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2 **Biology of the world's largest invertebrate, the colossal squid**
3 **(*Mesonychoteuthis hamiltoni*): a short review**

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6 **Rui Rosa ^{1*}, Vanessa M. Lopes ¹, Miguel Guerreiro ¹, Kathrin Bolstad ², José C.**
7 **Xavier ^{3,4}**

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11 ¹ MARE – Marine Environmental Sciences Centre, Laboratório Marítimo da Guia,
12 Faculdade de Ciências da Universidade de Lisboa, Portugal.

13 ² Institute for Applied Ecology New Zealand, Auckland University of Technology,
14 Auckland, New Zealand.

15 ³ MARE – Marine and Environmental Sciences Centre (MARE), Department of Life
16 Sciences, University of Coimbra, 3004-517 Coimbra, Portugal.

17 ⁴ British Antarctic Survey, Natural Environment Research Council, High Cross,
18 Madingley Road, Cambridge CB3 0ET, United Kingdom.

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20
21 * Corresponding author: rrosa@fc.ul.pt

34 **Abstract**

35 The present study aims to review the current biological knowledge on the largest
36 (heaviest) living invertebrate, the colossal squid *Mesonychoteuthis hamiltoni*
37 (Robson, 1925). This squid is known to be endemic off the Southern Ocean (SO),
38 with a circumpolar distribution spreading from the Antarctic continent up to the
39 Sub-Antarctic Front. Small juveniles (< 40 mm mantle length) are mainly found from
40 the surface to 500 m, and the late juvenile stages are assumed to undergo
41 ontogenetic descent to depths reaching 2000m. Thus, this giant spends most part of
42 its life in the meso- and bathypelagic realms, where it can reach a total length of 6
43 meters. The maximum weight recorded so far was 495 kg. *Mesonychoteuthis*
44 *hamiltoni* is presently reported from the diets of 17 different predator species,
45 comprising penguins, sea birds, fishes and marine mammals, and feeds on
46 myctophids, Patagonian toothfish, sleeper shark and other squids. Isotopic analysis
47 places the colossal squid as one of the top predators in the SO. Based on phylogenetic
48 inferences, it is assumed that this squid is not capable of high-speed predator-prey
49 interactions, but it is rather an ambush predator. Their eyes, the largest in the planet,
50 seemed to have evolved to detect very large predators (e.g. sperm whales) rather
51 than to detect mates or preys at long distances. On the other hand, and like many
52 other deep-sea animals, it possesses light-emitting organs on the eyes, which may
53 provide ventral camouflage and counter-illumination or some sort of deceptive
54 technique to capture their prey. Although *M. hamiltoni* is quite abundant in the SO,
55 its life existence remains one of the ocean's great mysteries. This unique
56 invertebrate giant continues to attract considerable attention from media and the
57 public in general, but its study also constitutes a valuable source of insight into the
58 biophysical principles behind body-size evolution.

59

60 **Keywords:** colossal squid, *Mesonychoteuthis hamiltoni*, cranchiids, Southern Ocean;
61 gigantism

62

63 **Introduction**

64 The Southern Ocean consists of a system of deep-sea basins separated by the
65 Scotia Ridge, the Kerguelen plateau (Indian section) and the Macquarie Ridge (South
66 of New Zealand). While the south is limited by the Antarctic continent, the northern
67 part is surrounded by the Antarctic Polar Frontal Zone (APFZ), beginning at the
68 Antarctic convergence / Antarctic Polar Front (APF). The main surface current is the
69 Antarctic Circumpolar Current (ACC), which runs eastwards around the continent
70 (Orsi et al. 1995); Moore et al. (1997); (Moore et al. 1999). These associated fronts
71 create an obstacle to north-south “meridional” circulation, and the discontinuities
72 of temperature and salinity in the APFZ constitute an important barrier in
73 biogeographical interactions (Barnes et al. 2006). Nonetheless, Antarctic life is rich
74 and diverse with high levels of endemism (Arntz et al. 1994; Clarke and Johnston
75 2003).

