



Latitudinal and bathymetric patterns in the distribution and abundance of mesopelagic fish in the Scotia Sea

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ABSTRACT

Mesopelagic fish are a key component of the pelagic ecosystem throughout the world's oceans. Opening and closing nets were used to investigate patterns in the distribution and abundance of mesopelagic fish from the surface to 1000 m on a series of transects across the Scotia Sea from the ice-edge to the Antarctic Polar Front. A total of 141 non-target net hauls were undertaken during three cruises (Nov 2006, Jan 2008 and Mar 2009), with 7852 teleost fish captured, representing 43 species in 17 families. A further 1517 fish were caught in targeted net hauls. The dominant families were the Myctophidae (6961 specimens; 21 species) and Bathylagidae (1467 specimens; 4 species). Few fish were caught in the upper 400 m during daylight, which was attributed to a combination of net avoidance and diurnal vertical migration. Species composition was linked to depth and location and was closely associated with oceanographic features. Diversity was lowest in cold water at the most southerly stations, which were dominated by *Electrona antarctica*, *Gymnoscopelus braueri* and *Bathylagus antarcticus*. Further north, diversity increased with the addition of species such as *Krefflichthys anderssoni*, *Protomyctophum bolini* and *Electrona carlsbergi*. The depth integrated biomass of myctophids was similar across the latitudinal transect and produced an estimate of 4.5 million tonnes in the Scotia Sea. Bathylagids were patchily distributed, but were abundant in the lower mesopelagic zone (> 400 m) and are potentially significant zooplankton consumers. Given the biomass of the myctophids and bathylagids coupled with the vertical migrations of many species, these fish are likely to play a significant role in carbon export from the surface waters to the deep ocean.

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1. Introduction

Mesopelagic fish, which occupy the upper 1000 m of the world's oceans, play a key role linking primary consumers such as copepods and macro-zooplankton to higher predators such as birds, large pelagic fish and marine mammals. Lantern fish (Myctophidae) are one of the dominant mesopelagic fish families (see Gjøsaeter and Kawaguchi, 1980) and are ubiquitous in the world's oceans, with high diversity and abundance.

In the Southern Ocean the myctophid fauna includes 33 species (Hulley, 1981; McGinnis, 1982), with an estimated biomass of 70–130 million tonnes (Lubimova et al., 1987). They are a key dietary component of king penguins (Cherel et al., 2002; Olsson and North,

1997), and are a significant component of the diet of many other higher predators such as toothfish, elephant and fur seals and macaroni penguins (Collins et al., 2007; Reid et al., 2006). Guinet et al. (1996) estimated that the population of king penguins on the Crozet Islands consume 745,000 tonnes of lantern fish per year. Southern Ocean myctophids are themselves predators of macro-zooplankton such as copepods, amphipods and euphausiids, including Antarctic krill (*Euphausia superba*) (Pakhomov et al., 1996; Pusch et al., 2004; Shreeve et al., 2009), with evidence of dietary specialisation in different myctophid species (Shreeve et al., 2009).

The Scotia Sea, which includes 2 million km² of the Atlantic sector of the Southern Ocean (Hewitt et al., 2004), is a region of complex bathymetry and oceanography. It is bounded on three sides by the Scotia Arc (which includes South Georgia, the South Sandwich Islands and the South Orkneys), and is open to the Drake Passage to the west (Fig. 1). The Scotia Sea is influenced by two oceanographic regimes: the generally eastward flowing Antarctic Circumpolar Current (ACC) and the cyclonic circulation of the Weddell Gyre, which meet in the

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JR200 in the austral autumn (Mar 2009). A winter cruise to the southern Scotia Sea would be very difficult due to the sea-ice and hence no comparative winter sampling was undertaken. During each cruise oceanographic (Venables et al., 2012), acoustic (Fielding et al., 2012) and biological data were collected at a series of stations occupying a transect from the edge of the sea-ice to the Polar Front (PF). Stations were selected to sample the different water-masses and frontal zones.

2.2. Oceanographic background

Details of the oceanographic transects are provided in Venables et al. (2012).

2.3. Fishing methods and locations

Mesopelagic fish and pelagic invertebrates were sampled using an opening and closing 25-m² rectangular mid-water trawl (RMT25). The RMT25 (see Piatkowski et al., 1994) consists of two nets that are opened and closed on command to sample discrete depth layers. The net was monitored in real-time using a custom-built net monitoring system that logged depth and ambient temperature. Each net had a theoretical mouth opening of 25 m², with a cod-end mesh of 5 mm and was towed obliquely at 2.5 knots for 30–60 min in each depth horizon. The net was fitted with a protected cod-end to keep captured animals in good condition.

Net hauls were undertaken at six nominal stations (Southern Scotia Sea (SSS), Mid Scotia Sea (MSS), Western Scotia Sea (WSS), Northern Scotia Sea (NSS), Georgia Basin (GB) and Polar Front (PF); Fig. 1). At each station depth stratified RMT 25 hauls were undertaken at depths 0–200, 200–400, 400–700 and 700–1000 m. During the spring and summer cruises stratified hauls were repeated day and night, whilst during the autumn cruise all hauls were undertaken in darkness. Net hauls were undertaken sequentially, with the upper nets (0–200 and 200–400 m) undertaken as close to local midday or midnight as practical.

Additional net hauls were undertaken on acoustically detected fish aggregations. These net hauls were not included in similarity analyses or to generate estimates of abundance and biomass.

Net haul catches were sorted to the lowest taxonomic level using published guides (Gon and Heemstra, 1990; Hulley, 1981), and our own reference collection and experience. Total catch weights were obtained for each fish species using a motion compensated balance. All fish were measured (standard length (SL) and/or total length (TL) to the nearest mm).

2.4. Data analysis

The density of mesopelagic fish was calculated from the stratified (non-target) RMT25 net hauls. Densities were calculated as individuals per filtered volume of water for each depth zone (ind. 1000 m⁻³), with day and night hauls treated separately. Volume filtered was estimated from distance of the tow multiplied by the nominal area of the net (25 m²).

Patterns in the mesopelagic ichthyofaunal community structure were investigated using the Plymouth Routines in Multivariate Ecological Research (PRIMER v.6) Software (Clarke and Warwick, 2001). Shannon–Wiener diversity indices were derived for each net haul. Similarities between RMT25 net hauls were investigated using the numbers of each species in each net haul. The dataset was restricted to night-time hauls that caught more than 15 fish and a square-root transformation was applied to reduce the weighting of dominant species. Bray–Curtis similarities were calculated for each pair of net hauls to produce a similarity matrix, which was classified by Multi-dimensional Scaling (MDS) and cluster analysis. MDS used the group average linking method. Clusters were tested

using the SIMPROF procedure and the SIMPER procedure was applied to identify the key species.

