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Diet of Antarctic toothfish (*Dissostichus mawsoni*) from the continental slope and oceanic features of the Ross Sea region, Antarctica

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Abstract: The diet of *Dissostichus mawsoni* captured by bottom longline in the Ross Sea region was examined during 2003, 2005 and 2010. The diet of sub-adult toothfish was similar to adult toothfish, comprising mainly benthic fishes and cephalopods. Sub-adult toothfish ate a greater variety of smaller prey than adults, including smaller fish and prawns. Grenadiers (*Macrourus* spp.) were the most important fish and overall prey species. On the continental slope, icefish (Channichthyidae) and eel cods (Muraenolepididae) were also important fish prey, while *Psychroteuthis glacialis* was the most important cephalopod prey. On oceanic features, toothfish fed mainly on *Macrourus* spp. but also fed on *Antimora rostrata*, cephalopods and the occasional mesopelagic to epipelagic fish. Diet varied significantly with toothfish size and location on northern parts of the Mawson and Iselin banks of the Ross Sea continental slope. There was no significant temporal change in diet composition.

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Key words: feeding selectivity, trophic relationships

Introduction

The genus *Dissostichus* (Nototheniidae) comprises two commercially important fishes: the Patagonian toothfish, *D. eleginoides* Smitt, which is found throughout much of the Southern Ocean, and the Antarctic toothfish, *D. mawsoni* Norman, which is found in the sub-zero waters south of the Antarctic Polar Front. *Dissostichus mawsoni* supports a longline fishery in the Ross Sea, which is managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) as an exploratory fishery. This status requires that the fishery has a precautionary catch limit, set at a level that is not substantially above that necessary to obtain information on the biology and potential yield of the target species, the potential impacts on dependent and related species, and to allow guidance on harvest levels to be set (CCAMLR 2012). Research to address the potential impact of the fishery on dependent and related species has included a programme to determine and monitor the diet of *D. mawsoni*.

A number of publications have examined the diet of *D. eleginoides* (e.g. Pilling *et al.* 2001, Goldsworthy *et al.* 2002, Arkhipkin *et al.* 2003), but the diet of *D. mawsoni* is less well studied. Previous studies of *D. mawsoni* include the opportunistic examination of fish preyed on by Weddell seals (Wohlschlag 1968, Calhaem & Christoffel 1969) and sperm whales (Yukov 1971), and some specific feeding studies (Eastman 1985a, 1985b, Gröhsler 1992, Pakhomov & Tseytlin 1992, Takahashi & Iwami 1997, Fenaughty *et al.* 2003, Kokorin 2010, Petrov & Tatarnikov 2011, Roberts *et al.* 2011). Prior to Fenaughty *et al.* (2003), all *D. mawsoni* diet studies were based on fewer than 60 fish.

Fenaughty *et al.* (2003) studied the stomach contents of 9363 *D. mawsoni* from the western Ross Sea over two summers. Only the frequency of prey occurrence was recorded as the examinations took place aboard a commercial fishing vessel where facilities were limited. Furthermore, due to the advanced digestion of many prey, the identification to genus or species level was difficult and most prey were only identified to high taxa. Therefore, the study provided important, but preliminary, information on the diet of *D. mawsoni*. The main prey were finfish, with icefish (Channichthyidae) and grenadiers being the most commonly identified; some squid and prawns were also common, along with rocks and bait (Fenaughty *et al.* 2003).

Kokorin (2010) studied the stomach contents of 2058 *D. mawsoni* from the Ross and Amundsen seas. The main prey in 1336 Ross Sea toothfish was finfish (predominantly *Macrourus whitsoni* (Regan), *Muraenolepis* spp., *Chionobathyscus dewitti* Andriashev and Neelov, and *Trematomus* spp.).

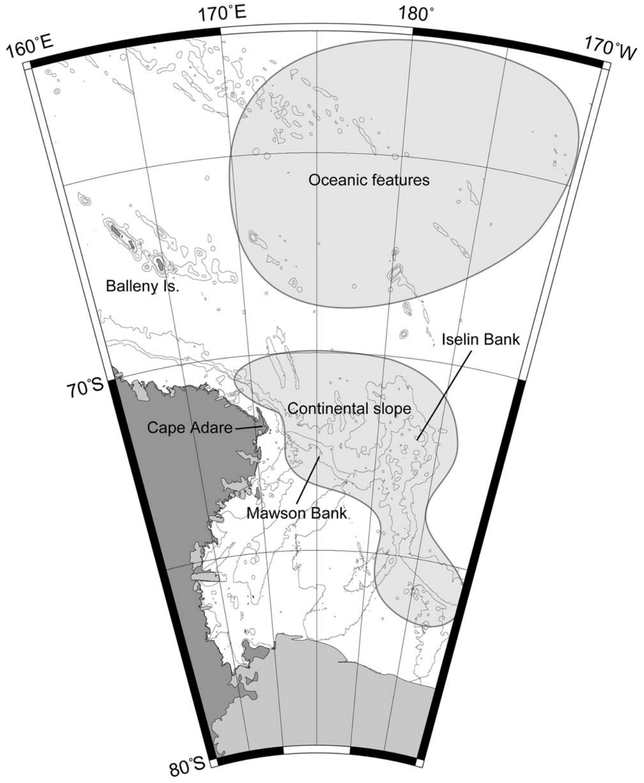

Fig. 1. Locality map showing the general position of non-empty stomach samples. Lines indicate the 500 m, 1000 m and 2000 m isobaths.

Petrov & Tatarnikov (2011) studied the stomach contents of *D. mawsoni* from the Lazarev Sea. By frequency of occurrence and weight, the main prey were finfish (predominantly *C. dewitti* and *Macrourus whitsoni*) and cephalopods (predominantly *Mesonychoteuthis hamiltoni* Robson and *Kondakovia longimana* Filippova).

