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Comparison of cephalopods eaten by sooty albatross *Phoebetria fusca* breeding in subtropical and subantarctic waters, and teuthofauna of the southern Indian Ocean

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ABSTRACT

Using a total of ~7000 accumulated beaks sorted from 92 food samples, the cephalopod diet of sooty albatross *Phoebetria fusca* was determined for the first time at the subtropical Amsterdam Island (3898 beaks from 53 food samples), and it was compared with prey eaten at the subantarctic Crozet Islands (3085 beaks from 39 samples). At Amsterdam Island, sooty albatross fed on 42 cephalopod taxa that included the dominant *Histioteuthis atlantica* (34.7% by number of beaks) and juvenile *Ommastrephes cylindraceus/Todarodes filippovae* (10.1%). They preyed primarily upon cephalopods that have a wide latitudinal distribution (55.1%), with subtropical species ranking second (25.8%), and Southern Ocean endemics third (19.1%). By contrast, birds from Crozet Islands fed primarily on Southern Ocean endemics (80.7%), followed by subtropical species (14.8%), and taxa with a wide distribution (4.5%). There, the main prey were adult *Histioteuthis eltaninae* (24.6%), *Batoteuthis skolops* (27.2%) and *Galiteuthis glacialis* (16.2%). Sympatric sooty and light-mantled sooty *P. palpebrata* albatrosses from Crozet Islands segregated by feeding on different prey indicating different foraging grounds north and south of the archipelago, respectively. Light-mantled sooty albatross fed almost exclusively on Southern Ocean endemics (98.2%), such as *G. glacialis* (44.4%), *Psychroteuthis glacialis* (21.4%), *H. eltaninae* (13.4%) and *Moroteuthopsis longimana* (10.2%). Including cephalopod prey of sooty albatross to the previous investigations on teuthofauna from the southern Indian Ocean added southern subtropical species to Southern Ocean taxa. Overall, teuthofauna of this vast oceanic zone hosts at least 71 cephalopod species, including two bathyteuthids, 56 oegopsids, two sepiolids, three cirrate and seven incirrate octopods, and the vampyroteuthid *Vampyroteuthis infernalis*.

1. Introduction

Albatrosses are the largest seabirds and among the world's most endangered taxa of birds (IUCN, 2023). Most of the albatross species breed in the Southern Ocean (water masses south of the Subtropical Front, STF) and migrate northward to the Subtropical Zone (STZ) during the non-breeding period (Cherel et al., 2013). By contrast, they breed at only a few scattered localities within the STZ and at the STF, namely the Tristan da Cunha Group in the Atlantic, Amsterdam and the closely-related Saint-Paul Island in the Indian Ocean, and Tasmania and the Chatham Islands in the western Pacific Ocean. Those islands host endemic species, as the Amsterdam albatross *Diomedea amsterdamensis*, shy albatross *Thalassarche cauta* (Tasmania) and Chatham albatross *T. eremita*, together with species that have a larger distribution and breed both in the subtropics and further south. The latter species include the Atlantic *T. chlororhynchos* and Indian *T. carteri* yellow-nosed albatrosses, Buller's albatross *T. bulleri*, and sooty albatross *Phoebetria fusca* (ACAP, 2012; Shirihai, 2002).

The Southern Ocean can be split into three broad oceanographic zones, from South to North, the Antarctic Zone (AZ) between Antarctica and the Polar Front, the Polar Frontal Zone (PFZ) between the Polar Front and the Subantarctic Front, and the Subantarctic Zone (SAZ) between the Subantarctic Front and STF (Pollard et al., 2002). The sooty albatross breeds on oceanic islands of the southern Atlantic and Indian Oceans encompassing different oceanic zones. The species does not breed in the AZ, but major populations occur within the PFZ (Prince Edward Islands, ~2500 annual breeding pairs; Crozet Islands, ~2100 pairs), the SAZ (Gough Island, <5000 pairs), and north of the Southern Ocean within the STZ (Tristan da Cunha Group, ~3000 pairs; Amsterdam Island, ~480 pairs) (ACAP, 2012). Population declines have been

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reported at all sites where repeated surveys have been carried out and, consequently, the species has been uplisted to endangered in the IUCN Red List of Threatened species (IUCN, 2023). For example, censuses in the French Territories indicate a 75% decline of the sooty albatross during the period 1980-2017 at the Crozet Islands, and a 17% decline during the period 2003-2012 at Amsterdam Island (Weimerskirch et al., 2018). These population decreases are generally considered to be the result of low survival of adult and immature birds caused by at sea mortality associated with fisheries in the subtropics, particularly tuna longline fishing vessels (Delord et al., 2008, 2013; ACAP, 2012).

The food and feeding ecology of the sooty albatross is one of the least well known of albatrosses breeding in the Southern Ocean and fringing subtropical waters. Chick food was detailed at Prince Edward and Crozet Islands (Ridoux, 1994; Cooper and Klages, 1995; Connan et al., 2014), but only anecdotal dietary information is available from the subtropical populations (Marchant and Higgins, 1990). Satellite- and GPS-tracking was performed on incubating and brooding adults from subantarctic islands (Pinaud and Weimerskirch, 2007; ACAP, 2012; Schoombie et al., 2017; Carpenter-Kling et al., 2020a,b), with only a few birds having been tracked from the Tristan da Cunha Group (Schoombie et al., 2017) and Amsterdam Island (Delord et al., 2013). Hence, the foraging ecology of sooty albatross breeding at subtropical islands is virtually unknown, especially during the chick-rearing period.

The five aims of this study were: (i) to detail for the first time the cephalopod diet of sooty albatross in the subtropics during the chick-rearing period, since cephalopods constitute a major prey group of the species elsewhere (41%-79% by mass; Ridoux, 1994; Cooper and Klages, 1995; Connan et al., 2014); (ii) to compare the cephalopod diet of sooty albatrosses breeding either in subtropical or subantarctic waters at two localities from the Southern Indian Ocean, Amsterdam and Crozet Islands, respectively; (iii) to review and update the cephalopod diet of sooty albatross from previous investigations (Ridoux, 1994; Cooper and Klages, 1995); (iv) to compare the cephalopod prey between the two sibling species of *Phoebetria* albatrosses, the sooty and light-mantled sooty albatrosses *P. palpebrata* at the Crozet Islands where they breed in sympatry; and (v) to use sooty albatross as bio-sampler of cephalopods to examine their biodiversity and abundance in the southern Indian Ocean.

Albatrosses is the group of seabirds that feed the most on cephalopods (Cherel and Klages, 1998; Cherel et al., 2017). Sclerotized beaks of squids and octopuses accumulate over the long-term in their stomachs, thus with potential to provide valuable information on the cephalopod prey from large numbers of accumulated beaks (*e.g.*, Cherel et al., 2017, 2023; Xavier et al., 2022). The importance of cephalopods in the diet of predators highlights the key role of oceanic squids in the marine food webs of the Southern Ocean and fringing subtropical waters (Clarke, 1980; Rodhouse and White, 1995; Collins and Rodhouse, 2006; Rodhouse, 2013). The biology of southern subtropical and Southern Ocean cephalopods is nonetheless poorly known (Xavier et al., 2018; Cherel, 2020), with the main limitations being the small number of research cruises targeting squids (Rodhouse, 1990). Most previous oceanographic and fishery cruises had been conducted in the Atlantic and Pacific Oceans, with the result that teuthofauna of the Indian Ocean is the less known of the three major oceans. A complementary tool to gather information on cephalopods is to use their predators as bio-samplers to investigate their biodiversity, biogeography and abundance. The method has already provided relevant information on pelagic squid and octopuses from the southern Indian Ocean over the last decades (*e.g.*, Cherel and Weimerskirch, 1995, 1999; Cherel et al., 2004, 2023; Cherel, 2020).

The present article is a companion paper to a previous article on cephalopod prey of the light-mantled sooty albatross (Cherel et al., 2023). Unlike the sooty albatross, the light-mantled sooty albatross breeds within the AZ and not in the subtropics, but both species co-exist within the PFZ of the southern Indian Ocean (Weimerskirch et al., 2018; Shirihai, 2002).

2. Materials and methods

2.1. Study sites and sampling

Amsterdam Island (37°50′S, 77°33′E) is located within the STZ, while the Crozet Archipelago (45°55′-46°50′S, 50°33′-52°58′E), including Possession Island where fieldwork was conducted, is located within the PFZ of the southern Indian Ocean (Park et al., 1993). Food samples included stomach contents, spontaneous regurgitations and regurgitated boluses, all from chicks. At Amsterdam Island, in total, 53 food samples including 16 stomach contents, 12 regurgitations and 25 boluses were collected mainly in April over five years (n = 10, 8, 7, 20 and 8, in 1993, 1995, 1996, 1997 and 2003, respectively). At Crozet Islands, 39 food samples were collected over two breeding seasons, *i.e.,* 26 boluses in April-May 1993 and 13 stomach contents in late January-early February 1996. Boluses were collected near nests either at the end of the chick-rearing period or right after fledging. Cephalopod prey identified from boluses and stomach contents compare well, and collection and analysis of boluses is therefore a simple and efficient method for assessing the cephalopod diet of albatrosses (Xavier et al., 2005).

