# 1 Distribution, habitat and trophic ecology of Antarctic

# 2 cephalopods: inferences from predators and stable isotopes

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# 15 Abstract:

16 Cephalopods play a key role in the marine environment but knowledge of their 17 feeding habits is limited by a lack of observations and this is particularly true for 18 Antarctic species. Toothfish species are key predators of cephalopods and may be 19 viewed as ideal biological samplers of these species. A total of 256 cephalopod lower 20 beaks were identified from the stomachs of Patagonian (Dissostichus eleginoides) and 21 Antarctic toothfish (D. mawsoni), captured in fisheries of South Georgia and the 22 South Sandwich Islands in the South Atlantic. Long-armed octopus squid 23 (Kondakovia longimana) and smooth-hooked squid (Moroteuthis knipovitchi) were 24 the main cephalopod prey and both were predated upon wherever toothfish were 25 captured, though inhabit deeper waters at the South Sandwich Islands than at South Georgia. Measurements of  $\delta^{13}$ C from beak material indicated a clear segregation of 26 habitat use comparing adult and sub-adult sized K. longimana. Variation in  $\delta^{15}$ N with 27 28 size indicated an ontogenetic shift in the diet of cephalopods and also suggested 29 trophic plasticity, with variation in diet in response to prey availability. This study 30 provides new insights in to private life of elusive Antarctic cephalopods in a largely 31 unexplored region of the South Atlantic. 32 33 34 35

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# 1 Introduction

2 Cephalopods play an important role in the Antarctic marine ecosystem both as 3 predators and prey of top predators (Clarke 1996), though there is still a general lack 4 of knowledge about their ecology and distribution, particularly of deep sea species 5 (Cherel et al. 2004; Clarke 1983; Southward et al. 2006; Xavier et al. 1999). This is largely because of the small amount of dedicated survey cruises targeting oceanic 6 7 squid species allied with the fact that several species (particularly myopsid Antarctic 8 species) are extremely difficult to catch using scientific nets (Clarke 1977; Rodhouse 9 1990; Xavier et al. 2002). One solution is to use observations from the diet of squid 10 predators such as toothed whales (e.g. Mikhalev et al., 1981;), seals (e.g. Slip et al. 11 1995), seabirds (Xavier et al. 2003) and fish (Xavier et al. 2002).

12 The identification of cephalopod species from beak (keratinous mandibles) 13 morphology is now possible for a large number of commonly occurring Antarctic 14 species (Xavier and Cherel 2009). We can also use information from the ratio of 15 stable isotopes ( $\delta^{15}$ N and  $\delta^{13}$ C) of keratin from cephalopod beaks to complement the 16 spatial distribution of presence in the diet of predators (Cherel et al. 2011; Cherel and 17 Hobson 2005). Heavy nitrogen is enriched in beak material with increasing trophic level (> $\delta^{15}$ N), consequently  $\delta^{15}$ N measurements serve as indicator of individual 18 trophic position (Hobson & Welch 1992). Carbon ( $\delta^{13}$ C) is mainly used to determine 19 20 primary sources in a trophic network, indicating the lower versus higher-latitude 21 plankton and inshore versus offshore, or pelagic versus benthic, contribution to food 22 intake (Cherel and Hobson 2005; Hobson et al. 1994).

23 In this study, squid beaks were obtained from the stomachs of toothfish 24 species captured in demersal longline fisheries of South Georgia and the South 25 Sandwich Islands: Patagonian toothfish (Dissostichus eleginoides) which are found 26 mainly around sub-Antarctic Islands and Patagonian region and Antarctic toothfish 27 (Dissostichus mawsoni), which has several adaptations to very cold water 28 temperatures and is endemic to the austral seasonal pack-ice zone (De Witt et al. 29 1990). Dissostichus spp. are opportunistic predators feeding on a wide range of taxa, 30 including fish, crustaceans and cephalopods (Collins et al. 2010; Collins et al. 2007; 31 Fenaughty et al. 2003; Garcia de la Rosa et al. 1997; Pilling et al. 2001; Roberts et al. 32 2011; Stevens et al. 2012). This generalist feeding behaviour and generally low rates 33 of dispersal (Williams et al. 2002) make *Dissostichus* spp. ideal biological samplers 34 of deep water cephalopods and other prey taxa.

1 The distributions of the two toothfish congeners overlap in only a few places 2 including at the South Sandwich Islands, an island arc along the Scotia Ridge 3 (Roberts et al. 2011). The South Sandwich Islands are bisected by the Weddell Front, 4 which separates the marine habitat of this region in to two separate water bodies with 5 distinct hydrographical characteristics: the eastward-flowing Weddell-Scotia 6 Confluence (WSC) to the north and Weddell Gyre to the south (Orsi et al. 1995). The 7 segregation between these two water mass is evident from a north to south gradient in 8 water temperature and habitat type that causes the observed distributions of toothfish 9 species along the island chain (Roberts et al. 2011).

