# Accounting for local scale variability in benthos: implications for future assessments of latitudinal trends in the coastal Ross Sea

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**Abstract:** This paper is a contribution to the Latitudinal Gradient Project. It describes macro and epifaunal assemblages and habitats at three shallow water locations at the southern end of the western Ross Sea coast, and investigates relationships between faunal composition and environmental characteristics. Many variables (e.g. substrate type, sediment composition, depth, latitude, longitude) contributed to explaining the differences in community composition between locations, with latitude (a likely surrogate for broader scale factors, e.g. ice cover) one of the most important. The percentage explained by environmental characteristics was strongly scale dependent, decreasing with increasing scale of observation. As much as 66% and 75% of the variability in macrofaunal and epifaunal assemblages, respectively, was explained at the smallest scale (i.e. between transects within a location), compared to 9–18% and 11–32%, respectively, at the scale of the entire study. This relationship was also true for species richness and total abundance. This suggests that while small-scale habitat variability will not confound our ability to detect latitudinal gradients in future studies, adequately quantifying the environmental factors important in structuring these communities at larger (latitudinal) spatial scales will be important. Finally, large differences in habitat structure did not translate into large differences in the diversity of fauna, illustrating the difficulty of predicting faunal composition in the Ross Sea based on seafloor topography alone.

## Introduction

There is strong evidence that locally reduced habitat complexity can cause reductions in biodiversity, and vice versa (e.g. Schumude *et al.* 1998, Charbonnel *et al.* 2002, Valdemarsen & Suuronen 2003). However, this relationship does not always hold (e.g. Angel & Ojeda 2001), and the links between the various components of habitat and biodiversity have been extensively debated in recent decades (Symstad *et al.* 2003). A good understanding of these links is important to enable predictions and protection of areas and habitats likely to be important in terms of biodiversity.

In coastal marine ecosystems, local patterns of structural and functional biodiversity may be constrained by broad-scale environmental variables, such as food supply/energy input (Pearson & Rosenberg 1987) or salinity. These and other broad-scale environmental variables can strongly influence the observed patterns in species diversity, such that comparisons between locations in which these variables differ are not likely to reveal simple, consistent patterns or responses (Hewitt *et al.* 2002). The potential strong influence of environmental factors, operating over a range of spatial and temporal scales, on benthic diversity underlines the importance of moving beyond traditional point measurements of diversity and utilizing techniques that enable us to identify how these broad-scale factors interact with biotic and environmental processes operating on smaller-scales.

In the Antarctic marine environment sea ice conditions are likely to have a strong influence on benthic communities (Thrush *et al.* 2006). Strong seasonality in sea ice cover and, consequently, the light regime means that primary production and input of food to marine benthic communities is pulsed. Thus, benthic biomass is strongly influenced by advection of food from elsewhere, sinking of material through the water column, and *in situ* production (Greibmeier & Barry 1991), and the relative importance of these food sources is affected by sea ice conditions (e.g. spatial and temporal extent of ice cover).

Antarctic benthic communities are predicted to closely reflect local conditions (i.e. local sediment type, productivity and history of ice disturbance). Dayton &
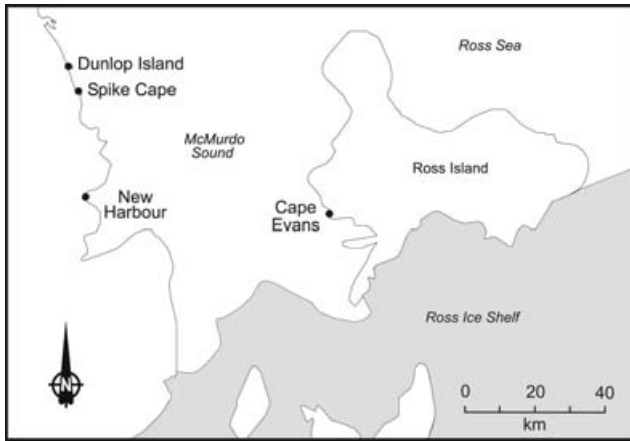
**Fig. 1.** Map of the south-western Ross Sea study area.

**Table I.** Broad-scale environmental characteristics at the study locations.

| Environmental factor | DI | SC | NH |
|---|---|---|---|
| Ice conditions | | | |
| − ice cover | annual | annual | semi-permanent |
| − ice thickness (m) | 2.6 | 2.4 | 3.5 |
| Below ice incident irradiance (%) | 0.25 | 0.12 | 0.20 |
| Water temperature (°C) | -1.92 | -1.92 | -1.92 |
| Current velocity (cm s$^{-1}$) | | | |
| − mean ± SD | 3.8 ± 2.6 | 2.6 ± 1.3 | 2.6 ± 0.8 |
| − minimum– maximum | 0.0–14.0 | 0.0–7.6 | 1.2–4.6 |

DI = Dunlop Island, SC = Spike Cape, NH = New Harbour. SD = standard deviation

## Methods

### Sites

We developed a modular survey design that nests macrobenthic and biogeochemical core samples within videoed transects of the seafloor (Thrush *et al.* 2001, Hewitt *et al.* 2002). The survey was implemented at three locations (Dunlop Island, Spike Cape and New Harbour) on the western side of McMurdo Sound, in October/November of 2001 and 2002. These locations span *c.* 32 km of coastline: the southernmost site, New Harbour, is 24 km south of Spike Cape, and Dunlop Island is 8 km north of Spike Cape (Fig. 1). Table I identifies key environmental characteristics of each location (details of how these were measured are given below).

At each location, three sites, separated by at least 50 m, were surveyed (Table II). Each site was accessed through holes in the sea ice and sampled using SCUBA. Two 20 m transect lines were laid on the seafloor within a 14–25 m depth stratum and videoed using a diver-held digital video camera, at fixed heights of 70 cm and 40 cm above the bottom. Five randomly chosen positions along Transect 1 were marked with labelled pegs. At each position, small (26 mm diameter, 50 mm deep) and large (70 mm diameter, 100 mm deep) cores were collected to determine sediment grain size, organic and chlorophyll *a* (Chl *a*) content, and the abundance and diversity of macrofauna, respectively.

To provide information on broader scale characteristics of

Oliver (1977) found that species biomass, abundance and diversity varied between the east and west sides of McMurdo Sound, Ross Sea. Due to prevailing circulation patterns and its proximity to the Ross Ice Shelf, the continental margin of McMurdo Sound (New Harbour) exhibits consistently low primary productivity, while Cape Evans (eastern McMurdo Sound) supports macroalgae populations, abundant sea ice algae during spring, and a phytoplankton bloom typically occurs each December/January. Along the latitudinal gradient encompassed by the western Ross Sea coast, physico-chemical conditions and coastal marine communities are expected to vary in a predictable, but non-linear, fashion due to the proximity to the Ross Ice Shelf, variation in the extent of the sea ice and coastal polynyas and frequency of iceberg disturbance. Quantitative between-location comparisons of species richness, diversity, evenness and functionality along this coastline have not yet been made at latitudinal scales.