76 Within this unique region, cephalopods are known to play a key role in the
77 marine food webs, because they constitute a vital alternate food source to Antarctic
78 krill *Euphausia superba* (Collins and Rodhouse 2006). They are important prey, and
79 thus sustain large populations of penguins, procellariiform birds, seals and toothed
80 whales (Clarke 1980; Xavier et al. 2002a; Cherel and Duhamel 2004; Cherel et al.
81 2004; Cherel and Hobson 2005; Cherel and Hobson 2007; Cherel et al. 2007; Xavier
82 et al. 2011). Yet, despite their important ecological role, the basic knowledge of the
83 bio-ecology of Southern Ocean cephalopods is still poorly known (Xavier et al. 1999;
84 Xavier et al. 2014; Alvito et al. 2015; Guerreiro et al. 2015), probably due to an
85 absence of a fishery industry. This may be related to the low number of exploitable
86 species (Xavier et al. 2007), lack of basic knowledge of the species' biology, stocks'

87 unpredictability, and the relative inaccessibility of these stocks for exploration and
88 study (Rodhouse et al. 1996; Rodhouse 1998; Collins and Rodhouse 2006).

89 The majority of the resident Southern Ocean cephalopod fauna comprises
90 endemic species of octopods (cirrate and incirrate), and oegopsid squids, which
91 differ greatly from the taxa found at lower latitudes. There is also a total absence of
92 myopsid squids and cuttlefish, and normally abundant families are rare. Unique
93 Southern Ocean taxa include the squid families Psychroteuthidae and
94 Batoteuthidae, and the genera *Psychroteuthis*, *Kondakovia*, *Alluroteuthis*,
95 *Slosarczykovia*, *Batoteuthis* and *Mesonychoteuthis*. Moreover, several of these
96 cephalopods occupy similar niches to (and compete with) some pelagic top
97 predators, namely sharks and large fishes (Rodhouse and White 1995; Rodhouse et
98 al. 1996; Cherel and Duhamel 2004; Cherel and Hobson 2005). One of these is the
99 most massive living cephalopod - the colossal squid *Mesonychoteuthis hamiltoni*
100 (Robson 1925)(Fig. 1). This squid is known to be a Southern Ocean endemic, and
101 although it is preyed by many top predators, its basic biology and ecology remain
102 one of the ocean's great mysteries. This review aims to summarize the currently
103 scattered bio-ecological knowledge of the elusive, largest living invertebrate; an
104 overview of the species' taxonomy and detailed treatment of the morphology will be
105 treated in a separate forthcoming publication (Bolstad et al. in prep).

106

107 ***Polar gigantism and some key morphological features of the colossal squid***

108 For a long time polar scientists have observed that organisms of such areas
109 can reach remarkably large sizes. Polar gigantism is notable tool for understanding
110 the biophysical principles and ecological theories (e.g. temperature-size rule,
111 Bergmann rule, oxygen availability coupled with low metabolic rates hypothesis)

112 behind body size evolution (Atkinson 1994; Chapelle and Peck 1999; Chapelle and
113 Peck 2004; Vermeij 2016). Although not consensual, some argue that this
114 phenomenon may be linked to the fact that polar giant taxa share common
115 evolutionary histories with deep-sea taxa. In other words, polar gigantism is
116 associated with abyssal gigantism. Yet, it is worth noting that the evolutionary
117 history of (benthic) Southern Ocean fauna is complex and the respective “invasions”
118 worked both ways (i.e. shelf to deep and vice versa) (Brandt et al. 2007; Strugnell et
119 al. 2011). One extreme case of polar gigantism in the Southern Ocean (where other
120 examples of this phenomenon include foraminiferans, sponges, ctenophores,
121 isopods, copepods, amphipods, pycnogonids, pteropods, annelids, echinoderms) is
122 the colossal squid (Fig. 1), which was first described by Robson (1925) from
123 fragments from two squids obtained from sperm whale stomach contents.
124 Posteriorly, the description of its beaks was done by Klumov and Yukhov (1975),
125 McSweeney (1970), and then reviewed by Clarke (1980) and Xavier and Cherel
126 (2009).