10 Commercial interest in Southern Ocean cephalopods has increased over the 11 past few decades. Cephalopod species including Martialia hyadesi, Kondakovia 12 longimana, Moroteuthis knipovitchi and Gonatus antarcticus are potential candidates 13 for commercial exploration (Xavier et al. 2007). However, the poor understanding of 14 ecology and distribution will hamper the estimation of stock size and the effective 15 management of any future cephalopod fisheries that may develop in the Southern 16 Ocean. In addition, these cephalopod species have been recorded regularly in the diet 17 of numerous predators and are likely to perform a relevant ecosystem function, at 18 least in particular areas of the Southern Ocean. As such it is desirable to improve our 19 knowledge on the ecology of the populations of cephalopod species of this region. 20 The main goals of this study were: (1) to describe the cephalopod fauna in the diet of 21 *Dissostichus* spp., in terms of diversity and quantity; (2) to characterise the vertical 22 and horizontal distribution of cephalopods; and (3) to assess the trophic level and the 23 habitat of the cephalopods fauna, using stable isotopes analysis.

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## 25 Materials and Methods

Whole stomachs from *D. mawsoni* and *D. eleginoides* were collected on board the demersal longline fishing vessel *San Aspiring* at the South Sandwich Islands (from 55.7–59.9° S and 25–29° W) at depths ranging from 917 to 1720 m during March and April 2009 (See Roberts *el al.* 2011 for a more detailed description). The southern arrow squid (*Nototodarus sloanii*) were used as bait and do not naturally occur at the study site. As such they were omitted from this analysis where found in stomachs.

The stomach contents from both toothfish species were analysed following the
method of Roberts *et al.* (2011). The cephalopods beaks were preserved in 90%

1 ethanol prior to identification. Lower beaks were counted and identified to species 2 level using Xavier & Cherel (2009) while upper beaks were only counted. The lower 3 rostral length (LRL) was measured to the nearest 0.1 mm using Vernier callipers and 4 used to estimate reconstituted mass and mantle length for each individual using 5 allometric equations for each species given by Xavier & Cherel (2009). The 6 frequency of occurrence (% O) of cephalopods in the diet (count of sampled in which 7 a species was present divided by the total number of stomach sampled), the 8 proportion (% N) of lower beak beaks (count of lower beak of a species divided by 9 the total count of lower beaks) and the contribution to the estimated total prey mass 10 (% M) (estimated mass, M, of a species divided by the total estimated mass of all 11 cephalopod individuals) were calculated. 12 Lower beaks were selected for isotopic analyses (C and N) for the three 13 species that comprised the greatest proportion of reconstituted mass (% M; 14 Kondakovia longimana, Moroteuthis knipovitchi and Psychroteuthis glacialis) from 15 stomach sampled collected from D. mawsoni (beaks from stomachs of D. eleginoides 16 were not used because the sample size was small). For K. longimana sampled subsets 17 were taken based on beak LRL that were assumed to have belonged to sub-adults 18 (LRL  $\leq$  10mm) or adults (>10mm). Cleaned whole beaks were dried and reduced to a fine powder. Stable isotope ratios of nitrogen ( $\delta^{15}N$ ) and carbon ( $\delta^{13}C$ ) were measured 19 20 using a Continuous Flow Isotope Ratio Mass Spectrometer (CFIRMS) at IMAR-21 CMA following Ceia et al. (2012) (Ceia et al. 2012). The results are presented in  $\delta$ 22 notation as deviations from the standard references in parts per thousand (‰) 23 according to the following equation: 24 25  $\delta$  X=[(Rsample / Rstandard) -1]×1000 26 where X represents  ${}^{13}$ C or  ${}^{15}$ N and Rsample the ratios  ${}^{13}$ C/ ${}^{12}$ C or  ${}^{15}$ N/ ${}^{14}$ N. Rstandard 27 28 represents the international reference standard V-PDB ("Vienna" - PeeDee formation) 29 and atmospheric N2 (AIR) is the standard for  $\delta^{13}$ C and  $\delta^{15}$ N, respectively. Data were 30 statistically analysed using R for Macintosh (R Core Team 2013). 31 32 **Results** The cephalopod diet of Antarctic toothfish Dissostichus mawsoni 33