This work is conducted as part of the Latitudinal Gradient Project (LGP; see http://www.lgp.aq), whose overarching theme is that "ice driven dynamics controls the structure and function of ecosystems at high latitudes". The results presented in this paper address the key LGP questions investigating latitudinal-scale changes in the structure and function of marine benthic ecosystems, and the effect of ice conditions (such as ice extent, persistence) on light, primary producers and key marine biological processes (Howard-Williams *et al.* 2006). We provide a comparison of seafloor communities and habitat structure at three locations along the western McMurdo Sound coastline, at the southern end of the latitudinal gradient of the western Ross Sea coast. Our aim is to identify the environmental variables likely to be important determinants of habitat at the scale of this study and consider how relevant they are likely to be when integrating data on community structure and species diversity along this entire coastline.

**Table II.** Locations and depths of the three sites sampled at each location. Dunlop Island (DI) was sampled from 22–25 October 2002, Spike Cape (SC) from 30 October–2 November 2002, and New Harbour (NH) from 29 October–4 November 2001.

| Location | Site | Depth (m) | Latitude | Longitude |
|---|---|---|---|---|
| DI | 1 | 19.0 | 77°14.161'S | 163°27.940'E |
| DI | 2 | 21.0 | 77°14.176'S | 163°27.997'E |
| DI | 3 | 15.5 | 77°14.141'S | 163°27.917'E |
| SC | 1 | 18.5 | 77°18.024'S | 163°33.935'E |
| SC | 2 | 20.0 | 77°18.040'S | 163°33.880'E |
| SC | 3 | 14.8 | 77°18.050'S | 163°33.958'E |
| NH | 1 | 24.0 | 77°34.578'S | 163°31.668'E |
| NH | 2 | 19.0 | 77°34.555'S | 163°31.279'E |
| NH | 3 | 22.0 | 77°34.610'S | 163°31.895'E |

the environment, water current velocity, and under-ice light climate were quantified at one site at each location. An S4 current meter was deployed 4 m above the seafloor for 3–5 days. Photosynthetically available radiation (PAR) was measured using a LiCor Li190SA quantum sensor for incident irradiance (background irradiance above the ice) and a Li192SB for underwater irradiance attached to a Li-1000 logger. Five replicate recordings were made at positions above and just below the sea ice. The latter measurements were made well away from the dive holes.

Finally, to extend the generality of the survey results and determine how representative our sites were of each location, a remotely operated video camera (SplashCam) was used to video additional sites. The camera was lowered on an umbilical through small holes drilled in the sea ice. The camera was fitted with three lasers, which allowed for sizing of dominant animals and habitat features.

### Sample processing and analysis

Macrofauna core samples were sieved (500 μm mesh), preserved in 70% isopropyl alcohol, sorted and identified to the lowest taxonomic level possible. Sediment from each small core was homogenized and subsampled for Chl *a*, grain size and organic content analysis. Chl *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). Sediments for particle size analysis were digested in 6% hydrogen peroxide for 48 h to remove organic matter, and dispersed using Calgon. A Galai particle analyser (Galai Cis−100; Galai Productions Ltd, Midgal Haemek, Israel) was then used to calculate percentage volumes for the coarse, medium and fine sand, silt and clay fractions. Organic content was determined by drying the sediment at 60°C for 48 h, followed by combustion at 400°C for 5.5 h.

### Video imagery

A video frame grab was taken at each of the five marked positions along Transect 1. Each frame (or sample "quadrat") corresponded to an area of either 1.3 m$^2$ or 0.3 m$^2$, for the footage taken at 70 cm or 40 cm above the bed, respectively. The specific video height (i.e. 70 or 40 cm above the seafloor) analysed for quantitative estimates of habitat structure depended on the habitat (see below). Additional frame grabs were taken on either side of the marked position, resulting in three adjacent quadrats from each position and a total of 15 quadrats along the transect.

Habitat structure and epifaunal abundance were quantified for each quadrat by splitting the video screen into a regular grid of 10 by 8 squares. Each square was classed as containing a particular habitat type based on the dominant (i.e. > 50% cover) habitat category found within

it. This information was then used to determine the relative proportions of the different habitat categories (i.e. rock, cobble, pebble and sand) contained within each quadrat. At sites dominated by larger rock and cobble, only the video footage from 40 cm above the seafloor was used as this provided the best quality video for distinguishing between them. At sites dominated by relatively featureless soft sediments, only the 70 cm height video footage was used. Hereafter the quadrats from the 70 cm and 40 cm heights will be referred to as 1.3 m$^2$ and 0.3 m$^2$ quadrats, respectively. Epifaunal abundance was also determined along the full transect length, thus providing information on the rarer taxa with patchy distributions, and a more complete estimate of species composition at a site.

### Statistical analyses

Variations in species composition and relative abundance of benthic fauna within and between sites were determined using a combination of visual examination of univariate measures, and multivariate analytical procedures (Clarke & Warwick 1994, Legendre & Legendre 1998).

The macrofaunal community core data is presented as numbers of individuals and taxa core$^{-1}$. Counts of epifaunal taxa from the video quadrats were converted to density m$^{-2}$. These conversions were calculated using the combined count from three consecutive quadrats, as these generally gave better abundance estimates than those using a single quadrat. The total number of taxa and individuals and species richness (Margalef's index) were calculated for both the epifauna and macrofauna using the DIVERSE procedure within PRIMER (Clarke 1993). The ability of our video sampling design to adequately estimate the total number of large epifaunal taxa at each site had previously been tested using the data obtained from each video quadrat and a randomisation procedure, giving us confidence in our estimates of species richness.