3. Results

3.1. Oceanographic context of different stations/locations

During each cruise, an oceanographic transect ran from south of the Southern Boundary, within the Seasonal Ice Zone northwards across the Scotia Sea, crossing the Southern Boundary and SACCF (Fig. 2, Venables et al., 2012). The North Scotia Sea (NSS) station showed characteristics of the very southern edge of the PF, especially in JR161. The Georgia Basin (GB), downstream of South Georgia, is north of the Scotia Ridge but, due to a retroflexion of the flow, it had a slightly lower dynamic height than the NSS station and was more similar, by water mass properties, to the stations in the middle of the Scotia Sea. The physical oceanography is discussed in more detail in Venables et al. (2012).

3.2. Species composition and distribution

A total of 141 non-target net hauls were undertaken (Table 1; Fig. 1) during the three cruises. Weather and operational limitation meant that it was not possible to sample all stations in all cruises. The western Scotia Sea station was only sampled in the first cruise. An additional 82 target net hauls were undertaken at stations, mostly targeting aggregations of krill, but some targeted mesopelagic fish aggregations, particularly at the PF.

In all net hauls a total 9369 teleost fish were captured, representing 43 species in 17 families (Tables 2 and 3), the majority of which 7852 (83%) were caught in non-target hauls. The dominant families were the Myctophidae (6961 specimens (74.3%; 21 species) and Bathylagidae (1467 specimens (15.7%; 4 species). Owing to its small size, the Gonostomatidae (*Cyclothone* spp.) were probably under-sampled by the RMT25, but still represented 5.5% of the catch (515 individuals). Target hauls accounted for 1517 fish, with *Gymnoscopelus braueri* and *Electrona carlsbergi* accounting for 47% of them. The only species that was caught more frequently in target hauls was *Electrona*

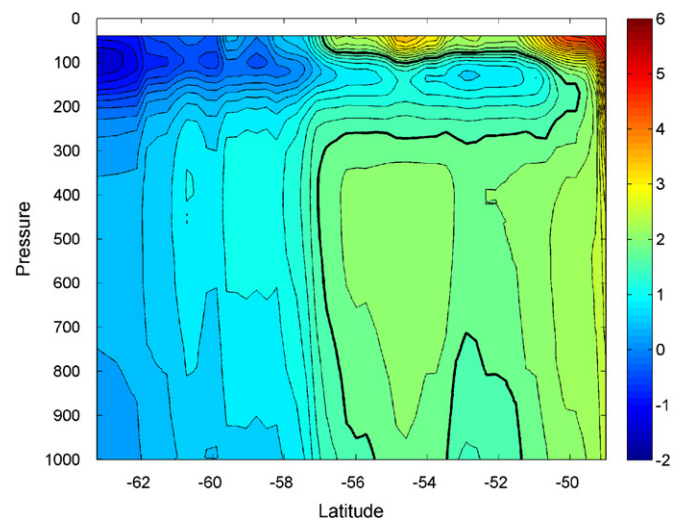


Fig. 2. Argo-derived temperature section along the sampling transect in the Scotia Sea. Profiles were averaged within dynamic height bins and then plotted against latitude using the average dynamic height for each position along the transect. The surface 40 m is excluded as seasonal effects are not accounted for. The temperature scale (°C) is on the right-hand side.

carlsbergi, which was caught in acoustically identified target hauls in the region of the PF.

Myctophids were caught at all sampling locations and from all depths (at night) (Figs. 3 and 4). Among the myctophids the most abundant species were *Electrona antarctica*, *Gymnoscopelus braueri*, *Krefflichthys anderssoni* and *Protomyctophum bolini* (Table 2), which were caught at all stations, although *K. anderssoni* and *P. bolini* were only caught in small numbers at the more southerly stations. *G. nicholsi* was also caught across the latitudinal range, but only in small numbers. Three species (*G. fraseri*, *P. tenisoni* and *E. carlsbergi*) were rarely caught in the SSS stations, but were more abundant

further north. Some species were caught in reasonable numbers throughout the sampled depth range (e.g. *E. antarctica*, *G. braueri*), whilst others (e.g. *E. carlsbergi*, *P. tenisoni* and *P. choriodon*) were largely confined to the upper 400 m (Tables 2 and 4). *Krefflichthys anderssoni* was principally caught deeper than 200 m, whilst *P. bolini* was mostly (85%) caught between 200 and 400 m.

In some myctophid species the sampled size range was limited to adults (e.g. *E. carlsbergi*, *P. bolini*, *P. choriodon*), whilst in other species (*E. antarctica*, *G. braueri*, *K. anderssoni*) a greater range of sizes were sampled (Table 2).

Bathylagids were particularly abundant in the SSS and MSS stations and also at the PF (Table 3; Figs. 5 and 6) and were generally caught in the deeper nets (Table 4). Specific identification of the bathylagids was difficult, but preliminary DNA sequence analysis using the mitochondrial cytochrome oxidase I gene identified four phylogenetically reciprocally monophyletic groups that corresponded to *B. antarcticus*, *B. tenuis*, *B. gracilis*, plus another potentially undescribed species (SB Piertney, University of Aberdeen unpublished). The four putative species occurred in the northern stations, while there was a single species, which was assumed to be *Bathylagus antarcticus*, in the southern Scotia Sea. The other species caught in large numbers were *Cyclothone* spp., which were caught in deeper hauls and *Notolepis coatsi*, the majority of which were larvae.

3.3. Day–night comparisons

Comparative day–night RMT25 net hauls were undertaken during the spring (JR161) and summer (JR177) cruises (see Figs. 3–6). Clear differences between day and night hauls were apparent, with consistently more fish caught during night than during day. Catches in the upper 400 m were generally low during daylight. Some species (e.g. *Electrona carlsbergi*) were rarely caught in the top 400 m in daylight, but were abundant at night, particularly in target hauls. The day–night difference is probably best illustrated with

Table 1
Numbers of RMT25 depth-discrete non-target net hauls in the Scotia Sea during three cruises on the RRS James Clark Ross. D=day; N=night.

