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

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1 RESEARCH PAPER

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

5

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16

17

18 ABSTRACT

19 The sperm whale is the largest toothed whale that feeds almost exclusively on oceanic  
20 cephalopods. Since it was actively hunted commercially, considerably more is known about  
21 its food than for many other large marine apex predators. However, the use of those unique  
22 dietary information is today hampered by out-of-date cephalopod taxonomy. Here, the names  
23 of cephalopod prey of sperm whales were revisited by reviewing taxonomic investigations  
24 and tracking over time the names of sclerotized beaks that accumulate in predators' stomachs.  
25 The study focused on the seminal investigations by [Clarke \(1980\)](#) and [Clarke and MacLeod](#)  
26 [\(1982\)](#), which form the basis of our knowledge on the feeding habits of sperm whales in the  
27 Southern Hemisphere. Forty-five different beaks were identified, of which the labelling of  
28 24% taxa is valid today, 7% are still undetermined, and the name of the 69% remaining beaks  
29 had to be changed due to improvement in both taxonomy (31%) and beak identification  
30 (27%), and to initial misidentifications (11%). Few taxonomic changes occurred at the family  
31 level, but changes at the species level are substantial and reveal the dietary importance of  
32 poorly known squid species (*e.g. Galiteuthis suhmi, Histioteuthis macrohista*). Within the  
33 southern subtropics, sperm whales feed primarily on five histioteuthids, with *Histioteuthis*  
34 *atlantica* ranking first numerically, and on octopoteuthids, cranchiids and onychoteuthids. In  
35 contrast, whales caught in the Antarctic prey mainly upon three species of Southern Ocean  
36 endemics, the cranchiid *Mesonychoteuthis hamiltoni*, and the onychoteuthids *Filippovia*  
37 *knipovitchi* and *Moroteuthopsis longimana*. In conclusion, revisiting taxonomy allowed a  
38 better understanding of the deep-sea ecosystem by improving our knowledge on oceanic  
39 cephalopods and on the feeding habits of sperm whales, a cephalopod predator that has a key  
40 trophic role in the oceans.

41

42 *Keywords:* Antarctica, cetacean, Histioteuthidae, odontocete, squid, trophic relationships

## 43 1. Introduction

44

45 The sperm whale *Physeter macrocephalus* is the largest of the toothed whales  
46 (odontocetes) and the commonest large cetacean today. It has a wide geographic range from  
47 the equator to high latitudes, where its diet consists almost exclusively of oceanic  
48 cephalopods, mainly oegopsids, with fish being a significant prey group in some areas (Clarke  
49 1996). The sperm whale is an apex predator that was estimated to consume ~110 (96-320)  
50 million tons of cephalopods each year, thus highlighting its major role and the importance of  
51 cephalopods both as prey and as consumers within the trophic web of the pelagic ecosystem  
52 of the World Ocean (Clarke 1977, Santos et al. 2001). Since the sperm whale was historically  
53 heavily harvested, considerably more is known about its food than about other cephalopod-  
54 eating whales (Clarke 1986b).

55 The initial step in studying the feeding habits of sperm whales was to identify  
56 cephalopods morphologically, with unfortunately no or little quantification of the species  
57 involved (Kawakami 1980, Mikhalev et al. 1981). The second step was to use the cephalopod  
58 beaks that accumulate by hundreds and thousands in the whale stomach (over 18,000 beaks in  
59 a single stomach; Clarke 1986b). Identification and quantification of cephalopod prey of  
60 marine predators by using the morphology of their sclerotized beaks was initiated in the 60s  
61 and subsequently developed with an initial focus on sperm whale food (Clarke 1986a,b,  
62 1972, 1986a). The method was at its best in a seminal and beautifully illustrated monography  
63 that depicts the feeding habits of sperm whales caught in the southern subtropics and the  
64 Southern Ocean (Clarke 1980). Tens of thousands of lower beaks were described, illustrated,  
65 numbered and measured, thus allowing detailed identification of the cephalopod prey of  
66 sperm whales in South Africa, western Australia and in the Antarctic. This and subsequent  
67 publications (Clarke and MacLeod 1982, Pascoe et al. 1990, Clarke and Roper 1998, Evans

68 [and Hindell 2004](#), [Gomez-Villota 2007](#)) form the basis of our knowledge about the food of  
69 this overwhelmingly important cephalopod predator worldwide.

70 Unfortunately, several limitations now hinder an easy use of those data. Firstly, the  
71 initial monograph ([Clarke 1980](#)) was published in an important journal that is now difficult to  
72 get access to a copy. Secondly, and more fundamentally, our knowledge of cephalopod  
73 taxonomy has developed over the last 40 years, thus obscuring the picture regarding beak  
74 names in previous investigations. Four features are notable within that context. Cephalopod  
75 taxonomy improved, thus inducing (i) new names for well-known species (*e.g. Filippovia*  
76 *knipovitchi*, formerly *Moroteuthis knipovitchi*; [Bolstad 2010](#)), and (ii) the description of new  
77 species to science (*e.g. Asperoteuthis lui*; [Braid 2017](#)). Moreover, improvement in the  
78 identification of lower beaks resolved (iii) previous mismatches between beak names and  
79 well-described species (*e.g. ?Psychroteuthis*, now *Discoteuthis discus*; [Clarke and Roeleveld](#)  
80 [1998](#)), and (iv) the links between well-described beaks and the corresponding squid species  
81 (*e.g. Moroteuthis A* and *Moroteuthopsis ingens*; [Clarke 1986a](#)). Hence, a recent review of  
82 taxonomy and of the tracking of beak names over time increased substantially the diversity of  
83 pelagic squids in the Southern Ocean and underlined the importance of previously poorly  
84 known taxa as prey of seabirds and marine mammals ([Cherel 2020](#)).

85 The main goal of the present work was to synthesize the dispersed information on  
86 cephalopod taxonomy and on identification of cephalopod beaks to upgrade the list of  
87 cephalopod prey of sperm whales in southern subtropical waters and in the Southern Ocean.  
88 Its ultimate objective was to facilitate the use of this important scientific literature to  
89 researchers developing programs on cetaceans and on cephalopods, their trophic relationships,  
90 and on the functioning of the pelagic ecosystems of the Southern Hemisphere. Revisiting the  
91 food of sperm whales caught commercially brings up to date unique data sets that cannot be  
92 collected again, because commercial whaling has ceased and the species is protected

93 worldwide. The sperm whale is today globally designated as Vulnerable on the IUCN Red  
94 List of Threatened species ([Taylor et al. 2019](#)).