| 1  | A total of 269 stomachs were collected, of which 205 (76.2%) contained prey.                          |
|----|---|
| 2  | The main prey was fish (62% <i>M</i> of <i>D. mawsoni</i> ), followed by cephalopods (35% <i>M</i> ). |
| 3  | Seven species of cephalopods were identified from a total of 205 stomachs, of which                   |
| 4  | 76.2% of stomachs containing prey. A total of 311 beaks (71 uppers and 240 lowers)                    |
| 5  | were collected. Kondakovia longimana was (122 fresh lower beaks; 65.2% of total                       |
| 6  | fresh lower beaks) followed by Moroteuthis knipovitchi (48 beaks; 25.7%), these two                   |
| 7  | species (both Onychoteuthids) represented 90.9% of the total number of fresh lower                    |
| 8  | beaks found (Table 1). The estimated mass of cephalopods consumed by D. mawsoni                       |
| 9  | was 999.7 Kg (average of 4.9 kg for each <i>D. mawsoni</i> that had consumed squid). <i>K.</i>        |
| 10 | longimana was also the most important cephalopod species in terms of estimated                        |
| 11 | mass (96.4% of the total estimated mass for all cephalopods) followed by $M$ .                        |
| 12 | knipovitchi (2.9%) (Table 1).   |
| 13 | Lower rostral lengths of beaks in the stomachs of D. mawsoni ranged from                              |
| 14 | 5.3-19.8 mm (mean: 12.3 ±0.37 mm [SE]), slightly below that of the dominant                           |
| 15 | species K. longimana (mean: 15.6 ± 0.26mm [SE]). The smallest beak was identified                     |
| 16 | as a single Slosarczykovia circumantarctica (3.2 mm).   |
| 17 | There were no significant effect of predator size on beak LRL (ANOVA: F5,                             |
| 18 | 175 = 1.2; p= 0.31), or of predator sex (Mann- Whitney; U = 3395; p=0.22).                            |
| 19 |   |
| 20 |   |
| 21 | The cephalopod diet of Patagonian toothfish Dissostichus eleginoides                                  |
| 22 | A total of 775 stomachs were collected, of which only 56 contained prey                               |
| 23 | (7.2% O). The main prey was fish $(73.6% M)$ , followed by cephalopods $(18% M)$ .                    |
| 24 | Only three species were identified. A total of 21 beaks (5 uppers and 16                              |
| 25 | lowers) were collected. K. longimana and M. knipovitchi were, again, the most                         |
| 26 | important species by number (each species: 5 fresh lower beaks and 45.5% of total                     |
| 27 | fresh lower beaks; Table 2).  |
| 28 | The estimated mass of cephalopods consumed by D. eleginoides was 34.5 kg                              |
| 29 | (average of 0.62 kg for each individual that had consumed squid). K. longimana was                    |
| 30 | also the most important cephalopod species by estimated mass (89.3% of the total                      |
| 31 | estimated mass for all cephalopods) followed by M. knipovitchi (10.2%; Table 2)                       |

| 1  | Lower rostral lengths of beaks in the stomachs of D. mawsoni ranged from                                 |
|----|--|
| 2  | 18.2 to 5.7mm (mean = $9.65 \pm 1.31$ mm [SE]). The smaller beak found was from a                        |
| 3  | specimen of <i>M. knipovitchi</i> (3.2 mm).  |
| 4  | There were no significant effect of predator size on beak LRL (ANOVA: F <sub>6,5</sub>                   |
| 5  | = 1.56; $p=0.32$ ), or of predator sex (Mann- Whitney; $U = 8$ ; $p=0.23$ ).                             |
| 6  |  |
| 7  |  |
| 8  | Vertical and horizontal distribution of toothfish species in relation to                                 |
| 9  | cephalopods consumed   |
| 10 | Cephalopod beaks were found in fish caught from 1000 to 1800m depth. The                                 |
| 11 | majority of beaks came from the range depth 1300 to 1600 m (60% of total fresh                           |
| 12 | lower beaks found on the diet of Dissostichus spp.; Figure 1; Figure 2).                                 |
| 13 | The most important cephalopod species, K. longimana and M. knipovitchi,                                  |
| 14 | were distributed across the depth range over which fish were captured, though no $M$ .                   |
| 15 | knipovitchi were found at depths >1700m. Both cephalopod species were most                               |
| 16 | common at intermediate depths (1300-1600m). The sizes of Dissostichus spp. that                          |
| 17 | feed on cephalopod was not significantly comparing depth ranges (Kruskal-Wallis;                         |
| 18 | H=27.07; p < 0.01), neither was beak LRL (Kruskal-Wallis; H= 8.16 ; p= 0.03).                            |
| 19 | Cephalopods beaks were found in all locations where fish were captured and may                           |
| 20 | have greatest frequency of occurrence in south-eastern areas of the South Sandwich                       |
| 21 | Islands (Figure 1b from Roberts et al. 2011). There was no evidence for a location of                    |
| 22 | capture effect on the frequency of occurrence of the main cephalopod prey.                               |
| 23 |  |
| 24 | Habitat and trophic level of Antarctic cephalopods according to stable isotope                           |
| 25 | signatures   |
| 26 | There was a clear delineation of adults and sub-adult from K. longimana                                  |
| 27 | based on $\delta^{15}N$ (a proxy for their trophic level): $\delta^{15}N$ of sub-adult beaks ranged from |
| 28 | 6.77-5.88, compared with 6.11-8.33 for adults (ANOVA; $F_{3, 28}$ = 8.55; p < 0,01;                      |
| 29 | Figure 3), indicating that they are at a greater trophic level. The value of $\delta^{13}C$ (a proxy     |
| 30 | for their habitat) indicates that K. longimana (adult) and Psychroteuthis glacialis                      |
| 31 | occupy similar habitat types and are spatially segregated from <i>M. knipovitchi</i> and <i>K</i> .      |
| 32 | <i>longimana</i> (sub-adult) (ANOVA; F $_{3,28} = 20.22$ ; p < 0.01; Figure 3).                          |
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#### 1 Discussion

