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Revisiting taxonomy of cephalopod prey of sperm whales caught commercially in subtropical and Southern Ocean waters

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ABSTRACT

The sperm whale is the largest toothed whale that feeds almost exclusively on oceanic cephalopods. Since it was actively hunted commercially, considerably more is known about its food than for many other large marine apex predators. However, the use of those unique dietary information is today hampered by out-of-date cephalopod taxonomy. Here, the names of cephalopod prey of sperm whales were revisited by reviewing taxonomic investigations and tracking over time the names of sclerotized beaks that accumulate in predators' stomachs. The study focused on the seminal investigations by Clarke (1980) and Clarke and MacLeod (1982), which form the basis of our knowledge on the feeding habits of sperm whales in the Southern Hemisphere. Forty-five different beaks were identified, of which the labelling of 24% taxa is valid today, 7% are still undetermined, and the name of the 69% remaining beaks had to be changed due to improvement in both taxonomy (31%) and beak identification (27%), and to initial misidentifications (11%). Few taxonomic changes occurred at the family level, but changes at the species level are substantial and reveal the dietary importance of poorly known squid species (*e.g. Galiteuthis suhmi, Histioteuthis macrohista*). Within the southern subtropics, sperm whales feed primarily on five histioteuthids, with *Histioteuthis atlantica* ranking first numerically, and on octopoteuthids, cranchiids and onychoteuthids. In contrast, whales caught in the Antarctic prey mainly upon three species of Southern Ocean endemics, the cranchiid *Mesonychoteuthis hamiltoni*, and the onychoteuthids *Filippovia knipovitchi* and *Moroteuthopsis longimana*. In conclusion, revisiting taxonomy allowed a better understanding of the deep-sea ecosystem by improving our knowledge on oceanic cephalopods and on the feeding habits of sperm whales, a cephalopod predator that has a key trophic role in the oceans.

1. Introduction

The sperm whale *Physeter macrocephalus* is the largest of the toothed whales (odontocetes) and the commonest large cetacean today. It has a wide geographic range from the equator to high latitudes, where its diet consists almost exclusively of oceanic cephalopods, mainly oegopsids, with fish being a significant prey group in some areas (Clarke 1996). The sperm whale is an apex predator that was estimated to consume ~110 (96–320) million tons of cephalopods each year, thus highlighting its major role and the importance of cephalopods both as prey and as consumers within the trophic web of the pelagic ecosystem of the World Ocean (Clarke 1977; Santos et al., 2001). Since the sperm whale was historically heavily harvested, considerably more is known about its food than about other cephalopod-eating whales (Clarke 1986b).

The initial step in studying the feeding habits of sperm whales was to identify cephalopods morphologically, with unfortunately no or little quantification of the species involved (Kawakami 1980; Mikhalev et al., 1981). The second step was to use the cephalopod beaks that accumulate by hundreds and thousands in the whale stomach (over 18,000 beaks in a single stomach; Clarke 1986b). Identification and quantification of cephalopod prey of marine predators by using the morphology of their sclerotized beaks was initiated in the 60s and subsequently developed with an initial focus on sperm whale food (Clarke, 1962a,b, 1972, 1986a). The method was at its best in a seminal and beautifully illustrated monography that depicts the feeding habits of sperm whales caught in the southern subtropics and the Southern Ocean (Clarke 1980). Tens of thousands of lower beaks were described, illustrated, numbered and measured, thus allowing detailed identification of the cephalopod prey of sperm whales in South Africa, western Australia and in the Antarctic. This and subsequent publications (Clarke and MacLeod 1982; Pascoe et al., 1990; Clarke and Roper 1998; Evans and Hindell 2004; Gomez-Villota 2007) form the basis of our knowledge about the food of this overwhelmingly important cephalopod predator worldwide.

Unfortunately, several limitations now hinder an easy use of those

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data. Firstly, the initial monograph (Clarke 1980) was published in an important journal that is now difficult to get access to a copy. Secondly, and more fundamentally, our knowledge of cephalopod taxonomy has developed over the last 40 years, thus obscuring the picture regarding beak names in previous investigations. Four features are notable within that context. Cephalopod taxonomy improved, thus inducing (i) new names for well-known species (*e.g. Filippovia knipovitchi*, formerly *Moroteuthis knipovitchi*; Bolstad 2010), and (ii) the description of new species to science (*e.g. Asperoteuthis lui*; Braid 2017). Moreover, improvement in the identification of lower beaks resolved (iii) previous mismatches between beak names and well-described species (*e.g.* ?*Psychroteuthis*, now *Discoteuthis discus*; Clarke and Roeleveld 1998), and (iv) the links between well-described beaks and the corresponding squid species (*e.g. Moroteuthis* A and *Moroteuthopsis ingens*; Clarke 1986a). Hence, a recent review of taxonomy and of the tracking of beak names over time increased substantially the diversity of pelagic squids in the Southern Ocean and underlined the importance of previously poorly known taxa as prey of seabirds and marine mammals (Cherel 2020).

The main goal of the present work was to synthesize the dispersed information on cephalopod taxonomy and on identification of cephalopod beaks to upgrade the list of cephalopod prey of sperm whales in southern subtropical waters and in the Southern Ocean. Its ultimate objective was to facilitate the use of this important scientific literature to researchers developing programs on cetaceans and on cephalopods, their trophic relationships, and on the functioning of the pelagic ecosystems of the Southern Hemisphere. Revisiting the food of sperm whales caught commercially brings up to date unique data sets that cannot be collected again, because commercial whaling has ceased and the species is protected worldwide. The sperm whale is today globally designated as Vulnerable on the IUCN Red List of Threatened species (Taylor et al., 2019).

2. Materials and methods

2.1. Study sites, physical oceanography and biogeography

The study focused on two sperm-whale dietary investigations that complement each other in terms of geographical coverage of the Southern Hemisphere, from the southwestern Atlantic to the southwestern Pacific Ocean, thus including the southern Atlantic and Indian Oceans (Clarke 1980; Clarke and MacLeod 1982). Food samples came firstly from three whaling stations that were located on the west coast (Donkergat) and on the east coast (Durban) of South Africa, and on the west coast of Australia (Albany) (Clarke 1980). Secondly, some samples

Table 1
Improvement in cephalopod identification and taxonomy over time: revisiting and updating cephalopod prey of sperm whales from the Southern Hemisphere.