95

## 96 **2. Materials and methods**

97

### 98 *2.1. Study sites, physical oceanography and biogeography*

99

100 The study focused on two sperm-whale dietary investigations that complement each  
101 other in terms of geographical coverage of the Southern Hemisphere, from the southwestern  
102 Atlantic to the southwestern Pacific Ocean, thus including the southern Atlantic and Indian  
103 Oceans ([Clarke 1980](#), [Clarke and MacLeod 1982](#)). Food samples came firstly from three  
104 whaling stations that were located on the west coast (Donkergat) and on the east coast  
105 (Durban) of South Africa, and on the west coast of Australia (Albany) ([Clarke 1980](#)).  
106 Secondly, some samples were collected from pelagic factories operating in the Tasman Sea  
107 ([Clarke and MacLeod 1982](#)) and in the Antarctic, including South Georgia and the pelagic  
108 Antarctic (the South Shetland Islands and South Orkney Islands) ([Clarke 1980](#)).

109 According to physical oceanography, sperm whales were caught in subtropical waters  
110 and within the Southern Ocean. The latter is defined as water masses located south of the  
111 Subtropical Front (STF). The main marine fronts within the Southern Ocean are the  
112 Subantarctic and the Polar Fronts; they delineate the following oceanic zones, from North to  
113 South: the subantarctic Zone (SAZ), Polar Frontal Zone (PFZ) and Antarctic Zone (AZ)  
114 ([Pollard et al. 2002](#)). The oceanic zone north of the Southern Ocean (north of the STF) is the  
115 Subtropical Zone (STZ). Hence, sperm whales from Donkergat (western South Africa),  
116 Durban (eastern South Africa) and Albany (western Australia) ([Clarke 1980](#)) were caught  
117 within the STZ of the eastern Atlantic, and of the western and eastern Indian Ocean,

118 respectively. Whales from the Tasman Sea (Clarke and MacLeod 1982) were killed mainly  
119 within the STZ of the western Pacific, with some of them coming from the SAZ (to 47°S).  
120 Finally, sperm whales from South Georgia, and from the South Orkney and South Shetland  
121 Islands (Clarke 1980) were caught further south, within the AZ of the southwestern Atlantic.

122

## 123 *2.2. Analysis and nomenclature*

124

125 Cephalopod beaks that were identified in sperm whale food samples (Clarke 1980, Clarke and  
126 MacLeod 1982) were listed and the validity of each taxon was thoroughly examined using  
127 various means (Table 1), including successive updates by M Clarke (Clarke and MacLeod  
128 1982, Clarke 1986a, Clarke et al. 1993, Clarke and Roeleveld 1998, Clarke and Roper 1998,  
129 Clarke and Young 1998). Synonymies of beak names were tracked over publications and time  
130 (details in Cherel 2020). The work also benefited from the opportunistic examination of beaks  
131 from Clarke's collection by the author, because beaks from sperm whale stomachs (Clarke  
132 1980) were deposited to several museums and scientific organizations, including the British  
133 Antarctic Survey (Cambridge, UK), and the Port Elizabeth Museum at Bayworld (South  
134 Africa). The work on beaks was completed by a review of articles (1980-2020) and of recent  
135 grey literature (PhD) devoted to species, species groups and assemblages to complete and  
136 update both taxonomy and biogeography (e.g. Braid 2017, Evans 2018, Fernandez-Alvarez  
137 2018, Kelly 2019).

138 The three following issues limited the retrospective analysis of dietary data on fresh  
139 items. Firstly, the lack of detailed information precludes knowing which cephalopods were  
140 caught within the STZ and/or within the SAZ of the Tasman Sea (Clarke and MacLeod 1982).  
141 However, since only one whaling position lied within the SAZ, it was assumed that all the  
142 cephalopods from the Tasman Sea refer to the STZ (Tables 2 and 3). Secondly, while it is

143 expected that the southernmost caught fresh *Octopoteuthis* specimens in the Tasman Sea (in  
144 the SAZ, at 47°S) refer to *Octopoteuthis fenestra* (see below), it was not detailed how many  
145 individuals were eaten by the whales, thus explaining why *O. fenestra* was not listed in [Table](#)  
146 [2](#). Thirdly, I removed two *Filippovia knipovitchi* and added two *Onykia robsoni* amongst the  
147 fresh remains of cephalopods from South Georgia ([Table 2](#)), because (i) fresh remains of *O.*  
148 *robsoni* were identified from sperm whales caught at South Georgia, but no fresh specimens  
149 were recorded in the corresponding table ([Clarke 1980](#)), (ii) there was a mismatch in the  
150 number of fresh *F. knipovitchi* when comparing different tables (two more or less specimens),  
151 and (iii) beaks of the two species are closely-related and easy to confuse, thus likely  
152 explaining why their accumulated beaks were pooled ([Clarke 1980](#)).

153       It is important to consider the following issues regarding data on accumulated beaks.  
154 Retrospective analysis necessitated back calculation of the beak numbers of some species by  
155 using percentages that were indicated within the text and tables ([Clarke 1980](#)). There were  
156 also some limitations due to the initial data analysis ([Table 3](#)). Firstly, lower beaks of  
157 *Liguriella podophtalma* included those from *Galiteuthis glacialis* (see below). Secondly,  
158 beaks of *Histioteuthis eltaninae* at South Georgia and in the pelagic Antarctic were pooled  
159 with those of *H. atlantica*, as were beaks from *O. robsoni* with those of *F. knipovitchi* ([Clarke](#)  
160 [1980](#)). Thirdly, according to beak size and location, *Octopoteuthis* spp. included two to three  
161 different taxa (see below) that were numbered in [Clarke and MacLeod \(1982\)](#) but pooled in  
162 [Clarke \(1980\)](#). Fourthly, beaks called “Others” included those from *Discoteuthis discus* at  
163 Donkergat and Durban ([Clarke 1980](#)). Finally, the lack of a database including detailed beak  
164 measurements (lower rostral length, LRL) precluded updating the estimation of cephalopod  
165 size (mantle length, body mass) and thus of the absolute and relative species-specific  
166 biomasses consumed by sperm whales.

