

Distribution, habitat and trophic ecology of Antarctic squid *Kondakovia longimana* and *Moroteuthis knipovitchi*: inferences from predators and stable isotopes

J. Seco¹ · J. Roberts² · F. R. Ceia¹ · A. Baeta¹ · J. A. Ramos¹ · V. H. Paiva¹ · J. C. Xavier^{1,3}

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Abstract Cephalopods have a key role in the marine environment though knowledge of their distribution and trophic ecology is limited by a lack of observations. This is particularly true for Antarctic species. Toothfish species are key predators of cephalopods and may be viewed as ideal biological samplers of these species. A total of 256 cephalopod lower beaks were identified from the stomachs of Patagonian toothfish (*Dissostichus eleginoides*) and Antarctic toothfish (*Dissostichus mawsoni*), captured in fisheries of South Georgia and the South Sandwich Islands in the South Atlantic between March and April 2009. Long-armed octopus squid (*Kondakovia longimana*) and smooth-hooked squid (*Moroteuthis knipovitchi*) were the main cephalopod prey and both were predated upon wherever toothfish were captured, though this cephalopod species appear to inhabit deeper waters at the South Sandwich Islands than at South Georgia. Measurements of $\delta^{13}\text{C}$ from beak material indicated a clear segregation of habitat use comparing adult and sub-adult sized *K.*

longimana. Variation in $\delta^{15}\text{N}$ with size indicated an ontogenetic shift in the diet of cephalopods and also suggested some trophic plasticity among years. This study provides new insights into the private life of some elusive Antarctic cephalopods in an underexplored region of the South Atlantic.

Keywords *Dissostichus eleginoides* · *Dissostichus mawsoni* · Cephalopod · South Sandwich Islands · Southern Ocean · $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

Introduction

Cephalopods play an important role in the Antarctic marine ecosystem both as predators and prey of top predators (Clarke 1996; Roberts et al. 2011), though there is still a general lack of knowledge about their ecology and distribution, particularly of deep water species (Clarke 1983; Cherel et al. 2004; Collins and Rodhouse 2006). This is largely because of the small amount of dedicated survey cruises targeting oceanic squid species allied with the fact that several species (particularly myopsid Antarctic species) are extremely difficult to catch using scientific nets (Clarke 1977; Xavier et al. 2002). One solution is to use observations from the diet of squid predators such as toothed whales (Mikhalev et al. 1981), seals (Split 1995), seabirds (Xavier et al. 2003) and fish (Xavier et al. 2002).

The identification of cephalopod species from beak (chitinous mandibles) morphology is now possible for a large number of commonly occurring Antarctic species (Xavier and Cherel 2009). We can also use information from the ratio of stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) from cephalopod beaks to complement the spatial distribution of presence in the diet of predators (Cherel and Hobson 2005,

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✉ J. Seco
joses.seco@gmail.com

- ¹ MARE - Marine and Environmental Science Center, University of Coimbra, 3004-517 Coimbra, Portugal
- ² Natural Institute of Water and Atmospheric Research, 301 Evans Bay Parade, Greta Point, PO Box 14-901, Kirbirnie, Wellington, New Zealand
- ³ British Antarctic Survey, NERC, High Cross, Madingley Road, Cambridge CB3 0ET, UK

2007; Cherel et al. 2011). Heavy nitrogen is enriched in beak material with increasing trophic level ($>\delta^{15}\text{N}$), consequently $\delta^{15}\text{N}$ measurements serve as an indicator of individual trophic position (Hobson and Welch 1992). Carbon ($\delta^{13}\text{C}$) is mainly used to determine primary sources in a trophic network, e.g.: low versus high-latitude; inshore versus offshore; pelagic versus benthic (Cherel and Hobson 2005; Hobson et al. 1994).

In this study, squid beaks were obtained from the stomachs of toothfish species captured in demersal longline fisheries of South Georgia and the South Sandwich Islands: Patagonian toothfish (*Dissostichus eleginoides*) which are found mainly around sub-Antarctic islands and the Patagonian region and Antarctic toothfish (*Dissostichus mawsoni*), which has several adaptations to very cold water temperatures and is endemic to the austral pack-ice zone (De Witt et al. 1990).

