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Latitudinal variation of demersal fish assemblages in the western Ross Sea

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Abstract: Demersal fishes were sampled using a large fish trawl during two surveys carried out in February and March 2004 and 2008 in the Ross Sea, and around seamounts and islands just to the north at 66°S. The distribution and abundance of 65 species collected in these surveys were examined to determine if demersal fish communities varied throughout the area, and what environmental factors might influence this. Species accumulation with sample frequency did not reach an asymptote, but the rate of new species was low suggesting data were adequate for describing the main components of the communities. Three broad assemblages were identified, in the southern Ross Sea (south of 74°S), central–northern Ross Sea (between latitudes 71°–74°S), and the seamounts further north (65°–68°S) where some species more typical of sub-Antarctic latitudes were observed. Multivariate analyses indicated that environmental factors of seafloor rugosity (roughness), temperature, depth, and current speed were the main variables determining patterns in demersal fish communities.

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Key words: Antarctica, environmental factors, fish communities, seamounts

Introduction

In over one hundred years of research there has been limited scientific sampling of fishes in the Ross Sea, with few systematic surveys aimed at describing the community of fishes and how the community might be structured by environmental factors. Most of the sampling has been opportunistic or has been limited by resources or conditions. Sampling the Ross Sea for fishes presents numerous challenges, because the area is remote, the Ross Sea has a permanent ice zone in southern areas, and it is subject to seasonal pack ice which in some years can be extensive. Hence our knowledge of the fish fauna, and structure of fish communities, is limited.

Major studies of the Ross Sea fish fauna in recent decades include Eastman & Hubold (1999) who reported on 979 specimens from 20 bottom trawl stations from the south-western Ross Sea. They recorded a total of 47 species including four new species, and concluded that "even in relatively shallow water, knowledge of specific and intraspecific diversity in the Ross Sea fauna is incomplete". Donnelly *et al.* (2004) reported 45 species of benthic and pelagic fishes sampled from 41 midwater and six bottom trawl stations in the eastern Ross Sea, and found highest diversity between 450 and 500 m depth. Other historical fish sampling was summarized in Headland (1990) and Eastman & Hubold (1999).

A number of studies have investigated whether faunal composition in the Antarctic marine region may vary with latitude, but most have focused on benthic invertebrate communities (e.g. Cummings *et al.* 2006, De Domininco *et al.* 2006, Thrush *et al.* 2006) and results are mixed (Cummings *et al.* this issue). Studies that have examined geographical and depth distribution of Ross Sea fishes include those of La Mesa *et al.* (2006) who compared site, depth, and diversity of plunderfishes (Artedidraconidae) using an Agassiz trawl at five sites spanning four degrees latitude from Cape Adare to Cape Russell at depths of 100–500 m. They reported that sampling site was the main factor affecting species composition with both north–south and depth related trends in the distribution of species. Vacchi *et al.* (2000) described species composition, abundance, depth distribution, and biology for fishes sampled down to 700 m using gill and trammel nets, longlines and traps in the area of Terra Nova Bay. They recorded 26 species with the highest diversity at the shallow end of the depth range.

In this paper we describe fish assemblages in the western Ross Sea (south of 71°S), and also from some of the islands and seamounts just to the north of it (65–68°S). The main aim was to improve our knowledge of fish species diversity and distribution, and to determine if community composition changed with latitude. In addition we examine a range of environmental factors in an attempt to establish key drivers for variation in fish assemblages with location. For these purposes we use data from surveys in 2004 and 2008 which were designed to sample a range of latitudes and depths to provide data on fish diversity, relative abundance, and distribution.

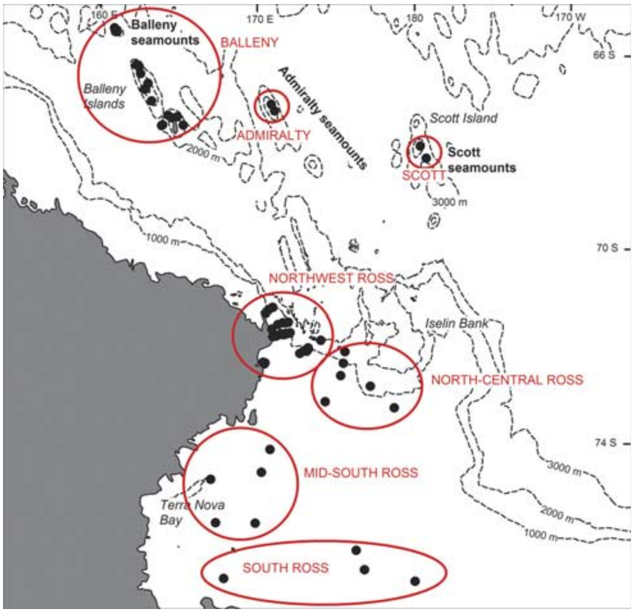

Fig. 1. Survey area, showing demersal trawl tow locations (black dots) and the initial area groupings.

Materials and methods

Survey area

Sampling was carried out on two separate surveys of the biodiversity of the Ross Sea. The first (termed "BioRoss") survey took place in January–March 2004, and sampling was carried out along a series of five transects at depths of 123–1165 m between Cape Adare and Cape Hallet in the north-west Ross Sea and on four separate locations aound the Balleny Islands (Mitchell & Clark 2004). The second (termed "IPY-CAML") survey was carried out in January–March 2008, and was designed to sample a wide range of habitats and depths from 150 m to 3554 m covering the shelf, slope, abyss, and seamounts in the Ross Sea (Hanchet *et al*. 2008). The sampling locations of the bottom trawl stations from both surveys are shown in Fig. 1.