167

168 **3. Results**

169

170 Overall, forty-five different beaks were identified and described in [Clarke \(1980\)](#) and  
171 [Clarke and MacLeod \(1982\)](#). Amongst those 45 cephalopod taxa ([Table 1](#)), the labelling of 11  
172 (24.4%) beaks was right, three (6.7%) are still undetermined at the species level, and the  
173 name of the 31 (68.9%) remaining taxa had to be changed due to improvement in both  
174 taxonomy (n = 14, 31.1%) and beak identification (n = 12, 26.7%), and to initial  
175 misidentifications (n = 5, 11.1%).

176

177 *3.1. Taxonomic updates and species notes*

178

179 Most taxonomic updates were detailed in [Cherel \(2020\)](#), but some taxa required some  
180 additional information.

181

182 *3.1.1. Chiroteuthidae*

183 Five *Chiroteuthis* beaks, namely *C. joubini*, *C. ?joubini*, *Chiroteuthis* sp. A,  
184 *Chiroteuthis* sp. B and *Chiroteuthis* sp. C were described in [Clarke \(1980\)](#) and [Clarke and](#)  
185 [MacLeod \(1982\)](#). While *Chiroteuthis* sp. A and *Chiroteuthis* sp. C were subsequently  
186 synonymized with *C. joubini* and *C. veranyi*, respectively ([Clarke et al. 1993](#)), the species  
187 identification of *C. ?joubini*, and *Chiroteuthis* sp. B was problematic. The presence of  
188 luminous patches on eyes rather than photophores and its Antarctic location of capture  
189 suggests that the single head of *Chiroteuthis* sp. B corresponds to *C. veranyi*. *C. ?joubini*  
190 beaks are closely similar to those described as *Chiroteuthis* A from sperm whales caught off  
191 Peru ([Clarke and MacLeod 1982](#)). Drawings of *Chiroteuthis* A beaks ([Clarke et al. 1976](#)) look  
192 like those of *C. veranyi*, which is the single species of *Chiroteuthis* recorded in the area ([Nesis](#)

193 1987, Alexeiev 1994). Overall, this suggests that *C. ?joubini* and *Chiroteuthis* sp. also  
194 correspond to *C. veranyi*.

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

### 199 3.1.2. Cranchiidae

200 Lower beaks of *Galiteuthis armata* refer to three different species of cranchiids (Cherel  
201 2020), namely *Galiteuthis suhmi* in Clarke and MacLeod (1982), and *L. podophtalma* and *G.*  
202 *glacialis* in Clarke (1980 Text-fig. 225). Clarke (1980) found two modes in beak size of *G.*  
203 *armata*, suggesting two species, the largest being *G. armata* (= *L. podophtalma*) and the  
204 smallest a second species he also found in albatross food samples. Indeed, lower beaks from  
205 *L. podophtalma* and *G. glacialis* are pretty similar, but those from *L. podophtalma* darken at,  
206 and reach, a larger size than those from *G. glacialis*, the latter species being one of the  
207 commonest cephalopod prey of albatrosses within the Southern Ocean (Cherel 2020).  
208 Confusion was increased when beaks named ?*Taonius megalops* (Clarke 1980 Text-fig. 209)  
209 were re-named *G. armata*, because one head was in sufficiently good condition to indicate  
210 that the species was not a *Taonius* but a *Galiteuthis* species (Clarke and MacLeod 1982).  
211 Indeed, both ?*Taonius megalops* (Clarke 1980) and *G. armata* (Clarke and MacLeod 1982)  
212 now correspond to the rarely reported *Galiteuthis suhmi* (Evans 2018, Cherel 2020).

213 Voss (1985) synonymized *Galiteuthis* (= *Teuthowenia*) sp. B (Clarke and MacLeod  
214 1982, misnamed as *G. armata* within the text p 33 but not in Tables 1 and 2) with  
215 *Teuthowenia pellucida* (details in Cherel 2020).

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

### 219 3.1.3. Cycloteuthidae

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

### 224 3.1.4. Octopoteuthidae

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

- 229 - The smallest *Octopoteuthis* species (mode at 8-9 mm LRL) from Donkergat, Durban  
230 and Albany remains undetermined. Clarke (1980) tentatively identified it as *O.*  
231 *sicula*, but the species is endemic to the Atlantic and is not recorded from the Indian  
232 Ocean (Kelly 2019).
- 233 - *O. rugosa* corresponds to the peak at 10-11 mm LRL, max 12.5 mm LRL  
234 (Donkergat, Durban and Albany) (Clarke 1980) and to beaks with LRL <11.5 mm  
235 (Tasman Sea) (Clarke and MacLeod 1982). The species has a southern circumglobal  
236 distribution (Kelly 2019).
- 237 - The third peak occurred at 13.0-14.5 mm LRL at Albany (Clarke 1980) and it  
238 corresponds to beaks with LRL >11.5 mm of *Octopoteuthis* sp. A in the Tasman Sea  
239 (Clarke and MacLeod 1982). Clarke (1980) tentatively identified the corresponding

240 species as *O. longiptera*, which is today a *nomen dubium* (Kelly 2019). The species  
241 remains unidentified, but the newly described *O. fenestra* (Kelly 2019) is a good  
242 candidate because: i) its maximum LRL is 13.6 mm, a larger size than that of all the  
243 other small *Octopoteuthis* species (Kelly 2019), (ii) *O. fenestra* has been collected  
244 south of Tasmania and in New Zealand waters (Kelly 2019), which fits well with its  
245 presence in the diet of sperm whales caught in Australian waters and not in South  
246 Africa (Clarke 1980, Clarke and MacLeod 1982), and (iii) *Octopoteuthis* flesh  
247 recorded from sperm whales caught within the SAZ in the Tasman Sea (Clarke and  
248 MacLeod 1982) is likely to correspond to *O. fenestra*, which is the southernmost  
249 and single *Octopoteuthis* species living in the Southern Ocean (Kelly 2019).

250 - In the Tasman Sea, large beaks with a LRL >15 mm were called *Octopoteuthis* sp.  
251 (giant) B (Clarke and MacLeod 1982). They correspond to the still undescribed  
252 giant Pacific *Octopoteuthis* sp. that lives in the western Pacific and possibly has a  
253 southern circumglobal distribution (Kelly 2019).

254 Two size modes of *Taningia danae* lower beaks were found in the diet of sperm whales  
255 caught at Donkergat and Durban (Clarke 1980), and in the Tasman Sea (Clarke and MacLeod  
256 1982), thus suggesting that the genus *Taningia* is composed to two species (Clarke and  
257 MacLeod 1982). Indeed, a recent taxonomic revision split the monotypic *T. danae* into five  
258 different taxa, including the cosmopolitan tropical-subtropical *T. danae* and the newly  
259 described Southern Hemisphere *T. fimbria* (Kelly 2019). The correspondence between beak  
260 size and species is not established but available information suggest that the large and the  
261 small LRL peaks correspond primarily to *T. danae* and *T. fimbria*, respectively.