127 The colossal squid belongs to the family Cranchiidae, or “glass” squids, which
128 are generally small-to-medium sized species; *M. hamiltoni* is several orders of
129 magnitude larger than some other cranchiid species, attaining a maximum mantle
130 length (ML) of 2.5 meters and total length (TL) of 6 meters. The maximum weight
131 recorded to date was 495 kg (Fig. 1) (Jereb and Roper 2010). Apart from the coelom
132 (fluid-filled buoyancy chamber), while most cranchiids have translucent bodies (see
133 examples in Fig. 2 A, B and C), *M. hamiltoni* has much more muscle density (Fig. 2 D
134 and E). A further notable difference between the colossal squid and other cranchiids
135 is the presence of swivelling hooks on its tentacle clubs (Voss 1980; Voss et al. 1992)
136 (Fig. 2 G). Thus, the colossal squid is a clear “outlier” in the cranchid group.

137

138 ***Early stages***

139 Records of egg masses and hatchlings are essentially non-existent. Between
140 1962 and 1985, only 33 juveniles were reported, all caught using RMT and IKMT
141 nets (Fig. 3). Their mantle length (ML) ranged from 3 to 146 mm, with a clear
142 relationship between juvenile size and depth of capture. In fact, individuals below
143 ML 40 mm have been mostly found between the surface and 500 m (Fig. 3) (see
144 more juvenile morphometric information in McSweeney 1970; Filippova 1972;
145 Filippova 1979; Rodhouse and Clarke 1985; Filippova 1991; Filippova and
146 Pakhomov 1994; Lu and Williams 1994; Anderson and Rodhouse 2002; Filippova
147 2002). Nonetheless, the majority of the specimens known so far have been collected
148 by trawls (N = 155; Fig. 3) but besides their location no other relevant data (e.g. ML,
149 life stage) are available.

150

151 ***Age, growth and reproduction***

152 Besides the characteristic low temperatures, the Southern Ocean is also well
153 known by the drastic annual cycles of productivity. The oscillations from abundance
154 to famine are thought to be associated with increased resistance to starvation,
155 reduced competition and unusually slow growth rates (Lindstedt and Boyce 1985;
156 Arnett and Gotelli 2003; Clarke 2003). Deep-sea and polar environments are also
157 usually linked with low metabolic rates and longer longevity. For instance, Robison
158 et al. (2014) recently reported a female deep-sea benthic octopus *Graneledone*
159 *boreopacifica* undertaking an astonishing 53-month brooding period (by far the
160 longest egg-brooding period ever reported for any animal). If brooding comprises
161 about a quarter of this octopod lifespan, this species may be among the longest-lived

162 of all cephalopods. Their findings are unparalleled by those from the well-studied
163 shallow-water species and highlights the notion of how little we know about life in
164 marine extreme environments (deep-sea and poles). Within this context, one might
165 imagine that *M. hamiltoni* may live much longer than their temperate and tropical
166 counterparts, i.e. far longer than 12 to 18 months. The most common method for
167 measuring growth in cephalopods, and consequent age determination, is counting
168 growth increments on statoliths (Lipinski 1986; Rodhouse and Hatfield 1990);
169 however, *M. hamiltoni* material reported to date has not yet been sufficient to
170 validate the periodicity of statolith-ring formation for this species.

171 The colossal squid takes longer to mature and reproduce than its more
172 northern relatives, becoming mature at lengths of at least 1m and weight above 30
173 kg (Jereb and Roper 2010). Although in colder waters cephalopods tend to produce
174 a low number of large eggs (Collins and Rodhouse 2006), the colossal squid's
175 potential fecundity has been estimated at a maximum of 4.2 million oocytes (Jereb
176 and Roper 2010), which makes it one of the most fecund cephalopods, especially
177 when compared to other polar cephalopod fauna (Collins and Rodhouse 2006).

