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1 RESEARCH PAPER

2

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22 dietary information is today hampered by out-of-date cephalopod taxonomy.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 Chérel 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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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)	(%)
	(n)	(n)	(n)	(n)				(n)	(n)	(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 podophtalma</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

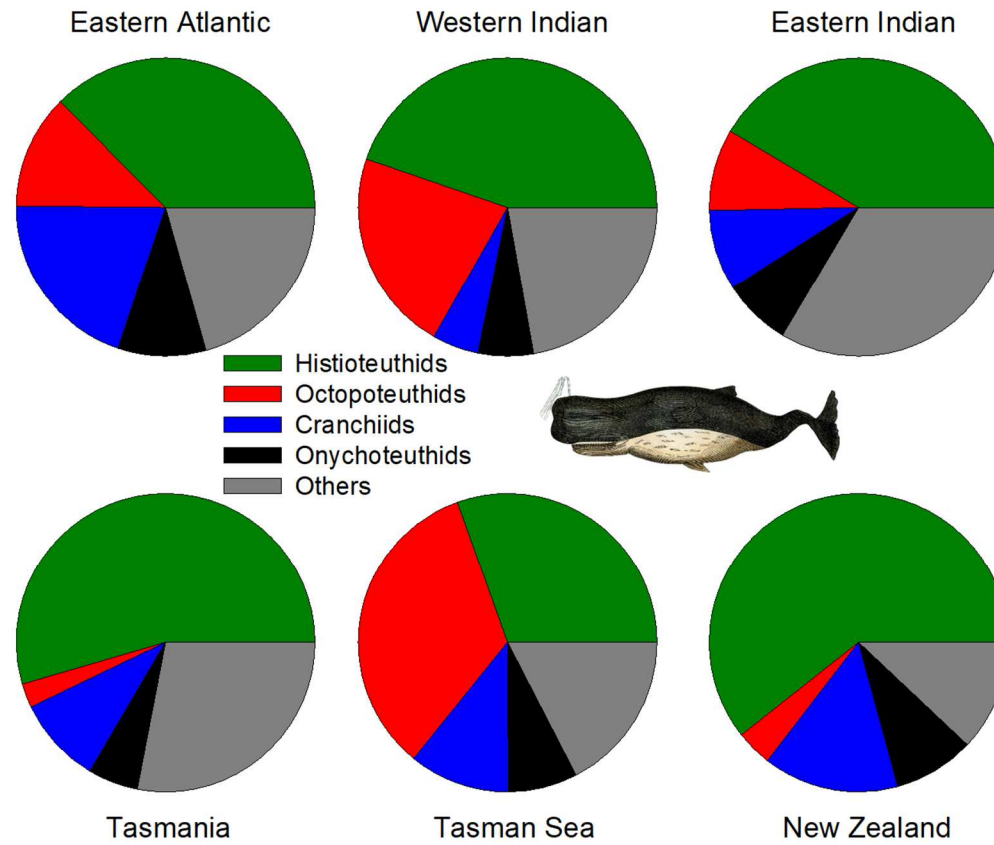
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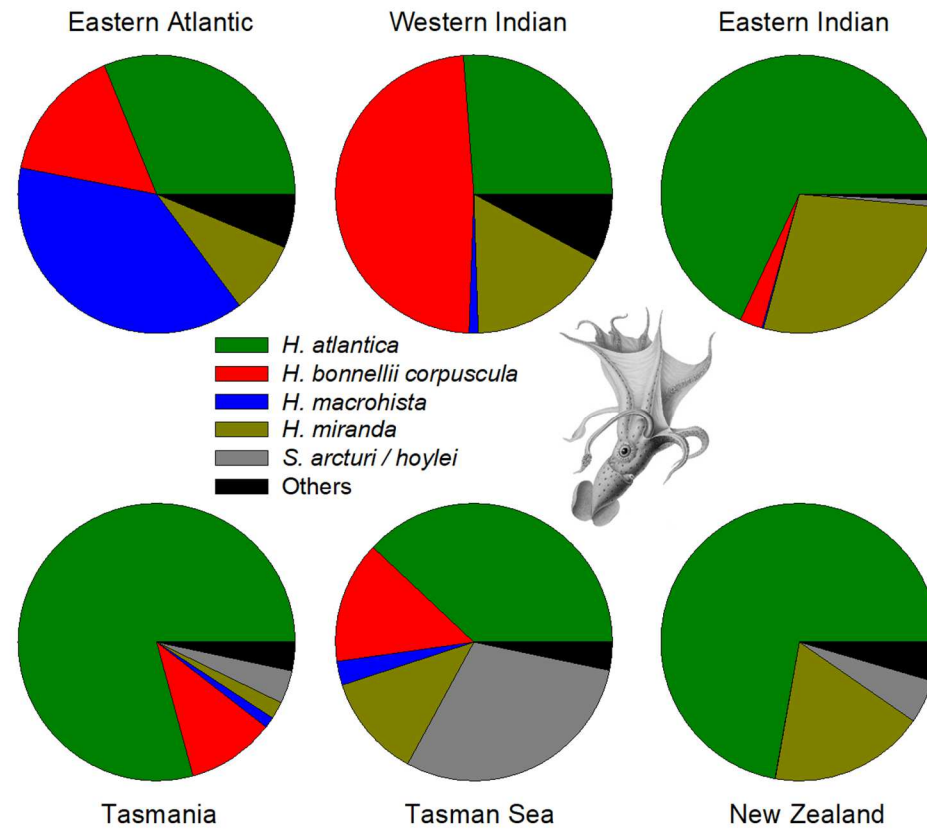
594 **Figure 1** Numerical importance of the four main families of cephalopods in the diet of sperm whales caught in the southern subtropics. The
 595 eastern Atlantic, western Indian and eastern Indian Ocean refer to Donkergat, Durban and Albany, respectively. Data from [Clarke \(1980\)](#), [Clarke](#)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