#### 262 3.1.5. Ommastrephidae

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

### 273 3.1.6. Pholidoteuthidae

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

### 278 3.1.7. Alloposidae

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

281

## 282 3.2. Cephalopods in the diet of sperm whales

283

284 A total of 1991 fresh remains were identified either morphologically or from beaks that  
285 were sorted from buccal masses (Table 2). Most of them (70%) came from Durban, which  
286 was the most investigated locality by far (Clarke 1980, Clarke and Roeleveld 1998). Two

287 oegopsid families dominated by number the diet of sperm whales in the southern subtropics,  
288 the octopoteuthids (25.0%) and histioteuthids (21.3%), while onychoteuthids (59.1%) and  
289 cranchiids (32.6%) were the two most important families within the Southern Ocean. Six  
290 squids totalled >5% by number of fresh items in the STZ, by decreasing order of importance:  
291 *T. filippovae/angolensis* > *O. rugosa* > *Ancistrocheirus lesueurii* > *Histioteuthis bonnellii*  
292 *corpuscula* > *H. miranda* > *G. suhmi*. In contrast, only three species dominated the whale diet  
293 in the Antarctic, *M. longimana* > *Mesonychoteuthis hamiltoni* > *F. knipovitchi*.

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

304 Within the STZ, histioteuthids ranked first at Donkergat (37.5%), Durban (44.7%) and  
305 Albany (41.4%) and second in the Tasman Sea (30.5%). *H. atlantica* was important  
306 everywhere, but *H. b. corpuscula*, *H. macrohista*, *H. miranda*, and *S. hoylei* were notably  
307 abundant at Durban, Donkergat, Albany and in the Tasman Sea, respectively (Table 3, Fig. 2).  
308 Octopoteuthids ranged from 8.8% in Albany to 33.7% in the Tasman Sea, the only locality  
309 where they dominated and where they were detailed at the species level, in the decreasing  
310 order: *O. ?fenestra* (11.7%) > *T. danae/fimbria* (10.5%) > *O. rugosa* (10.0%) > giant Pacific  
311 *Octopoteuthis* sp. (1.5%). Cranchiids were important at Donkergat (20.0%) with *G. suhmi* and

312 in the Tasman Sea (10.9%) where *Megalocranchia* sp. was a significant prey item. Other  
313 squids that amounted to >5% by number were *O. robsoni* at Donkergat, *A. lesueurii* and  
314 *Chiroteuthis* spp. (pooled *C. joubini* and *C. veranyi*) at Durban, *T. filippovae* at Albany, and  
315 *P. massyae* at Donkergat, Albany and in the Tasman Sea (Table 3).

316 Many more beaks were analyzed at Donkergat and Durban than elsewhere, with the  
317 same 32 taxa being identified at the two South African localities (Table 3). Statistical analyses  
318 (equality of two proportions tests) showed that proportions significantly differed (all  $p \leq$   
319 0.460, with  $p < 0.0001$  in 27 comparisons) for almost all taxa but three, the numerically  
320 important *H. atlantica* ( $Z = 0.24$ ,  $p = 0.814$ ), and the occasional *M. ingens* ( $Z = 0.23$ ,  $p =$   
321 0.816), and Others (including *D. discus*) ( $Z = 1.00$ ,  $p = 0.319$ ).

322

#### 323 4. Discussion

324

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

333

##### 334 4.1. Revisiting cephalopod taxonomy

335

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

350 In contrast, within-families changes at the species level are substantial (Table 1).  
351 Three issues are especially relevant: (i) the importance of *H. macrohista* (formerly *H.*  
352 *?meleagroteuthis*) in the diet of whales at Donkergat; (ii) the disentangling of the beaks  
353 previously named *?Taonius megalops* and *G. armata* adds significant new records and trophic  
354 information about the two rarely reported cranchiids *G. suhmi* and *L. podophtalma*, the former  
355 species being one of the main prey of sperm whales at Donkergat; and (iii), improving beak  
356 identification overall increases our knowledge on squid biodiversity and biogeography (e.g.  
357 the poorly-known *A. lui* and *A. acanthoderma*). Despite these changes, the initial analysis of  
358 lower beaks is remarkable and the hypothesis that various LRL modes of fully darkened beaks  
359 within a given taxa represent different species was validated (e.g. *G. armata* that corresponds  
360 to *G. suhmi*/*G. glacialis*) or in the process of being validated (e.g. *Octopoteuthis* spp. and

361 *Taningia danae/fimbria*). However, the absence of some beaks is puzzling and suggests that  
362 at least some of them were not recognized morphologically as distinct from others and, hence,  
363 that some taxa are a diverse mix of different species. Within the STZ and Southern Ocean,  
364 relevant missing species include *Batoteuthis skolops*, *Mastigoteuthis psychrophila*, the  
365 neoteuthid *Nototeuthis dimegacotyle*, the onychoteuthids *Moroteuthopsis* sp. B (Imber) and  
366 *Notonykia africanae*, and the recently described cranchiids *Taonius expositus* and possibly *T.*  
367 *tanuki* (Evans 2018, Cherel et al. 2020). Indeed, *B. skolops* was subsequently identified  
368 amongst fresh items in the stomach of sperm whales caught within the AZ (Lubimova 1985).

369

#### 370 4.2. Cephalopod prey within the Subtropical Zone (STZ)

371

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

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

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

405

#### 406 4.3. Cephalopod prey within the Southern Ocean

407

408 Three Southern Ocean endemics form the bulk (90.7% by number of fresh items) of  
409 the cephalopod diet of sperm whales in the Antarctic, the colossal squid *M. hamiltoni* and the  
410 two onychoteuthids *F. knipovitchi* and *M. longimana* (Table 2), which is in general agreement

411 with qualitative information collected from Soviet and Japanese factories (Mikhalev et al.  
412 1981, Nemoto et al. 1988, Filippova 2002). The other squids eaten within the AZ include *G.*  
413 *antarcticus* and two other Southern Ocean endemics (*A. lui* and *P. glacialis*). A review of the  
414 literature adds four species, again all endemics, to the squid prey of sperm whales in the  
415 Antarctic (*B. skolops*, *G. glacialis*, *A. antarcticus*, and *M. ingens*), and six species to the prey  
416 taken further north within the Southern Ocean (*A. dux*, *C. sirventi*, *H. atlantica*, *H. eltaninae*,  
417 *P. massyae* and *H. atlanticus*) (Vovk et al. 1978, Mikhalev et al. 1981, Lubimova 1985,  
418 Filippova 2002). Comparing fresh remains of cephalopods from sperm whales caught within  
419 the AZ and the STZ highlights the dietary importance of different squids living in these two  
420 contrasting oceanic environments (Table 2). Twenty-three species occurred in the STZ only,  
421 six in the AZ only, and three were recorded in the two zones. The latter species (*T.*  
422 *danae/fimbria*, *T. filippovae/angolensis* and *O. robsoni*) are primarily subtropical species  
423 whose distribution extends to the northern Southern Ocean (Cherel 2020), where, accordingly,  
424 they are minor prey items for sperm whales.