The contributions of the various macrofaunal and epifaunal taxa to the community differences observed within and between sites and locations were identified using the classification procedure SIMPER (PRIMER, Clarke 1993). The relationships within and between locations for (a) macrofaunal community composition (determined from the core data), and (b) epifaunal community composition (determined from the video) in relation to environmental drivers/surrogate variables were assessed using Canonical Correspondence Analysis (CCA; ter Braak 1986, 1987). The following environmental variables were included in this analysis: latitude, longitude, depth, habitat characteristics from video (i.e. cobble, rock, pebble, sand), sediment characteristics from cores (i.e. coarse, medium and fine sand, silt, clay, organic content, Chl *a*, phaeophytin, the ratio of Chl *a* to phaeophytin). As the information on light levels and current velocities were not available for every site, these variables were not used in this analysis.
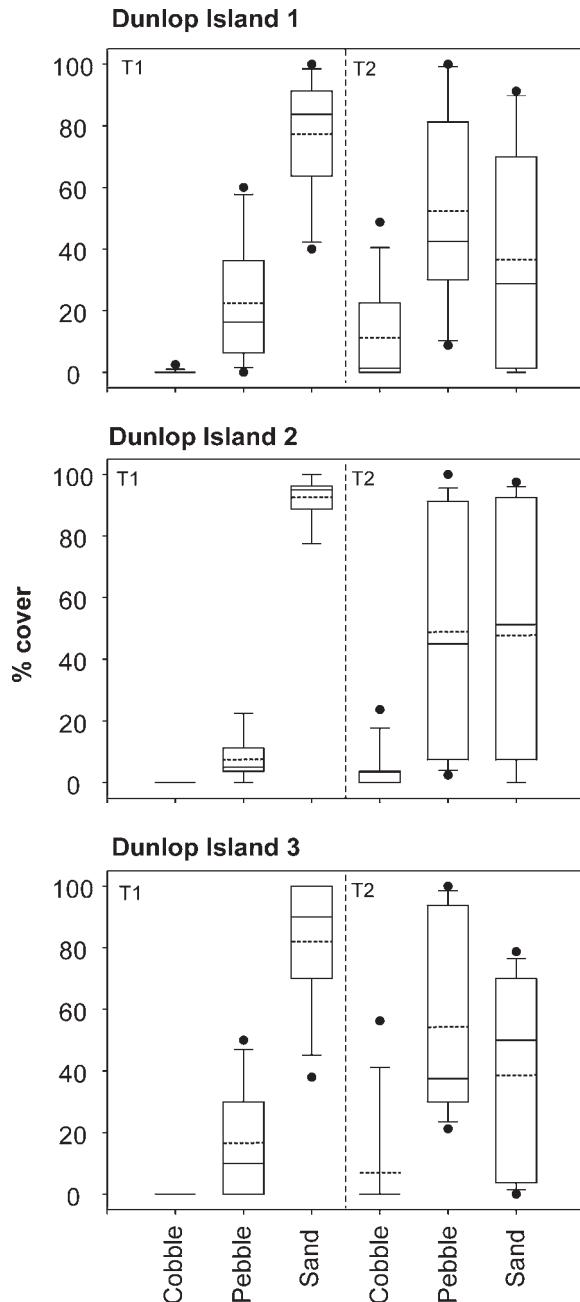
**Fig. 2.** Distribution of the major habitat types at the three sites at Dunlop Island. Whiskers located at the 10% and 90% percentiles encompass 80% of the data points and dots indicate the few values outside of this range. The upper and lower ends of the box are the 25% and 75% percentiles, respectively, and encompass 50% of the data. The solid line indicates the median and the dotted line the mean value.
T1 = Transect 1, T2 = Transect 2.

**Fig. 3.** Distribution of the major habitat types at the three sites at Spike Cape. Plot description as for Fig. 2.

To determine whether relationships between community composition and habitat variability were likely to interfere with the detection of large-scale latitudinal gradients, the effect of scale on these relationships were investigated. Forwards selection of important environmental variables
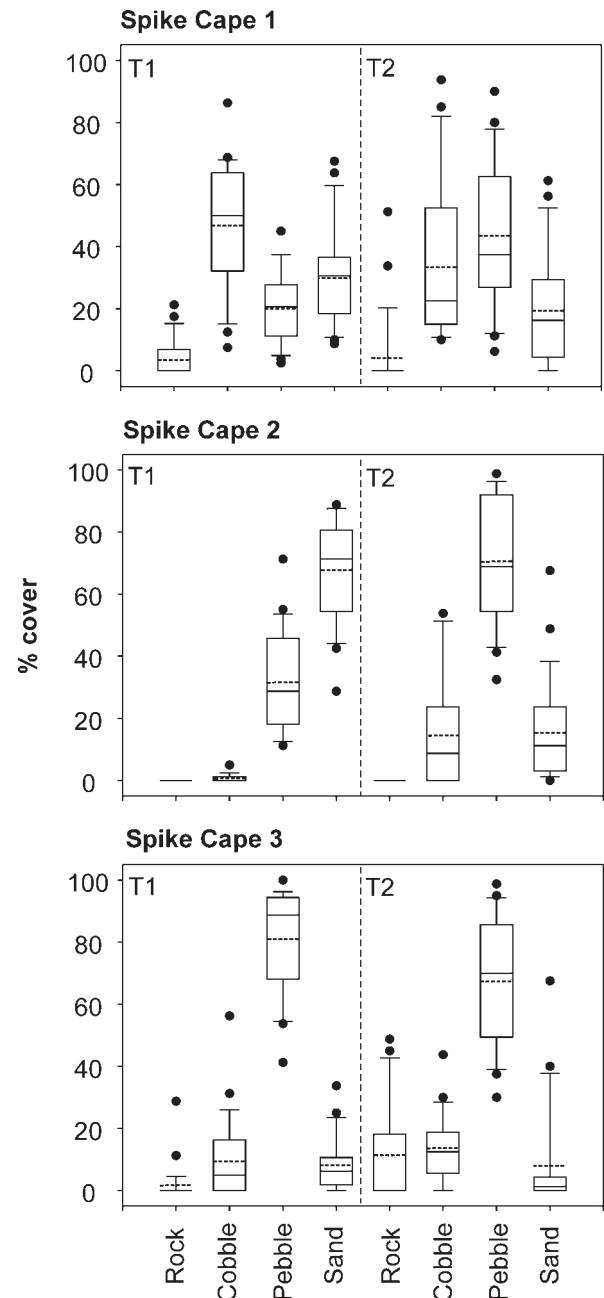
was carried out at three scales: (1) within a site at each location, (2) within each location and (3) among locations. For both the epifauna and macrofauna community analyses, raw data was used in a CCA with down weighting for rare taxa. The variables used were estimates from the video data of % cover of substrate type (rock, cobbles, sand, mud) over three quadrats, and measures of sediment particle size at each core. For macrofaunal data collected by coring, a further habitat variable, the percentage cover of sedentary epifauna and flora, was included. For both epifauna and macrofauna data, a similar analysis was carried out using

**Table III.** Sediment grain size (%), organic (%) and pigment (μg g⁻¹ sediment) content at the three locations. Data presented are mean ± SE.

