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Taihoro Nukurangi

Ecology and biodiversity of coastal benthic communities in McMurdo Sound, Ross Sea: emerging results

V. Cummings, S. Thrush, N. Andrew, A. Norkko, G. Funnell,
R. Budd, M. Gibbs, J. Hewitt, S. Mercer, P. Marriott, O. Anderson

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2. **Contractor:** NIWA

3. **Project Title:** Ecology and biodiversity of coastal benthic communities in Antarctica

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7. EXECUTIVE SUMMARY

This report presents the most recent results of a new research programme investigating the ecology and biodiversity of coastal benthic communities in the Ross Sea. The long-term objective of this programme is to quantify patterns in biodiversity and benthic community structure in the coastal Ross Sea region. In 2002/03 this involved implementation of a modular sampling design at three locations on the continental coast of the Ross Sea, and one adjacent to Ross Island. This sampling protocol was developed in McMurdo Sound in 2001/02, and allows rapid, cost-effective assessments of biodiversity of benthic communities. This report summarises the work conducted in 2002/03, and provides a preliminary temporal comparison with that collected in 2001/02.

The sampling design was successfully implemented and quantitative assessments were carried out in two new locations, Dunlop Island and Spike Cape. Repeat visits were also made to sites at New Harbour and Cape Evans, to provide initial information on temporal change in biodiversity and benthic community composition. Three sites were sampled at both Dunlop Island and Spike Cape, and one each at New Harbour and Cape Evans. There were clear differences between locations, with the New Harbour and Cape Evans locations being the most different.

There were large differences in habitat structure, macroalgae and microphytobenthic standing stock between locations. The New Harbour habitat is dominated by soft

sediments while Cape Evans is dominated by rocks and boulders interspersed with soft sediments and abundant macroalgae. Although Dunlop Island and Spike Cape are more similar to Cape Evans than New Harbour, there are also distinct differences between all three. The red alga *Phyllophora antarctica* and encrusting coralline algae are present at Dunlop Island, Spike Cape and Cape Evans, and their abundances differed between locations. New Harbour sediments had the lowest chlorophyll *a* and phaeophytin biomass of the four locations, while Cape Evans sediments had the highest levels. In addition, a higher proportion of the microphytobenthic biomass was in a degraded state at Spike Cape and New Harbour. There were also differences in the diversity and composition of large epibenthic taxa, and macro-infauna between locations.

Our assessments of the functional diversity of coastal benthic communities in McMurdo Sound in 2001/02 using natural stable isotopes demonstrated marked differences in trophic structure and functional diversity between New Harbour and Cape Evans. To strengthen our interpretations of food web structure and function, our 2002/03 work focussed on investigating the food sources of selected common epibenthic taxa at each location. We found differences in isotopic signatures of ice algae, microphytobenthos/detritus and macroalgae (*Phyllophora antarctica*) between locations, indicating differences in nutrient sources, and differences in the food sources of some common taxa dependent on location. The construction of a more detailed food web at Cape Evans is progressing well, and will ultimately enable us to better assess the relative importance of primary food sources, and of particular species to the wider ecological community. This information will help predict the consequences of change in trophic relationships.

The full potential of this sampling design will not be realised until we can incorporate additional locations with different environmental characteristics (i.e. sea ice conditions, light regime, water currents, magnitude and diversity of primary producers, etc.); only then will we be able to conduct a full-scale gradient analysis and make quantitative use of these factors.

Our sampling strategy was designed to enable us to make comparisons between sites while still including high levels of variation in habitat structure and diversity within sites (Thrush et al. 2001a). We developed a modular sampling design which nests macrobenthic and biogeochemical core samples within videoed transects of the seafloor. As the spatial characterisation of benthic biodiversity was identified as being highly dependent on obtaining good quality video-footage, this is a major thrust in our sampling protocol. This design enables analysis of relationships between habitat structure and macrobenthic diversity at a number of spatial scales.

10.1.1 Biodiversity Survey

At each location a minimum of three sites, separated by at least 50 m, were surveyed. Each site was sampled as described below through separate dive-holes in the sea-ice:

Two 20 m transect lines were laid on the seafloor within a 15–25 m depth stratum starting from haphazardly chosen starting points. This depth range was chosen as it is accessible by diving and below the immediate impact of ice scour and anchor ice, yet is shallow enough to be affected by changes in sea ice and land-associated processes (e.g., melt ponds). The transects were videoed using a diver-held digital video camera at a fixed height of (a) 70 cm above the bottom (for the broader-scale analysis of habitat structure), and (b) 40 cm above the bottom (to allow for more accurate species identifications).

Along one of the 20 m transects, core samples were collected from five randomly chosen positions. At each position, two small sediment cores (26 mm diam., 50 mm deep) are collected: one to determine sediment grain size and benthic chlorophyll *a* content, and one to determine the natural stable isotope signature of the sediment. Also at each position, one large core (70 mm diam., 100 mm deep) was collected to estimate the abundance and diversity of benthic macrofauna. Additional collections were made along this transect: (a) three surface sediment scrapes, to determine the species composition of microalgae, (b) three individuals of each of the numerically dominant epibenthic species, to determine their stable isotope signatures, and (c) additional specimens of animals and plants, and organic material (e.g. seal faeces) for isotopic analysis, to provide a more complete picture of the food-web structure of the community.

Algae on the undersurface of the sea-ice were sampled to determine their isotopic signature using five small cores (26 mm diam., 100 mm deep). Additional cores were obtained for the determination of chlorophyll *a* and species composition of sea-ice algae.

Video sampling is stratified by habitat type, e.g., hard substrates, sand, sponge gardens. The sizes of fauna along the transects can be determined using the scale markings on the transect line. Additional videos were taken of biota in the study area to allow a more general picture of the site to be developed.

Physical background variables (e.g. sea-ice conditions, light intensity) were quantified at each site, and water currents were estimated at each location using standard data-logging instruments.

Final Research Report

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10.1.2 Remote Sampling

A remotely operated video camera (SplashCam) was used to video additional sites, and increase our knowledge of the spatial extent of the habitats surveyed by diving, and the generality of our results. The camera was lowered on an umbilical through small holes drilled in the sea ice. The camera was fitted with three lasers, which allows for accurate sizing of dominant animals and habitat features. These images provided information on habitat type and overall biodiversity, and could also be used to make quantitative estimates of the relative abundance, size and diversity of epibenthic species.

10.2 Describe ecosystem function at selected locations in the Ross Sea (Objective 2)

At all sites from each location sampled as part of Objective 1, samples were taken to determine stable isotope signatures. Specific samples collected are detailed in the sampling protocol described for Objective 1 (see above). These include: tissues of large epibenthic taxa, sea-ice algae, surface sediment, phytoplankton, microphytobenthos, macroalgae and detritus (e.g. seal faeces), and macrofauna. Samples were frozen and returned to New Zealand, where they were freeze dried or oven dried (sea ice algae filters only) prior to analysis. Isotopic signature was determined using NIWA's Finnegan Delta-C, continuous flow Mass Spectrometer (Bury 1999).

Additional sampling was conducted to determine the importance of drift aggregations of the red alga *Phyllophora antarctica* to the benthic ecology of Cape Evans, and the relative contribution of these accumulations to the total organic carbon available to seafloor dwelling organisms. Drift aggregation biomass was determined from weights of *Phyllophora* collected within 0.25 m^2 quadrats. Biomass estimates were made from 27 replicate quadrats in the 15–25 m depth strata. The photosynthetic capacity and extent of degradation of 10 different drift accumulations on the seafloor was measured using pulse amplitude modulated fluorometry (PAM). Samples of sediment (26 mm diam., 50 mm deep sediment cores) and macrofauna (> 500 µm; 70 mm diam., 100 mm deep cores) were collected from beneath the 10 *Phyllophora* drift accumulations, and from 10 adjacent bare areas. The sediment cores will be processed and analysed for grain size, chlorophyll content and stable isotope signature, using methods described for Objective 1. The macrofaunal cores were sieved (500µm mesh), preserved in 70% isopropyl alcohol, sorted and identified to the lowest taxonomic level possible. To help determine the relative importance of primary production from different sources (e.g., macroalgae or microphytobenthos), and assess the food-web complexity (i.e., number of trophic levels, degree of omnivory etc.), additional macrofaunal cores were collected, and the individual animals obtained from them were analysed to determine their stable isotope signatures. The stable isotope of nitrogen (^{15}N) was used to estimate the trophic positions of benthic species, and stable isotopes of carbon (^{13}C) to determine patterns of carbon flow to these consumers.

10.3. Sample processing and analysis:

Sample processing and analysis was described in detail in our previous report (Norkko et al. 2002). It is briefly reiterated below.

10.3.1 Video-imagery:

The digital videos of the transects were analysed by estimating the abundance and percent cover of epifauna and flora in 15 frame grabs. Each frame (or sample 'quadrat') corresponds 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 two different video heights (i.e., 70 and 40 cm above the seafloor) were used in a complementary way and the specific height used for the actual analysis depended on the habitat. 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.

As well as determining the abundance of the large epibenthic taxa within quadrats, counts were also made along the full length of each transect. This enabled us to account for rare taxa with patchy distributions, and thus provide a more complete estimate of species composition at a site. The sizes of numerically dominant individual animals and macroalgae were estimated using calibration marks on the transect line.

Images obtained by remote video were processed in the same way. We analysed the remote video (SplashCam) at distances of 0.5 and 1.5 m above the seafloor.

10.3.2 Sediment and macrofauna samples:

Sediment from the small core collected for isotope analysis was sectioned so that only the top 5 mm was retained. Sediment from the other small core was homogenised prior to being subsampled for chlorophyll *a*, grain size and organic content analysis.

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 chlorophyll *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 % volumes for the 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 for 48 h, followed by combustion at 400°C for 5.5 h.

Macrofauna core samples were sieved on 500μm mesh, preserved in 70% isopropyl alcohol, sorted and identified to the lowest taxonomic level possible. Surface sediment scrapes were frozen prior to being examined for species composition of microalgae.

10.3.3 Sea-ice algae:

Ice cores for stable isotope analysis were slowly melted in the laboratory and filtered onto pre-combusted Whatman GF/C filters, and the filters oven dried (60°C) prior to analysis. Under-ice cores for taxonomic composition of sea-ice algae were immediately frozen. In all cases, samples were stored frozen and in the dark until they could be processed.

10.3.4 Stable Isotope Analysis:

All samples were kept frozen until they could be freeze dried (animals, sediment, macroalgae, detritus) or oven dried (ice algae filters). They were ground prior to analysis.

The stable isotope signatures of each sample were determined using NIWA's Finnegan Delta-plus continuous flow Mass Spectrometer (Bury 1999). The dried and ground samples obtained from sediments, primary producers, detritus and different tissues of the animals were combusted and examined by mass spectrometry, and compared to two standards. Standard reference materials were PDB limestone for carbon (a calibrated working standard of CO_2 gas was used), and air for nitrogen. Isotopic ratios are reported in delta (δ) notation in parts per thousand (‰). Ratios were calculated relative to a standard using the following formula:

$$\delta\ ^{13}C \text{ or } ^{15}N\ ‰ = ((R_{sample} - R_{standard}) - 1) \times 10^3, \text{ where } R = ^{13}C/^{12}C \text{ or } ^{14}N/^{15}N.$$

10.3.5 Numerical analysis:

Variations in species composition and relative abundance of benthic fauna and flora within and between sites were determined using a combination of visual examination of univariate measures, and multivariate analytical procedures (Clarke and Warwick 1994, Legendre and Legendre 1998, Warwick and Clarke 2001). As mentioned previously, our sampling regime involves nesting macrobenthic and biogeochemical core samples within videoed transects of the seafloor, and thus enables analysis of relationships between habitat structure and macrobenthic diversity at a number of spatial scales. Analyses of this type are described by Thrush et al. (2001a). When more locations have been sampled, meta-analysis will be used to investigate the relative importance of relationships between benthic diversity, local processes (e.g., rate of production, trophic structure) and broader-scale environmental variables such as sea ice cover, current velocity and temperature (see Thrush et al. 2000, 2001b).

For the macrofaunal community core data, numbers presented are individuals/taxa $core^{-1}$.

For the video transect data, all counts from each quadrat were converted to density m^{-2}. For all analyses of epifaunal taxa, 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.

For the stable isotope data, three replicate samples and standard statistical procedures were used to determine within site and location variability.

Multivariate statistical analysis: Non-metric multidimensional scaling ordination (MDS; Clarke and Gorley 2001) was used to assess the relationship within and between locations for (a) sediment characteristics (determined from the core data), (b) macrofaunal community composition (determined from the core data), (c) epifaunal community composition (determined from the video), and (d) all of the above plus the habitat characteristics (determined from the video). All data were untransformed. Bray-Curtis similarities were used in analyses (b) and (c), and Euclidian distances for analyses (a) and (d).

Differences in macrofauna community composition between sites and locations were tested using a non-parametric randomised permutation test on Bray-Curtis similarities (ANOSIM; Primer, Clarke 1993). After this an analytical classification procedure (SIMPER; Primer, Clarke 1993) was used to determine average similarities within

and between sites, along with the taxa that were most important in defining differences between sites.

The significance of the relationship between the macrofaunal and epifaunal communities was investigated using the RELATE routine within PRIMER (Clarke & Warwick 1994). This procedure investigates how well the multivariate pattern exhibited by the macrobenthic core data reflected the multivariate pattern of the large epifauna data derived from the video.

The sediment and habitat characteristics were related to the macrofauna and epifauna found at Dunlop Island and Spike Cape separately using Spearman's rho correlations and Bray-Curtis similarities on the untransformed data (BVSTEP; Clarke and Gorley 2001). New variables were added into the model by forward selection only if they increased the correlation coefficient by ≥ 0.05, and the most stable set of explanatory variables derived was used.

11. RESULTS

11.1 Quantify biodiversity in benthic and sea ice communities at three locations in the Ross Sea region (Objective 1).

The sampling design and analytical procedures described above were implemented at Dunlop Island, Spike Cape, New Harbour and Cape Evans in October/November 2002 (Figure 1).

11.1.1 Background Environmental Variables:

These are summarised in Table 1, and discussed further below. Note that the historical patterns in sea ice conditions and snow cover at each location is currently being investigated as part of our FRST research, and this information will be incorporated in a future report.

Sea ice: The thickness of the sea ice was similar at each of the locations visited. It was thickest at New Harbour (3.2 m) and thinnest at Cape Evans (approx. 2 m). The last known break-up of sea ice at New Harbour was in 1999. The ice at Cape Evans was new (photos of CE in January 2002 show there is no ice left in the bay). In our 2001 Cape Evans visit, the ice was slick and smooth; however in 2002 the surface was rougher and there was generally a good snow covering.

There was also considerable snow cover at Spike Cape and Dunlop Island. The sea ice at both of these locations is likely to be annual, although on some occasions the ice may linger in the area between Dunlop Island and the continent. This will be confirmed as part of the investigations into historical patterns in ice and snow cover mentioned above.

Currents and water temperature: The S4 current meter was deployed for a short time period at each location, during diving operations. However, there are some differences noted between locations.

With the exception of Dunlop Island, current velocities were generally <5 cm sec^{-1} at each location (Table 1; Figure 2). Highest velocities (up to 14 cm sec^{-1}) were noted at the northern most location, Dunlop Island (Figure 2), and this is consistent with what was experienced by the divers. The Dunlop Island sites were located in a relatively

narrow gap between Dunlop Island and the continent (Figure 1); which may have channelled the water flow and increased current speed. However, the current directions recorded by the S4 were not predominantly North-South as might be expected in a channel oriented in this direction (Figure 2). This could be due to local magnetic anomalies interfering with the instrument, or to local bathymetry (e.g., the grounded iceberg noted at the northern end of the channel) modifying flows.

While previous work by Goring and Pyne (presented in Norkko et al. 2002) would enable us to account for variations in tidal flow, we have presented the raw data in this report (Figure 2).

The water temperature 4 m above the seafloor was identical at each location (-1.92°C; Table 1).

Table 1. Background environmental conditions at the study locations in October/November 2002. DI = Dunlop Island, SC = Spike Cape, NH = New Harbour, CE = Cape Evans. * not measured in our study; patterns will be confirmed as part of the analysis conducted for our FRST work. ** measured directly under the ice layer. sd = standard deviation.

Environmental factor	DI	SC	NH	CE
Ice conditions				
– ice cover*	annual	annual	semi-permanent	annual
– ice thickness (m)	2.6	2.4	3.2	ca. 2.0
Light conditions				
– Light penetration (% of incident irradiance**)	0.25	0.12	0.08	0.20†
Water temperature (°C)	-1.92	-1.92	-1.92	-1.92
Current velocity (cm s^{-1})				
– mean ± sd	3.8±2.6	2.6±1.3	1.7±0.8	1.9±1.2
– minimum – maximum	0.0 – 14.0	0.0 – 7.6	0.4 – 3.8	0.0 – 5.9

† as measured in 2001 (see Norkko et al. 2002).

Under-ice light conditions: Very little of the above-ice incident light penetrated the sea ice at each location (i.e., ≤ 0.25%). There were differences between locations, with the least light measured immediately below the ice at New Harbour (0.08%), and comparatively more transmitted at Dunlop Island (0.25%).

11.1.2 Site Descriptions:

The GPS locations of each survey site, and a description of the benthic habitat and epifauna present, is given below.

Dunlop Island:
The three sites sampled at Dunlop Island ranged from 15.5–21.0 m in depth. The sites were located in the sound between the continent and Dunlop Island itself, and were separated by 36–73 m. The following sites were surveyed:

DI-1: depth 19.0 m	77° 14.161 S, 163° 27.940 E
DI-2: depth 21.0 m	77° 14.176 S, 163° 27.997 E
DI-3: depth 15.5 m	77° 14.141 S, 163° 27.917 E

The sound is quite shallow, and appears to be 25 m deep at its deepest The substrate is primarily sand interspersed with gravel/cobble/rocky 'banks' (possibly created by iceberg scour or glacial moraine). At the northern end of the sound is a grounded iceberg, which has apparently been in place for some time (Jim Cowie, AntNZ, pers comm.).

This location supported a combination of the fauna found at New Harbour and Cape Evans, with scallops (*Adamussium colbecki*) and sea urchins (*Sterechinus neumayeri*) the most common large epibenthic species (Photo 1). *Adamussium* sometimes has a very rich epibiont community. The sea star *Odontaster validus*, the bivalve *Laternula elliptica*, and nemertean worms (*Parborlasia*) were also common. Fronds of the red alga *Phyllophora antarctica* were observed adhered to sea urchins, but no attached plants were found at any of the sites surveyed. Encrusting coralline algae was also noted.

Dunlop Island was sampled from 22-25 October 2002. The S4 current meter was deployed at DI-1 from 22-27 October, and the light measurements were made at DI-3 on October 25th.

Spike Cape:
The Spike Cape sites were located in the bay immediately north of Spike Cape. The entire bay appears shallow, and fairly protected from iceberg disturbance. The sites ranged in depth from 15-20 m, and were separated by 36-49 m. The following sites were surveyed:

SC-1: depth 18.5 m	77° 18.024 S, 163° 33.935 E
SC-2: depth 20.0 m	77° 18.040 S, 163° 33.880 E
SC-3: depth 14.8 m	77° 18.050 S, 163° 33.958 E

The substrate is dominated by large rock, interspersed with some sandy/gravely sediment (Photo 2). As with Dunlop Island, Spike Cape supported a combination of the fauna found at New Harbour and Cape Evans. *Adamussium* are less abundant at Spike Cape than Dunlop Island, and had less epibionts associated with them. *Sterechinus* was once more abundant, and in addition had a rich epibiont community. *Adamussium colbecki*, *Odontaster validus*, *Laternula elliptica*, ophiuroids and sponges were also common. There were many pycnogonids, particularly at SC-2. While drift *Phyllophora* was noted on the sea urchins, there was little in comparison to Dunlop Island. Conversely, there was a lot of encrusting coralline algae noted at all of the Spike Cape sites.

Spike Cape was sampled between 30 October and 2 November 2002. The S4 current meter was deployed at SC-1 from 30 October to 3 November, and the light measurements were made at SC-3 on 2 November.

New Harbour:
The site surveyed in New Harbour was in Explorers Cove, at the mouth of the Taylor Valley. This site is in almost the same location as one of those sampled in 2001/02 (i.e., NH-1).

NH-1: depth 24.5 m 77° 34.572 S, 163° 31.667 E

The seafloor in this area is completely dominated by soft sediments. *Adamussium*, ophiuroids (*Ophionotus victoriae*), and heart urchins (*Abatus nimrodi*) were the dominant epifauna. Other conspicuous taxa include a variety of sponges (e.g. the bush sponge *Homaxinella balfourensis*), nemerteans (*Parborlasia corrugatus)*, a large ophiuroid (*Ophiosparte gigas),* a large sea star (*Diplasterias brucei)* and the pencil urchin (*Ctenocidaris perrieri*). Sponges[1] and other encrusting fauna in New Harbour were found growing on shells of *Adamussium* and spines of the pencil urchin. No macroalgae were observed at New Harbour, but there were visible growths of both seafloor and sea-ice microalgae.

New Harbour was sampled on 5–6 November 2002. The S4-current meter was deployed from 7–8 November.

Cape Evans:
The survey site at Cape Evans was in the vicinity of Scott's *Terra Nova* expedition hut, on the slopes of Mt Erebus. The site surveyed was in the same location as one of the sites sampled in 2001/02 (i.e., CE-3).

CE-3: depth 19.0 m 77° 38.095 S, 166° 24.843 E

The Cape Evans seafloor is dominated by rocky reefs, boulders and rocks, interspersed with soft sediments (mainly coarse sand/gravel) (Photo 3). Sea stars (*Diplasterias brucei* and *Odontaster validus*), sea urchins (*Sterechinus neumayeri*) and nemerteans (*Parborlasia corrugatus*) dominated the epifaunal community. Macroalgae were abundant at Cape Evans, with drift accumulations of *Phyllophora* a dominant habitat feature (Photo 3). Cape Evans is one of the furthest south locations where macroalgae is found on the Antarctic Continent. Coralline algae were also abundant at Cape Evans.

Cape Evans was surveyed on 12 November 2002. The S4 current meter was deployed from 13-16 November. No light measurements were made.

11.1.3 Physical habitat characteristics

Video-transects:
Habitats were characterised from frame-grabbed quadrats (0.3 m^2) from the video transects at all sites except New Harbour.

[1] identifications of many of the sponges noted during our 2002 visit are being confirmed by Dr. Carlo Cerrano, University of Genoa, Italian Antarctic Research Programme.

The New Harbour habitat was simple, and dominated by soft sediments. The complexity of this habitat was enhanced by the presence of numerous scallops (*Adamussium colbecki*) which make mounds and depressions in the soft sediments, and the shells of which provide a hard substrate for sponges and other epifauna to grow on.

The complexity of both the Dunlop Island and Spike Cape habitats was provided by the presence of pebbles, cobbles and rocks (0.5–6.0 cm, 6.0–18.0 cm, and >18.0 cm, respectively). At both locations, there was considerable variability in habitat structure, both between transects at a particular site, and between sites.

The Dunlop Island habitat was comprised of sand with varying amounts of pebble, and the occasional presence of cobble (Figure 3). The three sites were reasonably similar, with no one site being more or less cobbly than the others. While drift *Phyllophora* was observed on the seafloor at all three survey sites, it did not constitute a significant habitat feature in the way it does at Cape Evans, and therefore was not conspicuous in the video footage.

The Spike Cape habitat was less sandy than the Dunlop Island site, with more cobble and the occasional rock (Figure 4). One feature of this site was the large amount of coralline algae encrusting the rocks, boulders and pebbles. SC-1 was the most cobbled of the three Spike Cape sites, while SC-3 was the most rocky site and had high amounts of pebble. The habitat at SC-2 was predominately pebble and sand, with small amounts of cobble, and no rock.

The habitat structure at Cape Evans was very distinct from that of the remaining locations. It was comprised of 3 major habitat categories: crustose/bare rock, drift *Phyllophora* accumulations, and coarse sediments with detritus (Figure 5). Along both transects at CE-3, coarse sediments with detritus were the dominant habitat feature. In 2001 the habitat structure at CE-3 was more variable, and *Phyllophora* was a slightly more predominant feature (Figure 5).

Sediment characteristics:

Sediment characteristics at each site were determined from the small core samples. With the exception of one site at Spike Cape (SC-1), and the New Harbour site, all sites surveyed were comprised mostly of coarse sand and gravel/pebble (Table 2). Dunlop Island sediments were dominated by coarse sand at all three sites (41–55%). Gravel/pebble was also common at DI-1 and DI-3, while medium and fine sand were more abundant at DI-2. Two of the Spike Cape sites (SC-2 and SC-3) were dominated by gravel/pebble and coarse sand. The sediments at SC-1 were comprised mostly of fine sand (41.9%), although it also had some coarse sand (23%), The Cape Evans seafloor was predominantly gravel/pebble and coarse sand (i.e., 58.7% and 34.2%, respectively) while the New Harbour site was mostly fine, medium and coarse sand (39.3, 23.6 and 29.9%, respectively).

Sediment organic content was very low at all sites (<1%; Table 2). The lowest levels were at Dunlop Island Sites 1 and 3 (0.09 and 0.27%, respectively), and the highest at New Harbour (0.89%).

Figure 6 illustrates the comparability of the sediment characteristics at each site and location. There is considerable overlap between locations, and considerable variability between the three sites within a location. The New Harbour site samples were most

similar to each other of all the sites sampled (Figure 6). Conversely, the sediment characteristics of SC-2 and SC-3 were the most variable, as evidenced by the wide scatter of their distribution over the ordination plot.

New Harbour/Cape Evans temporal comparison:

Our 2001/02 survey results showed the sediments at both New Harbour and Cape Evans to be comprised mainly of coarse sand (Norkko et al. 2002). In 2002/03, the distribution was slightly different at both locations: Cape Evans had more gravel/pebble-sized sediments (i.e., 59% in 2002 cf. 6% in 2001), and New Harbour had a higher proportion of fine sand (i.e., 40% in 2002 cf. 18% in 2001).

The organic content was similar between years at Cape Evans (i.e., 0.61% in 2002, 0.60%–0.90% in 2001), and slightly higher at New Harbour in 2002 (i.e., 0.89% in 2002 cf. 0.60%–0.70% in 2001).

These temporal differences are all consistent with our observations of the variability in the seafloor sediments noted within each location.

Table 2. Sediment grain size and organic content (measured as loss on ignition) at the four locations. Data presented are mean % (± standard error). DI = Dunlop Island, SC = Spike Cape, NH = New Harbour, CE = Cape Evans.

Site	Organic content	Clay	Silt	Fine sand	Medium sand	Coarse sand	Gravel
DI-1	0.09±0.07	0.02±0.00	0.52±0.13	5.90±1.79	13.10±2.26	54.95±6.93	25.52±9.34
DI-2	0.45±0.04	0.03±0.01	1.19±0.21	23.31±1.71	29.03±2.32	41.49±2.49	4.95±2.89
DI-3	0.27±0.10	0.02±0.01	0.58±0.20	6.32±2.21	8.89±2.45	45.94±6.46	38.26±10.42
SC-1	0.64±0.22	0.06±0.02	3.11±0.77	41.89±7.04	22.53±3.25	23.06±5.64	9.35±9.01
SC-2	0.39±0.19	0.06±0.01	2.88±0.97	21.82±8.67	10.00±3.74	26.09±8.09	39.15±19.86
SC-3	0.73±0.23	0.14±0.08	4.96±3.49	12.39±8.08	6.24±3.35	26.12±11.30	50.15±22.17
NH-1	0.89±0.05	0.09±0.01	7.09±0.58	39.30±3.10	23.60±0.48	29.90±2.93	0.02±0.02
CE-3	0.61±0.14	0.09±0.04	1.92±0.53	2.90±1.07	2.26±1.16	34.15±12.05	58.68±13.20

11.1.4 Biomass of micro- and macroalgae

Sea ice algae:

Samples of ice algae were collected at each location to determine taxonomic composition. These samples are being processed as part of another NIWA project, and will be presented in a future report.

Microphytobenthos:

There were differences in levels of sediment microphytobenthos between locations (Figure 7). New Harbour sediments had the lowest chlorophyll *a* (healthy microphytobenthos) and phaeophytin (a chlorophyll degradation product) biomass of the four locations, while Cape Evans sediments had the highest levels (Figure 7). Levels of chlorophyll *a* were, on average, similar at Dunlop Island and Spike Cape, but the amount of phaeophytin was considerably higher in Spike Cape sediments (Figure 7). Within each of these locations, the three Dunlop Island sites had similar levels of chlorophyll (0.79–1.84 μg/g sediment) and phaeophytin (2.23–2.37 μg/g sediment). At Spike Cape, however, levels of chlorophyll *a* and phaeophytin were 1.8 and 2.5 times lower, respectively, at SC-1 and SC-2 than they were at SC-3.