425 Analysis of accumulated beaks fit well with quantification of fresh items, with the three  
426 same species (*M. hamiltoni*, *F. knipovitchi* and *M. longimana*) accounting together for 71.6%  
427 of the total number of lower beaks within the AZ (Table 3). This proportion is lower than for  
428 fresh items, however, which is the consequence of the much larger diversity of cephalopods  
429 identified from beaks than from fresh items, since most beaks were found in whales caught in  
430 both subtropical and Antarctic waters. Fresh items are indicative of local food, while the  
431 much larger number of beaks results primarily from their progressive accumulation in the  
432 stomach over time (maximum ~10 days; Clarke 1980). Male sperm whales migrate back and  
433 forth over years between their main feeding zone in cold waters and the reproductive zone in  
434 warmer waters where females and juveniles live all year-round. Hence, the presence of beaks  
435 of subtropical cephalopods in the stomach of adult males caught in the Antarctic indicates a

436 recent southward migration, and *vice-versa* (Clarke 1972, 1980). Within that context, the  
437 puzzling large number of eroded lower beaks of *S. arcturi* in two whales caught in the pelagic  
438 Antarctic (South Shetlands) likely results from their southward migration (Clarke 1980), since  
439 *S. arcturi* does not occur within the Southern Ocean (Cherel 2020), but it was recorded in  
440 subtropical waters of the southwest Atlantic (Voss et al. 1998).

441

#### 442 4.4. Predators, trophic niches, and the pelagic ecosystems

443

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

461

## 462 **5. Conclusion**

463

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

471

### 472 **Declaration of competing interest**

473 The author declare that he has no known competing financial interests or personal  
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### 484 **References**

485

486 Alexeyev DO (1994) New data on the distribution and biology of squids from the Southern Pacific. *Ruthenica*  
487 4:151-166

488 Bolstad KSR (2010) Systematics of the Onychoteuthidae Gray, 1847 (Cephalopoda: Oegopsida). *Zootaxa*  
489 2696:1-186

490 Braid HE (2017) Resolving the taxonomic status of *Asperoteuthis lui* Salcedo-Vargas, 1999 (Cephalopoda,  
491 Chiroteuthidae) using integrative taxonomy. *Mar Biodiv* 47:621-635

492 Cherel Y (2020) A review of Southern Ocean squids using nets and beaks. *Mar Biodiv* 50:98

493 Cherel Y (2021) ?*Mastigoteuthis* B Clarke, 1980, is a junior synonym of *Asperoteuthis acanthoderma* (Lu, 1977)  
494 (Cephalopoda, Oegopsida, Chiroteuthidae), a rare cosmopolitan deep-sea squid. *Mar Biodiv* in press

495 Cherel Y, Duhamel G (2004) Antarctic jaws: cephalopod prey of sharks in Kerguelen waters. *Deep-Sea Res I*  
496 51:17-31

497 Cherel Y, Weimerskirch H (1999) Spawning cycle of onychoteuthid squids in the southern Indian Ocean: new  
498 information from seabird predators. *Mar Ecol Prog Ser* 188:93-104

499 Cherel Y, Xavier JC, de Grissac S, Trouvé C, Weimerskirch H (2017) Feeding ecology, isotopic niche, and  
500 ingestion of fishery-related items of the wandering albatross *Diomedea exulans* at Kerguelen and Crozet  
501 Islands. *Mar Ecol Prog Ser* 565:197-215

502 Clarke M, Young R (1998) Description and analysis of cephalopod beaks from stomachs of six species of  
503 odontocete cetaceans stranded on Hawaiian shores. *J Mar Biol Assoc UK* 78:623-641

504 Clarke MR (1962a) The identification of cephalopod ‘beaks’ and the relationship between beak size and total  
505 body weight. *Bull Brit Mus Nat Hist Zool* 8:419-480

506 Clarke MR (1962b) Significance of cephalopod beaks. *Nature* 193:560-561

507 Clarke MR (1972) New technique for the study of sperm whale migration. *Nature* 238:405-406

508 Clarke MR (1977) Beaks, nets and numbers. *Symp Zool Soc Lond* 38:89-126

509 Clarke MR (1980) Cephalopoda in the diet of sperm whales of the Southern Hemisphere and their bearing on  
510 sperm whale biology. *Discovery Rep* 37:1-324

511 Clarke MR (1986a) A handbook for the identification of cephalopod beaks. Clarendon Press, Oxford, England

512 Clarke MR (1986b) Cephalopods in the diet of odontocetes. In: Bryden MM, Harrison R (eds) *Research on*  
513 *dolphins*, Clarendon Press, Oxford, pp 281-321

514 Clarke MR (1996) Cephalopods as prey. III. Cetaceans. *Phil Trans Biol Sci* 351:1053-1065

515 Clarke MR, MacLeod N, Paliza O (1976) Cephalopod remains from stomachs of sperm whales caught off Peru  
516 and Chile. *J Zool Lond* 180:477-493

517 Clarke MR, MacLeod N (1982) Cephalopod remains from the stomachs of sperm whales caught in the Tasman  
518 Sea. *Mem Nat Mus Victoria* 43:25-42

519 Clarke MR, Martins HR, Pascoe P (1993) The diet of sperm whales (*Physeter microcephalus* Linnaeus 1758) off  
520 the Azores. *Phil Trans R Soc Lond B* 339:67-82

521 Clarke MR, Roeleveld MAC (1998) Cephalopods in the diet of sperm whales caught commercially off Durban,  
522 South Africa. *S Afr J Mar Sci* 20:41-45

