

Macrobenthic communities of the north-western Ross Sea shelf: links to depth, sediment characteristics and latitude

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Abstract: In early 2004 the Victoria Land Transect project sampled coastal north-western Ross Sea shelf benthos at Cape Adare, Cape Hallett, Cape Russell and Coulman Island from 100–500 m deep. We describe the benthic macrofaunal assemblages at these locations and, to assess the use of seafloor sediment characteristics and/or depth measures in bioregionalizations, determine the extent to which assemblage compositions are related to measured differences in these factors. Percentages of fine sand and silt, the ratio of sediment chlorophyll *a* to phaeophytin, and depth were identified as important explanatory variables, but in combination they explained only 17.3% of between-location differences in assemblages. Consequently, these variables are clearly not strong determinants of macrofaunal assemblage structure. Latitude *per se* was not a useful measure of community variability and change. A significant correlation between both number of individuals and number of taxa and sediment phaeophytin concentration across locations suggests that the distribution of the benthos reflects their response to seafloor productivity. A number of factors not measured in this study have probably influenced the structure and function of assemblages and habitats. We discuss the implications of the results to marine classifications, and stress the need to incorporate biogenic habitat complexity into protection strategies.

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Introduction

Classifying Antarctic and Southern Ocean flora and fauna into biogeographic regions has been a discussion point for decades (e.g. see Dell 1972 and references therein). More recently, the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR), its scientific committee (SC-CAMLR) and the Committee for Environmental Protection (CEP) have begun developing bioregionalizations of the Southern Ocean. Bioregionalization is essentially a tool for biodiversity or conservation management that involves classifying Southern Ocean marine life into distinct biogeographic regions. The resultant maps are intended to be used to develop an ecologically representative system of marine protected areas (Grant *et al.* 2006). The question for managers is how well do these maps, usually based on easy to measure or model physico-chemical surrogate variables, capture the diversity and functioning of the seafloor communities we are trying to protect? The bioregionalization process is particularly difficult in subtidal marine systems (where direct observations of life are difficult), and even more so in the Antarctic, due to its remoteness, ice conditions and difficulty of access. Use of biological data in these classifications is generally impractical due to scarcity or poor geographical coverage of data (except perhaps in smaller subregions that have

been better studied; e.g. McMurdo Sound, Terra Nova Bay, Prince Edward Islands).

The first Southern Ocean bioregionalization was based on a combination of datasets of mostly physical variables (e.g. bathymetry, sea surface temperature, nutrient concentrations, proportion of year < 15% sea ice concentration, satellite observed sea surface chlorophyll; Grant *et al.* 2006). A later separation into pelagic and benthic bioregionalizations has allowed use of variables that are more relevant to these different (but interlinked) systems (e.g. Grant *et al.* unpublished). While considerable advances have been and are being made in this process (e.g. Sharp unpublished), their fitness-for-purpose will ultimately be judged on how well the bioregionalization captures the relationships between the biological communities under consideration and their environment. This assessment is urgently needed in order to ensure the ecological relevance of variables used to generate the classifications. It is also particularly relevant for Ross Sea marine benthic ecosystems, for which such data are scarce.

Given the spatially discrete nature of benthic sampling in the Ross Sea, and the natural variability in community composition, an ability to clearly link communities and environmental features such as depth, seafloor sediment type, or latitude, would ensure production of meaningful bioregionalizations. For example, in a survey of megabenthos

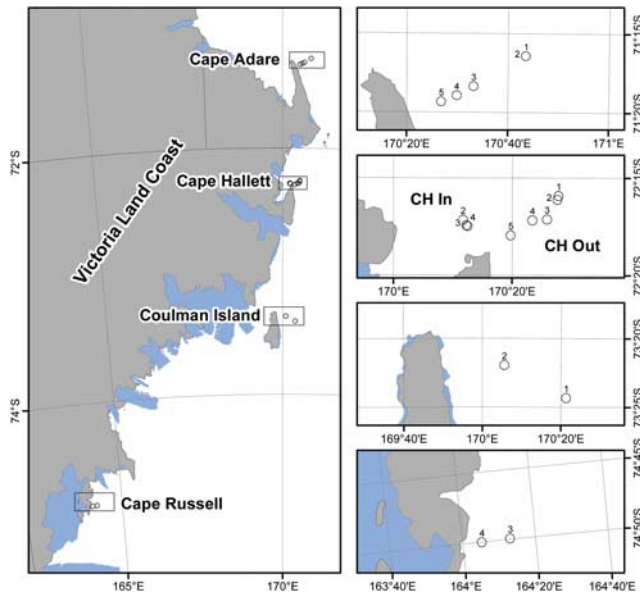


Fig. 1. Map of the north-western Ross Sea showing the locations sampled along the Victoria Land coast (left hand panel), and positions of sampling stations at each location (right hand panels). CH = Cape Hallett. Blue areas indicate large ice features.

at 270–1173 m deep sites, Barry *et al.* (2003) noted lower densities with increasing depth, a higher abundance of suspension feeding taxa in shallow waters and deposit-feeders at the deepest sites. Natural gradients in environmental conditions and productivity along the latitudinal range of the Ross Sea provide a useful framework in which to identify key physical variables and primary production pathways driving site-specific patterns in benthic community structure and function. With the exception of macroalgae (Miller & Pearse 1991, Wiencke & Clayton 2002), latitude *per se* in the Ross Sea is not generally a good descriptor of species diversity or community composition (e.g. Cummings *et al.* 2006, De Domenico *et al.* 2006, Schiaparelli *et al.* 2006), mostly due to the fact that the environmental variables that structure these communities are not monotonically related to latitude. For example, iceberg disturbance and very strong coastal currents are dominant factors north of Terra Nova Bay, while south of Terra Nova Bay the presence of fast ice and proximity to primary production originating in polynyas becomes increasingly important (Thrush *et al.* 2006a, Norkko *et al.* 2007). However, this picture is complicated by the fact that iceberg disturbance does occur in the south (e.g. McMurdo Sound), and there can be as much as 1–2 months difference in duration of open water in summer months within some regions (e.g. Terra Nova Bay). We also have little understanding of how benthic community structure and function are moderated by localized environmental or ecological factors.

Here we describe the macrofaunal assemblage composition of coastal Cape Adare, Cape Hallett, Cape Russell and

Table 1. GPS location of grab samples collected from each location and station. Stations 1, 2, 3, 4 and 5 correspond to targeted depths of 500, 400, 300, 200 and 100 m, respectively; the actual depths are also given.

