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RESEARCH ARTICLE

Distribution and diet of juvenile Patagonian toothfish on the South Georgia and Shag Rocks shelves (Southern Ocean)

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Abstract The distribution and diet of juvenile (<750 mm) Patagonian toothfish are described from four annual trawl surveys (2003–2006) around the island of South Georgia in the Atlantic sector of the Southern Ocean. Recruitment of toothfish varies inter-annually, and a single large cohort dominated during the four years surveyed. Most juveniles were caught on the Shag Rocks shelf to the NW of South Georgia, with fish subsequently dispersing to deeper water around both the South Georgia and Shag Rocks shelves. Mean size of juvenile toothfish increased with depth of capture. Stomach contents analysis was conducted on 795 fish that contained food remains and revealed that juvenile toothfish are essentially piscivorous, with the diet dominated by notothenid fish. The yellow-finned notothen, *Patagonotothen guntheri*, was the dominant prey at Shag Rocks whilst at South Georgia, where *P. guntheri* is absent, the dominant prey were Antarctic krill and notothenid fish. The diet changed with size, with an increase in myctophid fish and krill as toothfish grow and disperse. The size of prey also increased with fish size, with a greater range of prey sizes consumed by larger fish.

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Introduction

The Patagonian toothfish (*Dissostichus eleginoides*) belongs to the notothenioids or Antarctic cods that are endemic to the southern hemisphere and dominate Antarctic fish assemblages (Kock 1992). It is circumpolar in distribution, being found around sub-Antarctic islands such as South Georgia, Heard Island and Kerguelen Island and also extends north onto the Patagonian shelf. To the south it is replaced by the congeneric Antarctic toothfish (*Dissostichus mawsoni*), which is found at high latitudes around the Antarctic continent (Gon and Heemstra 1990).

Patagonian toothfish reach large size (>2 m, >100 kg) and are long lived with adult fish believed to reach 50 years old (Horn 2002). Growth is relatively quick for the first 10 years, while the fish inhabit relatively shallow water, but following the onset of maturity [700–800 mm total length (TL)] growth is very slow. Spawning is thought to occur in deep-water, with both eggs and larvae pelagic (Evseenko et al. 1995).

The large size of toothfish, coupled with high quality flesh, led to the development, in the mid 1980s, of a valuable long-line fishery, targeting large adult fish in deep water (>500 m) (Agnew 2004). The fishery began in Chilean waters, but rapidly expanded to cover the geographic range of toothfish (Agnew 2004). At South Georgia the long-line fishery began in 1988, targeting large adult fish in deep-water although toothfish had previously been taken in bottom trawls on the shelf. Since the mid 1990s the fishery has been managed under the auspices of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), with mean annual catches of around 4,000 tonnes (Agnew 2004).

Ecologically sustainable management of a fishery requires an understanding of the distribution and ecology of the exploited species throughout the life cycle and interactions with other species in the ecosystem, and this underpins CCAMLR's ecosystem approach to fisheries management (Constable et al. 2000). Whilst the distribution and ecology of the adult part of the toothfish population has been elucidated through the fishery (e.g. Pilling et al. 2001; Agnew 2004) and the use of baited cameras (Yau et al. 2002; Collins et al. 2006), the distribution and ecology of the pre-recruits or juveniles is poorly documented.

The diet of Patagonian toothfish has been studied across its geographic range (Duhamel 1981; McKenna 1991; Garcia de la Rosa et al. 1997; Goldsworthy et al. 2001, 2002; Pilling et al. 2001; Arkhipkin et al. 2003; Barrera-Oro et al. 2005), but most of these studies have focused on adult toothfish from the fishery. At South Georgia adult toothfish (>750 mm TL) are thought to be opportunistic predators and scavengers (Pilling et al. 2001), but data on the diet of fish prior to entering the fishery (TL ~750 mm) is limited to a study from a single survey in March–April 1996 (Barrera-Oro et al. 2005).

Here we examine the distribution and diet of pre-recruit toothfish from trawl surveys undertaken at South Georgia and Shag Rocks in four consecutive seasons and consider the role of toothfish in the South Georgia ecosystem.

Materials and methods

During January 2003, 2004, 2005 and 2006 bottom trawl surveys were undertaken on the FPRV *Dorada* in the area of South Georgia and Shag Rocks. South Georgia is situated between the Polar Front and the Southern Antarctic Circumpolar Current Front (SACCF), with circulation generally flowing from west to east in the Antarctic Circumpolar Current (see Fig. 1). The surveys used a commercial sized otter trawl (FP-120), which was fished, during daylight, for approximately 30 min at each station. The trawl had a headline height of 4 m, and fished with a wingspread of 18–20 m and a cod-end mesh of 40 mm. In January 2003 trawl stations were arranged in a series of transects radiating away from the island and covering depths of 100–900 m. In 2004–2006 the trawl stations were arranged in a random, stratified design, to assess the abundance of mackerel icefish and pre-recruit toothfish.

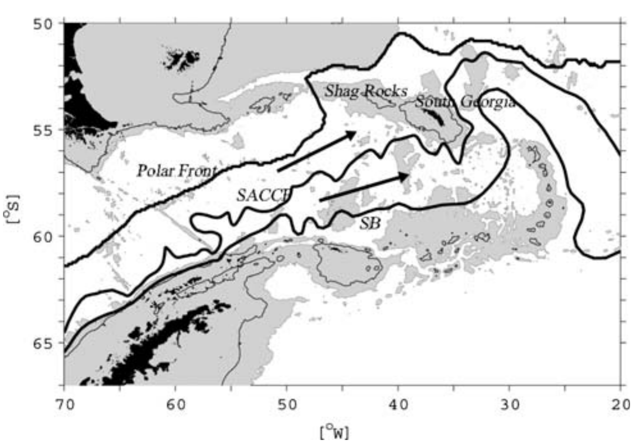


Fig. 1 The location of South Georgia and Shag Rocks in relation to the main fronts and currents in the Scotia Sea. *SACCF* Southern Antarctic Circumpolar Current Front, *SB* Southern Boundary of Antarctic Circumpolar Current

During all surveys, all captured toothfish were sampled, and were measured (to 10 mm category below), weighed and sexed. Except in 2003, when a subsample was taken, all toothfish stomachs that contained any food items were carefully dissected from the fish, and immediately frozen at –20°C.