Roberts *et al.* (2011) studied the stomach contents of *D. eleginoides* and *D. mawsoni* around the South Sandwich Islands, one of the few areas where the species co-exist. Despite large differences in the number of stomachs containing prey, the diets were broadly similar, with $>90\%$ of the prey mass comprising finfish (mainly grenadiers and eel cods) and cephalopods (mainly *K. longimana*).

In this study we describe the diet of *D. mawsoni* in the Ross Sea region using stomach contents. Our study had three specific aims: i) to determine whether the diet composition of toothfish varied between sub-adults and adults from the continental slope, ii) to determine whether the diet composition of adult toothfish varied between the continental slope and oceanic features to the north and iii) to determine whether there was significant variability in diet composition of adult toothfish from within a relatively well-sampled area of the continental slope.

Materials and methods

Stomach samples

Stomach samples from toothfish were obtained during voyages of commercial longliners fishing under exploratory permits in the western Ross Sea (CCAMLR subarea 88.1) (Fig. 1) during the 2003, 2005 and 2010 summer seasons. 'Season' refers to the period December–May, the main fishing period in the middle of the CCAMLR fishing year (e.g. 2010 refers to the 2009–10 fishing year).

Toothfish were caught by bottom longline at depths from 770–1890 m, using size 13–15 autoline hooks baited with jack mackerel (*Trachurus* spp.), arrow squid (*Nototodarus* spp.), blue mackerel (*Scomber australasicus* Cuvier) and barracouta (*Thyrsites atun* (Euphrasén)). Biological data (total length (TL), total weight, sex and macroscopic gonad stage) and stomachs were collected from toothfish by scientific observers (CCAMLR and New Zealand Ministry for Primary Industries) and Sanford Ltd company liaison Jack Fenaughty. In the laboratory each stomach was examined and graded on a qualitative scale according to its fullness as empty, trace, part full or full. Individual food items were identified to the lowest possible taxonomic level, counted and weighed. The state of prey digestion was recorded qualitatively as fresh, slightly digested, moderately digested or digested. Fish prey were identified using Gon & Heemstra (1990) and the otolith descriptions of Williams & McEldowney (1991). Cephalopod prey were identified using the cephalopod beak descriptions of Clarke (1986). Otoliths and beaks from reference collections were used to aid identification.

The unidentifiable prey, prey classified as digested and parasites, including gnathiid isopods, sphyrion copepods, anisakid nematodes and leeches, were excluded from detailed diet analyses. Small scavenging cirolanid isopods (*Natatolana* spp.) and lysianassid amphipods (*Orchomenella* spp.) were considered to be incidental prey ingested along with large prey and were also excluded from detailed diet analyses.

Analysis of diet composition

The data were too confounded to allow a single analysis of diet composition and variability across all fish sizes and areas. Therefore, three diet composition analyses were completed. First, the composition of the diet was compared between adult and sub-adult toothfish on the continental slope. Adult toothfish were assumed to be those ≥110 cm TL (Parker & Grimes 2009). Second, the composition of the diet of adult toothfish was compared between the continental slope and oceanic features of elevated topography to the north, such as ridges, hills and seamounts. Allocation of samples to slope or oceanic features was achieved by dividing the study area at 70°S, with oceanic features only fished to the north. Third, diet variability was examined for adult toothfish on the continental slope between 174°E–176°W and 70–73.5°S, where the majority of the stomach samples were obtained (Fig. 1).

The composition of the diet was described by the numerical importance (%N), frequency of occurrence (%F), weight (%W) and percentage index of relative importance (%IRI) (Pinkas *et al.* 1971). Bootstrap methods consisting of 1000 replicates of random samples with replacement from the original dataset, stratified by tow, were used to estimate 95% confidence intervals around the dietary statistics (Tirasin & Jørgensen 1999).

To conduct analyses of diet variability, the prey items were aggregated into taxonomic categories. To assess the adequacy of the samples, the cumulative diversity (Brillouin index of diversity, H) of categorized stomach contents was plotted against the cumulative number of stomachs containing food. The mean cumulative curve, and 95% credible intervals describing the shape of the curve, were calculated from 1000 curves based upon different random orders of the stomachs. The total sample was considered adequate once the mean sample diversity (H) was $\geq$95% of the asymptotic diversity (HA), estimated from a fitted curve of the form $H = aN(1 + bN)^{-1}$ (Dunn 2009). The asymptotic curves were also fitted to subsets of the data, for each subset the sample prey diversity was expressed as a percentage of the estimated asymptote.

Multivariate statistical analyses were used to determine which factors were influencing the diet composition of toothfish from the continental slope. Distance-based linear model (DistLM) analysis in PRIMER v6 (Clarke & Warwick 2006, Anderson *et al.* 2008) was used to identify which of nine biological, environmental and temporal predictors explained a significant proportion of the variability in diet composition. The weight of prey observed in each toothfish was first standardized, then square-root transformed and a dissimilarity matrix calculated using Bray-Curtis distances. The predictors investigated were biological (TL, sex and weight), temporal (season of sampling, i.e. summer between October–March, and month), spatial (latitude, longitude and a spatial model) and depth. Latitude and longitude were tested in addition to the spatial model because there were a priori hypotheses that diet might change with these predictors. The spatial model was a cubic trend surface, which allowed for more complex features such as gaps and patches (Legendre 1990, Borcard *et al.* 1992). To estimate the spatial model, the variables for longitude (x) and latitude (y) were first centred on their means, and then terms for a cubic trend surface regression were tested, i.e. x, y, x^2, y^2, x^3, y^3, xy, x^2y and xy^2. The spatial terms included were selected by sequential testing using the stepwise DistLM procedure and the Akaike Information Criterion (AIC) (Anderson *et al.* 2008), and the selected terms then included in subsequent tests as the 'spatial model'. The depth predictor was treated as independent because it was both a component of space (i.e. xyz) and also aliased for environmental conditions (i.e. light, temperature and pressure). The results of the subsequent DistLM analyses were conditional tests, fitting each predictor conditional on all other predictors already being in the model. This effectively tests the null hypotheses that each predictor has no effect after the effect of the other predictors has been removed, thereby attempting to control for potentially confounded sampling designs (Borcard *et al.* 1992, Anderson & Gribble 1998). When TL was tested weight was excluded from the conditional terms, and similarly when the spatial model was tested latitude and longitude were excluded (and vice versa).