#### 2 Regional variation in cephalopod prey of *Dissostichus* spp.

3 To our knowledge, this is the first detailed study to analyse the distribution, 4 habitat and trophic levels of cephalopods around South Sandwich Islands. The 5 cephalopod component of diet of D. mawsoni and D. eleginoides is typically quite different though was quite similar at the South Sandwich Islands. All cephalopod 6 7 species found in this study had been previously recorded in the diet of at least one 8 toothfish species (Cherel et al. 2004; Stevens et al. 2012; Xavier et al. 2002; Xavier 9 and Cherel 2009). D. eleginoides from the Argentinian shelf prey on Semirossia 10 tenera, Illex argentinus, Loligo gahi and Octopus tehuelchus (Garcia de la Rosa et al. 11 1997). None of these species were observed in our study and may not be present at the 12 South Sandwich Islands, though I. argentinus may also occur in colder waters (Xavier 13 et al. 2006). Around the sub-Antarctic islands of Kerguelen and Crozet, K. longimana, 14 Moroteuthis ingens and Gonatus antarcticus were the most important cephalopods in 15 terms of estimated mass (Cherel et al. 2004) – the latter two species did not occur in 16 our study, probably due to a slightly warmer water distribution (Anderson and 17 Rodhouse 2002; Nesis 1987; Rodhouse 1989; Xavier and Cherel 2009). However, G. 18 antarcticus was reported in the diet of D. eleginoides around South Georgia (Xavier 19 et al. 2002) indicating that the distribution of this species is limited to the northern 20 islands of the Scotia Arc (Ward et al. 2012). Even so, despite the hydrographical 21 segregation of the Scotia Sea, the cephalopod component in the diet of D. eleginoides 22 found in South Georgia is relatively similar to the component of cephalopods found in 23 the present study, where K. longimana and M. knipovitchi were also the most 24 important species by estimated mass (76.1% M and 10.7% M, respectively; Xavier et 25 al. 2002). 26 In the Ross Sea just two cephalopod species -K. longimana and

*Psychroteuthis glacialis* – were found in *D. mawsoni* stomachs, the latter having the greatest estimated mass (29.6% *M*; Stevens 2012). The dominance of *P. glacialis* could be due increased latitude and proximity to the mainland as this cephalopod species is considered to have a Antarctic distribution (Xavier et al. 1999). Comparing our study with those of toothfish species in other regions we see that these species have a high degree of trophic plasticity with respect to cephalopod prey and are likely to predate on the species that are locally abundant.

#### **1** Vertical/Horizontal distribution of Antarctic cephalopods

2 There is considerable potential in using top predators to better describe the 3 spatial distributions of cephalopod species that are not yet commercially exploited 4 (Rodhouse et al. 1996). Cephalopod beaks were found in the diets of toothfish at all 5 depths sampled (100 m to 1800 m) with most present in fish caught between 1300 and 6 1600 m. This conforms with present assumption that most Antarctic cephalopod 7 species are confined to continental slope habitat, the mesopelagic/bathypelagic zones 8 (Croxall and Prince 1994; Kock 1987). K. longimana and M. knipovitchi - the most 9 important cephalopod prey in this study, were mainly found between 1300 at 1600m, 10 contrary to a previous study conducted at South Georgia where they were only found 11 between depths of 300 to 900m (Xavier et al. 2002). Therefore, we can say that the 12 vertical distributions of K.longimana and M. knipovitchi vary between bathyal and 13 mesopelagic zones in the Scotia Sea, depending on the oceanographic regime. 14 Galiteuthis glacialis and P. glacialis were also found in deeper water when compared 15 to the South Georgia study (600-900m and 300-1200 in Xavier et al. (2002), 16 respectively). These results show that the South Sandwich Islands cephalopod 17 community inhabits at greater depths than the population from South Georgia. A 18 recent study found that hydrographic differences effectively split the Scotia Sea in to 19 North and South groupings where the structure of the food web is different (Ward et 20 al. 2012), which can explain why there is an different observed vertical distribution of 21 cephalopods.