2.2. Food sample analysis

Accumulated cephalopod beaks were sorted from all the food samples, together with a few fresh beaks with flesh still attached that were found in stomach contents and spontaneous regurgitations. Beaks were cleaned and stored in 70% ethanol before subsequent analysis. The morphology of both lower and upper beaks, instead of that of lower beaks only, was used to determine cephalopod prey (Cherel et al., 2000; Xavier et al., 2011). Beaks were numbered and identified by comparison with material held in our own collection and by reference to the available literature (Clarke, 1986; Imber, 1992; Cherel, 2020; Xavier and Cherel, 2021). Species names are based on a recent review on Southern Ocean squids (Cherel, 2020), which followed the Tree of Life Web Project (Tolweb, 2023) together with recent systematic investigations, *e.g.,* Octopoteuthidae (Kelly, 2019), *Ommastrephes cylindraceus* (Fernandez-Alvarez et al., 2020), and *Taonius expolitus* and *T. notalia* (Evans, 2018). At Amsterdam Island, both lower and upper beaks of juvenile ommastrephids refer to either *O. cylindraceus* (Fernandez-Alvarez et al., 2020) or/and *Todarodes filippovae* (Adam, 1975) whose beaks are similar, thus precluding identifying them with confidence at the species level. Upper beaks from *Histioteuthis atlantica, H. bonnellii corpuscula, H. miranda* and *Stigmatoteuthis hoylei* are so similar that they were pooled. Consequently, the percentage number of beaks of those histioteuthids referred to lower beaks only, thus contrasting with other cephalopod taxa whose relative numbers referred to the total number of identified beaks (both lower and upper beaks).

Lower rostral length (LRL) of squid beaks were measured using a Vernier calliper. Cephalopod dorsal mantle length (DML) and body mass were estimated using regression equations (Clarke, 1986; Adams and Klages, 1987; Rodhouse and Yeatman, 1990; Lu and Williams, 1994; Jackson, 1995; Roeleveld, 2000; Piatkowski et al., 2001; Lu and Ickeringill, 2002; Kelly, 2019; Xavier and Cherel, 2021). For the species where no relationships were available, length was estimated using equations for closely related species or for species with a similar morphology. Unlike accumulated wholly darkened beaks of adult squids, most undarkened or darkening lower beaks lose their fragile wings over time in chicks' stomachs, thus precluding measuring LRL of most juvenile and maturing squids, respectively.

2.3. A review of cephalopod prey of sooty albatross and comparison with the light-mantled sooty albatross

Comparison of the cephalopod diet of the sympatric sooty and light-mantled sooty albatrosses from Crozet Islands was made using two data sets. Firstly, both lower and upper beaks were sorted and identified from

Table 1

Numbers of accumulated cephalopod beaks identified from food samples of sooty albatross at the subtropical Amsterdam Island. Biogeography refers to Cherel (2020): Southern Ocean (SO) endemics (south of the Subtropical Front, STF), species with a wide latitudinal distribution (south and north of the STF), and subtropical species (north of the STF and/or occasionally south of it).

Year		1993		1995		1996		1997		2003		Total	
Food samples (n)	Biogeography	10 Number		8 Number		7 Number		20 Number		8 Number		53 Number	
		(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)
Architeuthidae													
Architeuthis dux	wide					2	0.29	2	0.12	4	0.82	8	0.22
Thysanoteuthidae													
Thysanoteuthis rhombus	subtropical					1	0.14					1	0.03
Ommastrephidae													
Martialia hyadesi	SO endemic					5	0.72					5	0.13
Ommastrephidae sp.	wide	146	28.02	13	3.65	128	18.39	55	3.33	68	13.96	410	11.04
Onychoteuthidae													
Filippovia knipovitchi	SO endemic					3	0.43	5	0.30			8	0.22
Moroteuthopsis ingens	SO endemic					1	0.14					1	0.03
Moroteuthopsis longimana	SO endemic					7	1.01			1	0.21	8	0.22
Moroteuthopsis sp. B (Imber)	SO endemic					8	1.15	3	0.18	1	0.21	12	0.32
Onychoteuthis bergii	subtropical							3	0.18			3	0.08
Onychoteuthis sp. 2 (Imber)	subtropical	4	0.77			4	0.57	1	0.06	2	0.41	11	0.30
Onykia robsoni	wide	3	0.58	21	5.90	23	3.30	124	7.50	25	5.13	196	5.28
Walvisteuthis rancureli	subtropical					8	1.15	56	3.39	15	3.08	79	2.13
Gonatidae													
Gonatus antarcticus	wide					12	1.72	1	0.06	1	0.21	14	0.38
Ancistrocheiridae													
Ancistrocheirus lesueurii	subtropical	14	2.69	14	3.93	12	1.72	72	4.35	14	2.87	126	3.39
Octopoteuthidae													
Octopoteuthis sp.	wide	1	0.19	2	0.56	9	1.29	50	3.02	22	4.52	84	2.26
Taningia danae	wide	4	0.77	1	0.28	3	0.43	6	0.36	2	0.41	16	0.43
Lepidoteuthidae													
Lepidoteuthis grimaldii	subtropical					3	0.43	3	0.18	2	0.41	8	0.22
Histioteuthidae													
Histioteuthis atlantica (lower beaks)	wide	79	15.16	54	15.17	108	15.52	280	16.93	89	18.28	610	16.42
Histioteuthis bonnellii corpuscula (lower beaks)	subtropical	3	0.58	9	2.53	4	0.57	11	0.67	6	1.23	33	0.89
Histioteuthis miranda (lower beaks)	subtropical	2	0.38			5	0.72	13	0.79	10	2.05	30	0.81
Stigmatoteuthis hoylei (lower beaks)	subtropical			3	0.84			1	0.06			4	0.11
Histioteuthis spp. (upper beaks)		94	18.04	70	19.66	120	17.24	385	23.28	101	20.74	770	20.73
Histioteuthis eltaninae (lower and upper beaks)	SO endemic					6	0.86	20	1.21			26	0.70
Histioteuthis macrohista (lower and upper beaks)	subtropical	48	9.21	32	8.99	23	3.30	235	14.21	33	6.78	371	9.99
Neoteuthidae													
Alluroteuthis antarcticus	SO endemic					2	0.29			2	0.41	4	0.11
Nototeuthis dimegacotyle	SO endemic	69	13.24	18	5.06	57	8.19	168	10.16	32	6.57	344	9.26
Cycloteuthidae													
Cycloteuthis sirventi	subtropical	5	0.96	5	1.40	10	1.44	22	1.33	8	1.64	50	1.35
Mastigoteuthidae													
Magnoteuthis osheai	subtropical	1	0.19			2	0.29	4	0.24			7	0.19
Mastigopsis hjorti	subtropical	4	0.77			1	0.14	6	0.36			11	0.30
Mastigoteuthis psychrophila	SO endemic	9	1.73	3	0.84	3	0.43	6	0.36	2	0.41	23	0.62
Chiroteuthidae													
Asperoteuthis lui	SO endemic			2	0.56	25	3.59	10	0.60	11	2.26	48	1.29
Chiroteuthis mega	subtropical	2	0.38	4	1.12	1	0.14	4	0.24	7	1.44	18	0.48
Chiroteuthis veranyi	wide	2	0.38	1	0.28			4	0.24	3	0.62	10	0.27
Batoteuthidae													
Batoteuthis skolops	SO endemic	3	0.58	5	1.40	26	3.74	10	0.60	8	1.64	52	1.40
Cranchiidae													
Galiteuthis glacialis	SO endemic			82	23.03	57	8.19	28	1.69			167	4.50
Galiteuthis suhmi	wide	7	1.34	2	0.56	4	0.57	7	0.42	3	0.62	23	0.62
Liguriella podophtalma	wide	1	0.19	3	0.84			9	0.54	3	0.62	16	0.43
Mesonychoteuthis hamiltoni	SO endemic							1	0.06			1	0.03
Taonius expolitus	subtropical	3	0.58	8	2.25	2	0.29	10	0.60	1	0.21	24	0.65
Taonius notalia	SO endemic	3	0.58			4	0.57	12	0.73	2	0.41	21	0.57
Teuthowenia pellucida	subtropical	11	2.11	4	1.12	5	0.72	25	1.51	7	1.44	52	1.40
Sepiolidae													
Heteroteuthis cf. *dagamensis*	subtropical	3	0.58			1	0.14			1	0.21	5	0.13
Vampyroteuthidae													
Vampyroteuthis infernalis	subtropical					1	0.14	2	0.12	1	0.21	4	0.11
Total		521	100.00	356	100.00	696	100.00	1654	100.00	487	100.00	3714	100.00
Eroded beaks		37		29		20		76		22		184	

Table 2
Measured lower rostral length (LRL), and estimated dorsal mantle length (DML) of squids eaten by sooty albatross at Amsterdam and Crozet Islands. Values are means ± SD with ranges in parentheses. Mann-Whitney U tests were performed to compare squid sizes between the two localities. Significant differences (p < 0.05) are highlighted in **bold**. na: not applicable (either no allometric equations, or n ≤ 2).