Previous taxonomy		Actual taxonomy
Clarke (1980)	Clarke and MacLeod (1982)	
Architeuthis sp.	*Architeuthis* sp.	*Architeuthis dux*
Todarodes sp. (*T. angolensis, T. filippovae*)	*Todarodes* sp.	*Todarodes angolensis* and *T. filippovae*
Kondakovia longimana	*Kondakovia longimana*	*Moroteuthopsis longimana*
Moroteuthis knipovitchi		*Filippovia knipovitchi*
Moroteuthis robsoni	*Moroteuthis robsoni*	*Onykia robsoni*
Moroteuthis A	*Moroteuthis* A	*Moroteuthopsis ingens*
Pholidoteuthis boschmai	*Pholidoteuthis boschmai* A and B	*Pholidoteuthis massyae*
Gonatus antarcticus		*Gonatus antarcticus*
Ancistrocheirus lesueuri	*Ancistrocheirus lesueuri*	*Ancistrocheirus lesueurii*
Octopoteuthis rugosa	*Octopoteuthis rugosa*	*Octopoteuthis rugosa*
Octopoteuthis ?*sicula*		Undetermined *Octopoteuthis*
Octopoteuthis ?*longiptera*	*Octopoteuthis* sp. A	*Octopoteuthis* ?*fenestra*
	Octopoteuthis sp. (giant) B	Giant Pacific *Octopoteuthis* sp.
Taningia danae	*Taningia danae*	*Taningia danae* and *T. fimbria*
Lepidoteuthis grimaldii	*Lepidoteuthis grimaldii*	*Lepidoteuthis grimaldii*
Chiroteuthis joubini		*Chiroteuthis joubini*
Chiroteuthis sp. A		*Chiroteuthis joubini*
Chiroteuthis sp. B		Undetermined *Chiroteuthis*, possibly *C. veranyi*
Chiroteuthis sp. C	*Chiroteuthis* sp. C	*Chiroteuthis veranyi*
	Chiroteuthis ?*joubini*	Undetermined *Chiroteuthis*, possibly *C. veranyi*
?*Mastigoteuthis* A		*Asperoteuthis lui*
?*Mastigoteuthis* B	?*Mastigoteuthis* B	*Asperoteuthis acanthoderma*
Cycloteuthis akimushkini	*Cycloteuthis akimushkini*	*Cycloteuthis sirventi*
?*Discoteuthis*	?*Discoteuthis*	*Discoteuthis laciniosa*
A1 *Histioteuthis* ?*meleagroteuthis*	*Histioteuthis* A1 ?*meleagroteuthis*	*Histioteuthis macrohista*
A2 *Histioteuthis bonnellii corpuscula*	*Histioteuthis* A2 *bonnellii corpuscula*	*Histioteuthis bonnellii corpuscula*
A3 *Histioteuthis miranda*	*Histioteuthis* A3 *miranda*	*Histioteuthis miranda*
A4 *Histioteuthis dofleini*	*Histioteuthis* A4 ?*dofleini*	*Stigmatoteuthis hoylei* and *S. arcturi*
A5 *Histioteuthis* sp.		*Stigmatoteuthis hoylei* and *S. arcturi*
B1 *Histioteuthis* ?*eltaninae*		*Histioteuthis eltaninae*
B2 *Histioteuthis reversa*		*Histioteuthis eltaninae*
B3 *Histioteuthis atlantica*	*Histioteuthis* B3 *atlantica*	*Histioteuthis atlantica*
B4 *Histioteuthis* sp.	*Histioteuthis* B4	*Histioteuthis atlantica*
Psychroteuthis		*Psychroteuthis glacialis*
?Large *Psychroteuthis*, ?*Psychroteuthis*		*Discoteuthis discus*
Liocranchia sp.		*Liocranchia reinhardti*
?*Crystalloteuthis glacialis*		*Alluroteuthis antarcticus*
?*Taonius megalops*	*Galiteuthis armata*	*Galiteuthis suhmi*
Taonius pavo	*Taonius pavo*	*Taonius notalia*
Phasmatopsis cymoctypus	*Megalocranchia* sp.	*Megalocranchia* sp.
Galiteuthis armata		*Liguriella podophtalma* and *Galiteuthis glacialis*
	Galiteuthis sp. B	*Teuthowenia pellucida*
Mesonychoteuthis hamiltoni	*Mesonychoteuthis hamiltoni*	*Mesonychoteuthis hamiltoni*
Alloposus mollis	*Alloposus mollis*	*Haliphron atlanticus*
Vampyroteuthis infernalis	*Vampyroteuthis infernalis*	*Vampyroteuthis infernalis*

were collected from pelagic factories operating in the Tasman Sea (Clarke and MacLeod 1982) and in the Antarctic, including South Georgia and the pelagic Antarctic (the South Shetland Islands and South Orkney Islands) (Clarke 1980).

According to physical oceanography, sperm whales were caught in subtropical waters and within the Southern Ocean. The latter is defined as water masses located south of the Subtropical Front (STF). The main marine fronts within the Southern Ocean are the Subantarctic and the Polar Fronts; they delineate the following oceanic zones, from North to South: the subantarctic Zone (SAZ), Polar Frontal Zone (PFZ) and Antarctic Zone (AZ) (Pollard et al., 2002). The oceanic zone north of the Southern Ocean (north of the STF) is the Subtropical Zone (STZ). Hence, sperm whales from Donkergat (western South Africa), Durban (eastern South Africa) and Albany (western Australia) (Clarke 1980) were caught within the STZ of the eastern Atlantic, and of the western and eastern Indian Ocean, respectively. Whales from the Tasman Sea (Clarke and MacLeod 1982) were killed mainly within the STZ of the western Pacific, with some of them coming from the SAZ (to 47°S). Finally, sperm whales from South Georgia, and from the South Orkney and South Shetland Islands (Clarke 1980) were caught further south, within the AZ of the southwestern Atlantic.

2.2. *Analysis and nomenclature*

Cephalopod beaks that were identified in sperm whale food samples (Clarke 1980; Clarke and MacLeod 1982) were listed and the validity of each taxon was thoroughly examined using various means (Table 1), including successive updates by M Clarke (Clarke and MacLeod 1982; Clarke 1986a; Clarke et al., 1993; Clarke and Roeleveld 1998; Clarke and Roper 1998; Clarke and Young 1998). Synonymies of beak names were tracked over publications and time (details in Cherel 2020). The work also benefited from the opportunistic examination of beaks from Clarke's collection by the author, because beaks from sperm whale stomachs (Clarke 1980) were deposited to several museums and scientific organizations, including the British Antarctic Survey (Cambridge, UK), and the Port Elizabeth Museum at Bayworld (South Africa). The work on beaks was completed by a review of articles (1980–2020) and of recent grey literature (PhD) devoted to species, species groups and assemblages to complete and update both taxonomy and biogeography (*e.g.* Braid 2017; Evans 2018; Fernandez-Alvarez 2018; Kelly 2019).

Table 2
Fresh remains (whole specimens, heads, buccal masses) of cephalopod prey of sperm whales from the Southern Hemisphere.