Vessel and gear specifications

The RV *Tangaroa* is a 70 m long, 2000 GRT, stern trawler owned and operated by the National Institute of Water and Atmospheric Research (NIWA). She has only an ice-strengthened hull and so was restricted to areas where ice cover was light.

A number of biological sampling gear types were deployed during both surveys (epibenthic sleds, beam trawls and fish trawls). However, there were clear differences in the catch composition of each gear type and therefore only data from a large demersal fish trawl, which was deployed widely during the surveys, were used in the analyses presented. The NIWA rough bottom (orange roughy) net was deployed to sample demersal species between about 50 and 1990 m. This has a mouth width of 25 m, a headline height of 6 m, a codend of 60 mm mesh fitted with a 40 mm liner to retain smaller fish. The gear was set up in an identical fashion for both surveys, which included reducing the width swept by the trawl to about 80 m by reducing the lengths of the sweeps and bridles. SCANMAR sensors and a netsonde were attached to the doors and net to record doorspread and headline height respectively, and to determine bottom contact time. Standard tows were of 20 min. duration at a speed over the ground of *c*. 3 knots. Tows where there was gear damage that may have affected the catch were excluded from analysis ($n = 7$).

Table I. Potential environmental factors used in the analyses of species richness and abundance (data compiled for Southern Ocean bioregionalisation workshops 2006, 2007 (Pinkerton *et al*. 2010)).

Predictor	Description
latitude	Mid point of tow
longitude	Mid point of tow
depth	Average of gear depth at start and finish of tow
temperature	Annual average near-bottom potential temperature (°C) from the remapped Southern Ocean Database (Orsi & Whitworth 2009)
salinity	Annual average near-bottom salinity (PSU) from the remapped Southern Ocean Database (Orsi & Whitworth 2009)
chl *a*	Average near-surface chlorophyll *a* concentration (mg chl *a* m^{-3}) in summer (Nov–Jan) calculated from natural-log transformed monthly composite measurements by SeaWIFS and MODIS ocean colour sensors between 1997 and 2007 (Pinkerton *et al*. 2010)
ice15	Fraction of year for which ice concentration is > 15% of the sea surface area, between 1979/80 and 2006/07 (National Snow and Ice Data Center; Cavalieri *et al*. 1990, updated 2007)
ice85	As ice15 but where ice concentration > 85% of the sea surface area
rugosity2	Slope area of seabed divided by horizontal area, and transformed as (x-1)^0.25 to improve normality. Based on GEBCO Digital Atlas (IOC 2003) bathymetry projected onto polar stereographic grid with 4 km spatial resolution.
rugosity2S	As rugosity2 but isotropically smoothed to 100 km scale
speed	Annual mean near-bottom current speed (cm s^{-1}), derived from the HiGEM 1.1 numerical circulation model of the Ross Sea (Shaffrey *et al*. 2009, Rickard *et al*. 2010)
area	A grouping of trawl stations into 7 arbitrary geographical regions

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Table II. List of demersal elasmobranch and fish species identified from the two surveys in the Ross Sea. Species caught but not used in the analyses are included (†). + indicates occurrence in the area (the seven areas are those shown in Fig. 1). Taxonomic species names are from Gon & Heemstra (1990), Eastman & Eakin (2000) and Eschmeyer & Fricke (2009). Family names are from Nelson (2006).

	Ross Sea				Seamounts		
Fish species	South	Mid-South	North-central	North-west	Admiralty	Balleny	Scott
Rajidae (hardnose skates)							
Amblyraja georgiana Norman, 1938						+	
Arhynchobatidae (soft-nose skates)							
Bathyraja maccaini Springer, 1971			+	+			
Bathyraja sp. (cf. *eatonii*) (Günther, 1876)	+		+	+			
Bathyraja sp. [Stehmann & Bürkel in Gon & Heemstra, 1990]†			+	+			
Muraenolepididae (eel cods)							
Muraenolepis sp. 1				+			
Muraenolepis sp. 2				+			
Macrouridae (grenadiers, rattails)							
Coryphaenoides ferrieri (Regan, 1913)†							+
Coryphaenoides lecointei (Dollo, 1900)†							+
Cynomacrurus piriei Dollo, 1909			+	+		+	
Macrourus whitsoni (Regan, 1913)			+	+	+	+	+
Moridae (deepsea cods)							
Antimora rostrata (Günther, 1878)						+	+
Halargyreus johnsonii Günther, 1862							+
Liparidae (snailfishes)							
Paraliparis sp.1				+			
Zoarcidae (eelpouts)							
Lycenchelys sp.1				+			
Lycodapus antarcticus Tomo, 1982						+	
Lycodichthys dearborni (DeWitt, 1962)			+	+			
Melanostigma sp.1							+
Ophthalmolycus amberensis (Tomo, Marschoff & Torno, 1977)	+						
Pachycara brachycephalum (Pappenheim, 1912)		+	+				
Seleniolycus sp.1						+	
Zoarcid sp.1				+			
Zoarcid sp.2				+			
Nototheniidae (cod icefishes)							
Aethotaxis mitopteryx DeWitt, 1962		+		+		+	+
Dissostichus eleginoides Smitt, 1898						+	
Dissostichus mawsoni Norman, 1937	+	+	+	+		+	+
Lepidonotothen larseni (Lönnberg, 1905)						+	
Lepidonotothen squamifrons (Günther, 1880)			+	+	+	+	+
Notothenia coriiceps Richardson, 1844				+		+	
Trematomus bernacchii (Boulenger, 1902)				+		+	
Trematomus eulepidotus Regan, 1914	+	+	+	+		+	
Trematomus hansoni Boulenger, 1902	+					+	
Trematomus lepidorhinus (Pappenheim, 1911)	+	+	+	+			
Trematomus loennbergii Regan, 1913	+	+		+			
Trematomus newnesi Boulenger, 1902		+		+		+	
Trematomus nicolai (Boulenger, 1902)	+			+		+	
Trematomus pennellii Regan, 1914		+		+		+	
Trematomus scotti (Boulenger, 1907)	+	+	+	+		+	
Trematomus tokarevi (Andriashev, 1978)				+			
Artedidraconidae (barbeled plunderfishes)							
Artedidraco loennbergi Roule, 1913	+			+			
Artedidraco orianae Regan, 1914				+			
Artedidraco shackletoni Waite, 1911				+			
Artedidraco skottsbergi Lönnberg, 1905		+					
Dolloidraco longedorsalis Roule, 1913	+	+					
Histiodraco velifer (Regan, 1914)	+	+					
Pogonophryne barsukovi Andriashev, 1967†	+						
Pogonophryne immaculata Eakin, 1981				+			
Pogonophryne marmorata Norman, 1938		+					
Pogonophryne mentella Andriashev, 1967	+						
Pogonophryne scotti Regan, 1914	+	+		+			
Bathydraconidae (Antarctic dragonfishes)							