Location	Station	Grab	Depth (m)	Latitude S	Longitude E
CA	1	1	488.4	71°16.468'	170°43.549'
CA		2	478.0	71°16.664'	170°42.993'
CA		3	476.4	71°16.446'	170°42.621'
CA	2	1	488.4	71°16.468'	170°43.549'
CA		2	476.4	71°16.446'	170°42.621'
CA	3	1	312.8	71°18.396'	170°33.215'
CA		2	308.0	71°18.168'	170°32.534'
CA		3	312.0	71°18.107'	170°32.485'
CA	4	1	223.6	71°18.982'	170°29.920'
CA		2	234.4	71°18.615'	170°29.348'
CA	5	1	124.4	71°19.382'	170°26.833'
CA		2	133.6	71°19.131'	170°26.849'
CA		3	136.0	71°19.056'	170°26.834'
CH In	2	1	400.0	72°17.182'	170°11.736'
CH In		2	406.8	72°17.169'	170°11.573'
CH In		3	414.0	72°17.017'	170°10.775'
CH In	3	1	312.8	72°17.456'	170°12.314'
CH In		2	330.0	72°17.415'	170°12.270'
CH In		3	369.2	72°17.146'	170°12.348'
CH In	4	1	266.0	72°17.506'	170°12.536'
CH In		2	228.0	72°17.756'	170°12.247'
CH In		3	152.8	72°17.699'	170°12.862'
CH Out	1	1	494.8	72°15.936'	170°27.804'
CH Out		2	525.6	72°15.709'	170°27.778'
CH Out		3	530.8	72°15.649'	170°28.631'
CH Out	2	1	475.2	72°16.140'	170°27.657'
CH Out		2	377.2	72°16.588'	170°26.483'
CH Out		3	332.8	72°16.738'	170°26.007'
CH Out	3	1	261.2	72°17.151'	170°25.883'
CH Out		2	246.0	72°17.280'	170°25.810'
CH Out	4	1	195.2	72°17.201'	170°23.414'
CH Out		2	231.6	72°16.798'	170°24.225'
CH Out	5	1	103.2	72°17.973'	170°19.768'
CH Out		2	105.6	72°18.017'	170°19.869'
CH Out		3	106.8	72°18.052'	170°19.971'
CI	1	1	480.8	73°24.344'	170°21.389'
CI		2	478.8	73°24.340'	170°21.489'
CI		3	480.8	73°24.302'	170°21.539'
CI	2	1	372.8	73°21.975'	170°05.622'
CI		2	375.2	73°21.996'	170°05.443'
CI		3	380.8	73°21.712'	170°05.512'
CR	3	1	307.2	74°49.964'	164°13.095'
CR		2	322.0	74°49.890'	164°12.885'
CR		3	329.0	74°49.865'	164°12.907'
CR	4	1	174.0	74°50.038'	164°05.254'
CR		2	156.4	74°49.951'	164°05.367'
CR		3	135.2	74°49.812'	164°05.568'

CA = Cape Adare, CH Out = Cape Hallett Outside, CH In = Cape Hallett Inside, CI = Coulman Island, CR = Cape Russell.

Coulman Island from 100–500 m deep, and assess the extent to which their similarities and differences are related to measured differences in seafloor sediment characteristics and/or depth and location along the coast. Specifically, we test the hypothesis that there are strong monotonic relationships between benthic communities and depth, sediment type and the quality and quantity of food resources derived from primary production.

Methods

Sampling

Sampling was conducted off the Victoria Land coastline, at four locations spanning three degrees of latitude: Cape Adare (one transect), Cape Hallett (two transects), Coulman Island (one transect) and Cape Russell (one transect) (Fig. 1, Table I). One of the Cape Hallett transects was located close to the cape itself (hereafter 'Cape Hallett Inside'), with the other further offshore (hereafter 'Cape Hallett Outside'). At each location, five stations (stations 1 to 5) were arranged along a depth gradient, at nominal depths of 500, 400, 300, 200 and 100 m, respectively. At some locations, ice conditions were such that fewer than five stations could be sampled (Table I).

At each station, three Van Veen grab samples (60 litre volume, 0.2 m² surface area) were collected. Where possible, three grabs were taken at each station, but in some cases only two grabs of sufficient quality were able to be collected, despite repeated attempts, due to the cobbled nature of the bottom. Grabs were subsampled by collecting a core (7 cm diameter) to quantify macrofaunal community composition, and surficial sediment scrapes to characterize sediments. Thus, in our study, one individual core⁻¹ equates to 260 individuals m⁻², assuming the spatial scale of heterogeneity from cores to m² are consistent. Core samples were sieved (500 µm mesh) and preserved in 70% isopropyl alcohol. Sediment scrapes were homogenized prior to being subsampled for chlorophyll *a* (chl *a*), particle size and organic content analysis. The sediment samples were stored frozen until they could be analysed.

Sample processing and analysis

Macrofauna core samples were sorted and identified to the lowest taxonomic level practical. Sediments for particle size

analysis were digested in 6% hydrogen peroxide to remove organic matter. A Galai particle analyser (Galai Cis – 100; Galai Productions Ltd., Midgal Haemek, Israel) was then used to determine percentage volumes for the gravel/shell hash, coarse, medium and fine sand, silt and clay fractions. The organic matter content of the sediment was measured as loss on ignition (LOI) by drying the sediment at 60°C to constant weight, followed by combustion at 400°C for 5.5 h. Chlorophyll *a* was extracted from freeze dried sediments by boiling in 90% ethanol. The extract was measured spectrophotometrically, and an acidification step was included to separate degradation products (phaeophytin) from chl *a* (Sartory 1982).

Numerical analysis

Variations in species composition and relative abundance of benthic fauna and flora within and between sites were determined using a combination of univariate (McCullagh & Nelder 1989) and multivariate analytical procedures (Legendre & Legendre 1998, Warwick & Clarke 2001). Total number of species, total number of individuals, Shannon-Wiener diversity (*H'*), species evenness (Pielou's *J*) and species richness (Margalef) were calculated using PRIMER (Clarke & Gorely 2001). Differences in these parameters between stations and locations were assessed with ANOVA (using the GLM procedure within SAS). Spearman's correlation coefficients were used to identify correlations between depth and a number of variables (i.e. number of individuals, number of taxa, feeding modes) using the CORR procedure within SAS (SAS Institute 1999). Relationships between phaeophytin concentrations and both number of individuals and number of taxa were similarly investigated. Similarities and differences in community composition at the different locations and stations were assessed using non-metric multidimensional

Table II. Sediment grain size and organic content (measured as loss on ignition) at the five locations. Data presented are mean % (\pm standard error). Location abbreviations as for Table I.