Localities	Amsterdam			Crozet			Statistics on LRLMann-Whitney U-tests
Species	n	Measured LRL (mm)	Estimated DML (mm)	n	Measured LRL (mm)	Estimated DML (mm)	
Architeuthis dux				2	5.9 (4.6-7.2)	183 (135-232)	na
Thysanoteuthis rhombus	1	2.1	115				na
Martialia hyadesi	1	5.2	254	1	4.7	241	na
Filippovia knipovitchi	2	8.3 (8.1-8.5)	413 (401-425)	18	7.9 ± 0.4 (7.0-8.5)	389 ± 26 (333-426)	na
Moroteuthopsis ingens				15	10.3 ± 0.8 (7.7-11.6)	430 ± 37 (316-491)	na
Moroteuthopsis longimana	2	15.2 (13.6-16.8)	544 (483-605)	36	12.7 ± 1.2 (10.7-15.5)	451 ± 44 (377-556)	na
Moroteuthopsis sp. B (Imber)	7	6.8 ± 0.3 (6.5-7.2)	271 ± 9 (260-284)	1	5.7	233	na
Onychoteuthis bergii	1	3.2	107	3	3.2 ± 0.1 (3.2-3.3)	109 ± 2 (106-110)	na
Onychoteuthis sp. 2 (Imber)	3	2.5 ± 0.3 (2.2-2.7)	83 ± 8 (76-92)	4	2.3 ± 0.2 (2.1-2.5)	78 ± 6 (71-85)	U = 9.0, p = 0.077
Walvisteuthis rancureli	44	4.9 ± 0.3 (4.2-5.6)	162 ± 10 (139-185)				na
Onykia robsoni	82	9.9 ± 0.7 (7.5-11.1)	839 ± 101 (486-1025)	1	7.8	531	na
Gonatus antarcticus	6	6.7 ± 0.5 (6.2-7.5)	246 ± 22 (222-279)	7	6.4 ± 0.6 (5.6-7.1)	230 ± 25 (198-259)	U = 30.0, p = 0.199
Ancistrocheirus lesueurii	50	8.3 ± 1.1 (5.0-10.3)	297 ± 46 (162-377)	8	7.3 ± 1.4 (4.4-8.8)	257 ± 59 (136-319)	**U = 297.0, p = 0.029**
Octopoteuthis sp.	17	12.4 ± 2.2 (8.9-15.5)	214 ± 38 (154-268)	1	10.5	182	na
Taningia danae	5	13.6 ± 7.4 (5.2-22.8)	599 ± 496 (35-1217)				na
Lepidoteuthis grimaldii	2	24.8 (22.9-26.8)	898 (828-969)				na
Histioteuthis atlantica	464	5.3 ± 0.7 (3.0-7.4)	125 ± 17 (66-180)	52	4.8 ± 0.7 (3.1-6.4)	113 ± 17 (70-154)	**U = 17215.0, p <0.0001**
Histioteuthis bonnellii corpuscula	27	5.0 ± 0.5 (3.6-5.7)	77 ± 8 (57-89)	109	5.0 ± 0.3 (3.9-5.7)	78 ± 5 (60-88)	U = 1444.0, p = 0.881
Histioteuthis eltaninae	14	3.5 ± 0.3 (2.9-4.1)	83 ± 8 (68-96)	316	3.5 ± 0.2 (2.5-4.2)	82 ± 6 (58-99)	U = 2433.0, p = 0.527
Histioteuthis macrohista	162	3.8 ± 0.3 (3.0-5.0)	57 ± 5 (45-74)	2	4.0 (3.5-4.5)	60 (53-67)	na
Histioteuthis miranda	25	6.8 ± 0.6 (5.4-8.3)	206 ± 22 (159-256)	29	6.6 ± 0.6 (3.8-7.3)	200 ± 22 (103-225)	U = 386.0, p = 0.683
Stigmatoteuthis hoylei	4	6.2 ± 2.2 (3.5-8.7)	98 ± 32 (59-135)	1	6.7	105	na
Alluroteuthis antarcticus	3	5.4 ± 0.4 (4.9-5.7)	183 ± 15 (167-196)	14	5.3 ± 0.3 (4.8-5.9)	183 ± 12 (165-202)	U = 21.0, p = 1.000
Nototeuthis dimegacotyle	141	4.1 ± 0.3 (3.1-4.8)	na	5	3.6 ± 0.3 (3.1-3.9)	na	**U = 620.0, p = 0.004**
Cycloteuthis sirventi	19	12.1 ± 3.0 (5.6-16.1)	374 ± 94 (174-500)	32	13.0 ± 1.7 (9.3-16.3)	403 ± 53 (287-504)	U = 271.5, p = 0.527
Discoteuthis laciniosa				3	7.3 ± 0.3 (7.0-7.6)	na	na
Magnoteuthis osheai	5	5.1 ± 0.3 (4.7-5.4)	147 ± 7 (136-154)	1	4.7	136	na
Mastigopsis hjorti	5	4.5 ± 0.9 (3.4-5.3)	130 ± 25 (98-151)	4	4.9 ± 0.4 (4.5-5.3)	140 ± 11 (129-153)	U = 8.0, p = 0.624
Mastigoteuthis psychrophila	8	3.9 ± 0.3 (3.5-4.3)	119 ± 2 (116-121)	10	3.9 ± 0.2 (3.6-4.2)	119 ± 1 (117-121)	U = 40.0, p = 1.000
Asperoteuthis lui	19	7.3 ± 0.6 (6.3-8.2)	na	5	5.8 ± 0.4 (5.2-6.2)	na	**U = 95.0, p = 0.001**
Chiroteuthis mega	4	5.5 ± 0.1 (5.4-5.6)	145 ± 2 (143-148)	2	5.8 (5.6-6.0)	153 (149-157)	na
Chiroteuthis veranyi	5	6.7 ± 1.2 (4.7-7.9)	176 ± 30 (127-204)	9	6.5 ± 0.4 (5.8-7.1)	171 ± 10 (154-184)	U = 32.0, p = 0.205
Batoteuthis skolops	20	4.6 ± 0.5 (3.5-5.6)	na	376	4.3 ± 0.3 (3.5-5.4)	na	**U = 5460.0, p = 0.001**
Galiteuthis glacialis	77	5.1 ± 0.4 (3.5-5.8)	435 ± 34 (302-493)	241	5.2 ± 0.4 (3.8-6.3)	445 ± 32 (321-532)	**U = 7592.0, p = 0.016**
Galiteuthis suhmi	10	8.2 ± 0.9 (6.1-9.4)	346 ± 36 (261-396)	1	8.9	374	na
Liguriella podophtalma	9	6.2 ± 0.8 (4.5-6.9)	265 ± 32 (197-293)				na
Taonius expolitus	8	4.8 ± 0.3 (4.2-5.1)	284 ± 18 (248-299)	39	5.0 ± 0.3 (4.4-5.9)	296 ± 21 (258-348)	U = 95.0, p = 0.084
Taonius notalia	8	8.3 ± 1.9 (6.5-11.3)	496 ± 115 (386-683)	1	10.5	632	na
Teuthowenia pellucida	30	4.4 ± 0.4 (3.5-5.1)	155 ± 13 (126-174)				na
Total	1290			1349			

10 stomach contents of large chicks of light-mantled sooty albatrosses collected in March-April 1997. They were then compared with those of the sooty albatross. Secondly, the lower beaks identified in Ridoux (1994) were pooled with those from the present study to increase the number of lower beaks per albatross species and thus to strengthen species comparison. Like the latter data set, the review on the cephalopod prey of sooty albatross focused on lower beaks only, since previous investigations did not identify upper beaks. Species names of squids from Ridoux (1994), and Cooper and Klages (1995) were updated following Cherel (2020).

2.4. Data analysis

All the beaks (both lower and upper beaks) of a given cephalopod taxon from all the food samples were summed for a given albatross species and locality. The numerical importance (%) of each cephalopod

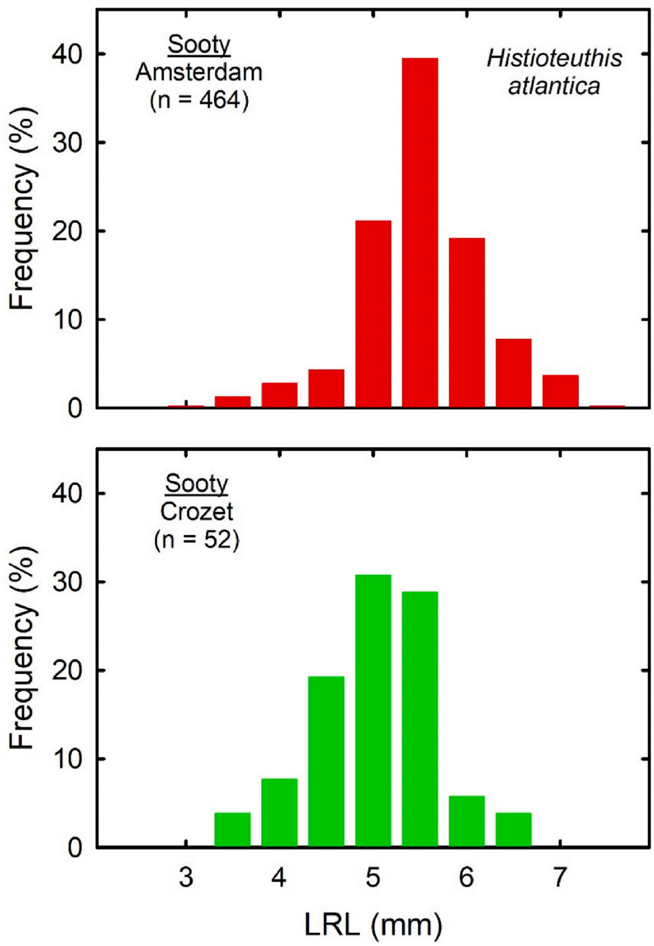

Fig. 1. Length-frequency distribution of lower rostral length (LRL) of *Histioteuthis atlantica* eaten by sooty albatross at Amsterdam (red, upper panel) and Crozet (green, lower panel) Islands.