Table II. Continued

Fish species	South	Mid-South	Ross Sea North-central	North-west	Seamounts Admiralty	Balleny	Scott
Akarotaxis nudiceps (Waite, 1916)	+	+					
Bathydraco macrolepis Boulenger, 1907	+	+					
Bathydraco marri Norman, 1938	+	+	+	+			
Bathydraco scotiae Dollo, 1906[†]			+				
Bathydraco sp.1				+			
Cygnodraco mawsoni Waite, 1916	+			+			
Gerlachea australis Dollo, 1900	+	+					
Gymnodraco acuticeps Boulenger, 1902			+	+		+	
Prionodraco evansii Regan, 1914	+						
Racovitzia glacialis Dollo, 1900	+						
Vomeridens infuscipinnis (DeWitt, 1964)		+					
Channichthyidae (crocodile icefishes)							
Chaenodraco wilsoni Regan, 1914	+	+	+				
Chionobathyscus dewitti Andriashev & Neyelov, 1978				+	+		+
Chionodraco hamatus (Lönnberg, 1905)	+	+		+			
Chionodraco myersi DeWitt & Tyler, 1960	+	+	+	+			
Cryodraco antarcticus Dollo, 1900	+	+	+	+			
Cryodraco atkinsoni Regan, 1914	+	+	+				
Dacodraco hunteri Waite, 1916	+	+					
Neopagetopsis ionah Nybelin, 1947	+	+	+	+			
Pagetopsis macropterus (Boulenger, 1907)	+			+			
Pagetopsis maculatus Barsukov & Permitin, 1958	+	+					

Catch sampling and identification

Catch samples were sorted at sea, identified to the lowest possible taxonomic level (OTU, operational taxonomic unit) and weighed on motion-compensating 100 kg Seaway scales to the nearest 0.1 kg. Species were identified following Gon & Heemstra (1990) supplemented by subsequently published taxonomic papers on Southern Ocean fishes (e.g. Schneppenheim *et al*. 1994, Eastman & Eakin 1999). Voucher specimens of each OTU were taken, and registered into the New Zealand National Fish Collection at the Museum of New Zealand Te Papa Tongarewa. Some specimens were examined again onshore to confirm accuracy and consistency of identifications.

Environmental data

Data were obtained for several environmental factors considered to be biologically relevant (Table I). Temperature and salinity layers were obtained from the Southern Ocean Database (SODB: Orsi & Whitworth 2009). Chlorophyll *a* (chl *a*) concentration measurements were obtained from SeaWiFS and MODIS satellite sensors (Pinkerton *et al*. 2010). Near-bottom current speed in the study area was obtained from the HiGEM 1.1 numerical circulation model (Shaffrey *et al*. 2009, Rickard *et al*. 2010). GEBCO Digital Atlas (2003) bathymetry data were used to generate the rugosity layers. Observations of sea-ice concentration were obtained from the National Snow and Ice Data Center (University of Colorado, USA; Cavalieri *et al*. 1990, updated 2007).

Data analyses

The cumulative species richness was plotted against the cumulative number of tows to assess the adequacy of the survey data for describing species richness. The mean and 95% confidence interval were calculated from 1000 curves based

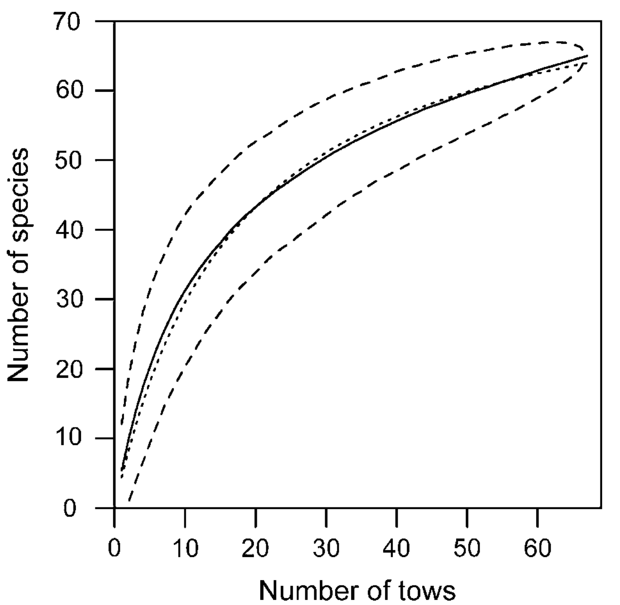

Fig. 2. Number of tows and the cumulative number of demersal fish species sampled. Dashed lines indicate the 95% CIs. Dotted line is a fitted curve from which asymptotic species richness was estimated.