Species	Donkergat Clarke (1980)	Durban Clarke (1980) Clarke and Roeleveld (1998)	Albany Clarke (1980)	Tasman Sea Clarke and MacLeod (1982)	Subtropical Zone			South Clarke (1980)	Pelagic Clarke (1980))	Antarctic	Zone
	(n)	(n)	(n)	(n)	FO (n)	(n)	(%)	(n)	(n)	(n)	(%)
Ancistrocheirus lesueurii	5	144	4	33	4	186	10.3				
Architeuthis dux	19	8	4	6	4	37	2.1				
Asperoteuthis lui								2		2	1.0
Chiroteuthis joubini		34	2		2	36	2.0				
Chiroteuthis veranyi		9		5	2	14	0.8				
Undetermined *Chiroteuthis*								1		1	0.5
Galiteuthis suhmi	37	40		13	3	90	5.0				
Liguriella podophtalma		2			1	2	0.1				
Liocranchia reinhardti		3			1	3	0.2				
Megalocranchia sp.		4	1	18	3	23	1.3				
Mesonychoteuthis hamiltoni								33	30	63	32.6
Taonius notalia	6			1	2	7	0.4				
Cycloteuthis sirventi	4	12	6	2	4	24	1.3				
Discoteuthis discus		1			1	1	0.1				
Discoteuthis laciniosa	1	1			2	2	0.1				
Gonatus antarcticus								1	2	3	1.6
Histioteuthis atlantica	1	36	2	17	4	56	3.1				
Histioteuthis bonnellii corpuscula	7	171		2	3	180	10.0				
Histioteuthis eltaninae		4			1	4	0.2				
Histioteuthis macrohista	7				1	7	0.4				
Histioteuthis miranda	6	108	18	4	4	136	7.6				
Lepidoteuthis grimaldii	1	2	2	5	4	10	0.6				
Octopoteuthis rugosa	15	326	1	23	4	365	20.3				
Giant Pacific *Octopoteuthis* sp.				1	1	1	0.1				
Taningia danae/fimbria	1	42	7	33	4	83	4.6	4		4	2.1
Ommastrephes cylindraceus		2			1	2	0.1				
Todarodes filippovae/ angolensis	3	378	5		3	386	21.5	4		4	2.1
Filippovia knipovitchi								13	14	27	14.0
Moroteuthopsis longimana								55	30	85	44.0
Onykia robsoni	10	60	6	7	4	83	4.6	2		2	1.0
Pholidoteuthis massyae	30	5	9	13	4	57	3.2				
Psychroteuthis glacialis									1	1	0.5
Other decapods	2				1	2	0.1		1	1	0.5
Haliphron atlanticus		1			1	1	0.1				
Total	155	1393	67	183	4	1798	100.0	115	78	193	100.0

Table 3
Accumulated cephalopod beaks identified from stomach contents of sperm whales caught in the Southern Hemisphere.

Location	Donkergat		Durban		Albany		Tasman Sea		South Georgia		Pelagic Antarctic	
Number of whales	89		72		6		30		28		12	
	Clarke (1980)		Clarke (1980)		Clarke (1980)		Clarke and MacLeod (1982)		Clarke (1980)		Clarke (1980)	
Species	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)
Ancistrocheirus lesueurii	2319	4.48	3914	6.02	75	2.77	116	3.52	46	2.81	48	0.67
Architeuthis dux	153	0.30	153	0.24	10	0.37	54	1.64	18	1.10	2	0.03
Asperoteuthis acanthoderma	164	0.32	63	0.10	6	0.22	16	0.48				
Asperoteuthis lui									57	3.48	53	0.74
Chiroteuthis spp.	404	0.78	5392	8.30	36	1.33	46	1.39			12	0.17
Galiteuthis suhmi	7153	13.82	975	1.50	73	2.69	68	2.06	8	0.49	26	0.36
Liguriella podophtalma	405	0.78	827	1.27	14	0.52			7	0.43	27	0.38
Liocranchia reinhardti	7	0.01	49	0.08					1	0.06		
Megalocranchia sp.	1087	2.10	377	0.58	4	0.15	246	7.46	16	0.98	51	0.71
Mesonychoteuthis hamiltoni	942	1.82	713	1.10	120	4.42	11	0.33	377	23.00	989	13.78
Taonius notalia	766	1.48	342	0.53	27	1.00	21	0.64	16	0.98	27	0.38
Teuthowenia pellucida							15	0.45				
Cycloteuthis sirventi	386	0.75	708	1.09	78	2.88	29	0.88	4	0.24	11	0.15
Discoteuthis laciniosa	418	0.81	681	1.05			22	0.67				
Gonatus antarcticus	59	0.11	12	0.02					3	0.18	274	3.82
Histioteuthis atlantica	6046	11.68	7617	11.72	764	28.17	382	11.58	49	2.99	54	0.75
Histioteuthis bonnellii corpuscula	3060	5.91	14012	21.56	30	1.11	143	4.33	1	0.06		
Histioteuthis eltaninae	1206	2.33	2257	3.47	8	0.29			yes	?	yes	?
Histioteuthis macrohista	7425	14.34	314	0.48	2	0.07	28	0.85				
Histioteuthis miranda	1656	3.20	4831	7.43	312	11.50	121	3.67	25	1.53	25	0.35
Stigmatoteuthis hoylei and *S. arcturi*	5	0.01	24	0.04	8	0.29	298	9.03	47	2.87	729	10.16
Undetermined histioteuthids							33	1.00				
Lepidoteuthis grimaldii	268	0.52	133	0.20	38	1.40	57	1.73	14	0.85	46	0.64
Alluroteuthis antarcticus	31	0.06	326	0.50	5	0.18			3	0.18	104	1.45
Octopoteuthis spp.	5568	10.75	12756	19.63	157	5.79	764	23.16	3	0.18	34	0.47
Taningia danae and *T. fimbria*	828	1.60	1577	2.43	83	3.06	348	10.55	177	10.80	50	0.70
Todarodes filippovae	91	0.18	1853	2.85	394	14.53	38	1.15	34	2.07	5	0.07
Filippovia knipovitchi	150	0.29	66	0.10					292	17.82	3180	44.30
Onykia robsoni	3188	6.16	1543	2.37	83	3.06	135	4.09	yes	?	yes	?
Moroteuthopsis ingens	231	0.45	284	0.44			10	0.30	34	2.07	175	2.44
Moroteuthopsis longimana	1366	2.64	1990	3.06	118	4.35	102	3.09	354	21.60	1124	15.66
Pholidoteuthis massyae	5656	10.92	291	0.45	263	9.70	172	5.21	1	0.06	25	0.35
Psychroteuthis glacialis									1	0.06	22	0.31
Vampyroteuthis infernalis	34	0.07	110	0.17			1	0.03			2	0.03
Haliphron atlanticus	63	0.12	29	0.04	1	0.04	6	0.18	49	2.99	42	0.59
Others (including *Discoteuthis discus*)	637	1.23	758	1.17	3	0.11	17	0.52	2	0.12	41	0.57
Total	51772	100.00	64977	100.00	2712	100.00	3299	100.00	1639	100.00	7178	100.00