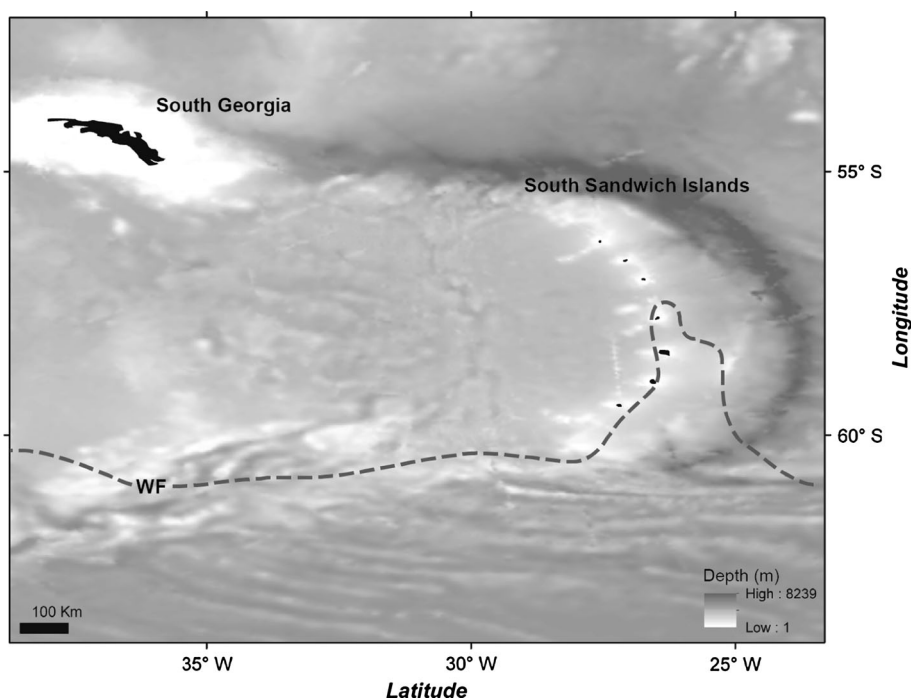
The distributions of the two toothfish congeners overlap in only a few places including at the South Sandwich Islands—an island arc along the Scotia Ridge (Roberts et al. 2011). *Dissostichus* spp. are opportunistic predators feeding on a wide range of taxa, including fish, crustaceans and cephalopods (Garcia de la Rosa et al. 1997; Pilling et al. 2001; Fenaughty et al. 2003; Roberts et al. 2011; Stevens et al. 2012). This generalist feeding behaviour and generally low rates of dispersal (Williams et al. 2002) make *Dissostichus* spp. ideal biological samplers of deep water cephalopods and other prey taxa.

The South Sandwich Islands (Fig. 1) are bisected by the Weddell Front, which divides the marine habitat into two

separate water bodies with distinct hydrographical characteristics: the eastward-flowing Weddell-Scotia Confluence (WSC) to the north and Weddell Gyre to the south (Orsi et al. 1993). The segregation between these two water masses is evident from a north to south gradient in water temperature and habitat type, which influences the observed distributions of toothfish species along the island chain (Roberts et al. 2011).

Commercial interest in Southern Ocean cephalopods has increased over the past few decades. Cephalopod species including *Martialia hyadesi*, *Kondakovia longimana*, *Moroteuthis knipovitchi* and *Gonatus antarcticus* are potential candidates for commercial exploitation (Xavier et al. 2007), although *K. longimana* and *M. knipovitchi* may be unpalatable as they contain ammonium (Lu and Williams 1994; Nesis 2000). However, at present, a poor understanding of ecology and distribution will hamper the estimation of stock size and the effective management of any cephalopod fisheries, which may develop in the Southern Ocean. In addition, these cephalopod species have been recorded regularly in the diet of numerous predators and are likely to perform significant ecosystem function in the Southern Ocean (Ducklow et al. 2007; Murphy et al. 2007, 2013). The main goals of this study were: (1) to describe the cephalopod fauna in the diet of *Dissostichus* spp., in terms of diversity and quantity; (2) to characterise the vertical and horizontal distribution of cephalopods; and (3) to assess the trophic level and the habitat of the cephalopod fauna, through stable isotopes analysis.