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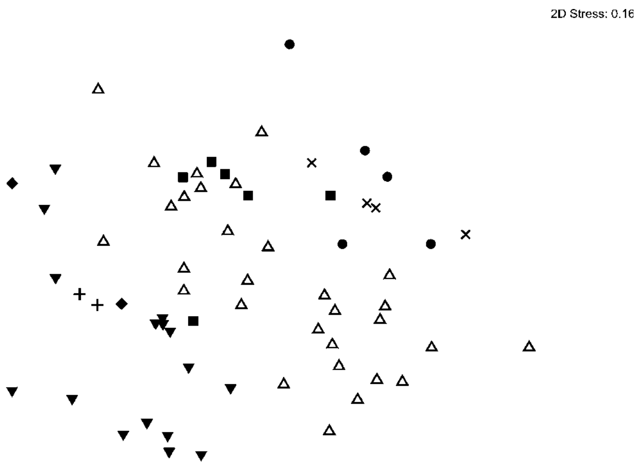

Fig. 3. Non-parametric multidimensional scaling ordination plot for demersal fish species presence/absence in trawl catches in the Ross Sea by subarea (▼ = Balleny seamounts, ● = mid-south Ross, ■ = north-central Ross, ◆ = Scott seamounts, △ = north-west Ross, + = Admiralty seamounts, × = south Ross).

upon different random orders of the tows. The asymptotic richness was estimated from a fitted curve of the form $H = aN/(1 + bN)$, where a and b are constants, N is the number of tows sampled, and the asymptote is given by a/b (Dunn 2009).

An initial subjective grouping of tows by geographical location (Fig. 1) was made to examine whether community composition varied with location. Subsequently a Distance-based Linear Model (DistLM) analysis was used to identify which environmental predictors (Table I) explained most of the variability in species occurrence and abundance (Anderson *et al*. 2008). Analyses were performed on species presence/absence or catch rate (kg per nautical mile). Catch rates were standardized, by expressing the catch rate of each species item as a proportion of the total catch rate in each tow. A dissimilarity matrix was then calculated using Bray-Curtis distances. The most significant predictors were selected using the "best" selection method, using the Akaike Information Criterion (AIC) (Anderson *et al*. 2008). The results of the DistLM analysis were a marginal test, fitting each predictor individually, and a conditional test, fitting each predictor conditional on the predictor(s) already in the model (Anderson *et al*. 2008). Because of the small dataset, the conditional model was restricted to the best model having no more than three predictors.

In order to further investigate the effects of the predictors identified from the DistLM analysis, the continuous predictors were binned. Six bins were used, with bin limits chosen so that the number of observations in each bin was approximately equal. This was considered objective given that there were no *a priori* known biologically meaningful boundaries for these predictors. The binned data were analysed using non-parametric multidimensional scaling (MDS), followed by SIMPER (similarity percentages), using PRIMER v6 (Clarke & Warwick 2006). Similarity levels were indicated on MDS plots following a cluster analysis using the average linkage method (Clarke & Warwick 2006). The SIMPER was used to describe, based on the contribution to the overall Bray-Curtis dissimilarity, which species were characteristic within each group.

Results

Species composition

In total from the two surveys there were 70 OTUs of demersal fishes at the species level (with a further 21 pelagic OTUs) (Table II). The catch from the 67 valid trawl

Table III. Demersal fish species presence/absence or abundance (kg n.mile^{-1}) in trawl catches in the Ross Sea, results of the DistLM analysis marginal models and the best 3-predictor sequential model chosen using the Akaike Information Criterion after excluding the Area predictor.

		Presence/absence			Abundance	
Factor	df	*P*	r^2		*P*	r^2
Marginal model						
Longitude	2	0.001	0.080		0.005	0.033
Latitude	2	0.001	0.173		0.001	0.063
Temperature	2	0.001	0.164		0.001	0.074
Salinity	2	0.001	0.052		0.008	0.031
Chl *a*	2	0.001	0.083		0.001	0.043
Ice85	2	0.002	0.051		0.066	0.023
Ice15	2	0.001	0.058		0.001	0.037
Rugosity 2S	2	0.001	0.188		0.001	0.068
Rugosity 2	2	0.001	0.161		0.001	0.054
Speed	2	0.001	0.082		0.001	0.041
Depth	2	0.001	0.120		0.001	0.071
Area	7	0.001	0.304		0.001	0.180
Best sequential model (excluding Area)						
Rugosity 2S	2	0.001	0.188	Temperature	0.001	0.074
+ Depth	3	0.001	0.307	+ Depth	0.001	0.138
+ Speed	4	0.001	0.371	+ Speed	0.001	0.181

Table IV. SIMPER percentage contribution of species to within rugosity 2S subgroup similarity, using presence/absence. Only the 5 species contributing most to the SIMPER within each subgroup, or contributing at least 90% of the similarity, are shown.