The three following issues limited the retrospective analysis of dietary data on fresh items. Firstly, the lack of detailed information precludes knowing which cephalopods were caught within the STZ and/or within the SAZ of the Tasman Sea (Clarke and MacLeod 1982). However, since only one whaling position lied within the SAZ, it was assumed that all the cephalopods from the Tasman Sea refer to the STZ (Tables 2 and 3). Secondly, while it is expected that the southernmost caught fresh *Octopoteuthis* specimens in the Tasman Sea (in the SAZ, at 47°S) refer to *Octopoteuthis fenestra* (see below), it was not detailed how many individuals were eaten by the whales, thus explaining why *O. fenestra* was not listed in Table 2. Thirdly, I removed two *Filippovia knipovitchi* and added two *Onykia robsoni* amongst the fresh remains of cephalopods from South Georgia (Table 2), because (i) fresh remains of *O. robsoni* were identified from sperm whales caught at South Georgia, but no fresh specimens were recorded in the corresponding table (Clarke 1980), (ii) there was a mismatch in the number of fresh *F. knipovitchi* when comparing different tables (two more or less specimens), and (iii) beaks of the two species are closely-related and easy to confuse, thus likely explaining why their accumulated beaks were pooled (Clarke 1980).

It is important to consider the following issues regarding data on accumulated beaks. Retrospective analysis necessitated back calculation of the beak numbers of some species by using percentages that were indicated within the text and tables (Clarke 1980). There were also some limitations due to the initial data analysis (Table 3). Firstly, lower beaks of *Liguriella podophtalma* included those from *Galiteuthis glacialis* (see below). Secondly, beaks of *Histioteuthis eltaninae* at South Georgia and in the pelagic Antarctic were pooled with those of *H. atlantica*, as were beaks from *O. robsoni* with those of *F. knipovitchi* (Clarke 1980). Thirdly, according to beak size and location, *Octopoteuthis* spp. included two to three different taxa (see below) that were numbered in Clarke and MacLeod (1982) but pooled in Clarke (1980). Fourthly, beaks called "Others" included those from *Discoteuthis discus* at Donkergat and Durban (Clarke 1980). Finally, the lack of a database including detailed beak measurements (lower rostral length, LRL) precluded updating the estimation of cephalopod size (mantle length, body mass) and thus of the absolute and relative species-specific biomasses consumed by sperm whales.

3. Results

Overall, forty-five different beaks were identified and described in Clarke (1980) and Clarke and MacLeod (1982). Amongst those 45 cephalopod taxa (Table 1), the labelling of 11 (24.4%) beaks was right, three (6.7%) are still undetermined at the species level, and the name of the 31 (68.9%) remaining taxa had to be changed due to improvement in both taxonomy (n = 14, 31.1%) and beak identification (n = 12, 26.7%), and to initial misidentifications (n = 5, 11.1%).

3.1. Taxonomic updates and species notes

Most taxonomic updates were detailed in Cherel (2020), but some taxa required some additional information.

3.1.1. *Chiroteuthidae*

Five *Chiroteuthis* beaks, namely *C. joubini*, *C. ?joubini*, *Chiroteuthis* sp. A, *Chiroteuthis* sp. B and *Chiroteuthis* sp. C were described in Clarke (1980) and Clarke and MacLeod (1982). While *Chiroteuthis* sp. A and *Chiroteuthis* sp. C were subsequently synonymized with *C. joubini* and *C. veranyi*, respectively (Clarke et al., 1993), the species identification of *C. ?joubini*, and *Chiroteuthis* sp. B was problematic. The presence of luminous patches on eyes rather than photophores and its Antarctic location of capture suggests that the single head of *Chiroteuthis* sp. B corresponds to *C. veranyi*. *C. ?joubini* beaks are closely similar to those described as *Chiroteuthis* A from sperm whales caught off Peru (Clarke and MacLeod 1982). Drawings of *Chiroteuthis* A beaks (Clarke et al., 1976) look like those of *C. veranyi*, which is the single species of *Chiroteuthis* recorded in the area (Nesis 1987; Alexeiev 1994). Overall, this suggests that *C. ?joubini* and *Chiroteuthis* sp. B also correspond to *C. veranyi*.

Two recent taxonomic studies synonymized ?*Mastigoteuthis* A and ?*Mastigoteuthis* B (Clarke 1980) with two species of the chiroteuthid genus *Asperoteuthis*, *A. lui* (Braid 2017) and *A. acanthoderma* (Cherel 2021), respectively. ?*Mastigoteuthis* B beaks were erroneously named *Mastigoteuthis* A in Table 1, but not in the text of Clarke and MacLeod (1982).

3.1.2. *Cranchiidae*

Lower beaks of *Galiteuthis armata* refer to three different species of cranchiids (Cherel 2020), namely *Galiteuthis suhmi* in Clarke and MacLeod (1982), and *L. podophtalma* and *G. glacialis* in Clarke (1980 Text-fig. 225). Clarke (1980) found two modes in beak size of *G. armata*, suggesting two species, the largest being *G. armata* (= *L. podophtalma*) and the smallest a second species he also found in albatross food samples. Indeed, lower beaks from *L. podophtalma* and *G. glacialis* are pretty similar, but those from *L. podophtalma* darken at, and reach, a larger size than those from *G. glacialis*, the latter species being one of the commonest cephalopod prey of albatrosses within the Southern Ocean (Cherel 2020). Confusion was increased when beaks named ?*Taonius megalops* (Clarke 1980 Text-fig. 209) were re-named *G. armata*, because one head was in sufficiently good condition to indicate that the species was not a *Taonius* but a *Galiteuthis* species (Clarke and MacLeod 1982). Indeed, both ?*Taonius megalops* (Clarke 1980) and *G. armata* (Clarke and MacLeod 1982) now correspond to the rarely reported *Galiteuthis suhmi* (Evans 2018; Cherel 2020).

Voss (1985) synonymized *Galiteuthis* (= *Teuthowenia*) sp. B (Clarke and MacLeod 1982, misnamed as *G. armata* within the text p 33 but not in Tables 1 and 2) with *Teuthowenia pellucida* (details in Cherel 2020).

The genus *Liocranchia* includes two species, with only one, *L. reinhardti*, living in subtropical waters where it is common (Nesis 1987), thus explaining the shift here from *Liocranchia* sp. (Clarke 1980) to *L. reinhardti*.