22 One of the more interesting characteristics of the South Sandwich Islands Arc 23 is the clear spatial segregation of the two Dissostichus spp. (Roberts et al. 2011) and 24 also of other fish species and benthic invertebrate communities (Roberts 2012). The 25 north to south gradient in temperature at bathyal depths is likely to be a key driver of 26 this bio-regionalisation (Roberts 2012), though does not appear to be a barrier to the 27 dispersal of key cephalopod prey of toothfish species in this study. In this study we 28 found the main cephalopod prey species in the diet of toothfish species both to the north and south of the Weddell front. The relatively broad niche of these species has 29 30 been observed before by Xavier et al. (1999).

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#### 33 Habitat assessment from cephalopod beaks

- Based on the ratio of <sup>13</sup>C isotopic signatures of cephalopod beaks found in the 1 2 stomachs of *D. mawsoni* and comparing with reference values, all three species 3 analysed (K. longimana, M. knipovitchi e P. glacialis) have mainly inhabited 4 Antarctic waters (Stowasser et al. 2012). However, our results show differences 5 between species, indicating that they may feed in different areas of the ocean. There is a clear segregation between sub-adults and adults of K. longimana, suggesting that 6 7 younger individuals of the South Sandwich Islands population inhabit more northerly 8 regions with a southward redistribution likely to occur as they increase in size. 9 In previous studies,  $\delta^{13}$ C values of K. longimana and M. knipovitchi were relatively high ( $[\delta^{13}C \text{ of } K. longimana \text{ and } M. knipovitchi \text{ caught by Black-browed albatrosses}$ 10 were  $-21.85 \pm 1.53$  and  $-21.24 \pm 1.04$ , respectively (Alvito, Rosa, Phillips, Ceia, Seco 11 12 and Xavier (unpublished data)]; (Anderson et al. 2009)) at South Georgia). The South Sandwich Islands are ate higher latitude that can explain the difference on the  $\delta^{13}$ C. 13
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#### 15 Trophic assessment of cephalopods beaks

We found a clear segregation between the <sup>15</sup>N signatures of sub-adults and
adults of *K. longimana*, suggesting an ontogenetic dietary shift in this species. The
trophic ecology of *K. longimana* is poorly understood, though through comparing
with the results of another study (Cherel and Hobson 2005) we can infer an
ontogenetic shift in *K. longimana* from a crustacean to a mesopelagic fish diet at
South Sandwich Islands.

The values of  $\delta^{13}$ C from sub-adults of *K. longimana* and adults of *M. knipovitchi* are very similar, though the  $\delta^{15}$ N values for these two species are significantly different, from which we can infer that they occupy similar habitat, though have a different trophic ecology.

Comparing with other studies in the Scotia Sea region,  $\delta^{15}$ N values found in this study were relatively low ([ $\delta^{15}$ N of *K. longimana* and *M. knipovitchi* caught by Black-browed albatrosses were 8,00 ± 0.82 and 8.82 ± 0.76, respectively (Alvito , Rosa, Phillips, Ceia, Seco and Xavier (unpublished data)]; (Anderson et al. 2009)). – especially when compared with the study of Anderson et al (2009) ( $\delta^{15}$ N of *K.longimana* = 7.5; *M. knipovitchi* = 10.8, *P. glacialis* = 10.5). The large difference

32 between studies may indicate strong location or year effects on foodweb structure

- 33 beneath these cephalopod species. Antarctic Krill (*Euphasia superba*) perform a key
- 34 central role in the marine foodweb of the Scotia Sea region and in years of low krill

1 biomass in the Subantarctic region (as in 2009 – the year of this study) (Hill et al. 2 2009; Waluda et al. 2012). Intermediates species in the foodweb may switch to 3 feeding on species at a lower trophic level such as copepods, which will affect a decrease in the value of  $\delta^{15}$ N in cephalopods further up the foodweb (Tarling et al. 4 5 2012). The study of cephalopods present in the diet of albatrosses in 2009 around the South Georgia confirms this inference (Alvito et al. (unpublished data)). 6 7 Nevertheless, cephalopods from the Scotia Sea had a greater  $\delta^{15}$ N than those of the 8 Kerguelen Plateau (Cherel et al. 2011) indicating that the former are feeding prey at a 9 higher trophic level.