| Location | Clay | Silt | Fine sand | Medium sand | Coarse sand | Gravel | OC | Chl $a$ | Phaeo | Chl $a$:phaeo |
|---|---|---|---|---|---|---|---|---|---|---|
| DI1 | 0.02 ± 0.00 | 0.52 ± 0.13 | 5.90 ± 1.79 | 13.10 ± 2.26 | 54.95 ± 6.93 | 25.52 ± 9.34 | 0.09 ± 0.07 | 1.84 ± 0.31 | 2.31 ± 0.58 | 0.87 ± 0.08 |
| DI2 | 0.03 ± 0.01 | 1.19 ± 0.21 | 23.31 ± 1.71 | 29.03 ± 2.32 | 41.49 ± 2.49 | 4.95 ± 2.89 | 0.45 ± 0.04 | 0.79 ± 0.16 | 2.37 ± 0.35 | 0.36 ± 0.10 |
| DI3 | 0.02 ± 0.01 | 0.58 ± 0.20 | 6.32 ± 2.21 | 8.89 ± 2.45 | 45.94 ± 6.46 | 38.26 ± 10.42 | 0.27 ± 0.10 | 1.31 ± 0.33 | 2.23 ± 0.27 | 0.56 ± 0.10 |
| SC1 | 0.06 ± 0.02 | 3.11 ± 0.77 | 41.89 ± 7.04 | 22.53 ± 3.25 | 23.06 ± 5.64 | 9.35 ± 9.01 | 0.64 ± 0.22 | 1.23 ± 0.20 | 4.29 ± 0.84 | 0.31 ± 0.04 |
| SC2 | 0.06 ± 0.01 | 2.88 ± 0.97 | 21.82 ± 8.67 | 10.00 ± 3.74 | 26.09 ± 8.09 | 39.15 ± 19.86 | 0.39 ± 0.19 | 1.65 ± 0.25 | 4.79 ± 0.28 | 0.35 ± 0.05 |
| SC3 | 0.14 ± 0.08 | 4.96 ± 3.49 | 12.39 ± 8.08 | 6.24 ± 3.35 | 26.12 ± 11.30 | 50.15 ± 22.17 | 0.73 ± 0.23 | 3.08 ± 0.58 | 11.86 ± 2.54 | 0.28 ± 0.05 |
| NH1 | 0.03 ± 0.00 | 6.21 ± 1.36 | 18.39 ± 1.36 | 19.66 ± 1.65 | 52.28 ± 1.64 | 3.44 ± 2.99 | 0.63 ± 0.05 | 0.28 ± 0.04 | 1.59 ± 0.28 | 0.19 ± 0.03 |
| NH2 | 0.02 ± 0.01 | 2.56 ± 0.38 | 15.52 ± 1.53 | 15.09 ± 0.76 | 60.45 ± 2.36 | 6.36 ± 2.64 | 0.55 ± 0.04 | 0.51 ± 0.09 | 2.33 ± 0.44 | 0.22 ± 0.02 |
| NH3 | 0.03 ± 0.01 | 5.88 ± 1.49 | 17.61 ± 1.73 | 18.19 ± 0.92 | 57.40 ± 3.35 | 0.89 ± 0.31 | 0.69 ± 0.07 | 0.61 ± 0.21 | 2.28 ± 0.33 | 0.24 ± 0.05 |

OC = organic content, Chl $a$ = chlorophyll $a$, Pphaeo = phaeophytin. DI = Dunlop Island, SC = Spike Cape, NH = New Harbour.

multiple regression with species richness and total abundance as dependent variables.

## Results

### Broad-scale environmental characteristics

The sea ice was thickest at New Harbour (3.5 m), and almost 1 m thinner at Dunlop Island and Spike Cape (Table I). New Harbour sea ice is relatively persistent, breaking out only every 5 to 10 years; the last known breakout prior to our visit was 1999/2000 (Sam Bowser, personal communication 2001). In contrast, the sea ice at Dunlop Island and Spike Cape is likely to be annual, although on some occasions the ice may linger in the area between Dunlop Island and the continent. Less than 0.25% of the above-ice incident light penetrated the sea ice at each location. There were differences between locations, with the least light transmitted through the ice at Spike Cape (Table I). However, there was considerable snow cover on the ice at Spike Cape and Dunlop Island in 2002, but little at New Harbour in 2001. Mean current velocities were similar at all locations, with highest velocities (up to 14 cm sec⁻¹) noted at Dunlop Island (Table I).

### Physical habitat characteristics

At both Dunlop Island and Spike Cape there was considerable variability in habitat structure both between transects at a particular site, and between sites. The Dunlop Island sites were comprised of sand with varying amounts of pebble, and the occasional patch of cobble (Fig. 2). The Spike Cape habitats contained comparatively more cobble (Fig. 3). Site 1 was the cobbliest of the three Spike Cape sites, while Site 3 was rocky and had high amounts of pebble. The habitat at Site 2 was predominately pebble and sand, with small amounts of cobble, and no rock. One feature of this location was the large amount of coralline algae encrusting the rocks, boulders and pebbles. In contrast, the New Harbour habitats were entirely dominated by soft sediments. The Splash Cam footage at each location showed similar habitats to those revealed from the intensive
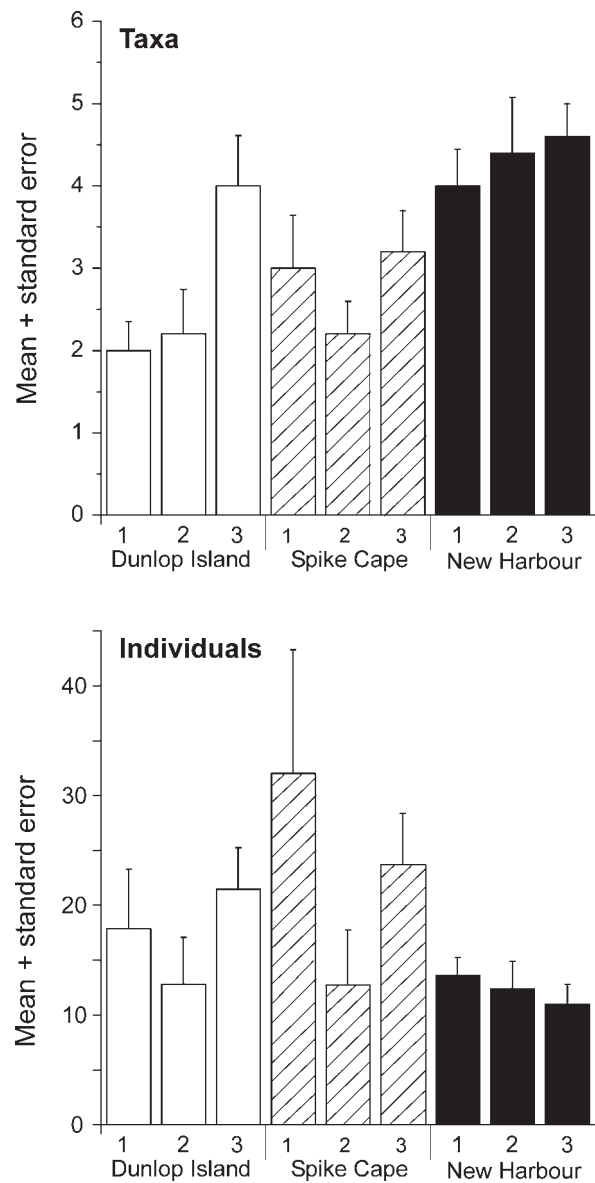