3.1.3. *Cycloteuthidae*

Beaks described as ?Large *Psychroteuthis* and ?*Psychroteuthis* (Clarke 1980), and as ?*Discoteuthis* (Clarke 1980; Clarke and MacLeod 1982) correspond to those of the two species of the genus *Discoteuthis*, *D. discus* and *D. laciniosa*, respectively (Clarke et al., 1993; Clarke and Roeleveld 1998; Clarke and Young 1998).

3.1.4. *Octopoteuthidae*

Two and three size modes of *Octopoteuthis* lower beaks were found in the diet of sperm whales caught at Donkergat and Durban (Clarke 1980), and at Albany and in the Tasman Sea (Clarke 1980; Clarke and MacLeod 1982), respectively. Modes refer either to gender because females have larger beaks than males (Kelly 2019), or more likely to different taxa.

- The smallest *Octopoteuthis* species (mode at 8–9 mm LRL) from Donkergat, Durban and Albany remains undetermined. Clarke (1980) tentatively identified it as *O. sicula*, but the species is endemic to the Atlantic and is not recorded from the Indian Ocean (Kelly 2019).
- *O. rugosa* corresponds to the peak at 10–11 mm LRL, max 12.5 mm LRL (Donkergat, Durban and Albany) (Clarke 1980) and to beaks with LRL <11.5 mm (Tasman Sea) (Clarke and MacLeod 1982). The species has a southern circumglobal distribution (Kelly 2019).
- The third peak occurred at 13.0–14.5 mm LRL at Albany (Clarke 1980) and it corresponds to beaks with LRL>11.5 mm of *Octopoteuthis* sp. A in the Tasman Sea (Clarke and MacLeod 1982). Clarke (1980) tentatively identified the corresponding species as *O. longiptera*, which is today a *nomen dubium* (Kelly 2019). The species remains unidentified, but the newly described *O. fenestra* (Kelly 2019) is a good candidate because: i) its maximum LRL is 13.6 mm, a larger size than that of all the other small *Octopoteuthis* species (Kelly 2019), (ii) *O. fenestra* has been collected south of Tasmania and in New Zealand waters (Kelly 2019), which fits well with its presence in the diet of sperm whales caught in Australian waters and not in South Africa (Clarke 1980; Clarke and MacLeod 1982), and (iii) *Octopoteuthis* flesh recorded from sperm whales caught within the SAZ in the Tasman Sea (Clarke and MacLeod 1982) is likely to correspond to *O. fenestra*, which is the southernmost and single *Octopoteuthis* species living in the Southern Ocean (Kelly 2019).
- In the Tasman Sea, large beaks with a LRL >15 mm were called *Octopoteuthis* sp. (giant) B (Clarke and MacLeod 1982). They correspond to the still undescribed giant Pacific *Octopoteuthis* sp. that lives in the western Pacific and possibly has a southern circumglobal distribution (Kelly 2019).

Two size modes of *Taningia danae* lower beaks were found in the diet of sperm whales caught at Donkergat and Durban (Clarke 1980), and in the Tasman Sea (Clarke and MacLeod 1982), thus suggesting that the genus *Taningia* is composed to two species (Clarke and MacLeod 1982). Indeed, a recent taxonomic revision split the monotypic *T. danae* into five different taxa, including the cosmopolitan tropical-subtropical *T. danae* and the newly described Southern Hemisphere *T. fimbria* (Kelly 2019). The correspondence between beak size and species is not established but available information suggest that the large and the small LRL peaks correspond primarily to *T. danae* and *T. fimbria*, respectively.

3.1.5. *Ommastrephidae*

Beaks of *Todarodes* sp. were collected at Donkergat, Durban, Albany and in the Tasman Sea (Clarke 1980; Clarke and MacLeod 1982). Morphology and biogeography indicate that they were either *T. angolensis*, *T. filippovae* or a mix of both. The picture is even more complicated because firstly, the taxonomic status of *T. angolensis* outside South African waters needs to be investigated (Cherel 2020), and secondly, beaks from the *Ommastrephes bartramii* species complex that occurs in the area (Fernandez-Alvarez 2018) are morphologically similar to those of the genus *Todarodes* (Cherel 2020). Indeed, a subsequent analysis of new material that included whole specimens from sperm whales caught at Durban found two *O. bartramii* (now *O. cylindraceus*, Fernandez-Alvarez 2018) and showed that all *Todarodes* specimens were *T. filippovae* (Clarke and Roeleveld 1998).

3.1.6. *Pholidoteuthidae*

According to size and morphology, beaks of *P. massyae* eaten by sperm whales clustered into three groups (Clarke 1980, 1986a), including *P. boschmai* (= *massyae*) A and B (Clarke and MacLeod 1982), thus suggesting that there may well be three species in the Southern Hemisphere (Clarke 1986a).

3.1.7. *Alloposidae*

Alloposus mollis (Clarke 1980; Clarke and MacLeod 1982) is a junior synonym of *Haliphron atlanticus* (Kristensen and Knudsen 1983).

3.2. Cephalopods in the diet of sperm whales

A total of 1991 fresh remains were identified either morphologically or from beaks that were sorted from buccal masses (Table 2). Most of them (70%) came from Durban, which was the most investigated locality by far (Clarke 1980; Clarke and Roeleveld 1998). Two oegopsid families dominated by number the diet of sperm whales in the southern subtropics, the octopoteuthids (25.0%) and histioteuthids (21.3%), while onychoteuthids (59.1%) and cranchiids (32.6%) were the two most important families within the Southern Ocean. Six squids totalled >5% by number of fresh items in the STZ, by decreasing order of importance: *T. filippovae/angolensis* > *O. rugosa* > *Ancistrocheirus lesueurii* > *Histioteuthis bonnellii corpuscula* > *H. miranda* > *G. suhmi*. In contrast, only three species dominated the whale diet in the Antarctic, *M. longimana* > *Mesonychoteuthis hamiltoni* > *F. knipovitchi*.

A total of 131,577 lower beaks were sorted from the stomach of 237 sperm whales (Table 3). Thirty-six taxa from 16 families were identified, almost all oegopsids, but two species of Octopodiformes, the vampire squid *Vampyroteuthis infernalis* and the incirrate seven-arm octopus *H. atlanticus*. The number of taxa ranged from 26 (Albany) to 32 (Donkergat and Durban), thus depending on localities. There was a strong difference in the main squid prey in the AZ and STZ, and items were locality-specific in the subtropics. In Antarctic waters, three families including four species overall dominated the whale diet, the onychoteuthids (58.5% by number) with *F. knipovitchi* (39.4%) and *M. longimana* (16.8%), the cranchiids (17.5%) with *M. hamiltoni* (15.5%), and the histioteuthids (10.5%) with *S. arcturi* (8.8%).