The ratio of chlorophyll *a* to phaeophytin provided useful information on the quality of food available to the macro- and epifauna. All locations had more degraded than healthy microphytobenthos (Figure 7). In addition, a higher proportion of the microphytobenthic biomass was in a degraded state at Spike Cape and New Harbour than at Dunlop Island or Cape Evans (Figure 7). There was comparatively more chlorophyll available at DI-1 and Cape Evans (ratios of 0.87 and 0.77, respectively).

New Harbour/Cape Evans temporal comparison:

A comparison of the microphytobenthic biomass at NH-1, and at CE-3, in 2001 and 2002 are shown in Figure 8. While levels were similar at New Harbour in both years, there was only half as much chlorophyll *a* in the Cape Evans sediments in 2002 (Figure 8).

Macroalgae:

Macroalgae was present at 3 of the 4 locations sampled: Dunlop Island, Spike Cape and Cape Evans. At Dunlop Island and Spike Cape, the red alga *Phyllophora* occurred as drift only, attached to the spines of *Sterechinus*. As noted above, drift accumulations of *Phyllophora* were an important habitat feature at Cape Evans, and fronds were also attached to sea urchin spines. No attached *Phyllophora* were observed at 15–25 m at any of the sites surveyed. *Iridaea cordata* was also found at Cape Evans, but only as drift algae.

No macroalgae was found at New Harbour. Its absence is likely due to the lack of hard substrates (Table 1).

Encrusting algae:

The crustose coralline algae *Phymatolithon foecundum*[2] was a common feature at Cape Evans, Dunlop Island and Spike Cape. While we have not quantitatively assessed the coverage of *Phymatolithon* from the video, in terms of relative abundance the most coralline was noted at Spike Cape, and the least at Dunlop Island.

[2] referred to as ?*Leptophytum coulmanicum* in Norkko et al. (2002)

11.1.5 Community composition of large epibenthic taxa and macrofauna

Since our last report, the identifications of several macrofaunal taxa have been confirmed by taxonomic experts. Thus we are able to provide a more detailed taxonomic list in this report.

Community composition of large epibenthic taxa:

We identified a total of 44 large epibenthic taxa at the four locations in 2002: 19 at Dunlop Island, 23 at Spike Cape, 24 at New Harbour and 18 at Cape Evans (Appendix 1). This list was compiled using the data collected in 2002 only, and includes those taxa identified on the video and individual specimens collected for isotope analysis. Only 8 taxa were found at all locations, i.e. the sea urchin *Sterechinus neumayeri*, the seastars *Diplasterias brucei*, *Psilaster charcotti* and *Odontaster validus*, the brittle star *Ophionotus victoriae*, the gastropod *Neobuccinium eatoni*, the large nemertean *Parborlasia corrugatus* and pycnogonids (sea spiders). When comparing taxa found at the 3 continental locations with those found at Cape Evans, the Antarctic scallop, *Adamussium colbecki*, and the bush sponge, *Homaxinella balforensis,* were the only taxa found only at the continental sites.

From our video quadrat counts, the number of epifaunal taxa observed at each location ranged from an average of 2-5 taxa m^{-2}. Cape Evans and New Harbour had the most taxa m^{-2}, while DI-1, DI-2 and SC-2 had the least (Figure 9). The number of taxa was similar at each of the Spike Cape sites; however, DI-3 had twice as many taxa on average than the other Dunlop Island sites.

The lowest epifaunal abundances were recorded at DI-2 and SC-2 (around 13 individuals m^{-2}), and the highest at SC-1 and Cape Evans (32 and 27 individuals m^{-2}, respectively). At both Dunlop Island and Spike Cape, the abundances varied between sites (Figure 9).

Adamussium and *Odontaster* numerically dominated the epifaunal communities at Dunlop Island; *Sterechinus* was present in reasonable numbers at DI-3 only (Figure 10). *Sterechinus* was the most abundant epifaunal taxa at Spike Cape, and *Odontaster* was also common. *Adamussium* were also present at this site, but in much lower numbers than at Dunlop Island. *Adamussium* were the dominant epifauna at New Harbour (Figure 10), along with *Homaxinella* (which was mostly attached to scallop shells, or to spines of the pencil urchin *Ctenicidaris perrieri*). *Ophionotus* was also reasonably common at New Harbour.

Odontaster was very abundant at Cape Evans, with more than 20 individuals m^{-2} observed. *Sterechinus* and *Parborlasia* (the large nemertean worm) were also common (Figure 10).

The MDS ordination of the epifaunal community at each location is shown in Figure 11. New Harbour and Cape Evans locations are separated from the other locations, and from each other, in ordination space, reflecting the different assemblages. There is considerable variability between sites at both Dunlop Island and Spike Cape (Figure 11).

New Harbour and Cape Evans, temporal comparison:

The average number of taxa recorded per metre squared was not appreciably different between New Harbour and Cape Evans in 2001 (Norkko et al. 2002). This pattern was also apparent in our 2002 survey. On average, we recorded around 4–5 different large epibenthic taxa m^{-2} at each location (Figure 12).

Our 2001 survey noted a much greater abundance of large epibenthic taxa (i.e. number of individuals) at Cape Evans than at New Harbour, and this was still apparent in our 2002 repeat survey (cf. Norkko et al. 2002).

Abundances of the common epifaunal taxa were also similar at these sites between years (Figure 12).

Macrofaunal community composition:
We identified a total of 64 macrofaunal taxa at the four locations (Appendix 2). Forty taxa were collected from Dunlop Island, 38 from Spike Cape, 21 from New Harbour, and 25 from Cape Evans. Only 4 taxa were found at all four locations. Between 5 and 10 taxa were found at only 1 of the 4 locations (Appendix 2). When comparing the continental locations (Dunlop Island, Spike Cape and New Harbour) with Cape Evans, 4 taxa were found at all three continental locations only (Appendix 2).

Despite sampling 2 additional locations in 2002, the total number of macrofaunal taxa found was almost identical to the number found at Cape Evans and New Harbour in 2001 (i.e., 65 taxa; Norkko et al. 2002). Also in 2001, 18 of these taxa were collected at both New Harbour and Cape Evans: however in 2002 only 5 taxa were found at both locations. This is likely due to the fact that only one site was surveyed at each location in 2002.

The average number of macrofaunal taxa found at each site ranged from 8–14 taxa $core^{-1}$ (Figure 13). NH-1 and SC-3 had the lowest diversity (8.3 and 9.0 taxa $core^{-1}$ on average, respectively). The total abundance of macrofauna found was more variable between locations (Figure 13). The highest abundances were recorded at Cape Evans (134.2 individuals $core^{-1}$), and the lowest at New Harbour and Spike Cape site 3 (14.4 and 17.0 individuals/core, respectively). Abundances at the 3 Dunlop Island sites were remarkably similar (i.e., 64.0–71.6 individuals $core^{-1}$), as were those at SC-1 and SC-2 (i.e., 64.8 and 75.2, respectively; Figure 13).

The MDS ordination of macrofaunal community composition at each of the sites/location is shown in Figure 14. The communities at New Harbour (NH1), SC-3 and CE-3 are clearly separated from each other and from the other sites. The remaining Spike Cape sites, and all of the Dunlop Island sites, are clustered together in ordination space, indicating there are similarities between the macrofaunal communities at these sites. These differences are further illustrated by the SIMPER analysis (Table 3).

Table 3. Average percentage dissimilarity in macrofaunal community composition between sites and locations (unshaded side of the matrix). Bold values indicate the percentage within-site similarity. The shaded side of the matrix indicates the level of statistical significance determined using ANOSIM (non-significant values are in italics). Pairwise contrasts between sites based on ANOSIM provide an indication of differences between locations.

	Dunlop Island			Spike Cape			New Harbour	Cape Evans
	DI-1	DI-2	DI-3	SC-1	SC-2	SC-3	NH-1	CE-3
DI-1	**25**	*0.83*	*0.53*	*0.06*	*0.15*	<0.05	<0.05	<0.05
DI-2	65	**40**	*0.75*	<0.05	*0.23*	<0.05	<0.05	<0.05
DI-3	67	58	**42**	<0.05	<0.05	<0.05	<0.05	<0.05
SC-1	73	64	77	**55**	*0.15*	<0.05	<0.05	<0.05
SC-2	70	60	66	55	**44**	<0.05	<0.05	<0.05
SC-3	87	88	88	86	86	**29**	<0.05	<0.05
NH-1	96	97	97	97	95	98	**34**	<0.05
CE-3	89	88	82	92	84	92	98	**50**

The macrofaunal community composition at the New Harbour site (NH-1) was significantly different from those at all other locations/sites (i.e., % dissimilarity ≥95%, ANOSIM $P < 0.05$; Table 3). Within locations, the communities at the three Dunlop Island sites were not significantly different from each other, nor were the communities at Spike Cape sites 1 and 2 different to each other. Across locations, SC-2 and both DI-1 and DI-2 had similar macrofaunal communities, as did SC-1 and DI-1 (Table 3).

SIMPER analysis revealed the importance of different taxa in accounting for variability in macrobenthic community composition between sites and locations. At all locations, only 2–5 taxa explained 80% of the variability in community composition (Table 4). The Dunlop Island sites were all dominated by myodocopid ostracods (15.6–28.4 individuals core^{-1}); the anemone *Edwardsia* sp. was also common at DI-1 and DI-2 (around 13 core^{-1}), and ?Nematoda Type A at DI-3 (11.6 core^{-1}). The distinction between SC-3 and the other Spike Cape sites noted in the MDS (Figure 14) can be explained by the completely different suite of macrofaunal species and the low abundances found at SC-3. While SC-1 and SC-2 were dominated by *Edwardsia* sp. (33.8 and 22.8 core^{-1}, respectively), along with *Spiophanes tcherniai* and maldanids (polychaetes), myodocopid ostracods and ?Nematoda type A (2.8–13 core^{-1}), none of these taxa were important at SC-3. SC-3 was dominated by a gastropod (*Onoba gelida*; 2.8 core^{-1}), polychaetes (Cirratulidae type A, *Aglaophamus* sp., *Syllidia inermis*; 0.6–2.6 core^{-1}), and a different type of ostracod (podocopids; 1.4 core^{-1}) (Table 4). Nematodes, tanaids and an isopod (*Austrosignum grande*) were important at Cape Evans (21.4–52.0 core^{-1}), while polychaetes (*Aricidea* sp., Oweniidae and Paraonidae Type A; 1.5–2.75 core^{-1}) were common at New Harbour.

Relationships between epifauna and macrofauna

The epifaunal and macrofaunal community MDS ordinations (Figures 11 and 14) were significantly different (P=0.0060), indicating that epifaunal communities are not a good predictor of macrofaunal community composition, and vice versa.

Relationships between fauna and habitat

An MDS ordination was developed to investigate the overall relationship between fauna (both epifauna and macro-infauna), habitat (obtained from video) and sediment (obtained by coring) characteristics. The fauna and habitat associations characteristic of each site and location are shown in Figure 15.

Each of the 4 locations is clearly distinct from the others. At Dunlop Island, while DI-2 is tightly clustered, all three of the Dunlop Island sites overlap in ordination space. At Spike Cape, the three sites are grouped together but still clustered by site, indicating that while they are similar to each other, there are distinctions between sites (Figure 15).

A Spearman's rho correlation was used to relate macrofauna and epifauna at each location to sediment and habitat characteristics.

At Dunlop Island, the Spearmans rho correlation coefficient between epifauna and habitat characteristics was very low (i.e., 0.110) with % silt, % medium sand and % gravel the best explanatory environmental variables. The corresponding Spearmans rho correlation coefficient between macrofauna and habitat characteristics was also poor (i.e., 0.190), with % cobble the important explanatory environmental variable.

At Spike Cape, the Spearmans rho correlations were slightly better. The relationship between epifauna and habitat characteristics was 0.250 using % rock, % cobble and % pebble as explanatory environmental variables. The corresponding Spearmans rho correlation coefficient between macrofauna and habitat characteristics at Spike Cape was the most successful (i.e., 0.795), using % cobble, % coarse sand, % silt and sediment phaeophytin as the explanatory environmental variables.

Thus, unlike our analysis of fauna-habitat associations for Cape Evans and New Harbour in 2001, which demonstrated a very strong link between habitat structure and the distribution and diversity of both epifauna and macrofauna, only weak relationships could be distinguished for epifauna and macrofauna at Dunlop Island, and for epifauna at Spike Cape. The best relationship found was for Spike Cape macrofauna. It is important to remember that these relationships do not preclude broader relationships emerging as we sample more locations. This analysis simply points to how important the environmental variables are at accounting for variability within locations.

Table 4. The macrofaunal taxa contributing to 80% of the variability in community composition at each site. For each site, taxa are ranked according to their dominance, with 1 the most dominant taxa. The percentage contribution of each individual taxa to community variability is given in brackets. DI = Dunlop Island, SC = Spike Cape, NH = New Harbour, CE = Cape Evans.

Taxa	DI-1	DI-2	DI-3	SC-1	SC-2	SC-3	NH-1	CE-3
Nematodes								
?Nematoda Type A			2 (19.32)		2 (22.69)			1 (17.96)
Oligochaetes								
Oligochaeta	4 (6.84)							
Gastropods								
Onoba turquetti	5 (9.09)		3 (15.11)					
Onoba gelida						1 (27.27)		
Polychaetes								
Aglaophamus sp.						6.5 (7.80)		
Aricadea sp.							2 (28.04)	
Cirratulidae						2 (21.59)		
Haploscoloplos sp.	3 (24.53)							
Maldanidae					4 (7.16)			
Oweniidae							1 (30.52)	
Paraonidae Type A							3.5 (11.77)	
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)	–		
Crustaceans								
Podocopida						3 (13.52)		
Myodocopida	1 (28.11)	1 (52.50)	1 (45.84)	3 (11.00)	3 (20.47)	–		
?Nototanais sp.								2 (36.03)
Austrosignum grande								3 (25.88)

11.1.6.Remote video of additional sites using SplashCam

Three main areas were sampled using remote video (SplashCam). The general locations of these, and of the sites surveyed using ROV, are shown in Figure 16.

Dunlop Island:

A total of 18 sites were sampled along two transects in the Dunlop Island 'sound', ranging in depth from 4.8 to 35.0 m (Table 5). This sampling was conducted on 20 October 2002

RV-DI 1: depth 16.0 m	77° 14.191 S, 163° 28.041 E
RV-DI 2: depth 21.0 m	77° 14.197 S, 163° 27.999 E
RV-DI 3: depth 22.0 m	77° 14.204 S, 163° 27.959 E
RV-DI 4: depth 22.5 m	77° 14.220 S, 163° 27.869 E
RV-DI 5: depth 23.0 m	77° 14.236 S, 163° 27.773 E
RV-DI 6: depth 22.0 m	77° 14.247 S, 163° 27.716 E
RV-DI 7: depth 20.5 m	77° 14.255 S, 163° 27.654 E
RV-DI 8: depth 4.8 m	77° 14.265 S, 163° 27.589 E
RV-DI 9: depth 18.0 m	77° 14.267 S, 163° 27.548 E
RV-DI 10: depth 14.2 m	77° 14.175 S, 163° 28.133 E
RV-DI 11: depth 10.5 m	77° 14.170 S, 163° 28.177 E
RV-DI 12: depth 19.0 m	77° 14.156 S, 163° 27.570 E
RV-DI 13: depth 25.5 m	77° 14.280 S, 163° 27.962 E
RV-DI 14: depth 28.5 m	77° 14.366 S, 163° 28.153 E
RV-DI 15: depth 35.0 m	77° 14.454 S, 163° 28.333 E
RV-DI 16: depth 32.0 m	77° 14.544 S, 163° 28.551 E
RV-DI 17: depth 32.5 m	77° 14.585 S, 163° 28.976 E
RV-DI 18: depth 8.0 m	77° 14.618 S, 163° 22.362 E

The major habitat category at all sites videoed was sand and/or cobble. Boulders were characteristic of 3 sites (RV-DI 5, 7 and 8). Visable growths of microalgae were observed on the sand at RV-DI 1 and RV-DI 2. This combination of habitat types, and the major types of fauna observed (Table 5), are similar to those surveyed through diving.

Cape Roberts:

Five sites were remotely sampled in the vicinity of Cape Roberts, on 26 October 2002.

RV-CR 1: depth 20.0 m	77° 01.804 S, 163° 09.587 E
RV-CR 2 depth 19.8 m	77° 01.797 S, 163° 09.713 E
RV-CR 3 depth 19.8 m	77° 01.781 S, 163° 10.025 E
RV-CR 4 depth 21.0 m	77° 01.764 S, 163° 10.158 E
RV-CR 5 depth 21.0 m	77° 01.767 S, 163° 10.315 E

The seafloor in these sites was a combination of sand and/or cobble, with boulders also present at RV-CR3 (Table 6). The large epibenthic taxa noted include a significant number of *Odontaster* at RV-CR 1. *Phyllophora* was significant at RV-CR5.

Spike Cape:
These 8 remotely sampled sites covered a wide area, and encompassed a range of habitat categories (Table 7). Sampling took place on 29 October 2002.

RV-SC 6: depth 64.0 m	77° 16.121 S, 163° 29.929 E
RV-SC 7: depth 75.0 m	77° 17.565 S, 163° 32.710 E
RV-SC 8: depth 2.5 m	77° 18.095 S, 163° 31.741 E
RV-SC 9: depth 6.4 m	77° 18.092 S, 163° 31.940 E
RV-SC 10: depth 8.6 m	77° 18.087 S, 163° 32.122 E
RV-SC 11: depth 15.8 m	77° 18.077 S, 163° 32.536 E
RV-SC 12: depth 21.7 m	77° 18.079 S, 163° 32.988 E
RV-SC 13: depth 23.2 m	77° 18.082 S, 163° 33.457 E

Sponges (both erect and flat growth forms) were a significant feature of RV-DEBSC 6.

As noted in our previous report, SplashCam did not provide the same resolution and quality of video footage as obtained through the diving video survey. In some cases, it was difficult to positively discriminate between different habitat types, to positively identify epifaunal taxa, or to obtain good counts of epibenthic taxa. However, we found remote sampling to be extremely useful for conducting supplementary biodiversity assessments, as it was still possible to differentiate between major habitat types and to determine the dominant fauna present. With the SplashCam information presented here, and the small amount of information obtained using the ROV, we now have knowledge of the seafloor habitat and depth from Spike Cape up to Cape Roberts. This is a significant advance over our site specific sampling at Dunlop Island and Spike Cape (Figure 16). It has also given us valuable information on environmental variables such as depth of some areas – which was unavailable to us previously due to the lack of charts and the fact that these sites have not been sampled before.

11.1.7 Summary

Previous research involving comparisons of benthic communities and habitats have contrasted Cape Evans and New Harbour (e.g., Dayton refs). However, to date there have been no comparisons of locations on the continental side of the Ross Sea. Our work has begun to investigate this region, along the latitudinal gradient northwards from McMurdo Sound. Although we intend to sample more northerly locations along this gradient, there are already clear contrasts between New Harbour, Spike Cape and Dunlop Island. While Spike Cape and Dunlop Island may look similar at first glance (e.g., cf. Photos 1 and 2), we have documented interesting differences in habitat features, as well as epifaunal and macro-infaunal communities. The additional information obtained from Remote Video sampling north of Spike Cape has provided evidence that our dive locations are representative, and that in future we will be able to interpolate our detailed survey information to wider spatial extents.

Table 5. Habitat characteristics and the dominant large epibenthic taxa of sites surveyed at Dunlop Island using SplashCam. Results from video footage obtained at two different heights above the bottom (0.5, 1.5 m, corresponding to areas of 0.15 m^2 and 0.90 m^2, respectively) are presented. Habitat categories represent % cover on the seafloor. nd = not determined. * = Numbers of large epibenthic taxa are number per 0.15 m^2 and 0.90 m^2, for video footage 0.5 m and 1.5 m above the seafloor, respectively.

			Habitat category (% cover)					Large epibenthic taxa*						
RV SITE	Depth (sea ice thickness) (m)	Height above seafloor	Sand	Cobble	Boulder (< 40 cm)	Microalgae	Sponge	*Adamussium*	*Parborlasia*	*Ophionotis*	*Odontaster*	*Sterechinus*	*Abatus*	Sponge
DI 1	16.0	0.5	100			85		0						
		1.5	100					1						
DI 2	21.0	0.5	100			80			0	0				
		1.5	100			93			1	0				
DI 3	22.0 (2.4)	0.5	74	26						0				
		1.5	94	6						1				
DI 4	22.5	0.5	39	61						1		0		
		1.5	11	89						1		2		
DI 5	23.0 (2.6)	0.5		93	7					0				
		1.5		95	5					2				
DI 6	22.0 (2.6)	0.5	31	69								1		
		1.5	12	88								1		
DI 7	20.5	0.5		100	0		0					2		0
		1.5		82	18		6					0		3
DI 8	4.8	0.5		94	6								0	
		1.5		94	6								1	
DI 9	18.0 (2.6)	0.5		100							1	1		
		1.5		100							0	0		
DI 10	14.2 (2.6)	0.5		100				1						
		1.5		100				2						
DI 11	10.5 (2.5)	0.5	100					2		0				
		1.5	100					5		1				
DI 12	19.0 (2.5)	0.5	100								2			
		1.5	100								2			
DI 13	25.5 (2.6)	0.5	100							1				
		1.5	100							1				
DI 14	28.5 (2.5)	0.5		100							0			
		1.5		100							4			
DI 15	35.0 (2.5)	0.5		100										
		1.5		nd										
DI 16	32.0 (2.6)	0.5	100					0						
		1.5	100					2						
DI 17	32.5 (2.6)	0.5	100							0				
		1.5	100							2				
DI 18	8.0 (2.6)	0.5		100								3		
		1.5		100								3		

Table 6. Habitat characteristics and the dominant large epibenthic taxa of sites surveyed at Cape Roberts using SplashCam. Legend as for Table 5.

			Habitat category (% cover)					Large epibenthic taxa					
RV SITE	**Depth (sea ice thickness) (m)**	**Height above sea floor**	**Sand**	**Cobble**	**Boulders <40 cm**	**Sponge†**	***Phyllophora***	***Odontaster***	***Ophionotus***	***Alcyonium***	**Sponge**	**Lge starfish**	***Sterechinus***
CR 1	20.0 (2.6)	0.5	100					2					
		1.5	100					8					
CR 2	19.8 (2.6)	0.5	6	94									
		1.5	4	96									
CR 3	19.8	0.5	20	80	0	4				1	0	0	
		1.5	10	83	7	1				1	0	0	
CR 4	21.0 (2.6)	0.5	100					1	0		0		2
		1.5	100					1	2		1		2+
CR 5	21.0 (2.6)	0.5	100				93						2
		1.5	100				nd						nd

† as sponges grow on or over another habitat element, total % cover may be >100%.

Table 7. Habitat characteristics and the dominant large epibenthic taxa of sites surveyed around Spike Cape using SplashCam. Legend as for Table 5.

				Habitat category (% cover)					Large epibenthic taxa*					
RV SITE	**Depth (sea ice thickness) (m)**	**General habitat charact-eristics**	**Height above seafloor**	**Sand**	**Cobble**	**Boulder <40 cm**	**Boulder >40 cm**	**Sponge†**	***Sterechinus***	***Ophionotus***	***?Poriana*††**	***Adamussium***	**Pycnogoind**	**Sponge**
SC 6	64 (2.2)	Rocky; lots of sponges	0.5 1.5	nd nd	nd nd		53 63	12 10	2 0	1 0				13 8
SC 7	75 (2.0)	Rocky; Starfish, corallines, ophiuroids	0.5 1.5	66 nd		34 nd		75 nd		1 nd	1 nd			
SC 8	2.5 (2.1)	Anchor ice; 0.5 m clear water	0.5			100								
SC 9	6.4 (2.1)	Barren rock; fish	0.5 1.5		100 74	0 11	0 15							
SC 10	8.6 (2.4)	Mostly barren rock	0.5 1.5				100 100							
SC 11	15.8 (2.2)	Rock; some corallines	0.5 1.5		100 100				1 1			1 6		
SC 12	21.7 (2.2)	Fairly barren	0.5 1.5	100 32	0 68									
SC 13	23.2 (2.2)	Cobble, silt; scallops	0.5 1.5	85 60	15 40					1 2		1 2	1 0	

† as sponges grow on or over another habitat element, total % cover may be >100%.; ††*?Poriana antarctica*.

11.2 Describe ecosystem function at selected locations in the Ross Sea (Objective 2).

11.2.1. Ecological role of *Phyllophora antarctica* drift accumulations in coastal soft-sediment communities.

A study was conducted at Cape Evans to investigate the influence of drift accumulations of *Phyllophora* on macrofaunal community composition. This research has been written in publishable form, and will be submitted to an international journal for publication shortly. The draft paper, detailing methodology and findings of the study, is presented in Appendix 3, and is very briefly summarised below.

Whilst decomposition and incorporation of macroalgal drift material into the food web is rapid in temperate ecosystems, these processes are predicted to be slow in Antarctica. This work addresses the functional role of macroalgal detritus (i.e., drift *Phyllophora* accumulations) in fuelling the biodiversity of benthic communities at Cape Evans during the summers of 2001 and 2002. Specifically we (a) described the distribution and biomass of attached and drift algae, (b) assessed the photosynthetic capacity and degradation of drift accumulations using in situ fluorometry (c) assessed the structuring effect of patches of drift *Phyllophora* on underlying macrofaunal communities, and, (d) investigated the possible uptake by macrofauna using stable isotopes. We found significant reductions in the abundance of soft sediment macrofaunal assemblages under algae. This structuring effect was more pronounced in 2002 than in 2001, matching patterns of increasing degradation of the algal accumulations over this time period determined using in situ fluorometry. However, there were no clear differences in the numbers or types of macroinfaunal taxa found in bare sand or under algae.

Apart from providing structural complexity and refuge to benthic invertebrates, our results provide clear evidence that slowly decomposing *Phyllophora* may be an important source of carbon to higher trophic levels. The $^{13}C/^{12}C$ ratios of macrofauna collected under the drift algal accumulations were more reduced than those found on bare sand, while the $^{14}N/^{15}N$ ratios of macrofauna found under algae indicate that they feed at a lower trophic level than those on bare sand. Our results also suggest that although structurally intact *Phyllophora* from the bottom of drift-algal accumulations might not be a direct food source, detritus originating from *Phyllophora* is still utilised as food.

The persistence and slow degradation of *Phyllophora* detritus may serve to dampen the seasonality in food supply by providing a more consistent source of food to the benthic fauna. Macroalgal detritus clearly plays an important trophic role in Antarctic coastal waters, but the time scales for its incorporation into food web appear to be long, and very little is known about the utilisation of this resource by higher trophic levels. Thus, the ecological role of *Phyllophora* reported in this study is in stark contrast to the often rapid decomposition and incorporation into the food web reported for phaeophytes from lower Antarctic latitudes and temperate waters.

11.2.2. Determining community structure using stable isotopes

Understanding stable isotopes in ecological studies

Carbon (C) and nitrogen (N), two of the main building blocks of biological material, have two stable isotopes, ^{12}C and ^{13}C, and ^{14}N and ^{15}N, with the heavy isotope occurring at a natural abundance of 1.10 and 0.366% of each element, respectively. Because the heavy isotope makes a molecule larger, during assimilation molecules

with the lighter isotope pass through the cell wall in preference to molecules with the heavier isotope of that element. The preference is not exclusive but results in a shift in the ratio of heavy to light isotope, commonly referred to as isotopic 'fractionation'. Because isotopic fractionation results in very small changes in actual isotopic composition, delta (δ) notation with the units 'per mil' (‰) is used to describe the resultant isotopic signatures. The δ value refers to the enrichment of the heavy isotope relative to a specific reference standard, Pee Dee Belemnite (PDB) limestone = 0 ‰ for C and atmospheric nitrogen = 0 ‰ for N, and is calculated from the equation:

$$\delta X = (R_{sample}/R_{standard} - 1) \times 1000‰$$

where X is ^{13}C or ^{15}N and R is the ratio $^{13}C:^{12}C$ or $^{15}N:^{14}N$, respectively.

Fractionation for each element is different and has a finite enrichment step range with respect to the heavy isotope, typically 0.8-1 ‰ for carbon (^{13}C) and 3.5-4 ‰ for nitrogen (^{15}N). The process is accumulative and always positive. Because assimilation of food also involves excretion and respiration, the "predator" will always have more isotopically enriched $\delta^{13}C$ and $\delta^{15}N$ signatures than the prey. This is the basis of using stable isotopic composition for the determination of food webs.