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### 11 Final remarks

12 This study once again confirms the importance that cephalopods have the 13 Antarctic food web, though we still know very little about their ecology and 14 distribution. Due to their high degree of trophic plasticity and generally low rates of 15 dispersal, D. eleginoides and D. mawsoni are two species that show great potential as 16 biological samplers of bathyal cephalopod species across the South Ocean. The 17 isotopic analysis indicated that habitat types of different cephalopod species vary 18 along the Scotia Arc, maybe due to variation in hydrographic conditions. Stable 19 isotopes also indicate ontogenetic shifts in diet of cephalopods and that they may be 20 generalist predators, with diet varying in response to the availability of prey. 21 22 23 24 Ackowledgements 25 The authors would like to thank the crew of the San Aspiring, particularly 26 Jack Fenaughty, for assistance with the at-sea collection of samples. We would also

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| 2                    | References:  |
| 3                    |  |
| 4                    |  |
| 5<br>6               | Anderson C, Rodhouse PG (2002) Distribution of juvenile squid in the Scotia Sea in relation to regional oceanography. Bulletin of marine science 71:97–108.  |
| 7<br>8<br>9          | Anderson ORJ, Phillips RA, McDonald RA, et al. (2009) Influence of trophic position<br>and foraging range on mercury levels within a seabird community. Marine<br>Ecology Progress Series 375:277–288. doi: 10.3354/meps07784  |
| 10<br>11<br>12       | Ceia FR, Phillips RA, Ramos JA, et al. (2012) Short- and long-term consistency in the foraging niche of wandering albatrosses. Marine Biology 159:1581–1591. doi: 10.1007/s00227-012-1946-1  |
| 13<br>14             | Cherel Y, Duhamel G, Gasco N (2004) Cephalopod fauna of subantarctic islands:<br>new information from predators. Marine Ecology Progress Series 266:143–156.   |
| 15<br>16<br>17<br>18 | Cherel Y, Gasco N, Duhamel G (2011) Top predators and stable isotopes document<br>the cephalopod fauna and its trophic relationships in Kerguelen waters. The<br>Kerguelen Plateau: marine ecosystem and fisheries Société Française<br>d'Ichtyologie, Paris 99–108. |
| 19<br>20<br>21<br>22 | Cherel Y, Hobson KA (2005) Stable isotopes, beaks and predators: a new tool to study the trophic ecology of cephalopods, including giant and colossal squids. Proceedings of the Royal Society B: Biological Sciences 272:1601–1607. doi: 10.1007/s00442-003-1270-z  |
| 23<br>24<br>25       | Clarke M (1996) Cephalopods as prey. The role of cephalopods in the World's oceans.<br>Philosophical Transactions of the Royal Society of London Series B: Biological<br>Sciences Special Volume:1053–1165.  |
| 26<br>27             | Clarke M (1983) Cephalopod Biomas - Estimation from Predation. Memoirs of National Museum Victoria 95–107.   |
| 28                   | Clarke M (1977) Beaks, nets and numbers. Symp zool Soc Lond 89–126.  |
| 29<br>30<br>31       | Collins MA, Brickle P, Brown J, Belchier M (2010) The Patagonian Toothfish:<br>Biology, Ecology and Fishery. In: Lesser M (ed) Advances in Marine Biology,<br>1st ed. Academic Press, Burlington, pp 227–300   |
| 32<br>33<br>34       | Collins MA, Ross KA, Belchier M, Reid K (2007) Distribution and diet of juvenile<br>Patagonian toothfish on the South Georgia and Shag Rocks shelves (Southern<br>Ocean). Marine Biology 152:135–147. doi: 10.1007/s00227-007-0667-3                                 |
| 35<br>36             | Croxall JP, Prince PA (1994) Dead or alive, night or day: how do albatrosses catch squid? Antarctic Science 6:155–155.   |
| 37<br>38             | De Witt HH, Heemstra PC, Gon PC (1990) Nototheniidae. In: Gon PC, Heemstra PC (eds) <i>Fishes of the Southern Ocean</i> . JLB Smith  |