**Fig. 4.** Number of large epifaunal taxa and individuals (mean ± SE m⁻²) at each site at each location.
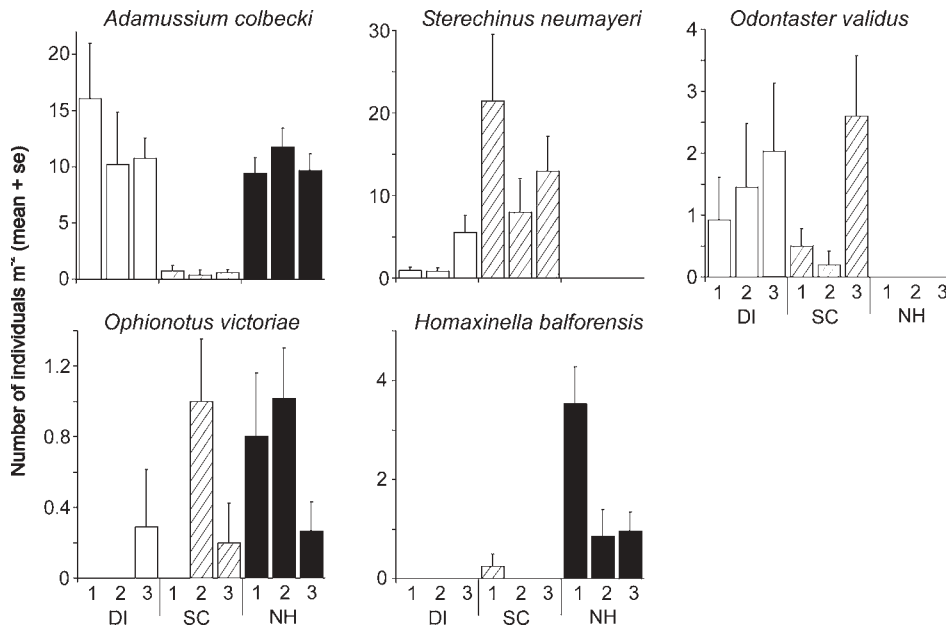
**Fig. 5**. The abundance (mean ± SE m$^{-2}$) of the numerically dominant, large epibenthic taxa at Dunlop Island, Spike Cape and New Harbour. DI = Dunlop Island, SC = Spike Cape, NH = New Harbour.

survey sampling using transects, indicating the local representativeness of habitats sampled at the survey sites.

### Sediment characteristics

At all three Dunlop Island sites coarse sand was the largest sediment component (41−55%; Table III). Gravel/pebble was also common at Dunlop Island Sites 1 and 3, while medium and fine sand were more abundant at Site 2. The sediments at Spike Cape Site 1 were comprised of fine sand (41.9%), with some coarse and medium sand (each 23%). Sites 2 and 3 were predominantly gravel/pebble and coarse sand. The New Harbour sites were mostly coarse sand (52–60%), with equal amounts of fine and medium sand (each 15–20%). Sediment organic content was low at all locations (< 1%; Table III).

There were differences in levels of sediment Chl *a* between locations (Table III), with the lowest levels measured in New Harbour sediments. Chl *a* was, on average, similar at Dunlop Island and Spike Cape. Within each of these locations, the three Dunlop Island sites had similar chlorophyll levels (0.79–1.84 µg g$^{-1}$ sediment), as did the three New Harbour sites (0.28–0.61 µg g$^{-1}$ sediment). At Spike Cape, however, between site variability was large, with levels considerably higher at Site 3 than at Sites 1 or 2 (Table III). Sediments at all three locations had more degraded than healthy microphytobenthos (Table III). In addition, a higher proportion of the microphytobenthic biomass was in a degraded state at Spike Cape and New Harbour than at Dunlop Island, with comparatively more chlorophyll available at Dunlop Island Site 1 (i.e. Chl *a*: phaeophytin = 0.87; Table III).

### Epifaunal community composition

Epifaunal diversity was similar between locations, ranging from an average of 2–4 taxa m$^{-2}$ (Fig. 4). Epifaunal abundances ranged from 10–24 ind. m$^{-2}$. At both Dunlop

**Table IV.** The epifaunal taxa contributing to 80% of the variability in community composition at each site (from SIMPER analysis). For each site, the top ranked taxa are given, with 1 the most abundant taxa. The percentage contribution of each individual taxa to community variability is given in brackets.

| Taxa<br>% within-site similarity | DI1<br>54.65% | DI2<br>48.10% | DI3<br>57.88% | SC1<br>50.89% | SC2<br>34.92% | SC3<br>54.39% | NH1<br>75.90% | NH2<br>77.26% | NH3<br>74.04% |
|---|---|---|---|---|---|---|---|---|---|
| Bivalvia | | | | | | | | | |
| *Adamussium colbecki* | 1 (92.49) | 1 (87.13) | 1 (70.57) | | | | 1 (71.23) | 1 (90.52) | 1 (91.49) |
| Echinodermata | | | | | | | | | |
| *Sterechinus neumayeri* | | | 2 (20.05) | 1 (93.43) | 1 (71.77) | 1 (77.33) | | | |
| *Ophionotus victoriae* | | | | | 2 (28.23) | | | | |
| *Odontaster validus* | | | | | | 2 (19.11) | | | |
| Porifera | | | | | | | | | |
| *Homaxinella balforensis* | | | | | | | 2 (24.46) | | |
| Total taxa | 1 | 1 | 2 | 1 | 2 | 2 | 2 | 1 | 1 |

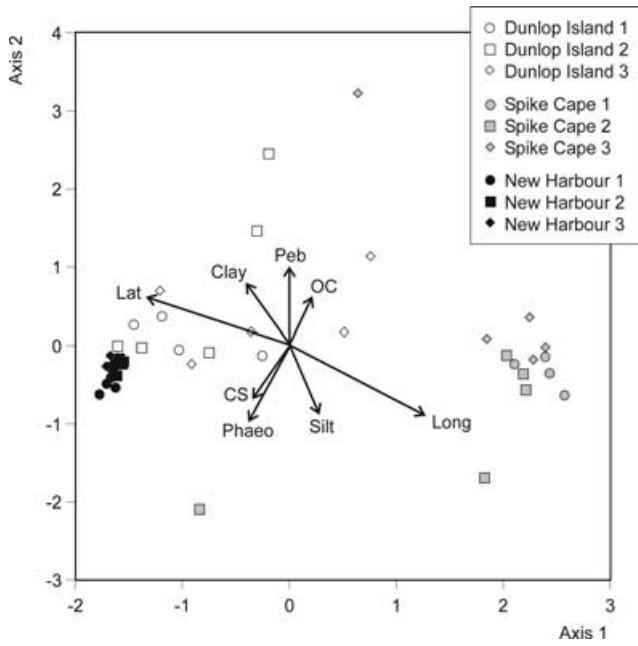DI = Dunlop Island, SC = Spike Cape, NH = New Harbour.

**Fig. 6**. Canonical Correspondence Analysis ordination plot of epifaunal community composition at each site/location, and the environmental variables important in explaining community composition. Lat = latitude, Long = longitude, Peb = pebble, OC = organic content, CS = coarse sand, Phaeo = phaeophytin.

Island and Spike Cape, the abundances varied between sites, ranging from 13–22 and 10–24 ind. m$^{-2}$, respectively. New Harbour abundances were comparatively low and evenly distributed between sites (12–14 ind. m$^{-2}$).

*Adamussium colbecki* numerically dominated the epifaunal communities at both Dunlop Island and New Harbour (Fig. 5, Table IV). *Sterechinus neumayeri* was the most abundant taxa at each of the Spike Cape sites, with *Ophionotus victoriae* and *Odontaster validus* occurring at Sites 2 and 3, respectively. *Homaxinella balfourensis* was a dominant taxa at New Harbour, where it was found attached to *Adamussium* or to spines of the pencil urchin *Ctenocidaris perrieri*.

### Relationship between epifaunal community composition and environmental variables

Despite the three locations sharing similar dominant epifaunal taxa (Fig. 5; Table IV), their separation from each other in ordination space indicates they have distinct assemblage compositions (Fig. 6). The highest within-site variation in epifaunal community composition was noted at Spike Cape (i.e. Sites 2 and 3). Conversely, the New Harbour epifaunal communities are very similar. The epifaunal communities at Dunlop Island showed similar variability within and between sites.