523 Clarke MR, Roper MAC (1998) Cephalopods represented by beaks in the stomach of a sperm whale stranded at  
524 Paekakariki, North Island, New Zealand. *S Afr J Mar Sci* 20:129-133

525 Evans AB (2018) A systematic review of the squid family Cranchiidae (Cephalopoda: Oegopsida) in the Pacific  
526 Ocean. PhD, Auckland University of Technology

527 Evans K, Hindell MA (2004) The diet of sperm whales (*Physeter macrocephalus*) in southern Australian waters.  
528 ICES J Mar Sci 61:1313-1329

529 Fernandez-Alvarez FA (2018) An onto-phylogenetic journey through the life history of flying squids  
530 (Cephalopoda: Ommastrephidae). PhD, Universitat Politècnica de Catalunya, Barcelona

531 Filippova JA (2002) Review of Soviet/Russian studies on squids in the Antarctic Ocean. Bull Mar Sci 71:255-  
532 267

533 Foskolos I, Koutouzi N, Polychronidis L, Alexiadou P, Frantzis A (2020) A taste for squid : the diet of sperm  
534 whales stranded in Greece, Eastern Mediterranean. Deep-Sea Res I 155:103164

535 Gaskin DE, Cawthorn MW (1967a) Squid mandibles from the stomachs of sperm whales (*Physeter catodon* L.)  
536 captured in the Cook Strait region of New Zealand. NZ J Mar Freshwater Res 1:59-70

537 Gaskin DE, Cawthorn MW (1967b) Diet and feeding habits of the sperm whale (*Physeter catodon* L.) in the  
538 Cook Strait region of New Zealand. NZ J Mar Freshwater Res 2:156-179

539 Gomez-Villota F (2007) Sperm whale diet in New Zealand. Master thesis, Auckland University of Technology

540 Imber MJ (1973) The food of grey-faced petrels (*Pterodroma macroptera gouldi* (Hutton)), with special  
541 reference to diurnal vertical migration of their prey. J Anim Ecol 42:645-662

542 Kawakami T (1980) A review of sperm whale food. Sci Rep Whales Res Inst 32:1--218

543 Kelly JT (2019) Systematics of the Octopoteuthidae Berry, 1912 (Cephalopoda: Oegopsida). PhD, Auckland  
544 University of Technology

545 Kristensen TK, Knudsen J (1983) A catalogue of the type specimens of Cephalopoda (Mollusca) in the  
546 Zoological Museum, University of Copenhagen. Steenstrupia, 9:217-227

547 Lubimova TG (1985) Results of Soviet investigation of the distribution and ecology of pelagic squids  
548 (Oegopsida) in the Southern Ocean. Selected Papers SC-CCAMLR 1985:79-111

549 Mikhalev JA, Savusin VP, Kishiyan NA (1981) To the problem of the feeding of sperm whales from the  
550 Southern Hemisphere. Rep Int Whal Commn 31:737-745

551 Nemoto T, Okiyama M, Iwasaki N, Kikuchi T (1988) Squid as predators on krill (*Euphausia superba*) and prey  
552 for sperm whales in the Southern Ocean. In: Sarhage D (ed) Antarctic ocean and resources variability,  
553 Springer Verlag, Berlin, pp 292-296

554 Nesis KN (1987) Cephalopods of the world. Squids, cuttlefishes, octopuses and allies. TFH Publications,  
555 Neptune City, New Jersey, USA

556 Pascoe PL, Mickiewicz MC, Castello HP (1990) Cephalopod remains from the stomach of a sperm whale  
557 stranded off Patagonia. Mar Biol 104:1-4

558 Pollard RT, Lucas MI, Read JF (2002) Physical controls on biogeochemical zonation in the Southern Ocean.  
559 Deep-Sea Res II 49:3289-3305

560 Ridoux V (1994) The diets and dietary segregation of seabirds at the subantarctic Crozet islands. Mar Ornithol  
561 22:1-192

562 Rodhouse PG, Clarke MR, Murray WA (1987) Cephalopod prey of the wandering albatross *Diomedea exulans*.  
563 Mar Biol 96:1-10

564 Santos MB, Clarke MR, Pierce GJ (2001) Assessing the importance of cephalopods in the diets of marine  
565 mammals and other top predators: problems and solutions. *Fish Res* 52:121-13

566 Spitz J, Cherel Y, Bertin S, Kiszka J, Dewez A, Ridoux V (2011) Prey preferences among the community of  
567 deep-diving odontocetes from the Bay of Biscay, Northeast Atlantic. *Deep Sea Res I* 58:273-282

568 Taylor BL, Baird R, Barlow J, Dawson SM, Ford J, Mead JG, Notarbartolo di Sciara G, Wade P, Pitman RL  
569 (2019) *Physeter macrocephalus* (amended version of 2008 assessment). The IUCN Red List of  
570 Threatened Species 2019: e.T41755A160983555.  
571 <https://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T41755A160983555.en>.

572 Voss NA (1985) Systematics, biology and biogeography of the cranchiid cephalopod genus *Teuthowenia*  
573 (Oegopsida). *Bull Mar Sci* 36:1-85

574 Voss NA, Nesis KN, Rodhouse PG (1998) The cephalopod family Histiotteuthidae (Oegopsida): systematics,  
575 biology, and biogeography. *Smithson Contrib Zool* 586:293-372

576 Vovk AN, Nesis KN, Panfilov NG (1978) Distribution of deep sea cephalopods in the South Atlantic and  
577 adjacent waters (mainly analyses of sperm whales feeding). *Malacol Rev* 11:131-132

578 Vukhov VL (1972) The range of fish of the genus *Dissostichus* (Fam. Nototheniidae) in Antarctic waters of the  
579 Indian Ocean. *J Ichthyol* 12:346-347

580 Xavier JC, Walker K, Elliot G, Cherel Y, Thompson D (2014) Cephalopod fauna of South Pacific waters: new  
581 information from breeding New Zealand wandering albatrosses. *Mar Ecol Prog Ser* 513:131-142  
582  
583