Subgroup Rugosity	1 0.015–0.076	2 0.077–0.098	3 0.105–0.138	4 0.142–0.157	5 0.163–0.208	6 0.209–0.241
Pagetopsis macropterus	7.9	–	–	–	–	–
Trematomus scotti	22.0	–	–	–	–	–
Trematomus pennellii	–	7.7	–	–	–	–
Chionodraco hamatus	7.1	34.4	–	–	–	–
Artedidraco orianae	–	14.2	11.6	–	–	–
Trematomus lepidorhinus	16.5	8.5	34.3	44.5	–	–
Neopagetopsis ionah	–	–	–	6.1	–	–
Bathyraja sp. (cf. *eatonii*)	–	–	15.3	12.0	–	–
Trematomus hansoni	–	–	–	–	5.2	–
Trematomus eulepidotus	7.2	9.4	6.2	–	–	4.0
Macrourus whitsoni	–	–	13.9	18.9	27.1	29.7
Dissostichus mawsoni	–	–	–	5.2	–	4.8
Lepidonotothen squamifrons	–	–	–	–	58.3	46.1
Antimora rostrata	–	–	–	–	–	3.7
Similarity	60.8	74.1	81.3	86.6	90.6	88.3

tows used in the analyses comprised 65 species. The cumulative species richness curve was not yet asymptotic, indicating the richness was not fully sampled (Fig. 2). The fitted curve estimated the asymptotic richness at 81 species. However, the curve is flattening towards an asymptote, and so sampling can be regarded as adequate for describing the main components of fish communities in the area.

Assemblage composition

Multivariate analyses showed a clear separation of the Area groupings (Fig. 3). The nMDS plot clustered the three seamount chains (Scott, Balleny, Admiralty) in the bottom left, the north-west Ross and north-central Ross within a broad band through the central section of MDS space, and the mid-south and south Ross in the top right. The pattern was the same for catch rate data, and so the nMDS for abundance is not plotted. Although each of the seven groups did not separate, the clustering into three matches a latitudinal gradient from the southern Ross Sea, through central parts, to the seamounts in the north.

The Area grouping variable was the most influential of the environmental factors analysed. It accounted for the greatest proportion of the deviance in species richness (0.3) and abundance (0.18) (Table III). When the area predictor was excluded, the best conditional model had the predictors rugosity2S (presence/absence) or temperature (abundance), followed by depth and speed (Table III). There were significant correlations in the sample between the predictors rugosity2S, temperature, area and latitude (all

Table V. SIMPER percentage contribution of species to within depth (m) subgroup similarity, using presence/absence. Only the five species contributing most to the SIMPER within each subgroup, or contributing at least 90% of the similarity, are shown.

Subgroup Depth	1 80–225	2 238–351	3 369–471	4 477–552	5 562–756	6 765–1972
Trematomus hansoni	14.4	–	–	–	–	–
Trematomus bernacchii	5.1	–	–	–	–	–
Trematomus scotti	5.0	–	–	–	–	–
Trematomus pennellii	17.6	5.8	–	–	–	–
Artedidraco orianae	–	14.3	–	–	–	–
Lepidonotothen squamifrons	40.8	–	30.6	–	3.7	–
Chionodraco hamatus	–	25.6	–	8.6	–	–
Trematomus eulepidotus	–	28.0	20.6	–	3.9	–
Bathyraja sp. (cf. *eatonii*)	–	–	–	14.7	–	–
Cryodraco antarcticus	–	–	8.8	8.8	–	–
Neopagetopsis ionah	–	4.9	–		–	7.8
Trematomus lepidorhinus	–	–	9.6	42.7	13.4	19.6
Pagetopsis maculatus	–	–	–		3.1	–
Macrourus whitsoni	–	–	16.6	14.7	63.3	31.6
Cynomacrurus piriei	–	–	–	–	–	13.4
Aethotaxis mitopteryx	–	–	–	–	–	11.0
Similarity	82.9	78.6	86.1	89.6	87.4	83.3

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Table VI. SIMPER percentage contribution of species to within bottom current speed (cm s^{-1}) subgroup similarity, using presence/absence. Only the five species contributing most to the SIMPER within each subgroup, or contributing at least 90% of the similarity, are shown.

Subgroup Bottom current speed	1 0.2–0.5	2 0.6–1.3	3 1.4–1.7	4 2.3–6.6	5 16.9–23.8	6 24.9–34.9
Notothenia coriiceps	3.3	–	–	–	–	–
Pagetopsis macropterus	–	4.1	–	–	–	–
Trematomus hansoni	4.3	–	7.6	–	–	–
Trematomus scotti	–	–	5.1	–	–	–
Chionodraco myersi	–	4.1	–	8.8	–	–
Lepidonotothen squamifrons	64.3	11.2	57.2	–	–	–
Macrourus whitsoni	14.0	32.8	10.9	11.8	–	24.7
Cryodraco antarcticus	–	–	–	8.7	–	–
Trematomus eulepidotus	3.3	–	6.1	9.1	11.3	–
Chionodraco hamatus	–	–	–	–	13.4	6.7
Trematomus lepidorhinus	–	14.8	–	19.5	19.9	51.0
Artedidraco orianae	–	–	–	–	12.0	–
Bathyraja sp. (cf. *eatonii*)	–	–	–	–	10.4	8.5
Similarity	89.1	66.9	86.9	57.9	67.6	90.9

permutations had $r^2 \geq 0.72$, $P \leq 0.01$), with the strongest correlations between rugosity2S and latitude ($r^2 = 0.90$, $P \leq 0.001$), and rugosity2S and temperature ($r^2 = 0.86$, $P \leq 0.001$).