Depth (m)	Southern Scotia Sea		Western Scotia Sea		Mid Scotia Sea		Northern Scotia Sea		Georgia Basin		Polar Front	
	D	N	D	N	D	N	D	N	D	N	D	N
JR161												
0–200	3	2	1	1	1	1	1	1		2	1	1
201–400	3	2	1	1	1	1	1	1		1	1	1
401–700	2	1	1	2	1	1	1	1	1		1	1
701–1000	2	2	1		1	1	1	1	1		1	1
JR177												
0–200	2	2			1	1	1	1	3		1	2
201–400	3	2			1	1	1	1	3		1	2
401–700	3	2			2	1	1	1	2			2
701–1000	3	2			1	1	1	1	2			2
JR200												
0–200		3			3		1					2
201–400		2			3		1					2
401–700		3			3		1		1			2
701–1000		2			3		1		1			2

Table 2
Myctophid species caught in RMT25 net hauls in each region in each season, with depth ranges, size ranges and numbers caught. SSS=south Scotia Sea; WSS=west Scotia Sea; MSS=mid Scotia Sea; NSS=north Scotia Sea; GB=Georgia Basin & PF=Polar Front.

Species name	Spring: JR161						Summer: JR171						Autumn: JR200						Depth range	SL range (mm)	Total numbers
	SSS	WSS	MSS	NSS	GB	PF	SSS	WSS	MSS	NSS	GB	PF	SSS	MSS	NSS	GB	PF				
<i>Electrona antarctica</i>	459	5	66	10	61	3	625	–	180	44	230	4	419	177	9	13	47	1–1010	24–115	2352	
<i>Electrona carlsbergi</i>	–	30	–	210	2	2	–	3	78	15	1	175	–	30	–	–	14	1–1008	68–88	560	
<i>Electrona subaspera</i>	–	–	–	–	–	1	–	–	–	–	–	2	–	–	–	–	2	16–402	107–119	5	
<i>Electrona</i> sp.	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	19–178	36–37	2	
<i>Gymnoscopelus bolini</i>	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	–	1	199–1001	178–208	3	
<i>Gymnoscopelus braueri</i>	136	62	61	46	80	62	100	–	54	34	182	214	212	197	10	5	96	1–1010	34–162	1551	
<i>Gymnoscopelus fraseri</i>	–	–	–	2	5	6	–	–	–	–	70	20	1	4	6	1	29	3–704	39–115	144	
<i>Gymnoscopelus hintonoides</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	399–701	170	1	
<i>Gymnoscopelus nicholsi</i>	10	1	5	8	1	5	8	–	5	1	16	–	5	4	2	–	1	8–1002	34–165	72	
<i>Gymnoscopelus opisthopterus</i>	16	–	–	–	–	–	18	–	7	–	11	–	1	–	–	–	–	199–1010	55–187	53	
<i>Gymnoscopelus piabilis</i>	–	1	5	–	–	3	–	–	–	–	–	–	–	–	–	–	–	16–703	80–149	9	
<i>Gymnoscopelus</i> sp.	2	–	–	1	1	–	–	–	1	2	2	–	–	–	–	–	–	191–1010	37–106	9	
<i>Krefflichthys anderssoni</i>	2	153	24	167	172	115	2	–	11	50	127	2	–	7	30	45	146	1–1010	15–74	1053	
<i>Lampadena</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	400–705	123	1	
<i>Lampanyctus</i> sp.	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	695–992	43	1	
<i>Nannobranchium achirus</i>	1	12	3	8	11	12	–	–	–	3	8	–	1	5	9	2	13	191–1005	65–167	88	
<i>Protomyctophum andriaeshevi</i>	–	–	–	–	1	9	–	–	–	–	–	1	–	–	–	–	–	199–702	44–53	14	
<i>Protomyctophum bolini</i>	14	49	23	44	59	83	21	–	11	10	139	16	15	10	15	–	206	1–1008	23–66	715	
<i>Protomyctophum choriodon</i>	–	–	–	–	–	–	–	–	–	–	31	19	8	2	5	–	–	3–701	55–85	65	
<i>Protomyctophum gemmatum</i>	–	–	–	3	–	–	–	–	–	1	–	–	–	–	–	–	–	398–704	54–66	4	
<i>Protomyctophum luciferum</i>	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	704–997	33	1	
<i>Protomyctophum parallelum</i>	–	2	–	4	–	22	–	–	–	–	–	–	–	–	–	–	1	398–705	29–53	29	
<i>Protomyctophum tenisoni</i>	–	11	3	36	9	22	–	–	–	–	–	99	–	–	–	–	41	10–998	32–55	221	
<i>Protomyctophum</i> sp.	1	1	–	4	–	–	–	–	–	–	–	2	–	–	–	–	–	192–980	21–45	8	

Table 3

Non-mycetophid species caught in RMT25 net hauls in each region in each season, with depth ranges, size ranges and numbers caught. SS=south Scotia Sea; WS=west Scotia Sea; MS=mid Scotia Sea; NS=north Scotia Sea; GB=Georgia Basin and PF=Polar Front.