Location	Station	Organic content	Clay	Silt	Fine sand	Medium sand	Coarse sand	Gravel
CA 1	1	1.06 \pm 0.39	0.00 \pm 0.00	0.02 \pm 0.00	3.17 \pm 0.92	8.15 \pm 0.63	73.90 \pm 3.71	14.76 \pm 4.26
CA 2	2	3.43 \pm 0.48	0.00 \pm 0.00	0.05 \pm 0.01	4.65 \pm 1.82	2.73 \pm 1.11	27.05 \pm 18.82	65.53 \pm 15.88
CA 3	3	1.30 \pm 0.24	0.00 \pm 0.00	0.04 \pm 0.02	5.35 \pm 3.06	1.59 \pm 0.91	23.62 \pm 15.50	69.40 \pm 18.40
CA 4	4	2.48 \pm 0.44	0.00 \pm 0.00	0.09 \pm 0.00	6.46 \pm 2.17	2.12 \pm 0.92	29.39 \pm 8.26	61.94 \pm 5.17
CA 5	5	0.81 \pm 0.15	0.00 \pm 0.00	0.12 \pm 0.06	16.11 \pm 8.55	3.90 \pm 1.73	38.70 \pm 6.52	41.17 \pm 16.68
CH In	2	1.33 \pm 0.07	0.01 \pm 0.01	2.22 \pm 0.62	64.64 \pm 15.99	1.41 \pm 0.29	5.33 \pm 1.21	26.39 \pm 17.96
CH In	3	1.18 \pm 0.26	0.03 \pm 0.02	2.05 \pm 0.70	63.54 \pm 4.00	2.39 \pm 0.63	12.47 \pm 5.79	19.52 \pm 7.27
CH In	4	1.77 \pm 0.35	0.02 \pm 0.00	2.80 \pm 1.97	61.98 \pm 21.46	1.38 \pm 0.69	11.16 \pm 5.88	22.66 \pm 19.19
CH Out	1	2.08 \pm 0.20	0.03 \pm 0.02	0.71 \pm 0.14	28.90 \pm 10.35	2.57 \pm 1.15	29.65 \pm 3.96	38.14 \pm 13.75
CH Out	2	2.12 \pm 0.77	0.00 \pm 0.01	0.63 \pm 0.15	20.02 \pm 11.95	0.66 \pm 0.38	7.64 \pm 5.75	71.05 \pm 18.24
CH Out	3	2.34 \pm 0.26	0.01 \pm 0.01	0.70 \pm 0.50	25.00 \pm 19.06	1.01 \pm 0.55	13.44 \pm 1.02	59.83 \pm 19.11
CH Out	4	2.69 \pm 0.06	0.01 \pm 0.02	1.02 \pm 0.41	26.33 \pm 21.01	0.75 \pm 0.66	9.13 \pm 8.64	62.77 \pm 30.70
CH Out	5	2.16 \pm 1.03	0.01 \pm 0.01	1.65 \pm 1.61	33.75 \pm 24.01	2.64 \pm 1.87	20.39 \pm 9.02	41.56 \pm 30.35
CI	1	2.03 \pm 0.09	0.07 \pm 0.02	5.49 \pm 1.60	60.83 \pm 11.94	2.50 \pm 0.34	23.27 \pm 7.16	7.84 \pm 6.46
CI	2	1.99 \pm 0.21	0.03 \pm 0.00	4.44 \pm 0.37	52.82 \pm 3.91	2.78 \pm 0.94	25.43 \pm 3.08	14.50 \pm 6.60
CR	3	0.98 \pm 0.17	0.01 \pm 0.00	3.02 \pm 1.05	56.26 \pm 20.62	3.92 \pm 1.44	25.28 \pm 9.27	11.51 \pm 14.09
CR	4	0.76 \pm 0.10	0.02 \pm 0.01	2.26 \pm 1.60	39.38 \pm 22.36	2.79 \pm 0.83	29.97 \pm 9.48	25.58 \pm 26.58

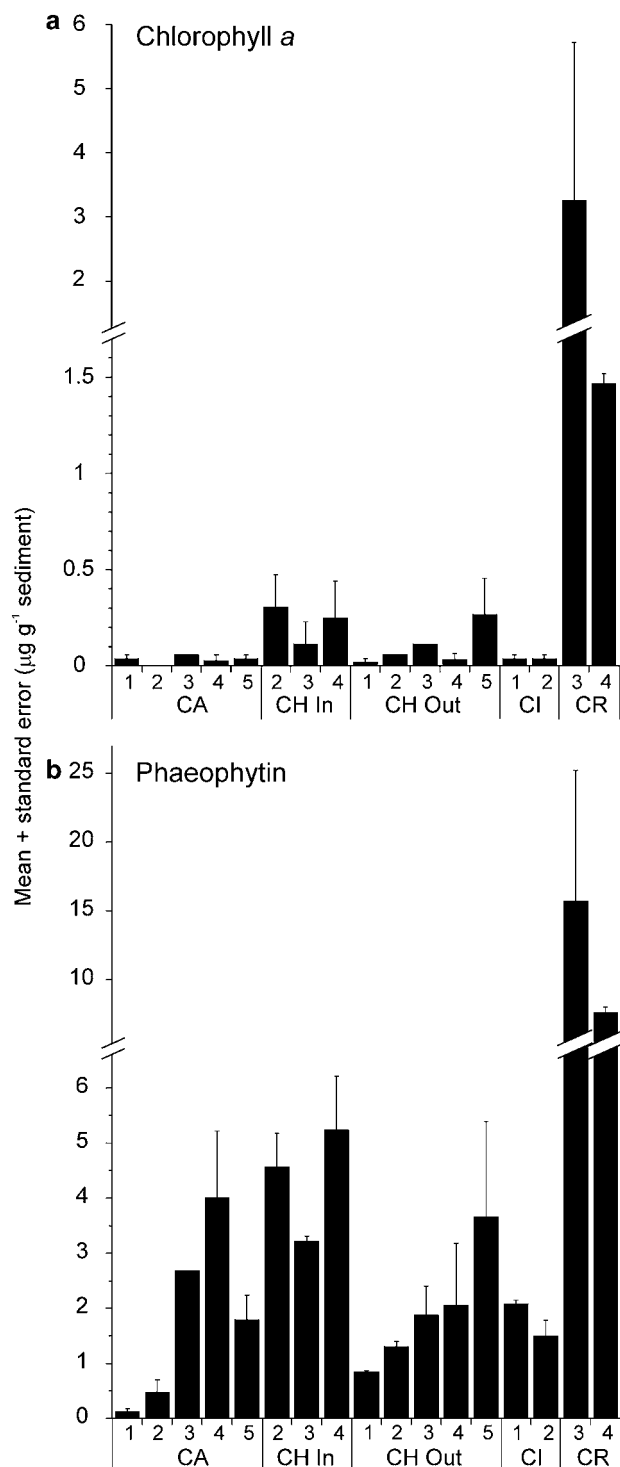


Fig. 2. Levels of **a.** chl *a* (mean \pm standard error), and **b.** phaeophytin present in seafloor sediments at each station and location in February 2004. Location abbreviations as for Table I.

scaling ordinations (MDS) of the untransformed and presence/absence transformed data using PRIMER. Canonical correspondence analysis (CCA, ter Braak 1986, 1987), using untransformed community data, was then used to

identify the contribution of measured environmental factors (e.g. sediment characteristics and depth) to the observed patterns in community composition.