The nMDS analysis indicated rugosity2S subgroups 5 and 6 (0.163–0.241) were similar, and most dissimilar from subgroups 1–4 (0.015–0.157). SIMPER identified the main discriminatory species as *Trematomus scotti*, *Lepidonotothen squamifrons* and *Trematomus lepidorhinus*. The low rugosity areas were characterized predominantly by *Trematomus scotti*, *Trematomus lepidorhinus*, and *Chionodraco hamatus*, and the high rugosity areas predominantly by *Macrourus whitsoni* and *Lepidonotothen squamifrons* (Table IV).

For depth, nMDS indicated subgroups 2–4 (238–552 m) were most similar, with subgroup 6 (765–1972 m) the least similar to other depth groups. SIMPER identified the best discriminatory species as *Macrourus whitsoni*, *Lepidonotothen squamifrons* and *Trematomus lepidorhinus*. Deeper tows (562–1972 m) were characterized predominantly by *Macrourus whitsoni* and *Trematomus lepidorhinus*, intermediate tows (238–552 m) by *Trematomus lepidorhinus*, *Trematomus eulepidotus*, and *Lepidonotothen squamifrons*, and shallow tows (80–225 m) by *Lepidonotothen squamifrons*, *Trematomus pennellii* and *Trematomus hansoni* (Table V).

For bottom speed, nMDS indicated subgroups 5 and 6 (16.9–34.9 cm s^{-1}) were most similar, and the slow speed subgroup 1 (0.2–0.5 cm s^{-1}) relatively dissimilar to other groups. SIMPER identified the best discriminatory species as *Macrourus whitsoni*, *Trematomus lepidorhinus* and *Lepidonotothen squamifrons*. Slower current speeds (0.2–1.7 cm s^{-1}) were characterized predominantly by *Lepidonotothen squamifrons* and *Macrourus whitsoni*, and faster currents (16.9–34.9 cm s^{-1}) by *Trematomus lepidorhinus*, *Bathyraja* sp. (cf. *eatonii*) and *Chionodraco hamatus* (Table VI).

The nMDS of temperature, the main factor determining abundance, indicated subgroups 4 and 5 (0.09–0.40°C) were similar, and least similar to subgroups 1–3 (-1.92–0.08°C) and subgroup 6 (0.41–0.75°C). SIMPER identified the best discriminatory species as *Macrourus whitsoni*, *Chionodraco*

Table VII. SIMPER percentage contribution of species to within bottom temperature subgroup similarity, using abundance (kg n.mile^{-2}). Only the five species contributing most to the SIMPER within each subgroup, or contributing at least 90% of the similarity, are shown.

Subgroup Bottom temperature	1 -1.92 to -1.50°C	2 -1.46 to -0.39°C	3 -0.36 to 0.08°C	4 0.09–0.14°C	5 0.16–0.40°C	6 0.41–0.75°C
Chionodraco myersi	35.1	–	–	–	–	–
Pagetopsis maculatus	6.4	–	–	–	–	–
Trematomus nicolai	3.4	–	–	–	–	–
Trematomus pennellii	–	7.7	–	–	–	–
Chionodraco hamatus	14.4	82.4	5.0	–	–	–
Trematomus lepidorhinus	8.6	–	11.8	–	–	–
Notothenia coriiceps	–	–	7.5	–	–	–
Bathyraja sp. (cf. *eatonii*)	–	–	9.2	–	34.6	–
Lepidonotothen squamifrons	–	–	–	35.9	8.6	22.5
Macrourus whitsoni	–	–	53.4	61.1	51.0	48.2
Dissostichus mawsoni	–	–	–	–	–	23.4
Similarity	67.8	90.1	86.8	96.9	94.2	94.1