178

179 ***Distribution***

180 Part of the known distribution of the colossal squid is based on the rare
181 encounters with live or recently dead specimens aboard (mainly) toothfish fishing
182 (e.g. Fig. 1 D and E) vessels and the stomach contents of the squid's predators.
183 *Mesonychoteuthis hamiltoni* has a circumpolar distribution, ranging from the
184 Antarctic continent (excluding respective shelves and Kerguelen Plateau) up to the
185 Sub-Antarctic Front (SAF) (Fig. 4). Based on Xavier et al. (2015b), the highest values
186 of the species' predicted habitat suitability are found: i) between the Weddell Sea

187 (Atlantic sector) and the west of the Kerguelen archipelago (~60°E), and ii) between
188 180°E and 120°W in the Ross/Amundsen areas.

189

190 ***Vertical (ontogenetic) movements***

191 Available information on colossal squid's vertical migrating habits is very
192 scarce. As shown in Figure 3, small juveniles (< 40 mm ML) are mainly found from
193 the surface to 500 m. The higher productivity near the surface may confer the young
194 higher chances of feeding between hatching and their probable migration to deeper
195 waters. At late juvenile stages, *M. hamiltoni* is assumed to conduct an ontogenetic
196 descent to depths around 2000m (Lu and Williams 1994). Thus, the colossal squid
197 likely spends the majority of its life (late juvenile, subadult and adult stages) in the
198 meso- and bathypelagic zones of the Southern Ocean. Nonetheless, it is worth noting
199 that female specimens have been captured by fishing vessels at depths shallower
200 than the abovementioned range, suggesting that females may migrate to shallower
201 waters to spawn, as do other cranchiids.

202

203 ***Predator and prey interactions***

204 The undigested remains of colossal squid (beaks, tentacular hooks or sucker
205 rings) have been found in a great variety of predators' stomach contents. Presently,
206 *M. hamiltoni* is known from the diets of 17 different predator species, comprising
207 penguins, sea birds, fishes and marine mammals (Table 1). The larger predators of
208 the colossal squids are the sperm whales (Clarke 1980) and the sleeper sharks
209 (Cherel and Duhamel 2004) (Fig. 5), but in contrast to the former, the latter is a
210 bottom scavenger and ambush predator. One of the more remarkable predator

211 observations has been made at the Kerguelen Islands, where 66% of the shark
212 stomachs contained colossal squid remains (Cherel and Duhamel 2004).

213 Colossal squid beaks have also been found quite frequently in the Patagonian
214 toothfish (*Dissostichus eleginoides*) stomach contents (Fig. 5), and in turn, beak-
215 shaped bites and scratches from club hooks (matching the colossal squid's) have
216 also been found along the bodies of captured Patagonian toothfish (Remeslo et al.
217 2015). This may suggest reciprocal predator-prey dynamics. Patagonian toothfish
218 may be able to forage squids larger themselves because they attack dead or
219 moribund colossal squids. Remeslo et al. (2015) also argue that, due to anatomical
220 constraints (namely tooth shape), the toothfish may only scavenge the leftovers of
221 other predators, including the colossal squid itself. Cannibalism is also very common
222 among cephalopods, including giant squids (Bolstad and O'Shea 2004; Ibáñez and
223 Keyl 2010).

224 Seabirds, namely albatrosses, are also known to scavenge *M. hamiltoni* (Fig. 5).
225 Albatross stomachs often contain the remains of cephalopod prey that would have
226 been several times heavier than their own mean size (Croxall and Prince 1994;
227 Xavier et al. 2003b; Xavier and Croxall 2007; Alvito et al. 2015; Guerreiro et al.
228 2015). In fact, in certain periods (e.g. end of interbreeding/beginning of breeding
229 period) scavenging plays a crucial role in the diets of wandering (*Diomedea exulans*),
230 black-browed (*Thalassarche melanophrys*) and grey-headed (*Thalassarche*
231 *chrysostoma*) albatrosses, as more than 60% of the cephalopod remains recovered
232 had potentially been scavenged (more than 95% of the total estimated mass of
233 cephalopods consumed) (Alvito et al. 2015).