Within the STZ, histioteuthids ranked first at Donkergat (37.5%), Durban (44.7%) and Albany (41.4%) and second in the Tasman Sea (30.5%). *H. atlantica* was important everywhere, but *H. b. corpuscula*, *H. macrohista*, *H. miranda*, and *S. hoylei* were notably abundant at Durban, Donkergat, Albany and in the Tasman Sea, respectively (Table 3, Fig. 2). Octopoteuthids ranged from 8.8% in Albany to 33.7% in the Tasman Sea, the only locality where they dominated and where they were detailed at the species level, in the decreasing order: *O. ?fenestra* (11.7%) > *T. danae/fimbria* (10.5%) > *O. rugosa* (10.0%) > giant Pacific *Octopoteuthis* sp. (1.5%). Cranchiids were important at Donkergat (20.0%) with *G. suhmi* and in the Tasman Sea (10.9%) where *Megalocranchia* sp. was a significant prey item. Other squids that amounted to >5% by number were *O. robsoni* at Donkergat, *A. lesueurii* and *Chiroteuthis* spp. (pooled *C. joubini* and *C. veranyi*) at Durban, *T. filippovae* at Albany, and *P. massyae* at Donkergat, Albany and in the Tasman Sea (Table 3).

Many more beaks were analyzed at Donkergat and Durban than elsewhere, with the same 32 taxa being identified at the two South African localities (Table 3). Statistical analyses (equality of two proportions tests) showed that proportions significantly differed (all $p \leq 0.460$, with $p < 0.0001$ in 27 comparisons) for almost all taxa but three, the numerically important *H. atlantica* ($Z = 0.24$, $p = 0.814$), and the occasional *M. ingens* ($Z = 0.23$, $p = 0.816$), and Others (including *D. discus*) ($Z = 1.00$, $p = 0.319$).

4. Discussion

Revisiting taxonomy changed considerably the species list of cephalopods initially identified from stomachs of sperm whales commercially hunted in the southern Atlantic, Indian and Pacific Oceans. This greatly improves our knowledge on cephalopod biodiversity and on trophic relationships within the deep-sea ecosystems of the subtropics and the Southern Ocean. By reviewing the existing literature, the study also highlights the marked contrast in the dietary habits of sperm whales caught within the STZ and AZ, which is related to the different teuthofaunas inhabiting temperate and cold waters of the Southern Hemisphere.

4.1. Revisiting cephalopod taxonomy

Dietary investigations from the 1970s–1990s contain out-of-date scientific names of prey species and include initial misidentifications, because identifying cephalopods from their beaks is challenging (Cherel 2020). This is especially problematic in pioneer studies that are either impossible (*e.g.* Imber 1973) or difficult (*e.g.* Rodhouse et al., 1987; Ridoux 1994) to use, including the seminal works on the cephalopod prey of sperm whales (Clarke 1980; Clarke and MacLeod 1982). Taxonomic updating of the latter studies changed the name of a majority (69%) of the 45 different cephalopods that were identified morphologically and/or from their lower beaks (Table 1). Shifts from one family to another family are restricted to four species that were not major prey of sperm whales (Table 3), namely the chiroteuthids *A. lui* and *A. acanthoderma* (formerly mastigoteuthids), the cycloteuthid *D. discus* (formerly a psychroteuthid) and the neoteuthid *A. antarcticus* (formerly a cranchiid). Hence, the relative importance of cephalopod families in the diet of sperm whales remains essentially unchanged (Clarke 1980; Clarke and MacLeod 1982) and conclusions about them worldwide are likely valid today (Clarke 1986b, 1996).

In contrast, within-families changes at the species level are substantial (Table 1). Three issues are especially relevant: (i) the importance of *H. macrohista* (formerly *H. ?meleagroteuthis*) in the diet of whales at Donkergat; (ii) the disentangling of the beaks previously named ?*Taonius megalops* and *G. armata* adds significant new records and trophic information about the two rarely reported cranchiids *G. suhmi* and *L. podophtalma*, the former species being one of the main prey of sperm whales at Donkergat; and (iii), improving beak identification overall increases our knowledge on squid biodiversity and biogeography (*e.g.* the poorly-known *A. lui* and *A. acanthoderma*). Despite these changes, the initial analysis of lower beaks is remarkable and the hypothesis that various LRL modes of fully darkened beaks within a given taxa represent different species was validated (*e.g. G. armata* that corresponds to *G. suhmi/G. glacialis*) or in the process of being validated (*e.g. Octopoteuthis* spp. and *Taningia danae/fimbria*). However, the absence of some beaks is puzzling and suggests that at least some of them were not recognized morphologically as distinct from others and, hence, that some taxa are a diverse mix of different species. Within the STZ and Southern Ocean, relevant missing species include *Batoteuthis skolops*, *Mastigoteuthis psychrophila*, the neoteuthid *Nototeuthis dimegacotyle*, the onychoteuthids *Moroteuthopsis* sp. B (Imber) and *Notonykia africanae*, and the recently described cranchiids *Taonius expolitus* and possibly *T. tanuki* (Evans 2018; Cherel et al., 2020). Indeed, *B. skolops* was subsequently identified amongst fresh items in the stomach of sperm whales caught within the AZ (Lubimova 1985).

4.2. Cephalopod prey within the Subtropical Zone (STZ)

Fresh remains of 10 squids were identified at all the four subtropical localities (*A. lesueurii*, *A. dux*, *C. sirventi*, *H. atlantica*, *H. miranda*, *L. grimaldii*, *O. rugosa*, *T. danae/fimbria*, *O. robsoni* and *P. massyae*), thus indicating they form the basis of cephalopod prey of sperm whales within the STZ circumglobally (Table 2). Accumulated beaks confirmed that general pattern with the diet being dominated by histioteuthids and to a lesser extent octopoteuthids, while *A.dux*, *C. sirventi* and *L. grimaldii* were not numerically important (<3%) (Table 3). Histioteuthids also accounted for 54.7% and 60.6% of accumulated beaks in stranded individuals from Tasmania and New Zealand, respectively (Evans and Hindell 2004; Gomez-Villota 2007), thus highlighting the importance of this family in the diet of sperm whales within the STZ (Fig. 1). Five species were involved and *H. atlantica* ranked first or second everywhere (Fig. 2). Moreover, it is likely that numerous *H. atlantica* beaks from Tasmania were misidentified as *H. eltaninae* (Evans and Hindell 2004), because LRL measurements are too large for the latter species and fit well with the former. The four other histioteuthids are *H. miranda* (1.1%–11.5%), *H. b. corpuscula* (1.1%–21.6%, excluding New Zealand),