In the laboratory stomachs were thawed and the total contents weighed prior to being sorted into species or species groups. Contents were identified to the lowest taxonomic level using published guides (Hulley 1981; Nesis 1987; Gon and Heemstra 1990) and reference collections. Partially digested fish were identified from sagital otoliths using reference material and published guides (Hecht 1987; Reid 1996). Partially digested cephalopods were identified using reference collections of beaks. Individual prey items were weighed and measured (TL for fish; ML for cephalopods), with the size of highly digested prey estimated from otolith to length relationships (Hecht 1987; Reid 1996). Items that were completely undigested were considered to represent trawl feeding and were excluded from subsequent analyses.

Diet was expressed using percent mass (% M), percent frequency of occurrence (% F), percent number (% N) and percent index of relative importance (% IRI: see Cortes 1996). Percent mass was based on the weight of the prey found in the stomach and not on reconstituted mass.

Percent mass: $$\%M_i = \frac{M_i}{\sum_{i=1}^{n} M_i} \times 100$$

Percent frequency of occurrence: $$\%F_i = \frac{F_i}{S} \times 100$$

S = number of stomachs containing food remains

Percent number: $$\%N_i = \frac{N_i}{\sum_{i=1}^{n} N_i} \times 100$$

Percent index of relative importance:

$$\%IRI_i = \frac{(\%N_i + \%M_i) \times \%F_i}{\sum_{i=1}^{n} (\%N_i + \%M_i) \times \%F_i} \times 100$$

Statistical analyses were undertaken using the statistical software MINITAB Release 14 and Sigma Plot 9.01. Inter-annual comparisons of stomach fullness (expressed as % body weight) were investigated using a one-way ANOVA on arcsin-transformed data. Regression analyses were undertaken to investigate the relationships between depth (independent) and fish length and between toothfish size (independent) and prey size. Assumptions about normality and constant variance were tested prior to analyses.

Results

Distribution of juvenile toothfish

Juvenile Patagonian toothfish (<750 mm TL) were found throughout the South Georgia and Shag Rocks shelves, but the density of juvenile fish was considerably greater on the Shag Rocks shelf, where 84% of the juveniles were caught (Table 1; Figs. 2, 3). Toothfish comprised 2.8–9.1% (by weight) of the fish catches at Shag Rocks and

Table 1 Numbers of trawl stations undertaken in each depth zone at Shag Rocks and South Georgia during each of the surveys, with the numbers of toothfish caught (excludes hauls that targeted toothfish for tagging)

Depth	Shag Rocks								South Georgia							
	100–200		200–300		300–400		>400		100–200		200–300		300–400		>400	
	Haul	Fish	Haul	Fish	Haul	Fish	Haul	Fish	Haul	Fish	Haul	Fish	Haul	Fish	Haul	Fish
January 2003	1	218	1	10	2	13	6	25	8	0	3	0	3	5	15	63
January 2004	6	24	10	237	4	88	2	10	15	4	18	32	8	9	2	0
January 2005	3	108	5	114	3	35	1	9	12	0	11	55	5	10	3	5
January 2006	5	133	10	308	2	11	0	0	13	9	19	40	14	20	0	0
Total	15	483	26	669	11	147	9	44	48	13	51	127	30	44	20	68

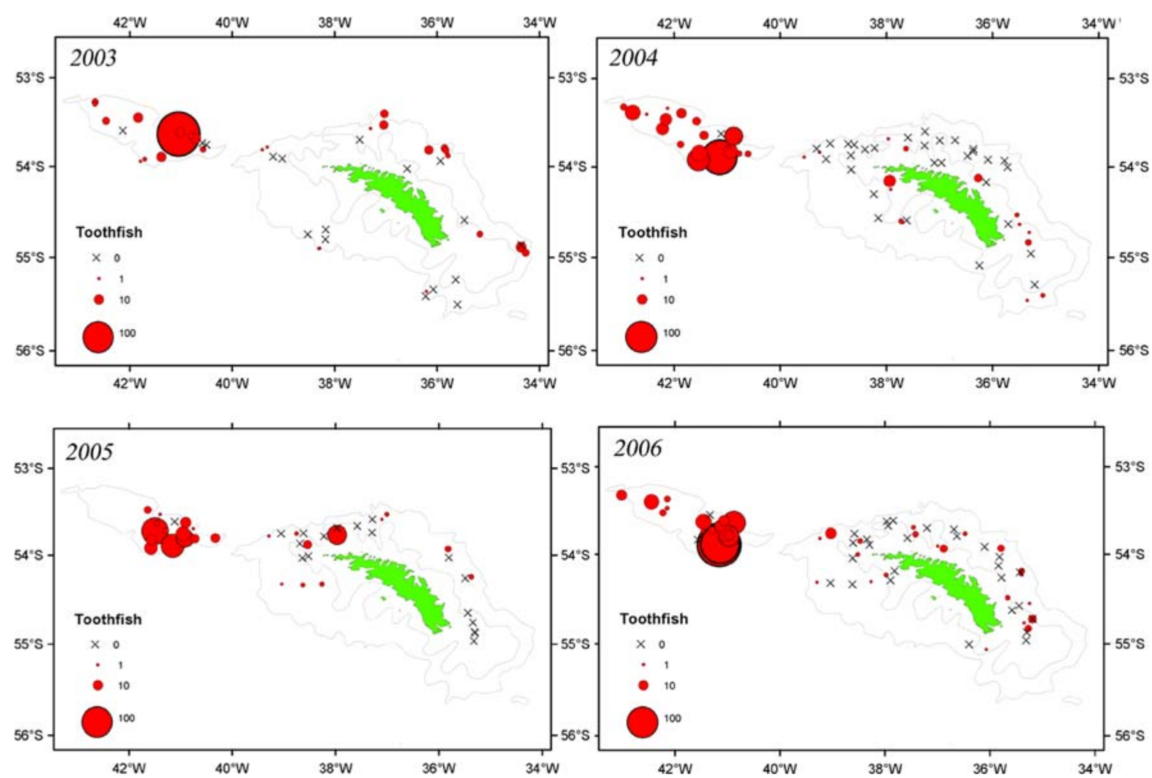


Fig. 2 Distribution (numbers caught) of juvenile Patagonian toothfish (*Dissostichus eleginoides*) (<750 mm TL) around South Georgia and Shag Rocks from surveys in 2003, 2004, 2005 and 2006