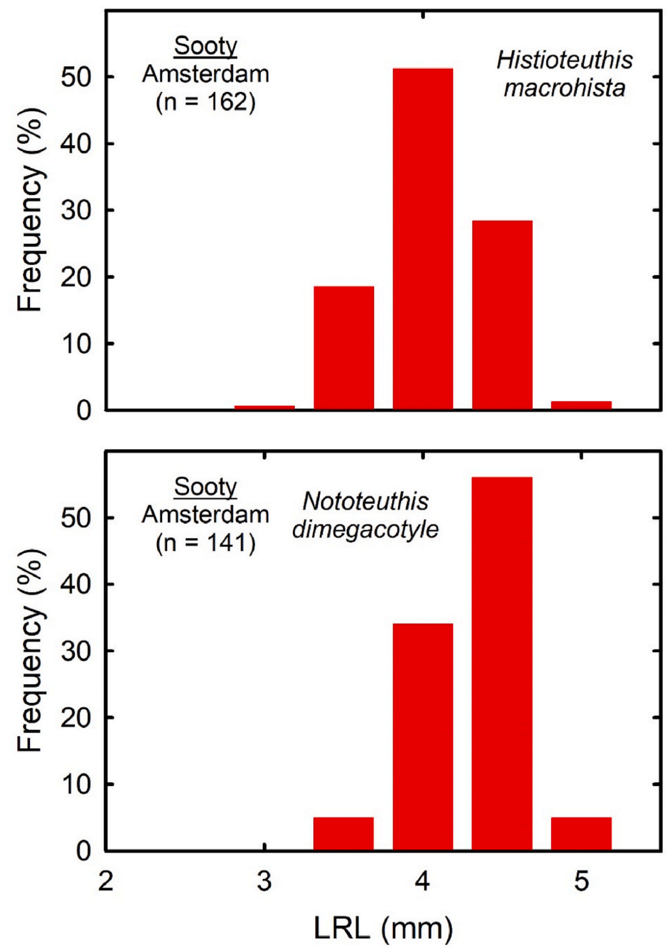

Fig. 2. Length-frequency distribution of lower rostral length (LRL) of *Histioteuthis macrohista* (upper panel) and *Nototeuthis dimegacotyle* (lower panel) eaten by sooty albatross at Amsterdam Island.

taxon refers to the total number of beaks of that taxon over the total number of cephalopod beaks from all taxa in all food samples. Biogeography of cephalopods refers mainly to a recent review on oceanic squids from the Southern Ocean (Cherel, 2020). They were classified as either subtropical species (that live north of the STF, or only occasionally south of it), Southern Ocean endemics (that live south of the STF), or species having a wide latitudinal distribution (that live both north and south of the STF).

Data were statistically analyzed using SYSTAT 13. Equality of proportion tests (large-sample tests) were performed to compare relative prey numbers between sooty and light-mantled sooty albatrosses. Nonparametric tests (either Mann-Whitney or Kruskal-Wallis tests) were performed to compare squid sizes (LRL) between years and localities. Kruskal-Wallis tests were followed by Conover-Inman post-hoc tests for pairwise comparisons.

3. Results

3.1. Amsterdam Island

Flesh of 18 cephalopods was found from 16 stomach contents and 12 spontaneous regurgitations of sooty albatross from Amsterdam Island. They included six *H. atlantica*, two *H. macrohista*, one *Octopoteuthis* sp., one *Mastigopsis hjorti*, one *Teuthowenia pellucida* and seven unidentified oegopsids (flesh with no corresponding beaks).

In total, 3898 accumulated beaks were sorted from 53 food samples. Since 184 beaks were too eroded to be identified with confidence, beaks that were identified to the lowest possible taxon numbered 3714 (1958 and 1756 upper and lower beaks, respectively) (Table 1). Forty-two cephalopod taxa were identified, including 40 oegopsids, one sepiolid and the vampyroteuthid *Vampyroteuthis infernalis*. In terms of species richness, the cephalopod diet of sooty albatross was dominated by the families onychoteuthids (eight species, 8.6% of the total number of identified beaks), cranchiids (seven species, 8.2%), and histioteuthids (six species, 49.6%). At the species level, *H. atlantica* was by far the most abundant prey (34.7% of the lower beaks). The complex *O. cylindraceus*/*T. filippovae* ranked second, *H. macrohista* third, the neoteuthid *Nototeuthis dimegacotyle* fourth, and the onychoteuthid *Onykia robsoni* fifth (11.0%, 10.0%, 9.3%, and 5.3% of the total number of identified beaks, respectively).

The estimated DML of squids eaten by sooty albatross ranged widely (Table 2), from a small (35 mm) to a large (over 1.2 m) specimen of the octopoteuthid *Taningia danae*. Depending on squid species, sooty albatross fed on juveniles, immatures and/or adult specimens (lower beaks with undarkened, darkening and darkened wings, respectively; Clarke, 1986). All beaks of ommastrephids were from juvenile squids, with the loss of wings of lower beaks precluding measuring their LRL. By contrast, most or all beaks of *H. atlantica, H. macrohista, N. dimegacotyle* and *O. robsoni* were wholly darkened, thus indicating that albatrosses fed on adult squids. Accordingly, LRL frequency distribution of each species presented a single mode (Figs. 1–3).

Substantial inter-annual variations and consistency in the numerical importance of the main squid prey were found when comparing the five years (Table 1). *Histioteuthis atlantica* was always the dominant

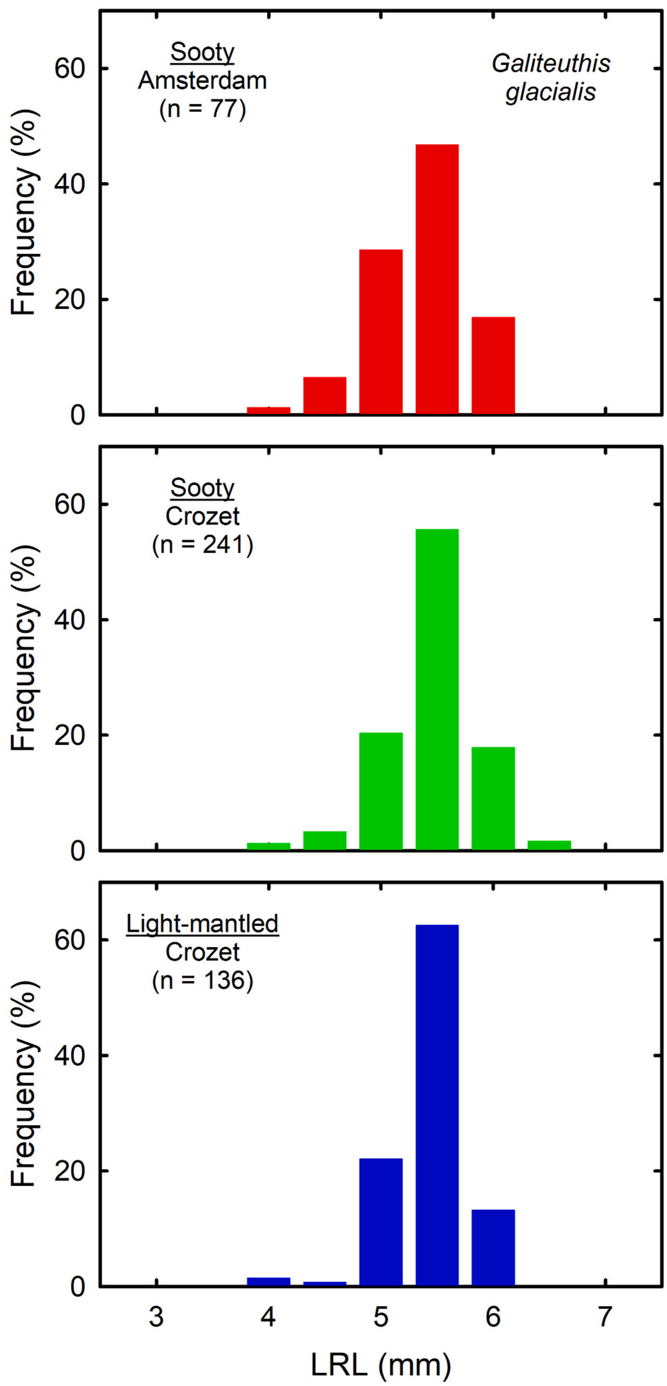

Fig. 3. Length-frequency distribution of lower rostral length (LRL) of *Galiteuthis glacialis* eaten by sooty albatross at Amsterdam Island (red, upper panel), and by sooty (green, middle panel) and light-mantled sooty (blue, lower panel) albatrosses at Crozet islands.