The variables most important in explaining between-location and between-site differences in epifaunal
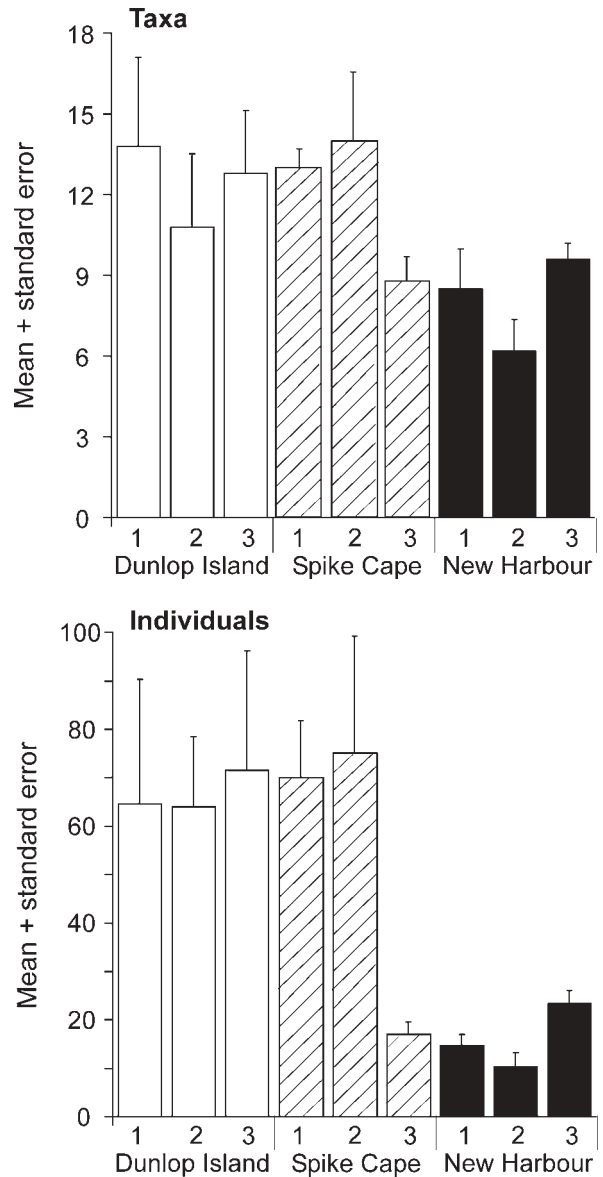


**Fig. 7.** Number of macrofauna taxa and individuals (mean ± SE core[1]) at each site at each location.

assemblage composition were latitude and longitude (overall variance explained = 50.4%). Site depth, pebble (from video), and % coarse sand, % medium sand, % fine sand, % silt and % organic content of the sediment (all from the cores) were also important. The fact that so many environmental variables contributed to explaining these assemblage patterns illustrates the complexity of the relationship between habitat characteristics and epifauna at these locations.

### Macrofaunal community composition

The average number of macrofaunal taxa found at each site ranged from 6–14 taxa core$^{-1}$ (Fig. 7). Numbers of taxa at the New Harbour sites was slightly lower than at the other

**Table V.** The macrofaunal taxa contributing to 80% of the variability in community composition at each site (from SIMPER analysis). For each site, the top five ranked taxa are listed, with 1 the most abundant taxa. The percentage contribution of each individual taxa to community variability is given in brackets.

| Taxa<br>% within-site similarity | DI1<br>24.91% | DI2<br>39.48% | DI3<br>41.95% | SC1<br>55.01% | SC2<br>43.59% | SC3<br>28.91% | NH1<br>27.51% | NH2<br>30.15% | NH3<br>33.14% |
|---|---|---|---|---|---|---|---|---|---|
| Nematodes | | | | | | | | 2 (29.49) | |
| Oligochaetes | | | | | | | | | |
|   Oligochaeta | 5 (6.84) | | | | 4 (6.55) | | | | |
| Gastropods | | | | | | | | | |
|   *Onoba turquetti* | | | 3 (15.11) | | | | | | |
|   *Onoba gelida* | | | | | | 1 (27.27) | | | |
| Polychaetes | | | | | | | | | |
|   *Aglaophamus* sp. | | | | | | 6 (7.80) | | | |
|   *Aricadea* sp. | | | | | | | | | 4 (12.14) |
|   Cirratulidae | 4 (5.44) | | | | | 2 (21.59) | 4.5 (15.57) | | 5.5 (14.41) |
|   *Haploscoloplos* sp. | 3 (24.53) | | | | | | | | 5.5 (8.38) |
|   Maldanidae | | | | | 5 (7.16) | | | | |
|   *Ophelina* sp. | | | | | | | | 3 (15.20) | |
|   Oweniidae | | | | | | | 1 (13.46) | | 2 (15.01) |
|   Paraonidae Type A | | | | | | | 4.5 (15.57) | | |
|   *Polygordus antarcticus* | | 3 (11.95) | 2 (19.32) | 4 (4.14) | 2 (22.69) | | | 1 (20.07) | 1 (15.52) |
|   *Spiophanes tcherniai* | | | | | 2 (16.65) | | | | |
|   *Syllidia inermis* | | | | | | 4.5 (7.53) | | | |
| Anemones | | | | | | | | | |
|   *Edwardsia* sp. | 2 (8.64) | 2 (19.77) | | 1 (46.46) | 1 (26.53) | | 3 (15.99) | 2 (49.6) | |
| Crustaceans | | | | | | | | | |
|   *Austrosignum grande* | | | | | | 4.5 (7.10) | | | |
|   Myodocopida | 1 (28.11) | 1 (52.50) | 1 (45.84) | 3 (11.09) | 3 (20.47) | | | | |
|   ?*Nototanais* sp. | | | | | | | | | 3 (9.24) |
|   Podocopida | | | | | | 3 (13.52) | | | |
| Total taxa | 5 | 3 | 3 | 4 | 5 | 6 | 5 | 3 | 6 |

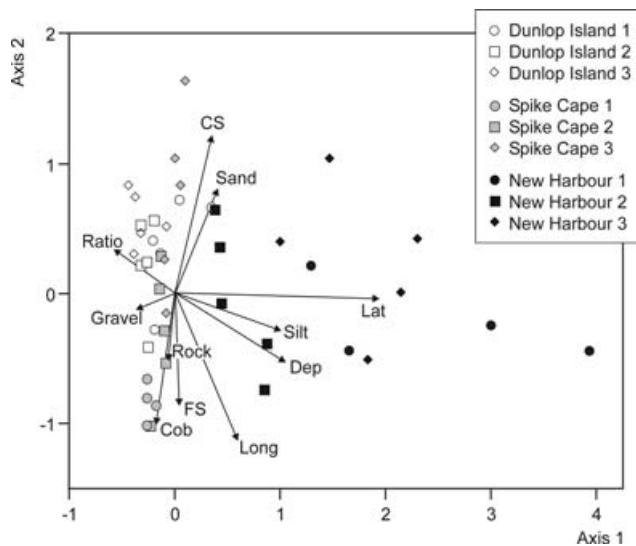DI = Dunlop Island, SC = Spike Cape, NH = New Harbour.