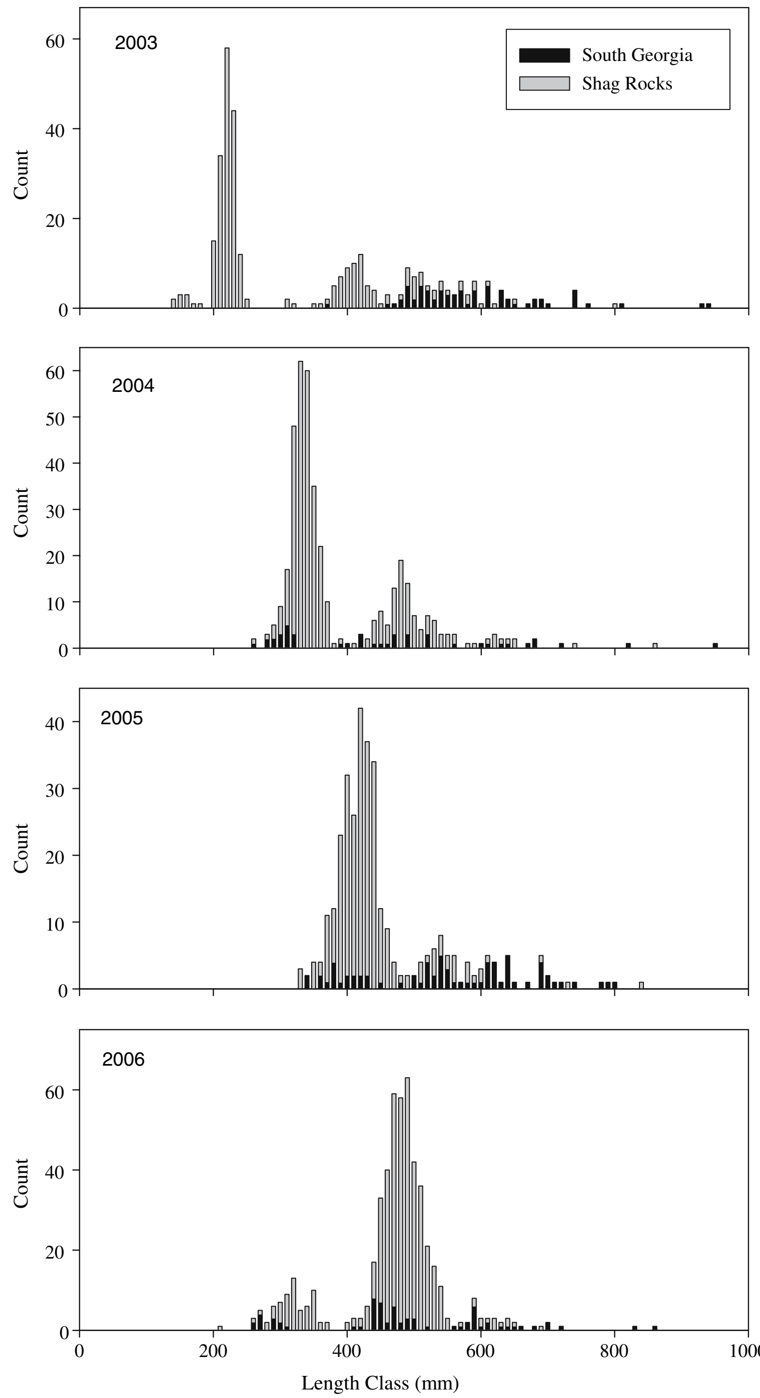


Fig. 3 Length frequency distribution of Patagonian toothfish (*Dissostichus eleginoides*) from each survey showing the size of fish sampled (excludes trawls that targeted toothfish for tagging)

0.7–6.7% of catches at South Georgia (Table 2). No Antarctic toothfish (*Dissostichus mawsoni*) were caught during the surveys.

In each year the catch was dominated by a single cohort that was of size 200–250 mm in 2003 (putative 1+ year old), 300–360 mm in 2004, 380–460 mm in 2005 and 430–530 mm in 2006 (Fig. 3). A second, numerically smaller, cohort was seen in 2003 at around 400 mm TL, which was present in small numbers in 2005 and 2006. A third cohort was detected in 2006 at size 260–340 mm (putative 2+ years old) that was not seen the previous year.

Juvenile fish were generally confined to the continental shelf areas, with the largest catches taken at depths of less than 300 m and larger fish were more frequently caught at South Georgia (Fig. 3). For trawls that caught three or more Patagonian toothfish, mean size increased significantly with depth of capture (regression: $F = 43.61$; $P < 0.001$; Fig. 4), and although large fish are occasionally

Table 2 Percentage composition (of mass) of the main fish species caught in non-target trawls (mean depth <400 m) on the South Georgia and Shag Rocks shelves. Total catch is given in kg

	South Georgia				Shag Rocks			
	2003	2004	2005	2006	2003	2004	2005	2006
Champsocephalus gunnari	59.43	63.46	12.79	68.44	10.82	50.72	4.94	35.01
Gobionotothen gibberifrons	19.47	10.67	20.94	9.45	0.55	0.49	0.70	0.86
Notothenia rossii	2.44	6.25	26.15	8.61	0.00	0.01	0.00	0.22
Chaenocephalus aceratus	8.27	6.50	8.72	5.33	0.07	0.00	0.05	0.13
Pseudochaenichthys georgianus	4.37	8.58	9.26	5.31	0.00	0.00	0.00	0.00
Lepidonotothen squamifrons	0.77	0.28	1.58	0.38	2.42	4.00	47.69	25.91
Dissostichus eleginoides	0.83	0.74	6.70	0.65	2.81	9.07	5.09	5.79
Patagonotothen guntheri	0.00	0.00	0.00	0.00	82.57	33.29	40.17	31.83
Other	4.43	3.51	13.85	1.83	0.77	2.42	1.36	0.25
Total catch (kg)	1,225	9,040	1,830	13,895	2,258	2,282	3,966	7,898

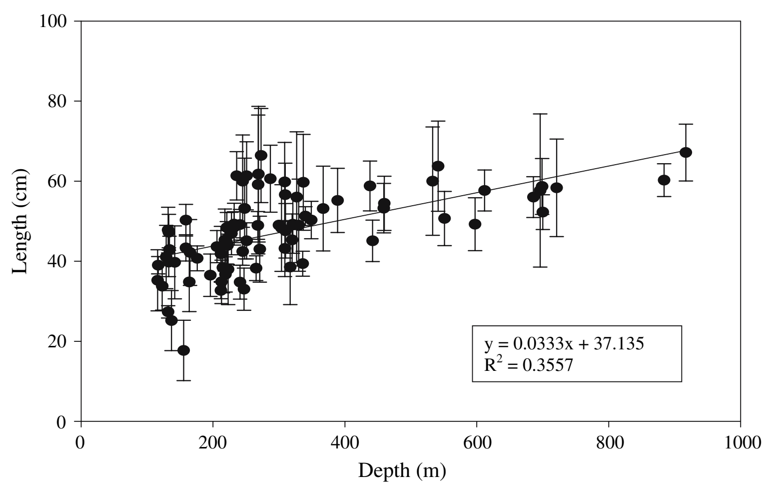


Fig. 4 Mean length of Patagonian toothfish (*Dissostichus eleginoides*) in relation to depth of capture from the four surveys. Error bars show standard deviations of length, only trawls with 3 or more fish included

caught in shallow water, smaller fish are restricted to shallow depths.