Fig. 1 Localisation of the South Sandwich Islands with the general position of Weddell front (WF; Orsi. et al. 1993)



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 to 25.0–29.0° W) at depths ranging from 917 to 1720 m, in March and April 2009 (See Roberts et al. 2011 for a more detailed description of sample collection). The southern arrow squid (*Nototodarus sloanii*) were used as bait and do not naturally occur at the study site; therefore, it was omitted from any analysis.

The stomach contents from both toothfish species were assessed following the method of Roberts et al. (2011). Briefly, the cephalopods beaks were preserved in 90 % ethanol prior to identification. Lower beaks were counted and identified to species level using Xavier and Cherel (2009), while upper beaks were only counted. The lower rostral length (LRL) was measured to the nearest 0.1 mm using vernier callipers and used to estimate reconstituted mass and mantle length for each individual using species-specific allometric equations given by Xavier and Cherel (2009). Only fresh beaks (with the lateral walls still intact and not eroded by digestive action) were included in the analysis to avoid overestimation. The frequency of occurrence (% *O*) of cephalopods in the diet (proportion of stomach samples in which a species was present), the abundance (% *N*) of a particular species (count of lower beaks of a species divided by the total count of lower beaks) and the contribution to the estimated total prey mass (% *M*; estimated mass, *M*, of a species divided by the total estimated mass of all cephalopod individuals) were calculated.

Lower beaks were selected for isotopic analyses ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) for the three species that comprised the greatest proportion of reconstituted mass (*K. longimana*, *M. knipovitchi* and *Psychroteuthis glacialis*) from stomach samples collected from *D. mawsoni* (beaks from stomachs of *D. eleginoides* were not used because the sample size was small). For *K. longimana*, sampled subsets were taken based on beak LRL that was assumed to have belonged to sub-adults (LRL ≤ 10 mm) or adults (>10 mm). Beaks were cleaned, then dried and reduced to a fine powder. Stable isotope ratios of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) were measured using a Continuous Flow Isotope Ratio Mass Spectrometer (CFIRMS) at IMAR-CMA following Ceia et al. (2012). The results are presented in δ notation as deviations from the standard references in parts per thousand (‰) according to the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where X represents ^{13}C or ^{15}N and R_{sample} the ratios $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. R_{standard} represents the international reference standard V-PDB (Vienna Pee-Dee Belemnite)

and atmospheric N_2 (AIR) is the standard for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Long-term performance of the mass spectrometer was monitored by analysis of secondary isotopic reference material (acetanilide STD: C and N contents of 71.09 and 10.36 %, respectively) in every batch, indicating precision <0.2 ‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Data were statistically analysed within R (R Core Team 2013).

Results

The cephalopod diet of Antarctic toothfish

A total of 269 stomachs were collected, of which 205 (76.2 %) contained prey. The main preys were fish (62 % *M* of *D. mawsoni*) and then cephalopod species (35 % *M*). Seven species of cephalopods were identified from a total of 205 stomachs. A total of 311 beaks (71 uppers and 240 lowers) were collected. *K. longimana* was the dominant species (122 fresh lower beaks; 65.2 % of total fresh lower beaks) followed by *M. knipovitchi* (48 beaks; 25.7 %). These two species (both onychoteuthids) represented 90.9 % of the total number of fresh lower beaks found (Table 1). The estimated mass of cephalopods consumed by *D. mawsoni* was 999.7 kg (average of 4.9 kg for each *D. mawsoni* that had consumed squid). *K. longimana* was also the most important cephalopod species in terms of estimated mass (96.4 % of the total estimated mass for all cephalopods) followed by *M. knipovitchi* (2.9 %; Table 1).