cephalopod prey (30.9%-37.2% of the lower beaks), while the importance of all the other main taxa varied from year to year: *O. cylindraceus/T. filippovae* (from 3.3% to 28.0% of the total number of identified beaks), *H. macrohista* (from 3.3% to 14.2%), *N. dimegacotyle* (from 5.1% to 10.2%), and *O. robsoni* (from 0.6% to 7.5%). Noticeably, no beaks of *Galiteuthis glacialis* were found in two years (1993 and 2003), while they accounted for 1.7% of the total number of beaks in 1997, 8.2% in 1996 and up to 23.0% in 1995. Potential inter-annual variations in squid size were tested on 17 species during two to five years using non-parametric tests (either Mann-Whitney or Kruskal-Wallis tests). Overall, sooty albatross fed on the same size-class of squids over years, but LRL of *O. robsoni* (four years, $H = 10.42$, $p = 0.015$) and *H. atlantica* (five years, $H = 59.43$, $p < 0.0001$) showed significant inter-annual variations. LRL of *H. atlantica* was larger in 1997 (5.5 ± 0.6 mm) than in 1993, 1995, 1996 and 2003 (4.7 ± 0.8, 5.0 ± 0.7, 5.2 ± 0.5 and 5.2 ± 0.5 mm, respectively), and it was significantly smaller in 1993 than in 1996, 1997 and 2003 (Conover-Inman tests for pairwise comparisons, data not shown).

Ten anthropogenic-related items were found in eight food samples. They included seven pieces of plastic and three of fishing lines.

3.2. Crozet Islands

Flesh of five cephalopods was found from 13 stomach contents of sooty albatross at the Crozet Archipelago. They included two specimens of *G. glacialis*, one *Taonius expolitus*, and two unidentified oegopsids.

In total, 3085 accumulated beaks were sorted from the 39 food samples. Excluding 20 eroded beaks, beaks that were identified to the lowest possible taxon numbered 3065 (1522 and 1543 upper and lower beaks, respectively) (Table 3). Thirty-nine cephalopod taxa were identified, including 38 oegopsids and one pelagic octopod. In terms of species richness, the cephalopod diet was dominated by the families onychoteuthids (eight species, 5.6% of the total number of identified beaks), histioteuthids (six species, 40.0%), and cranchiids (four species, 18.7%). At the species level, the batoteuthid *Batoteuthis skolops* ranked first (27.2%), closely followed by *Histioteuthis eltaninae* (24.6%). *G. glacialis* ranked third (16.2%), and *H. bonnellii corpuscula* fourth (9.1% of the lower beaks).

At Crozet Islands, sooty albatross preyed on squids of different sizes (Table 2), from a small *H. macrohista* (53 mm estimated DML) to a large *Taonius notalia* (63 cm). Depending on squid species, sooty albatross fed on juveniles, immatures and adult specimens. Overall, adults predominated, as most or all beaks of histioteuthids, *B. skolops* and *G. glacialis* were wholly darkened, and, accordingly, their LRL frequency distribution presented a single mode (Fig. 3). Lower beak morphology (Bolstad, 2006) indicated that all the 15 specimens of *Moroteuthopsis ingens* were females, including 14 large mature individuals.

Inter-annual variations and consistencies in the numerical importance of the main squid prey were found when comparing the two years. *Batoteuthis skolops* was a minor prey in 1993 (1.4% of the total number of beaks) and the main item, by far, in 1996 (63.4%). The reverse is true for *H. eltaninae* (40.4% and 2.4%, respectively). On the other hand, the relative importance of both *G. glacialis* (15.4%-17.4%) and *H. bonnellii corpuscula* (9.3%-8.9% of the lower beaks) did not show pronounced inter-annual variations (Table 3). Potential inter-annual differences in squid size was tested on eight species. LRL differed significantly between 1993 and 1996 for the two species *B. skolops* and *G. glacialis*, but size differences were so small that statistics (Mann-Whitney U-tests) carried little biological value (LRL: 4.7 ± 0.4 *versus* 4.3 ± 0.3 mm, and 5.2 ± 0.4 *versus* 5.3 ± 0.3 mm, $U = 3444.5$ and 5364.5, $p = 0.001$ and <0.0001, respectively).

Twelve anthropogenic-related items were found in five boluses collected in 1993. They included six pieces of polystyrene foam and six of plastic.

3.3. A review of cephalopod prey of sooty albatross

Five features are notable as characterizing and differentiating cephalopod prey of sooty albatross at the subtropical Amsterdam Island and subantarctic Crozet and Prince Edward Islands (Table 4).

1. Species richness of cephalopod prey was overall similar at the three localities (n = 41, 42 and 37 taxa at Amsterdam, Crozet and Prince Edward Islands, respectively).
2. Amongst the commonest prey (>1% by number of lower beaks), *O. cylindraceus/T. filippovae* and *Walvisteuthis rancureli* were only

Table 3
Numbers of accumulated cephalopod beaks identified from food samples of sooty and light-mantled sooty albatrosses at the subantarctic Crozet Archipelago. 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.

Species	Sooty albatross						Light-mantled sooty albatross		Statistics on numbers (%)
Year	1993		1996		Total		1997		
Food samples (n)	26		13		39		10		Sooty albatross *versus* light-mantled sooty albatross
	Number		Number		Number		Number		
	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)	
Architeuthidae									
Architeuthis dux	6	0.34			6	0.20			na
Ommastrephidae									
Martialia hyadesi			3	0.24	3	0.10	4	0.61	**Z = 2.75, p = 0.006**
Todarodes sp.	2	0.11	1	0.08	3	0.10			na
Ommastrephidae sp.	2	0.11	7	0.55	9	0.29			na
Onychoteuthidae									
Filippovia knipovitchi	35	1.96	4	0.31	39	1.27	9	1.37	Z = 0.21, p = 0.834
Moroteuthopsis ingens	27	1.51	2	0.16	29	0.95	2	0.31	Z = 1.64, p = 0.102
Moroteuthopsis longimana	67	3.74	16	1.25	83	2.71	67	10.23	**Z = 8.88, p <0.0001**
Moroteuthopsis sp. B (Imber)			2	0.16	2	0.07			na
Notonykia africanae			1	0.08	1	0.03			na
Onychoteuthis bergii	5	0.28			5	0.16			na
Onychoteuthis sp. 2 (Imber)	11	0.61			11	0.36			na
Onykia robsoni	2	0.11			2	0.07			na
Psychroteuthidae									
Psychroteuthis glacialis							140	21.37	na
Psychroteuthis sp. B (Imber)							4	0.61	na
Gonatidae									
Gonatus antarcticus	5	0.28	10	0.78	15	0.49	4	0.61	Z = 0.40, p = 0.693
Ancistrocheiridae									
Ancistrocheirus lesueurii	16	0.89	7	0.55	23	0.75			na
Octopoteuthidae									
Octopoteuthis sp.	2	0.11			2	0.07			na
Taningia danae	5	0.28	1	0.08	6	0.20	2	0.31	Z = 0.55, p = 0.583
Histioteuthidae									
Histioteuthis atlantica (lower beaks)	59	3.30	4	0.31	63	2.06			na
Histioteuthis bonnellii corpuscula (lower beaks)	83	4.64	58	4.55	141	4.60			na
Histioteuthis miranda (lower beaks)	29	1.62	4	0.31	33	1.08			na
Stigmatoteuthis hoylei (lower beaks)	1	0.06			1	0.03			na
Histioteuthis spp. (upper beaks)	175	9.78	57	4.47	232	7.57			na
Histioteuthis eltaninae (lower and upper beaks)	724	40.45	30	2.35	754	24.60	88	13.44	**Z = 6.20, p <0.0001**
Histioteuthis macrohista (lower and upper beaks)	2	0.11			2	0.07			na
Neoteuthidae									
Alluroteuthis antarcticus	24	1.34	3	0.24	27	0.88	16	2.44	**Z = 3.39, p = 0.001**
Nototeuthis dimegacotyle	4	0.22	7	0.55	11	0.36	2	0.31	Z = 0.55, p = 0.833
Cycloteuthidae									
Cycloteuthis sirventi	70	3.91	18	1.41	88	2.87			na
Discoteuthis laciniosa	5	0.28			5	0.16			na
Mastigoteuthidae									
Magnoteuthis osheai	2	0.11			2	0.07			na
Mastigopsis hjorti	6	0.34	1	0.08	7	0.23			na
Mastigoteuthis psychrophila	18	1.01	2	0.16	20	0.65	1	0.15	Z = 1.55, p = 0.121
Chiroteuthidae									
Asperoteuthis lui	11	0.61			11	0.36	1	0.15	Z = 0.85, p = 0.398
Chiroteuthis mega			3	0.24	3	0.10			na
Chiroteuthis veranyi	18	1.01			18	0.59	5	0.76	Z = 0.52, p = 0.602
Batoteuthidae									
Batoteuthis skolops	25	1.40	808	63.37	833	27.18	19	2.90	**Z = 13.42, p <0.0001**
Cranchiidae									
Galiteuthis glacialis	275	15.36	222	17.41	497	16.22	291	44.43	**Z = 16.04, p <0.0001**
Galiteuthis suhmi	2	0.11			2	0.07			na
Taonius expolitus	67	3.74	1	0.08	68	2.22			na
Taonius notalia	4	0.22	3	0.24	7	0.23			na
Alloposidae									
Haliphron atlanticus	1	0.06			1	0.03			na
Total	1790	100.00	1275	100.00	3065	100.00	655	100.00	
Eroded beaks	12		8		20		2		

Table 4
A review of accumulated cephalopod lower beaks identified from food samples of sooty albatross at various localities. Beaks from Crozet Islands refer to those from Ridoux (1994), which were pooled with lower beaks analyzed in the present study. Species names of squids from previous investigations were updated following Cherel (2020). Only cephalopods accounting for >1% by number at one locality are detailed. Abbreviations: PFZ, Polar Frontal Zone; STZ, Subtropical Zone (for definitions, see text).