Diet of juvenile toothfish

Stomach fullness was generally high, and less than 25% of stomachs were empty (23% in 2004, 19% in 2005; 24% in 2006). Average stomach fullness (ratio of stomach weight to body weight) was significantly higher in 2004 (2.52% BW) than 2005 (1.86%) and 2006 (2.12%) (ANOVA: $F = 4.632$; $P < 0.01$) (2003 excluded as full set of data not available). For stomachs containing food, contents weight averaged 2.78% of body weight (range 0.01–12.6%). There was no relationship between stomach fullness and time of day, but all trawls were conducted during daylight.

Stomach contents were examined from 795 toothfish that had full or partially full stomachs, of which 636 were from fish caught at Shag Rocks and 159 from South Georgia caught fish. The size distribution of sampled fish was approximately proportional to the size range caught, with the exception of the small sized fish (200–250 mm TL) caught in 2003, which were under-represented.

Juvenile toothfish (<750 mm) were predominantly ichthyophagous, with fish accounting for 95% of the diet by mass, 51% numbers, 88% frequency and 89% IRI (Table 3). The diet composition differed between South Georgia and Shag Rocks (Table 3; Fig. 5), with more crustaceans taken at South Georgia, but this may reflect the larger average size of fish caught off South Georgia compared to Shag Rocks (see above). At South Georgia more krill (52% by number) was taken, but when the diet is considered in terms of percent mass fish prey accounted for 89% of the diet at South Georgia, compared to 97% at Shag Rocks.

The fish component of the diet differed substantially between the two locations. At Shag Rocks the yellow-finned notothen (*Patagonotothen guntheri*) dominated the diet in each of the years (85% by mass; 95% IRI). Catches of both toothfish (Fig. 2) and *P. guntheri* (Fig. 6) were

Table 3 Diet composition of Patagonian toothfish (*Dissostichus eleginoides*) expressed as percent mass, percent numbers, percent frequency of occurrence and percent IRI for the South Georgia and Shag Rocks shelves and the two areas combined

Prey	% Mass			% Numbers			% Occurrence			% IRI			Rank
	SR	SG	All	SR	SG	All	SR	SG	All	SR	SG	All	
Antarctomysis sp.	0.00	1.05	0.26	0.07	20.08	7.37	0.16	8.18	1.76	0.00	4.39	0.23	6
Euphausia triacantha	0.00	0.00	0.00	0.07	0.00	0.05	0.16	0.00	0.13	0.00	0.00	0.00	
Euphausia superba	1.75	8.10	3.34	21.12	52.07	32.42	10.69	39.62	16.48	2.70	60.56	10.27	2
Eusiridae	0.00	0.00	0.00	0.00	0.13	0.05	0.00	0.63	0.13	0.00	0.00	0.00	
Notocrangon	0.00	1.05	0.26	0.00	2.63	0.96	0.00	9.43	1.89	0.00	0.88	0.04	
Natatolana sp. (Isopoda)	0.03	0.00	0.03	0.43	0.00	0.27	0.63	0.00	0.50	0.00	0.00	0.00	
Isopoda indet.	0.01	0.00	0.01	0.14	0.00	0.09	0.31	0.00	0.25	0.00	0.00	0.00	
Themisto gaudichaudii	0.10	0.08	0.09	9.16	2.13	6.59	2.67	4.40	3.02	0.27	0.25	0.35	5
Vibilia antarctica	0.00	0.00	0.00	0.29	0.00	0.18	0.63	0.00	0.50	0.00	0.00	0.00	
Copepoda (parasitic)	0.00	0.00	0.00	0.22	0.00	0.14	0.47	0.00	0.38	0.00	0.00	0.00	
Crustacea indet	0.13	0.02	0.10	0.58	0.38	0.50	1.26	1.26	1.26	0.01	0.01	0.01	
Crustacea total	2.04	10.30	4.10	32.08	77.42	48.63	15.25	47.17	21.64	2.99	66.09	10.92	
Gastropoda	0.01	0.00	0.01	0.07	0.00	0.05	0.16	0.00	0.13	0.00	0.00	0.00	
Adelieledone polymorpha	0.00	1.02	0.25	0.00	0.25	0.09	0.00	1.26	0.25	0.00	0.04	0.00	
Octopoda	0.00	0.00	0.00	0.07	0.00	0.05	0.16	0.00	0.13	0.00	0.00	0.00	
Psychroteuthis glacialis	0.22	0.00	0.16	0.07	0.00	0.05	0.16	0.00	0.13	0.00	0.00	0.00	
Cephalopoda indet	0.01	0.00	0.01	0.07	0.00	0.05	0.16	0.00	0.13	0.00	0.00	0.00	
Mollusca total	0.25	1.02	0.44	0.29	0.25	0.27	0.63	1.26	0.75	0.00	0.04	0.00	
Electrona antarctica	0.32	0.19	0.28	1.37	0.38	1.01	1.89	0.63	1.64	0.04	0.01	0.04	
Electrona carlsbergi	0.26	0.00	0.20	0.79	0.00	0.50	1.42	0.00	1.13	0.02	0.00	0.01	
Gymnoscopelus bolini	1.11	0.00	0.84	0.07	0.00	0.05	0.16	0.00	0.13	0.00	0.00	0.00	
Gymnoscopelus braueri	0.07	0.04	0.06	0.14	0.13	0.14	0.31	0.63	0.38	0.00	0.00	0.00	
Gymnoscopelus fraseri	0.26	0.33	0.28	0.43	0.25	0.37	0.94	1.26	1.01	0.01	0.02	0.01	
Gymnoscopelus hintonoides	0.10	0.00	0.08	0.29	0.00	0.18	0.63	0.00	0.50	0.00	0.00	0.00	
Gymnoscopelus nicholsi	3.82	0.31	2.94	3.39	0.13	2.20	6.29	0.63	5.16	0.50	0.01	0.46	4
Gymnoscopelus sp.	0.54	0.00	0.41	0.72	0.00	0.46	1.42	0.00	1.13	0.02	0.00	0.02	
Krefftichthys anderssoni	0.02	0.00	0.02	0.65	0.00	0.41	0.94	0.00	0.75	0.01	0.00	0.01	
Protomyctophum bolini	0.82	0.00	0.62	3.82	0.00	2.43	3.62	0.00	2.89	0.19	0.00	0.15	7=
Protomyctophum choriodon	0.29	0.00	0.22	1.01	0.00	0.64	1.57	0.00	1.26	0.02	0.00	0.02	
Protomyctophum parallelum	0.03	0.00	0.02	0.07	0.00	0.05	0.16	0.00	0.13	0.00	0.00	0.00	
Myctophidae indet.	0.51	0.41	0.48	1.23	0.50	0.96	2.04	1.89	2.01	0.04	0.04	0.05	
Myctophidae total	8.16	1.27	6.44	13.99	1.38	9.39	17.92	3.77	15.09	0.84	0.08	0.78	
Chaenocephalus aceratus	0.00	1.62	0.41	0.00	0.13	0.05	0.00	0.63	0.13	0.00	0.03	0.00	
Chaenodraco wilsoni	0.00	0.11	0.03	0.00	0.13	0.05	0.00	0.63	0.13	0.00	0.00	0.00	
Champsocephalus gunnari	0.76	12.94	3.80	0.22	1.51	0.69	0.47	7.55	1.89	0.01	2.77	0.15	7=
Channichthyidae	0.01	0.04	0.02	0.07	0.13	0.09	0.16	0.63	0.25	0.00	0.00	0.00	
Gobionotothen gibberifrons	0.00	2.88	0.72	0.00	0.25	0.09	0.00	1.26	0.25	0.00	0.10	0.00	
Gobionotothen marionensis	0.23	0.00	0.17	0.07	0.00	0.05	0.16	0.00	0.13	0.00	0.00	0.00	
Lepidonotothen larseni	0.00	20.22	5.05	0.00	7.78	2.84	0.00	28.93	5.79	0.00	20.57	0.80	
Lepidonotothen nudifrons	0.06	0.00	0.04	0.14	0.00	0.09	0.31	0.00	0.25	0.00	0.00	0.00	
Lepidonotothen squamifrons	0.00	9.91	2.48	0.00	0.13	0.05	0.00	0.63	0.13	0.00	0.16	0.01	
Patagonotothen guntheri	85.19	0.00	63.90	46.58	0.00	29.58	65.72	0.00	52.58	95.47	0.00	85.68	1
Pseudochaenichthys georgianus	0.00	7.79	1.95	0.00	0.63	0.23	0.00	2.52	0.50	0.00	0.54	0.02	
Trematomus hansoni	0.00	22.80	5.70	0.00	1.63	0.60	0.00	6.29	1.26	0.00	3.90	0.14	9
Notothenioid indet	0.65	2.29	1.06	1.80	2.38	2.01	3.93	11.95	5.53	0.11	1.42	0.30	
Notothenioid total	86.90	80.61	85.33	48.88	14.68	36.40	70.60	54.09	67.30	95.59	29.50	87.08	