- 1 Institute of Ichthyology, Grahamstown, pp 279–331
- Fenaughty JM, Stevens DW, Hanchet SM (2003) Diet of the Antarctic toothfish
  (Dissostichus mawsoni) from the Ross Sea, Antarctica (subarea 88.1). CCAMLR
  Science 10:113–123.
- Garcia de la Rosa SB, Sánchez F, Figueroa D (1997) Comparative feeding ecology of
   patagonian toothfish (Dissostichus eleginoides) in the Southwestern Atlantic.
   CCAMLR Science 4:105–124.
- Hill S, Belchier M, Collins MA, et al. (2009) Multiple indicators suggest a strong
   ecosystem anomaly at South Georgia in 2009. British Antarctic Survey, UK
- Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird
   trophic relationships. Journal of Animal Ecology 786–798.
- Kock K-H (1987) Marine consumer: Fish and Squid. Environment International
   13:37–45.
- 14 Nesis KN (1987) Cephalopods of the world. TFH, Neptune City
- Orsi A, whitworth T, Nowlin W (1995) On the meridional extent and fronts of the
   Antarctic circumpolar current. Deep Sea Research I 42:641–673.
- Pilling GM, Purves MG, Daw TM, et al. (2001) The stomach contents of Patagonian
  toothfish around South Georgia (South Atlantic). Journal of Fish Biology
  59:1370–1384. doi: 10.1006/jfbi.2001.1748
- Roberts J (2012) Ecology and management of range edge populations: the case of
   toothfish species at the South Sandwich Islands. In: Faculty of Science of
   Imperial College London, pp 1–240
- Roberts J, Xavier JC, Agnew DJ (2011) The diet of toothfish species Dissostichus
   eleginoides and Dissostichus mawsoni with overlapping distributions. Journal of
   Fish Biology 79:138–154. doi: 10.1111/j.1095-8649.2011.03005.x
- Rodhouse PG (1990) Cephalopod Fauna of the Scotia Sea at South Georgia: Potential
   for Commercial Exploitation and Possible Consequences. In: Kerry KR, Hempel
   G (eds) Antarctic Ecosystems. Springer Berlin Heidelberg, pp 289–298
- Rodhouse PG (1989) Pelagic cephalopods caught by nets during the Antarctic
  research cruises of the 'Polarstern' and 'Walther Herwig'. Arch Fischereiweiss
  39:111–121.
- Rodhouse PG, Prince PA, Trathan PN, et al. (1996) Cephalopods and mesoscale
   oceanography at the Antarctic Polar Front: satellite tracked predators locate
   pelagic trophic interactions. Marine Ecology Progress Series 136:37–50.
- Southward AJ, Young CM, Fuiman LA (2006) Advances in Marine Biology.
  Academic Press, San Diego
- 37 Stevens DW, Dunn MR, Pinkerton MH, Forman JS (2012) Diet of Antarctic toothfish

| 1                    | (Dissostichus mawsoni) from the Ross Sea region, Antarctica. Unpublished report   |
|----------------------|---|
| 2<br>3<br>4          | Stowasser G, Atkinson A, McGill RAR, et al. (2012) Food web dynamics in the<br>Scotia Sea in summer A stable isotope study. Deep Sea Research 59-60:208–221.<br>doi: 10.1016/j.dsr2.2011.08.004   |
| 5<br>6<br>7          | Tarling GA, Ward P, Atkinson A, et al. (2012) DISCOVERY 2010 Spatial and<br>temporal variability in a dynamic polar ecosystem. Deep Sea Research 59-60:1–<br>13. doi: 10.1016/j.dsr2.2011.10.001  |
| 8<br>9<br>10         | Waluda CM, Hill SL, Peat HJ, Trathan PN (2012) Diet variability and reproductive performance of macaroni penguins Eudyptes chrysolophus at Bird Island, South Georgia. Marine Ecology Progress Series 466:261–274. doi: 10.3354/meps09930                             |
| 11<br>12<br>13       | Ward P, Atkinson A, Venables HJ, et al. (2012) Food web structure and bioregions in the Scotia Sea A seasonal synthesis. Deep Sea Research 59-60:253–266. doi: 10.1016/j.dsr2.2011.08.005   |
| 14<br>15<br>16       | Williams R, Tuck GN, Constable AJ, Lamb T (2002) Movement, growth and available abundance to the fishery of Dissostichus eleginoides Smitt, 1898 at Heard Island, derived from tagging experiments. CCAMLR Science 9:33–48.   |
| 17<br>18<br>19       | Xavier JC, A Tarling G, P Croxall J (2006) Determining prey distribution patterns from stomach contents of satellite tracked high predators of the Southern Ocean. Ecography 29:260–272.  |
| 20<br>21             | Xavier JC, Cherel Y (2009) Cephalopod beak guide for the Southern Ocean. British<br>Antarctic Survey, Cambridge   |
| 22<br>23<br>24<br>25 | Xavier JC, Croxall JP, Trathan PN, Rodhouse PG (2003) Inter-annual variation in the cephalopod component of the diet of the wandering albatross, Diomedea exulans, breeding at Bird Island, South Georgia. Marine Biology 142:611–622. doi: 10.1007/s00227-002-0962-y |
| 26<br>27<br>28       | Xavier JC, Rodhouse PG, Purves MG, et al. (2002) Distribution of cephalopods<br>recorded in the diet of the Patagonian toothfish (Dissostichus eleginoides) around<br>South Georgia. Polar Biology 25:323–330. doi: 10.1007/s00300-001-0343-x                         |
| 29<br>30<br>31       | Xavier JC, Rodhouse PG, Trathan PN, Wood AG (1999) A Geographical Information<br>System (GIS) Atlas of cephalopod distribution in the Southern Ocean. Antarctic<br>Science 11:61–62.  |
| 32<br>33<br>34<br>35 | Xavier JC, Wood AG, Rodhouse PG, Croxall JP (2007) Interannual variations in<br>cephalopod consumption by albatrosses at South Georgia: implications for future<br>commercial exploitation of cephalopods. Mar Freshwater Res 58:1136–1143. doi:<br>10.1071/MF06237   |
| 26                   |   |