Species	Family	Spring: JR161						Summer: JR177					Autumn: JR200					Depth Range (m)	SL (mm)	Number
		SS	WS	MS	NS	GB	PF	SS	MS	NS	GB	PF	SS	MS	NS	GB	PF			
<i>Bathylagus antarcticus</i>	Bathylagidae	270	-	-	-	-	-	370	-	-	-	-	181	-	-	-	-	1-1010	35-190	821
<i>Bathylagus</i> spp.		-	22	34	10	17	39	-	174	18	108	2	-	163	4	3	52	12-1010	28-173	472
<i>Icichthys australis</i>	Centrolophidae	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	14-205	295	1
<i>Champocephalus gunnari</i>	Channichtyidae	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	16-206	44	2
<i>Pseudoscopelus</i> sp.	Chiasmodontidae	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	702-1006	115	1
<i>Paradiplospinus gracilis</i>	Gempylidae	6	-	1	-	-	-	2	1	-	2	2	9	3	-	-	-	1-1001	289-415	26
<i>Cyclothone</i> spp.	Gonostomatidae	4	11	41	34	6	26	50	50	68	87	-	25	7	25	24	57	1-1010	25-93	515
<i>Cynomacurus piriei</i>	Macrouridae	1	3	4	1	-	3	-	2	9	2	-	-	2	1	-	1	1-1010	79-332	29
Macrouridae sp.		-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	693-1002	73-79	2
<i>Poromitra crassiceps</i>	Melamphidae	-	4	-	8	3	4	-	-	2	6	-	-	1	-	2	5	1-1008	40-114	35
<i>Sio nordenskjoeldii</i>		-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	399-998	78-92	2
<i>Nansenia antarctica</i>	Microstomatidae	-	3	-	2	2	-	-	2	1	5	-	-	1	1	-	1	3-997	65-167	18
<i>Muraenolepis</i> sp.	Muraenolepididae	-	-	-	-	-	-	-	-	1	-	-	-	3	-	1	-	3-212	38-51	5
<i>Nemichthys curvirostris</i>	Nemichthyidae	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	400-705	607-607	2
<i>Notothenia rossii</i>	Nototheniidae	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	399-701	35	1
<i>Notolepis coatsi</i>	Paralepididae	41	-	-	2	2	2	18	20	33	57	-	19	2	1	3	13	1-1006	179-361	213
<i>Benthalbella elongata</i>	Scopelarchidae	-	-	1	-	1	-	-	-	2	1	1	2	2	-	-	-	14-998	134-251	10
<i>Benthalbella macropinna</i>		-	1	-	2	1	-	-	-	-	2	-	-	4	1	1	5	201-1005	142-231	17
<i>Borostomias antarcticus</i>	Stomiidae	-	4	3	8	2	1	-	-	6	5	-	-	1	1	-	4	1-1008	107-224	35
<i>Stomias gracilis</i>		-	-	-	3	-	6	-	-	1	1	-	-	-	-	-	2	16-998	144-267	13
<i>Stomias</i> sp.		-	-	-	-	-	-	-	-	-	2	-	-	2	-	-	1	399-1003	139-225	5
<i>Melanostigma gelatinosum</i>	Zoarcidae	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	199-400	-	6
Unidentified fish	Unidentified	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	400-1000	25-30	3

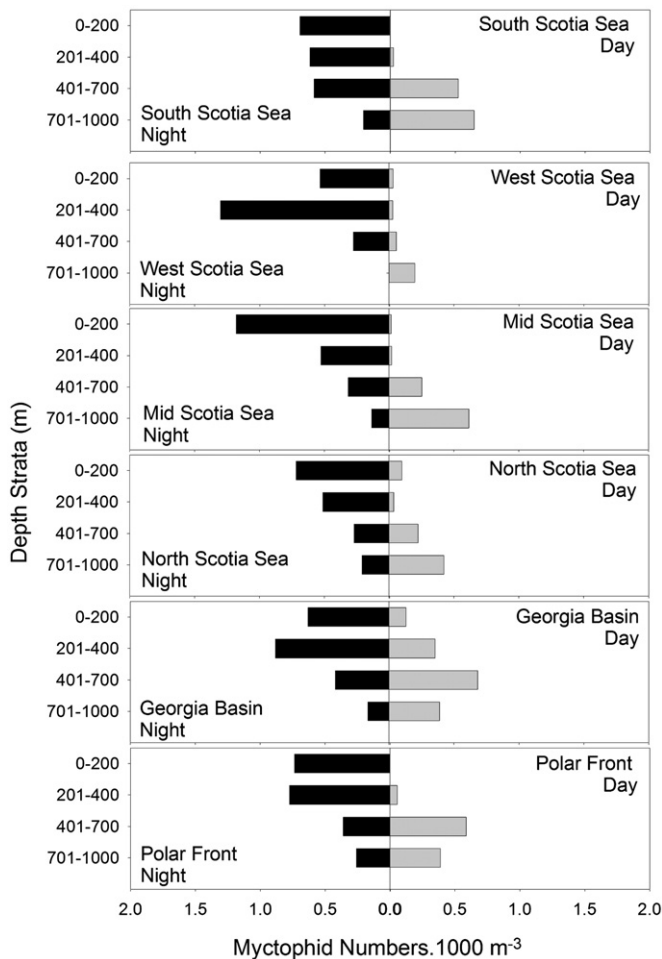


Fig. 3. Abundance of myctophid fish in each depth zone and each station. Data from non-target hauls only. No day hauls undertaken during JR200.

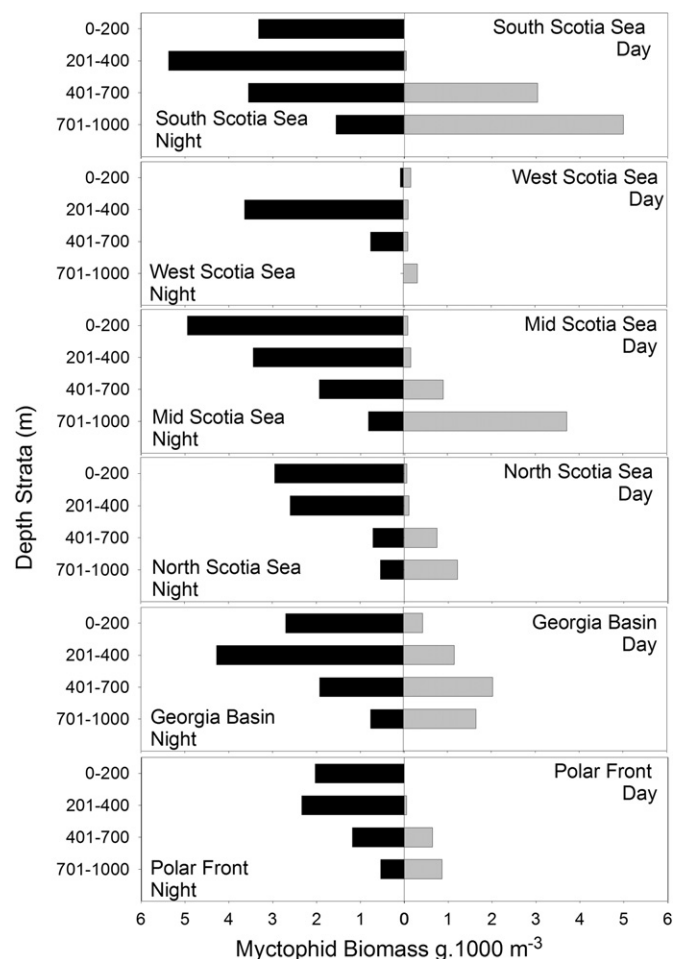


Fig. 4. Biomass of myctophid fish in each depth zone and each station. Data from non-target hauls only. No day hauls undertaken during JR200.

Table 4
Numbers of each mesopelagic fish species caught in each depth zone during stratified RMT 25 net hauls in the Scotia Sea.