Results

Seafloor sediment characteristics

Sediment grain size composition differed between locations: Cape Hallett Inside and the two southernmost locations (Coulman Island and Cape Russell) had a high proportion of fine sediments, while Cape Adare and Cape Hallett Outside were predominantly coarse sand and gravel (Table II). The Coulman Island and Cape Russell sediments were the most heterogeneous (Table II). There was no consistent pattern in sediment grain size distribution with station depth across locations.

The sediment organic content was $< 3.5\%$ at all stations and locations. Levels were most variable between stations at Cape Adare (average 0.81–3.43%), and most similar at the Cape Hallett Outside stations (average 2.08–2.69%) (Table II). There was no relationship with latitude or depth (Table II).

There was no gradient in sediment chl *a* or phaeophytin concentration with latitude or depth, although both were highest at the southernmost location, Cape Russell (Fig. 2). Not surprisingly, deep sites generally had very low levels of chl *a* (i.e. $< 0.5 \mu\text{g g}^{-1}$ sediment; Fig. 2a). The exception was Cape Russell, where seafloor sediment at 200 and 300 m depth contained on average 1.5–3.3 $\mu\text{g chl } a \text{ g}^{-1}$ sediment (Fig. 2a). The amount of phaeophytin (a chl *a* degradation product) was comparatively high (i.e. 0.1–15.7 $\mu\text{g g}^{-1}$ sediment, recorded at Cape Adare (500 m) and Cape Russell (200 m), respectively; Fig. 2b), with sediments at all stations having more phaeophytin than chl *a* (i.e. by 2 to > 10 times).

Macrofauna

At Cape Adare the macrobenthic assemblage was comprised mostly of bivalves and crustaceans (amphipods, isopods and ostracods), while at Cape Hallett Outside polychaetes were amongst the dominant taxa at all but the shallowest station (100 m, station 5) (Table III). In comparison, the dominant taxa at Cape Russell and Coulman Island were polychaetes, nematodes and oligochaetes. The most common taxa at the Cape Hallett Inside assemblages were a bivalve, crustaceans and polychaetes. The bivalve, *Genaxinus debilis* Thiele, 1912, the most abundant species at stations 2 and 3, did not feature amongst the dominant taxa at any other location (Table III).

Average numbers of macrofaunal taxa collected in each core ranged from 3–21 across all locations and stations (Table IV). The number of taxa was most variable between stations at Cape Adare (4.0–20.5 taxa core⁻¹), and most similar between Cape Hallett Outside stations (2.5–8.0 taxa core⁻¹). The Cape Hallett Outside and Coulman Island stations had the lowest diversity and the fewest number of

Table IIIa. Dominant macrofaunal taxa (number of individuals core⁻¹, mean ± standard error) at each location and station. Location abbreviations as for Table I.

	Station 1	Station 2	Station 3	Station 4	Station 5
CA	<i>Leptanthuria glacialis</i> (0.33 ± 0.41)	<i>Leptanthuria glacialis</i> (2.50 ± 2.12)	Myodocopida (2.33 ± 1.78)	Myodocopida (13.00 ± 15.56)	Ophiuroid 3 (2.00 ± 1.87)
	Lysianassidae (0.33 ± 0.41)	Nematoda (2.50 ± 2.12)	Ischyroceridae (1.67 ± 2.04)	<i>Leptanthuria glacialis</i> (7.00 ± 2.83)	Ischyroceridae (1.67 ± 0.41)
	Oligochaeta (0.33 ± 0.41)	<i>Philobrya sublaevis</i> (1.00 ± 1.41)	Ophiuroid 2 (1.33 ± 1.63)	Ischyroceridae (6.00 ± 8.49)	Ophiuroid 1 (1.67 ± 1.08)
	Glyceridae (0.33 ± 0.41)	Myodocopida (1.00 ± 1.41)	<i>Leptanthuria glacialis</i> (1.33 ± 1.08)		Ophiuroid 2 (1.00 ± 1.22)
		<i>Nucula</i> sp. (1.00 ± 1.41)	<i>Kiklonana</i> sp. (1.33 ± 0.82)		<i>Leptanthuria glacialis</i> (1.00 ± 1.71)
	Foraminifera (1.00 ± 1.41)				
CH Out	<i>Philobrya sublaevis</i> (0.67 ± 0.82)	<i>Euchone</i> sp. (0.50 ± 0.71)	Ophiuroid sp.1 (1.00 ± 1.41)	Hydroida (2.00 ± 0.00)	Ophiuroid 1 (1.33 ± 1.08)
	Glyceridae (0.33 ± 0.41)	Glyceridae (0.50 ± 0.71)	Serpulidae 1 (0.50 ± 0.71)	Syllinae (1.00 ± 0.00)	Hydroida (1.33 ± 0.82)
	<i>Aricidea</i> sp. (0.33 ± 0.41)	Lumbrineridae (0.50 ± 0.71)	Syllinae (0.50 ± 0.71)	Brachiopoda (1.00 ± 1.41)	Nematoda (1.0 ± 1.22)
	Lumbrineridae (0.33 ± 0.41)	Nemertean (0.50 ± 0.71)	Serpulidae 2 (0.50 ± 0.71)		Pycnogonida (1.00 ± 0.71)
	<i>Galathowenia wilsoni</i> (0.33 ± 0.41)				
	Ophiuroid 1 (0.33 ± 0.41)				
	Ophiuroid 3 (0.33 ± 0.41)				
CH In	Not sampled	<i>Genaxinus debilis</i> (3.00 ± 1.22)	<i>Genaxinus debilis</i> (1.33 ± 0.41)	Cumacea 2 (5.33 ± 4.81)	Not sampled
		Oligochaeta (2.33 ± 2.27)	Phoxocephalidae 2 (1.00 ± 0.71)	<i>Maldane sarsi antarctica</i> (4.33 ± 4.08)	
		Lumbrineridae (2.00 ± 0.71)	<i>Notoproctus oculatus antarcticus</i> (1.00 ± 0.71)	Oligochaeta (2.33 ± 2.27)	
				<i>Rhodine</i> sp. (2.33 ± 2.27)	
CI	Cirratulid (1.00 ± 0.71)	Nematoda (1.67 ± 2.04)	Not sampled	Not sampled	Not sampled
	<i>Spiophanes tcherniai</i> (1.00 ± 1.22)	Oligochaete (1.33 ± 1.63)			
	Lumbrineridae (0.67 ± 0.41)	Lumbrineridae (1.00 ± 0.00)			
CR	Not sampled	Not sampled	Nematoda (4.00 ± 4.90)	Oligochaeta (7.67 ± 3.34)	Not sampled
			Oligochaeta (3.67 ± 2.48)	Nematoda (5.00 ± 1.87)	
			<i>Maldane sarsi antarctica</i> (2.67 ± 0.82)	<i>Maldane sarsi antarctica</i> (3.67 ± 4.49)	

individuals of all locations (< 11.3 individuals core⁻¹; Table IV). The highest numbers of individuals and taxa were found at Cape Adare station 4 (69.0 individuals, 20.5 taxa core⁻¹).

