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

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Abstract

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

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

Introduction

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

Within this unique region, cephalopods are known to play a key role in the marine food webs, because they constitute a vital alternate food source to Antarctic krill *Euphausia superba* (Collins and Rodhouse 2006). They are important prey, and thus sustain large populations of penguins, procellariform birds, seals and toothed whales (Clarke 1980; Xavier et al. 2002a; Cherel and Duhamel 2004; Cherel et al. 2004; Cherel and Hobson 2005; Cherel and Hobson 2007; Cherel et al. 2007; Xavier et al. 2011). Yet, despite their important ecological role, the basic knowledge of the bio-ecology of Southern Ocean cephalopods is still poorly known (Xavier et al. 1999; Xavier et al. 2014; Alvito et al. 2015; Guerreiro et al. 2015), probably due to an absence of a fishery industry. This may be related to the low number of exploitable species (Xavier et al. 2007), lack of basic knowledge of the species' biology, stocks' unpredictability, and the relative inaccessibility of these stocks for exploration and study (Rodhouse et al. 1996; Rodhouse 1998; Collins and Rodhouse 2006).

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

Polar gigantism and some key morphological features of the colossal squid

For a long time polar scientists have observed that organisms of such areas can reach remarkably large sizes. Polar gigantism is notable tool for understanding the biophysical principles and ecological theories (e.g. temperature-size rule, Bergmann rule, oxygen availability coupled with low metabolic rates hypothesis) behind body size evolution (Atkinson 1994; Chapelle and Peck 1999; Chapelle and Peck 2004; Vermeij 2016). Although not consensual, some argue that this phenomenon may be linked to the fact that polar giant taxa share common evolutionary histories with deep-sea taxa. In other words, polar gigantism is associated with abyssal gigantism. Yet, it is worth noting that the evolutionary history of (benthic) Southern Ocean fauna is complex and the respective “invasions” worked both ways (i.e. shelf to deep and vice versa) (Brandt et al. 2007; Strugnell et al. 2011). One extreme case of polar gigantism in the Southern Ocean (where other examples of this phenomenon include foraminiferans, sponges, ctenophores, isopods, copepods, amphipods, pycnogonids, pteropods, annelids, echinoderms) is the colossal squid (Fig. 1), which was first described by Robson (1925) from fragments from two squids obtained from sperm whale stomach contents. Posteriorly, the description of its beaks was done by Klumov and Yukhov (1975), McSweeny (1970), and then reviewed by Clarke (1980) and Xavier and Cherel (2009).

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

Early stages

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

Age, growth and reproduction

Besides the characteristic low temperatures, the Southern Ocean is also well known by the drastic annual cycles of productivity. The oscillations from abundance to famine are thought to be associated with increased resistance to starvation, reduced competition and unusually slow growth rates (Lindstedt and Boyce 1985; Arnett and Gotelli 2003; Clarke 2003). Deep-sea and polar environments are also usually linked with low metabolic rates and longer longevity. For instance, Robison et al. (2014) recently reported a female deep-sea benthic octopus *Graneledone boreopacifica* undertaking an astonishing 53-month brooding period (by far the longest egg-brooding period ever reported for any animal). If brooding comprises about a quarter of this octopod lifespan, this species may be among the longest-lived of all cephalopods. Their findings are unparalleled by those from the well-studied shallow-water species and highlights the notion of how little we know about life in marine extreme environments (deep-sea and poles). Within this context, one might imagine that *M. hamiltoni* may live much longer than their temperate and tropical counterparts, i.e. far longer than 12 to 18 months. The most common method for measuring growth in cephalopods, and consequent age determination, is counting growth increments on statoliths (Lipinski 1986; Rodhouse and Hatfield 1990); however, *M. hamiltoni* material reported to date has not yet been sufficient to validate the periodicity of statolith-ring formation for this species.

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

Distribution

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

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

Vertical (ontogenetic) movements

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

Predator and prey interactions

The undigested remains of colossal squid (beaks, tentacular hooks or sucker rings) have been found in a great variety of predators' stomach contents. Presently, *M. hamiltoni* is known from the diets of 17 different predator species, comprising penguins, sea birds, fishes and marine mammals (Table 1). The larger predators of the colossal squids are the sperm whales (Clarke 1980) and the sleeper sharks (Cherel and Duhamel 2004) (Fig. 5), but in contrast to the former, the latter is a bottom scavenger and ambush predator. One of the more remarkable predator observations has been made at the Kerguelen Islands, where 66% of the shark stomachs contained colossal squid remains (Cherel and Duhamel 2004).

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

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

Regarding the squid's own feeding ecology, *M. hamiltoni* specimens with intact or undigested stomach contents remain unknown. Moreover, dietary studies in cephalopods are difficult to conduct as gut contents are usually in an advanced state of digestion, making identification of prey items difficult to impossible. Cephalopods also macerate their preys finely before ingestion, using their beaks and radula. It has been suggested that *M. hamiltoni* feeds on myctophids, Patagonian toothfish, sleeper sharks and other squids (Jereb and Roper 2010; Roberts et al. 2011). Based on phylogenetic (metabolic) inferences and polar gigantism constraints, Rosa and Seibel (2010) argued that the colossal squid is probably not a predator capable of high-speed predator–prey interactions (see also section 3.5). Therefore, the very large but immobilized (or weakened) toothfish specimens captured by longline would present easy, opportunistic prey for *M. hamiltoni* (Yukhov 2012; Remeslo et al. 2015).