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

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



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

Species	Donkergat	Durban	Albany	Tasman Sea	Subtropical Zone			South	Pelagic	Antarctic Zone	
	Clarke (1980)	Clarke (1980) Clarke and Roeleveld (1998)	Clarke (1980)	Clarke and MacLeod (1982)	FO (n)	(n)	(%)	Georgia Clarke (1980)	Antarctic Clarke (1980)	(n)	(%)
<i>Ancistrocheirus lesueurii</i>	5	144	4	33	4	186	10.3				
<i>Architeuthis dux</i>	19	8	4	6	4	37	2.1				
<i>Asperoteuthis lui</i>								2		2	1.0
<i>Chiroteuthis joubini</i>		34	2		2	36	2.0				
<i>Chiroteuthis veranyi</i>		9		5	2	14	0.8				
Undetermined <i>Chiroteuthis</i>								1		1	0.5
<i>Galiteuthis suhmi</i>	37	40		13	3	90	5.0				
<i>Liguriella podophthalma</i>		2			1	2	0.1				
<i>Liocranchia reinhardti</i>		3			1	3	0.2				
<i>Megalocranchia</i> sp.		4	1	18	3	23	1.3				
<i>Mesonychoteuthis hamiltoni</i>								33	30	63	32.6
<i>Taonius notalia</i>	6			1	2	7	0.4				
<i>Cycloteuthis sirventi</i>	4	12	6	2	4	24	1.3				
<i>Discoteuthis discus</i>		1			1	1	0.1				
<i>Discoteuthis laciniosa</i>	1	1			2	2	0.1				
<i>Gonatus antarcticus</i>								1	2	3	1.6
<i>Histioteuthis atlantica</i>	1	36	2	17	4	56	3.1				
<i>Histioteuthis bonnellii corpuscula</i>	7	171		2	3	180	10.0				
<i>Histioteuthis eltaninae</i>		4			1	4	0.2				
<i>Histioteuthis macrohista</i>	7				1	7	0.4				
<i>Histioteuthis miranda</i>	6	108	18	4	4	136	7.6				
<i>Lepidoteuthis grimaldii</i>	1	2	2	5	4	10	0.6				
<i>Octopoteuthis rugosa</i>	15	326	1	23	4	365	20.3				
Giant Pacific <i>Octopoteuthis</i> sp.				1	1	1	0.1				
<i>Taningia danae/fimbria</i>	1	42	7	33	4	83	4.6	4		4	2.1

<i>Ommastrephes cylindraceus</i>		2			1	2	0.1				
<i>Todarodes filippovae/angolensis</i>	3	378	5		3	386	21.5	4		4	2.1
<i>Filippovia knipovitchi</i>								13	14	27	14.0
<i>Moroteuthopsis longimana</i>								55	30	85	44.0
<i>Onykia robsoni</i>	10	60	6	7	4	83	4.6	2		2	1.0
<i>Pholidoteuthis massyae</i>	30	5	9	13	4	57	3.2				
<i>Psychroteuthis glacialis</i>									1	1	0.5
Other decapods	2				1	2	0.1		1	1	0.5
<i>Haliphron atlanticus</i>		1			1	1	0.1				
Total	155	1393	67	183	4	1798	100.0	115	78	193	100.0

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

Location Number of whales	Donkergat 89		Durban 72		Albany 6		Tasman Sea 30		South Georgia 28		Pelagic Antarctic 12	
	Clarke (1980)		Clarke (1980)		Clarke (1980)		Clarke and MacLeod (1982)		Clarke (1980)		Clarke (1980)	
Species	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)
<i>Ancistrocheirus lesueurii</i>	2319	4.48	3914	6.02	75	2.77	116	3.52	46	2.81	48	0.67
<i>Architeuthis dux</i>	153	0.30	153	0.24	10	0.37	54	1.64	18	1.10	2	0.03
<i>Asperoteuthis acanthoderma</i>	164	0.32	63	0.10	6	0.22	16	0.48				
<i>Asperoteuthis lui</i>									57	3.48	53	0.74
<i>Chiroteuthis</i> spp.	404	0.78	5392	8.30	36	1.33	46	1.39			12	0.17
<i>Galiteuthis suhmi</i>	7153	13.82	975	1.50	73	2.69	68	2.06	8	0.49	26	0.36
<i>Liguriella podophthalma</i>	405	0.78	827	1.27	14	0.52			7	0.43	27	0.38
<i>Liocranchia reinhardti</i>	7	0.01	49	0.08					1	0.06		
<i>Megalocranchia</i> sp.	1087	2.10	377	0.58	4	0.15	246	7.46	16	0.98	51	0.71
<i>Mesonychoteuthis hamiltoni</i>	942	1.82	713	1.10	120	4.42	11	0.33	377	23.00	989	13.78
<i>Taonius notalia</i>	766	1.48	342	0.53	27	1.00	21	0.64	16	0.98	27	0.38
<i>Teuthowenia pellucida</i>							15	0.45				
<i>Cycloteuthis sirventi</i>	386	0.75	708	1.09	78	2.88	29	0.88	4	0.24	11	0.15
<i>Discoteuthis laciniosa</i>	418	0.81	681	1.05			22	0.67				
<i>Gonatus antarcticus</i>	59	0.11	12	0.02					3	0.18	274	3.82
<i>Histioteuthis atlantica</i>	6046	11.68	7617	11.72	764	28.17	382	11.58	49	2.99	54	0.75
<i>Histioteuthis bonnellii corpuscula</i>	3060	5.91	14012	21.56	30	1.11	143	4.33	1	0.06		
<i>Histioteuthis eltaninae</i>	1206	2.33	2257	3.47	8	0.29			yes	?	yes	?
<i>Histioteuthis macrohista</i>	7425	14.34	314	0.48	2	0.07	28	0.85				
<i>Histioteuthis miranda</i>	1656	3.20	4831	7.43	312	11.50	121	3.67	25	1.53	25	0.35
<i>Stigmatoteuthis hoylei</i> and <i>S. arcturi</i>	5	0.01	24	0.04	8	0.29	298	9.03	47	2.87	729	10.16
Undetermined histioteuthids							33	1.00				
<i>Lepidoteuthis grimaldii</i>	268	0.52	133	0.20	38	1.40	57	1.73	14	0.85	46	0.64
<i>Alluroteuthis antarcticus</i>	31	0.06	326	0.50	5	0.18			3	0.18	104	1.45
<i>Octopoteuthis</i> spp.	5568	10.75	12756	19.63	157	5.79	764	23.16	3	0.18	34	0.47