Localities	Amsterdam		Crozet		Marion	
Oceanic zone	STZ		PFZ		PFZ	
References	this study		Ridoux (1994), this study		data from Cooper and Klages (1995)	
	(n)	(%)	(n)	(%)	(n)	(%)
Ommatrephes cylindraceus/ Todarodes filippovae	178	10.1				
Filippovia knipovitchi	5	0.3	71	2.6	256	5.6
Moroteuthopsis longimana	2	0.1	67	2.5	339	7.4
Onykia robsoni	95	5.4	2	0.1	38	0.8
Walvisteuthis rancureli	45	2.6				
Gonatus antarcticus	7	0.4	15	0.6	77	1.7
Ancistrocheirus lesueurii	61	3.5	13	0.5	2	<0.1
Octopoteuthis sp.	34	1.9	2	0.1	4	0.1
Histioteuthis atlantica	610	34.7	63	2.3	11	0.2
Histioteuthis bonnellii corpuscula	33	1.9	245	9.1	81	1.8
Histioteuthis eltaninae	15	0.9	549	20.3	911	19.9
Histioteuthis macrohista	174	9.9	2	0.1	10	0.2
Histioteuthis miranda	30	1.7	33	1.2	22	0.5
Alluroteuthis antarcticus	3	0.2	25	0.9	207	4.5
Nototeuthis dimegacotyle	145	8.3	5	0.2	10	0.2
Cycloteuthis sirventi	30	1.7	45	1.7	3	0.1
Asperoteuthis lui	24	1.4	12	0.4	32	0.7
Batoteuthis skolops	20	1.1	578	21.4	805	17.5
Galiteuthis glacialis	80	4.6	826	30.6	1610	35.1
Taonius expolitus	10	0.6	39	1.4	31	0.7
Teuthowenia pellucida	33	1.9			1	<0.1
Other taxa	122	6.9	106	3.9	137	3.0
Total	1756	100.0	2698	100.0	4587	100.0

identified from Amsterdam food samples. Five other squids were present in greater proportions at Amsterdam Island than at the two subantarctic localities, by decreasing order of numerical importance: *H. atlantica, H. macrohista, N. dimegacotyle* and *O. robsoni.* Hence, at the family level, sooty albatrosses from Amsterdam Island fed more on histioteuthids (49.3% *versus* 22.6-33.1%) and ommastrephids (10.4% versus 0.1-0.2%).

3. Conversely, sooty albatrosses from the two subantarctic localities fed more on *G. glacialis, H. eltaninae* and *B. skolops* than albatrosses from Amsterdam Island, the three taxa forming the bulk of the cephalopod diet at Crozet and Prince Edward Islands.
4. In the subantarctic, albatrosses from Crozet Islands caught more *H. bonnellii corpuscula*, but less *Filippovia knipovitchi* and *Moroteuthopsis longimana* than birds from Prince Edward Islands. Hence, at the family level, sooty albatrosses from Crozet Islands fed more on histioteuthids (33.1% *versus* 22.6%), and birds from Prince Edward Islands more on onychoteuthids (14.4% *versus* 6.3%).
5. Comparing LRL of the same squid species eaten at Amsterdam and Crozet Islands showed that sooty albatross preyed upon individuals of the same size class at both localities, even if some size differences were statistically significant (Table 2, Figs. 1 and 3).

3.4. Sympatric sooty and light-mantled sooty albatrosses from Crozet Islands

Flesh of 11 cephalopods was found from eight stomach contents of light-mantled sooty albatross at the Crozet Archipelago. They included three specimens of *H. eltaninae,* three *G. glacialis*, one *M. longimana*, one *Psychroteuthis glacialis* and three unidentified oegopsids.

In total, 657 accumulated lower and upper beaks were sorted from 10 food samples. They were compared to the 3085 beaks sorted from samples of sooty albatross (first data set). Four features are notable as characterizing and differentiating cephalopod prey of sympatric sooty and light-mantled sooty albatrosses at the subantarctic Crozet Islands (Table 3).

1. Species richness is 2.3 higher for sooty albatross than light-mantled sooty albatross (37 and 16 taxa, respectively). Sooty albatross included more onychoteuthids (8 *versus* 3 species), histioteuthids (6 *versus* one), and cranchiids (4 *versus* one) in its diet than light-mantled sooty albatross.
2. Psychroteuthids only occurred in food samples of light-mantled sooty albatross.
3. All the other 14 taxa eaten by light-mantled sooty albatross were also identified from food samples of sooty albatross. Eight minor taxa (<1.4% by number) occurred in similar proportions in samples from the two species, but light-mantled sooty albatross fed more on *M. longimana* (10.2% *versus* 2.7%) and *G. glacialis* (44.4 *versus*

Table 5
A review of numbers of accumulated lower beaks of cephalopods identified from food samples of sooty and light-mantled sooty albatrosses at the subantarctic Crozet Archipelago (pooled data from Ridoux, 1994 and this study). Species names of squids from Ridoux (1994) were updated following Cherel (2020). Only cephalopods accounting for >1% by number for one albatross species are detailed. Equality of proportion tests (large-sample tests) were performed to compare relative prey numbers between the two albatrosses. Significant differences (p < 0.05) are highlighted in **bold**; na: not applicable.

Species	Sooty albatross		Light-mantled sooty albatross		Statistics on numbers (%)
	(n)	(%)	(n)	(%)	
Filippovia knipovitchi	71	2.6	11	1.1	**Z = 2.78, p = 0.006**
Moroteuthopsis longimana	67	2.5	104	10.5	**Z = 10.27, p <0.0001**
Psychroteuthis glacialis			146	14.7	na
Histioteuthis atlantica	63	2.3			na
Histioteuthis bonnellii corpuscula	245	9.1			na
Histioteuthis eltaninae	549	20.3	97	9.8	**Z = 7.47, p <0.0001**
Histioteuthis miranda	33	1.2			na
Alluroteuthis antarcticus	25	0.9	21	2.1	**Z = 2.90, p = 0.004**
Cycloteuthis sirventi	45	1.7	1	0.1	**Z = 3.80, p <0.0001**
Batoteuthis skolops	578	21.4	68	6.9	**Z = 10.31, p <0.0001**
Galiteuthis glacialis	826	30.6	504	50.9	**Z = 11.37, p <0.0001**
Taonius expolitus	39	1.4			na
Other taxa	157	5.8	38	3.8	**Z = 2.38, p = 0.017**
Total	2698	100.0	990	100.0	

16.2%), and sooty albatross more on *H. eltaninae* (24.6% *versus* 13.4%) and *B. skolops* (27.2% *versus* 2.9%).

4. Comparing LRL of seven squid species showed that only LRL of *B. skolops* and *G. glacialis* differed significantly between sooty and light-mantled sooty albatrosses. However, the size-difference was small, carried little biological value, and both albatrosses fed on individuals of the same size class, mainly adults (Fig. 3).

The second data set that pooled the lower beaks from Ridoux (1994) together with those from the present study emphasized trophic segregation between the two albatross species (Table 5). Amongst the main cephalopod prey (12 taxa), four species (*H. atlantica, H. bonnellii corpuscula, H. miranda* and *T. expolitus*) occurred only in sooty albatross food samples, and a single one (*P. glacialis*) in the diet of light-mantled sooty albatross. The remaining seven taxa were more important items for either the sooty albatross (four species, including *H. eltaninae* and *B. skolops*) or the light-mantled sooty albatross (three species, including *M. longimana* and *G. glacialis*).

4. Discussion

At the subtropical Amsterdam Island, the cephalopod diet of sooty albatross was diverse and included five dominant oceanic squids that have a large latitudinal distribution. At the subantarctic Crozet Islands, the species fed on different dominant squid taxa that are mainly endemic to the Southern Ocean. Sympatric sooty and light-mantled sooty albatrosses segregated by their cephalopod prey. Sooty albatross included subtropical cephalopods in its diet, while light-mantled sooty albatross fed almost exclusively on Southern Ocean endemics, including the Antarctic *P. glacialis*. Prey of sooty albatross provided additional information on the southern Indian Ocean cephalopods by increasing the spatial coverage from which samples are available to the subtropics, thus complementing previous investigations that used bony fishes, sharks and seabirds from subantarctic islands.