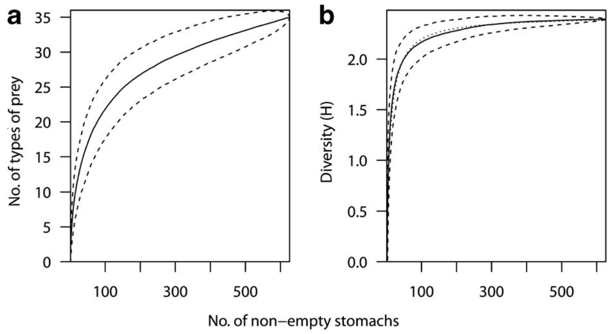

Fig. 2. a. The mean cumulative number of prey types identified. **b.** The mean cumulative diversity of prey categories (measured using the Brillouin index of diversity, H). Dashed lines indicate 95% credible intervals. Dotted line in b. is a fitted curve from which asymptotic diversity was estimated.

The variability in diet composition for toothfish on the continental slope was examined only for the predictors that were significant ($P \leq 0.05$) in the conditional DistLM tests. The spatial model allowed complex spatial variability. The diet (standardized prey weight) was examined by first objectively grouping samples with similar diets using hierarchical agglomerative clustering (Clarke & Warwick 2006, Forman & Dunn 2012), using a dissimilarity matrix calculated using Bray-Curtis distances and cluster analysis performed using the average linkage method. Groups (clusters) were significant (at the 1% level) using the PRIMER permutation test SIMPROF (Clarke & Warwick 2006), and had a sample size greater than 20 stomachs. Samples not included in the significant groups were considered to be 'outliers'. The sample statistics for the significant predictors, the spatial distribution (if selected) and the diet composition were then examined for each significant group. Prey types characteristic of the diet composition of each group were identified using SIMPER (similarity percentages; Clarke & Warwick 2006). The actual mean percentage weight of the prey groups identified by SIMPER was then calculated to show the main differences in diet composition between groups. The locations of samples in each significant group were

Table I. Comparison of the percentage by weight (%W) and percentage by Index of Relative Importance (%IRI) of prey items in the diet of sub-adult *Dissostichus mawsoni* sampled from oceanic features and the continental slope in the western Ross Sea during 2003, 2005 and 2010. The 95% confidence intervals estimated by bootstrap resampling are given in brackets.

		2003		2005		2010	
		%W	%IRI	%W	%IRI	%W	%IRI
Coelenterata							
Coral		0.01 (0.0–0.1)	6.4 (0.0–4.2)	0.01 (0.0–0.0)	0.01 (0.0–0.1)		
Crustacea							
Decapoda							
Nematocarcinidae	*Nematocarcinus* spp.	2.2 (0.0–7.5)	10.0 (0.0–33.4)	0.2 (0–0.6)	0.9 (0.1–3.5)	0.3 (0.0–0.9)	1.8 (0.0–7.2)
Amphipoda				0.01 (0.0–0.0)	0.1 (0.0–0.4)		
Isopoda		0.4 (0.0–1.5)	0.8 (0.0–8.7)				
Mollusca							
Cephalopoda							
Teuthoidea							
Onychoteuthidae	*Kondakovia longimana*			1.2 (0.0–4.6)	0.02 (0.0–0.3)		
Psychroteuthidae	*Psychroteuthis glacialis*	0.2 (0.0–1.2)	1.6 (0.0–10.3)	19.5 (9.6–34.5)	42.8 (20.4–65.3)	27.7 (2.9–56.1)	35.2 (4.9–72.0)
Octopoda							
Octopodidae				0.1 (0.0–0.4)	0.02 (0.0–0.1)	0.01 (0.0–0.1)	0.2 (0.0–1.9)
Opisthoteuthidae	*Cirroctopus* sp.	0.03 (0.0–0.1)	0.4 (0.0–3.6)				
Echinodermata				0.02 (0.0–0.1)	0.2 (0.0–1.2)		
Pisces							
Osteichthyes							
Paralepididae	*Notolepis coatsi*			0.06 (0.0–0.3)	0.01 (0.0–0.1)		
Muraenolepididae	*Muraenolepis* spp.	12.8 (0.0–38.4)	9.2 (0.0–39.9)	5.4 (1.5–12.2)	2.8 (0.4–10.6)	4.9 (0.1–14.1)	4.7 (0.2–19.9)
Macrouridae	*Macrourus* spp.	28.4 (4.8–60.4)	28.6 (1.3–71.3)	16.2 (5.5–28.0)	9.7 (2.4–20.5)	17.9 (1.1–22.3)	8.5 (0.4–28.0)
Oneirodidae	*Oneirodes notius*			0.3 (0.0–1.5)	0.01 (0.0–0.2)		
Zoarcidae				0.5 (0.0–2.2)	0.2 (0.0–0.4)		
Nototheniidae		7.8 (0.0–23.5)	6.2 (0.0–29.4)	14.6 (7.2–26.1)	14.7 (5.2–29.7)	1.9 (0.0–6.3)	1.1 (0.0–8.0)
Liparidae		7.3 (0.0–26.5)	1.3 (0.0–16.9)	1.0 (0.0–3.3)	0.05 (0.0–0.4)		
Artedidraconidae		3.7 (0.0–12.4)	0.8 (0.0–8.0)	0.7 (0–3.4)	0.01 (0.0–0.4)	7.7 (0.0–25.3)	2.0 (0.0–14.3)
Bathydraconidae				2.1 (0.5–5.7)	1.7 (0.3–5.1)	2.0 (0.0–6.6)	2.2 (0.0–11.9)
Channichthyidae		37.3 (8.6–66.3)	40.8 (3.5–73.1)	38.1 (17.8–53.0)	27.0 (6.9–47.5)	46.3 (14.4–73.1)	44.3 (6.6–76.5)
Fish discards				0.1 (0.0–0.3)	0.01 (0.0–0.1)		
n		20		144		28	
TL (median, min–max)		107 (72–110)		92 (51–110)		99 (78–110)	
Depth (median, min–max)		1171 (971–1613)		1100 (408–1497)		1193 (774–1568)	
% of prey diversity asymptote		55.5		94.3		67.9	

n = number of stomachs containing food, TL = fish total length.