**Fig. 8.** Canonical Correspondence Analysis ordination of macrofaunal community composition at each site/location, and the environmental variables important in explaining community composition. Lat = Latitude, Long = longitude, Dep = depth, Cob = cobble, Ratio = Chl *a*:phaeophytin, CS = coarse sand, FS = fine sand.

locations (6–10 taxa core$^{-1}$ on average). The taxa comprising these communities differed between locations (Table V). At New Harbour, the polychaetes Owenidae and *Polygordus antarcticus*, and the anemone *Edwardsia* sp. were numerically dominant. Myocopid ostracods were the most abundant species at Dunlop Island, where *Edwardsia*, *Polygordus* and the orbinid polychaete *Haploscoloplos* were also common. *Edwardsia*, *Polygordus*, myocopid ostracods and the tube building polychaete *Spiophanes tcherniai* were dominant at Spike Cape Sites 1 and 2. Spike Cape Site 3 did not share any of the dominant species found at Sites 1 or 2; the small gastropod *Onoba gelida*, cirratulid polychaetes, and podocopid ostracods were the most abundant species. The dominant macrofaunal taxa found at our locations are considered intermediate opportunistic species (e.g. *Polygordus*, cirratulidae, *Haploscoloplos*) or sedentary species (e.g. *Spiophanes*, *Nototanais*, *Edwardsia* sp.; *sensu* Lenihan & Oliver 1995). The exception are myocopid ostracods, which are highly motile.

Highest abundances were recorded at all Dunlop Island sites (64–72 individuals core$^{-1}$), Sites 1 & 2 at Spike Cape (70 and 75 ind. core$^{-1}$, respectively), while the lowest abundances were recorded from all New Harbour sites (10–23 ind. core$^{-1}$) and Site 3 at Spike Cape (17 ind. core$^{-1}$).
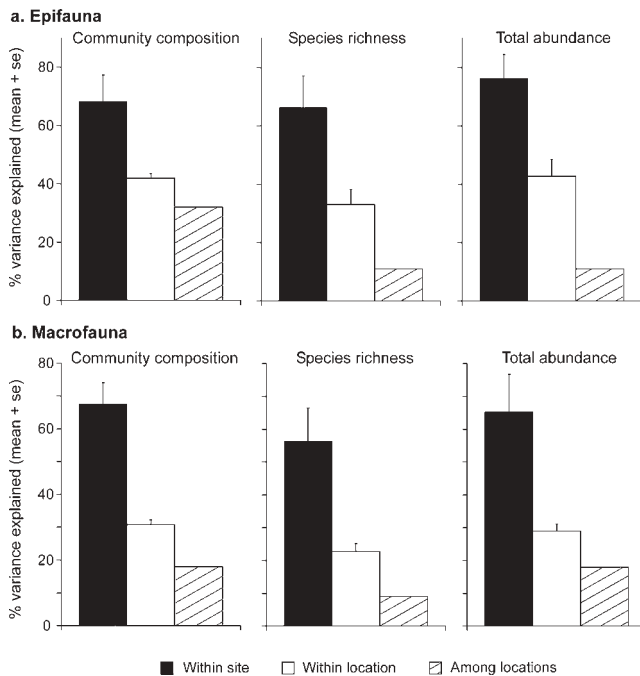
**Fig. 9.** Percentage explained in community composition, species richness and total abundance of **a.** epifauna and **b.** macrofauna, by habitat structure variables, at different scales. Percentage explained for community composition = sum of canonical eigenvalues x 100 / sum of all eigenvalues (using CCA). % explained for species richness and total abundance = $r^2$ (using multiple regression).

*Relationship between macrofaunal community composition and environmental variables*

The New Harbour macrofaunal communities were distinct from the other locations in ordination space (Fig. 8). The three Dunlop Island sites had the most similar macrofaunal communities, and the site 1 and 2 communities also shared similar characteristics to Spike Cape Sites 2 and 3. The Spike Cape Site 1 community was distinctly different to all other sites/locations except Spike Cape Site 2. Latitude and % coarse sand were the most important environmental variables contributing to these assemblage differences between and within locations (Fig. 8), with 58% of the variability explained overall. Of slightly less importance were longitude, cobble, depth, % fine sand, % silt, % sand, rock, Chl *a*:phaeophytin and gravel. Higher latitude and % silt content and greater depth influenced the New Harbour assemblages. As noted for the epifauna CCA, the fact that so many environmental variables contributed to this pattern illustrates the complex relationship between habitat characteristics and fauna at these locations.

*Relationship between habitat structure and community composition at different scales*

The percentage variability that is explained by habitat

structure characteristics is strongly scale dependent, and decreases with increasing scale of observation (Fig. 9). This was true for the macrofauna and the epifauna, and both this scale-relationship and the actual % explained at each scale, was similar when species richness and number of individuals were investigated (Fig. 9).

## Discussion

This study has shown that habitat structure is not the most important factor influencing the diversity of benthic communities in the south western Ross Sea (at least in shallow coastal areas). Habitat structure differed at the three locations, with New Harbour comprised of simple soft sediments. However, this habitat difference did not translate into large differences in the numbers of epifaunal or macrofaunal taxa found. Thus, 'low' habitat structure does not necessarily imply low diversity. This is especially evident from studies of the deep sea and continental shelf fauna (e.g. Gray 1994, Gage 1996). Despite the apparent simplicity of the New Harbour habitat, the diversity of large epifauna was comparable to that found in the more structurally complex physical habitats of Dunlop Island and Spike Cape (Fig. 6, Tables IV & V). We found no obvious influence of sediment composition on the macrofaunal assemblage found at the sites/locations, suggesting that these species are adapted to multiple sediment types. This contrasts with studies of deeper areas in Terra Nova Bay, where Gambi *et al.* (1997) found polychaete diversity to be lower in shallow bottoms with coarse sediments than in deeper more heterogeneous habitats (>100 m; fine sands, boulders and rocks). Cattaneo-Vietti *et al.* (2000) found sediment grain size preferences controlled the distribution of molluscs in Terra Nova Bay, indicating differences associated with deeper and/or more productive locations. Antarctic fauna appear to be very adaptable, in that the same species are found, often in high abundances, in markedly different habitat types and depths (e.g. see Ragua-Gil *et al.* 2004).

The structure of the New Harbour habitat was enhanced by the presence of numerous scallops (*Adamussium colbecki*), which make mounds and depressions in the soft sediment, and the shells of which provide a hard substrate for sponges and other encrusting epifauna. *Adamussium* also create patchiness of seafloor sediments by depletion of benthic algae via filter feeding. In addition, the heart urchin *Abatus nimrodi* was reasonably abundant at New Harbour (although not detected in our core or video sampling due to its size and cryptic nature) and disturbs the seafloor by bulldozing through the subsurface sediments. These fauna provide heterogeneity on the seemingly featureless New Harbour seafloor, which will persist in an environment that is constantly covered by ice and not subjected to sedimentation or water turbulence (e.g. Gage 1996). It is important to be cautious when attempting to identify

relationships between habitat structure and diversity over a range of locations; locations with homogeneous habitats (such as New Harbour) may strongly influence the patterns seen across locations/latitudinal gradients. In addition, this result illustrates the difficulty of predicting faunal composition in the Ross Sea based on seafloor topography alone.