There were no significant effects of predator size on beak LRL (ANOVA: $F_{5, 175} = 1.2$; $p = 0.31$), or of sex of toothfish (Mann–Whitney; $U = 3395$; $p = 0.22$; Table 2).

The cephalopod diet of Patagonian toothfish

A total of 775 stomachs were collected, of which only 56 contained prey items (7.2 % *O*). The main prey was fish (73.6 % *M*), followed by cephalopods (18 % *M*).

Only three species of cephalopods were found in the stomachs of *D. eleginoides*. A total of 21 beaks (five uppers and 16 lowers) were collected. *K. longimana* and *M. knipovitchi* were, again, the most important species by number (each species: five fresh lower beaks and 45.5 % of total fresh lower beaks; Table 3).

The estimated mass of cephalopods consumed by *D. eleginoides* was 34.5 kg (average of 0.62 kg for each individual that had consumed squid). *K. longimana* was also the most important cephalopod species by estimated mass (89.3 % of the total estimated mass for all cephalopods) followed by *M. knipovitchi* (10.2 %; Table 2).

There were no significant effects of predator size (ANOVA: $F_{6, 5} = 1.56$; $p = 0.32$; Table 4) or of predator sex (Mann–Whitney; $U = 8$; $p = 0.23$) on beak LRL.

Table 1 Species, frequency of occurrence, number and mass of cephalopods identified from *Dissostichus mawsoni* diet caught around South Sandwich Islands between March and April 2009

Taxa	Frequency	%	Number lower beaks	%	Estimated mass (g)	%
<i>Kondakovia longimana</i>	60	22.30	122	65.2	963,660.4	96.40
<i>Moroteuthis knipovitchi</i>	35	13.01	48	25.7	29,391.4	2.94
<i>Psychroteuthis glacialis</i>	6	2.22	6	3.3	3168.0	0.32
<i>Alluroteuthis antarcticus</i>	1	0.37	3	1.6	1865.6	0.19
<i>Mesonychoteuthis hamiltoni</i>	1	0.37	1	0.5	846.9	0.08
<i>Galiteuthis glacialis</i>	5	1.86	5	2.7	559.8	0.05
<i>Taonius</i> sp. (Voss)	1	0.37	1	0.5	186.4	0.02
<i>Slosarczykovia circumantarctica</i>	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			

Table 2 Lower rostral length (LRL) measurements and mantle length (ML) and mass estimations of cephalopods identified in *Dissostichus mawsoni* diet

Taxa	Number lower beaks	LRL (mm)				ML (mm)				Estimated mass (g)			
		Mean	Min	Max	SD	Mean	Min	Max	SD	Mean	Min	Max	SD
<i>Kondakovia longimana</i>	122	15.54	6.9	19.8	2.86	622.01	239.75	810.45	126.63	7964.13	85.73	21,482.06	5244.11
<i>Moroteuthis knipovitchi</i>	48	6.35	5.4	7.1	0.39	300.25	200.22	379.23	40.69	612.32	341.86	890.99	128.13
<i>Psychroteuthis glacialis</i>	6	7.01	5.3	8	0.94	278.86	201.58	323.13	42.56	527.99	139.03	879.01	257.28
<i>Galiteuthis glacialis</i>	5	5.5	5.3	5.7	0.15	236.49	228.33	244.65	6.45	111.96	102.56	121.59	7.52
<i>Alluroteuthis antarcticus</i>	3	5.83	5.3	6.1	0.46	199.80	181.14	209.14	16.16	621.86	463.46	701.07	137.18
<i>Mesonychoteuthis hamiltoni</i>	1	7.3	7.3	7.3		436.13	436.14	436.14		846.93	846.93	846.93	
<i>Taonius</i> sp. B (Voss)	1	7.6	7.6	7.6		454.56	454.57	454.57		186.35	186.35	186.35	
<i>Slosarczykovia circumantarctica</i>	1	3.2	3.2	3.2		80.88	80.89	80.89		8.93	8.93	8.93	

Vertical and horizontal distribution of toothfish species in relation to cephalopods consumed

Cephalopod beaks were found in fish caught from 917 to 1720 m depth. The majority of beaks came from the range depth 1300 to 1600 m (60 % of total fresh lower beaks found in the diet of *Dissostichus* spp.; Fig 2).