Fig. 2. – Bivariated isotopic signals of South American sea lion pups before and after parturition, once corrected in accordance with the expected total diet-to-pup isotopic enrichment for blood cells (before parturition) and serum (after parturition). Bivariated isotopic signals of the main potential prey of sea lion females and the primary producers shown as mean  $\pm$  SD. Sample size n = 5 for all the species, except for *O*. *flavescens* (n = 26 for each tissue), *L. gahi* (n = 4) and phytoplankton (n = 2; collective samples of diatoms and dinoflagellates).

**Drago M, Cardona L, Crespo EA, Aguilar A (2009)**. Ontogenic dietary changes in South American sea lions. J. Zool. 279:251–261

Table 1. Frequency of occurrence, number and mass of cephalopods identified from *Dissostichus mawsoni* diet.

| Таха  | Frequency |       | Number<br>lower beaks |      | Estimated mass (g) |       |
|---|-----------|-------|-----------------------|------|--------------------|-------|
|   |           | %     |                       | %    |                    | %     |
| Kondakovia longimana                        | 60        | 22.30 | 122                   | 65.2 | 963660.4           | 96.40 |
| Moroteuthis knipovitchi                     | 35        | 13.01 | 148                   | 25.7 | 29391.4            | 2.94  |
| Psychroteuthis glacialis                    | 6         | 2.22  | 6                     | 3.2  | 3168.0             | 0.32  |
| Alluroteuthis antarcticus                   | 1         | 0.37  | 3                     | 1.6  | 1865.6             | 0.19  |
| Mesonychoteuthis hamiltoni                  | 1         | 0.37  | 1                     | 0.5  | 846.9              | 0.08  |
| Galiteuthis glacialis                       | 5         | 1.86  | 5                     | 2.7  | 559.8              | 0.06  |
| Taonius sp. (Voss)                          | 1         | 0.37  | 1                     | 0.5  | 186.4              | 0.02  |
| Slosarczykovia circumantarctica             | 1         | 0.37  | 1                     | 0.5  | 8.9                | 0.00  |
| Total lower beaks                           |           |       | 240                   |      |                    |       |
| Total fresh lower beaks                     |           |       | 187                   |      |                    |       |
| Total upper beaks                           |           |       | 71                    |      |                    |       |
| Number of stomachs analysed                 |           |       | 269                   |      |                    |       |
| Number of stomachs with material            |           | 205   |                       |      |                    |       |
| Number of stomachs with cephalopods present |           |       | 158                   |      |                    |       |

|   | Frequency |       | Number<br>lower beaks |      | Estimated<br>Mass (g) |       |
|---|-----------|-------|-----------------------|------|-----------------------|-------|
| Taxa  |           |       |                       |      |                       |       |
|   |           | %     |                       | %    |                       | %     |
| Kondakovia longimana                        | 4         | 52    | 5                     | 45,5 | 30788,4               | 89,29 |
| Moroteuthis knipovitchi                     | 4         | 52    | 5                     | 45,5 | 3505,2                | 10,27 |
| Taonius sp. (Voss)                          | 1         | 13    | 1                     | 9    | 186,4                 | 0,54  |
| Total lower beaks                           |           |       |                       | 16   |                       |       |
| Total fresh lower beaks                     |           |       |                       | 11   |                       |       |
| Total upper beaks                           |           |       |                       | 5    |                       |       |
| Number of stomachs analysed                 |           |       |                       | 775  |                       |       |
| Number of stomachs with material            |           |       |                       | 56   |                       |       |
| Number of stomachs with cephalopods present |           | esent |                       | 13   |                       |       |

Table 2. Frequency of occurrence, number and mass of cephalopods identified from *Dissostichus eleginoides* diet



**Figure 1.** Number of cephalopods beaks found according to the depth where *Dissotichus mawsoni* were found.



**Figure 2.** Number of cephalopods beaks found according to the depth where *Dissotichus eleginoides* were found.

**Figure 3.** Signatures of stable isotopes of carbon and nitrogen for main cephalopod species found in the diet of *Dissostichus mawsoni* (Mean  $\pm$  SE). Abbreviations: AZ, Antarctic Zone; PF, Polar Front; SAZ, Sub-Antarctic Zone. Standard value for Carbon signature on the Polar Front given by Stowasser et al. (2012).