Species authorities: *Kondakovia longimana* Filippova, *Psychroteuthis glacialis* Thiele, *Notolepis coatsi* Dollo, *Oneirodes notius* Pietsch.

Table II. Comparison of the percentage by weight (%W) and percentage by Index of Relative Importance (%IRI) of prey items in the diet of adult *Dissostichus mawsoni* sampled from oceanic features and the continental slope in the western Ross Sea during 2003 and 2010. The subarea of the continental slope lies between 174°E–176°W and 70–73.5°S. The 95% confidence intervals estimated by bootstrap resampling are given in brackets.

		2003 slope		2003 oceanic features		2010 oceanic features		2003 subarea		2010 subarea	
		%W	%IRI	%W	%IRI	%W	%IRI	%W	%IRI	%W	%IRI
Coelenterata											
Jellyfish				0.5 (0–1.3)	0.2 (0–0.9)						
Coral		0.01 (0–0.1)	0.04 (0–0.2)	0.01 (0–0.1)	0.03 (0–0.3)			0.01 (0–0.1)	0.03 (0–0.2)	0.01 (0–0.1)	0.02 (0–0.1)
Sponge		0.01 (0–0.01)	0.01 (0–0.1)								
Crustacea											
Decapoda											
Lithodidae	*Paralomis* spp.			0.3 (0–0.6)	0.2 (0–0.3)	0.1 (0–0.3)	0.1 (0–8.2)				
Nematocarcinidae	*Nematocarcinus* spp.	0.06 (0–0.1)	0.2 (0–0.9)	0.01 (0–0.1)	0.01 (0–0.1)			0.06 (0–0.1)	0.3 (0–1.1)	0.02 (0–0.1)	0.01 (0–1.0)
Amphipoda				0.04 (0–0.2)	0.01 (0–0.1)					0.03 (0–0.1)	0.02 (0–0.1)
Isopoda	*Eurythenes gryllus*									0.01 (0–0)	0.01 (0–0.1)
Mollusca											
Cephalopoda											
Teuthoidea											
Cranchiidae		0.1 (0–0.3)	0.01 (0–0.1)	0.02 (0–0.1)	0.1 (0–0.4)	1.2 (0–6.3)	0.1 (0–14.0)	0.1 (0–0.3)	0.01 (0–0.1)	0.8 (0–2.5)	0.01 (0–0.1)
Onychoteuthidae	*Kondakovia longimana*	6.4 (1.5–12.8)	1.6 (0.2–4.8)	11.3 (1.6–22.4)	10.3 (2.6–24.2)	33.5 (2.3–67.8)	68.1 (2.6–93.6)	7.1 (1.4–14.0)	1.7 (0.2–5.5)	0.8 (0–2.7)	0.03 (0–0.2)
Psychroteuthidae	*Psychroteuthis glacialis*	4.9 (0.6–11.0)	2.2 (0.4–6.4)	0.01 (0–0.1)	0.1 (0–0.4)			5.4 (0.9–12.1)	2.4 (0.4–6.7)	22.2 (2.9–13.3)	17.9 (9.1–27.4)
Octopoda											
Octopodidae		0.3 (0–0.9)	0.1 (0–0.3)	0.4 (0–1.2)	0.1 (0–0.5)			0.1 (0–0.4)	0.01 (0–0.1)	1.5 (0.1–3.8)	0.1 (0–0.6)
Opisthoteuthidae	*Cirroctopus* sp.	1.1 (0–3.1)	0.3 (0–1.0)	1.0 (0–3.7)	0.1 (0–0.5)			1.1 (0–3.4)	0.2 (0–1.3)	1.0 (0.1–2.4)	0.1 (0–0.5)
Stauroteuthidae	*Stauroteuthis gilchristi*			0.3 (0–0.8)	0.1 (0–0.5)	7.5 (0–27.3)	5.0 (0–34.8)				
Chordata											
Ascidacea		0.01 (0–0.1)	0.01 (0–0.1)					0.01 (0–0.1)	0.01 (0–0.1)		
Echinodermata											
Ophuiroidea		0.1 (0–0.1)	0.2 (0–1.0)	0.02 (0–0.1)	0.1 (0–0.4)			0.2 (0–0.7)	0.1 (0–1.3)	0.01 (0–0.1)	0.01 (0–0.1)
Holothuroidea				0.3 (0–1.0)	0.01 (0–0.1)						
Bryozoa						0.2 (0–0.3)	0.8 (0–8.3)				
Chondrichthyes											
Rajidae	*Amblyraja georgiana*	0.2 (0–0.6)	0.01 (0–0.1)					0.2 (0–0.8)	0.01 (0–0.1)	1.6 (0.2–3.6)	0.2 (0–0.8)
Pisces											
Osteichthyes											
Paralepididae	*Notolepis coatsi*	0.4 (0–1.7)	0.1 (0–0.4)	0.3 (0–1.1)	0.2 (0–1.2)			0.5 (0–1.9)	0.1 (0–0.6)	0.1 (0–0.2)	0.04 (0–0.2)
Anotopteridae	*Anotopterus pharao*			1.2 (0–3.1)	0.2 (0–1.2)						
Myctophidae	*Gymnoscopelus* sp.			0.2 (0–0.5)	0.04 (0–0.2)						
Muraenolepididae	*Muraenolepis* spp.	11.8 (5.6–19.0)	11.3 (3.9–22.5)	1.2 (0–2.9)	0.6 (0.1–2.2)			12.4 (5.8–20.5)	12.5 (3.9–25.7)	13.1 (5.9–21.3)	8.4 (2.6–18.0)
Moridae	*Antimora rostrata*	3.2 (0–9.1)	0.2 (0–1.1)	42.9 (26.8–56.7)	23.0 (9.1–41.7)	28.8 (0–61.0)	18.3 (0–68.1)	3.5 (0–11.1)	0.2 (0–1.5)	0.2 (0–0.5)	0.01 (0–0.1)
Macrouridae	*Macrourus* spp.	39.9 (28.4–51.3)	40.1 (22.4–56.7)	38.5 (25.8–53.0)	64.6 (43.1–80.4)	8.3 (0–30.3)	1.9 (0–26.1)	38.6 (25.3–50.2)	41.0 (20.8–57.7)	47.0 (34.0–58.4)	53.4 (35.4–68.6)
Carapidae	*Echiodon* sp.			0.01 (0–0.1)	0.01 (0–0.1)						
Melanocetidae	*Melanocetus rossi*									0.2 (0–0.6)	0.01 (0–0.1)
Zoarcidae		0.4 (0–0.6)	0.1 (0–0.7)					0.3 (0–0.7)	0.1 (0–0.6)	0.02 (0–0.1)	0.01 (0–0.1)
Nototheniidae		2.9 (1.2–5.1)	2.1 (0.5–4.9)					2.8 (1.2–5.2)	1.9 (0.4–5.0)	2.1 (0.8–3.8)	0.9 (0.1–2.0)
Centrolophidae	*Icichthys australis*					19.6 (0–54.1)	3.4 (0–38.5)				
Liparidae		0.1 (0–0.4)	0.02 (0–0.1)					0.1 (0–0.4)	0.02 (0–0.2)		
Artedidraconidae		0.3 (0–1.2)	0.01 (0–0.1)							1.1 (0.2–2.7)	0.2 (0–0.7)
Bathydraconidae		0.4 (0–0.9)	0.1 (0–0.6)					0.4 (0–1.0)	0.1 (0–0.6)	0.2 (0–0.5)	0.03 (0–0.2)
Channichthyidae		27.3 (18.2–37.3)	41.2 (23.7–59.1)	1.0 (0–3.5)	0.3 (0–1.4)	0.9 (0–4.2)	0.9 (0–13.9)	26.6 (17.3–37.3)	39.1 (21.1–57.9)	23.1 (13.7–34.4)	18.6 (8.4–33.6)