Species	Family	Depth zone			
		0–200	201–400	401–700	701–1000
<i>Bathylagus antarcticus</i>	Bathylagidae		78	229	523
<i>Bathylagus</i> spp.		30	87	247	264
<i>Ichthyos australis</i>	Centrolophidae	1			
<i>Champscephalus gunnari</i>	Channichthyidae	2			
<i>Pseudoscopelus</i> sp.	Chiasmodontidae				1
<i>Paradiplospinus gracilis</i>	Gempylidae	7	5	7	6
<i>Cyclothone</i> spp.	Gonostomatidae	3	9	194	305
<i>Cynomacurus piriei</i>	Macrouridae	1		2	24
Macrouridae sp.					2
<i>Poromitra crassiceps</i>	Melamphaidae			8	26
<i>Sio nordenskjoeldii</i>				1	1
<i>Nansenia antarctica</i>	Microstomatidae	1	2	14	1
<i>Muraenolepis</i> sp.	Muraenolepididae	5			
<i>Electrona antarctica</i>	Myctophidae	596	385	823	523
<i>Electrona carlsbergi</i>		396	141	12	2
<i>Electrona subaspera</i>		3	2		
<i>Electrona</i> sp.		2			
<i>Gymnoscopelus bolini</i>			1	1	1
<i>Gymnoscopelus braueri</i>		784	459	184	118
<i>Gymnoscopelus fraseri</i>		85	53	6	
<i>Gymnoscopelus hintonoides</i>				1	
<i>Gymnoscopelus nicholsi</i>		26	33	12	1
<i>Gymnoscopelus opisthopterus</i>			1	11	41
<i>Gymnoscopelus piabilis</i>		3	1	5	
<i>Gymnoscopelus</i> sp.			1	5	2
<i>Krefflichthys anderssoni</i>		67	202	397	352
<i>Lampadena</i> sp.				1	
<i>Lampanyctus</i> sp.					1
<i>Nannobranchium achirus</i>			9	40	39
<i>Protomyctophum andriashevi</i>		1	12	1	
<i>Protomyctophum bolini</i>		62	605	41	5
<i>Protomyctophum choriodon</i>		54	10	1	
<i>Protomyctophum gemmatum</i>				4	
<i>Protomyctophum luciferum</i>					1
<i>Protomyctophum parallelum</i>				29	
<i>Protomyctophum tenisoni</i>		211	1	8	1
<i>Protomyctophum</i> sp.		2	1	4	1
<i>Nemichthys curvirostris</i>	Nemichthyidae			2	
<i>Notothenia rossii</i>	Nototheniidae			1	
<i>Notolepis coatsi</i>	Paralepididae	6	40	108	56
<i>Benthalbella elongata</i>	Scopelarchidae	2	4	3	1
<i>Benthalbella macropinna</i>			1	11	5
<i>Borostomias antarcticus</i>	Stomiidae		1	21	12
<i>Stomias gracilis</i>		2	3	7	1
<i>Stomias</i> sp.		2		2	1
<i>Melanostigma gelatinosum</i>	Zoarcidae		6		

data on *Gymnoscopelus braueri*. No *G. braueri* were caught in the upper 200 m in daylight, but more fish were caught in the top 200 m at night (294), than in all sampled depths during the day (133). Given the clear day–night differences and lack of fish caught in the top 400 m in daylight, effort was focussed on night-time hauls in the autumn cruise (JR200).

3.4. Patterns in species composition

Shannon–Wiener ($\log e$) diversity index was calculated for each net haul which caught > 15 fish. Species diversity was

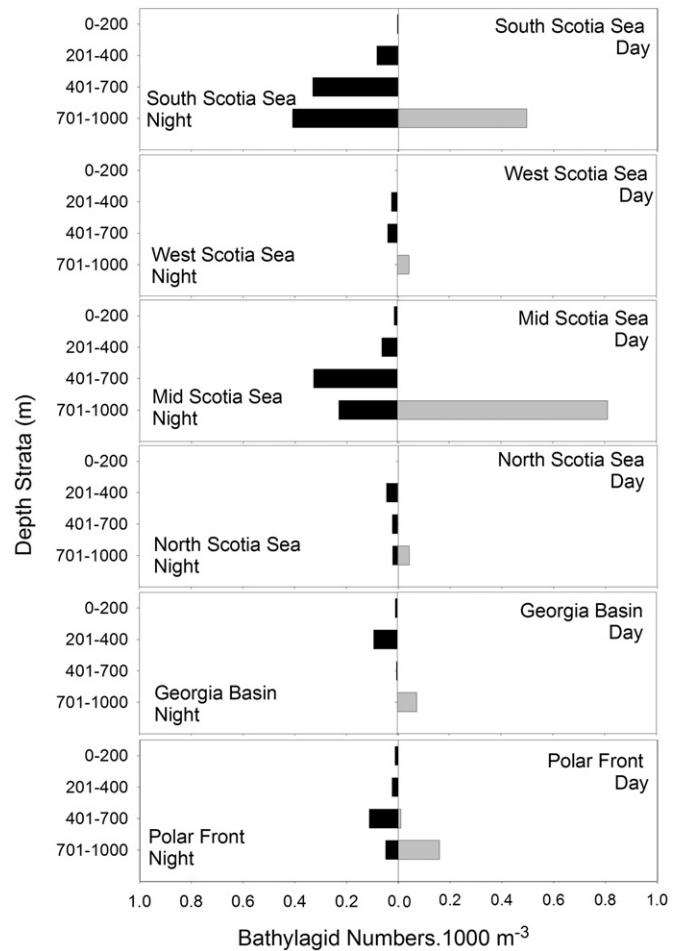


Fig. 5. Abundance of bathylagid fish in each depth zone and each station. Data from non-target hauls only. No day hauls undertaken during JR200.

significantly correlated with latitude (Spearman's $r=0.565$; $p < 0.01$), SST ($r=0.532$; $p < 0.01$) and net temperature ($r=0.637$; $p < 0.01$), but not with mean net depth ($r=0.132$) or water depth ($r=0.228$) (Fig. 7). In general the more southerly, cooler stations had lower diversity, with catches dominated by *Electrona antarctica*, *Gymnoscopelus braueri* and *Bathylagus antarcticus*. Further north, in warmer conditions, diversity increased.

Bray–Curtis similarities between night-time, depth stratified, non-target RMT25 hauls revealed significant structure to the data. The MDS plots reveal distinct patterns with respect to both sampling location (Fig. 8A) and depth (Fig. 8B). In the MDS plot there is a clear gradation with depth range (Fig. 8B), but the patterns with area (Fig. 8A) are less clear. Samples from the SSS and MSS formed a cluster, whilst samples from the NSS had affinity with those from the PF. Samples from the GB were intermediate between these groups.