However, while the isotopic signature of carbon can be used as a good indicator of food web position or "trophic" level, the nitrogen isotopic signature of plants and hence grazers can be 'blurred' by recycling of DIN through biological processes of excretion and decomposition, and other microbial processes. Effectively, the ambient concentration of CO_2 in seawater dilutes the isotopically depleted CO_2 signature below the level where it has a measurable effect on the $\delta^{13}C$ signature of algae. In contrast, the recycled DIN may be a large component of the DIN available for plant growth and hence it is more likely to have a measurable effect on the $\delta^{15}N$ signatures. Consequently, the nitrogen isotopic signature can only be used to assess the likely rate of processes occurring in the ecosystem rather than the trophic level within the food web.

A. Isotopic composition of algal material:

Algae are essentially at the base of the food web. They use dissolved inorganic nutrients of phosphate[3], dissolved inorganic nitrogen (DIN), and CO_2 for growth via photosynthesis. The $\delta^{15}N$ isotopic signature of DIN will have a range from about -3‰, for sources associated with atmospheric inputs (e.g. rainfall, lightening, nitrogen fixation of atmospheric N_2), to c. +8‰ or higher for DIN released from local sediments by microbial recycling and decomposition processes, or advected into the area from upwelling of deep oceanic waters.

Dissolved CO_2 has a $\delta^{13}C$ isotopic signature that also reflects its source. Atmospheric CO_2 dissolved in seawater has a $\delta^{13}C$ isotopic signature of 0 ‰ but, because of fractionation through the algal cell walls, marine algae have depleted $\delta^{13}C$ isotopic signatures in the range of -18‰ to -32 ‰. For Southern Ocean algae, the typical range is likely to be –20‰ to –25‰.

[3] With only one stable isotope, ^{31}P, phosphorus cannot be used as a natural isotopic tracer

Table 8. Mean isotopic composition (range) ‰ of the main groups of algae sampled from the 4 locations in October/November 2002 (n = number of samples).

Group			n	$\delta^{13}C$	$\delta^{15}N$	C/N ratio
Macroalgae						
Phyllophora antarctica						
	Cape Evans					
		Clean (drift)	3	-36.53 (0.5)	1.57 (1.7)	7.49
		Clean (attached)	3	-36.85 (2.5)	-1.08 (1.8)	6.54
	Dunlop Island					
		Clean (drift)	9	-37.68 (1.3)	-0.65 (1.4)	6.68
		Encrusted (drift)	3	-37.93 (0.7)	-0.13 (0.6)	6.70
Sea-ice algae						
Epicryophiles		Dunlop Island	9	-23.37 (3.3)	1.81 (0.6)	7.15
		Spike Cape	9	-22.29 (4.4)	2.03 (1.6)	6.52
		New Harbour	3*	-25.32 (3.0)	6.49 (0.2)	9.89
		Cape Evans	3	-20.19 (1.7)	2.44 (0.6)	7.27
Benthic algal material						
Benthic microphytes		Dunlop Island	15	-12.49 (6.3)	5.44 (3.3)	9.98
plus detritus		Spike Cape	15	-17.52 (1.6)	4.89 (3.2)	6.49
		New Harbor	5	-15.82 (1.0)	4.98 (0.8)	9.23
		Cape Evans	5	-19.18 (1.9)	5.75 (1.3)	6.76

* The $\delta^{15}N$ value for New Harbour sea ice algae was calculated from 2 samples.

The data in Table 8 show that the $\delta^{13}C$ isotopic signature of sea-ice algae all lie within the typical range, as do samples of pelagic phytoplankton from Cape Evans and Spike Cape (i.e., -23.88 ± 0.14 ‰; samples were not obtained from Dunlop Island or New Harbour). Macroalgae are more complex than ice algae and tend to have more depleted $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures, while benthic microphytes will have $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures that tend to reflect the recycling of nutrients within the sediments. Note 'benthic algal material' includes detritus.

Macroalgae:

The red alga *Phyllophora antarctica* was found as drift material at Dunlop Island, Spike Cape and Cape Evans. The $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures at Cape Evans were slightly enriched and depleted, respectively, over those at Dunlop Island (Table 8; Spike Cape drift *Phyllophora* was sparse and was not sampled). The encrusting species on the surface of the *Phyllophora* blades slightly enriched the $\delta^{13}C$ value and slightly depleted the $\delta^{15}N$ value (although not to the same extent as noted in our 2001 samples). In later assessments, we use isotopic values from cleaned *Phyllophora* only. As noted last year, all values are more depleted than those measured in *Phyllophora* from the vicinity of Anvers Island on the Antarctic Peninsula (^{15}N = 8.8 ‰, ^{13}C = -35.2 ‰; Dunton 2001), and probably indicate a difference in nutrient source between these locations (e.g., Dayton and Oliver 1977). However, the $\delta^{13}C$ isotopic signatures of *Phyllophora* from Cape Evans is more enriched by about 4 ‰ in 2002 (Table 8) compared with the 2001 values of -40.28 ‰ (Norkko et al. 2002). This is a substantial change and, as *Phyllophora* adsorb nutrients and CO_2 directly from the water, indicates a possible change in the water quality or source of water flowing through this location.

Sea-ice algae:

The isotopic signatures of the ice algae are distinctly different at the four locations. The ice algae at Spike Cape and Cape Evans are more enriched than those at Dunlop Island and New Harbour (Table 8; Figure 17). Interestingly, the $\delta^{15}N$ signature of the New Harbour ice algae is distinctly enriched relative to the $\delta^{15}N$ signatures of ice algae from the other locations. As ice algae also adsorb nutrients and CO_2 directly from the water, this indicates that either New Harbour is receiving a very different water mass from the other locations — an unlikely scenario given the geographical location of New Harbour relative to the other three locations, or the DIN at New Harbour has a higher proportion of locally recycled nutrients. Assuming that the ice algal species composition is comparable between locations, the more depleted $\delta^{13}C$ and enriched $\delta^{15}N$ signatures are consistent with a nutrient depleted water body and a nutrient supply dominated by sediment decomposition and recycling processes. The higher C:N ratio of the algae (Table 8) is also consistent with a nutrient depleted system. This implies that the seawater at New Harbour may have been very slow to exchange in 2002 compared with 2001. Exchange obviously does occur in the long term, as the $\delta^{13}C$ and $\delta^{15}N$ signatures of ice algae at New Harbour and Cape Evans in 2001 (Norkko et al. 2002) were very different, with more enriched $\delta^{13}C$ signatures at New Harbour than at Cape Evans, and more depleted $\delta^{15}N$ signatures at both locations (Figure 17).

Benthic algal material:

As noted for the ice algae, the isotopic signature for the benthic algal material was also distinctly different between locations. The Dunlop Island material has the most enriched $\delta^{13}C$ values, while the Cape Evans material has the least (Table 8, Figure 18). The benthic algal material comprises a mixture of benthic microphytes (algae attached to the sediment grains or living in the interstitial water spaces between them), faecal pallets of the larger epifauna and macroinfauna, sedimenting ice algae and water column phytoplankton, other detritus, and the microbial assemblages that decompose the detritus. It was not possible to separate the components of this mixture, and hence the isotopic signatures measured may to some extent reflect differences in their relative proportions.

The $\delta^{13}C$ values at Spike Cape are comparable with those at Cape Evans (Table 8, Figure 18) suggesting that similar processes probably occur at these locations, (e.g., sedimentation of advected phytoplankton blooms). The higher degree of ^{13}C enrichment at Dunlop Island (Figure 18) is more likely to be associated with detritus and faecal pellets rather than sedimenting pelagic phytoplankton. The large variability in the $\delta^{13}C$ values at this location is consistent with a wide range of settling detritus, which in turn will promote a greater degree of microbial processing in the sediments. This does not preclude the presence of benthic microphytes at Dunlop Island, but suggests that either they have taken on an enriched isotopic signature from nutrients released by decomposition processes, or that they are a minor component of the benthic algal 'mixture'.

There is a substantial difference in the $\delta^{13}C$ values of the sediments at New Harbour in 2002 compared to 2001 (cf. Norkko et al. 2002). This difference was not noted at Cape Evans, which suggests a continuation of previous conditions (e.g., annual phytoplankton blooms being advected and sedimenting in summer). The depletion in

the $\delta^{13}C$ isotopic signatures of the benthic community at New Harbour in 2002 suggests a major change in the relative proportions of the benthic algal components. In addition, the range of $\delta^{13}C$ values at New Harbour in 2002 (Figure 18, Table 8) is considerably less than it was in 2001 (see Norkko et al. 2002), a further indication that water exchange at New Harbour and the input of shoreline melt water may differ between years.

B. Isotopic composition of selected epifauna at each location:

Ice algae and benthic algal material are at the base of the food web and their isotopic signatures will pass into the filter feeders and detritivors that consume them. As previously discussed (Norkko et al. 2002), the isotopic value of the food changes during assimilation into the consumer due to isotopic fractionation associated with cell transfers into tissue with different turnover rates and excretion of waste products. Consequently, the epifauna have been dissected to separate short-term tissue and recently eaten food from long-term tissue, which is an integration of all food eaten over time, and places the organism within the food web.

Our approach was to use the isotopic signatures of (1) a 'long-term' tissue (such as test or integument) which integrates all the food sources consumed over a longer period of time, and (2) a 'short term' tissue (i.e., the gut) which represents the food consumed immediately prior to sampling. This strategy was continued for the new species examined in 2002 with a full tissue separation analysis being made to determine the most appropriate tissue to represent the long-term tissue. For the epibenthic taxa already assessed, we present only the signatures of the two tissues identified in 2001.

Below we describe and present the isotopic signatures of six of the common large epibenthic taxa, from a number of the locations surveyed. For those taxa that were not sampled in 2001, we use the isotopic signatures from the tissue separations to determine the 2 most appropriate tissues for routine analysis (Table 9).

In the filter-feeding bivalve, *Laternula elliptica*, all body tissues (except the gonad) have $\delta^{13}C$ values more enriched than the gut, which is consistent with intercellular fractionation as the food from the gut is assimilated into those tissues. The gonad is a specialised organ which experiences rapid turnover of nutrients and accumulation of lipids that are excreted from within the animal and consequently has a more depleted $\delta^{13}C$ value than the rest of the tissues. In this case it is also more depleted than the gut. As the digestive gland that produces lipids was not separated from the gut, the $\delta^{13}C$ value may be slightly depleted relative to the true value of the food recently ingested, i.e. phytoplankton and ice algae. The $\delta^{15}N$ values of most tissues is about one fractionation step more enriched than the gut and the $\delta^{15}N$ value of the gut is comparable with those of the ice algae at Dunlop Island (Table 9). Similar patterns were seen in the tissue separations for the other epibenthic taxa (Table 9). These tissue separation results are similar to those which were analysed in 2001 — i.e., *Adamussium colbecki*, *Sterechinus neumayeri* and *Ophionotus victoriae* (Norkko et al. 2002).

Table 9. Mean carbon and nitrogen % (± % range) and δ values (‰) of a variety of tissue types from three large epibenthic taxa.

Dissected tissue	%C (± %)	$\delta^{13}C$	%N (± %)	$\delta^{15}N$
Laternula elliptica (n = 3; Dunlop Island Site 1)				
Gut	41.50 (2.9)	-25.39	8.38 (0.9)	3.74
Muscle	39.50 (4.3)	-22.93	10.09 (1.2)	6.05
Foot	39.90 (3.91)	-22.36	10.87 (1.1)	6.25
Gonad	36.84 ( )	-26.83	5.46 ( )	5.42
Gill	38.23 (5.23)	-22.62	9.58 (1.4)	6.39
Siphon (inner)	40.63 ( )	-23.71	9.09 ( )	5.53
Siphon (skin)	10.80 ( )	-22.71	2.97 ( )	4.23
Siphon (tentacle)	37.72 ( )	-21.74	10.21 ( )	6.46
Hinge			1.03 ( )	3.91
Shell			0.21 ( )	2.36
Neobuccinum eatoni (n = 3; New Harbour Site 1)				
Gut	47.28 (5.1)	-22.23	7.43 (2.7)	8.45
Gonad	50.52 ()	-22.06	9.29 ()	10.96
Foot	39.56 (2.9)	-18.83	10.61 (2.4)	11.04
Operculum	29.68 ()	-17.40	11.91 ()	10.13
Shell	10.51 ()	0.44	0.02 ()	9.92
Spire	11.01 ()	1.29	0.06 ()	5.90
Odontaster validus (n = 3; Dunlop Island Site 1)				
Gut	41.58 (2.9)	-15.24	9.64 (0.8)	9.11
Gonad	42.32 (3.3)	-14.09	11.37 (1.0)	7.96
Central integument	28.55 (5.3)	-10.87	7.02 (2.6)	10.05
Arm integument	27.21 (2.5)	-11.08	5.97 (0.8)	9.72

In the figures presented below, a shift in $\delta^{13}C$ values to the right is an indication of isotopic fractionation and enrichment in those tissues relative to the gut. A shift in $\delta^{15}N$ value upwards also indicates isotopic fractionation and enrichment. The dual enrichment signature allows us to identify the tissue that has the slowest turn-over rates and, potentially, is the most useful for food-web studies.

1. *Adamussium colbecki*

Figure 19 illustrates the variability in stable isotope signature of the Antarctic scallop, *Adamussium,* at New Harbour, Spike Cape and Dunlop Island. The tissues shown are the gut and the gill; the gut indicated the signature of the most recently ingested food, while the gill signature indicates the combined signature of the food ingested longer term (i.e., the gill's lifetime). While the isotopic signatures for the Dunlop Island and Spike Cape sites show considerable overlap, the signatures the New Harbour individuals are considerably more enriched (Figure 19). This indicates that the *Adamussium* at New Harbour are utilising a different food source. Comparison of the gut $\delta^{13}C$ values with values for ice algae and benthic algal material (Figures 17, 18 and 19) at the respective locations suggests that *Adamussium* is more likely to be feeding on pelagic phytoplankton rather than benthic algal material. There is also some suggestion that sedimenting ice algae may be a minor food source for *Adamussium* at Dunlop Island and New Harbour. Benthic microphytes in the sediment may also be selectively separated from the associated detritus by *Adamussium*'s feeding strategy (i.e., re-suspending surface material by flapping the valves). Our sampling did not allow such a separation of the benthic algal material.

2. *Laternula elliptica*

The soft-shelled clam, *Laternula elliptica*, buries in the sand and filter feeds via a large siphon at the sediment surface. Based on the tissue separations at Dunlop Island (Table 9), the most appropriate long term tissue was the gill, as used for *Adamussium*, and hence only gut and gill tissue were routinely analysed for *Laternula* from the other sites.

While the isotopic signatures of *Laternula* (Figure 20) from all locations are similar to those of *Adamussium* (Figure 19) (*Adamussium* was not found at Cape Evans), there is a large range in the isotopic values for the gut at New Harbour, suggesting a wide range of food particles are being ingested. This range encompasses the depleted ice algae at New Harbour (Table 8).

3. *Sterechinus neumayeri*

In contrast to the filter feeders, the main food of the sea urchin, *Sterechinus neumayeri*, is derived from the amorphous benthic algal material. Gut isotopic values (Figure 21) are essentially the same as the benthic algal material (cf. Figures 18 and 20) at all locations. The degree of enrichment in the food source suggests it could be associated with detritus from higher organisms (e.g. biodeposits) and/or the consumption of macrofauna. There is considerable $\delta^{13}C$ isotopic enrichment during assimilation into the long-term tissue, i.e., the test (skin). There is also a high degree of $\delta^{15}N$ isotopic enrichment and variability in the $\delta^{15}N$ signatures that may also indicate a degree of omnivory that includes macrofauna within the available food sources.

4. *Ophionotus victoriae*

As noted in the previous report (Norkko et al. 2002), the small ophiuroid *Ophionotus* is an opportunistic predator and scavenger. Consequently, there is an expectation of a variable food source and hence a large range in the isotopic values of the gut, but this was not seen in the samples collected in 2002, except at New Harbour (Figure 22). The small range in the isotopic values of the gut at Dunlop Island and Spike Cape may reflect an abundance of or preference for a specific food. At New Harbour, the range of isotopic values is distinctly different, and variable (Figure 22). Interestingly, the isotopic values of the long-term tissue, i.e., the disc integument, are remarkably similar from all locations, including New Harbour, suggesting that the cause of the apparent scavenging at New Harbour may be a recent phenomenon.

5. *Neobuccinum eatoni*

The Antarctic whelk, *Neobuccinum eatoni*, is a large (up to 9 cm) gastropod. Tissue separations (Table 9) show $\delta^{13}C$ isotopic enrichment between the gut and other soft tissue but indicate that the shell and spire are precipitations of calcium carbonate. The operculum is chitinous and has similar $\delta^{13}C$ values to the soft tissue of the foot. While either tissue could be used, we selected the foot as the most appropriate long-term tissue in this study.

Neobuccinum is known to eat dead animals (necrophagous) and its prey includes *Adamussium* and damaged *Laternula*. Given these apparent preferences, there is an expectation for the isotopic values of the gut (Figure 23) to reflect the isotopic signatures of the long-term tissue of *Adamussium* and *Laternula* (Figures 19 and 20). This is the case at Dunlop Island, Spike Cape and New Harbour (Figure 23). However, at Cape Evans, the isotopic value of the *Neobuccinum* gut is substantially different from *Laternula* (*Adamussium* is not found at Cape Evans) indicating a different food source.

Of all the specimens analysed from Cape Evans in order to build a picture of the food web linkages (see below), few had long-term isotopic signatures comparable with the isotopic values of the *Neobuccinum* gut content. One likely food source is the macrofaunal polychaete, *Flabelligera mundata*, which has an isotopic signature that is a good match for that of the *Neobuccinum* gut.

6. *Odontaster validus*

The seastar, *Odontaster validus,* is an omnivorous predator with a broad selection of prey, capable of filter feeding and scavenging. Tissue separations show substantial $\delta^{13}C$ isotopic enrichment between the gut and the disk and arm integuments but only a small enrichment for the gonad (Table 9). As previously suggested, the gonad may be rapid turnover tissue and hence is less appropriate than the central integument for long-term tissue. While there is little difference in the $\delta^{13}C$ values between arm and central integument, the $\delta^{15}N$ values of these tissues suggest isotopic enrichment in the central integument, but depletion in the arm. Consequently, we used the central integument as the most appropriate long-term tissue.

The isotopic values of *Odontaster* gut (Figure 24) show relatively large ranges in both $\delta^{13}C$ and $\delta^{15}N$ values, which is consistent with what we know of the feeding range of this predator. However, while *Odontaster* is reported to include *Adamussium* and *Laternula* in its diet, the isotopic values of its gut are more enriched than the long term tissue of either of these shellfish and hence, the specimens examined were unlikely to have eaten *Adamussium* or *Laternula* recently. Of interest is the narrower range and more enriched $\delta^{13}C$ values in the gut of *Odontaster* from Cape Evans. Apart from a range of benthic macrofauna including polychaetes, amphipods, and crustaceans, these isotopic values most closely match the long-term tissue of the Antarctic whelk, *Neobuccinum eatoni*, which may be a preferred food at this location.

C. Trophic relationships at Cape Evans

A wide range of individual specimens of macrofauna, epifauna and primary production sources were collected from Cape Evans in order to examine some possible or potential food-consumer and predator-prey relationships. The ultimate objective of constructing a food web from this extremely complex data set (Figure 25) is not a simple task and only general statements on trophic relationships can be made at this time. Examples already cited above demonstrate that, whereas a predator may prefer a specific prey as food at one location, the absence of that prey at another location can result in an apparent switch to omnivory rather than the selection of a new preferred prey. This observation could highlight an increase in local abundance of the original preferred prey, rather than an active seeking of that prey in preference to other available prey species or food.

In general terms, the isotopic composition of samples collected from Cape Evans (Figure 25) show some consistent patterns. Macro- and microalgae (pale blue dots) all have lower isotopic values than the large epifauna (black dots), consistent with there being isotopic enrichment progressively up through the food web. Although we have not shown the specific species on this figure, some species do exhibit significantly different isotopic signatures from the rest, which imply no link with any of the other specimens collected to date. For example, the macroalgae, *Phyllophora antarctica*, is situated in the lower left hand corner of the figure (i.e., 2 pale blue dots at $\delta^{13}C$ value of c. -36.5 ‰). As it is clearly isolated from all other specimens, it is unlikely to be consumed by any of the species collected thus far at Cape Evans. This is consistent with *Phyllophora* being unpalatable and potentially toxic to most benthic macrofauna and epifauna. *Sterechinus neumayeri* is known to cover itself with drift *Phyllophora* as protection against predation.

Figure 25 also highlights the fact that there are differences between the isotopic signatures of macro-infauna living in sediments under drift *Phyllophora* accumulations (green dots), and those from bare sediment areas (red dots). The general pattern is that the macrofauna from the bare sediments are more enriched, indicating that detritus originating from decomposed *Phyllophora* is utilised as food by the macrofauna under the accumulations. This point was highlighted by our investigation into the role of *Phyllophora* in structuring macrobenthic communities in the first part of this Objective (see Appendix 3 for more details).
Interpretation of the Cape Evans food web data is currently in progress, and will be presented in more detail in a later report.

12. Summary and Conclusions

The aims of this project were to quantify biodiversity of benthic and sea-ice communities and to describe ecosystem function in the coastal areas of the Ross Sea. The research is designed to increase our understanding of the environmental processes that influence the biodiversity of coastal benthic communities in Antarctica.

Studies of biodiversity should have both a structural and functional component, since this allows observations to be placed in an ecological context (Lamont 1995, Gray 1997, Anon 2000; The New Zealand Biodiversity Strategy). While it is important to compare biodiversity at different locations and times, we also need to increase our understanding of how the different components of the ecosystem are linked together. Such understanding will strengthen predictions about how the biota might respond to environmental change.

Location-dependent differences in habitat and benthic biodiversity:

Our results demonstrate patterns in species diversity, abundance, and associations with habitat characteristics between locations. We found:

- Differences in habitat structure. The extremes were New Harbour and Cape Evans. New Harbour is dominated by soft sediments while Cape Evans was dominated by hard substrates (rocks and boulders) interspersed with soft sediments and abundant macroalgae. Dunlop Island and Spike Cape are similar to Cape Evans in that the seafloor is dominated by rocks and pebbles. However,

there are also distinct differences in the habitat elements between these 3 locations. The soft sediments at all 4 locations were generally comprised of coarse sand and gravel/pebble and had very low organic content.

- Differences in macroalgae between locations. The red alga *Phyllophora antarctica,* and encrusting coralline algae are present at 3 of the 4 locations sampled: Dunlop Island, Spike Cape and Cape Evans. However, abundances of these macroalgae differ between locations.

- Differences in the microphytobenthic standing stock between locations. New Harbour sediments have the lowest chlorophyll *a* and phaeophytin biomass of the four locations, while Cape Evans sediments have the highest levels. In addition, a higher proportion of the microphytobenthic biomass was in a degraded state at Spike Cape and New Harbour than at Dunlop Island or Cape Evans.

- Differences in the diversity and abundance of large epibenthic taxa, and macro-infauna between and within locations. The dominant epifaunal taxa were similar across locations, but their abundances varies considerably. The macrofaunal communities at New Harbour, Cape Evans and one of the Spike Cape sites were distinctly different from each other. The remaining Spike Cape sites and all three of the Dunlop Island sites had similar macrofaunal communities.

- Differences in fauna/habitat characteristics between locations. The three Dunlop Island sites had similar characteristics while the Spike Cape sites were distinct from each other. The macrofauna communities at Spike Cape were correlated with a number of sediment characteristics (i.e., cobble,coarse sand, silt and phaeophytin), and between sites at Spike Cape.

- Our findings of habitat structure and the diversity of epibenthic taxa obtained from the dive surveys were extended using Remote Video. We obtained new information on the seafloor habitat and depth between Cape Roberts and Spike Cape.

As stated in our first report (Norkko et al. 2002), it is important to note that, in isolation, these results describing patterns in structural biodiversity would provide little basis for predicting the likely impact of environmental change. For example, predicting the effect of changes in sea-ice conditions on ecosystem productivity and diversity would be difficult without supplementary data on the ecological processes linking the flora and fauna in an ecological community (functional biodiversity).

Ecological role of *Phyllophora antarctica* drift accumulations in coastal soft-sediment communities.

- Our study of the effect of drift accumulations of the macroalga *Phyllophora* on the underlying macrobenthic communities detected significant reductions in the abundance of soft sediment macrofaunal assemblages under algae. This structuring effect was more pronounced in 2002 than in 2001, matching patterns of increasing degradation of the algal accumulations. There were no clear differences in the numbers or types of macroinfaunal taxa found in bare sand or under algae.

Emerging patterns in functional diversity using stable isotope techniques:

The use of stable isotope techniques to demonstrate linkages between various fauna and their food source has proved to be very insightful, even in the early stages of this work. We have demonstrated:

- Differences in isotopic signatures of ice algae, microphytobenthos/detritus and macroalgae (*Phyllophora antarctica*) between locations, indicating differences in nutrient sources.

- Differences in isotopic signatures of tissues of selected common large epibenthic taxa between locations, indicating that the important food source(s) of a particular taxa may also differ between locations.

The construction of a more detailed food web at Cape Evans is progressing well, and will provide valuable information on trophic relationships. Ultimately, it will enable us to better assess the importance of the various primary food sources, or of a particular species, and thus help predict the consequences of change, to the wider ecological community.

Future research directions

In February 2004 we plan to implement this sampling design from the *RV Italica*, at several coastal locations in the north-western Ross Sea. Future sampling plans will depend in part on the success of this cruise. However, we envisage sampling additional locations in order to adequately encompass the latitudinal 'gradient' of the western Ross Sea, in conjunction with process-based research to provide important information on the functioning of these systems.

As discussed above, the potential of this sampling design will not be fully realised until we can incorporate additional locations, encompassing a range of environmental characteristics (i.e. sea ice conditions, light regime, water currents, magnitude and diversity of primary producers, etc.) along the latitudinal gradient of the western Ross Sea.

13. Acknowledgements

We are grateful to New Zealand Ministry of Fisheries for funding this Project (ZDB2002/01), and to Antarctica New Zealand for their excellent logistical support. We particularly thank the D6 drivers (Kim Dudek and Gus McGregor) and field guides (Ewan Paterson and Jim Spencer) for their invaluable assistance on the sea ice traverse. Thanks also to Joanna Norkko and our Italian collaborators at the University of Genova (Carlo Cerrano and Marta Guidetti) for their help on the ice, to the taxonomists who helped with macro-infauna identifications [Graham Fenwick, Niel Bruce (NIWA) and Bruce Marshall (Te Papa)], and to Nicole Hancock, Ron Ovenden and Burns Macaskill (NIWA) for processing samples.

14. Publications

Schwarz A, Hawes I, Andrew N, Norkko A, Cummings V, Thrush S (in press). Macroalgal photosynthesis near the southern global limit for growth; Cape Evans, Ross Sea, Antarctica. *Polar Biology.*

15. Data Storage

The data, recorded on excel spreadsheets, will be stored on the purpose built biodiversity database, which NIWA is currently under contract by the Ministry of Fisheries to build. Duplicates of digital videos are archived in room 3.20 of the Allen building at Greta Point, NIWA.

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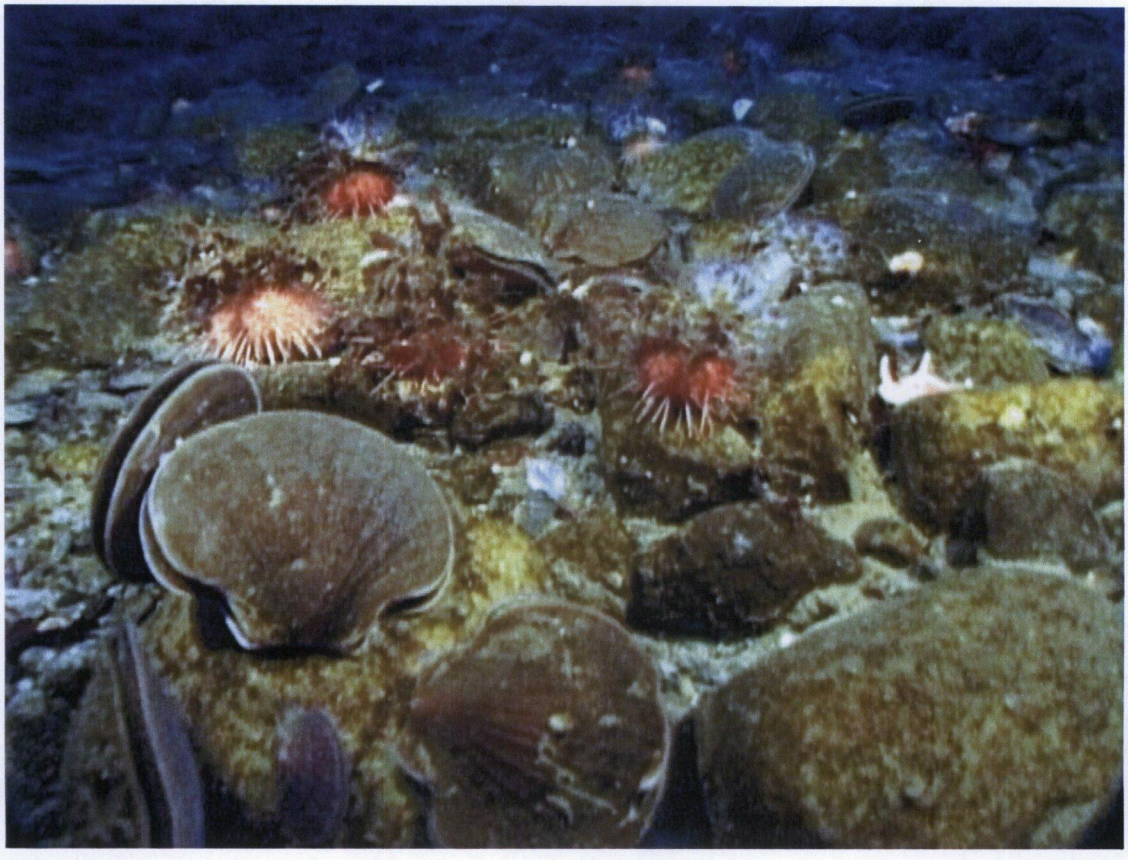

Photo 1. The seafloor at Dunlop Island. The Antarctic scallop *Adamussium colbecki* was the dominant epibenthic taxon at this location. The sea urchin *Sterechinus neumayeri* and the sea star *Odontaster validus* were also common. Drift macroalgae *Phyllopohora antarctica* was noted attached to the spines of *Sterechinus*.