Across all locations, the relationship between number of individuals and/or taxa and depth was weak (Spearman's $r = -0.4233$, $P = 0.0904$ for number of individuals;

Spearman's $r = -0.4140$, $P = 0.0985$ for number of taxa). However, strong differences were noted within locations. For example, at Cape Adare, significantly more individuals and taxa were found at station 4 (200 m deep) than at stations 1, 2 and 5 (500, 400 and 100 m deep, respectively; number of individuals: $P = 0.0458$, number of species: $P = 0.0508$). Station 4 also had more individuals than

Table IIIb. Feeding mode of the macrofauna found in this study. d = deposit feeder, det = detritus feeder, g = grazer, s = suspension feeder, p = predator, sc = scavenger, * could be either, but specific information not available for this species, misc = large group containing a variety of feeding modes.

Amphipoda	
Ischyroceridae	d/g*
Lysianassidae	p/sc
Phoxocephalidae 2	d
Brachiopoda	s
Cumacea 2	det
Echinodermata	
Ophiuroid 1	p/sc
Ophiuroid 2	p/sc
Ophiuroid 3	p/sc
Ophiuroid sp.1	p/sc
Foraminifera	misc
Hydroida	s
Isopoda	
Kiklonana sp.	d/g*
Leptanthuria glacialis	d/g*
Mollusca	
Genaxinus debilis	d
Nucula sp.	d
Philobrya sublaevis	s?
Myodocopida	d/g*
Nematoda	misc
Nemertea	p
Oligochaeta	d
Pycnogonida	d
Polychaeta	
Euchone sp.	s
Glyceridae	p/sc
Lumbrineridae	p/sc
Maldane sarsi Antarctica	d
Notoproctus oculatus antarcticus	d
Rhodine sp.	d
Serpulidae 1	s
Serpulidae 2	s
Syllinae	p/sc

station 3 (300 m deep; $P = 0.0458$). At Cape Hallett Outside, significantly more individuals were found at the shallowest station (100 m, station 5) than at the 500–300 m

deep stations (stations 1, 2 and 3; $P = 0.0542$). At Cape Hallett inside (where only the 200–400 m deep stations were sampled) more individuals were found at station 4 (200 m) than at station 3 (300 m) ($P = 0.0314$). There were no significant differences noted for the number of taxa found at stations within either the Cape Hallett Outside or Cape Hallett Inside locations, and no differences in numbers of individuals or taxa at Coulman Island or Cape Russell ($P > 0.05$).

Interestingly, the pattern in number of taxa and number of individuals at the Cape Adare, Cape Hallett Inside and Cape Hallett Outside stations was very similar to the pattern noted in the sediment phaeophytin levels at these stations/locations (compare Figs 3 & 2b). There was a significant correlation between both number of individuals and number of taxa and phaeophytin concentration of the sediments across all locations (Spearman's $r = 0.6564$, $P = 0.0042$ for number of individuals; Spearman's $r = 0.5565$, $P = 0.0203$ for number of taxa). This correlation is being driven by the patterns at Cape Adare and Cape Hallett Outside in particular, where there were highly significant and very strong correlations between phaeophytin concentrations and numbers of individuals and taxa ($P < 0.0001$; $r = 1.00$ in all cases).

Evenness was high at all locations/stations (i.e. 0.9–1.0; Table IV), indicating a lack of numerical dominance (a value of 1.0 indicates all taxa are equally abundant). The Shannon-Wiener diversity index was highest at sites with high numbers of taxa/individuals: Cape Adare stations 3 and 4, Cape Hallett Inside stations 2 and 4, and Cape Russell station 4 all had levels ≥ 2 . This index is affected by rare taxa, and increases both with increasing numbers of taxa and a more even distribution of individuals amongst taxa.

Examination of the distribution of functional groups (i.e. feeding modes) of the common macrofaunal taxa revealed no clear relationship with depth, either across all locations, or within individual locations ($P > 0.05$ in all cases).

Table IV. Diversity at the five locations. Data presented are mean \pm standard error core⁻¹. n = number of grab samples on which statistics are based. SW = Shannon-Wiener diversity index. Location abbreviations as for Table I.

Location	Station	n	Number of taxa	Number of individuals	Richness (d)	Evenness (J')	SW (H')
CA	1	1	4.0	4.0	2.2	1.0	1.4
CA	2	2	8.5 \pm 3.5	13.5 \pm 5.5	2.8 \pm 0.9	0.9 \pm 0.0	1.9 \pm 0.5
CA	3	2	13.0 \pm 0.0	25.0 \pm 5.0	3.8 \pm 0.2	0.9 \pm 0.0	2.4 \pm 0.1
CA	4	2	20.5 \pm 3.5	69.0 \pm 22.0	4.8 \pm 1.2	0.9 \pm 0.1	2.7 \pm 0.3
CA	5	3	9.0 \pm 1.5	14.0 \pm 3.0	3.1 \pm 0.4	1.0 \pm 0.0	2.1 \pm 0.2
CH In	2	3	10.3 \pm 3.2	17.7 \pm 4.7	3.2 \pm 0.9	0.9 \pm 0.0	2.1 \pm 0.3
CH In	3	3	8.0 \pm 2.6	9.0 \pm 3.1	3.1 \pm 0.7	1.0 \pm 0.0	1.9 \pm 0.4
CH In	4	3	13.3 \pm 2.3	28.3 \pm 3.5	3.7 \pm 0.8	0.9 \pm 0.1	2.2 \pm 0.3
CH Out	1	2	4.0 \pm 1.0	4.5 \pm 1.5	2.0 \pm 0.2	1.0 \pm 0.0	1.3 \pm 0.2
CH Out	2	2	2.5 \pm 0.5	2.5 \pm 0.5	1.6 \pm 0.2	1.0 \pm 0.0	0.9 \pm 0.2
CH Out	3	2	3.0 \pm 0.0	3.5 \pm 0.5	1.6 \pm 0.2	1.0 \pm 0.0	1.1 \pm 0.0
CH Out	4	2	6.0 \pm 1.0	7.5 \pm 1.5	2.5 \pm 0.2	1.0 \pm 0.0	1.7 \pm 0.2
CH Out	5	3	8.0 \pm 2.3	11.3 \pm 2.4	2.8 \pm 0.7	1.0 \pm 0.0	1.9 \pm 0.3
CI	1	2	5.5 \pm 1.5	7.0 \pm 1.0	2.3 \pm 0.6	0.9 \pm 0.0	1.6 \pm 0.3
CI	2	3	7.3 \pm 3.8	11.3 \pm 6.9	2.6 \pm 0.9	0.9 \pm 0.0	1.6 \pm 0.4
CR	3	3	7.3 \pm 3.9	17.7 \pm 9.4	2.0 \pm 1.0	0.8 \pm 0.0	1.3 \pm 0.5
CR	4	3	10.3 \pm 0.9	32.0 \pm 10.0	2.8 \pm 0.1	0.9 \pm 0.0	2.0 \pm 0.1