Table 3 continued

Prey	% Mass			% Numbers			% Occurrence			% IRI			Rank
	SR	SG	All	SR	SG	All	SR	SG	All	SR	SG	All	
Pseudoscopelus sp. (Chiasmodontidae)	0.14	0.00	0.11	0.07	0.00	0.05	0.16	0.00	0.13	0.00	0.00	0.00	
Macrouridae	0.00	0.67	0.17	0.00	0.13	0.05	0.16	0.00	0.13	0.00	0.00	0.00	
Micromesistius australis	0.09	0.00	0.07	0.07	0.00	0.05	0.00	0.63	0.13	0.00	0.00	0.00	
Muraenolepis sp.	0.28	1.89	0.69	0.36	2.89	1.28	0.79	10.69	2.77	0.01	1.30	0.09	10
Paradiplospinosus gracilis	0.36	0.00	0.27	0.07	0.00	0.05	0.16	0.00	0.13	0.00	0.00	0.00	
Fish indet.	1.78	4.24	2.39	4.11	3.26	3.80	8.96	15.72	10.31	0.58	3.00	1.11	3
Other fish total	2.65	6.80	3.69	4.69	6.27	5.27	10.06	25.79	13.21	0.70	3.50	1.22	

The ten main prey items are ranked by % IRI in the right hand column

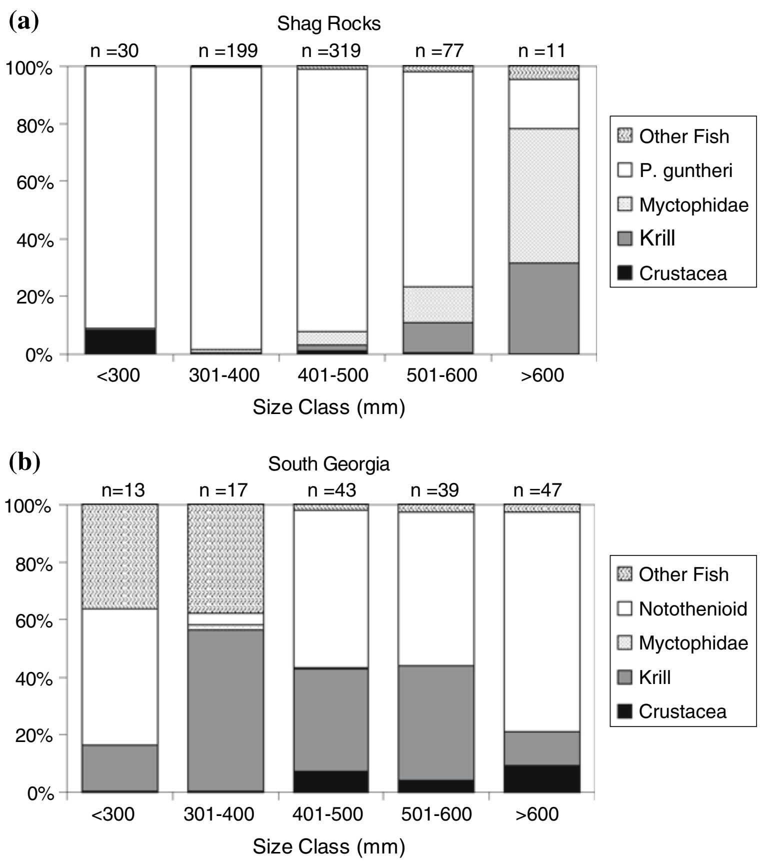


Fig. 5 Diet of juvenile toothfish by size category from Shag Rocks (**a**) and South Georgia (**b**)

highest at the eastern end of the Shag Rocks shelf, although there was no significant correlation between catches of the two species at Shag Rocks. On the South Georgia shelf the diet was more diverse with the notothenids *Lepidonotothen larseni* (20% mass; 21% IRI) and *Trematomus hansoni* (23% mass; 3.9% IRI) the main fish prey species. Myctophid fish were also consumed, with *Gymnoscopelus nicholsi* and *Protomyctophum bolini* the most common species taken. There was a single incidence of southern blue whiting (*Micromesistius australis*), which is rarely found at South Georgia and a single incidence of an undescribed species of the Chiasmodontidae genus *Pseudoscopelus* (Marcelo Melo, personal communication; specimen lodged at the Natural History Museum, London: BMNH.2006.8.19.1).