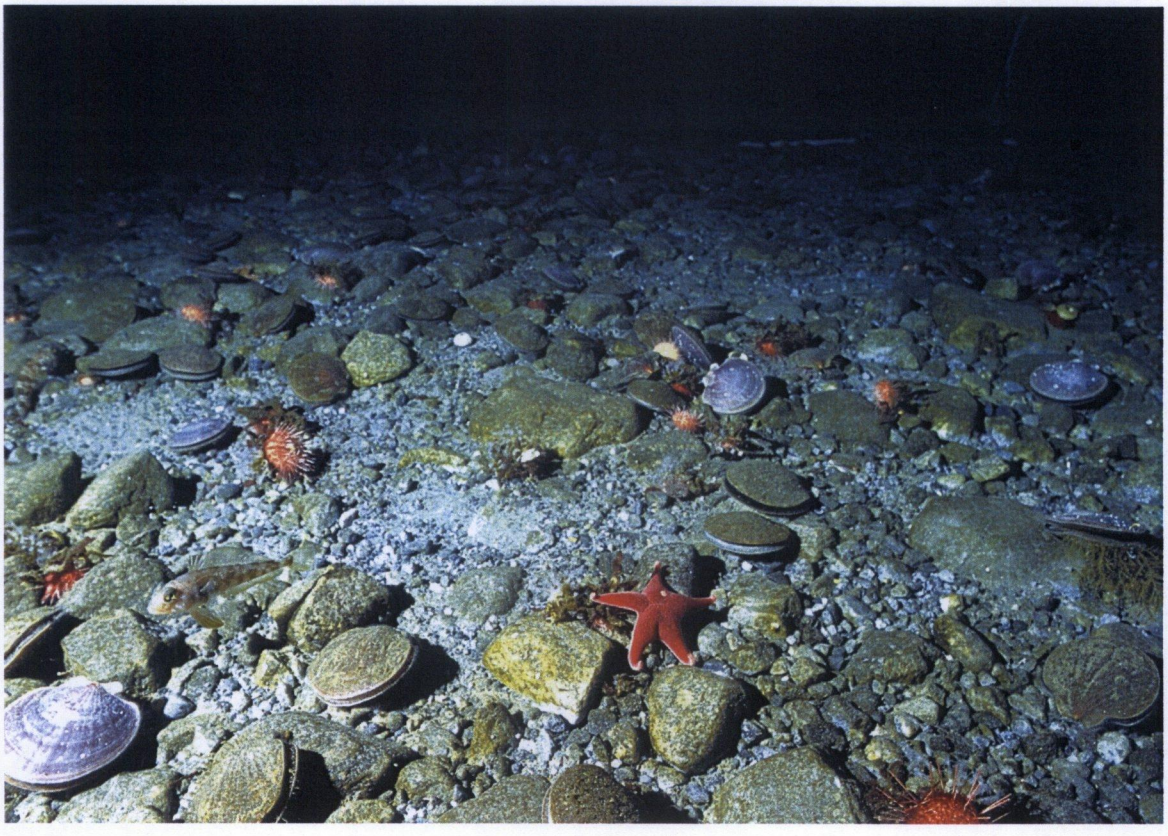

Photo 2. The seafloor at Spike Cape. The sea urchin *Sterechinus neumayeri* was the dominant epibenthic taxon at this location. The scallop *Adamussium colbecki* and the seastar *Odontaster validus* were also common.

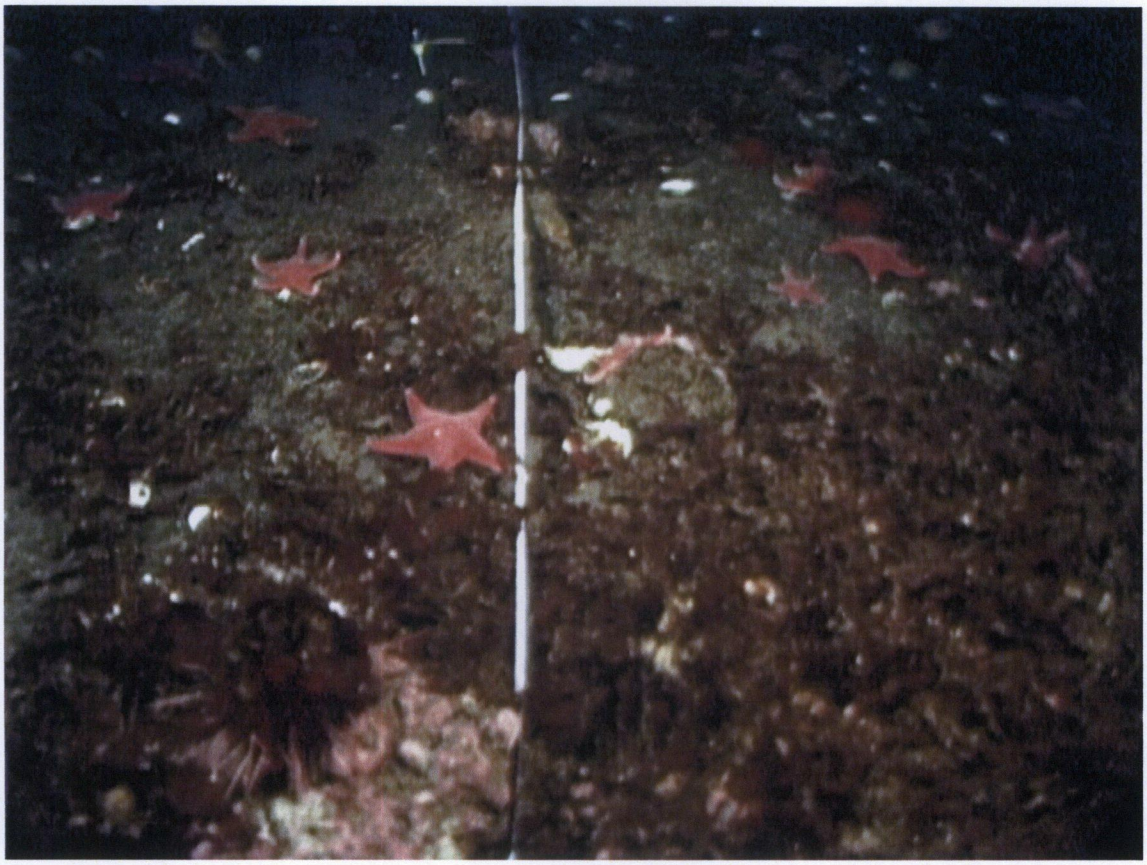

Photo 3. The seafloor at Cape Evans. Note the accumulations of drift *Phyllophora antarctica.* The sea star *Odontaster validus* was the dominant epibenthic taxon, and the sea urchin *Sterechinus neumayeri* and the nemertean *Parborlasia corrugatus* were also common.

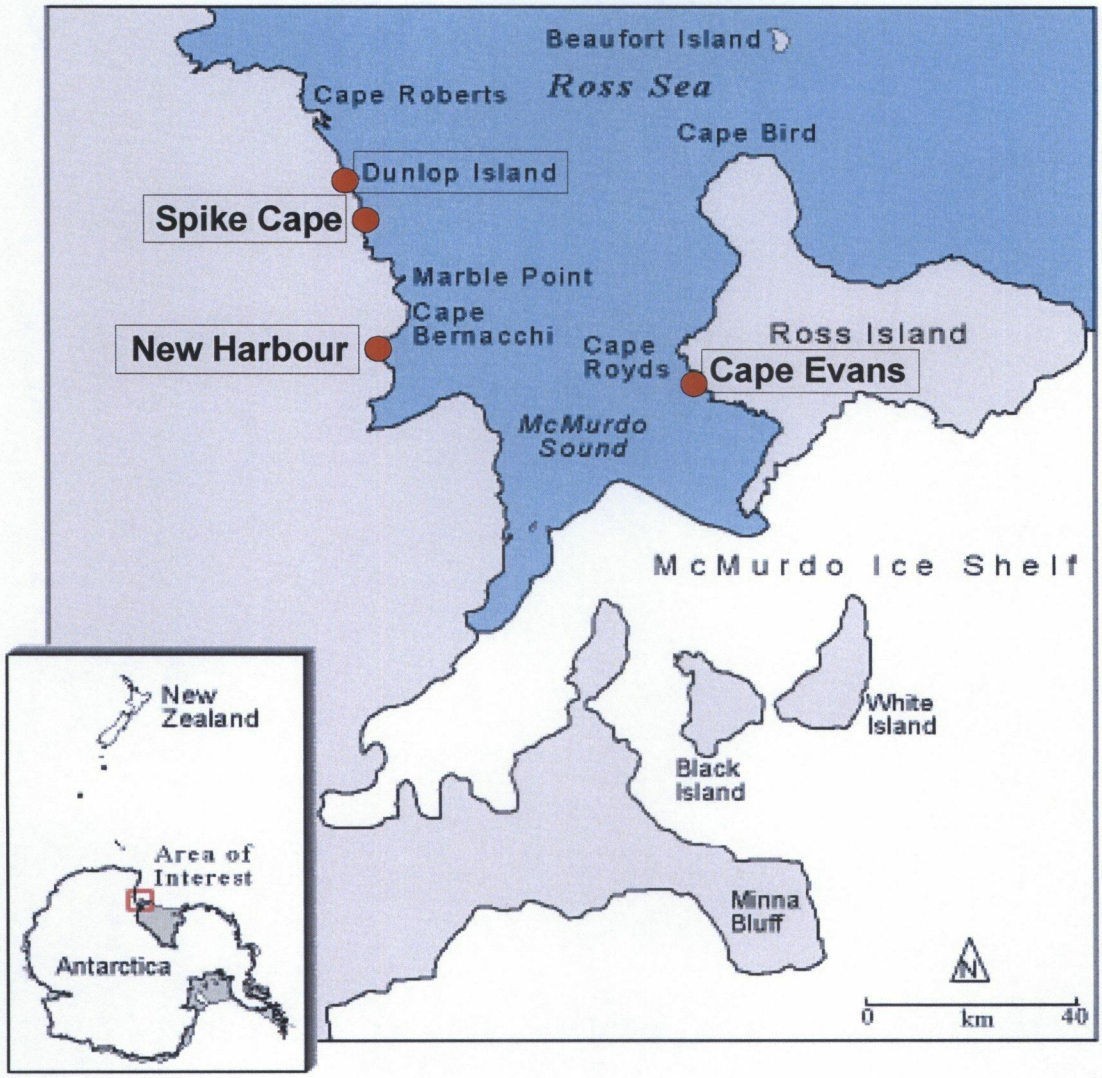

Figure 1. Map showing the four locations surveyed in 2002.

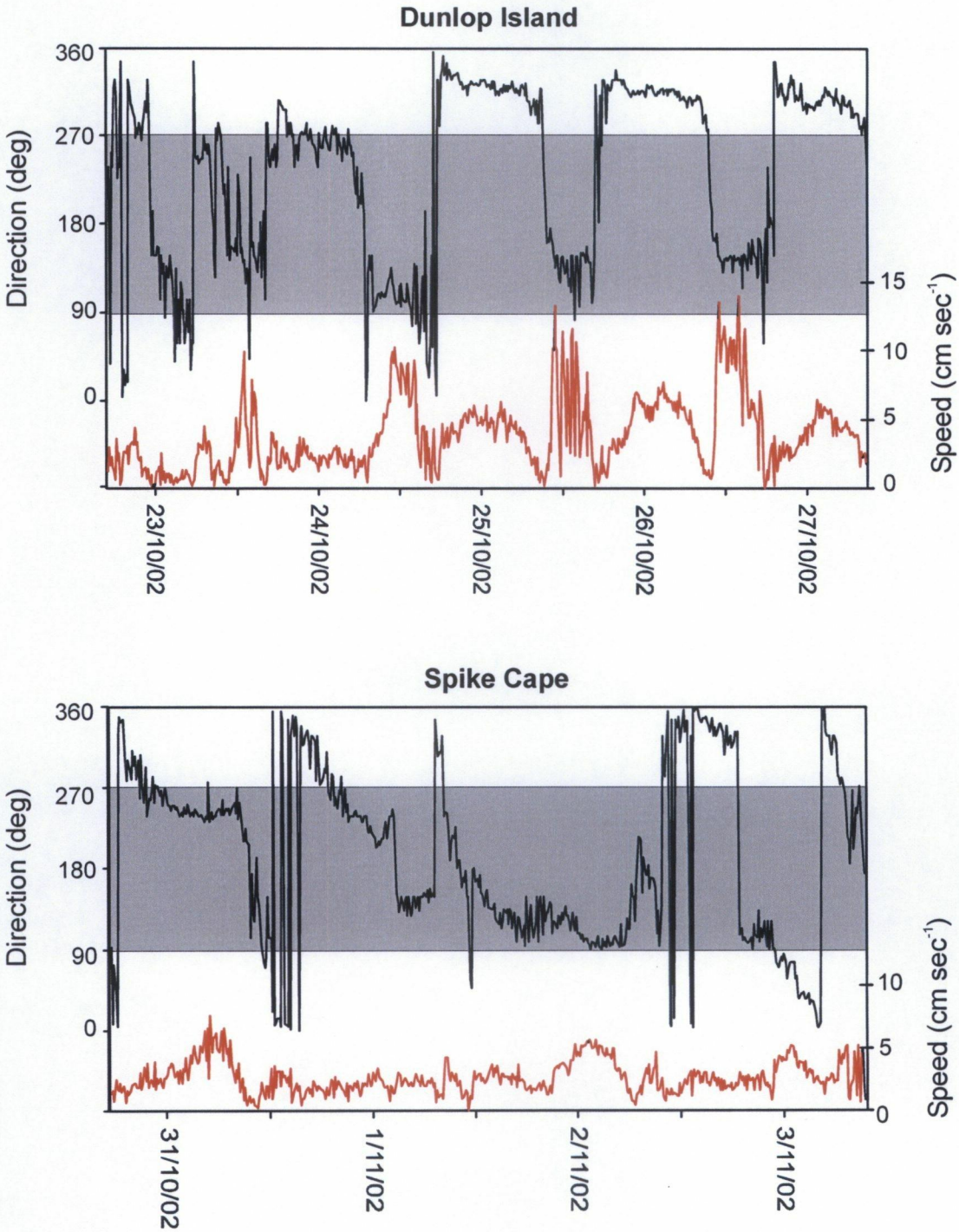

Figure 2. Measured current velocities (cm s^{-1}) and direction (degrees north) at Dunlop Island and Spike Cape. Note the differences in scale on the x-axes. The apparent abrupt shifts in direction are misleading as they only reflect a few degrees change at around 360° (e.g. 355° to 5° is only a 10 ° change in current direction). The shaded area indicates the range of southerly current direction.

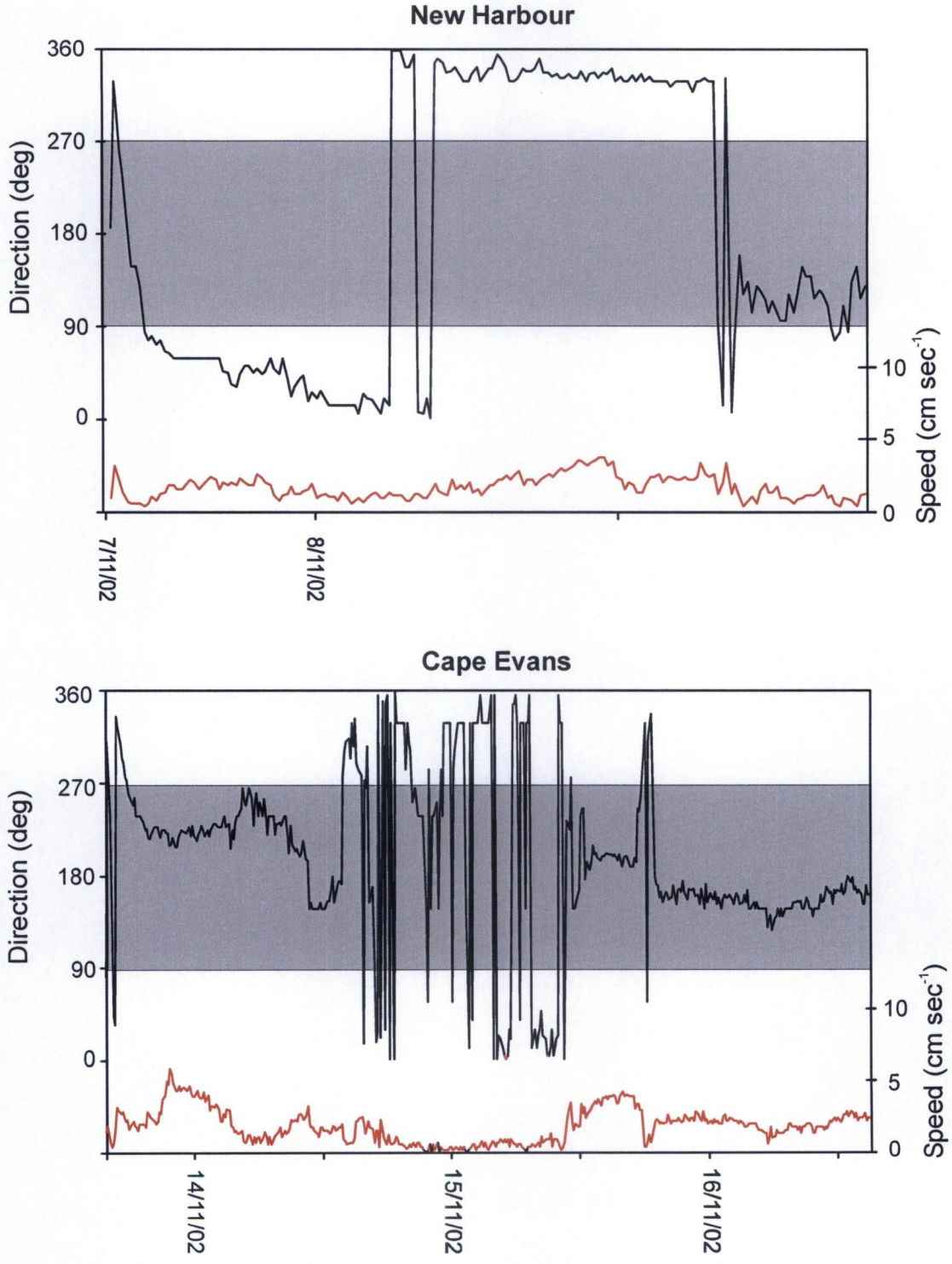

Figure 2 (continued). Measured current velocities (cm s^{-1}) and direction (degrees north) at New Harbour and Cape Evans.

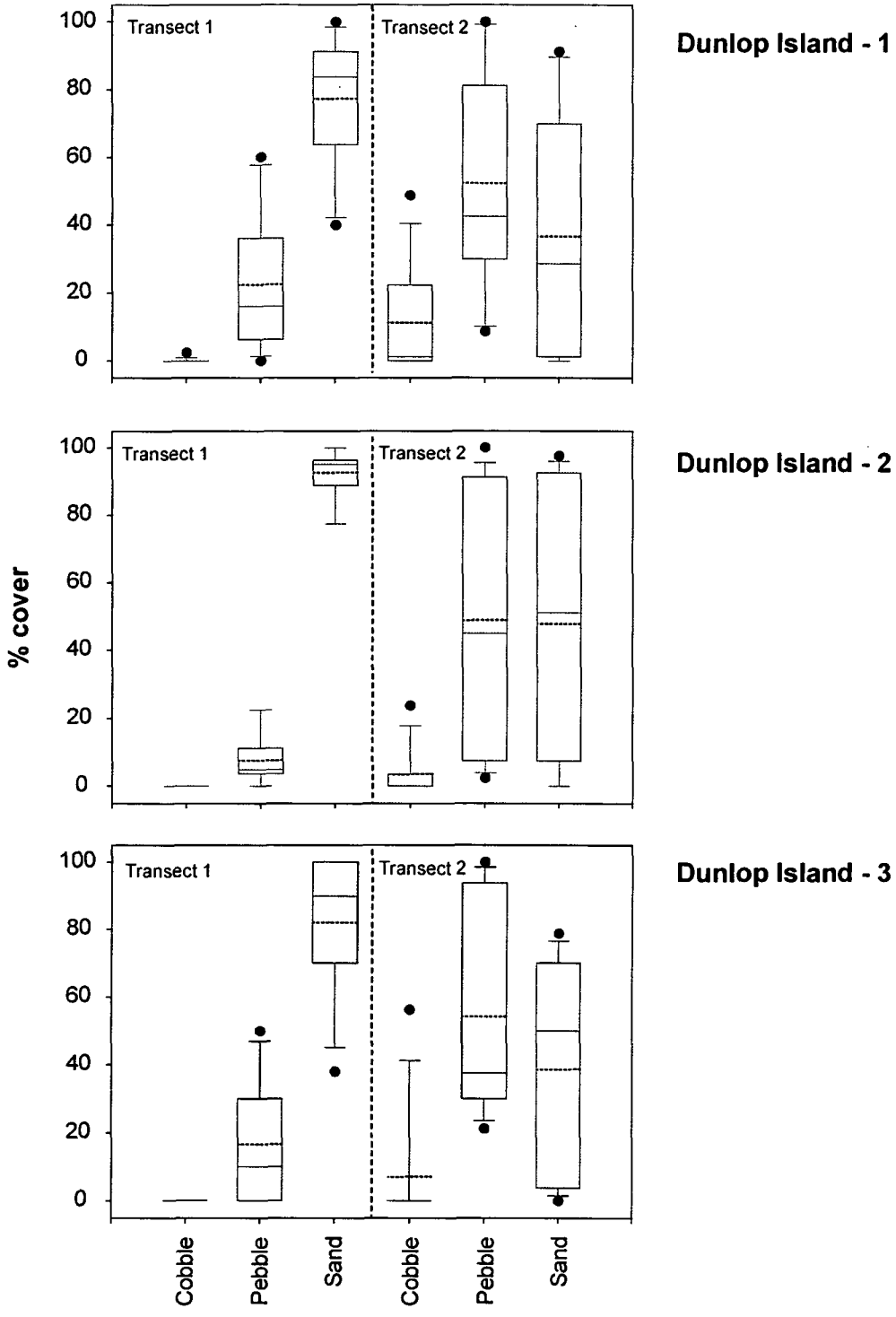

Figure 3. Boxplots illustrating the distribution of the major habitat types at the three sites at Dunlop Island. Whiskers located at the 10% and 90% percentiles encompass 80% of the data points and dots indicate the few values outside of this range. The upper and lower ends of the box are the 25% and 75% percentiles, respectively, and encompass 50% of the data. The solid line indicates the median and the dotted line the mean value.

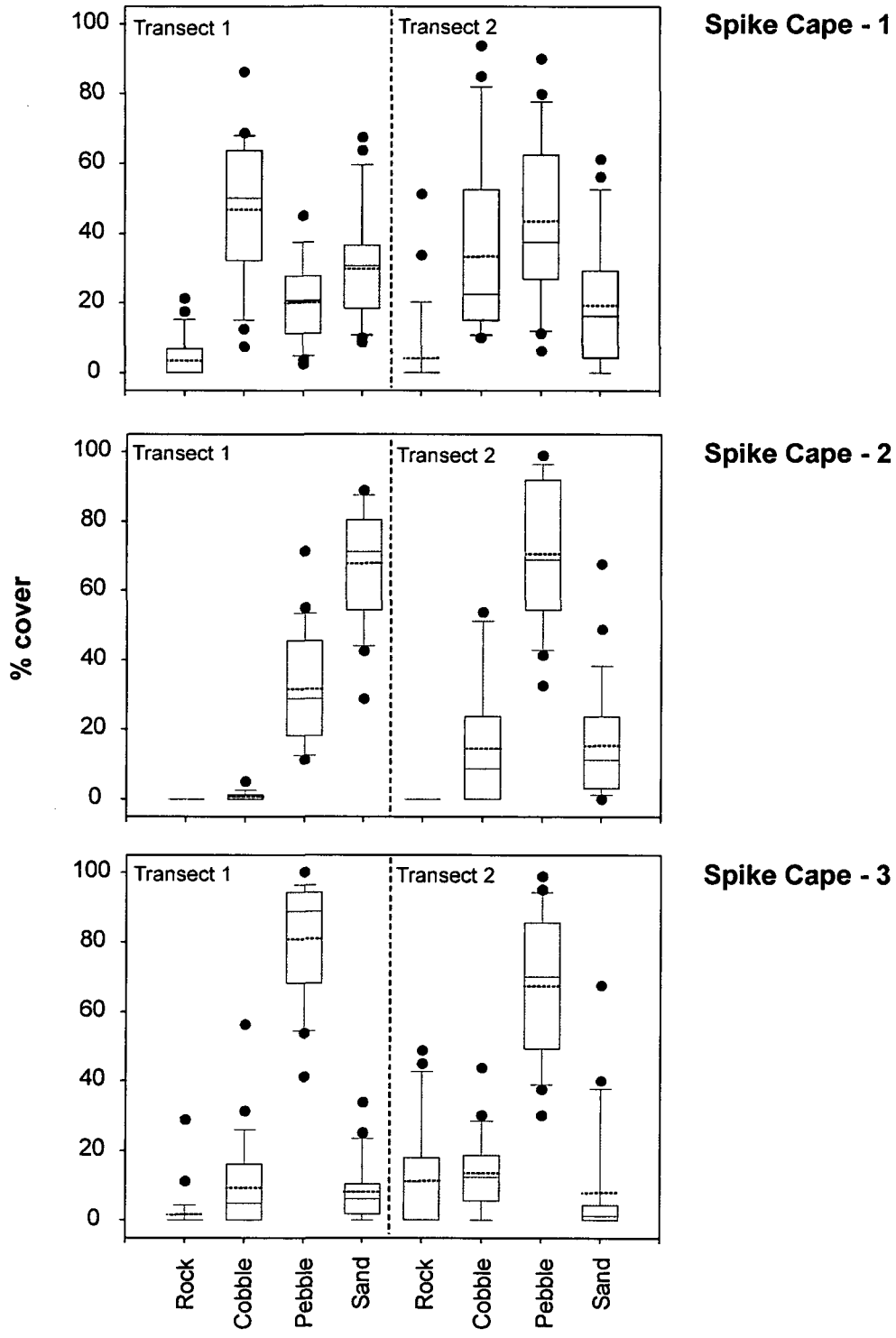

Figure 4. Boxplots illustrating the distribution of the major habitat types at the three sites at Spike Cape. Whiskers located at the 10% and 90% percentiles encompass 80% of the data points and dots indicate the few values outside of this range. The upper and lower ends of the box are the 25% and 75% percentiles, respectively, and encompass 50% of the data. The solid line indicates the median and the dotted line the mean value.