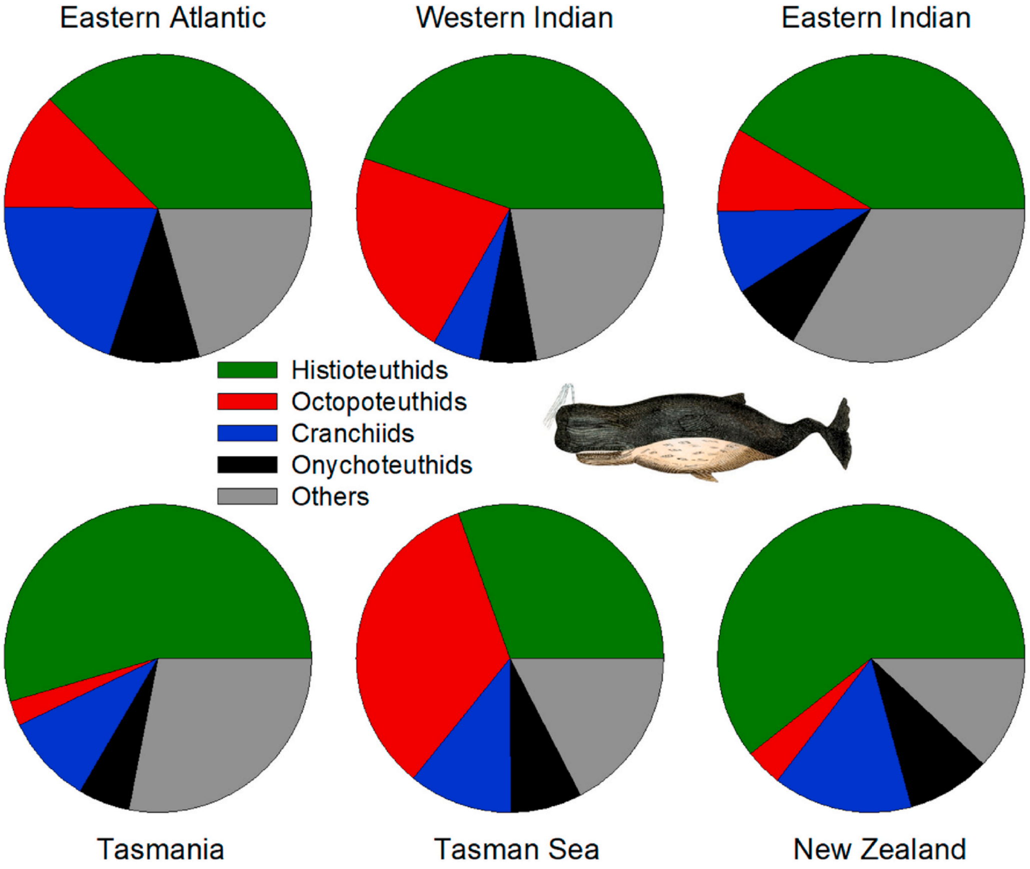

Fig. 1. Numerical importance of the four main families of cephalopods in the diet of sperm whales caught in the southern subtropics. The eastern Atlantic, western Indian and eastern Indian Ocean refer to Donkergat, Durban and Albany, respectively. Data from Clarke (1980), Clarke and MacLeod (1982), Evans and Hindell (2004) and Gomez-Villota (2007).

H. macrohista at Donkergat, and finally *S. hoylei* in the western Pacific (3.1%–9.0% in Tasmania, the Tasman Sea and New Zealand). All the above species were commonly recorded in nets in subtropical waters and at the Subtropical Front (Voss et al., 1998). Elsewhere, histioteuthids are dominant numerically (73.2%–76.9%) in the diet of sperm whales from the northern Atlantic and the Mediterranean Sea, where *H. b. bonnellii* is the main prey item (Clarke et al., 1993; Spitz et al., 2011; Foskolos et al., 2020).

At the family level, octopoteuthids, cranchiids and onychoteuthids are also important food items of sperm whales within the STZ (Fig. 1). Octopoteuthids dominated numerically in the Tasman Sea, ranked second at Durban, and third at Donkergat and Albany, with *Octopoteuthis* spp. being more abundant than *T. danae/fimbria* at every locality (Table 3). Cranchiids ranked second at Donkergat and in Tasmania (Evans and Hindell 2004) and New Zealand (Gomez-Villota 2007), and third at Albany and in the Tasman Sea. Several species were involved but *G. suhmi* and *Megalocranchia* sp. were notably abundant (>5%) at Donkergat, and in the Tasman Sea and New Zealand, respectively. Finally, onychoteuthids amounted to >5% everywhere, mainly due to the abundance of *O. robsoni* circumglobally and of the subantarctic endemic *M. ingens* in New Zealand waters (Gaskin and Cawthorn 1967a, b, Clarke and Roper 1998, Gomez-Villota 2007). Onychoteuthids also included the two Southern Ocean endemics *F. knipovitchi* and *M. longimana*, which indicate a recent northward migration of some of the whales (see below).

4.3. *Cephalopod prey within the Southern Ocean*

Three Southern Ocean endemics form the bulk (90.7% by number of fresh items) of the cephalopod diet of sperm whales in the Antarctic, the colossal squid *M. hamiltoni* and the two onychoteuthids *F. knipovitchi* and *M. longimana* (Table 2), which is in general agreement with qualitative information collected from Soviet and Japanese factories (Mikhalev et al., 1981; Nemoto et al., 1988; Filippova 2002). The other squids eaten within the AZ include *G. antarcticus* and two other Southern Ocean endemics (*A. lui* and *P. glacialis*). A review of the literature adds four species, again all endemics, to the squid prey of sperm whales in the Antarctic (*B. skolops*, *G. glacialis*, *A. antarcticus*, and *M. ingens*), and six species to the prey taken further north within the Southern Ocean (*A. dux, C. sirventi, H. atlantica, H. eltaninae, P. massyae* and *H. atlanticus*) (Vovk et al., 1978; Mikhalev et al., 1981; Lubimova 1985; Filippova 2002). Comparing fresh remains of cephalopods from sperm whales caught within the AZ and the STZ highlights the dietary importance of different squids living in these two contrasting oceanic environments (Table 2). Twenty-three species occurred in the STZ only, six in the AZ only, and three were recorded in the two zones. The latter species (*T. danae/fimbria, T. filippovae/angolensis* and *O. robsoni*) are primarily subtropical species whose distribution extends to the northern Southern Ocean (Cherel 2020), where, accordingly, they are minor prey items for sperm whales.