4.1. Sooty albatross breeding in subtropical and subantarctic waters

At Amsterdam Island, sooty albatross fed on 42 taxa, with five oceanic squids being important prey, in a decreasing numerical order: *H. atlantica*, juvenile *O. cylindraceaus/T. filippovae*, *H. macrohista, N. dimegacotyle,* and *O. robsoni*. Three of those taxa are known to live in both subtropical and subantarctic waters, *H. macrohista* is a subtropical species that occurs occasionally in subantarctic waters, while *N. dimegacotyle* is considered as a Southern Ocean endemic (Cherel, 2020). Overall, sooty albatross preyed primarily on cephalopods that have a wide latitudinal distribution (55.1% of the lower beaks, 11 species), with subtropical species ranking second (25.8%, 19 species), and Southern Ocean endemics third (19.1%, 13 species). At the subantarctic Prince Edward and Crozet Islands, sooty albatross preyed upon the same large diversity of cephalopod taxa as in Amsterdam Island (Table 4), but they fed primarily on Southern Ocean endemics (92.8% and 80.7%, respectively), followed by subtropical species (3.5% and 14.8%), and by taxa with a wide distribution (3.6% and 4.5%). The most important squid prey were all different between Amsterdam Island and the two subantarctic localities (adult *H. eltaninae, B. skolops* and *G. glacialis*). *Histioteuthis atlantica* and *G. glacialis* illustrate well how sooty albatross fed overall on the same cephalopod taxa whatever the breeding locality, but with their relative importance differing markedly between the subtropical Amsterdam Island and subantarctic Prince Edward and Crozet Islands (34.7% *versus* 0.2-2.3%, and 4.6% *versus* 30.6-35.1%, respectively). Hence, a well-defined dietary segregation occurs amongst the different populations of sooty albatross breeding north and south of the STF in the southern Indian Ocean. The lack of detailed information precludes generalizing this pattern to the southern Atlantic, which therefore merits further dietary investigation at the subtropical Tristan da Cunha Group and subantarctic Gough Island.

Site-specific cephalopod prey together with prey biogeography emphasized the trophic importance of teuthofauna near the breeding islands for sooty albatross during the chick-rearing period. Indeed, tracked incubating adults from Amsterdam Island forage primarily within the subtropics, and birds from Prince Edward and Crozet Islands primarily in subantarctic waters (Weimerskirch and Guionnet, 2002; Pinaud and Weimerskirch, 2007; Delord et al., 2013; Carpenter-Kling et al. 2020a, 2020b). Sooty albatrosses from Prince Edward and Crozet Islands also move northward to forage within the STZ, as indicated by both the presence of subtropical cephalopods in their diet (this study), and satellite- and GPS-tracking (Pinaud and Weimerskirch, 2007; Delord et al., 2013; Carpenter-Kling et al. 2020a, 2020b). Conversely, prey biogeography showed that sooty albatross from Amsterdam Island moved southward to forage in subantarctic waters, a new feature that was not indicated by satellite-tracking (Delord et al., 2013). Hence, the different populations of sooty albatross forage over the same wide latitudinal range that includes the PFZ, SAZ and STZ, with birds breeding in the subtropics favoring the STZ, and those from subantarctic sites the PFZ and SAZ.

Large inter-annual variability in cephalopod prey occurred at both Amsterdam and Crozet Islands during the chick-rearing period. Two non-exclusive explanations of this pattern are inter-annual variations in either prey availability or foraging areas. No direct information is available on year-to-year changes in prey abundance, but tracking of incubating birds showed substantial differences in the core latitudinal foraging areas among years (Carpenter-Kling et al., 2020b). Hence, inter-annual changes of the importance of Southern Ocean squids in the diet of sooty albatross from Amsterdam Island may be explained by foraging more or less south of the STF. For example, the low percentages of Southern Ocean endemics suggests that sooty albatross foraged less within the Southern Ocean, and thus more in the subtropics, in 1993, 1997 and 2003. In agreement with that hypothesis, no beaks of the Southern Ocean endemic *G. glacialis* were identified in food samples from Amsterdam Island in 1993 (Table 1), while *G. glacialis* was a main cephalopod prey of sooty albatross from Crozet Islands (Table 3), being thus available to the birds in subantarctic waters on that year.

4.2. Sympatric sooty and light-mantled sooty albatrosses from Crozet Islands

Reproductive cycles of sooty and light-mantled sooty albatrosses overlap greatly in time (Berruti, 1979; Weimerskirch et al., 1986), thus raising the question of niche partitioning in these taxonomically closely-related species. Evolutionary biology predicts that, potential competitors coexisting in a community should exhibit niche differentiation (Begon et al., 1990). Indeed, dietary differences related to different foraging grounds are a species-specific trophic segregating mechanism allowing co-existence during breeding of the two *Phoebetria* species at Crozet Islands, which is in agreement with previous studies on sympatric albatrosses (*e.g.,* Weimerskirch et al., 1986; Cherel et al., 2002; Cherel and Waugh, 2023). Breeeding sooty and light-mantled sooty albatrosses fed either on the same squid species, but in different proportions, or on different squids. Overall, sooty albatrosses preyed more on subtropical cephalopods (14.8% *versus* 0.1% of the lower beaks), while light-mantled sooty albatross fed almost exclusively on Southern Ocean endemics (98.2% *versus* 80.7%). The presence of *P. glacialis*, the only endemic species of the AZ (Cherel, 2020), in the diet of light-mantled sooty albatros indicated foraging in Antarctic waters. Southern foraging grounds of the species was also indicated by the lower diversity of its cephalopod prey, as squid diversity increases with decreasing latitudes in the Southern Ocean and fringing subtropical waters (Cherel, 2020). Hence, biogeography of cephalopod prey indicated that Crozet albatrosses segregated by partitioning latitudinal feeding grounds during the chick-rearing period. Sooty albatross favored warmer waters (SAZ and STZ), light-mantled sooty albatross colder waters (AZ), and their foraging areas overlapped within the PFZ, where they caught

Table 6
A summary of cephalopod taxa from the southern Indian Ocean recorded in the diet of top predators, as fishery bycatches, and those listed in oceanographic literature. Unpublished data refer to cephalopod prey of Patagonian toothfish that were not listed in Cherel et al. (2004, 2011).

	Cherel et al. (2004, 2011), unpublished data	Cherel et al. (2023), additional taxa only	Cherel (2023), this study additional taxa only	Additional references
Bathyteuthoidea				
Bathyteuthidae	*Bathyteuthis abyssicola*			
Chtenopterygidae			*Chtenopteryx sicula*	
Oegopsida				
Architeuthidae	*Architeuthis dux*			Cherel (2003)
Neoteuthidae	*Alluroteuthis antarcticus*			
	Nototeuthis dimegacotyle			
Brachioteuthidae	*Brachioteuthis linkowskyi*			
	Slosarczykovia circumantarctica			
Batoteuthidae	*Batoteuthis skolops*			
Chiroteuthidae	*Asperoteuthis acanthoderma*			Cherel (2021b)
	Asperoteuthis lui			
	Chiroteuthis mega			
	Chiroteuthis veranyi			
Mastigoteuthidae		*Magnoteuthis osheai*		Cherel (2020)
			Mastigopsis hjorti	
	Mastigoteuthis psychrophila			
Cranchiidae	*Galiteuthis glacialis*			
		Galiteuthis suhmi		
			Leachia sp.	
	Liguriella podophtalma			
			Megalocranchia sp.	
	Mesonychoteuthis hamiltoni			
		Taonius expolitus		Evans (2018)
	Taonius notalia			Evans (2018), Cherel (2020)
	Teuthowenia pellucida			
Cycloteuthidae	*Cycloteuthis sirventi*			
		Discoteuthis laciniosa		
Ancistrocheiridae		*Ancistrocheirus lesueurii*		
Enoploteuthidae	*Abraliopsis gilchristi*			
Lycoteuthidae		*Lycoteuthis lorigera*		
Pyroteuthidae			*Pyroteuthis margaritifera*	
Gonatidae	*Gonatopsis octopedatus*			Cherel (2020)
	Gonatus antarcticus			
Histioteuthidae	*Histioteuthis atlantica*			
		Histioteuthis bonnellii corpuscula		
	Histioteuthis eltaninae			
	Histioteuthis macrohista			
		Histioteuthis miranda		
		Stigmatoteuthis hoylei		
Psychroteuthida		*Psychroteuthis glacialis*		
	Psychroteuthis sp. B (Imber)			Cherel (2020)
Lepidoteuthidae		*Lepidoteuthis grimaldii*		
Octopoteuthidae		*Octopoteuthis* sp.	*Octopoteuthis rugosa*	Kelly (2019)
	Taningia danae			Kelly (2019)
Pholidoteuthidae	*Pholidoteuthis massyae*			
Ommastrephidae	*Martialia hyadesi*			
			Ommastrephes cylindraceus	Fernandez-Alvarez et al. (2020)
	Todarodes cf. *angolensis*			Cherel (2020)
	Todarodes filippovae			Adam (1975)
Onychoteuthidae	*Filippovia knipovitchi*			
	Moroteuthopsis ingens			
	Moroteuthopsis longimana			
	Moroteuthopsis sp. B (Imber)			Cherel (2020)
		Notonykia africanae		
		Onychoteuthis bergii		
		Onychoteuthis sp. 2 (Imber)		
	Onykia robsoni			
	Walvisteuthis rancureli			
Thysanoteuthidae			*Thysanoteuthis rhombus*	
Sepioidea				
Sepiolidae			*Heteroteuthis* cf. *dagamensis*	
	cf. *Stoloteuthis leucoptera*			Nesis (1987)
Cirrata				
Opisthoteuthidae	*Opisthoteuthis* sp.			
Cirroteuthidae	*Cirrothauma magna* (=? Cirrata sp. A)			Guerra et al. (1998)
Stauroteuthidae	*Stauroteuthis gilchristi*			
Incirrata				
Argonautidae			*Argonauta nodosus*	
Alloposidae			*Haliphron atlanticus*	
Octopodidae	*Graneledone gonzalezi*			Guerra et al. (2000)