The most important cephalopod species, *K. longimana* and *M. knipovitchi*, were distributed across the whole depth range over which fish were captured, though no *M. knipovitchi* were found at depths >1700 m. Both cephalopod

species were most common at intermediate depths (1300–1600 m; Fig. 2).

When analysing the catch per unit effort (number of cephalopod beak divided by number of toothfish sampled in each depth range), the depths where more cephalopods were caught by fish were between 1100 and 1300 m. The value for the 1700 m deep is the highest, but at this depth, it was only one fish caught (Fig. 2).

The sizes of *Dissostichus* spp. that feed on cephalopod were not significantly different comparing depth ranges (Kruskal–Wallis; $H = 27.07$; $p = 0.07$). Also, there were

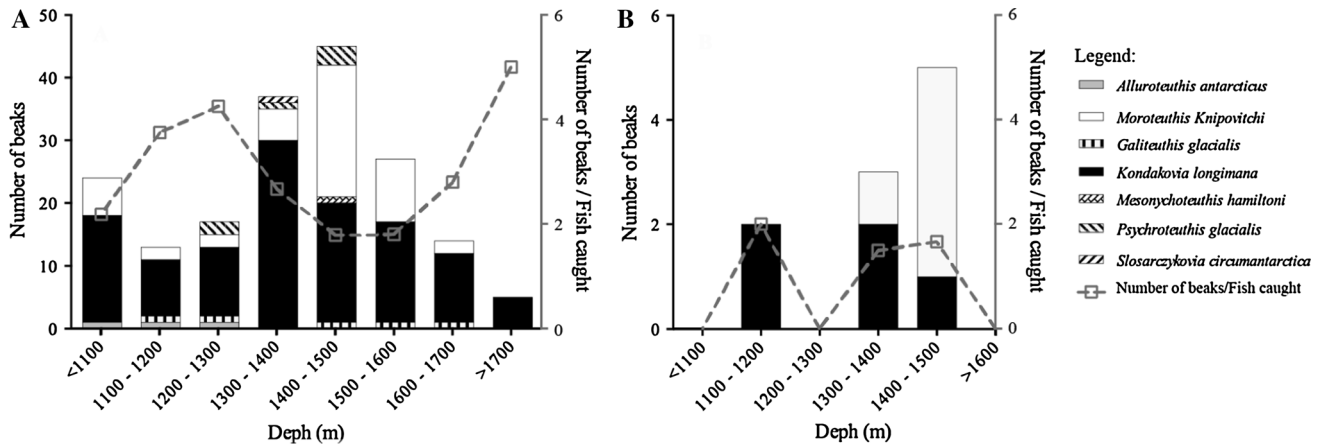


Fig. 2 Number of cephalopods beaks found and catch per unit effort (number of beak divided by the number of fish caught) according to the depth where *Dissostichus mawsoni* (a) and *Dissostichus*

eleginoides (b) were caught around South Sandwich Islands between March and April 2009

Table 3 Species, frequency of occurrence, number and mass of cephalopods identified from *Dissostichus eleginoides* diet caught around South Sandwich Islands between March and April 2009

Taxa	Frequency	%	Number lower beaks	%	Estimated mass (g)	%
<i>Kondakovia longimana</i>	4	52	5	45.5	30,788.4	89.29
<i>Moroteuthis knipovitchi</i>	4	52	5	45.5	3505.2	10.27
<i>Taonius</i> sp. (Voss)	1	13	1	9	186.4	0.53
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				13		

Table 4 Lower rostral length (LRL) measurements and mantle length (ML) and mass estimations of cephalopods identified in *Dissostichus eleginoides* diet