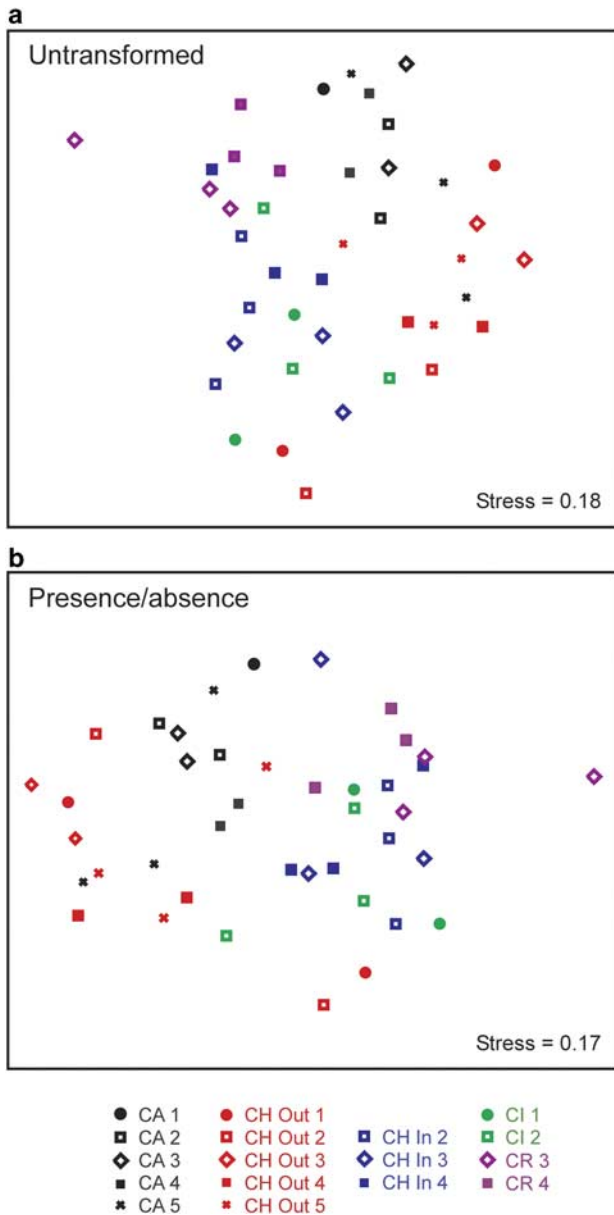


Fig. 3. Multidimensional scaling analysis ordination plot showing the similarities in macrofaunal assemblages within and between locations. Location abbreviations as for Table I.

In addition, closer examination of the composition of the Coulman Island and Cape Russell assemblages did not help elucidate potential reasons for the lack of correlation between number of species/individuals and phaeophytin levels at these locations noted above (e.g. absence of a particular functional group). Predator/scavengers and deposit feeders were common at all locations, while suspension feeders were more common at Cape Hallett Outside (Table III).

The relationship between macrofaunal assemblage composition at the different stations and locations are illustrated in two dimensions in Fig. 3. There is little similarity in macrofaunal assemblage composition across

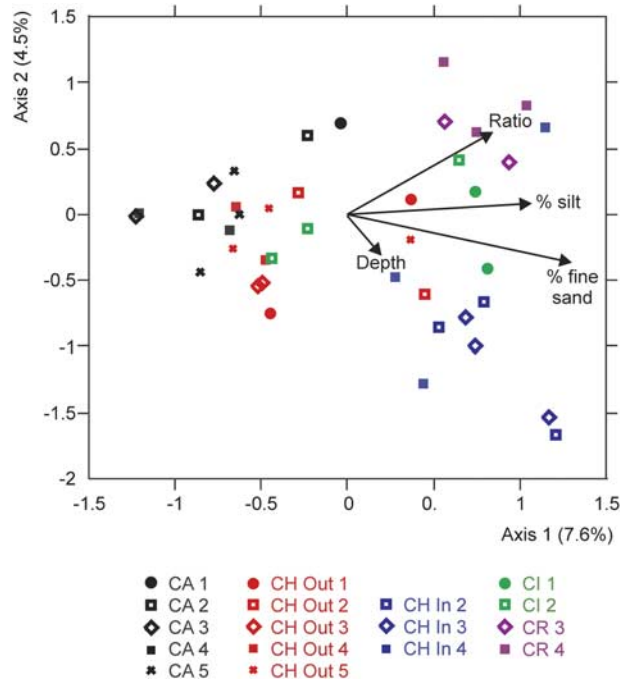


Fig. 4. Canonical correspondence analysis ordination plot showing the environmental variables important in explaining the macrofaunal assemblages at each location and station. Ratio = chl *a*:phaeophytin. Location abbreviations as for Table I.

locations at stations of similar depth (Fig. 3a). Generally, the assemblages varied considerably within locations and there was overlap of the different locations. Cape Adare is the most distinct within the ordination space, indicating that the macrofaunal assemblages at the five Cape Adare stations are the most similar to one another. Cape Hallett Outside exhibits the highest variability in macrofaunal assemblage composition, while Cape Hallett Inside stations are similar to those from Coulman Island. In order to isolate the effect of changes in the densities of species from changes in species composition, an ordination was also conducted on the presence/absence transformed data (Fig. 3b). While this shows a similar pattern to that of the untransformed MDS, with the exception of one Cape Hallett Inside station 3 sample, there is more overlap and tighter clustering of the Cape Hallett Inside, Coulman Island and Cape Russell assemblages (Fig. 3b), indicating that these communities were comprised of similar taxa (see previous discussion of individual taxa).