Abundances of epifauna and macrofauna were lower at New Harbour than at the other locations (Figs 3 & 6). We suggest that food availability is the most likely reason for this pattern: sediment chlorophyll levels were considerably lower at New Harbour than at the other locations. Another site, Spike Cape Site 3, exhibited relatively low macrofaunal abundance despite having 'normal' chlorophyll levels (Fig. 7); reasons for this may be disturbance-related (see below discussion).

We have also demonstrated a strong influence of the scale of observation on our ability to explain the variability in benthic assemblage composition. Habitat structure factors (i.e. substrate type, sediment composition, % cover of sedentary epifauna and flora) explained as much as 66% and 75% of the variability in macrofaunal and epifaunal assemblages, respectively, at the smallest scale (i.e. between transects within a location), compared to only 9–18% and 11–32%, respectively, at the scale of the entire study (Fig. 9). This finding suggests that small-scale habitat variability will not confound our ability to detect latitudinal gradients in future studies. The advantage of using sampling designs which nest small scale information (such as that collected via coring) within coarser scale information (e.g. collected using video), and which can be employed in a range of habitat types (e.g. soft sediment or rocky environments), when comparing diverse sites (e.g. gradient studies) is well recognized (e.g. Schneider *et al.* 1997, Thrush *et al.* 1997, Hewitt *et al.* 1998). This result suggests that the multi-scale approach of our study design is appropriate, but that it will be important to adequately quantify the environmental factors important in structuring these communities at larger (latitudinal) spatial scales.

Many environmental variables contributed to the differences in community composition between locations, illustrating the complexity of the relationships between habitat characteristics and fauna. Despite this, latitude was indicated as one of the most important explanatory variables, both for epifaunal and macrofaunal communities (Figs 5 & 7). Latitude may be a surrogate for broader scale environmental factors such as sea ice cover, although its role as a surrogate for environmental processes may change with spatial scale (Thrush *et al.* 2006). Sea ice has a strong influence on primary productivity, and is one of the most important factors in structuring Antarctic shallow benthic communities (e.g. Dayton *et al.* 1970). The more persistent sea ice cover at New Harbour (Table I) is likely to limit *in situ* productivity, and species at the lower levels of the food chain may be limited to obtaining food from advected

sources, settling ice algae, or locally via nutrient input associated with moats formed by melt water (Stockton 1984, Berkman 1994). The lower abundances of macrofauna and epifauna at New Harbour are in fact typical of patterns noted in productivity-limited systems (Dayton & Oliver 1977). In contrast, Dunlop Island and Spike Cape are predicted to be ice free more regularly, and benthic production is likely to be high when light is not limited. In a companion study, we have demonstrated a positive relationship between the amount of freshly produced algal material consumed by primary consumers and the degree of predatory behaviour of omnivores, and the proximity of the site to ice-free water (Norkko *et al.* unpublished data). These results demonstrate the relationship between sea ice distribution, *in situ* primary productivity and their influence on Antarctic food webs.

In comparison to other benthic marine ecosystems, the Antarctic environment has remarkably constant physical properties and is considered less affected by stress from physical disturbance than most other ecosystems in the world (Grebmeier & Barry 1991, Arntz *et al.* 1994). Many areas however, are affected by iceberg scour and anchor ice (e.g. Dayton *et al.* 1970, Gutt 2001, Gutt & Starmans 2001). Disturbance by icebergs in McMurdo Sound is generally infrequent (but see Lenihan & Oliver 1995), and anchor ice disturbance is more common than disturbance by grounded icebergs at the depths investigated in our study (e.g. Dayton *et al.* 1969).

Indeed, the constancy in the physical environment at New Harbour and the characteristics of its seafloor communities have led to previous descriptions of New Harbour as resembling a deep sea environment; both the ophiuroid *Ophionotus victoriae* and the pencil urchin *Ctenocidaris perrieri* resemble particular deep water (bathyal) taxa in terms of their population density, distribution, size and morphology (e.g. Dayton & Oliver 1977). Interestingly, while cidarids are found in McMurdo Sound and in the northern Victoria Land area, they are absent from the Terra Nova Bay region (Chiantore *et al.* 2006). In our study, *Ophionotus* was found at two of the Spike Cape sites (Sites 2 & 3), and at Dunlop Island Site 3, in similar numbers to New Harbour (Fig. 5). The number of macrofaunal and epifaunal taxa was similar at the three locations visited during this survey, despite the fact that the New Harbour habitat may be considered relatively more stable than Dunlop Island or Spike Cape. As noted above, the latter two locations are likely to be ice-free more often (Table I), and may occasionally be affected by disturbance from icebergs. However, the macrofaunal species comprising the dominant taxa differed at the three locations (Table V). The dominance of a mobile ostracod at all three Dunlop Island sites could be indicative of iceberg disturbance at this location (e.g. Lenihan & Oliver 1995), but this requires further investigation.

In deep Ross Sea environments (270–1173 m), seafloor

habitat characteristics (e.g. sediment organics) were found to be more important than upper ocean factors (e.g. the size and timing of ice cover, primary productivity) in regulating the spatial distribution of benthic megafauna over a range of habitat types (Barry *et al.* 2003). Barry *et al.* (2003) and Gambi & Bussotti (1999) also indicate the importance of current regime and bottom dynamics in influencing both sedimentary features and benthic community structure of deep Ross Sea sites. In the shallower (14–25 m) habitats investigated in our study, local ice cover conditions are likely to have a more direct link to the benthic fauna (i.e. settling of ice algae, effect on transmission of light and consequently on growth and photosynthesis of microphytobenthos) than in deep environments where light does not reach the seafloor, and where any ice algae detritus is likely to be consumed in the water column prior to reaching the benthos. Measurements of benthic chlorophyll will reflect water column as well as benthic processes.

## Concluding comments

The work presented here is part of a larger scale investigation of benthic ecosystems along the latitudinal gradient from McMurdo Sound to Cape Adare. We can already demonstrate contrasts between locations at the southern end of this gradient that support the importance of latitudinal-scale factors (e.g. variations in ice cover) in controlling benthic community composition. The percentage variability in epifaunal and macrofaunal assemblage composition able to be explained by environmental characteristics was strongly scale dependent, decreasing with increasing scale of observation. This suggests that adequately quantifying the environmental factors important in structuring these communities at larger (latitudinal) spatial scales will be important. We have documented interesting differences in habitat features between locations, but these are not reflected in expected diversity responses of epifaunal and macro-infaunal communities. However, while diversity *per se* appears to be weakly influenced by habitat structure/complexity in this extreme environment at the scale of our study, the taxa comprising these communities differed between locations (particularly for macrofauna), and the relatively low abundances of both epifauna and macrofauna at New Harbour suggest that food may be a limiting factor at this location.

## Acknowledgements

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