The main crustacean prey species were Antarctic krill (*Euphausia superba*), the mysids (*Antarctomysis ohlini* and *A. maxima*) and the pelagic amphipod (*Themisto gaudichaudii*), with the decapod, *Notocrangon antarcticus*, and isopods of the genus *Natatolana* (Family Cirolanidae)

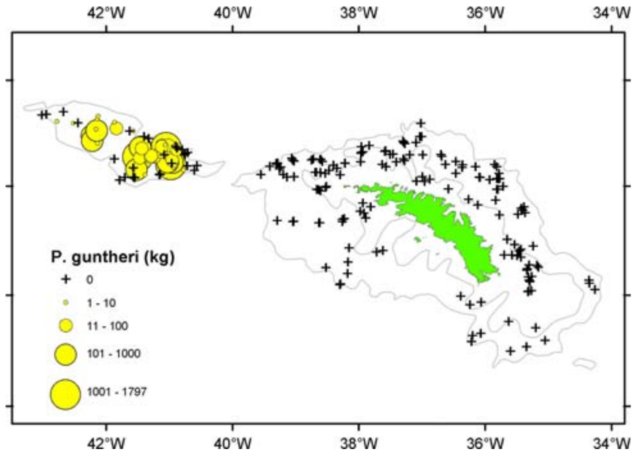


Fig. 6 Distribution of catches of the yellow-finned notothen (*Patagonotothen guntheri*) from surveys in 2003, 2004, 2005 and 2006

occasionally taken. Cephalopods were rare in the diet, with the octopus *Adelieledone polymorpha* and the squid *Psychroteuthis glacialis* the only species identified.

Ontogenetic changes in diet

The diet of toothfish changed with size at both Shag Rocks and South Georgia (Fig. 5: note sample sizes were smaller for larger fish and at South Georgia). At Shag Rocks the diet of fish size <500 mm TL was dominated by the notothenioid, *Patagonotothen guntheri*, which reflects the association with the Shag Rocks shelf. In fish greater than 400 mm TL there was an increase in krill and myctophids. At South Georgia, smaller fish consumed krill and other crustaceans, with larger fish taking notothenioid fish.

Fish prey size increased significantly with toothfish size (Regression: $F = 83.571$; $P < 0.001$; $n = 832$; Fig. 7) but, more clearly, the range of prey sizes taken increased with fish size. The main prey species, *Patagonotothen guntheri*, forms a cluster at sizes 70–200 mm TL, consumed by toothfish of 200–600 mm TL, but the relationship between predator size and prey size was still significant (Regression: $F = 49.706$; $P < 0.001$; $n = 546$). The larger prey items were other notothenioid fish, notably *Trematomus hansoni* and *Champsocephalus gunnari*. The myctophid prey, with the exception of a single large *Gymnoscopelus bolini* were of small size. The number of prey items consumed also increased with predator size.

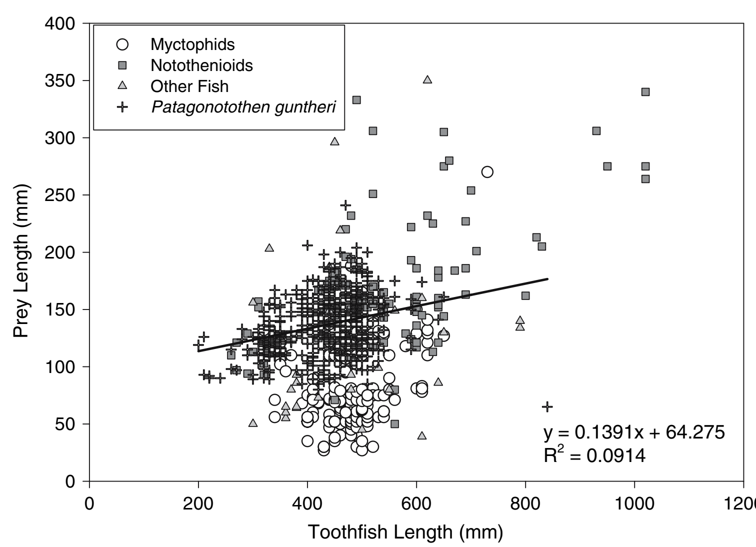
The length of *Patagonotothen guntheri* consumed by toothfish was generally slightly smaller than that caught by the survey (not illustrated), the exception being in 2005, when the survey caught relatively smaller *P. guntheri* than in the previous seasons.

Discussion

Distribution

Whilst adult toothfish are distributed in deep-water all around South Georgia and Shag Rocks (Agnew et al. 1999; Agnew 2004), the data from this study suggest that the recruitment of juvenile toothfish occurs predominantly at Shag Rocks, with small numbers of juvenile fish caught on the South Georgia shelf, most notably at the SW edge. This is consistent with the data of Garcia de la Rosa et al. (1997), who only found small toothfish at Shag Rocks. Barrera-Oro et al. (2005) did catch some small fish on the South Georgia shelf, but the majority of fish <600 mm TL were caught on the Shag Rocks shelf. The association between toothfish recruitment and Shag Rocks is not clear, but may be related to temperature and oceanography.

Fig. 7 Relationship between prey size and predator size in Patagonian toothfish (*Dissostichus eleginoides*)



Water temperatures at Shag Rocks are slightly warmer than on the South Georgia shelf (M.A. Collins, unpublished data) and, as the Patagonian toothfish is at the southern edge of its range, and, unlike *D. mawsoni*, does not possess anti-freeze glycoproteins (Gon and Heemstra 1990), temperature may be a limiting factor.