Taxa	Number lower beaks	LRL				Estimated ML				Estimated Mass			
		Mean	Min	Max	SD	Mean	Min	Max	SD	Mean	Min	Max	SD
<i>Kondakovia longimana</i>	5	14.50	9.90	18.20	3.33	575.98	372.48	739.67	147.52	6157.69	568.43	13,814.16	5632.22
<i>Moroteuthis knipovitchi</i>	5	6.58	5.70	7.30	0.58	324.47	231.81	400.29	61.13	701.05	413.08	981.97	205.18
<i>Taonius</i> sp. B (Voss)	1	7.60	7.60	7.60		454.57	454.57	454.57		186.35	186.35	186.35	

no significant differences in the beaks LRL and the depth ranges (Kruskal–Wallis; $H = 8.16$; $p = 0.3$).

Cephalopods beaks were found in all locations where fish were captured and may have greatest frequency of occurrence in south-eastern areas of the South Sandwich Islands (Roberts et al. 2011). There was no evidence for an effect of the capture location on the frequency of occurrence of the main cephalopod prey.

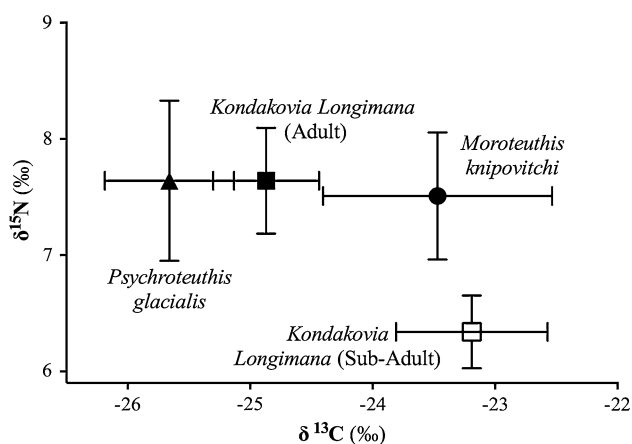
Habitat and trophic level of Antarctic cephalopods according to stable isotope signatures

Only 31 beaks of the main caught cephalopod species (*K. longimana*, *M. knipovitchi*, *P. glacialis*) were analysed (Table 5).

There was a clear delineation of adults and sub-adult from *K. longimana* based on $\delta^{15}N$ (a proxy for their trophic

Table 5 Lower rostral length (LRL) measurements and the isotopic signature of cephalopod beaks from main cephalopod species found in the diet of *Dissostichus mawsoni* caught around South Sandwich Islands between March and April 2009

Taxa	Number lower beaks	LRL				$\delta^{13}\text{C}$				$\delta^{15}\text{N}$			
		Mean	Min	Max	SD	Mean	Min	Max	SD	Mean	Min	Max	SD
<i>Kondakovia longimana</i> (Adult)	10	17.38	15.8	19.1	0.99	-24.87	-25.45	-24.3	0.43	7.64	6.78	8.25	0.46
<i>Kondakovia longimana</i> (Sub-adult)	5	8.66	7.7	9.8	0.83	-23.19	-23.79	-22.5	0.62	6.34	5.88	6.67	0.31
<i>Moroteuthis knipovitchi</i>	10	6.2	5.6	6.7	0.52	-23.47	-24.95	-21.97	0.94	7.51	6.58	8.83	0.55
<i>Psychroteuthis glacialis</i>	6	7	6.1	7.6	0.52	-25.66	-26.42	-25.31	0.53	7.64	6.11	8.15	0.69

**Fig. 3** $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures from mandibles for main cephalopod species found in the diet of *Dissostichus mawsoni* caught around South Sandwich Islands between March and April 2009 (Mean \pm SD)

level): $\delta^{15}\text{N}$ of sub-adult beaks ranged from 5.88 to 6.77 ‰, compared with 6.11 to 8.33 ‰ for adults (ANOVA $F_{3, 28} = 8.55$; $p < 0.01$; Fig. 3).