(continued on next page)

Table 6 (*continued*)

	Cherel et al. (2004, 2011), unpublished data	Cherel et al. (2023), additional taxa only	Cherel (2023), this study additional taxa only	Additional references
			Muusoctopus levis	Strugnell et al. (2011)
	Muusoctopus thielei			Strugnell et al. (2011)
			Octopus vulgaris	Guerra et al. (2010)
	Octopodidae sp. (Crozet, Prince Edward)			
Vampyromorpha				
Vampyroteuthidae			*Vampyroteuthis infernalis*	

specimens of the same size-class when feeding on the same squid species.

The use of cephalopod prey as bio-indicators of albatross feeding zones defined a species-specific spatial pattern during the chick-rearing period that is in agreement with the tracking of sooty and light-mantled sooty albatrosses conducted earlier during the breeding cycle. During incubation, both satellite-tracking at Crozet Islands (Pinaud and Weimerskirch, 2007; Delord et al., 2013) and GPS-tracking at the Prince Edward Islands (Carpenter-Kling et al., 2020b) showed both overlapping (PFZ) and species-specific foraging zones, with sooty and light-mantled sooty albatrosses foraging north and south of the two archipelagoes, respectively. At-sea observations during summer also indicates spatial segregation, with the limitations that the colonies of origin and breeding status of the individuals observed were unknown. Sooty and light-mantled sooty albatrosses range mainly between 30°S and 50°S, and 40°S to the pack-ice, respectively (Marchant and Higgins, 1990; Delord et al., 2013). In contrast to the sooty albatross, light-mantled sooty albatross occurs rarely in the subtropics and the species has the most southerly distribution of all albatrosses during summer that includes the chick-rearing period (Weimerskirch et al., 1986, Stahl et al. unpublished data).

No anthropogenic items were found in 10 stomach contents of light-mantled sooty albatrosses from Crozet Islands (this study) and only a few plastic debris items occurred in four out of 66 (6%) boluses at Kerguelen Islands (Cherel et al., 2023, Cherel unpublished data). By contrast, both plastic debris and fishery-related items occurred more frequently in food samples of sooty albatross from both Crozet (13%) and Amsterdam (15%) Islands, thus suggesting that interactions with human activities took place primarily in subtropical waters. *Phoebetria* albatrosses are primarily solitary foragers that are less attracted by fishing vessels than many other albatrosses (Weimerskirch et al., 1986; Banda et al., 2024). However, low exposure to the fishing boats does not preclude being killed by baited longlines (Huang and Liu, 2010; Banda et al., 2024), and this negative interaction is considered as the main driver of population decline of sooty albatross at all sites where long-term demographic surveys are carried out (ACAP, 2012; Weimerskirch et al., 2018). Consequently, more detailed information is needed on the at-sea behavior of sooty albatross in subtropical waters where Asian longlines operate (Huang and Liu, 2010). This means using state-of-the-art bird-borne satellite- and GPS-tags coupled with radar detectors (Weimerskirch et al., 2020) to quantify albatross-fishery interactions and to estimate the proportion of illegal fishing vessels.

4.3. Teuthofauna of the southern Indian Ocean

Using a combination of oceanographic cruises, fishery bycatches, and bio-sampling by cephalopod consumers, teuthofauna of the southern Indian Ocean was first described in slope waters surrounding the Crozet and Kerguelen Islands, which are the main fishing grounds for the Patagonian toothfish *Dissostichus eleginoides* (Cherel et al., 2004, 2011). A second step recently included the foraging grounds of albatrosses breeding at Kerguelen Islands, thus expanding the study area to vast oceanic zones south and north of the archipelago (Cherel et al., 2023). The present study on prey of sooty albatross at Amsterdam Island together with a recent review on cephalopods from Saint-Paul and Amsterdam Islands (Cherel, 2023) added southern subtropical waters to the study area. Interestingly, both sooty albatross and the wandering albatross *Diomedea exulans* from Kerguelen and Crozet Islands feed on the same cephalopod communities that occur within the STZ, SAZ and PFZ (with the latter species also foraging within the AZ), thus explaining their more diverse cephalopod prey when compared to other subantarctic albatrosses that do not forage within the STZ during the chick-rearing period (Cherel et al., 2017, 2023).

A synthesis of all the data now available indicates that the southern Indian Ocean hosts at least 71 cephalopod species, including two bathyteuthids, 56 oegopsids, two sepiolids, three cirrate and seven incirrate octopods, and the vampyroteuthid *V. infernalis* (Table 6). Excluding three endemic benthic octopods (*Graneledone gonzalezi, Muusoctopus levis* and *M. thielei*), it is likely that most of those cephalopod taxa have a circumpolar distribution due to the annular structure of fronts and, hence, of water masses all around Antarctica (Chapman et al., 2020).

Cephalopod prey of sooty albatross highlight the abundance and importance of some squids in the functioning of pelagic ecosystems of the southern Indian Ocean, such as juvenile ommastrephids, and adult histioteuthids, *B. skolops* and *N. dimegacotyle*. At Amsterdam Island, epipelagic shoals of juvenile *O. cylindraceus* and *T. filippovae* are targeted by sooty albatross (this study), Indian yellow-nosed albatross *Thalassarche carteri*, and subantarctic fur seal *Arctocephalus tropicalis* (Cherel, 2023), thus extending to southern subtropical waters the trophic role that other juvenile ommastrephids (*Martialia hyadesi* and *Todarodes* cf. *angolensis*) play in the nutrition of predators in the Southern Ocean (Cherel, 2020). Together with the subantarctic wandering albatross (Cherel et al., 2017), sooty albatross underlines the importance of histioteuthids in pelagic trophic webs of the southern Indian Ocean. The same six species of histioteuthids had been identified from food samples of sooty albatross (this study), wandering albatross (Cherel et al., 2017), and sperm whale *Physeter macrocephalus* (Clarke, 1980; Cherel, 2021a), with their relative dietary importance depending on predators and localities. The Southern Ocean endemic *H. eltaninae* generally predominates south of the STF (Cooper and Klages, 1995; Cherel et al., 2017, this study), being replaced by other species further north where *H. atlantica* is important everywhere, and *H. bonnellii corpuscula* and *H. macrohista* are also abundant prey of albatrosses and sperm whale (Cherel et al., 2017; Cherel, 2021a).

The cephalopod diet of sooty albatross added new information about the rarely reported and poorly known *B. skolops* and *N. dimegacotyle* (Cherel, 2020). It confirmed the high abundance of *B. skolops* in subantarctic waters of the southern Indian Ocean as the species accounted for up to 57.0% and 62.7% of the lower beaks from the Prince Edward Islands (misidentified as *Chiroteuthis* sp.) and Crozet Islands, respectively (Cooper and Klages, 1995, this study). Finally, the importance of *N. dimegacotyle* in the diet of sooty albatross from Amsterdam Island questions its status as an endemic species of the Southern Ocean (Cherel, 2020). The species belongs to the subantarctic squid assemblage in the Pacific (Nesis and Nikitina, 1992; Alexeyev, 1994), and it was recorded within the PFZ of the Indian Ocean (Cherel et al., 2004). Our results suggest that *N. dimegacotyle* also occurs in the vicinity of the STF and north of it, in the southern part of the STZ where Amsterdam Island is located.

A critical issue of using cephalopod beaks from predator food samples is taxonomic identification, which is notably difficult and requires expertise. The method is a powerful tool that complements, but not replaces, the more traditional mean of examining and dissecting well-preserved specimens, and DNA analysis of tissue samples. Consequently, caution is needed when critically evaluating studies based on the examination of beaks only (*e.g.,* Cherel, 2020). Moreover, it is likely that beak identification will be harder in the near future, since recent studies indicate that some taxa are species complexes, as *H. atlantica* (Braid and Bolstad, 2019) and *O. robsoni* (Bolstad et al., 2018). Hence, improvement in beak identification requires that both taxonomic revision and description of new species include drawings and photos of lower and upper beaks, ideally from early to adult cephalopods (Xavier et al., 2022).

CRediT authorship contribution statement

Yves Cherel: Conceptualization, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **Colette Trouvé:** Formal analysis.

Declaration of competing interest

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Data availability

Data will be made available on request.

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