Cluster analysis (using SIMPROF) revealed five significant clusters (Fig. 8C). The principal species in each cluster were identified with the SIMPER routine (Table 5). Cluster 1 included 13 net hauls from deep water (mostly 700–1000 m) in the SSS and MSS, with the dominant species being *Bathylagus antarcticus* and *Electrona antarctica*. Cluster 2 was dominated by *E. antarctica* and *Gymnoscopelus braueri* and included net hauls from the surface to 700 m, but mostly in the upper 400 m from the SSS and MSS. Cluster 3 included three net hauls dominated by *Electrona antarctica*, two from deep hauls in the SSS and one from the GB. Cluster 4 included shallow nets (0–400 m) from northern stations (NSS, GB and PF), dominated by *G. braueri*, *Protomyctophum bolini*

and *E. antarctica*. Clusters 5 included 18 deep nets from the NSS, GB and PF. The dominant species in Cluster 5 were *Krefflichthys anderssoni* and *Cyclothone* sp.

3.5. Estimates of biomass and abundance of myctophids and bathylagids

Using the night time biomass and abundance data for myctophids, the integrated biomass (upper 1000 m) under each m² of sea-surface was similar in all sampled areas (see Figs. 3 and 4), giving an average of 2.23 g m⁻² (standard deviation 0.79). Assuming this is

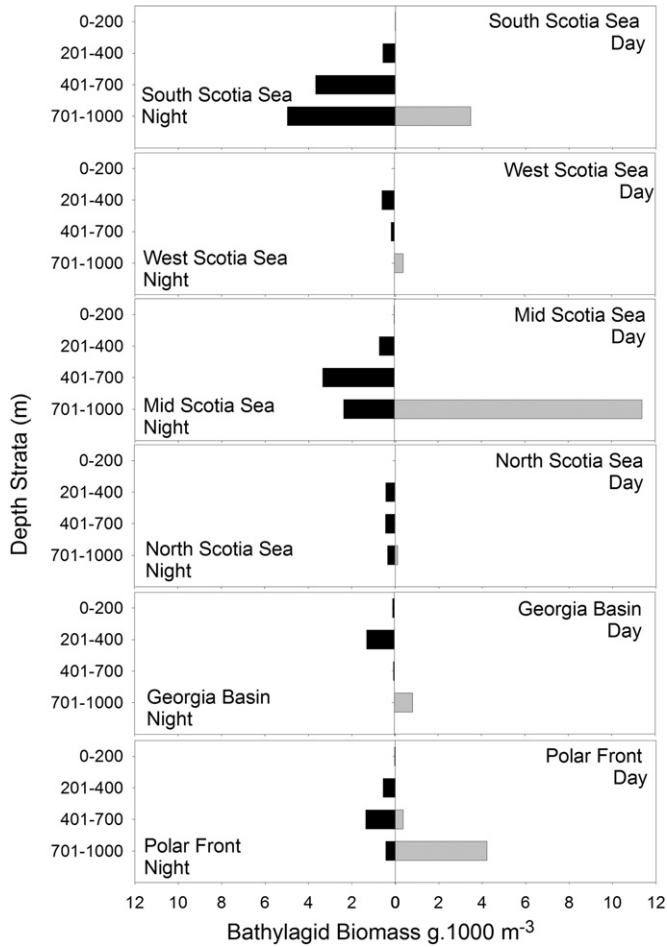


Fig. 6. Biomass of bathylagid fish in each depth zone and each station. Data from non-target hauls only. No day hauls undertaken during JR200.

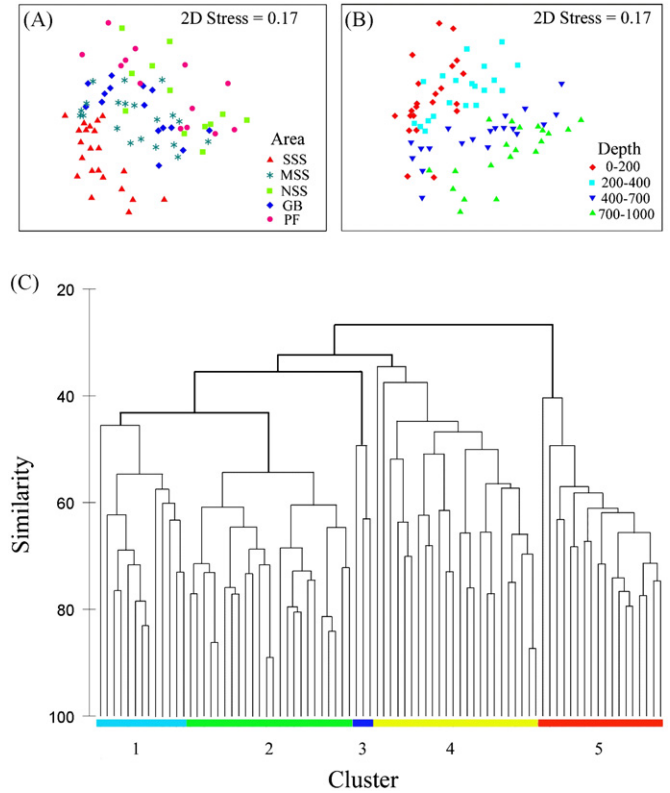


Fig. 8. MDS plot of the Bray-Cutis similarity between net hauls, showing sampling location (A) and depth (B) as factors. Cluster analysis of the same data showing clusters identified by SIMPROF routine (C). Based on night hauls only, with > 15 fish caught.