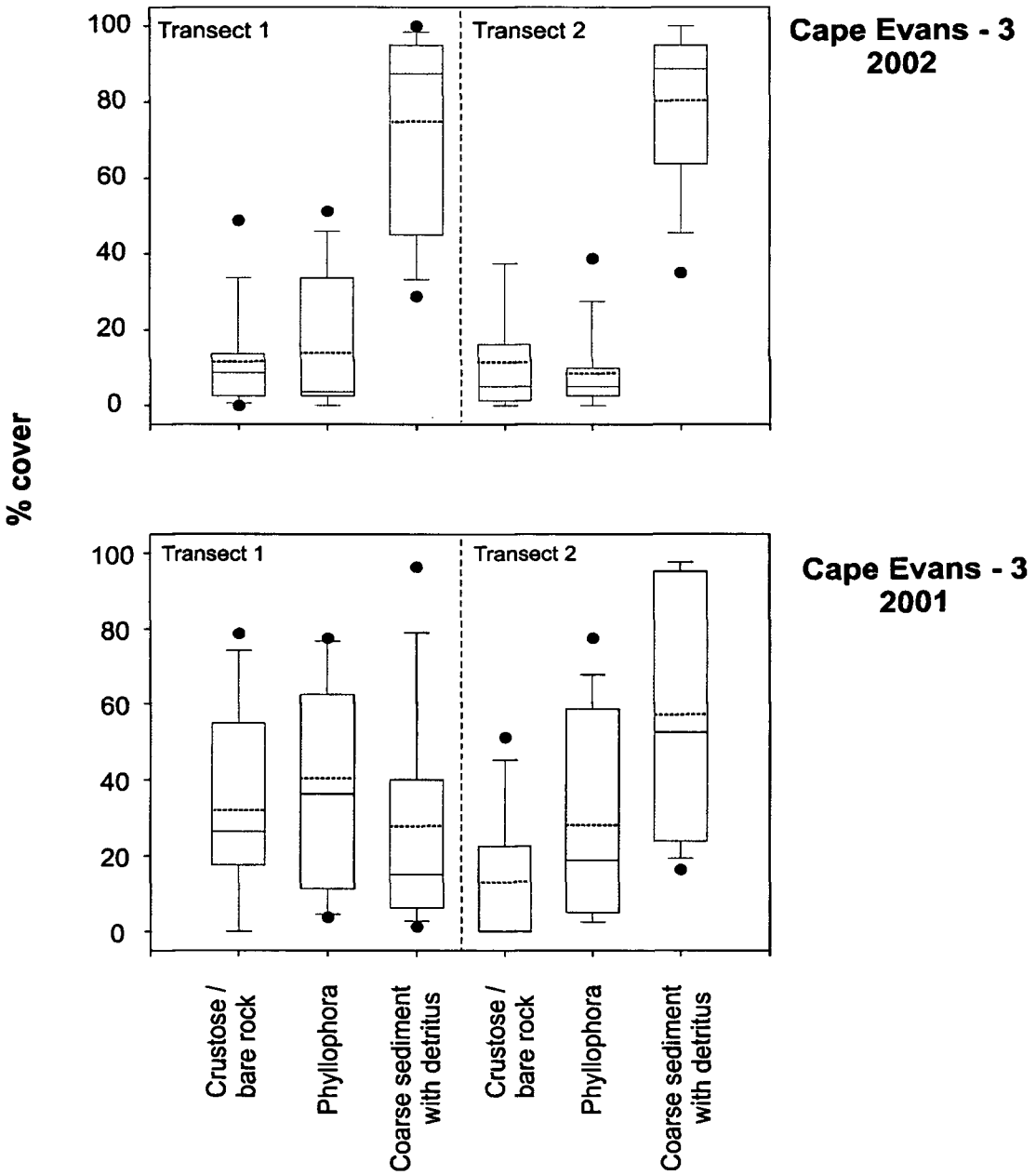

Figure 5. Boxplots illustrating the distribution of the major habitat types: *Crustose/bare rock, Phyllophora* and *Coarse sediment with detritus* from Cape Evans Site 3. The distributions in 2002 and 2001 are presented. Whiskers located at the 10% and 90% percentiles encompass 80% of the data points 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.

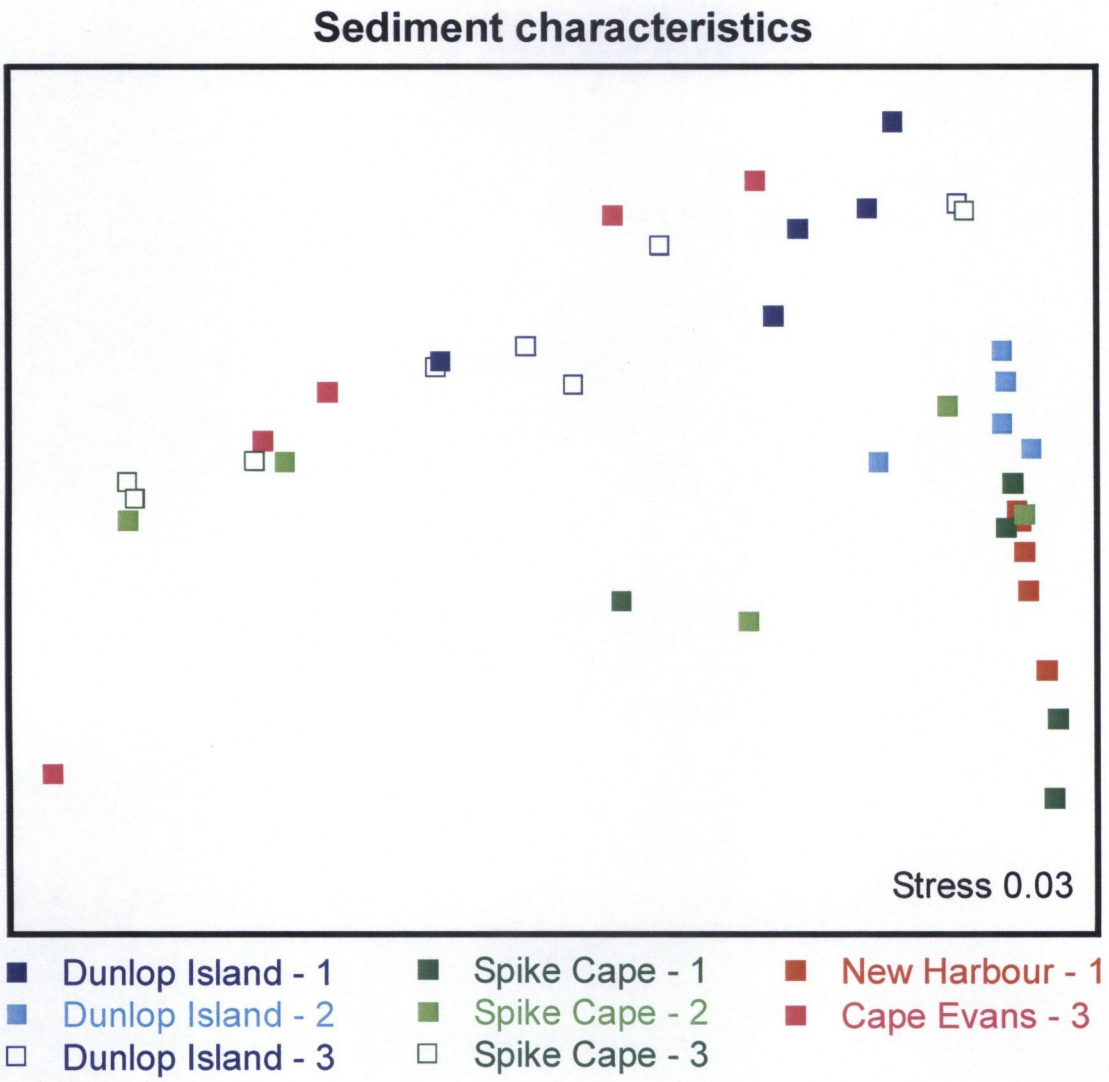

Figure 6. MDS ordination plot of sediment characteristics at each location. The axes have no labels as they have no meaning in absolute terms. Distances between sample points indicate the relative magnitude of differences in sediment characteristics.

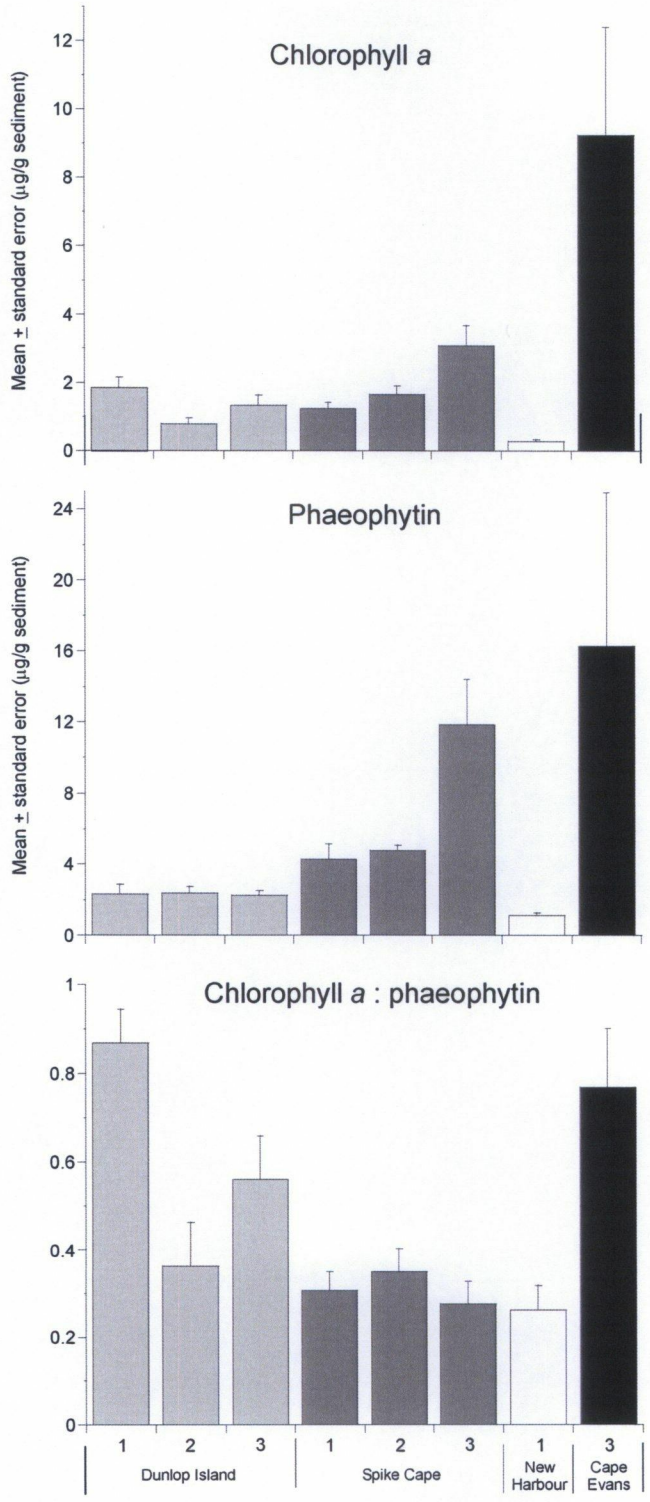

Figure 7. Concentrations (mean ± s.e.) of chlorophyll *a* and phaeophytin (degradation product of chlorophyll *a)*, and the chlorophyll *a*:phaeophytin ratio at the four locations.

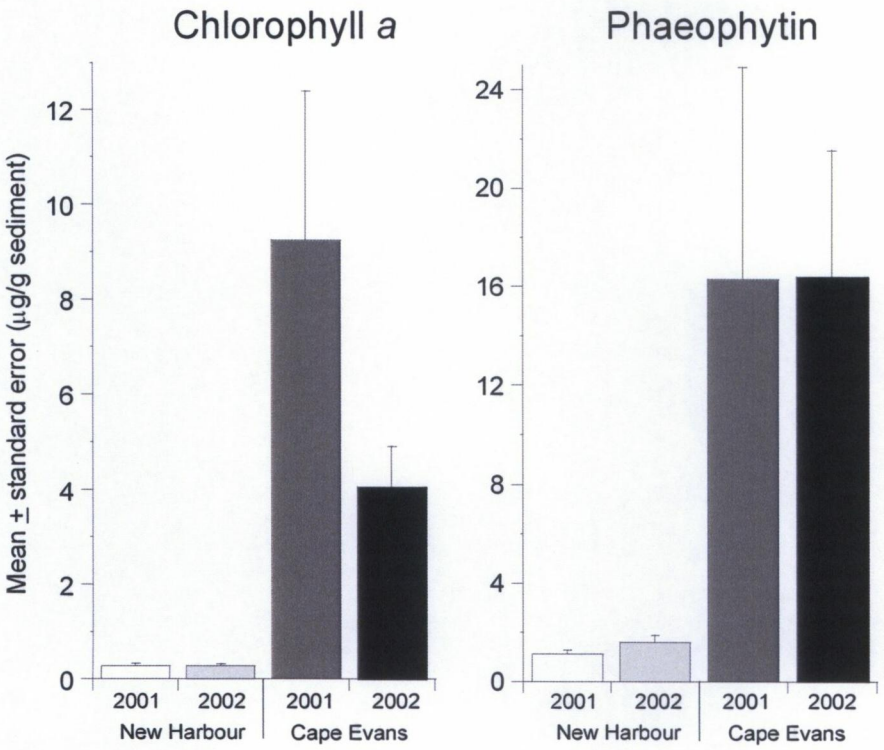

Figure 8. Concentrations (mean ± s.e.) of chlorophyll *a* and phaeophytin (degradation product of chlorophyll *a* at New Harbour and Cape Evans in 2001 and 2002.

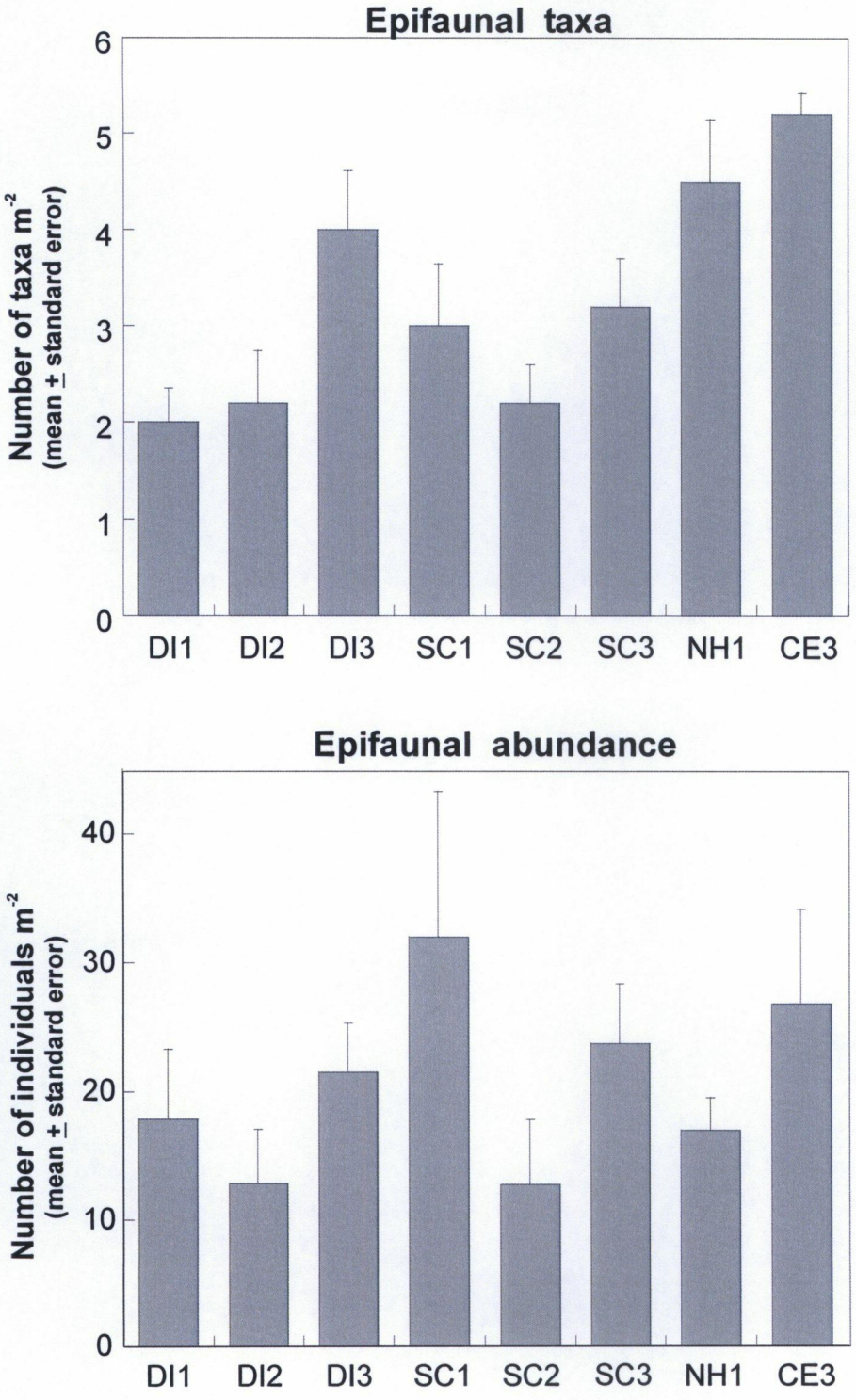

Figure 9. Number of taxa and individuals (mean ± s.e.) of the large epifauna at each location. DI = Dunlop Island, SC = Spike Cape, NH = New Harbour, CE = Cape Evans.

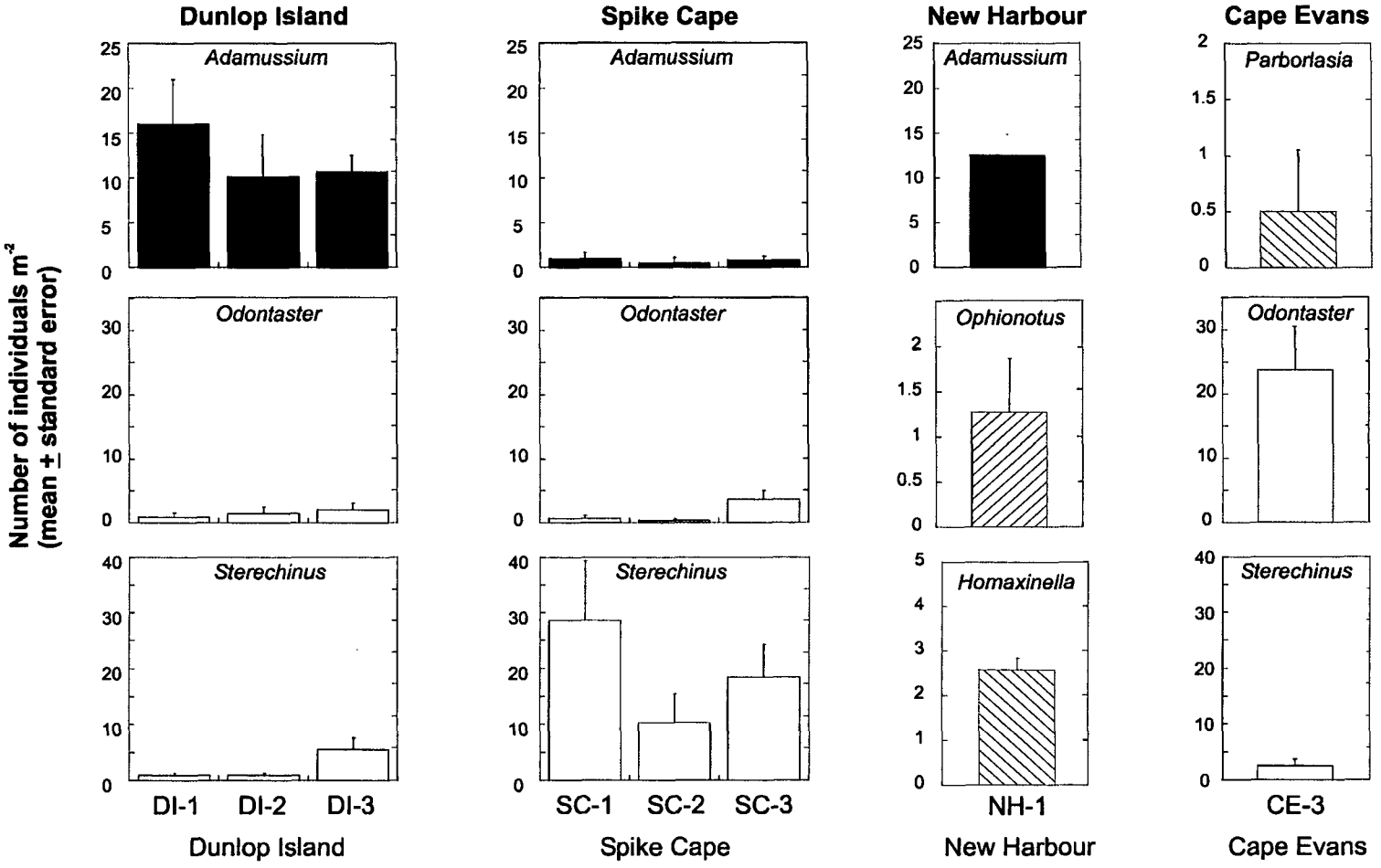

Figure 10. The abundance (mean ± s.e.) of the numerically dominant, large epibenthic taxa at Dunlop Island, Spike Cape, New Harbour and Cape Evans.

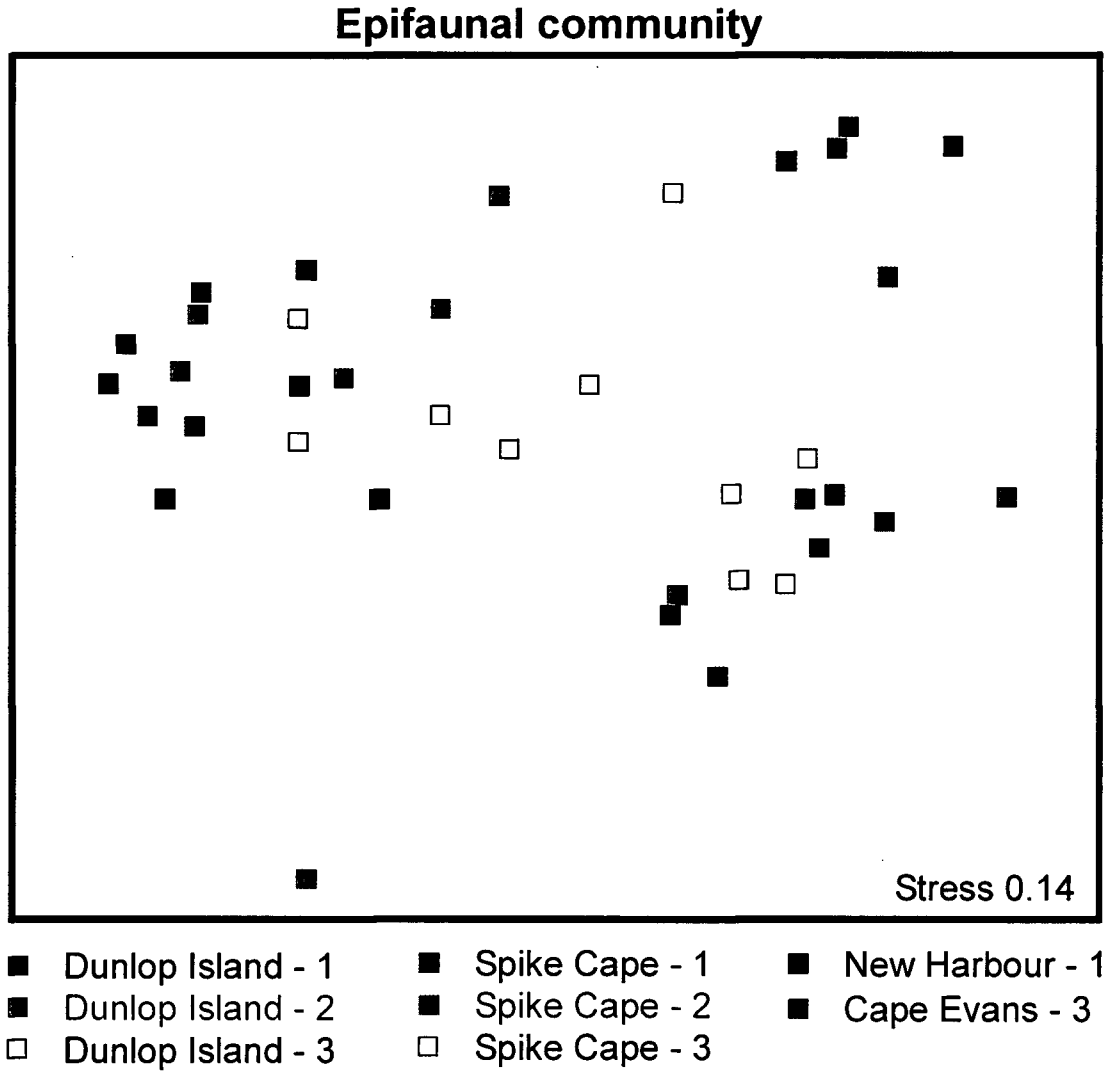

Figure 11. MDS ordination plot of the community composition of the large epibenthic taxa at each location. The axes have no labels as they have no meaning in absolute terms. Distances between sample points indicate the relative magnitude of differences in community composition.

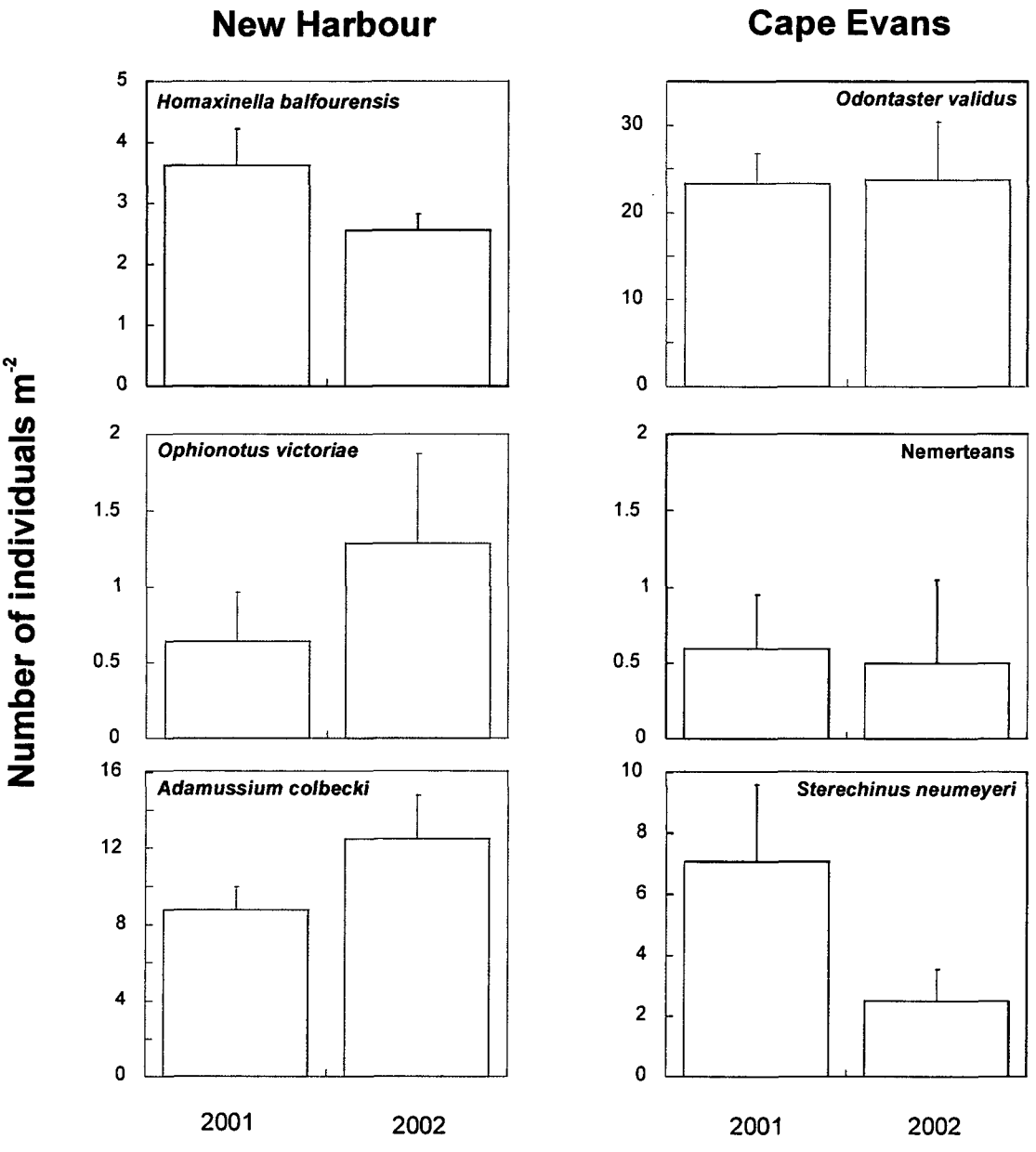

Figure 12. Comparison of abundances of common large epibenthic taxa (mean ± standard error) at New Harbour Site 1 and Cape Evans Site 3 in 2001 and 2002.