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

Vision

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

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

Metabolism

Rosa and Seibel (2010) calculated the metabolic rates and energy requirements of the colossal squid through a depth-temperature gradient representative of the Southern Ocean (Fig. 8). This phylogenetic inference was conducted based on other deep-sea cranchiid data and followed the expected allometric relationship between body size and metabolism (Seibel 2007; Seibel and Drazen 2007; Rosa et al. 2009). Based on their findings, the authors argued that the colossal squid *"is not a voracious predator capable of high-speed predator–prey interactions. It is, rather, an ambush or sit-and-float predator that uses the hooks on* *its arms and tentacles to ensnare prey that unwittingly approach".* The colossal squid was long thought to be an intrepid predator, due to the "kraken"-related myths and stories associated with its large size, but after this study, it has been postulated that the colossal squid perhaps does not deserve such a reputation. The question that we now raise is: does an organism need to be an active pursuit predator to be fearsome? For instance, white sharks, leopards, crocodiles, large monkfish and pythons are all ambush predators (many with low energy demands), and it is their capability to hide and strike without warning that makes them inherently aggressive.

Bioluminescence

Like the great majority of deep sea inhabitants, *M. hamiltoni* possesses light-emitting organs (photophores), in the form of two elongate structures on the ventral surface of each eye (Fig. 9) (Herring et al. 2002). The smaller is located anteriorly while the larger is crescent-shaped and located posteriorly around the outside rim of the iris (Voss 1980). *M. hamiltoni* photocytes contain crystalloids whose profiles appear as rectangular blocks or elongate needles, and the reflector platelets are unusual, being associated with a microtubular array that confers their edges a comb-like appearance (Fig. 9). Interestingly, within Cranchiidae, members of the subfamily Cranchiinae obliterate the silhouette of the eyeball by illuminating numerous small ventrally directed photophores, whereas the taoniines (including *M. hamiltoni*) use fewer, more elaborate, elongate reflectors to spread the light from the photophores over the entire projected ventral surface of the eyeball (Herring et al. 2002). Like all taoniines, the two photophores of the *M. hamiltoni* have a mirror-image arrangement in which the illuminated surface of each light-emitting organ extends towards the other, across the main ventral area of the eyeball. The subocular photophores of *M. hamiltoni* may serve as ventral camouflage and counter-illumination, to blend in with downwelling light when seen from below (Young 1975; Young 1977; Young et al. 1980). Yet, this seems to be not useful in large squid individuals since their main predators are not visually-orientated hunters. Photophores may also be used as a deceptive technique – when illuminated, other organisms may disregard the colossal squid as a threat, allowing it to approach its prey. Alternatively, the photophores may be used as "flashlights" to more accurately predict the distance needed to stretch its hooked tentacles and successfully capture unwitting prey.

Future directions

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

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

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

Marine mammals			
Southern elephant seal	*Mirounga leonina*	South Georgia	Rodhouse et al. (1992)
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)
Southern bottlenose whale	*Hyperoodon planifrons*	South America	Clarke and Goodall (1994)
Long-finned pilot whale	*Globicephala melaena*	South America	Clarke and Goodall (1994)

Figure captions

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

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

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

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

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

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

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

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

Figure 8 – Metabolic ecology of the colossal squid (*Mesonychoteuthis hamiltoni*) in the Southern Ocean. Panel A: Effect of size in the routine mass-specific metabolic rate of deep-sea cranchiid squids (blue circles, from a 0.017g *Liocranchia valdiviae* to 500 kg *M. hamiltoni*) and of other cephalopod counterparts, including loliginids (green line), coastal ommastrephids (dark red line), coastal benthic octopods (red line), pelagic gelatinous octopods (light blue line) and vampire squid (purple line). Value of 20 kg giant squid (*Architeuthis* spp.; solid triangle) was based on the activity of citrate synthase measured in mantle muscle (Seibel et al. 2000). Rates were standardized to 1.5ºC assuming a Q10 of 2. Data from Rosa and Seibel (2010) and Seibel (2007). Panels B and C represent depth-related changes in temperature in the circum-Antarctic Southern Ocean. Dashed lines represent sub-Antarctic areas (50.58S0.58E; 50.58S90.58E; 50.58S179.58W; 50.58S90.58W) and solid lines represent Antarctic areas (60.58S0.58E; 60.58S90.58E; 60.58S179.58W; 60.58S90.58W); (B) projected energy consumption (kcal day^{-1}; based on 4.7 kcal/l O_2) as a function of depth (temperature dependence of 2) in the circum-Antarctic Southern Ocean region. Thick solid line represents the mean values obtained from the different temperature profiles. Thin dashed line represents

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

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