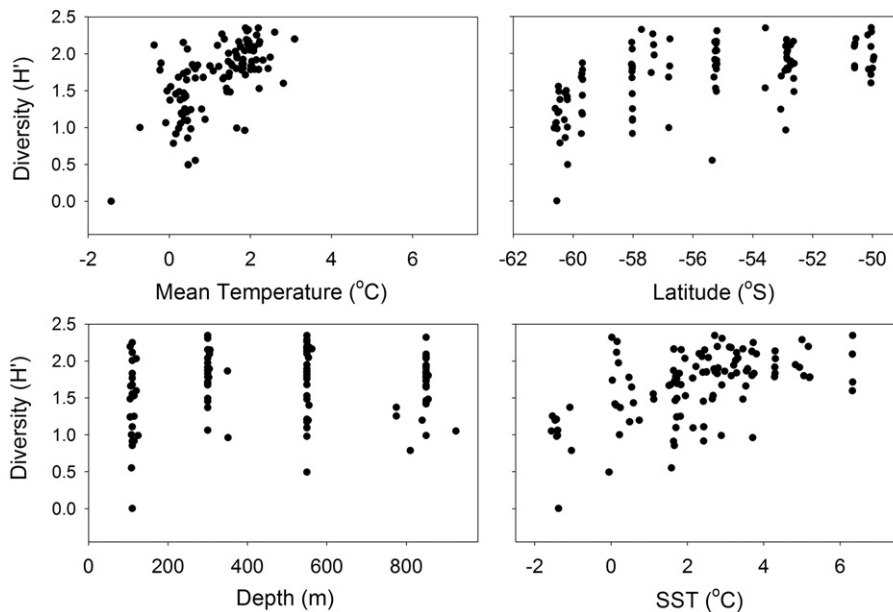


Fig. 7. Relationship between species diversity and net temperature, latitude, depth and sea-surface temperature. Based on non-target net hauls which captured > 15 fish.

Table 5
Clusters identified by the SIMPROF routine in PRIMER (see Fig. 7).

Depth Area	Cluster				
	1	2	3	4	5
	400–1000	0–700	0–200	0–400	400–1000
	Mid-SS	Mid-SS	South-SS	North-SS	North-SS
	South-SS	South-SS	SS	PF SG	PF SG
<i>Electrona antarctica</i>	28.51	48.45	90.8	17.48	11.56
<i>Bathylagus antarcticus</i>	46.75	11.72			
<i>Gymnoscopelus braueri</i>	5.55	33.44		29.19	5.64
<i>Krefflichthys anderssoni</i>				7.63	30.45
<i>Cyclothone</i> spp.	10.39				23.98
<i>Bathylagus</i> spp.					11.71
<i>Protomyctophum bolini</i>				18.59	
<i>Gymnoscopelus fraseri</i>				6.56	

Values are placed against the contributory species to each cluster identified by the SIMPER method, with bold indicating the main contributors.

representative of the Scotia Sea, with an area of 2 million km² (Hewitt et al., 2004), it gives a biomass estimate of 4.5 million tonnes of myctophids in the upper 1000 m of the Scotia Sea.

The variability in bathylagid abundance was considerably greater (Figs. 5 and 6), with a night mean of 0.92 g m⁻², but a standard deviation of 0.85. Given the high variability, the mean value is less likely to be representative, but would equate to 1.8 million tonnes in the upper 1000 m of the Scotia Sea.

4. Discussion

This study, which sampled the upper 1000 m of the Scotia Sea from the ice-edge to the Polar Front in three seasons (and years), provides a comprehensive baseline for the distribution of mesopelagic fish in the Southern Ocean. In common with other oceanic areas (Gjøsaeter and Kawaguchi, 1980), the ichthyofauna of the upper mesopelagic zone of the Scotia Sea (upper 500 m) is dominated by myctophids (see also Collins et al., 2008; Piatkowski et al., 1994; Pusch et al., 2004). Many of the species caught have broad circum-Antarctic distributions and have also been reported in similar assemblages in other parts of the Southern Ocean (Duhamel, 1998; Duhamel et al., 2000, 2005; Hulley, 1981; Pakhomov et al., 1996; Piatkowski et al., 1994; Pusch et al., 2004). In this study myctophids were caught in all parts of the Scotia Sea and clearly have an important and widespread role as secondary consumers. In the lower mesopelagic zone (400–1000 m), fish of the family Bathylagidae were dominant, although myctophids were still present in deeper nets. As the study primarily focussed on oceanic areas, the larval stages of shelf dwelling species were poorly represented in comparison to studies in the proximity of continental shelves (e.g. Pusch et al., 2004).

The clear day–night differences in the vertical distribution of myctophids are probably a consequence of both vertical migration (Robison, 2003) and net avoidance in the upper 400 m (see Fielding et al., 2012). Whilst the RMT25 is a reasonably large net, it is clear that larger myctophids (species and individuals) are capable of avoiding the net in the upper 400 m in daylight. The depth integrated myctophid abundance and biomass was greater at night at all locations. It is possible that myctophids migrate deeper than 1000 m during daylight, but it is much more likely that they are avoiding the relatively slow RMT25 net in daylight.

Target hauls conducted during the day also failed to catch acoustically detected aggregations of fish in the upper 400 m, which is consistent with previous work in the northern Scotia Sea (Collins et al., 2008). Further evidence of net avoidance comes from predators, such as king penguins (*Aptenodytes patagonicus*), that are able to catch myctophid prey in the upper 300 m during daylight (Scheffer et al., 2010) in areas that the RMT25 is not able to catch any fish. Larger pelagic trawls may be capable of catching myctophids in daylight (Collins et al., 2008) but, even with an IYGPT net, Duhamel (1998) and Duhamel et al. (2005) still had poor catches of mesopelagic fish in the upper 400 m on the Kerguelen Plateau during daylight. Furthermore, such nets cannot easily sample discrete depths and captured fish are often in poor condition. Duhamel (1998) also found that daylight catches off Kerguelen were of small sized fish, which he attributed to vertical migration, but it is possible that at least some larger fish were present, but able to avoid the net. Perhaps the best way of resolving the net-avoidance question would be using a video camera attached to the upper bar of the RMT25 or headline of an IYGPT.

Vertical migration is a common phenomenon in mesopelagic fish (Watanabe et al., 1999) and Southern Ocean fish appear to be no exception (Robison, 2003). There were indications of diel vertical migration in some of the species in this study (see also Collins et al., 2008), but the broad depth ranges sampled by the nets, the sequential (rather than synchronous) sampling of different depths, and the putative net avoidance in the upper layers during daylight make it difficult to accurately establish patterns. There may also be latitudinal variability in vertical migrations, associated with different water masses and fronts. The greater abundance of bathylagids in night hauls was certainly indicative of diel vertical migration, with fish presumably inhabiting depths greater than 1000 m during the day and moving closer to the surface at night. Ontogenetic vertical migrations have also been indicated in some species (Collins et al., 2008; Moteki et al., 2009), but species specific patterns were not addressed in this study.