The more negative value of $\delta^{13}\text{C}$ indicates that *K. longimana* (adult) and *P. glacialis* occupy further south habitat than *M. knipovitchi* and sub-adult *K. longimana* (ANOVA; $F_{3, 28} = 20.22$; $p < 0.01$; Fig. 3; Table 5).

Discussion

Regional variation in cephalopod prey of toothfish species

The cephalopod component of diet of *D. mawsoni* and *D. eleginoides* is typically quite different though was quite similar around South Sandwich Islands. All cephalopod species found in this study had been previously recorded in the diet of at least one toothfish species (Xavier et al. 2002; Cherel et al. 2004; Xavier and Cherel 2009; Stevens et al. 2012). *D. eleginoides* from the Argentinian shelf prey on *Semirossia tenera*, *Illex argentinus*, *Loligo gahi* and

Octopus tehuelchus (Garcia de la Rosa et al. 1997). None of these species were observed in our study and may not be present at the South Sandwich Islands, though *I. argentinus* may also occur in colder waters (Xavier et al. 2006). Around the sub-Antarctic islands of Kerguelen and Crozet, *K. longimana*, *Moroteuthis ingens* and *G. antarcticus* were the most important cephalopods in terms of reconstituted mass (Cherel et al. 2004)—the latter two species did not occur in our study, probably due to a preference for warmer waters (Anderson and Rodhouse 2002; Nesis 1987; Rodhouse 1989). *G. antarcticus* was reported in the diet of *D. eleginoides* around South Georgia (Xavier et al. 2002), indicating that the distribution of this species is limited to the northern islands of the Scotia Arc (Ward et al. 2012). Even so, despite the hydrographical segregation of the Scotia Sea, the cephalopod component in the diet of *D. eleginoides* found in South Georgia is relatively similar to that of the South Sandwich Islands population, for which *K. longimana* and *M. knipovitchi* were also the most important species by estimated mass (76.1 % *M* and 10.7 % *M*, respectively; Xavier et al. 2002).

In the Ross Sea, just two cephalopod species—*K. longimana* and *P. glacialis*—were found in *D. mawsoni* stomachs, the latter comprising the greatest estimated mass (29.6 % *M*; Stevens 2012). The dominance of *P. glacialis* could be due to 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 populations 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 those species that are locally abundant and available.

Vertical/horizontal distribution of Antarctic cephalopods

There is considerable potential in the use of top predators to better describe the spatial distributions of cephalopod species that are not yet commercially exploited (Rodhouse

et al. 1996); the toothfish are ones of few that can give information about the vertical distribution.

Cephalopod beaks were found in the diets of toothfish at all depths sampled (917–1720 m) with most present in fish caught between 1300 and 1600 m and the highest value of catch per unit of effort from 1100 to 1300 m. This observation conforms with the present assumption that most Antarctic cephalopod species are confined to continental slope habitats and the mesopelagic/bathypelagic zones (Croxford and Prince 1994; Kock 1987). *K. longimana* and *M. knipovitchi*—the most important cephalopod prey in this study—were mainly found between 1300 at 1600 m, contrary to previous studies conducted at South Georgia where they were only found between depths of 300–900 m (Xavier et al. 2002; Collins et al. 2004). Therefore, the vertical distributions of *K. longimana* and *M. knipovitchi* vary between bathyal and mesopelagic zones in the Scotia Sea, potentially with changes in ocean temperature. *Galiteuthis glacialis* (110–1700 m) and *P. glacialis* (1200–1400 m) were also found in deeper water when compared with the South Georgia study [600–900 and 300–1200 m in Xavier et al. (2002), respectively]. These results show that the South Sandwich Islands cephalopod community inhabits a greater depth than that of South Georgia.