234 Regarding the squid's own feeding ecology, *M. hamiltoni* specimens with
235 intact or undigested stomach contents remain unknown. Moreover, dietary studies

236 in cephalopods are difficult to conduct as gut contents are usually in an advanced
237 state of digestion, making identification of prey items difficult to impossible.
238 Cephalopods also macerate their preys finely before ingestion, using their beaks and
239 radula. It has been suggested that *M. hamiltoni* feeds on myctophids, Patagonian
240 toothfish, sleeper sharks and other squids (Jereb and Roper 2010; Roberts et al.
241 2011). Based on phylogenetic (metabolic) inferences and polar gigantism
242 constraints, Rosa and Seibel (2010) argued that the colossal squid is probably not a
243 predator capable of high-speed predator-prey interactions (see also section 3.5).
244 Therefore, the very large but immobilized (or weakened) toothfish specimens
245 captured by longline would present easy, opportunistic prey for *M. hamiltoni*
246 (Yukhov 2012; Remeslo et al. 2015).

247 A number of studies have also used a different approach to determine the
248 trophic position of the colossal squid, namely the use of isotopic analysis (e.g. Cherel
249 and Hobson 2005). Nitrogen isotopes ratio ($\delta^{15}\text{N}$) indicate the consumer's trophic
250 position, whereas carbon isotopes ratio ($\delta^{13}\text{C}$) can provide information on habitat
251 occupation. Assessment of the nitrogen signatures have demonstrated that *M.*
252 *hamiltoni* is definitely one of the top predators in the Southern Ocean (Fig. 6).

253

254 ***Vision***

255 Giant (*Architeuthis dux*) and colossal squids possess the largest eyes in the
256 World oceans (Fig. 7), and on the planet (Walls 1942; Land and Nilsson 2002). Since
257 both of these squid species are pelagic organisms that share (or compete for) similar
258 ecological niches with other (vertebrate) top predators, the tremendous differences
259 in eye size may indicate a different purpose for the use of eyes. Nilsson et al. (2012)

260 suggested that the very large eyes may have conferred an evolutionary advantage in
261 increased ability to detect large predators (especially sperm whales), rather for
262 utility in detecting mates or prey at long distances. These authors modelled large
263 squids' visual range and proposed that the giant eyes enable them to detect sperm
264 whales as they trigger plankton bioluminescence while swimming through the
265 water column. In other words, as whales conduct hunting dives, they attain
266 considerable speed and agitate the deep waters where a great variety of
267 bioluminescent organisms thrive. The colossal squid's eyes, due to their large retina,
268 are able to detect such small sources of light from a distance, although they may not
269 necessarily register the predators before being detected themselves by the whale's
270 sonar (the range of which can exceed 120 m). The squid may, however, be visually
271 warned in sufficient time to attempt an escape (Nilsson et al. 2012). Nonetheless, it
272 is worth noting that Schmitz et al. (2013) also argued that *M. hamiltoni*'s eyes are
273 within the expected allometric range for squids, and thus may be a simple result of
274 a phylogenetically conserved trait.

275

276 ***Metabolism***

277 Rosa and Seibel (2010) calculated the metabolic rates and energy
278 requirements of the colossal squid through a depth-temperature gradient
279 representative of the Southern Ocean (Fig. 8). This phylogenetic inference was
280 conducted based on other deep-sea cranchiid data and followed the expected
281 allometric relationship between body size and metabolism (Seibel 2007; Seibel and
282 Drazen 2007; Rosa et al. 2009). Based on their findings, the authors argued that the
283 colossal squid "*is not a voracious predator capable of high-speed predator-prey*
284 *interactions. It is, rather, an ambush or sit-and-float predator that uses the hooks on*

285 *its arms and tentacles to ensnare prey that unwittingly approach*". The colossal squid
286 was long thought to be an intrepid predator, due to the "kraken"-related myths and
287 stories associated with its large size, but after this study, it has been postulated that
288 the colossal squid perhaps does not deserve such a reputation. The question that we
289 now raise is: does an organism need to be an active pursuit predator to be fearsome?
290 For instance, white sharks, leopards, crocodiles, large monkfish and pythons are all
291 ambush predators (many with low energy demands), and it is their capability to hide
292 and strike without warning that makes them inherently aggressive.