Explaining variability in macrofaunal assemblage composition using environmental variables

The environmental variables measured during this study and initially included in the CCA model were sediment characteristics (grain size composition, organic content, chl *a*, phaeophytin, ratio of chl *a* to phaeophytin) and depth.

Table V. Summary of Ross Sea studies of distribution of benthic assemblages and important explanatory environmental variables identified.ROAVERRS: 270–1173 m deep, stations arrayed from Cape Hallett (CH) south to southern McMurdo Sound, and from the Victoria Land coast to *c.* 165°E (Barry *et al.* 2003).RV *Italica*: Cape Adare (CA), Cape Hallett, Coulman Island (CI), Cape Russell (CR), 100–500 m (this paper).RV *Tangaroa*: Cape Adare to Cape Hallett, plus the Balleny Islands, targeting three depth strata (50–750 m; e.g. Kröger & Rowden 2008).

Assemblage/ taxa studied	Sampling technique	Depth pattern?	Latitude pattern?	Important explanatory variables?	Voyage	Reference
benthos	box corer 500 µm	-	Sediment organic content higher at southern site.	Correlated with sediment features and sedimentary regime which reflect hydrodynamic conditions.	RV <i>Italica</i> 1994/95	Gambi & Bussotti 1999
megafauna	video transects	Density declined with depth. Deposit feeders most abundant at deeper sites	-	Habitat features and sediment organics	ROAVERRS 1996/97, 1997/98, 1998/99.	Barry <i>et al.</i> 2003
isopods	Rauschert dredge 500 µm	Gnathiidae abundance declined with depth at CA, CH in and CH out and CI (though latter has only 2 stations) but not at CR.	Biomass and abundance of Desmosomatidae and Munnidae increased to the south, Paramunnidae and Janidridae showed opposite pattern (Fig 4).	Sediment structure and iceberg disturbance.	RV <i>Italica</i> 2004	Choudhury & Brandt 2007
water column features, benthos	CTD (water), grab (sediments), AGT (benthos)	-	H ₂ O stratification (0–25 m, 25 m–bottom) and temperature increased and decreased, respectively, from CA to TNB area. Sediment phaeophytin increased to south. CA/CH low phytoplankton biomass and productivity and biogenic sedimentation cf. southern areas where fluxes are generally 2x as great.	Stronger benthic-pelagic coupling in TNB/CR than at CA/CH	RV <i>Italica</i> 2004	Povero <i>et al.</i> 2006
peracarid crustaceans	Rauschert dredge semi quantitative 59–575 m tows 1000–500 µm	-	Lowest diversity and number of cumacean species at CA (Table 6) Cumacean mean abundance increased with latitude (Table 6).	No explanation given	RV <i>Italica</i> 2004	Rehm <i>et al.</i> 2007
Macrozoo-benthos	as above	No change in community structure with depth.	Relative abundance and biomass of major taxa change along coast, but not monotonically (Fig 4).	Sediment type, iceberg disturbance	RV <i>Italica</i> 2004	Rehm <i>et al.</i> 2006
molluscs	grab, towed gear (epibenthic sled, rough bottom trawl, beam trawl, Agassiz trawl)	-	Species richness CA/CH > TNB/CR (but can't comment on latitudinal pattern because of gaps in sampling).	Increased habitat heterogeneity due to iceberg scouring in CA/CH area	RV <i>Tangaroa</i> 2004	Schiaparelli <i>et al.</i> 2006
echinoderms	as above	Differences in species depth distribution and abundance between locations, no indications of links to sediment grain size distribution.	Alpha diversity increases from north to south; beta diversity shows the opposite, but non-linear, trend.	Iceberg disturbance	RV <i>Italica</i> & <i>Tangaroa</i> 2004	De Domenico <i>et al.</i> 2006

Table V. Continued

Assemblage/ taxa studied	Sampling technique	Depth pattern?	Latitude pattern?	Important explanatory variables?	Voyage	Reference
polychaetes	grabs 1000 µm	Higher sediment chl <i>a</i> in shallows at all stations and also at deeper stations on transect 5	No decoupling between benthos/water column. Surface water and sediment chl <i>a</i> did not increase with latitude.	Sediment chl <i>a</i> , sponge spicules, sediment sorting coefficient, distance to nearest iceberg scour.	RV <i>Tangaroa</i> 2004	Kröger & Rowden 2008
macrofauna	grabs 500 µm	See Latitude pattern?	No clear pattern in assemblage composition, number of individuals or taxa with latitude or depth, but significant correlations with sediment phaeophytin. Latitude and depth are not good predictors of community composition.	Iceberg disturbance, ice cover, larval supply, hydrodynamics, primary food sources.	RV <i>Italica</i> 2004	this study

Those most important in explaining the differences in assemblage composition were % fine sand and silt, the ratio of sediment chl *a* to phaeophytin, and depth (Fig. 4). However, the overall percentage of community variability explained is low (17.3%), indicating that the environmental factors included in the model are having only a weak influence on macrofaunal assemblage composition.

Discussion

This paper has described the benthic macrofaunal assemblages at locations spanning three degrees of latitude along the coastal north-western Ross Sea shelf. Macrofaunal assemblages at Cape Adare were comprised mostly of bivalves and crustaceans, polychaetes were predominant at Cape Hallett Outside, polychaetes, nematodes and oligochaetes at Cape Russell and Coulman Island, and the Cape Hallett Inside assemblages comprised a mix of taxa found at the other locations. Average numbers of macrofaunal taxa collected in each core ranged from 3–21 across all locations and stations. Across all locations, the relationship between number of individuals and/or taxa and depth was weak.

To identify the use of seafloor sediment characteristics and/or depth measures in bioregionalizations, we also assessed the extent to which assemblage compositions are related to measured differences in these factors. Although our analyses identified % fine sand and silt, the ratio of sediment chl *a* to phaeophytin, and depth as important explanatory variables, in combination they explained only 17.3% of the between-location differences in assemblage composition. Consequently, these variables are clearly not strong determinants of macrofaunal assemblage structure. In addition, there was no clear pattern in assemblage structure with location along this coastline, indicating that latitude *per se* is not a useful measure of community variability and change. For reasons outlined in the Introduction, and similar to studies documented in Table V, the latter finding is not surprising. This lack of a clear link between these variables and assemblage composition highlights the need for caution when creating bioregionalizations based on such variables. This adds impetus to the need to gather data more appropriate for capturing seafloor diversity.