Table II. Continued

	2003 slope		2003 oceanic features		2010 oceanic features		2003 subarea		2010 subarea	
	%W	%IRI	%W	%IRI	%W	%IRI	%W	%IRI	%W	%IRI
Fish discards	0.7 (0–2.2)	0.05 (0–0.4)	1.3 (0–4.6)	0.03 (0–0.3)			0.8 (0–2.5)	0.1 (0–0.5)		
n	162		115		16		143		133	
TL (median, min–max)	140 (111–176)		148 (122–212)		150 (128–162)		140 (111–176)		141 (111–181)	
Depth (median, min–max)	1229 (857–1670)		1376 (1013–1715)		1587 (1268–1883)		1250 (857–1670)		1062 (748–2127)	
% of prey diversity asymptote	96.3		90.8		14.1		95.9		95.3	

n = number of stomachs containing food, TL = fish total length.

Species authorities: *Eurythenes gryllus* (Lichtenstein), *Kondakovia longimana* Filippova, *Psychroteuthis glacialis* Thiele, *Stauroteuthis gilchristi* (Robson), *Amblyraja georgiana* (Norman), *Notolepis coatsi* Dollo, *Anotopterus pharao* Zugmayer, *Antimora rostrata* (Günther), *Melanocetus rossi* Balushkin & Fedorov, *Icichthys australis* Haedrich.

Table III. Results of the DistLM analysis conditional tests using the subset from the continental slope, adults only, all stomachs containing prey ($n = 275$).

Predictor	df	P	r^2
Total length	2	0.001	0.018
Weight	2	0.002	0.015
Sex	3	0.868	0.001
Season	2	0.162	0.001
Month	4	0.359	0.011
Depth	2	0.015	0.010
Latitude	2	0.001	0.022
Longitude	2	0.011	0.012
Spatial model	5	0.001	0.055

examined but have not been included because the catch location information was considered commercially sensitive.

Results

Overall sample

Of 1022 stomachs examined, 9.8% were empty, 57.0% were part full and 7.6% were full. Between 1–17 prey items were identified per stomach, with most stomachs (75.4%) containing only a single prey item and 95.4% containing fewer than five prey items. There were 296 stomachs containing only well digested or unidentifiable prey (29.0%), leaving 626 (61.2%) for detailed analyses of diet composition. Of these, 454 stomachs were from fish caught on the continental slope between 174°E–176°W and 70–73.5°S. New types of prey continued to be identified with increasing sample size of non-empty stomachs. However, the diversity of prey categories reached 75% of the estimated asymptote after 28 stomachs, 90% after 94 stomachs and 95% after 198 stomachs (Fig. 2), indicating that the overall sample was large enough to describe the diversity of the diet.

Comparison of sub-adult and adult diet

Icefish (probably mainly *C. dewitti*) and *Macrourus* grenadiers were important prey in both sub-adult and adult toothfish. However, grenadiers were more important by %W and %IRI in adult fish (Tables I and II). Sub-adult toothfish ate smaller prey than adults, with smaller taxa such as *Trematomus* spp., dragonfish (mainly *Bathydraco* spp.) and *Nematocarcinus* sp. prawns being more important in the diet. Large onychoteuthid squid (*K. longimana*) were rarely eaten by sub-adults but smaller glacial squid (*Psychroteuthis glacialis* Thiele) were eaten more frequently.