293

294 ***Bioluminescence***

295 Like the great majority of deep sea inhabitants, *M. hamiltoni* possesses light-emitting
296 organs (photophores), in the form of two elongate structures on the ventral surface
297 of each eye (Fig. 9) (Herring et al. 2002). The smaller is located anteriorly while the
298 larger is crescent-shaped and located posteriorly around the outside rim of the iris
299 (Voss 1980). *M. hamiltoni* photocytes contain crystalloids whose profiles appear as
300 rectangular blocks or elongate needles, and the reflector platelets are unusual, being
301 associated with a microtubular array that confers their edges a comb-like
302 appearance (Fig. 9). Interestingly, within Cranchiidae, members of the subfamily
303 Cranchiinae obliterate the silhouette of the eyeball by illuminating numerous small
304 ventrally directed photophores, whereas the taoniines (including *M. hamiltoni*) use
305 fewer, more elaborate, elongate reflectors to spread the light from the photophores
306 over the entire projected ventral surface of the eyeball (Herring et al. 2002). Like all
307 taoniines, the two photophores of the *M. hamiltoni* have a mirror-image
308 arrangement in which the illuminated surface of each light-emitting organ extends
309 towards the other, across the main ventral area of the eyeball. The subocular

310 photophores of *M. hamiltoni* may serve as ventral camouflage and counter-
311 illumination, to blend in with downwelling light when seen from below (Young
312 1975; Young 1977; Young et al. 1980). Yet, this seems to be not useful in large squid
313 individuals since their main predators are not visually-orientated hunters.
314 Photophores may also be used as a deceptive technique – when illuminated, other
315 organisms may disregard the colossal squid as a threat, allowing it to approach its
316 prey. Alternatively, the photophores may be used as “flashlights” to more accurately
317 predict the distance needed to stretch its hooked tentacles and successfully capture
318 unwitting prey.

319

320 **Future directions**

321 Further efforts should be made to understand more about the life of this giant. It has
322 been assumed that *M. hamiltoni* is quite abundant in the Southern Ocean (biomass
323 of around 90 million tonnes) and there have been some reports on its interest to
324 fisheries (Jereb and Roper 2010). Every sample, fragment or sighting has proved to
325 be a highly valuable source of information and helped scientists to unveil more and
326 more about *M. hamiltoni*. Baited cameras and remotely operated vehicles could be
327 deployed in the search of live footage, as has happened recently for other deep sea
328 “giant” squids, e.g. *Architeuthis dux* (Kubodera and Mori 2005) and *Taningia danae*
329 (Kubodera et al. 2006). *M. hamiltoni* and other Antarctic organisms has been widely
330 used for education and outreach activities worldwide (Xavier et al. 2015a). Besides
331 the fact that these unique invertebrate giants continue to attract considerable
332 attention from media and the public in general, it is important to highlight, in the
333 words of Vermeij (2016), that: “*Gigantism is (...) a functionally distinct and*
334 *ecologically important condition that is both enabled by resources and compelled by*

335 *natural selection. The distribution of maximum size in time and space can therefore*
336 *inform our understanding of major patterns in the history of life.”*