An interesting characteristic of the South Sandwich Islands Arc is the clear spatial segregation of the two *Dissostichus* spp. (Roberts et al. 2011) and also of other fish species and benthic invertebrate communities (Roberts 2012). The north to south gradient in temperature at bathyal depths is likely to be a key driver of this bioregionalisation (Roberts 2012), though does not appear to be a barrier to the dispersal of key cephalopod prey of toothfish species in this study. Here, we found that the main cephalopod prey species of toothfish species were distributed both to the north and south of the Weddell front and the relatively broad niche of these species has been reported previously by (Xavier et al. 1999).

Habitat assessment from cephalopod beaks

In the Southern Ocean, plankton food bases have a well-defined gradient (lower-latitude plankton have higher $\delta^{13}\text{C}$ compared with plankton found on higher-latitude waters) that allows estimating the latitudes which predators forage (Cherel and Hobson 2007; Jaeger et al. 2010).

Based on the ratio of ^{13}C isotopic signatures of cephalopod beaks found in the stomachs of *D. mawsoni* and comparing with $\delta^{13}\text{C}$ reference values from the particulate organic matter (POM) caught in the Scotia Sea [were $\delta^{13}\text{C} < -20.2\text{‰}$ are associated to Antarctic waters (Stowasser et al. 2012)], all three species analysed (*K. longimana*, *M. knipovitchi* and *P. glacialis*) had $\delta^{13}\text{C}$ lower than -22‰ , so we can infer that they mainly inhabit

Antarctic waters. However, differences between species indicate that they may forage in different areas. There is a clear segregation between sub-adults and adults of *K. longimana*, suggesting that younger individuals of the South Sandwich Islands population inhabit more northerly regions with a southward redistribution occurring as they increase in size.

In previous studies, $\delta^{13}\text{C}$ values of *K. longimana* and *M. knipovitchi* were relatively enriched when compared with the present study (Alvito et al. 2014; Anderson et al. 2009). The higher-latitude location of the South Sandwich Islands arc may explain this difference in $\delta^{13}\text{C}$.

Trophic assessment of cephalopods beaks

We found that a clear segregation between the ^{15}N signatures of sub-adults and adults of *K. longimana* may suggest an ontogenetic dietary shift in this species (Cherel and Hobson 2005). Though as the $\delta^{13}\text{C}$ between adults and sub-adults are different, the $\delta^{15}\text{N}$ of primary producers from the foraging areas may be different; thus, the $\delta^{15}\text{N}$ of cephalopods will be different. Other possible explanations for the ^{15}N enrichment can on one hand be attributed to changes in prey type or size with increasing body size (Jennings et al. 2002). So the increase in $\delta^{15}\text{N}$ could be indicative that larger adults feed at higher trophic level than the smaller sub-adults. Habitat use can also be a reason for this difference of the $\delta^{15}\text{N}$ (Genner et al. 2003).

The values of $\delta^{13}\text{C}$ from sub-adults of *K. longimana* and adults of *M. knipovitchi* are very similar, though the $\delta^{15}\text{N}$ values for these two species are significantly different, this could be due to ontogenetic shift in feeding but could also be related with changes in prey type or size (Jennings et al. 2002). We can deduce that they occupy similar habitat though they have a different trophic ecology.

Cephalopods caught around South Georgia had $\delta^{15}\text{N}$ values relatively higher than cephalopods around South Sandwich Islands ([$\delta^{15}\text{N}$ of *K. longimana* and *M. knipovitchi* caught by black-browed albatrosses were 8.00 ± 0.82 and $8.82 \pm 0.76\text{‰}$, respectively]) (Alvito et al. 2014). The difference between studies indicates strong location effects on food web structure or in intake of ^{15}N .

Final remarks

This study confirms the importance of cephalopods in the Antarctic food web, though we still know very little about their ecology and distribution. Due to a high degree of trophic plasticity and typical low rates of spatial dispersion, *D. eleginoides* and *D. mawsoni* are two species that show great potential as biological samplers of bathyal cephalopod species across the South Ocean. The isotopic analysis indicated that habitat types of different cephalopod species

vary along the Scotia Arc, maybe due to variation in hydrographic conditions. Stable isotopes also indicate possible ontogenetic shifts in diet of cephalopods.

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