Comparison of adult diet on continental slope and oceanic features

On the continental slope, icefish (mainly *C. dewitti*) and *Macrourus* spp. (*Macrourus whitsoni* and *Macrourus caml*

Table IV. Mean of standardized percent prey weight within groups A–E using the subset from the continental slope, adults only, all stomachs containing prey ($n = 275$). Prey types shown are those which together contributed at least 95% of the SIMPER within group similarity for one or more groups.

	A	B	C	D	E
n	22	66	31	78	78
%PD	54	88	81	87	92
TL	134 (122–142)	140 (125–153)	138 (130–147)	146 (137–154)	137 (125–146)
Depth	1220 (1168–1354)	1262 (1159–1376)	1093 (986–1210)	1108 (893–1252)	1220 (1159–1310)
Muraenolepididae	1.0	95.1^{c}	0.9	0.2	8.7^{b}
Macrouridae	0.2	0.1	0.5	97.4^{c}	16.6^{b}
Channichthyidae	89.5^{c}	2.3	9.6	0.2	7.0^{a}
Psychroteuthidae	1.0	0.0	88.4^{c}	1.9	0.7
Nototheniidae	0.7	0.9	0.5	0.0	21.8^{b}
Onychoteuthidae	0.7	0.0	0.0	0.0	8.9^{a}
Opisthoteuthidae	0.2	0.1	0.0	0.1	6.6^{a}
Nematocarcinidae	0.1	0.2	0.0	0.0	4.2^{a}

The SIMPER percentage contribution to within group similarity: ^{a} 1–10%, ^{b} 10–50%, ^{c} >50%, no superscript = not identified by SIMPER as characteristic for that group.

n = sample size, %PD = sample total prey diversity as a percentage of the estimated asymptotic prey diversity, TL = mean total length in cm (interquartile range), depth = mean (interquartile range).

McMillan, Iwamoto, Stewart & Smith) were the main prey (Table II). Icefish were smaller but more numerous prey. Eel cods (mainly *Muraenolepis evseenkoi* Balushkin & Prirodina) were the third most important fish prey. Cephalopods were found in *c*. 20% of stomachs and, although relatively large prey, they were often incomplete or in advanced stages of digestion. The most important cephalopod prey were squids, particularly *P. glacialis* and *K. longimana*. The remaining prey species were a variety of small, mainly benthic fish, e.g. *Trematomus* spp., eelpouts (Zoarcidae), dragonfish and small invertebrates (prawns). A number of prey types were only found in toothfish taken from the continental slope (e.g. *Trematomus* spp., eelpouts, dragonfish), while violet cod (*Antimora rostrata* (Günther)) and *K. longimana* were rare in stomachs from the continental slope.

On oceanic features, *Macrourus* spp. were the dominant prey (Table II). Large violet cod (*Antimora rostrata*) were also important prey. The large onychoteuthid squid *K. longimana* was relatively common, but was usually well digested or incomplete, thus contributed less to prey weight. The remaining prey species were a variety of mainly pelagic fishes (e.g. daggertooths (*Anotopterus vorax* (Regan)), barracudinas (*Notolepis coatsi* Dollo) and myctophids) and jellyfish. Prey that was only found in samples from oceanic features included jellyfish, daggertooths, *Paralomis* sp. and *Stauroteuthis gilchristi* (Robson), while icefish and eel cods were rare.

Variability in adult diet composition on the continental slope

In the conditional DistLM tests of diet variability amongst adult toothfish from the subarea of the continental slope, there were significant relationships between diet composition and all predictors except sex, month and season, with the spatial model explaining the most deviance (Table III). The spatial model consisted of the terms $x + x^2 + xy + xy^2$. The overall model explained 14.1% of the variability in diet.

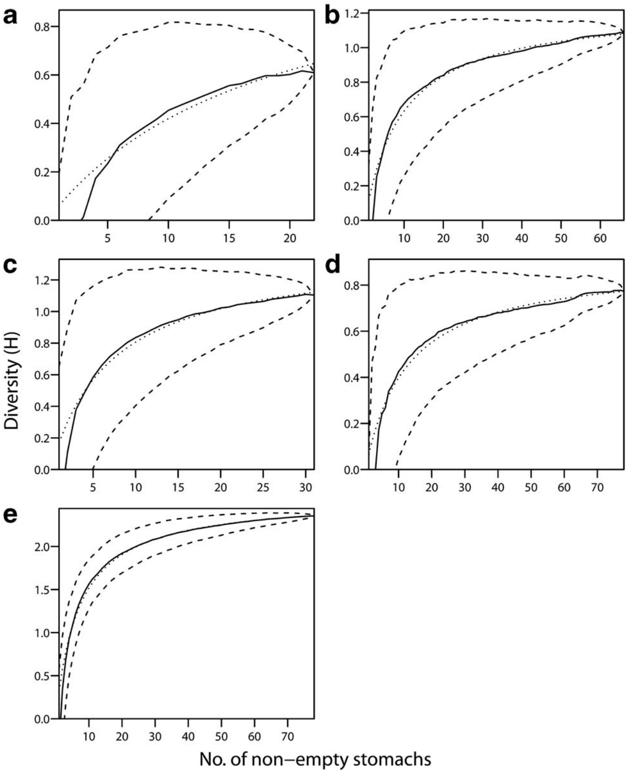

Fig. 3. a.–e. The mean cumulative diversity of prey categories for subgroups A–E (measured using the Brillouin index of diversity, *H*). Dashed lines indicate the 95% credible intervals. Dotted lines indicate the fitted curve from which asymptotic diversity was estimated.