337

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344

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598

599

600 Table 1 – List of known predators of the colossal squid (*Mesonychoteuthis hamiltoni*)

Predator groups and common names	Species	Geographical location	Reference
<i>Penguins</i>			
King penguin	<i>Aptenodytes patagonicus</i>	Crozet	Ridoux (1994)
Adélie penguin	<i>Pygoscelis adeliae</i>	Shirley Islands, East Antarctica	Kent et al. (1998)
Emperor penguin	<i>Aptenodytes forsteri</i>	Mawson	Robertson et al. (1994)
<i>Seabirds</i>			
Southern fulmar	<i>Fulmarus glacialisoides</i>	South Brazil	Fonseca and Petry (2007)
Wandering albatross	<i>Diomedea exulans</i>	Marion, Macquarie, Prince Edward, Crozet Is., South Georgia, Antipodes	(Clarke and Prince 1981; Imber and Berruti 1981; Rodhouse et al. 1987; Cooper and Brown 1990); Cooper et al. (1992); (Imber 1992; Ridoux 1994; Cherel and Klages 1998; Xavier et al. 2003a; Xavier et al. 2003b)
Black-browed albatross	<i>Thalassarche melanophrys</i>	South Georgia	Xavier et al. (2003a)
Grey-headed albatross	<i>Thalassarche chrysostoma</i>	Diego Ramirez; South Georgia,	(Cherel and Klages 1998; Xavier et al. 2003a; Arata et al. 2004; Alvito et al. 2015)
Light-mantled albatross	<i>Phoebetria palpebrata</i>	Crozet, Prince Edward Island, Marion Island; Macquarie and Heard islands	(Imber and Berruti 1981; Cooper and Brown 1990; Ridoux 1994; Cherel and Klages 1998; Green et al. 1998)
White-chinned petrel	<i>Procellaria aequinoctialis</i>	South Africa (Benguela Current); Marion Is.	Lipinski and Jackson (1989)
Sooty albatross	<i>Phoebetria fusca</i>	Marion and Crozet Islands	(Imber and Berruti 1981; Cooper and Brown 1990; Ridoux 1994; Cherel and Klages 1998)
<i>Fishes</i>			
Sleeper shark	<i>Somniosus cf. Microcephalus</i>	Kerguelen	Cherel and Duhamel (2004)
Patagonian toothfish	<i>Dissostichus eleginoides</i>	Crozet, South Georgia	(Xavier et al. 2002b; Cherel et al. 2004)
Antarctic toothfish	<i>Dissostichus mawsoni</i>	Lazarev Sea, South Sandwich Islands	(Petrov and Tatarnikov 2011; Roberts et al. 2011)

601

Marine mammals

602

Southern elephant seal

Mirounga leonina

South Georgia

Rodhouse et al. (1992)

603

Sperm whale

Physeter macrocephalus

Antarctica, South America, South
Georgia, Peru and Chile, Tasman
sea

(Korabelnikov 1959; Clarke et al. 1976; Clarke 1980; Clarke
and MacLeod 1982; Fiscus et al. 1989)

604

Southern bottlenose whale

Hyperoodon planifrons

South America

Clarke and Goodall (1994)

605

Long-finned pilot whale

Globicephala melaena

South America

Clarke and Goodall (1994)

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621 Figure captions

622

623 Figure 1 – Length and weight (logarithmic scale) of the marine invertebrate (grey
624 bars) and vertebrate giants (blue bars), with a special emphasis on the
625 cephalopods: giant octopus (*Enteroctopus dofleini*), giant squid (*Architeuthis*
626 *dux*) and colossal squid *Mesonychoteuthis hamiltoni* (red bar). Cephalopod
627 data from Jereb and Roper (2010) and Jereb et al. (2014). Other groups' data
628 from McClain et al. (2015) and references within.

629

630 Figure 2 – Morphological dissimilarities between the colossal squid
631 (*Mesonychoteuthis hamiltoni*) and other cranchiid species. Panels A, B and C
632 show the translucent bodies of deep-sea glass squids *Teuthowenia pellucida*
633 and *Taonius borealis* (copyright: MBARI). Panels D and E show the much
634 denser musculature of the colossal squid (photo credits: AP San Aspring crew
635 of Sanford Company). Panels F, G, H highlight the beak size, the presence of
636 rotating hooks on its tentacles, and eye lens size of the colossal squid
637 (copyright: Museum of New Zealand Te Papa Tongarewa).

638

639 Figure 3 – Number of colossal squid (*Mesonychoteuthis hamiltoni*) specimens caught
640 in nets (RMT- Rectangular midwater trawl, IKMT – Isaacs-Kidd Midwater
641 trawl, and other trawls) within the Southern Ocean, and the relationship
642 between juvenile mantle length (mm) and depth of capture.