Although two other cohorts were detected, this study essentially monitored a dominant cohort through four consecutive seasons. The cohort, first detected at size 200–250 mm TL, where probably 1+ years old in 2003 and would therefore be 4+ in 2006 (M. Belchier, unpublished data). The dominance of a single cohort through four years of sampling suggests strong interannual variability in recruitment. Toothfish are thought to spawn in winter in deep-water around South Georgia and Shag Rocks (Agnew et al. 1999). The eggs and larvae are both pelagic, with developmental stages thought to last 3 and 6 months respectively (Evseenko et al. 1995), and successful recruitment will be dependent on transport in near surface currents. The oceanography of the Scotia Sea is highly complex (Fig. 1) and subject to inter-annual variability, which may be the main factor driving recruitment variability. A detailed analysis of variability in growth and recruitment in Patagonian toothfish from 14 surveys from 1987 to 2006 is in progress (Belchier and Collins, in preparation).

In common with other species that scavenge as adults (see Collins et al. 2005), the Patagonian toothfish has a bigger-deeper trend (Arkhipkin et al. 2003; Laptikhovsky et al. 2006), and although this study was largely focused in shallow areas it showed a distinct pattern, which is supported by evidence from the fishery (Agnew et al. 1999). Larger fish do occasionally occur in shallow water and fish over a metre in length have been caught in trammel nets in <200 m depth in Cumberland Bay (personal observation).

Diet

Although this study only gives a summer snapshot of toothfish diet, it is clear that pre-recruit toothfish in the South Georgia/Shag Rocks area are essentially piscivorous, which is largely consistent with previous studies in the area (Zhivov and Krivoruchko 1990; Barrera-Oro et al. 2005) and dietary studies of similar sized toothfish in other parts of the range (Duhamel 1981; Garcia de la Rosa et al. 1997; Goldsworthy et al. 2002; Arkhipkin et al. 2003).

The difference in the specific composition of the toothfish diet between Shag Rocks and South Georgia is largely a consequence of distinct differences in the ichthyofauna between the two areas. The Shag Rocks and South Georgia shelves are separated by a deep (~1,500 m) channel, and many of the notothenids and channichthyids that are common on the South Georgia shelf are rare or absent at Shag Rocks (see Table 2). At Shag Rocks the demersal fauna is less diverse and dominated by *Lepidonotothen squamifrons*, mackerel icefish and *Patagonotothen guntheri*, with the latter being absent from South Georgia (Gon and Heemstra 1990). *Lepidonotothen squamifrons* are, in some years, abundant at Shag Rocks and were the main fish prey identified by Barrera-Oro et al. (2005), however they are usually large fish and maybe too large for a juvenile toothfish to consume. Hence the most abundant fish species of suitable size is usually *P. guntheri* and the dominance of this species in toothfish diet may simply be a consequence of the distribution of the two species, with conditions that favour toothfish recruitment also favouring *P. guntheri.* Both species are abundant at the eastern end of the Shag Rocks shelf, which may be more productive than other parts of the Shag Rocks shelf. Interestingly, on the Falkland shelf the congeneric *Patagonotothen ramsayi* is the main prey of pre-recruit toothfish of sizes <600 mm TL (Arkhipkin et al. 2003).

The specific composition of the toothfish diet in this study differs from that identified from sampling in March–April 1996 by Barrera-Oro et al. (2005) and from 1985 to 1986 by Zhivov and Krivoruchko (1990). The Barrera-Oro et al. (2005) study found *Lepidonotothen kempi* (=*L. squamifrons*) to be the main toothfish prey at South Georgia and Shag Rocks and neither study found *Patagonotothen guntheri* to be so dominant [10% occurrence in Zhivov and Krivoruchko (1990) and not recorded by Barrera-Oro et al. (2005)]. Differences between the studies may reflect seasonal or inter-annual variability in prey availability, but in both of the other studies a large part of the fish diet was unidentified (49% unidentified in Barrera-Oro et al. 2005).

Patagonotothen guntheri, the dominant prey species at Shag Rocks, is a semi-pelagic notothenid that is one of the most abundant species caught during trawl surveys at Shag Rocks (Table 2), but is at the southern end of its range (Gon and Heemstra 1990). It is a pelagic feeder, consuming large copepods (e.g. *Rhincalanus gigas*), pelagic amphipods (e.g. *Themisto gaudichaudii*) and krill (M.A. Collins, unpublished data). On the South Georgia shelf the most important prey species were *Lepidonotothen larseni* and *Trematomus hansoni*, which also feed on macro-zooplankton. The mackerel icefish (*Champsocephalus gunnari*), which is abundant at both South Georgia and Shag Rocks (Table 2) and is commercially fished, was only occasionally found in toothfish stomachs in this study.

Even within the limited size range studied here, a change in diet with size of toothfish was detected. The shift from *Patagonotothen guntheri* to other notothenioids is associated with dispersion of fish from Shag Rocks to the South Georgia shelf. There is also an increase in krill consumption and, to a lesser extent, myctophid fish

Table 4 Potential predators of Patagonian toothfish (*Dissostichus eleginoides*) on the South Georgia and Shag Rocks shelf