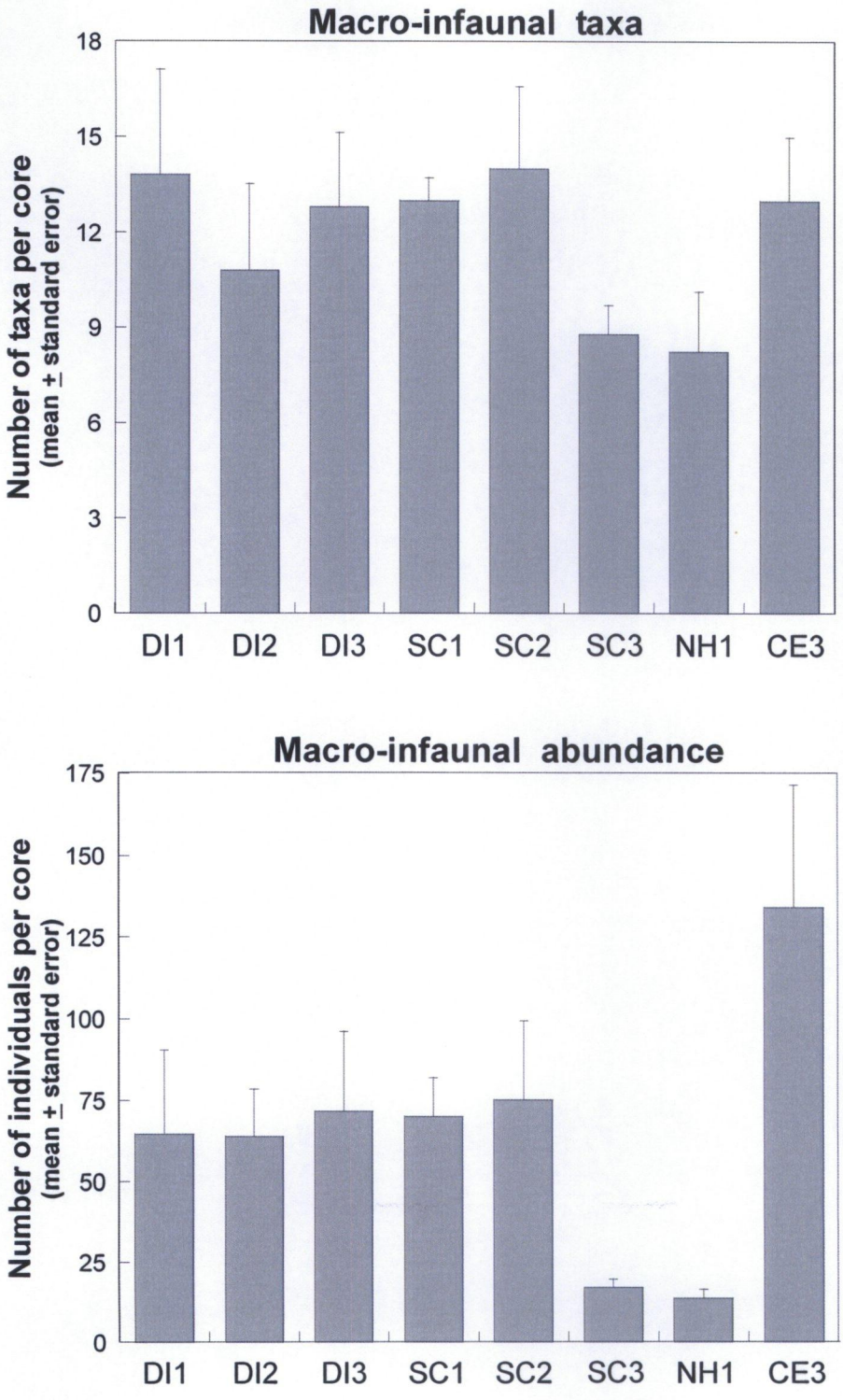

Figure 13. Number of taxa and individuals (mean ± s.e.) of macrofauna at the four locations. DI = Dunlop Island, SC = Spike Cape, NH = New Harbour, CE = Cape Evans.

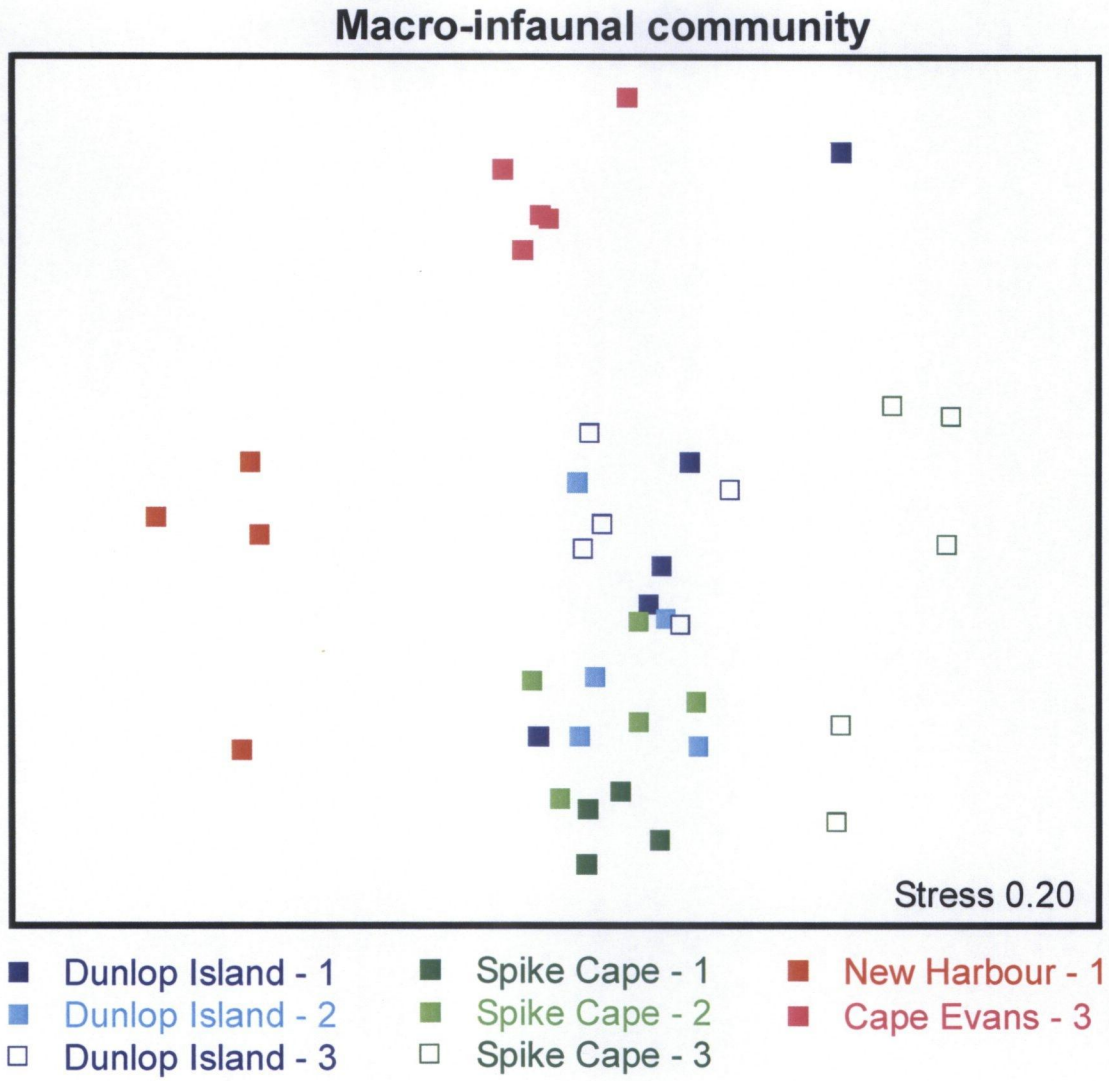

Figure 14. MDS ordination plot of macro-infaunal community composition at the four locations. The axes have no labels as they have no meaning in absolute terms. Distances between sample points indicate the relative magnitude of differences in fauna-habitat associations.

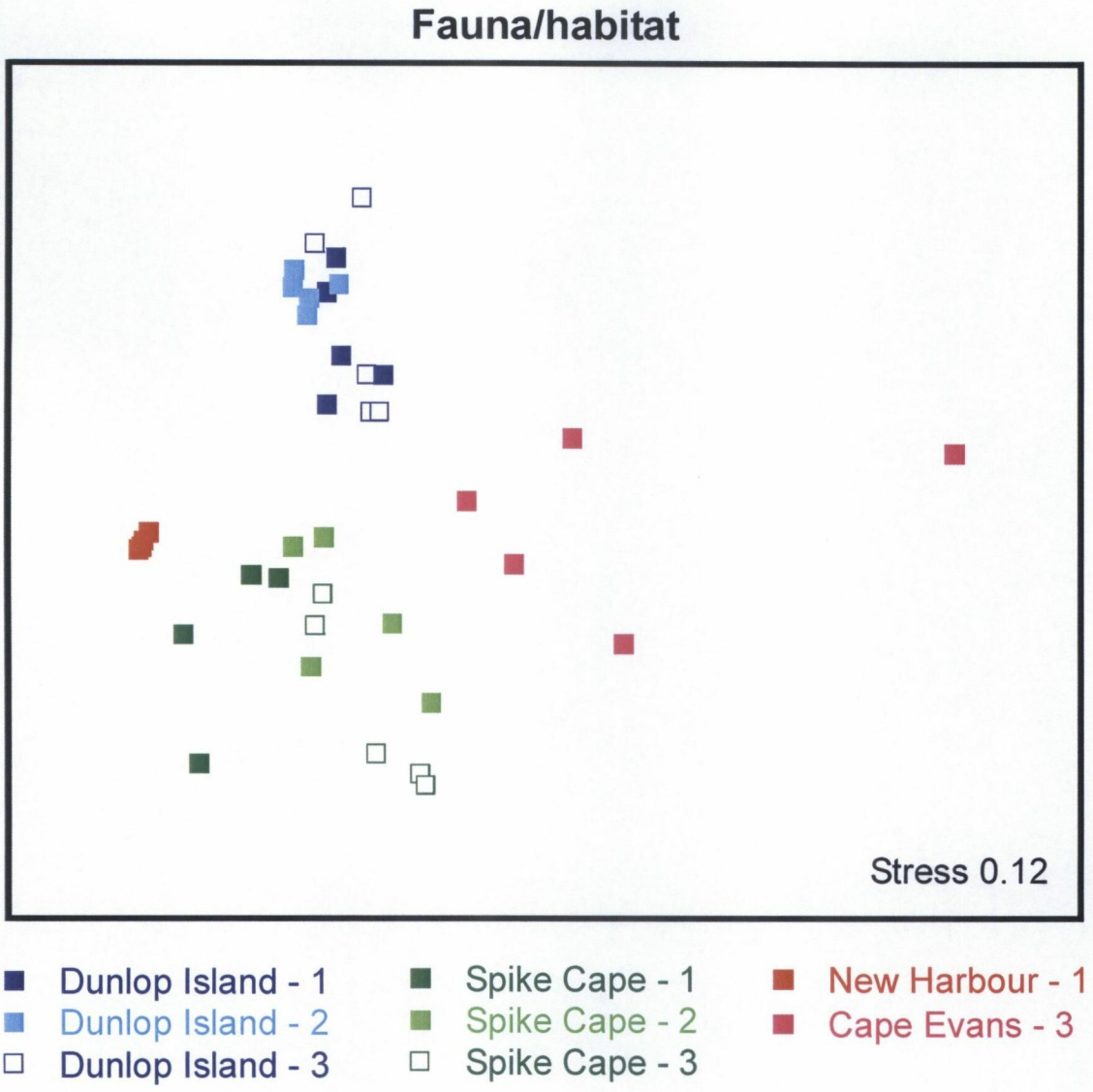

Figure 15. MDS ordination plot of large epibenthic taxa, macro infauna and habitat characteristics at the four locations (determined using Euclidian distances). The axes have no labels as they have no meaning in absolute terms. Distances between sample points indicate the relative magnitude of differences in fauna-habitat associations.

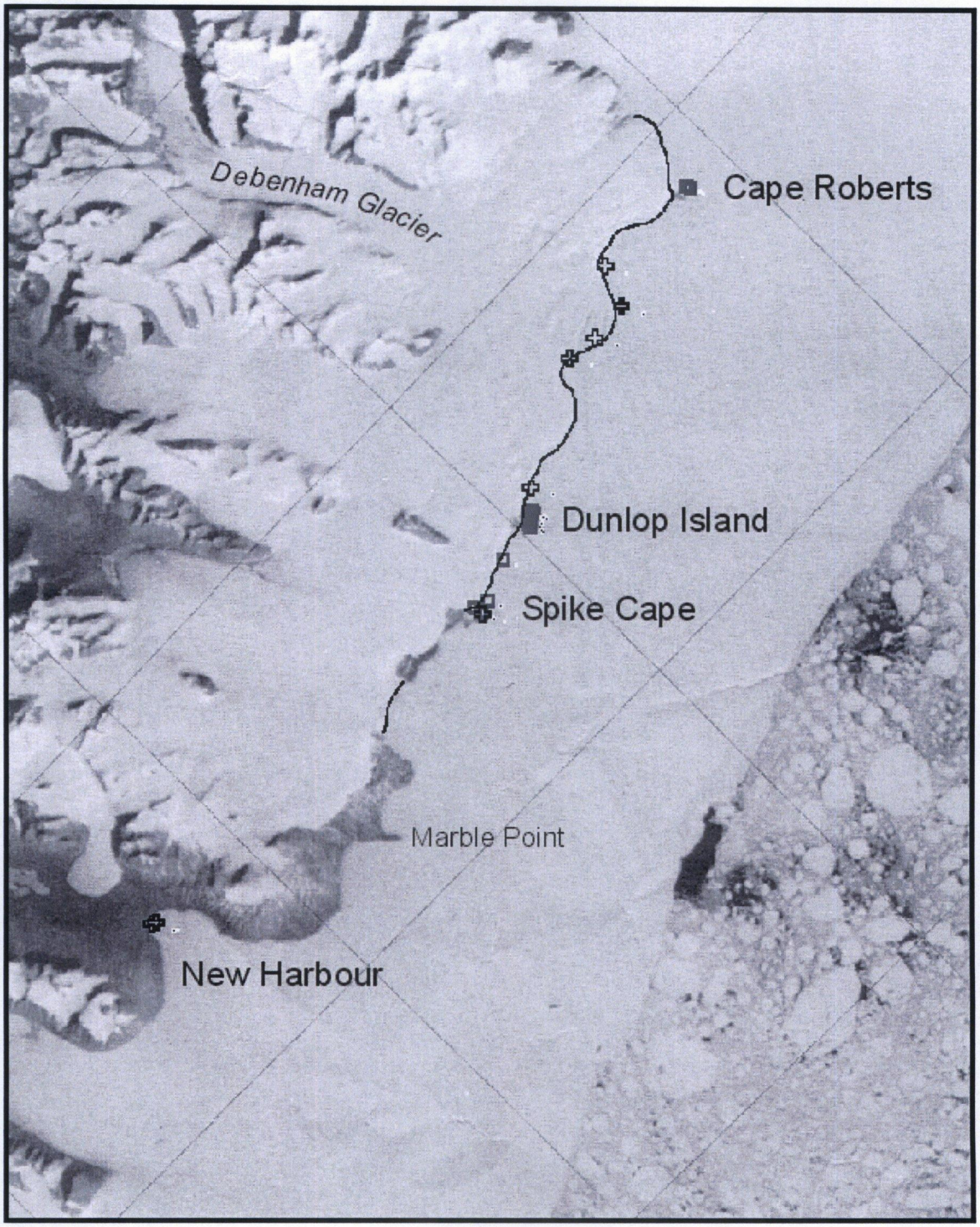

Figure 16. Map showing the location of the Remote Video sites. Squares indicate locations of Splash Cam sites, crosses indicate ROV sites.

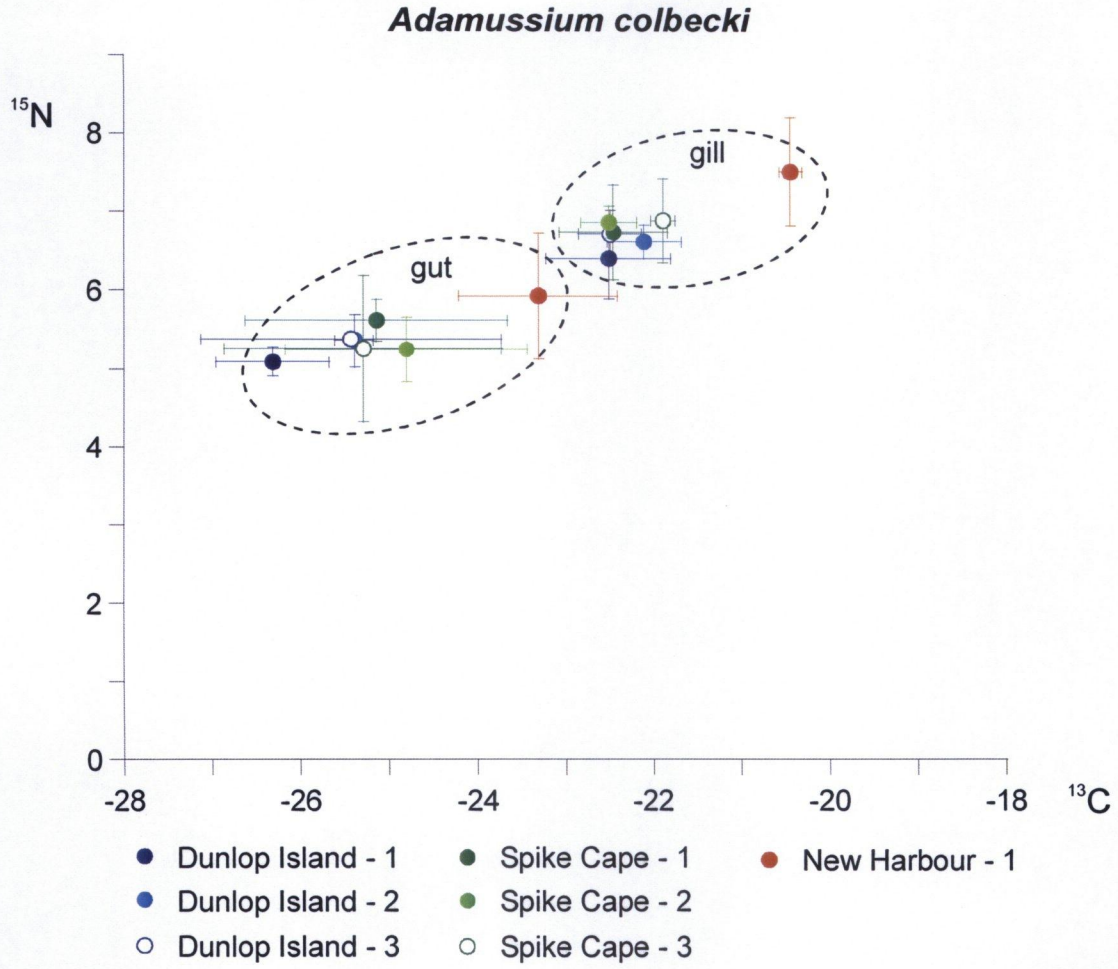

Figure 19. Mean isotopic (‰) distribution of the gut and gill of the Antarctic scallop, *Adamussium colbecki*, from the four locations. Error bars indicate the standard deviation of the data (n = 3 individuals per site/location).

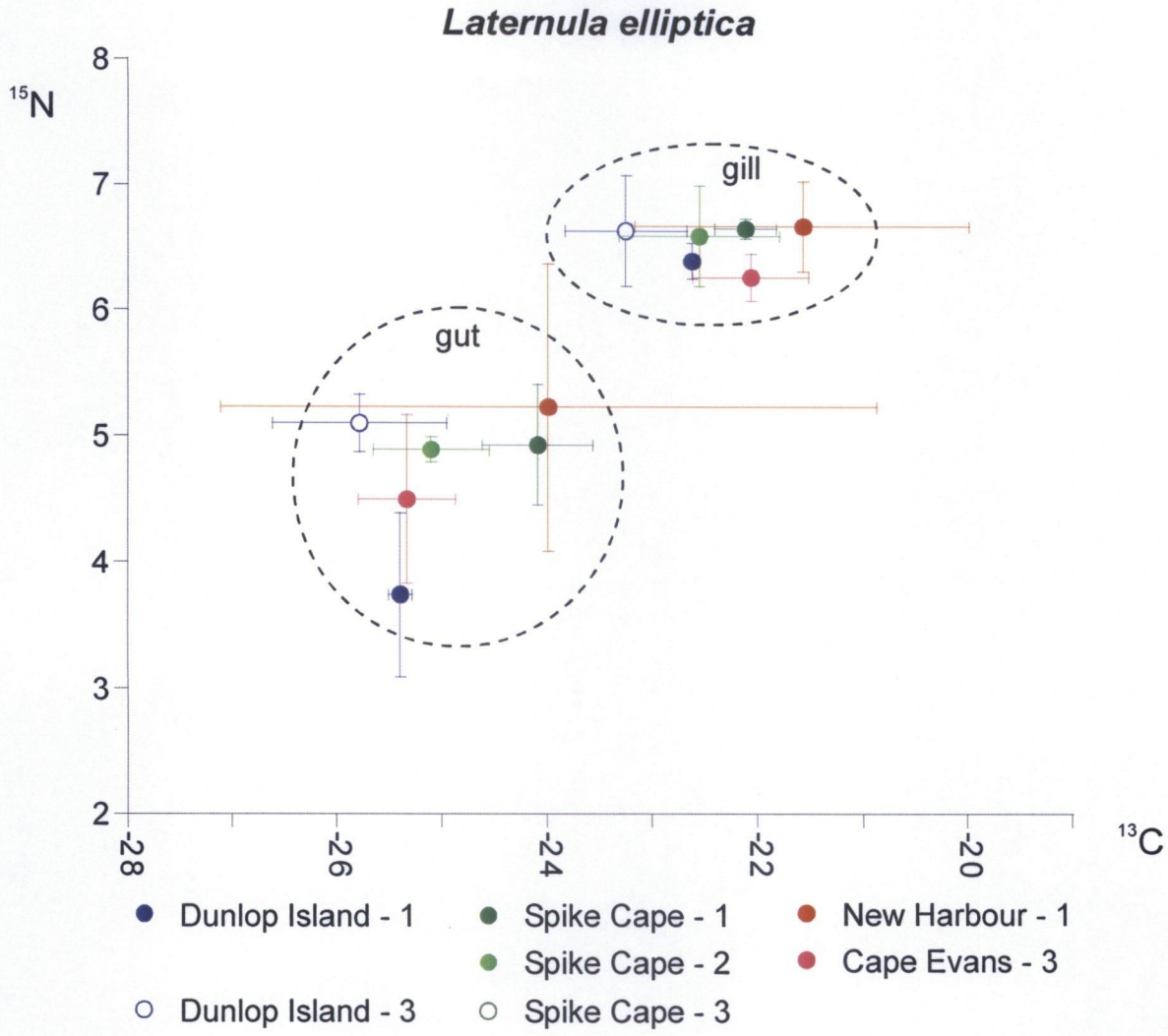

Figure 20. Mean isotopic (‰) distribution of the gut and gill of the Antarctic soft-shelled bivalve, *Laternula elliptica*, from the four locations. Error bars indicate the standard deviation of the data (n = 3 individuals per site/location).

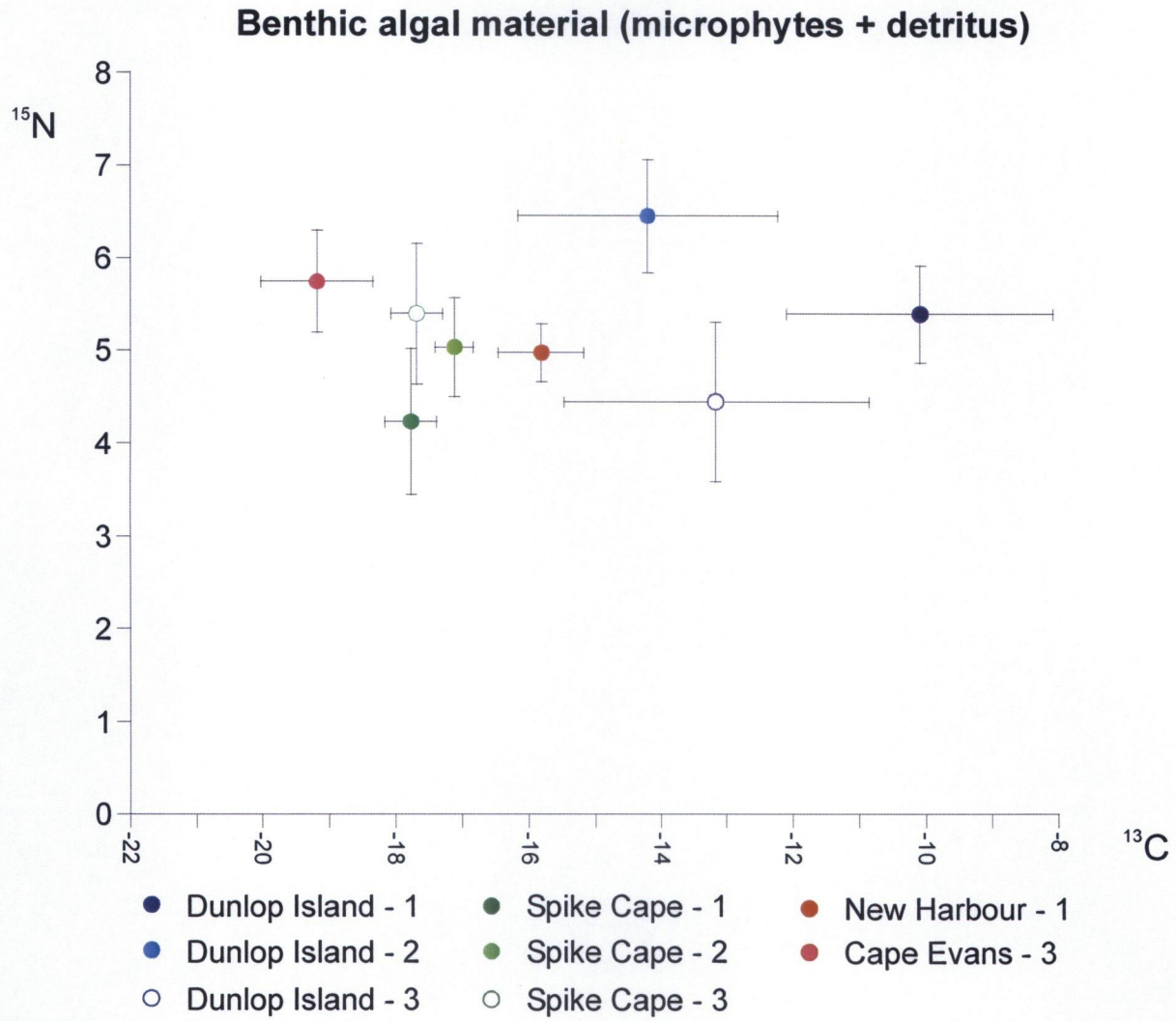

Figure 18. Mean isotopic (‰) distribution of the benthic algal material (microphytes and detritus) at each location. Error bars indicate the standard deviation of the data (n = 5 cores per site/location).