Barry *et al.* (2003) found that the Ross Sea megabenthos (sampled by video) was dominated by suspension feeders (87%), with a smaller proportion of deposit feeders and predators. These authors also noted that suspension feeders were more abundant in shallow waters (360 ± 105 m, mean \pm SD), deposit-feeding taxa increased at the deepest sites, and overall faunal densities decreased with depth. Arntz (1999) also noted that suspension feeders dominated the Ross Sea benthos. This depth-related pattern was not apparent for the macrofauna sampled by grab in our study (although the depths covered were not as wide ranging as those of Barry *et al.*), with a variety of functional groups found at all locations (Table III).

In coastal waters, one consistency that seems to be emerging is the high degree of heterogeneity that benthic communities exhibit (e.g. Hewitt *et al.* 2004, Thrush *et al.* 2006a). This is probably a reflection of local disturbance regimes (see below discussion of icebergs), larval supply, hydrodynamics, and the importance of ecosystem engineers along with changes in the relative proportions of primary food sources. We measured sediment organic content and pigment concentrations as an indication of primary food sources (i.e. sinking of material through the water column and *in situ* production). Sediment organic content was low, and showed no relationship with latitude or depth. Values of 0.5 to 1.5% C were noted for 270–1173 m deep stations in the south-western Ross Sea by Barry *et al.* (2003) and, although these values are not directly comparable to our organic content (which was measured as loss on ignition), they are also considered low. Sediment chl *a* and phaeophytin concentrations were variable and highest at the southernmost location, Cape Russell. All sediments contained more phaeophytin than chl *a*, indicating a stronger benthic-pelagic coupling in this area (Povero *et al.* 2006). Pusceddu *et al.* (2000) sampled sediment pigments from 12–127 m in Adélie Cove, Terra Nova Bay, and noted an increase with depth to 76 m and, as in this study, a predominance of phaeophytin amongst the sedimentary pigments. Interestingly, we found a significant correlation between both number of individuals and number of taxa and sediment phaeophytin concentration across all locations. This pattern may be due to the fact that both phaeophytin and macrofauna are time-integrated measures, and there is thus a better matching of macrofauna with phaeophytin than with chl *a*, and suggests that the distribution of the benthos in these locations reflects their response to time-averaged periods of productivity.

A number of factors not measured in this study have probably influenced the structure and function of assemblages and habitats. These include: strong near shore currents (particularly noticeable at Cape Hallett and Cape Adare) and bottom topography, rapid changes in sea ice conditions in the summer (e.g. over several hours in some locations), and iceberg disturbance. The latter in particular probably contributes to the variability between stations at some of our sampling locations, as local disturbance by ice and the subsequent recolonization creates a patchy pattern on the seafloor with epifaunal organisms exhibiting different life forms dominating in different stages of succession (Gutt 2001, Teixido *et al.* 2004). Studies have noted differences in macrofaunal biomass and taxa richness (Lenihan & Oliver 1995, Gerdes *et al.* 2003) and feeding types (Conlan *et al.* 1998) in relation to the degree of iceberg disturbance. While there was no clear pattern in distribution of functional groups in our study that would indicate that one station was more or less impacted by icebergs, video and multibeam imagery collected on the RV *Italica* and *Tangaroa* voyages demonstrate that iceberg scouring is a significant source of topographic variation to the seafloor in our sampling regions.

Dr R. Kvittek estimated iceberg disturbance had occurred in at least 40% of the seafloor off Cape Hallett (Thrush *et al.* 2006a). Kröger & Rowden (2008) reported considerably lower disturbance in the Cape Adare/Cape Hallett regions, and differences in disturbance rates with depth. Information on the distribution and track of icebergs and the spatial and temporal scales of disturbance in the Ross Sea, in tandem with observations of seafloor disturbance/community recovery dynamics, is needed to help interpret patterns in seafloor diversity. Icebergs can also affect phytoplankton production and distribution (e.g. Schwarz & Schodlok 2009) and thus benthic-pelagic coupling.

Good understanding of the ecological processes that underpin biodiversity in the Ross Sea's coastal regions (continental and islands) is vital in realistically assessing the threats to this environment (e.g. Agardy 2005). While there has been a long and productive history of taxonomic research on the benthos of the Ross Sea (e.g. Borchgrevink 1901, Bullivant 1967a, 1967b, Dell 1972), our understanding of the structure and function of these communities remains poor. Benthic communities have not been sampled in many areas and our understanding of functional relationships and their spatial and temporal variability is even more constrained. This limited knowledge is recognized as a major barrier to developing and testing bioregionalization (e.g. Lombard *et al.* 2007) and more broadly in predicting the consequences of change (e.g. removal of top predators, climate variability, tourism).

Importantly, we show that latitude and depth are not good predictors of community composition for north-western Ross Sea shelf macrofaunal communities. This provides insight into the role of changes in ecosystem structure and function directly associated with latitude along the Victoria Land coast (a Key Question within the Latitudinal Gradient Project). Several studies of Ross Sea fauna have looked for consistencies in assemblage composition with factors such as depth or latitude, but generally have not found evidence of simple patterns; rather their distributions are explained by sediment type, hydrodynamic conditions and iceberg disturbance (although these studies seldom measured the latter) (see summary in Table V). These findings emphasize the complexity of these marine systems, and the role of other environmental and biotic factors in governing abundance and distribution patterns. The low correlation found in this study between the infaunal community and the (largely physical) habitat characteristics measured highlights the need for caution when choosing marine protected areas (MPAs) based only on such variables.

Most researchers involved in marine bioregionalization development acknowledge the limited availability of benthic biological data (Sharp *et al.* 2010). This is unfortunate as seafloor habitats represent a major component of the biodiversity we are trying to protect. As technological improvements allow ecologists to better sample seafloor

habitats and communities, there is growing recognition of the essence of spatial variability (Levin & Dayton 2009). Often this important heterogeneity is generated by the presence and actions of organisms directly modifying habitats or generating important bio-physical or bio-geochemical feedback processes (e.g. Chiantore *et al.* 1998, Van de Koppel *et al.* 2005, Thrush *et al.* 2006b, Van Nes *et al.* 2007). Given their longevity and the potential of many Antarctic benthic species to create three-dimensional habitats we may expect such features to be especially important in the Antarctic (Arntz *et al.* 1997, Thrush *et al.* 2006a). The implementation of scale-dependent hierarchical approaches to bioregionalization recognizes that variability within scales can be functionally important (Legendre 1993), but cross-scale interactions and the maintenance of ecological connectivity across landscapes is also important for conservation (e.g. Zajac *et al.* 2003). While the challenge of improving bioregionalization processes via new data must be met we must also consider how to better incorporate dynamic process, such as variation in sea ice extent, thickness and snow cover. Also important is the need to incorporate biogenic habitat complexity into protection strategies and to define and understand the processes that contribute to seafloor biodiversity.

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