Analysis of accumulated beaks fit well with quantification of fresh items, with the three same species (*M. hamiltoni, F. knipovitchi* and *M. longimana*) accounting together for 71.6% of the total number of lower beaks within the AZ (Table 3). This proportion is lower than for fresh items, however, which is the consequence of the much larger diversity of cephalopods identified from beaks than from fresh items, since most beaks were found in whales caught in both subtropical and Antarctic waters. Fresh items are indicative of local food, while the much larger number of beaks results primarily from their progressive accumulation in the stomach over time (maximum ~10 days; Clarke 1980).

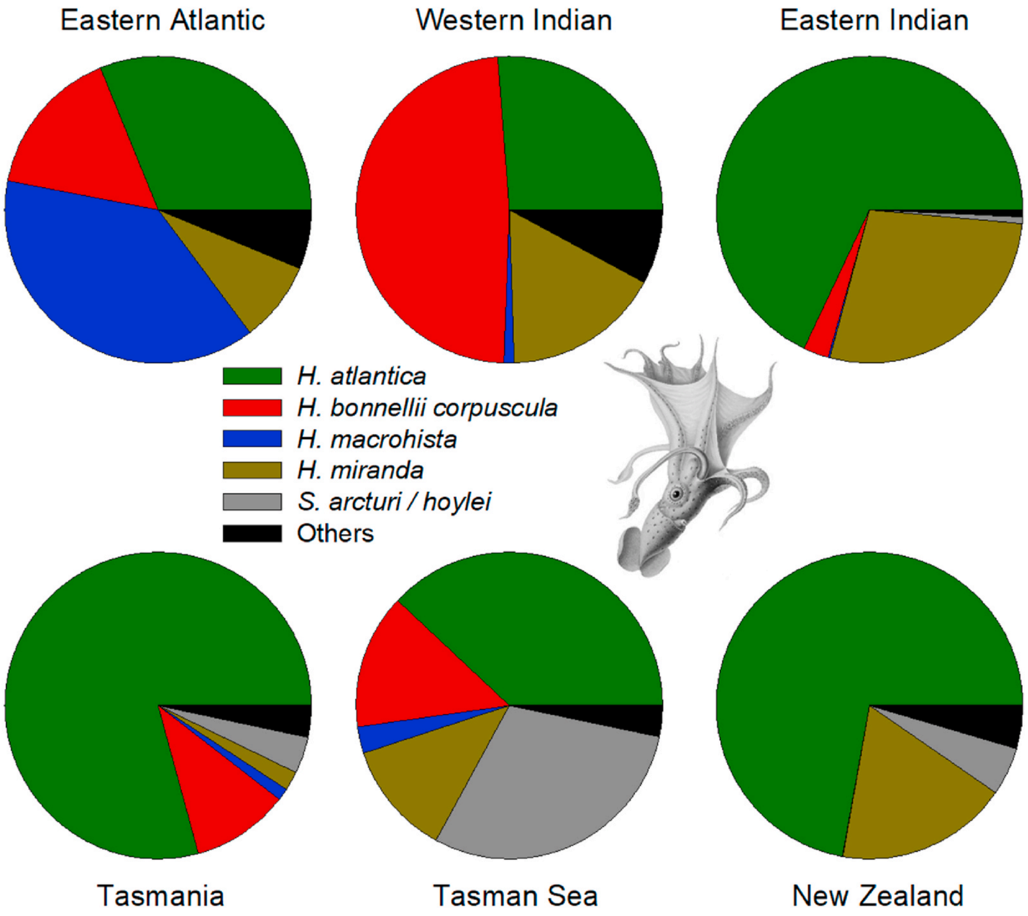

Fig. 2. Numerical importance of histioteuthid squids (*Histioteuthis atlantica, H. bonnellii corpuscula, H. macrohista, H. miranda* and *Stigmatoteuthis arcturi/hoylei*) in the diet of sperm whales caught in the southern subtropics. In Tasmania, *H. atlantica* and *H. eltaninae* were pooled (see text). The eastern Atlantic, western Indian and eastern Indian Ocean refer to Donkergat, Durban and Albany, respectively. Data from Clarke (1980), Clarke and MacLeod (1982), Evans and Hindell (2004) and Gomez-Villota (2007).

Male sperm whales migrate back and forth over years between their main feeding zone in cold waters and the reproductive zone in warmer waters where females and juveniles live all year-round. Hence, the presence of beaks of subtropical cephalopods in the stomach of adult males caught in the Antarctic indicates a recent southward migration, and *vice-versa* (Clarke 1972, 1980). Within that context, the puzzling large number of eroded lower beaks of *S. arcturi* in two whales caught in the pelagic Antarctic (South Shetlands) likely results from their southward migration (Clarke 1980), since *S. arcturi* does not occur within the Southern Ocean (Cherel 2020), but it was recorded in subtropical waters of the southwest Atlantic (Voss et al., 1998).

4.4. Predators, trophic niches, and the pelagic ecosystems

Within the STZ and AZ, sperm whales are apex predators that feed almost exclusively on medium-to large-sized cephalopods (Clarke 1980; Mikhalev et al., 1981), with the Patagonian toothfish being a significant prey item in some areas (Vukhov 1972). To my knowledge, only two other apex predators feed significantly on the same squids as the sperm whale, the Antarctic sleeper shark *Somniosus antarcticus* and large *Diomedea* albatrosses. The sleeper shark lives in slope waters surrounding subantarctic and Antarctic islands where it has a catholic diet including large *M. longimana*, *M. hamiltoni* and *T. danae/fimbria* (Cherel and Duhamel 2004). *Diomedea* albatrosses are endemic from the Southern Ocean and southern subtropical waters where they prey on large fish and squids, which include mainly adult onychoteuthids (*M. longimana*), histioteuthids (*H. atlantica*, *H. eltaninae*) and cranchiids (*G. glacialis*) (Xavier et al., 2014; Cherel et al., 2017). The sperm whale and sleeper shark feed in the deep-sea, but the former catch live prey, while the latter both predates and scavenges. *Diomedea* albatrosses are also scavengers that feed at the sea surface, where they catch dead or dying post-spawning squid species that have positive buoyancy (Cherel and Weimerskirch 1999). Hence, each apex consumer occupies a unique trophic niche, thus limiting or avoiding direct competition within the oceanic ecosystems of the Southern Ocean and subtropics.

5. Conclusion

Revisiting taxonomy of cephalopod prey of sperm whales improved our knowledge on their feeding habits and on cephalopods from the southern subtropics and the Southern Ocean. It reveals how important previously poorly known squid species are, as the histioteuthid *H. macrohista*, and the cranchiids *G. suhmi* and *Megalocranchia* sp. The study highlights the need to continue improving both the taxonomy of cephalopods and the description of their sclerotinized beaks, with the ecologically-fruitful outcome of using the numerous beaks of rarely net-caught species and adults of cephalopods that accumulate in predators' stomachs.

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