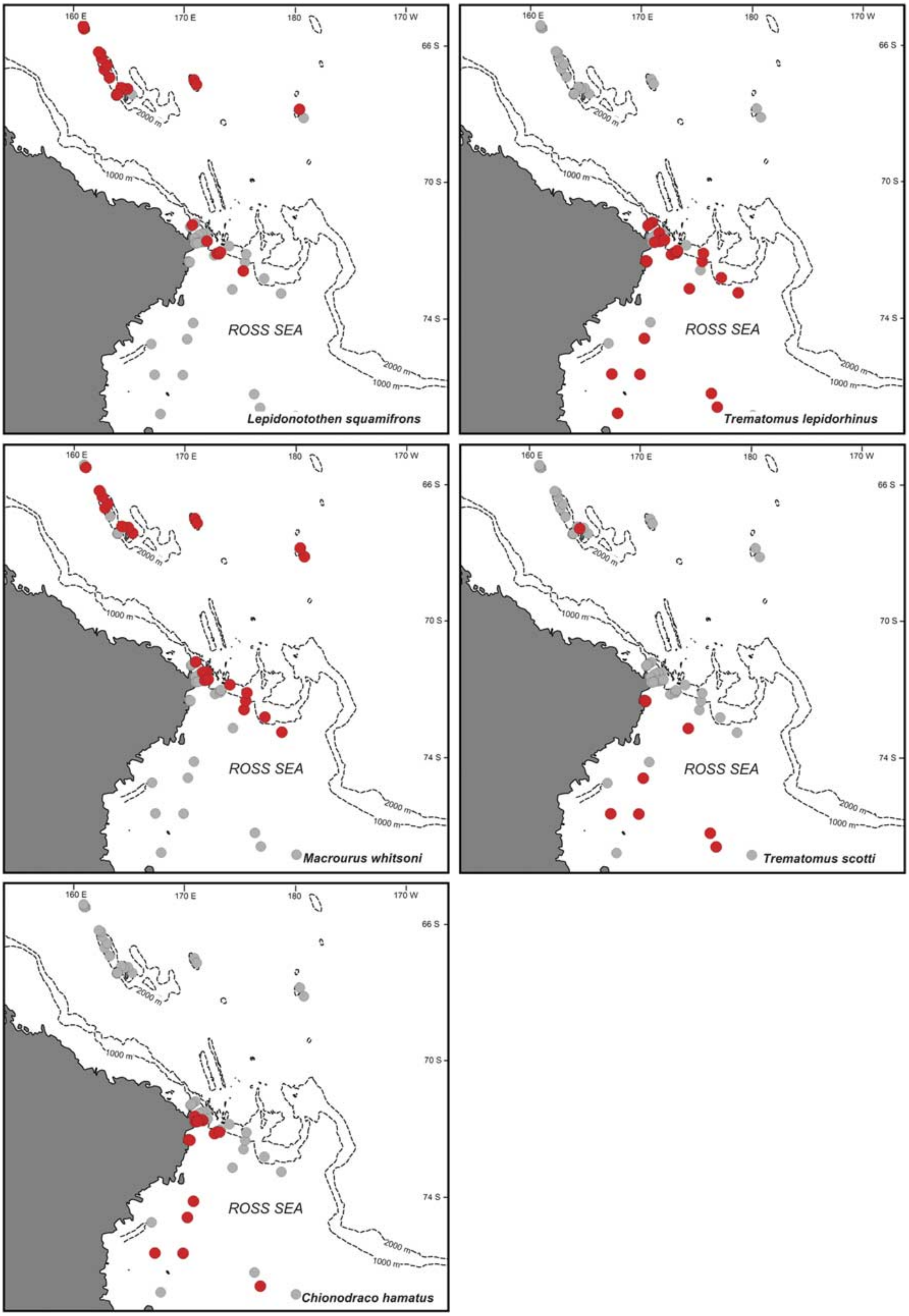

Fig. 4. Distribution of the main five discriminatory fish species: *Lepidonotothen squamifrons*, *Trematomus lepidorhinus*, *Macrourus whitsoni*, *Trematomus scotti*, *Chionodraco hamatus*. Trawl locations are shown as light grey, with red dots signifying the occurrence of the species.

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hamatus, and *Lepidonotothen squamifrons* (Table VII). Results using species abundance for depth and current speed effects were similar to those for occurrence, and are not shown. The main discriminating species for both factors were *Lepidonotothen squamifrons* and *Macrourus whitsoni*.

Three species dominated results of the SIMPER analyses:

1) *Lepidonotothen squamifrons* characterized areas of high rugosity, shallow to intermediate depths, slow to moderate bottom current speed, and moderate to high temperatures. The species was distributed in the north-western area of the Ross Sea, and in particular on the seamounts (Fig. 4).
2) *Trematomus lepidorhinus* was a distinguishing species in areas of low to moderate rugosity, intermediate to deep depths, moderate to high current speeds, and low temperatures. They were found on the shelf break near 1000 m depth, and scattered throughout the southern Ross Sea (Fig. 4).
3) *Macrourus whitsoni* discriminated areas of moderate to high rugosity, intermediate to deep depths, slow to high currents, and moderate to high temperature. They were common on the seamounts, and in northern-central sectors of the Ross Sea around 1000 m depth (Fig. 4).

Other important species were *Trematomus scotti* in low rugosity environments (central and southern Ross Sea), and *Chionodraco hamatus* in low rugosity, fast current, and low temperature areas along western and southern sectors of the Ross Sea (Fig. 4).

Discussion

The fish species recorded in this study are typical of an East Antarctic assemblage, with high frequency of the nototheniid genus *Trematomus*, together with artedidraconids, bathydraconids, and channichthyids (Kock 1992, Eastman 1993). This was found also by Eastman & Hubold (1999) from the western Ross Sea, and Donnelly *et al*. (2004) from the eastern Ross Sea. However, there are clear changes in the fauna from south to north, both within the Ross Sea, and especially between the Ross Sea and the seamounts. The seamount catches displayed clear sub-Antarctic influence in fish species composition, e.g. the morid cods *Halargyreus johnsonii* and *Antimora rostrata*, and the macrourids *Macrourus whitsoni* and *Cynomacrurus piriei* are more typical of temperate or sub-Antarctic waters (Gon & Heemstra 1990). The beginnings of a transition between Antarctic and sub-Antarctic fauna at the Balleny Islands has been documented for benthic invertebrates as well (e.g. Dawson 1970, Thatje & Lörz 2005).

Although this study has shown clearly that fish species composition varies with location within the Ross Sea, the environmental drivers of community composition are not necessarily as obvious or straightforward to interpret. All environmental factors were significant predictors of species composition when tested individually, but many were highly correlated. The decision to focus on the best three combined predictors was a pragmatic one, given the level of sampling effort and uneven distribution of stations throughout the survey area. It also reduces the potential to over-analyse and over-interpret when a large number of predictors are included. The final predictors analysed explained the greatest proportion of the deviance, but this did not necessarily mean these were key drivers of species composition; correlation does not necessarily imply causation, and the difference in deviance explained between alternative predictors was often small ($< 2\%$).