Because the spatial model was the best predictor of spatial variability, the individual latitude and longitude effects were not considered further. Fish TL was preferred over weight because the former explained more deviance. Therefore, diet variability was characterized in terms of TL, depth and the spatial model.

Five sub-groups of toothfish samples with similar diets were identified from cluster analysis. The number of samples in each group was sufficient to explain 81–92% of the estimated asymptotic prey diversity (%PD) in groups B–E, thus provided a near-complete estimate of diet in each group (Table IV). The cumulative diversity curve for group A was visually approaching an asymptote and was similar in shape to groups B–E. However, the relatively low %PD (54%) was considered unreliable because it was estimated from a poor fit of the asymptotic model to the data (Fig. 3).

There was substantial overlap in spatial, depth and TL distributions between the groups, but also some subtle differences. The mean TL in group D was significantly larger than all other groups (*t*-tests, $P \leq 0.01$), with no significant difference between groups A, B, C and E (*t*-tests, $P \geq 0.08$) (Table IV). The mean depths in groups A, B and E were significantly deeper than groups C and D (*t*-tests, $P \leq 0.05$), and were not significantly different from each other (*t*-tests, $P \geq 0.10$). The depths of groups C and D were not significantly different from each other (*t*-test, $P \geq 0.34$) (Table IV).

The diet of the groups from shallower water was characterized by Psychroteuthidae (*P. glacialis*), predominantly in the north-west region of Iselin Bank (group C), or by Macrouridae (*Macrourus caml* and *Macrourus whitsoni*) in virtually all samples taken from the south-east flank of Iselin Bank and in the largest fish throughout the region (group D). The diet of deeper water groups was characterized by Channichthyidae (group A), Muraenolepididae (group B) and a variety of other species (group E) throughout the region. Groups B and E accounted for virtually all samples taken from an area of deeper water to the north of Mawson Bank.

Discussion

The diet of sub-adult toothfish was broadly similar to that of adult toothfish in the Ross Sea continental slope region, comprising mainly benthic fishes and cephalopods. Not surprisingly, sub-adult toothfish ate a greater variety of smaller prey than adults, including smaller fishes (such as *Trematomus* spp. and *Bathydraco* spp.) and prawns (*Nematocarcinus* sp.). Larger toothfish ate a greater proportion of large demersal fishes such as grenadiers (*Macrourus* spp.).

Grenadiers were the most important fish and overall prey species. The grenadiers were often well digested and could usually only be identified as *Macrourus* spp. A few grenadiers were taken from toothfish captured north of 65°S where *Macrourus holotrachys* Günther occurs in small numbers (Marriott *et al*. 2003), but most *Macrourus* prey were probably *Macrourus whitsoni* or *Macrourus caml*. The new cryptic species *Macrourus caml* has only recently been identified (McMillan *et al*. 2012), hence, we did not distinguish between species of *Macrourus* in the present study. *Macrourus whitsoni* and *Macrourus caml* appear to occupy similar depths and be sympatric through the Ross Sea region (Pinkerton *et al*. 2012). Further research is needed to determine the relative proportion of *Macrourus whitsoni* and *Macrourus caml* consumed by toothfish in the Ross Sea region.

Glacial squid (*P. glacialis*) were the most important cephalopod prey and were particularly important in toothfish sampled from the north-west region of the Iselin Bank. Although most *P. glacialis* were incomplete, their lower beaks were generally fully chitinized indicating that they were mature adults. Based on lower rostral length measurements, and using the regression of Gröger *et al*. (2000), the *P. glacialis* eaten by toothfish in this study would have had estimated mantle lengths (ML) of 19–46 cm (mean = 33.4 cm, $n = 117$) (Stevens, unpublished data). Lu & Williams (1994) suggested that *P. glacialis* undergo an ontogenetic descent with larger individuals occurring at greater depth. Their largest specimens were 9.5–20.1 cm ML and were captured in 430–530 m depths. The *P. glacialis* taken from toothfish stomachs in this study were generally much larger than any examined by Lu & Williams (1994) and support an ontogenetic descent with adult *P. glacialis* occurring at much greater depths. The relative importance in the toothfish diet in the north-west region of the Iselin Bank suggest that adult *P. glacialis* may be aggregated in this region.

The large onychoteuthid *K. longimana* was the most abundant cephalopod prey on oceanic features. Most *K. longimana* were incomplete, comprising mainly brachial crowns, occasionally with mantle remnants attached. The beaks varied in the level of chitinization indicating that they were from both immature and mature individuals.

Other cephalopods identified from toothfish stomachs in the Ross Sea region (this study and Stevens, unpublished data) were the squids *Alluroteuthis antarcticus* Odhner, *Bathyteuthis abyssicola* Hoyle, *Filippovia knipovitchi* (Filippova), *Galiteuthis glacialis* Chun and *Mesonychoteuthis hamiltoni*, the incirrate octopi *Benthoctopus* sp., *Megaleledone setebos* (Robson), *Pareledone aequipapillae* Robson, *Pareledone turqueti* (Joubin) and *Thaumeledone* sp., and the cirrate octopi *Cirrata* sp. A (Cherel), *Cirrata* sp. B, *Cirroctopus* sp. and *Stauroteuthis gilchristi*.

Our results support the assumption that *D. mawsoni* is a demersal species. *Macrourus* grenadiers and eel cods (*Muraenolepis* spp.) are important prey for *D. mawsoni* (this study, Fenaughty *et al*. 2003, Kokorin 2010, Roberts *et al*. 2011) and are regarded as benthopelagic in habit (Gon & Heemstra 1990). Preliminary data for *Macrourus* grenadiers from the Ross Sea supports this assumption with benthic and pelagic components to their diet (Pinkerton *et al*. 2012). The icefish *C. dewitti* is regarded as a benthic species, having extensive thickening of the skin on the distal end of the pelvic fins used for resting on the substrate (Kock 2005). However, preliminary diet data supports a benthopelagic habit with mesopelagic prey, such as *Gymnoscopelus* spp. and euphausiids, important (Takahashi & Iwami 1997, Sutton *et al*. 2008, Forman, unpublished data). Therefore, the three key toothfish prey species appear to feed on benthopelagic prey. Large adult *P. glacialis* were also important prey and they are probably also abundant near the bottom as Gröger *et al*. (2000) reported specimens of *P. glacialis* larger than 100 mm ML have only been captured in big bottom and benthopelagic trawls.