643

644 Figure 4 – Map of the locations of all known colossal squid (*Mesonychoteuthis*
645 *hamiltoni*) occurrences. “Squid” symbol represents locations obtained from
646 nets and the other symbols represent predator diet studies (penguins,
647 seabirds, fish and sharks) [modified from Xavier et al. (2015b)].

648

649 Figure 5 – Predicted mantle length (mm) of the colossal squid (*Mesonychoteuthis*
650 *hamiltoni*) found in the stomachs remains (namely beaks) of its predators. The
651 estimated values are based on beaks' morphometrics (namely lower rostral
652 length) and the respective allometric equation (see Xavier and Cherel 2009).

653 Abbreviations: A.p. – *Aptenodytes patagonicus*; Dio.e. – *Diomedea exulans*;
654 Diss.e. - *Dissostichus eleginoides*; G.m. - *Globicephala melaena*; H.p. -
655 *Hyperoodon planifrons*; P.f. – *Phoebetria fusca*; P.m. – *Physeter macrocephalus*;
656 P.p. - *Phoebetria palpebrata*; S.m. – *Somniosus cf Microcephalus*; T.c. -
657 *Thalassarche chrysostoma*. The references for beak data (for the different
658 predator species) can be found in Table 1.

659

660 Figure 6 – $\delta^{15}\text{N}$ values (trophic level) of squid (grey bars) and other marine animals
661 collected in the Southern Ocean. * - corrected (beak) values. Data from
662 Guerreiro et al. (2015), Stowasser et al. (2012) and references within.

663

664 Figure 7 – Biggest eyes (mm) in the ocean. Data from Walls (1942), Land and Nilsson
665 (2002) and Nilsson et al. (2012).

666

667 Figure 8 – Metabolic ecology of the colossal squid (*Mesonychoteuthis hamiltoni*) in
668 the Southern Ocean. Panel A: Effect of size in the routine mass-specific
669 metabolic rate of deep-sea cranchiid squids (blue circles, from a 0.017g
670 *Liocranchia valdiviae* to 500 kg *M. hamiltoni*) and of other cephalopod
671 counterparts, including loliginids (green line), coastal ommastrephids (dark
672 red line), coastal benthic octopods (red line), pelagic gelatinous octopods
673 (light blue line) and vampire squid (purple line). Value of 20 kg giant squid
674 (*Architeuthis* spp.; solid triangle) was based on the activity of citrate synthase
675 measured in mantle muscle (Seibel et al. 2000). Rates were standardized to
676 1.5°C assuming a Q10 of 2. Data from Rosa and Seibel (2010) and Seibel
677 (2007). Panels B and C represent depth-related changes in temperature in the
678 circum-Antarctic Southern Ocean. Dashed lines represent sub-Antarctic areas
679 (50.58S0.58E; 50.58S90.58E; 50.58S179.58W; 50.58S90.58W) and solid lines
680 represent Antarctic areas (60.58S0.58E; 60.58S90.58E; 60.58S179.58W;
681 60.58S90.58W); (B) projected energy consumption (kcal day⁻¹; based on 4.7
682 kcal/l O₂) as a function of depth (temperature dependence of 2) in the circum-
683 Antarctic Southern Ocean region. Thick solid line represents the mean values
684 obtained from the different temperature profiles. Thin dashed line represents

685 the 95% confidence interval for the means (modified from Rosa and Seibel
686 2010).

687

688 Figure 9 – Photophores of the colossal squid (*Mesonychoteuthis hamiltoni*). Panel A
689 shows the light organ at the rear of the eyeball, while Panel B shows the eyelid
690 being pulled back to reveal part of the light organ (at the rear of the eyeball)
691 (copyright: Museum of New Zealand Te Papa Tongarewa). Panels C and D
692 show the colossal squid's photocytes containing paracrystalline aggregates
693 (needle-like or rectangle structures) and Panel E shows the reflector platelets
694 with edges of comb-like appearance (modified from Herring et al. 2002;
695 copyright: John Wiley & Sons, Inc.).

696