The four key environmental factors identified (rugosity, depth, bottom current speed, and temperature) vary with latitude in the Ross Sea. Depth progressively increases moving north from the southern sector of the Ross Sea, and bathymetry steepens at the shelf break about 700 m in the central–northern sector. The depth increases to over 3000 m going north, except for the seamounts, which have peaks at 500 m or less. Temperature is patchy, but generally increases moving northwards. Rugosity is a measure of seafloor "roughness" at large scales (4 km for rugosity2 and 100 km for rugosity2S) and increases where the seafloor is uneven (e.g. due to the presence of seamounts, canyons) or sloping. Rugosity is higher along the continental slope and Iselin Bank, around Admiralty and Scott seamounts and throughout the deep-sea fracture zone to the north of the Ross Sea sector. Bottom current speed is highly variable throughout the area, with high flow rates in the north-western and north-central sectors, probably along the shelf break, and around the seamounts. Depth and temperature are common environmental factors associated with distribution of fish communities (e.g. Francis *et al*. 2002, review by Carney 2005), and their influence on fish species composition is readily understood.

The key discriminating species occurred in different combinations of environmental conditions. *Lepidonotothen squamifrons* characterized areas of high rugosity, shallow to intermediate depths, relatively slow to moderate bottom current speed, and relatively warm environments. This species appears to be primarily benthic as observations made during the IPY-CAML survey using the NIWA Deep Towed Imaging System (DTIS) showed individuals in contact with pebble sea floor and also amongst rock, in crevices and behind encrusting invertebrates presumably sheltering against current flow. *Trematomus lepidorhinus* favoured areas of low to moderate rugosity, intermediate to high depths, moderate to high current speeds, and low temperatures. DTIS images showed individuals on soft sediment and mixed invertebrate sea floor types suggesting that the species is primarily benthic. *Macrourus whitsoni* was sampled from regions of moderate to high rugosity, intermediate to deep depths, slow to high currents, and moderate to high temperature. DTIS images revealed the species swimming close to soft sediment and pebble/rock sea floor i.e. typically just above the seafloor. *Trematomus scotti* was sampled in low rugosity environments and DTIS images showed individuals on soft sediment sea floor types suggesting that the species is primarily benthic. *Chionodraco hamatus* favoured low rugosity and low temperature areas but was not recorded in DTIS transects. A detailed analysis of assemblage composition relative to substrate type, or macrobenthic biogenic habitat was not possible at this time given the available data, but these factors can be important in species associations.

Environmental parameter values derived from well established compilations of data represent the best available information to characterize the oceanographic conditions of the Ross Sea benthic environment. Nevertheless, the spatial scale of variability in seafloor habitat conditions is often small (metres) relative to that of the environmental data (kilometres). This may introduce some spurious relationships, although it should be adequate for describing broad distributional patterns. Processing and analysis of the seafloor photographic data collected during the 2008 survey with DTIS will, in the future, improve the resolution of some of the environmental correlates with fish species distribution.

The Ross Sea fish fauna appears to be diverse compared with other Antarctic areas, with about 80 species in 12 families having been reported (Eastman & Hubold 1999). On-going returns of toothfish fishery by-catch species to the National Fish Collection has significantly increased this number to over 100 species (Museum of New Zealand, unpublished records). The two surveys reported here have also resulted in several new taxa being caught along with range extensions of species from elsewhere in the Southern Ocean. Many Southern Ocean species exhibit large depth ranges, possibly because the continental shelf extends out to 800–900 m in the Ross Sea, in contrast to many non-polar areas where the shelf break is at about 200 m (Kock 1992, Angel 1997). The species diversity recorded in this study includes almost all the known species, but small and benthic fishes are likely to have been poorly sampled using the large NIWA rough bottom trawl because the large bobbins used in the groundrope may have missed fishes hard down on the sea floor and also because the large mesh used in the front parts of the net may have enabled smaller fishes to escape. This sampling effect was noted during the BioRoss survey when different sampling gear types were deployed at the same sampling site resulting, for instance, in numerous specimens of small artedidraconids being captured in an epibenthic sled but being almost completely absent from the corresponding rough bottom trawl catch. It is therefore very likely that groups such as Rajidae (hardnose skates), Arhynchobatidae (soft-nose skates), Muraenolepididae (eel cods), Liparidae (snailfishes), Zoarcidae (eelpouts), Artedidraconidae (barbeled plunderfishes), and Bathydraconidae (Antarctic dragonfishes) were relatively poorly sampled and that in contrast larger fishes, especially those living just above the sea floor such as Macrouridae (grenadiers, rattails), Moridae (deepsea cods), many of the Nototheniidae (cod icefishes), and Channichthyidae (crocodile icefishes) were better sampled.

A number of fish specimens could not be identified to species. Although we were confident in assigning them unique OTUs, it reflects the fact that the fish fauna of the Ross Sea is still not completely known. The data used for this study therefore includes undescribed species, which are subject to on-going research by specialists in the groups. In addition, analysis of tissues collected from voucher material also revealed cryptic species in groups previously thought to be well understood, e.g. Macrouridae (NIWA, unpublished data). New species of fish are being discovered and new records published from most research surveys and the longline fishery in the Ross Sea (e.g. Eakin & Eastman 1998, Eastman & Eakin 1999, Chernova & Eastman 2001, Smith *et al*. 2008). Identification of fishes is a problem for some taxa and therefore diversity and ecological studies are limited to better known species. The groups that are not completely known or diagnosed and may contain new species include: Arhynchobatidae (soft-nose skates), Muraenolepididae (eel cods), Macrouridae (grenadiers, rattails), Liparidae (snailfishes), Zoarcidae (eelpouts) Artedidraconidae especially within *Pogonophryne* (barbeled plunderfishes), Bathydraconidae (Antarctic dragonfishes). In addition, although the continental shelf and upper slope down to about 800 m of the Ross Sea has been moderately well sampled, the rest of the slope and abyssal depths (to about 3000 m) have been less frequently sampled (Møller & Stewart 2006).

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