The diet of *D. mawsoni* in the Ross Sea region varies between the continental shelf, slope and oceanic features, probably reflecting latitudinal differences in habitat and species assemblages. In McMurdo Sound, under shore fast ice and heavy pack ice, *D. mawsoni* feeds mainly on fish, in particular *Pleuragramma antarctica* (Calhaem & Christoffel 1969, Eastman 1985a, 1985b). Preliminary data from the wider Ross Sea continental shelf suggests a more varied diet including small notothens and icefish (unpublished data). In deeper waters, largely over the continental slope, icefish, *Macrourus* grenadiers and eel cods comprise most of the diet (Fenaughty *et al*. 2003, Kokorin 2010, this study). In open oceanic waters, squid may dominate the diet (Yukhov, 1971).

We found substantial differences in toothfish diet in the offshore oceanic features versus continental slope habitats, although grenadiers were important in the diet in both regions. On the continental slope, the wide variety of benthic fish prey, and the presence of stones, ophiuroids and small coral fragments (probably accidentally ingested), indicate benthic foraging. On oceanic features, the prey included *Antimora rostrata*, cephalopods and the occasional mesopelagic to epipelagic fish and jellyfish. These differences probably reflect changes in assemblage of potential prey between the continental slope and oceanic features. It has been suggested that seamount habitats provide an enhanced horizontal flux of mesopelagic prey and extended contact with the mesopelagic layers. Seamounts are also favourable habitat for fishes because the seabed is closer and more rugged, thus provide refuges in which to rest or escape from predators (Morato & Clark 2007).

Toothfish may obtain a substantial component of their diet from scavenging. Fenaughty *et al*. (2003) and Roberts *et al*. (2011) reported penguin remains from toothfish stomachs captured in the Ross Sea and South Sandwich Islands while Petrov & Tatarnikov (2011) reported seal and ‘flying bird’ remains from the Lazarev Sea. Roberts *et al*. (2011) also reported that many of the *K. longimana* beaks had probably come from individuals > 10 kg in total mass and were ‘either torn from living animals or scavenged from the seafloor’. We agree that squid remnants found in toothfish stomachs from large cephalopod species, such as *K. longimana* and *Mesonychoteuthis hamiltoni* (misidentified as *Octopoteuthis rugosa* Clarke in Fenaughty *et al*. 2003), have probably been scavenged, possibly as discards from marine mammal feeding or spent adults. Conversely, octopus remains in toothfish stomachs were often intact, which is consistent with direct predation given that most Antarctic octopi are small enough to be eaten whole. In this study, we also found evidence for toothfish scavenging bait and depredation of captured fish from the longline. For example, one toothfish stomach contained six fresh *C. dewitti*, one of which had a hook, bait and snood in its mouth, two others had broken lower jaws (presumably where a hook had been ripped out of the mouth) and another was partially eaten internally by lysianassid amphipods (*Orchomenella* sp.) therefore was probably dead prior to ingestion. Furthermore, a small number of stomachs contained pilchard remains (*Sardinops* sp., Clupeidae) which were not used as bait by the vessels in this study indicating scavenging along longlines from other vessels in the fishery. Fishing discards (a pectoral fin, two caudal fins, intestines and male gonad from large nototheniids) were also recovered from five toothfish stomachs.

The aim of the analysis of diet variability of adult toothfish from within a relatively well-sampled area of the continental slope was to look for small-scale patterns in diet composition. Furthermore, to determine whether diet sampling for toothfish from the commercial fishery could be used to monitor ecosystem change in the Ross Sea region, pursuant to CCAMLR Article II, which commits managers to maintain the ecological relationships between species. One important set of interconnections in the ecosystem of the Ross Sea slope is the predator-prey (trophic) linkage between toothfish and benthopelagic fish prey, especially grenadiers, icefish and eel cods. Ecosystem modelling of the Ross Sea shelf and slope has suggested that large toothfish are the main predator of large fishes such as grenadiers and icefish, and consequently the toothfish fishery could lead to trophic cascades (Pinkerton *et al*. 2010). As fishing has been most intense on the continental slope near the Mawson and Iselin banks, any change in trophic interconnections due to fishing may first occur in this region. Consequently, in 2010 the sampling of toothfish stomachs was focussed on an area including the northern parts of the Mawson and Iselin banks (70°–73°S, 175°E–175°W). The majority of our toothfish stomach samples were from this area and within the subset analysed for diet variability.

The proportion of variance in diet composition explained by environmental and sampling factors was significant, although relatively small. Variability in the diet within the region will make it difficult to use fishery-based opportunist collection of toothfish diet samples as convincing temporal indicators of ecosystem status. To use toothfish diet as an ecosystem indicator will require a move away from opportunistic sampling, or at least enough opportunistic samples would need to be collected in order that a controlled subset of samples could be taken afterwards for analysis. Location and fish size had a significant influence on diet variability, but temporal factors did not, meaning that there was no change in diet between 2003 and 2010. In 2012, the spawning stock biomass of the Ross Sea toothfish stock was estimated to be 80% of the unfished level (Mormede *et al*. 2011). The current catch limit for toothfish in the Ross Sea region is anticipated to lead to a long-term biomass of the spawning stock of 50% of the unfished value, consistent with CCAMLR management. Given the relatively low current level of toothfish stock depletion, and the lack of temporal change, the present study may be considered to be a 'baseline' against which to monitor for change in toothfish diet in the future.

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