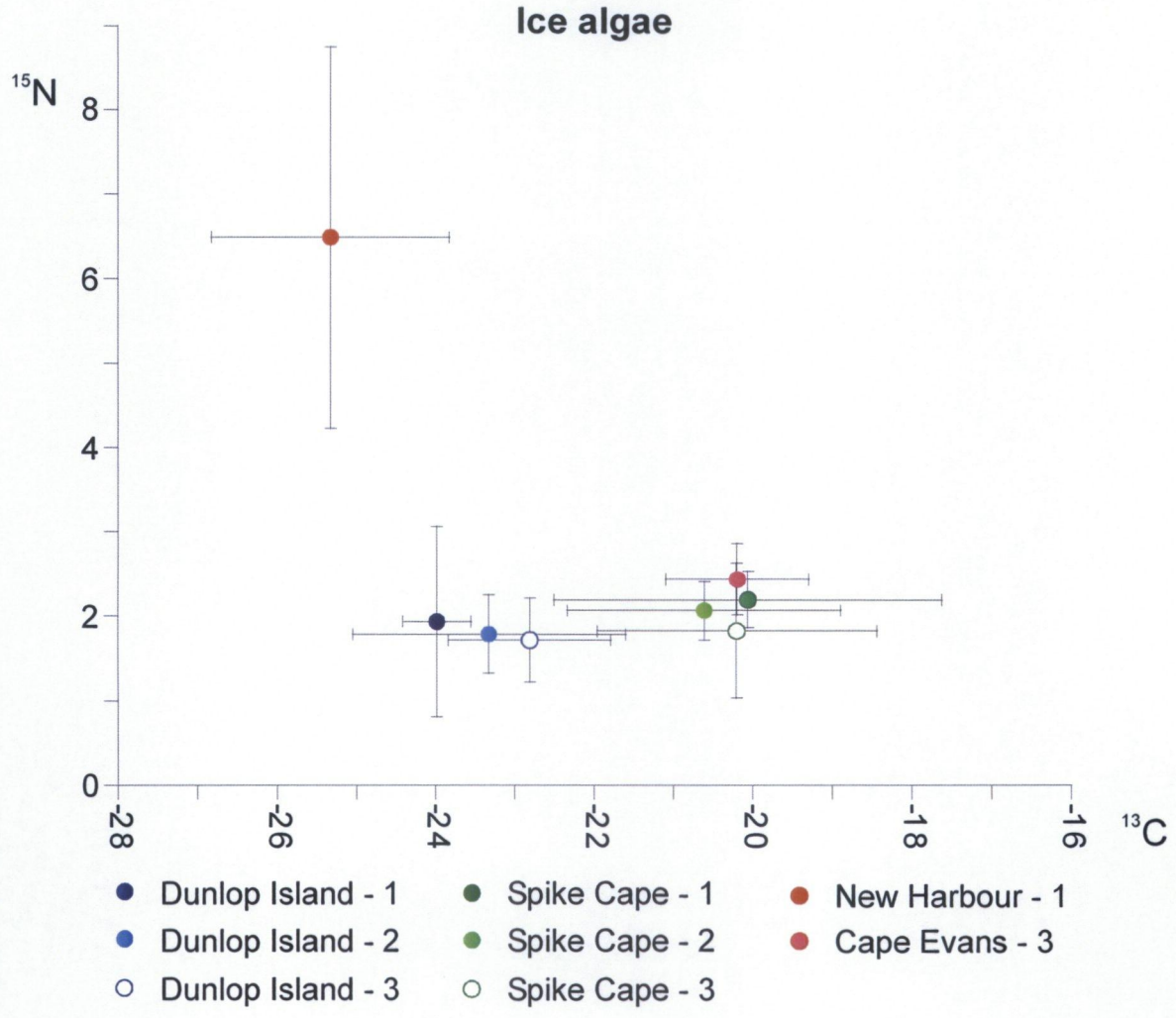

Figure 17. Mean isotopic (‰) distribution of the ice algae from the four locations. Error bars indicate the standard deviation of the data (n = 3 cores per site/location).

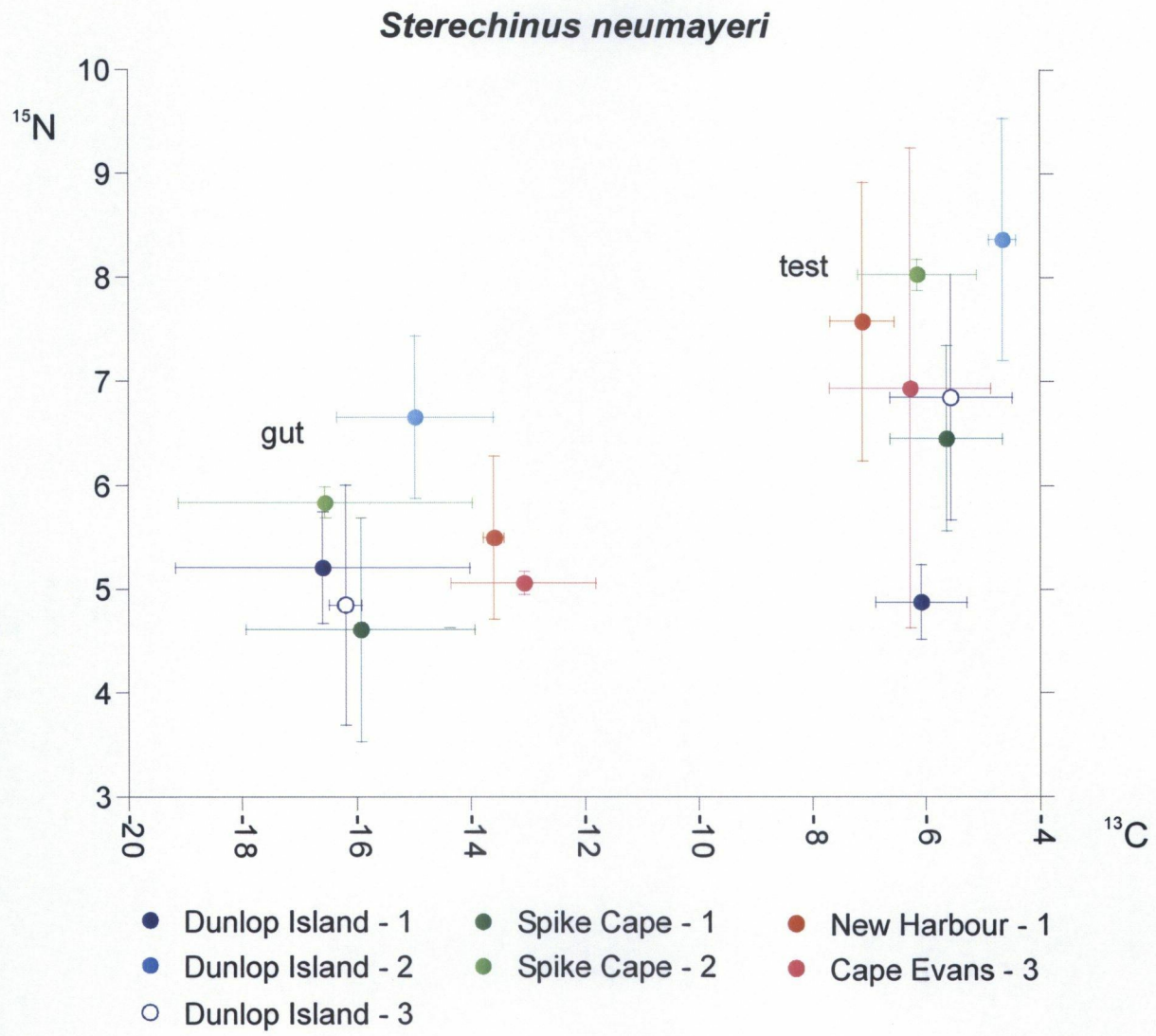

Figure 21. Mean isotopic (‰) distribution of the gut and test of the sea urchin, *Sterechinus neumayeri*, from the four locations. Error bars indicate the standard deviation of the data.

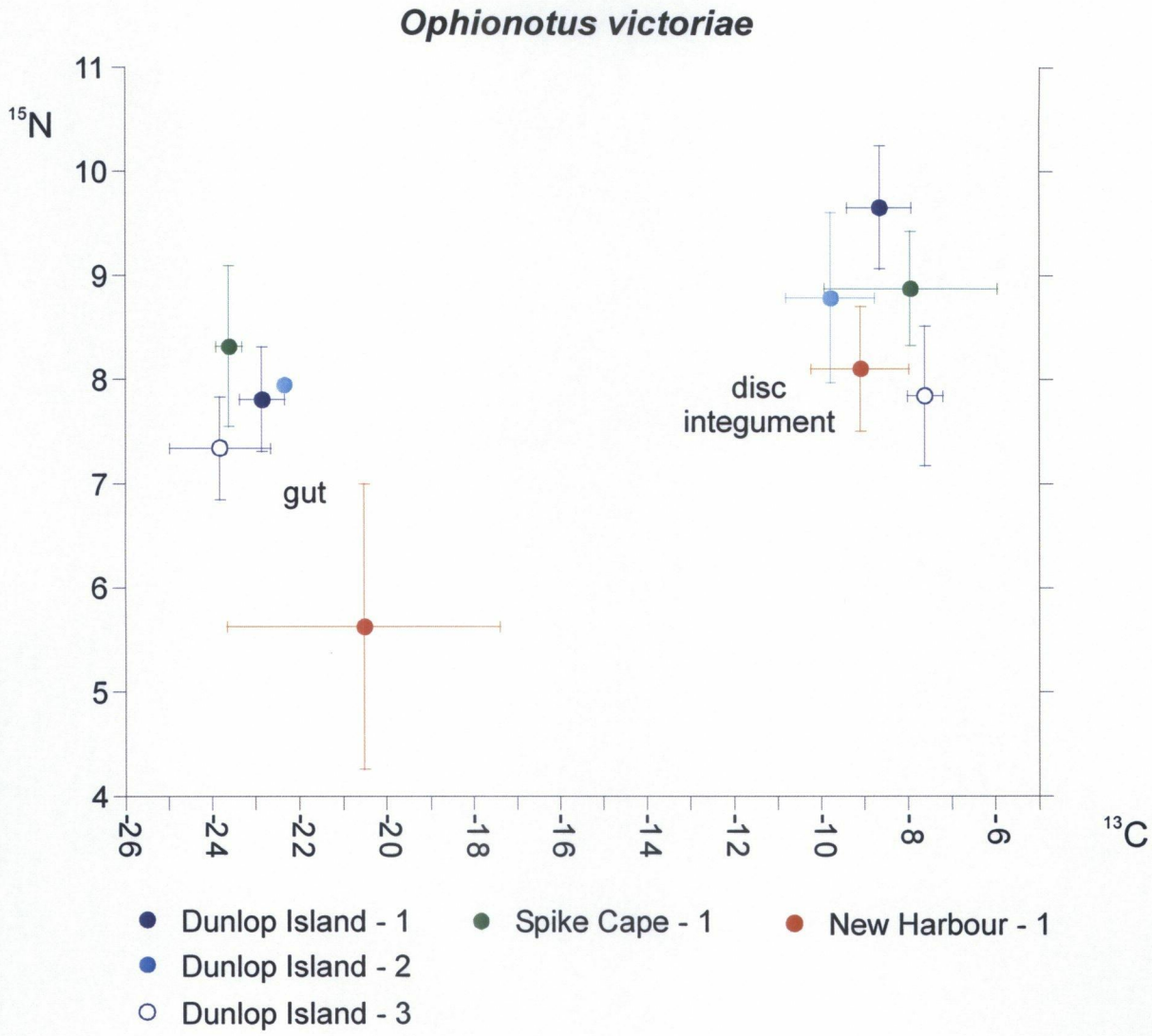

Figure 22. Mean isotopic (‰) distribution of the gut and disc integument of the ophiuroid, *Ophionotus victoriae*, from the four locations. Error bars indicate the standard deviation of the data.

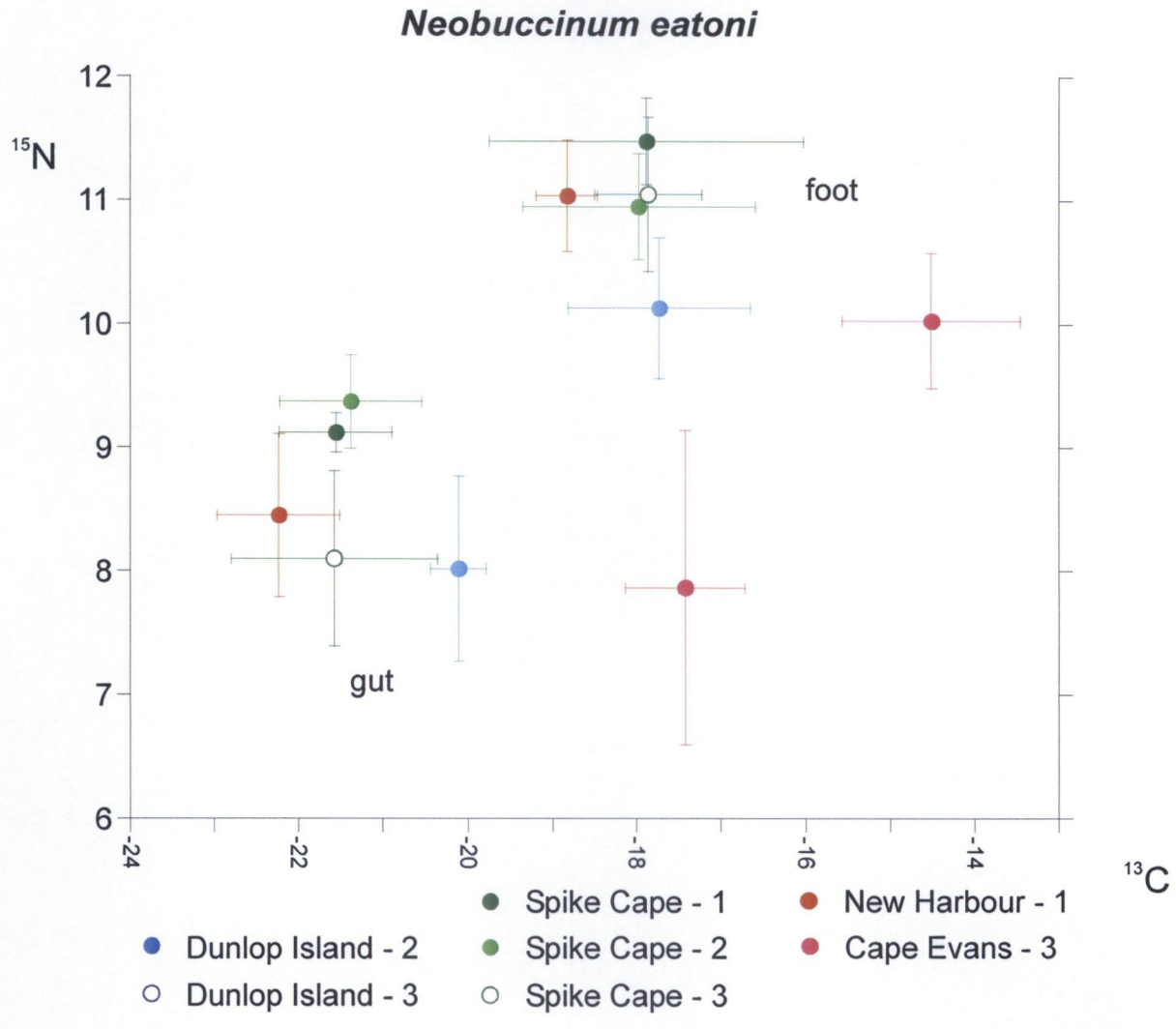

Figure 23. Mean isotopic (‰) distribution of the gut and foot of the gastropod, *Neobuccinum eatoni,* from the four locations. Error bars indicate the standard deviation of the data.

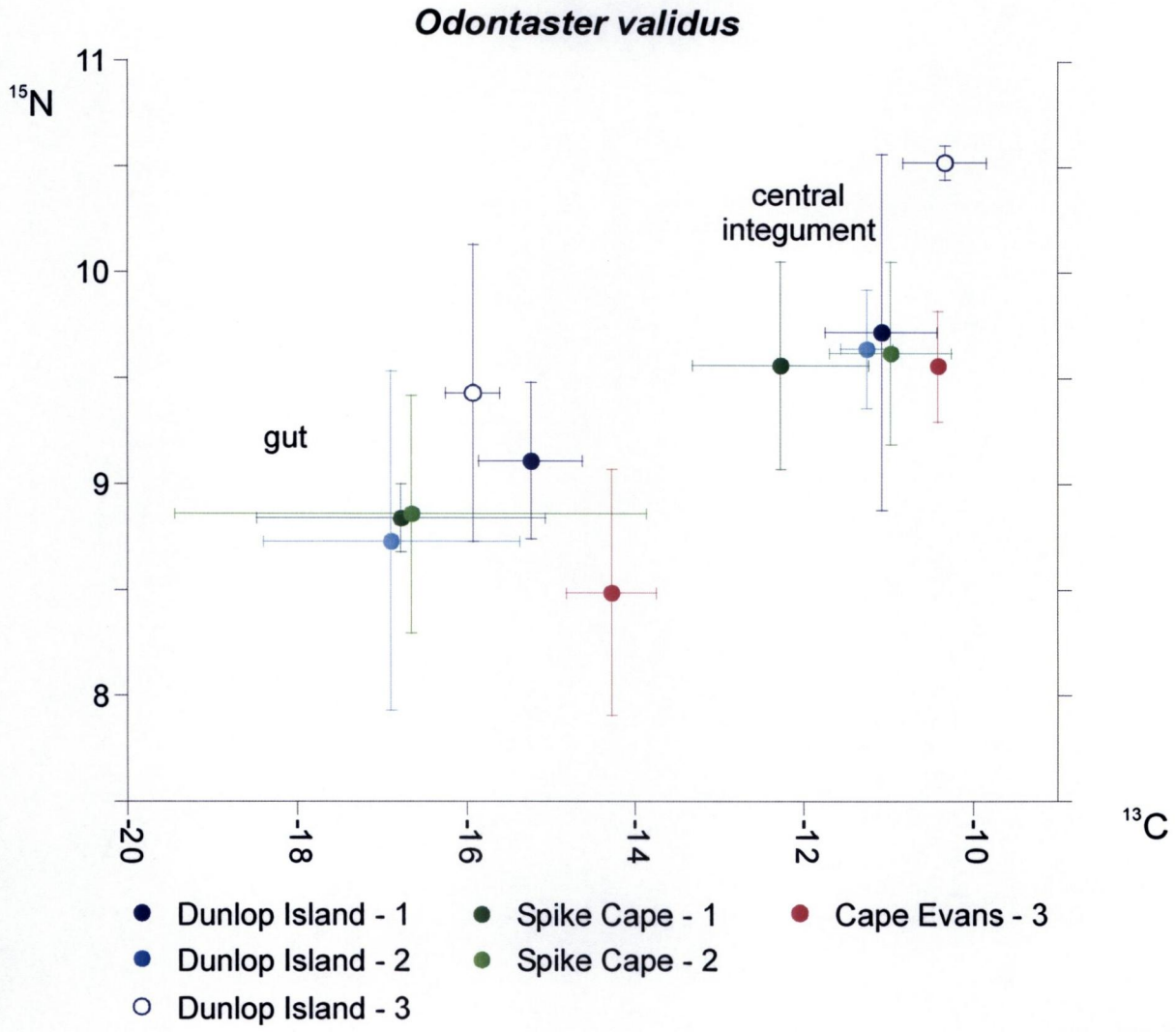

Figure 24. Mean isotopic (‰) distribution of the gut and central integument of the sea star, *Odontaster validus,* from the four locations. Error bars indicate the standard deviation of the data.

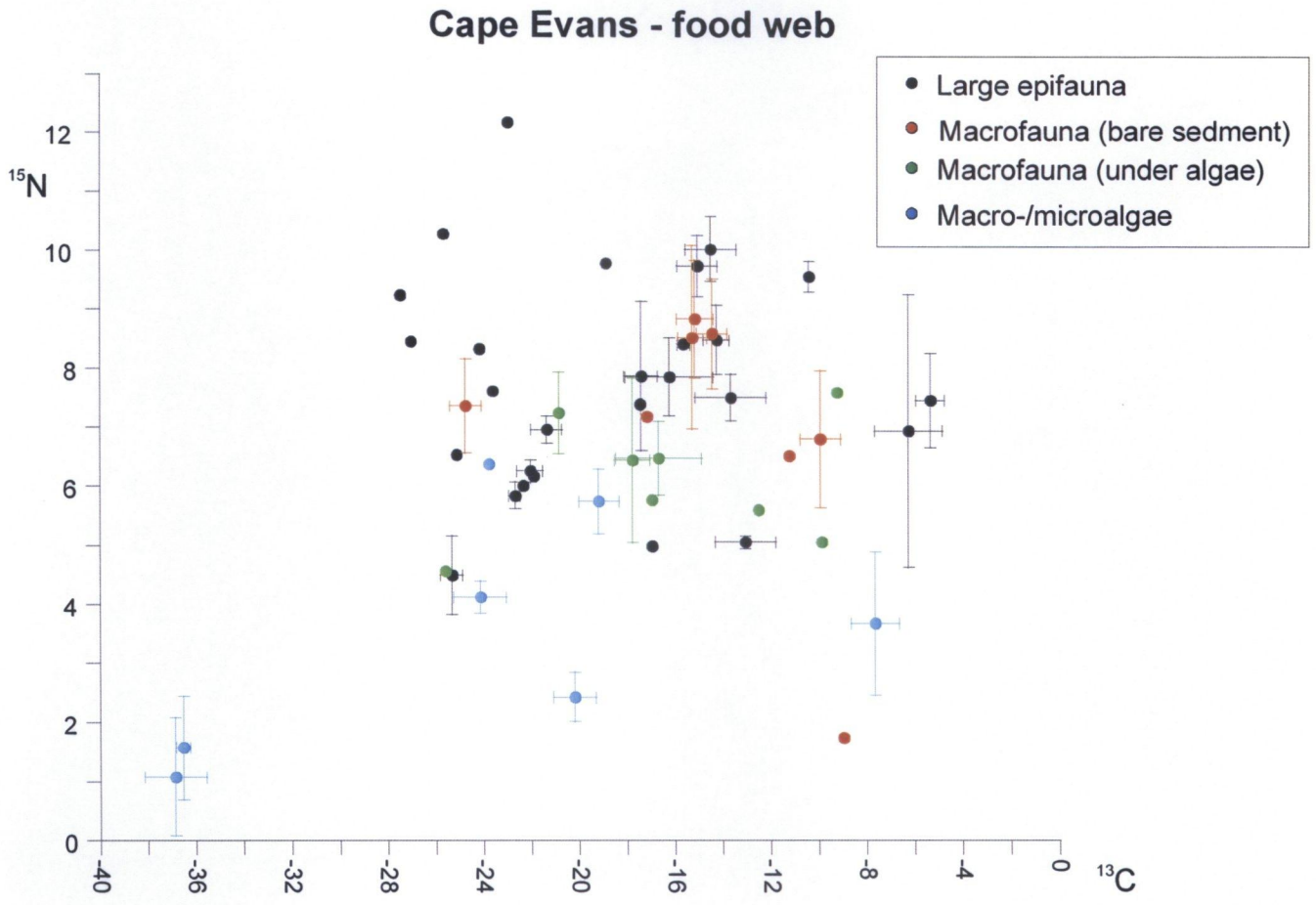

Figure 25. Mean isotopic (‰) distribution of a variety of flora and fauna at Cape Evans. Error bars indicate the standard deviation of the data. As it was not always possible to find replicate individuals of a particular epifaunal taxa, n = 0-3 individuals. For the macrofauna, individuals of several species (e.g., polychaetes) have sometimes been combined.

Appendix 1. A list of the large epifuanal taxa noted at each location in 2002. DI = Dunlop Island, SC = Spike Cape, NH = New Harbour, CE = Cape Evans. 'y' indicates taxa were present, 'n' indicates they were not.

		DI	SC	NH	CE
Kingdom: Animalia					
Phylum: Echinodermata					
Class: Echinoidea					
Order: Spatangoida					
Family: Schizasteridae	*Abatus shackletoni*	n	n	n	y
	Abatus nimrodi	n	n	y	n
Order: Echinoida					
Family: Echinidae	*Sterechinus neumayeri*	y	y	y	y
Subclass: Perischoechinoidea					
Order: Cidaroida	*Ctenocidaris perrieri*	n	n	y	n
Class: Stelleroidea	*Diplasterias brucei*	y	y	y	y
	Psilaster charcoti	y	y	y	y
	Stelleroidea type A	n	y	n	n
	Stelleroidea type B	n	y	n	n
Subclass: Asteroidea					
Order: Valvatida					
Family: Odontasteridae	*Odontaster validus*	y	y	y	y
	Odontaster ?meridonalis	n	n	y	n
Subclass: Ophiuroidea	Ophiuroidea type A	y	y	n	y
Order: Ophiurida	*Ophiosparte gigas*	n	n	y	n
Family: Ophiolepididae	*Ophionotis victoriae*	y	y	y	y
Class: Holothuroidea	Holothurian	n	n	n	y

Phylum: Cnidaria						
Class: Anthoza		Orange soft coral	y	y	n	y
		White soft coral	n	y	n	n
Order: Stolonifera						
Family: Clavulariidae		*Clavularia* sp.	y	y	n	n
Order: Alcyonacea						
Family: Alcyoniidae		*Alcyonium antarcticum*	y	n	n	n
Phylum: Arthropoda						
Class: Malacostraca						
Order: Isopoda		*Glyptonotus antarcticus*	n	n	n	y
Class: Pycnogonida		Pycnogonid	y	y	y	y
Phylum: Mollusca						
Class: Bivalvia						
Order: Pteroida						
Family: Pectinidae		*Adamussium colbecki*	y	y	y	n
Class: Gastropoda						
Order: Neogastropoda						
Family: Buccinidae		*Neobuccinum eatoni*	y	y	y	y
Order: Mesogastropoda						
Family: Lamellariidae		*Marseniopsis mollis*	n	n	n	y
Order: Neogastropoda						
Family: Muricidae		*Trophon longstaffi*	n	y	n	y
Order: Nudibranchia						

Family: Dorididae	*Austrodoris kerguelenensis*	n	n	y	n
Family: Dendronotidae	*Tritoniella belli*	y	y	n	n
Phylum: Nemertea					
Order: Heteronemertea	*Parborlasia corrugatus*	y	y	n	y
Phylum: Annelida					
Class: Polychaeta					
Subclass: Palpata					
Order: Terebellida					
Family: Flabelligeridae	*Flabelligera mundata*	n	y	y	y
Order: Sabellida					
Family: Sabellidae	Sabellid type A	n	y	n	n
Family: Surpulidae	Surpulid	y	n	n	n
Order: Spionida					
Family: Chaetopteridae	Chaetopteridae	n	n	y	n
Phylum: Porifera[4]	White sponge	n	y	y	n
	Sponge type-NH-N	n	n	y	n
	Sponge type-NH-M	n	n	y	n
	Sponge type-NH-Q	n	n	y	n
	Sponge type-NH-R	n	n	y	n
	Sponge type-NH-T	n	n	y	n
	Sponge type-NH-AA	n	n	y	n
Class: Calcarea					
Order: Leucettida					
Family: Leucettidae	?*Leucetta* sp.	n	y	n	n

[4] identifications of the sponges noted during our 2002 visit are being determined by Dr. Carlo Cerrano, Italian Antarctic Research Programme.

Class: Demospongiae						
Order: Axinellida						
Family: Axinellidae	*Homaxinella balfourensis*	y	y	y	n
Phylum: Bryozoa	Bryozoan	y	n	n	n
Kingdom: Protocista					
Phylum: Rhodophyta					
Class: Phodophyceae					
Order: Gigartinales					
Family: Gigartinaceae	*Iridaea cordata*	y	n	n	n
Family: Phyllophoraceae	*Phyllophora antarctica*	y	n	n	y
Order: Cryptonemiales					
Family: Corallinaceae	*Phymatolithon foecundum*	n	y	n	y

Appendix 2. A list of the macro-infaunal taxa noted at each location in 2002. DI = Dunlop Island, SC = Spike Cape, NH = New Harbour, CE = Cape Evans. 'y' indicates taxa were present, 'n' indicates they were not.