Given the putative net avoidance issues during daylight hauls, analysis of species diversity and composition and of biomass and abundance utilised night hauls only. The ichthyofauna diversity was lower in the cold water close to the ice-edge, and was dominated by *Electrona antarctica*, *Gymnoscopelus braueri* and *Bathylagus antarcticus*, with *Protomyctophum bolini*, *G. nicholsi* and *G. opisthopterus* also present in small numbers. Hauls in the upper 200 m in the southern Scotia Sea, where water temperatures were frequently below zero, were dominated by *E. antarctica*, which may be more tolerant to cold temperatures than the other species. The species composition in the southern Scotia Sea is consistent with the work of Pusch et al. (2004) north of King George Island and other studies in oceanic areas at high latitude in the Southern Ocean (Donnelly and Torres, 2008; Iwami and Kubodera, 1990; Moteki et al., 2009). Further north diversity increased with greater numbers of *G. nicholsi*, *P. bolini* and *Krefflichthys anderssoni* and with the addition of other more northerly species (e.g. *E. carlsbergi*, *P. choriodon*, *P. tenisoni* and *G. fraseri*), which is consistent with previous studies in similar locations (Collins et al., 2008; Piatkowski et al., 1994).

Species composition of net hauls was strongly related to both depth and location of capture (see MDS plots in Fig. 8). The mesopelagic fish community is clearly depth stratified with some species (in the sampled locations) occupying distinct depth bands. Across the latitudinal range *Protomyctophum bolini* was almost exclusively caught between 200 and 400 m, which is consistent with data from Collins et al. (2008) to the NW of South Georgia, although the species has been reported in the upper 200 m at night (Piatkowski et al., 1994). It is possible that the species is

intolerant to water less than 1.5 °C and remains just below the cold winter water layer (see Fig. 2). *Protomyctophum choriodon*, *P. tenisoni* and *E. carlsbergi* were caught primarily in the upper 200 m and may be associated with warm water eddies that emanate from the Polar Front. The deeper layers were dominated by the bathylagids, although the distribution of many myctophids extended to deeper layers during day and night.

Changes in species composition across the latitudinal transect were closely related to oceanographic features (Venables et al., 2012). Changes in community structure were not continuous across the latitudinal gradient, with the NSS station (SW of South Georgia) more similar to PF stations than those in the Georgia Basin (GB). The oceanography of this area is particularly dynamic, with the location of the PF highly variable and with warm water eddies forming (Venables et al., 2012). The GB area was oceanographically similar to the mid Scotia Sea area, whilst the NSS had characteristics of the PF (particularly in spring) and this was reflected in the mesopelagic fish community. It was notable that large numbers of the normally PF associated *E. carlsbergi* (Hulley, 1981) were caught in the northern Scotia Sea in the spring cruise and in both northern- and mid-Scotia Sea in the summer. *E. carlsbergi* otoliths have been reported in the diet of fur seals at Livingston Island in the South Shetlands (Osman et al., 2004), so the presence of *E. carlsbergi* in the southern Scotia Sea may not be unusual. Ward et al. (2012) detected a faunal transition associated with the SACCF, which is generally consistent with the pattern seen here, however the SACCF does move between seasons and years.

Whilst seasonal effects on community structure were not evident from the MDS plots, there was evidence of seasonal movements in some species. For instance, whilst *P. choriodon* was absent from all hauls during spring, it was caught at the PF in summer and further south in autumn. *Protomyctophum choriodon* is usually caught in the upper 300 m and although primarily associated with the PF and further north (Hulley, 1981), it regularly occurs in fur seal diets sampled from South Georgia in late summer and autumn (Reid et al., 2006). The abundance of *P. choriodon* in fur seal diets is strongly correlated with sea-surface temperature (Reid et al., 2006), which supports the idea that it migrates seasonally, often associated with periods of elevated SST.

Whilst the data from non-target net hauls in this study suggested that the biomass and abundance of myctophids was consistent across the Scotia Sea, there is evidence from multi-frequency acoustics (Fielding et al., 2012) and net hauls (Pakhomov et al., 1996) of elevated abundance at frontal zones. Where aggregations are detected acoustically, it is likely to be the species with well-developed swim-bladders (e.g. *E. carlsbergi*, *Protomyctophum* spp. and *K. anderssoni* (Marshall, 1960)) that are present. Species with small or residual swim-bladders (*Gymnoscopelus* spp. and *E. antarctica* (Marshall, 1960)) will be difficult to distinguish from macro-zooplankton. Taking the data from the net hauls and extrapolating to the Scotia Sea region, indicates that the total biomass of myctophids in the upper 1000 m is approximately 4.5 million tonnes, which is around 10% of the estimated biomass of krill in the same area (Hewitt et al., 2004). Myctophids are therefore likely to have a significant impact as predators of macro-zooplankton, including Antarctic krill.

The role of myctophids in the Southern Ocean ecosystem has been the source of considerable debate, particularly with respect to Antarctic krill (Pakhomov et al., 1996; Pusch et al., 2004; Shreeve et al., 2009). Whilst krill were not a major part of the diets of myctophids in the northern Scotia Sea (Shreeve et al., 2009), this may be a consequence of the predominance of large krill in this area and it is likely that the smaller krill that are available further south are important prey for many myctophid

species (see Pusch et al., 2004). Determining the diets of the abundant myctophid species at different sizes and across a broad latitudinal range will help resolve this question. Assuming myctophids consume 1.5% body weight per day (see Pakhomov et al., 1996); the Scotia Sea myctophids are estimated to consume approximately 25 million tonnes of macro-zooplankton per year, which could potentially include a significant amount of krill.

Myctophids have been targeted by commercial fisheries in the Southern Ocean, notably in the northern Scotia Sea area where ex-Soviet Union vessels targeted *Electrona carlsbergi* at or just south of the Polar Front to the north of South Georgia (Kock, 1991). Catches peaked at around 30,000 tonnes in the 1988/89 season, with the fish converted to meal, but since 1990 there has not been a targeted fishery. If a fishery for myctophids develops again, it will need careful management and consideration of impacts on dependent predators such as king penguins.

Data on the Bathylagidae are extremely limited, but the data from this study suggests they are highly abundant and potentially ecologically important. The bathylagids are taxonomically problematic, with the characters used to separate species difficult to determine even in well-preserved specimens. Preliminary genetic studies indicate that a single species was present in the southern Scotia Sea, which we assume is *Bathylagus antarcticus*. Further north, 3 additional species were caught, which were probably *B. tenuis*, *B. gracilis* and a putative new species. The ecological role of the bathylagids is poorly known but, given the abundance of this family, studies of their role as both predator and prey should be a high priority.

Finally, it is clear that both myctophids and bathylagids play a significant role in the ecology of the Southern Ocean and, through the consumption of primary consumers and the vertical migrations of certain species, play a major role in exporting carbon from the surface layers to deeper water.

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