<i>Taningia danae</i> and <i>T. fimbria</i>	828	1.60	1577	2.43	83	3.06	348	10.55	177	10.80	50	0.70
<i>Todarodes filippovae</i>	91	0.18	1853	2.85	394	14.53	38	1.15	34	2.07	5	0.07
<i>Filippovia knipovitchi</i>	150	0.29	66	0.10					292	17.82	3180	44.30
<i>Onykia robsoni</i>	3188	6.16	1543	2.37	83	3.06	135	4.09	yes	?	yes	?
<i>Moroteuthopsis ingens</i>	231	0.45	284	0.44			10	0.30	34	2.07	175	2.44
<i>Moroteuthopsis longimana</i>	1366	2.64	1990	3.06	118	4.35	102	3.09	354	21.60	1124	15.66
<i>Pholidoteuthis massyae</i>	5656	10.92	291	0.45	263	9.70	172	5.21	1	0.06	25	0.35
<i>Psychroteuthis glacialis</i>									1	0.06	22	0.31
<i>Vampyroteuthis infernalis</i>	34	0.07	110	0.17			1	0.03			2	0.03
<i>Haliphron atlanticus</i>	63	0.12	29	0.04	1	0.04	6	0.18	49	2.99	42	0.59
Others (including <i>Discoteuthis discus</i> )	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

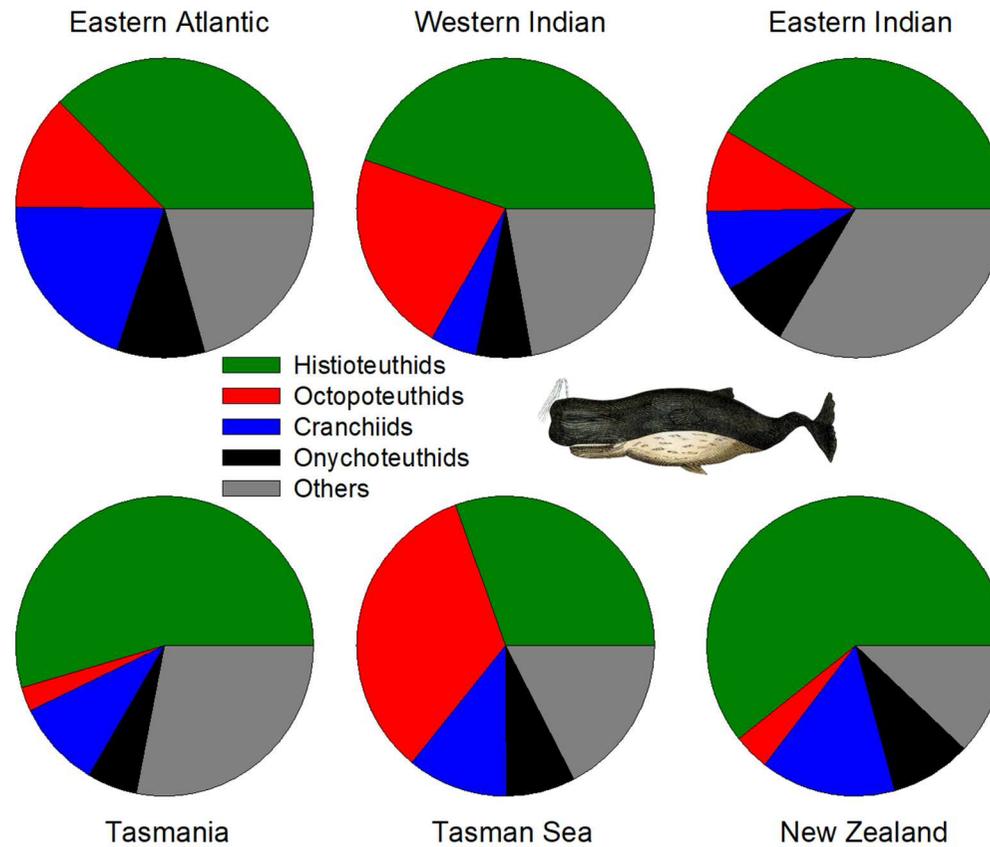
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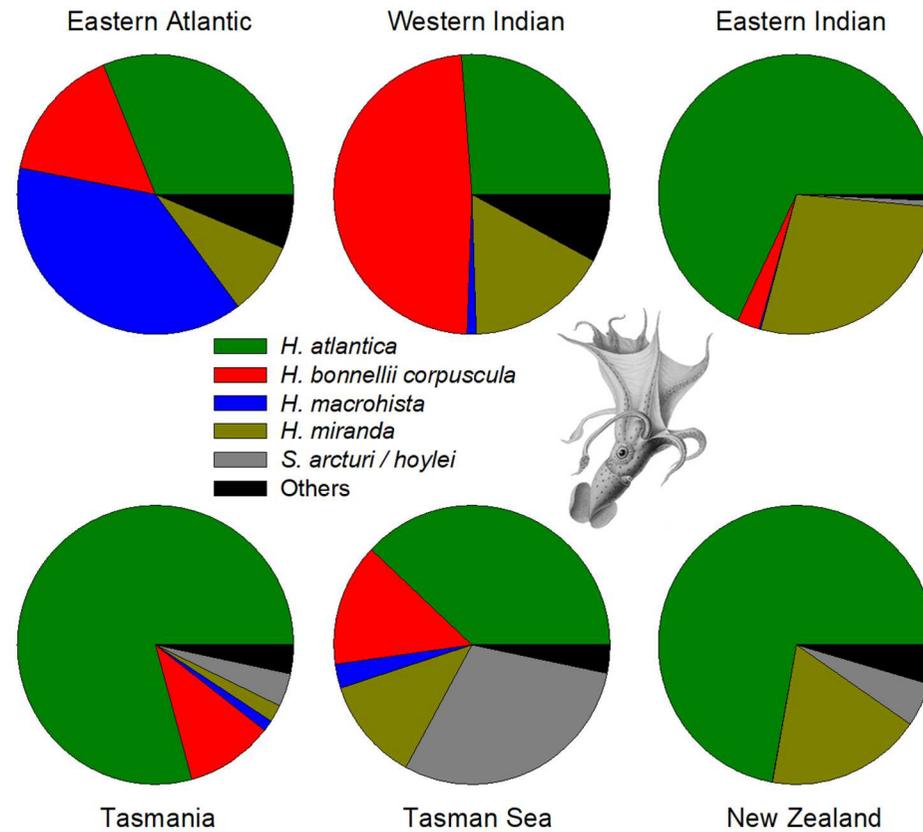
594 **Figure 1** Numerical importance of the four main families of cephalopods in the diet of sperm whales caught in the southern subtropics. The  
 595 eastern Atlantic, western Indian and eastern Indian Ocean refer to Donkergat, Durban and Albany, respectively. Data from [Clarke \(1980\)](#), [Clarke](#)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

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