Potential predator	Maximum depth	Comments	Sources
Southern elephant seal *Mirounga leonina*	Dive to >2,000 m.	Have been reported taking toothfish. Population size at South Georgia: ~100,000 breeding females potentially significant predator	Slip et al. (1994), Reid and Nevitt (1998), Boyd et al. (1996)
Antarctic fur seal *Artocephalus gazella*	Dive to 300 m	Toothfish otoliths occasionally in scats at South Georgia and Heard Island; unlikely to be a significant predator.	Green et al. (1989), Reid (1995), Reid and Arnould (1996)
Weddell seal *Leptonychotes weddelli*	Dive to 450 m	Know to take *D. mawsoni* in Weddell Sea; small South Georgia population may take *D. eleginoides*.	Calhaem and Christoffel (1969), Testa et al. (1985), Plotz (1986), Lake et al. (2003)
Sperm whale *Physeter macrocephalus*	Dive in excess of 2,000 m	Known to consume toothfish; take toothfish from longlines; population size at South Georgia is unknown.	Korabelnikov (1959), Clarke (1980), Abe and Iwami (1989), Watkins et al. (1993), Ashford et al. (1996), Purves et al. (2004), Kock et al. (2006)
Killer whale *Orcinus orca*	Dive to 200 m	Take toothfish off long-lines, but do not dive deep enough to catch adults	Ashford et al. (1996), Purves et al. (2004), Kock et al. (2006)
King penguin *Aptenodytes patagonicus*	Dive to 300 m	Piscivorous, but pelagic feeders generally taking small fish (myctophids) and squid; no toothfish reported in diet at South Georgia, but reported in diet at Crozet (n=2, 4.3 % occurrence).	Kooyman et al. (1992), Cherel et al. (1996), Olsson and North (1997)
Gentoo penguin *Pygocelis papua*	Dive to 150 m	Not known to take toothfish in South Georgia area, but toothfish recorded in diet at Maquarie Is (0.1-1.2 % occurrence) and Kerguelen (2.5 % occurrence)	Adams and Klages (1989), Robinson and Hindell (1996), Goldsworthy et al. (2001), Lescroel et al. (2004)
Macaroni penguin *Eudyptes chrysolophus*	Dive to 120 m	Single incidence of toothfish in diet at Marion Is., never recorded at South Georgia	Brown and Klages (1987)
Black-browed albatross *Thalassarche melanophris*	Surface feeders	Toothfish in stomachs probably from hooks and/or discards from fishing vessels	Cherel et al. (2000, 2002)
Grey-headed albatross *Thalassarche chrysostoma*	Surface feeders	Toothfish in stomachs probably from hooks and/or discards from fishing vessels	Cherel et al. (2002), Xavier et al. (2003)
White chinned petrels *Procellaria aequinoctialis*	10 m	Toothfish in stomachs probably from hooks and/or discards from fishing vessels	Catard et al. 2000
Patagonian toothfish *Dissostichus eleginoides*	2,500 m	Some cannibalism likely, with large fish taking smaller cohorts, but will be limited by the size-depth distribution pattern.	Arkhipkin et al. (2003)
Sleeper sharks *Somniosus* sp.	2,000 m	Toothfish recorded in stomachs, but may be net feeding and scavenging on discarded heads.	Cherel and Duhamel (2004)
Giant Antarctic squid *Mesonychoteuthis hamiltoni*	Unknown	Reach large size (>100 kg); incidentally caught on longline hooks targeting toothfish. Possible predator, abundance unknown.	Young (2003), M.A. Collins (unpublished data)

(particularly at Shag Rocks) with increased size. The principal myctophid species taken was *Gymnoscopelus nicholsi*, which is a relatively large species (upto 180 mm TL) abundant on the slope (300–1,000 m) around South Georgia and Shag Rocks, and although it is a pelagic species it is frequently caught in bottom trawls. This dietary change is associated with the ontogenetic migration into deeper water, where the available prey will differ, for instance *Patagonotothen guntheri* are rarely caught in depths greater than 300 m.

The migration to deep water is probably accompanied by changes in foraging behaviour as well as diet with large adults scavenging in addition to taking live prey (Garcia de la Rosa et al. 1997; Pilling et al. 2001; Arkhipkin et al. 2003), making them susceptible to baited long-lines and attracted to baited cameras (Collins et al. 1999, 2006; Yau et al. 2002). Arkhipkin et al. (2003) suggested that larger toothfish generally take less active prey than small toothfish, although adult fish are capable of bursts of high speed swimming (Yau et al. 2002), and consequently the diet of the larger toothfish is considerably different from that of the juveniles. At South Georgia the diet of adult fish appears more diverse than juveniles, with more cephalopods (Onychoteuthidae, Gonatidae, Chiroteuthidae and octopods) and crustaceans (krill, the decapod *Nauticaris* sp. and isopods) taken (Garcia de la Rosa et al. 1997; Pilling et al. 2001). The main fish families consumed were Myctophidae, Moridae and Zoarcidae, but in both studies over half the fish were not identified.

Although the size of prey increased with size of toothfish, it is clear that it is the range of prey size that increases, with the larger toothfish taking small prey as well as large prey items. The size of *P. guntheri* taken by toothfish was generally slightly smaller than that taken by the trawl survey and this is likely to be a consequence of both selectivity of the trawl and selectivity by the toothfish.

The diet of juvenile toothfish comprised a mixture of both pelagic and demersal species, and it is not known how much time toothfish spend foraging above the seafloor. For instance the main prey species *P. guntheri* feeds pelagically, but is also caught in bottom trawls. Time spent foraging above the seafloor will clearly impact their catchability in a bottom trawl, but potentially make toothfish more susceptible to diving predators (see below).

Given the importance of *P. guntheri* in the diet of toothfish recruits and the co-occurrence of the two species, it is likely that any exploitation of *P. guntheri* would impact on toothfish populations. Fishing for *P. guntheri* at Shag Rocks is likely to have a by-catch of small toothfish, and the removal of a large biomass of *P. guntheri* would reduce the available food for toothfish. Whilst there is currently no fishery for *P. guntheri* it has been estimated that around 170,000 tonnes were fished from the Shag Rocks area between 1969 and 1990 (Anon 1990a, b; Kock 1992). Currently a relatively small pelagic trawl fishery, targeting mackerel icefish (*Champsocephalus gunnari*), operates on the South Georgia and Shag Rocks shelves, which does have the potential to catch juvenile toothfish.

The role of toothfish in the South Georgia marine ecosystem

In order to have an ecologically sustainable fishery it is important to have knowledge of the diet of a target species and of potential predators that may be competing with the fishery. Whilst knowledge of the diet of toothfish is now substantial, little is known about the predators of toothfish. In shallow water, potential predators of juveniles include king and gentoo penguins, fur and elephant seals, but with increased size and habitat depth the range of potential predators is likely to decline (Table 4). From studies undertaken at on South Georgia, toothfish are rarely taken in the diets of fur seals or penguins, and only are occasionally taken by these species elsewhere (see Table 4). Toothfish have been reported in the diet of Weddell seals, of which there is a small population at South Georgia, and these are a potential predator. Albatross and white-chinned petrels are known to take toothfish, but these are, almost certainly, fish that escape from hooks or discards from fishing vessels. In deeper water, the only likely predators are elephant seals, sperm whales and large squid such as the Antarctic giant squid, *Mesonychoteuthis hamiltoni*. Both sperm and killer whales are known to take toothfish from longlines during hauling (Ashford et al. 1996; Kock et al. 2006; Purves et al. 2004), but toothfish habitat is beyond the normal diving capabilities of killer whales. Little is know about the ecology of *Mesonychoteuthis hamiltoni*, but these large squid are probably capable of catching and consuming large toothfish, and are occasionally caught on long-line hooks at South Georgia (M.A. Collins, unpublished data). Although cannibalism was not recorded in this study it has been recorded in larger toothfish (Arkhipkin et al. 2003) and may occur between cohorts. Overall the evidence from predators indicates low levels of predation, which is a consequence of the depth distribution and size of the toothfish.

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