		DI	SC	NH	CE
Kingdom: Animalia					
Phylum: Annelida					
Class: Oligochaeta	Oligochaeta	y	y	n	y
Class: Polychaeta					
Order: Eunicida					
Order: Dorvilleidae	Dorvillidae	n	y	n	n
Order: Eunicidae	Eunicidae	n	y	n	n
Order: Lumbrineriedae	Lumbrineridae	y	n	y	n
Order: Phyllodocida					
Family: Hesionidae	*Syllidia inermis*	y	y	n	y
Family: Nephtyidae	*Aglaophamus* sp.	y	y	y	n
Family: Polynoidae	*Barrukia cristata*	y	n	n	y
	Harmothoe sp.	n	y	n	n
	Lepidonotidae	y	y	n	y
Family: Syllidae	Exogond	n	y	n	n
Order: Sabellida					
Family: Oweniidae	Oweniidae	n	n	y	n
Family: Sabellidae	Sabellidae	n	n	y	n
	Euchone sp.	n	n	y	n
Order: Spionida					
Family: Cirratulidae	Cirratulidae type A	y	y	n	y

	Cirratulidae type B	n	n	y	n
Family: Spionidae	*Laonice* sp.	y	y	n	n
	Laonice weddellia	y	n	n	n
	Scolelepis sp.	y	y	n	n
	Spiophanes tcherniai	y	y	n	y
Order: Telebellida					
Family: Ampharetidae	Ampharetidae type A	y	n	n	n
	Ampharetidae type B	y	n	y	n
	Anobothrus sp.	n	y	y	n
Family: Terebellidae	Terebellidae type A	y	n	n	n
	Polycirrinae (Subfamily)	y	n	n	n
	Terebellinae (Subfamily)	y	n	n	n
Order: Scolecida					
Family: Maldanidae	Maldanidae	n	y	n	n
	Maldane sp.	n	n	y	y
	?*Nicomache* sp.	n	y	n	n
Family: Opheliidae	Opheliidae	y	y	n	n
	Ophelina sp.	y	y	n	n
Family: Orbiniidae	*Haploscoloplos* sp.	y	y	y	n
Family: Paraonidae	Paraonidae type A	n	n	y	n
	Paraonidae type B	n	n	y	n
	Aricidea sp.	n	n	y	n
Phylum: Arthropoda					
Class: Malacostraca					
Order: Amphipoda	Amphipoda type A	y	n	n	n

Family: Aoridae	*Kuphocheira* n.sp.	n	n	y	n
Family: Eusiridae	?*Oradarea* sp.	y	y	n	n
Family: Lysianassidae	*Orchomenella franklini*[i]	y	n	n	y
Family: Phoxocephalidae	*Heterophoxus videns*[ii]	y	y	n	y
Order: Cumacea	*Eudorella* sp.	y	y	y	n
Order: Tanaidacea					
Family: Nototanaidae	*?Nototanais* sp.	y	y	y	y
Order: Isopoda					
Suborder: Asellota					
Family: Microparasellidae	Microparasellidae	n	n	n	y
Family: Janiridae	*Austrofilius* sp.[iii]	n	n	n	y
Family: Paramunnidae	*Paramunna ?rostrata*[iv]	n	n	n	y
	Paramunna glacialis[v]	n	y	n	y
Family: Paramunnidae	*Austrosignum grande*	y	y	n	y
Class: Maxillopoda					
Subclass: Ostracoda					
Order: Myodocopida	Myodocopids	y	n	n	y
Order: Podocopida	Podocopids	y	y	n	y
Class: Pycnogonida	Pycnogonida	n	n	y	n
Phylum: Cnidaria					
Class: Anthozoa					
Order: Actinaria					

	Family: Edwardsiidae	*Edwardsia* sp.	y	n	y	y
Phylum: Echinodermata						
Class: Echinoidea		Echinoidea	n	n	n	y
Phylum: Mollusca						
Class: Bivalvia						
Order: Veneroida						
	Family: Thyasiridae	*Genaxinus debilis*	n	n	y	n
Order: Nuculoida						
	Family: Nuculanidae	*Yoldia eightsi*	y	y	n	n
	Family: Nuculidae	*Nucula* sp.	y	y	n	n
Order: Pholadomyoida						
	Family: Laternulidae	*Laternula elliptica*	y	y	y	y
Class: Gastropoda						
Order: Neogastropoda						
	Family: Muricidae	*Trophon longstaffi*	n	n	n	y
Order: Archaeogastropoda						
	Family: Trochidae	*Margarites crebriliratula*	y	y	n	n
Order: Mesogastropoda						
	Family: Rissoidae	*Onoba turquetti*	y	y	n	y
		Onoba gelida	y	y	n	y
	Family: Eatoniellidae	*Skenella paludinoides*	y	y	n	n
Phylum: Nemertea		Nemertea	y	y	n	n
Phylum: Nematoda		?Nematoda type A	y	y	n	y

	Nematoda type B	y	y	y	y
Kingdom: Protoctista					
Phylum: Granuloreticulosa					
Class: Foraminifera					
Order: Foraminiferida	Foraminifera	y	y	y	n

[i] 'Lysianassids' in Norkko et al. 2002.
[ii] 'Phoxocephalids' in Norkko et al. 2002.
[iii] 'Stenetriidae type A' in Norkko et al. 2002.
[iv] 'Stenetriidae type C' in Norkko et al. 2002.
[v] 'Stenetriidae type D' in Norkko et al. 2002.

Appendix 3.

Draft manuscript

Ecological role of *Phyllophora antarctica* drift accumulations in coastal soft-sediment communities of McMurdo Sound, Antarctica

Alf Norkko[1*], Simon F. Thrush[1], Vonda J. Cummings[1], Greig A. Funnell[1], Anne-Maree Schwarz[1], Neil L. Andrew[2] & Ian Hawes[1]

[1]National Institute of Water and Atmospheric Research
P.O. Box 11-115
Hamilton
New Zealand

[2]National Institute of Water and Atmospheric Research
P.O. Box 14-901
Wellington
New Zealand

*Present address:

Department of Marine Ecology
Göteborg University
Kristineberg Marine Research Station
S-450 34 Fiskebäckskil
Sweden

E-mail: alf.norkko@kmf.gu.se
Fax: +46 523 18502

Abstract

The diversity and magnitude of primary production is a key variable sustaining coastal food webs. At Cape Evans on Ross Island, Antarctica, the rhodophyte *Phyllophora antarctica* is the dominant primary producer in terms of biomass from 10 to >30 m depth. The vast majority of the biomass occurs as drifting accumulations. Whilst decomposition and incorporation of macroalgal drift material into the food web is rapid in temperate ecosystems, these processes are predicted to be slow in Antarctica. We address the functional role of macroalgal detritus in fuelling the biodiversity of benthic communities at Cape Evans during the summers of 2001 and 2002. Specifically we (a) describe the distribution and biomass of attached and drift algae, (b) assess the photosynthetic capacity and degradation of drift accumulations using in situ fluorometry (c) assess the structuring effect of patches of drift *Phyllophora* on underlying macrofaunal communities, and, (d) investigate the possible uptake by macrofauna using stable isotopes.

Introduction

Macroalgae play an important role in marine primary production and trophic dynamics. It is well established that macroalgae serve as an important food source for many grazers (Dayton 1985, Andrew 1993, Toth and Pavia 2002) with cascading effects on the structure and function of coastal food webs (Duggins et al. 1989, Tegner & Dayton 1991). Generally, only about 10% of the production is consumed directly by grazers, while 90% enters detrital food webs as particulate and dissolved organic matter (Pomeroy 1980, Mann 1982). The importance of allochtonous macroalgal detritus in fuelling higher trophic levels has been acknowledged for terrestrial (Polis & Hurd 1996) as well as marine coastal (Bustamente et al. 1995, Vetter 1995, Duggins & Eckman 1997), continental shelf (Vetter and Dayton 1998, 1999) and deep-sea habitats (Snelgrove et al. 1996). The fragmentation and bacterial degradation facilitates the ageing process, making drifting macroalgae more readily available to detritivores (Newell et al. 1982, Duggins & Eckman 1997). While some of the highest rates of benthic secondary production have been found associated with accumulations of drift algae (Vetter 1995), accumulations undergoing anaerobic degradation have also been shown to have a profound negative influence on underlying macrobenthic communities (Thrush 1986 a, b, Norkko & Bonsdorff 1996 a, b)

In Antarctic coastal ecosystems the input of primary production to benthic communities pulsed due to seasonal variations in sea-ice cover and light regime (Dayton et al. 1986, Clarke 1988, Arntz et al. 1994). At lower latitudes, along the Antarctic Peninsula, the subantarctic islands, and the Ross Sea, macroalgae have been shown to play an important trophic role by providing habitats for benthic macrofaunal communities (Klöser et al. 1996, Cattaneo-Vietti et al. 2000, Gambi et al. 2000, Cormaci et al. 1998) and macroalgal detritus has been shown to be important to coastal food webs (Reichardt & Dieckmann 1985, Fischer & Wiencke 1992, Kaehler et al. 2000, Dunton 2001). McMurdo Sound in the Ross Sea is the world's most southerly marine ecosystem (77-78°S) not permanently covered by thick glacial ice and it is here that the southernmost benthic macroalgae occur (Hodgson 1907, Zaneveld 1966, Dayton 1990, Miller & Pearse 1991). While the productivity of high latitude Antarctic benthic communities is thought to be primarily driven by the *in situ* production of benthic microalgae, sea ice algae and the lateral advection of phytoplankton (Dayton et al. 1986), the trophic role of decomposing macroalgae transferred through the detrital food web may also be significant, especially in areas with large biomasses of macrophytes (Dayton et al. 1986, Dayton 1990, Dunton 2001). However, especially at high Antarctic latitudes, information about the fate of primary production by macroalgae and the trophic relationship between macroalgal detritus and benthic macrofauna is lacking.

At Cape Evans on Ross Island in McMurdo Sound, three species of macroalgae have been recorded, the rhodophytes *Phyllophora antarctica* and *Iridea cordata* and the crustose coralline *Phymatolithon foecundum* (Miller & Pearse 1991, Schwarz et al. in press). *Phyllophora* is the dominant benthic primary producer in terms of biomass from 10 to >30 m depth. While a small proportion of the population grows attached, the vast majority of the biomass occurs as drift accumulations (Miller & Pearse 1991). Dayton (1990) describes occurrences of *Phyllophora* drift accumulations to depths of 60 m at Cape Evans. It is likely that anchor ice is responsible for the great amount of drift algal material as the ice forms on the bottom and detaches attached algae (Dayton et al. 1969, Amsler et al. 1998). Whilst decomposition and incorporation of macroalgal drift material into the detrital food web is rapid in temperate ecosystems, these processes are predicted to be slower in cold Antarctic waters. Previous experimental work has shown that *Phyllophora* is chemically defended and unpalatable to large epibenthic grazers such as the Antarctic sea urchin *Sterechinus neumayeri* (McClintock & Baker 1995, Amsler et al 1999) and a recent study conducted at Cape Evans demonstrates that *Phyllophora* further exhibit extreme shade adaptation and low respiration rates as a strategy to survive in this extreme environment with low irradiance levels (Schwarz et al in press). Schwarz et al. showed that it was only during a brief two-month ice-free period that irradiance levels exceeded compensation, enabling growth. However, despite extreme shade adaptation, low respiration rates and cold waters, we would still predict ongoing decomposition and the incorporation of *Phyllophora* drift accumulations into the detrital food web.

In this paper we address the functional role of macroalgal detritus in fuelling the biodiversity of high latitude Antarctic benthic communities. We present results from a study designed to examine the role of *Phyllophora* in structuring macrofaunal communities at Cape Evans during the austral summers of 2001 and 2002. Specifically we (a) describe and quantify the distribution and biomass of attached and drift algae, (b) assess the photosynthetic capacity (health) and extent of degradation of drift accumulations using *in situ* fluorometry, (c) assess the direct structuring effect of patches of drift *Phyllophora* on underlying macrofaunal communities, and, (d) investigate the possible nutrient enrichment of sediments and uptake by macrofauna using stable isotope techniques.

Materials and Methods

Study site

The study was conducted in November 2001 and November 2002 at Backdoor Bay, Cape Evans, Ross Island, McMurdo Sound, Antarctica (77° 38.1 S, 166° 24.9 E; Fig. 1). It is the site of Scott's 1910-1913 Terra Nova Expedition hut and in close proximity to the Barne Glacier. The geology is volcanic, dominated by moderately sloping boulder and cobble fields interspersed with gravel and sand. Sea ice varies in thickness from 1.5 to 2.5 m and it is common for the ice to break up annually in summer. Epifaunal communities are numerically dominated by the sea urchin *Sterechinus neumayeri*, the sea star *Odontaster validus* and the large nemertean *Parborlasia corrugatus*. During the study period water temperature was constant at –1.9°C. Tides in McMurdo Sound are diurnal with only one high and low tide every 24 hours (Goring & Pyne 2003); the study site at Cape Evans is quiescent, with current velocities averaging 3.5 cm s^{-1} (maximum:7 cm s^{-1}) four metres above the seafloor (Norkko et al. 2002). In 2001 the thick sea ice (2 m) filtered most of the light and only transmitted about 0.2% of the incident irradiance. Sea ice conditions were similar in 2002 (ca. 2 m thick), but with more snow drift cover. While light measurements were not made in 2002, under ice conditions were notably darker in comparison to 2001 (personal obs.). Three dive holes, each separated by approximately 50 m, were drilled through the ice. The holes were positioned over water depths from 19 to 21 m, and provided divers access to a wide depth range (2.8 – 31 m). Conditions at Cape Evans were similar to those described by Dayton et al. (1986).

Distribution and biomass of *Phyllophora*

Our first objective was to determine the depth distribution and biomass of drift *Phyllophora* accumulations at the site. This was done in 2001 only. Both attached and drift algal biomass was quantified using a 0.25 m^2 quadrat. A total of 61 quadrats were sampled along the 2.8 – 31 m depth-gradient using a stratified random sampling design. Depth was stratified into < 15 m, 15-25 m and > 25 m, with 25, 27 and 9 quadrats collected from each strata respectively. Dayton (1990) reports observations of large accumulations of *Phyllophora* at depths down to 60 m at Cape Evans. All algal material was cleaned of epifauna and epiphytes and then dried at 60°C to constant weight.

Ecological role of *Phyllophora*

As the greatest biomass of drift algal material was found at the 15 - 25 m depth strata, we concentrated our studies on the ecological role of *Phyllophora* here. At 20 m depth at each of the three dive holes, habitat structure and percent cover of *Phyllophora* was quantified from video-footage obtained along five 20 m transects. Fifteen digital frame grabs, each corresponding to an area of 1.3 m^2, were obtained from each transect and physical habitat structure was characterised 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 contained within each frame grab. Habitat categories were chosen from a list compiled after preliminary examination of the video footage and three major categories were determined: "crustose/bare rock", "*Phyllophora*" and, "coarse sediment with detritus". Habitats were quantified in 2001 only.

Photosynthetic capacity of drift algal accumulations

In order investigate the possible state of degradation of the *Phyllophora* drift accumulations we measured photosynthetic capacity (fluorescence yield) as a proxy for physiological health. This was done *in situ* using a diver operated submersible Pulse Amplitude Modulated (PAM) fluorometer (Diving-PAM, Walz). The principle measurement made using the Diving-PAM was the effective quantum yield (Y) of photosystem II (PS II), which can be used to investigate photosynthetic activity (Schreiber et al. 1986). We used the ratio of variable fluorescence to maximum fluorescence (F_v/F_m) as a parameter for physiological health. The F_v/F_m ratio is normally at its highest in non-inhibited material under dark acclimated conditions, when it represents the maximum quantum yield which, for healthy angiosperms, is typically close to 0.8 (Schreiber et al., 1986; Büchel and Wilhelm 1993). While F_v/F_m reflects the maximum quantum yield, $\Delta F/F_m'$ reflects the effective quantum yield (Y) of the plant under prevailing irradiance condition (Hanelt et al., 1992), there is strong evidence to suggest that yields measured using fluorescence techniques

accurately reflect the photosynthetic performance of plants (Hanelt et al., 1995, Beer and Björk, 2000; Beer et al., 2000).

Patches of drift algae were found settled in depressions and between rocks and they ranged in diameter from a few decimetres to metres. In November 2001 we haphazardly sampled a total of seven different patches of drift *Phyllophora* accumulations using PAM at 15 - 19 m depth. We sampled five replicate *Phyllophora* fronds from the top and the bottom of each accumulation, respectively. Fluorescence measurements of attached plants were also made, to provide a background (control) of the photosynthetic activity of healthy *Phyllophora*. Each measurement was made at a standard distance of 5 mm from the plant surface and within 5 cm of the apical tip of each frond. Care was taken to select fronds which were relatively free of epiphytes. In addition, three replicate measurements of the thickness of the drift algal accumulations in each patch were also made. This sampling was repeated for seven patches of drift algae, at the same location and depth strata in November 2002.

Sampling sediments and macrofaunal communities

To assess the structuring effect of drift *Phyllophora* accumulations on underlying macrofaunal communities we collected benthic core samples (7 cm diam., 10 cm deep) under the drift algae and from adjacent bare patches. One sample was collected from under algae, at least 30 cm in from the patch edge, and one from an adjacent bare sediment area at least 1 m from the algal patch. In 2001 we sampled 10 patch pairs, but in 2002 only five could be sampled due to time constraints. Macrofauna core samples were sieved (500 μm mesh), preserved in 70% isopropyl alcohol, stained with Rose Bengal, sorted and identified to the lowest taxonomic level possible.

Sediment characteristics from bare areas and from under algae were determined from small sediment cores (2.6 cm diam., 5 cm deep) collected in November 2001. Characteristics of sediments from bare areas were determined from cores collected at 5 positions along 3 of the video transects described above. Sediment characteristics under the algae were determined from cores collected from ten patches in 2001. Sampling involved collecting paired cores: one core was homogenised prior to being sub-sampled for sediment particle size, organic matter and benthic chlorophyll *a* content, while the other core was used to determine the natural stable isotope signature of carbon and nitrogen in the sediment (see below). All samples were stored frozen and in the dark until analysis. 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 % volumes for the coarse, medium and fine sand, silt and clay fractions. Organic matter was measured as loss on ignition (LOI) by drying the sediment at 60°C for 48 h, 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 chlorophyll *a* (Sartory 1982).

Stable isotope analysis

Stable isotope techniques can help determine major energy pathways and resource acquisition in benthic animals because the isotopic composition of consumers is closely related to that of their diet. As carbon is accumulated within organisms, carbon isotope ratios ($^{13}C/^{12}C$) pose a particularly valuable resource for mapping the importance of different organic carbon sources for secondary producers (e.g. Peterson & Fry 1987, Hobson & Welch 1992). The change in ^{13}C is usually approximately ~ 1‰ for each change in trophic level. The ratio of stable isotopes of nitrogen ($^{15}N/^{14}N$) is used to estimate trophic position; the ^{15}N of a consumer/secondary producer is typically enriched by 3-4 ‰ relative to its diet (Owens 1987, Hobson & Welch 1992).

We collected *Phyllophora* and benthic invertebrates to determine their trophic relationship using stable istope techniques. Samples were obtained from attached healthy *Phyllophora*, degrading *Phyllophora* from the bottom of drift algal accumulations, and from sediments and benthic invertebrates obtained from bare patches and from under algal accumulations Scraping, rather than coring was done in order to ensure that enough animals were obtained for the analysis. The samples were heterogeneous in terms of species composition and no species-specific comparisons could be made and therefore species were pooled into taxonomic groupings for analysis. All samples for stable isotope analyses were kept frozen until they could be freeze dried. Using a mortar and pestle the samples were then ground into a fine homogeneous powder before their stable isotope signatures were determined using a Finnegan Delta-plus continuous flow Mass Spectrometer. The standard reference materials used were PDB limestone for carbon (a calibrated working standard of CO_2 gas was used), and air for nitrogen. Isotopic ratios are reported in delta (δ) notation in parts per thousand (‰). Ratios were calculated relative to a standard using the following formula:

$$\delta\ ^{13}C \text{ or } ^{15}N\ ‰ = ((R_{sample} - R_{standard}) - 1) \times 10^3, \text{ where } R = ^{13}C/^{12}C \text{ or } ^{14}N/^{15}N.$$

Statistical analyses

Differences in the depth-distribution (biomass) of *Phyllophora* were tested using a one-way ANOVA with depth as fixed factor. The differences in photosynthetic capacity (*Fv/Fm*) of algal fronds from the top and bottom of drift algal accumulations, respectively, were tested using a two-way ANOVA with both time (year) and position (top or bottom) as fixed factors and a treatment*site interaction term. Differences in number of taxa and number of individuals of macrofauna in bare sediment patches and under algae were also tested using a two-way ANOVA. Data were examined for normality (one-sample Kolmogorov-Smirnov test) and homogeneity of variances (Levene's test) and were log-transformed where necessary. All univariate analyses were conducted using the software package SPSS 11.0. All data are presented as mean ± standard error.

Differences in the composition of macrobenthic assemblages found in bare sediment areas and under the algal accumulations were assessed using the Bray-Curtis similarity index (Bray and Curtis 1957), followed by non-metric multi-dimensional scaling (MDS) ordination. The MDS ordinations presented are based on √√-transformed data, and had a stress levels < 0.18 (indicating MDS provided a satisfactory representation of the relationship between samples). Differences in the assemblage composition were also tested using ANOSIM, a randomised permutation test on Bray-Curtis similarities (Clarke 1993). To examine the relative contribution of individual taxa clusters in the similarity matrix we used the similarity percentage procedure (SIMPER; Clarke 1993). All multivariate analyses were performed using the PRIMER v. 5 software package (Clarke & Gorley 2001). Because of the small sample sizes, statistical analyses were not performed on the stable isotope data. Instead the ranges of isotope values are presented graphically.

Results

Distribution and biomass of Phyllophora

Biomass estimates for *Phyllophora* were obtained from 2.8 to 31 m depth. Attached *Phyllophora* was only found at depths <15 m, with a biomass of 66 ± 15 g dwt m^{-2} (Fig. 2). In contrast drift *Phyllophora* accumulations occurred throughout the depth gradient, with peak biomasses of 140 ± 30 g dwt m^{-2} in the 15-25 m depth strata (Fig. 2). However, the differences in drift algae biomass between depth strata were not statistically significant ($F_{2,61}$=1.184; p=0.313).

Our quantitative estimates of habitat structure in the 15-25 m depth strata demonstrate that drift accumulations of *Phyllophora* is a conspicious habitat element at Cape Evans (Table 1). We identified three major habitat types from the video footage: crustose/bare rock, *Phyllophora*, and coarse sediments with detritus. Crustose/bare rock consisted of fist-sized rocks to large boulders with varying cover of the encrusting coralline algae, *Phymatolithon foecundum*. *Phyllophora* only occured as drift accumulations, and was found in cracks and crevices between rocks and boulders, in depressions on the seafloor, and attached to the spines of the sea urchin *Sterechinus neumayeri*. Coarse sediments with detritus were found between the rocks and boulders, and in larger scoria fields; often these coarse sediments were covered with fine sediment, microphytobenthos and detritus. There was substantial variation in habitat structure and *Phyllophora* cover between video transects (Table 1). The distribution of *Phyllophora* (drift and attached) was patchy, with the % cover ranging from 12.3 and 40.3. The average % cover of *Phyllophora* across all transects was 29.7 (Table 1).

Sediment composition at Cape Evans was predominantly coarse sand (77–81%) with low organic content (LOI: 0.6–0.9%; Table 1). In bare sediments chlorophyll *a* and phaeophytin varied from 2.4-4.1, and 7.4-16.4 μg g $sediment^{-1}$, respectively (Table 1).

Photosynthetic capacity of drift algal accumulations

There was no obvious change in the distribution and thickness of drift algal accumulations between 2001 and 2002. The thickness of the drift algal material averaged 4.1 ± 0.3 cm in 2001 and 3.9 ± 0.1 cm in 2002, indicating that additional material had not accumulated. In 2001 visual observations of the drift algal accumulations provided no clear indications that the algal material was degrading, apart from more fragmented *Phyllophora* fronds being found in the bottom of the accumulations compared to the top. However, in 2002 the drift algal accumulations appeared to be in a worse state.

These visual observations are corroborated by the measurements of photosynthetic yield (Fv/Fm; Fig. 3). For Fv/Fm we found a significant effect for both position (top vs. bottom of accumulation; $F_{1,28}$=7.315, p=0.012) and time (2001 vs. 2002; $F_{1,28}$=5.789, p=0.024) (Fig. 3), but a non-significant position*time interaction ($F_{1,28}$=0.052, p=0.822). Thus *Phyllophora* at the bottom of the accumulation were in significantly worse condition than at the top and overall in a worse condition in 2002 than in 2001. In 2001 the range of Fv/Fm for healthy plants was 0.67 to 0.83 while *Phyllophora* at the top of the accumulation had an overall average Fv/Fm value of 0.69 ± 0.03 across all seven patches,

i.e. within the range of healthy plants. In contrast, algae at the bottom of the accumulation had an average Fv/Fm value of 0.62 ± 0.09 (Fig. 3). Despite substantial variation between patches, drift algal accumulations showed clear signs of degradation in 2002. While the range of Fv/Fm values for attached *Phyllophora* in 2002 was basically identical to that in 2001, i.e. 0.68 to 0.79, the Fv/Fm values for *Phyllophora* in the top of the accumulations now averaged 0.63 ± 0.06 (corresponding to 93% of lowest level measured in attached 'healthy' plants) and only 0.54 ± 0.09 for algae in the bottom (corresponding to 79% of the capacity of attached plants). The differences in state of degradation between years become more apparent when examining the net difference in photosynthetic yield between *Phyllophora* in the drift algal accumulations in relation to the minimum value (here defined as the threshold value for degradation) recorded for 'healthy' attached plants (Fig. 4). In 2001, algae from the top of the accumulation were clearly in the range of healthy attached plants whereas plants from the bottom of the accumulation were degrading (Fig. 4), However, in 2002 degradation was apparent for both algae in the top and the bottom of the accumulation, respectively (Fig. 4).

Nevertheless, some evidence for degradation of *Phyllophora* in 2001 is already apparent when comparing concentrations of chlorophyll *a* and its degradation product phaeophytin in sediments under the algal accumulations, to concentrations in the adjacent bare sediments. Chlorophyll *a* and phaeophytin in the bare sediments averaged 3.1 and 11.4 μg g sediment^{-1}, respectively, while the corresponding concentrations under algae were 6.0 and 26.2 μg g sediment^{-1}, respectively (Fig. 5). These differences were significantly different (chlorophyll *a* $F_{1,24}$=5.856, p=0.0235; phaeophytin $F_{1,24}$=4.348, p=0.0479). Evidence for ongoing degradation under algae is further corroborated by a significantly higher phaeophytin to chlorophyll *a* ratio in sediments under algae (i.e. 4.4 under algae *vs.* 3.6 on bare sand; $F_{1,24}$=4.956, p=0.0357). However, some caution must be used when interpreting these results as it is possible that the chlorophyll *a* and phaeophytin could originate from the *in situ* production of microphytobenthos or from sedimenting phytoplankton or sea-ice algae.

Influences of *Phyllophora* on soft-sediment macrofaunal communities

In total we recorded 62 benthic invertebrate taxa in our samples. Fifteen of these taxa were only found either in bare sediment areas or under algae. However, these were mostly rare taxa and no clear patterns emerge when comparing bare sediment and algal patches. An average of 10-15 taxa were collected per core (Fig. 6), with no differences in the number of taxa between bare sediment and algal patches ($F_{1,28}$=0.025, p=0.876) or between years ($F_{1,28}$=1.576, p=0.220), and with no significant space*time interaction terms ($F_{1,28}$=1.908, p=0.179; Fig. 6). The average number of individuals of the ten most frequently occurring taxa varied between years, with abundances in bare sediment generally being higher than under algae in both years (Table 2-change tabs 2&3). Only one taxon, stenetriidae isopods, was persistently found in higher numbers under algae in both years (Table 2). Apart from ?Nematode type A, which was by far the most dominant taxon, six of the ten most frequently occurring taxa were crustaceans, two were gastropods and one a polychaete taxa (Table 2).

There were clear differences in total numbers of individuals between bare sediment and under algae, with lower abundances under algae compared to bare patches ($F_{1,28}$=5.185, p=0.031). There were no significant differences between years ($F_{1,28}$=1.35.1, p=0.256), and no significant space*time interaction ($F_{1,28}$=0.209, p=0.651; Fig. 5). The lack of a statistically significant effect of time (i.e. 2001 vs. 2002) for number of taxa and number of individuals was likely due to the large variability in our samples. However, for number of individuals in particular, the difference between bare sand and under algae appears stronger in 2002 (Fig, 6). In 2001 there were 50.6 % more individuals in the bare sediment than under the algae, and in 2002 this difference had increased to 71.8 %. These patterns in abundance correspond well with those of increasing degradation of the *Phyllophora* accumulations between 2001 and 2002 (Fig. 3 & 4).

The increasing structuring effect of degrading *Phyllophora* becomes apparent when examining the differences in macrofaunal community structure in bare sediment and under algae (Fig. 7). In 2001 there was a complete overlap in macrofaunal community composition with no significant difference between bare sediment and under algae (ANOSIM; p=0.424; Fig. 7). In contrast, the macrofaunal assemblages were significantly different in 2002 (ANOSIM; p=0.04; Fig. 7). The average dissimilarity between bare sediment and under algae was 56.5%, with 10 taxa accounting for just over 50% of this difference (SIMPER; Table 3). In 2002 three taxa (i.e., xnem, xneb and *Orchomenella franklini*) were only found in bare sediments, while in comparison, no taxa were found only under algae, and the most dominant taxa was ?Nematode type Awhich contributed more than 12% to differences in community composition (SIMPER; Table 3). However, in contrast to temperate benthic communities there is a higher diversity of taxa which contribute to the observed differences in macrofaunal assemblages.

Stable isotopes: enrichment effects and trophic role of Phyllophora

The $^{13}C/^{12}C$ signatures for attached *Phyllophora* as well as for drift plants found in the top and the bottom of the drift-algal accumulations were similar (Fig. 8). While the ^{13}C ratio for attached plants ranged between –37.8 and –35.4 ‰, the *Phyllophora* drift ranged between –37.4 and -36.3 ‰ (Fig. 8). In comparison to *Phyllophora*, the $^{13}C/^{12}C$ ratios of

surface sediments (which include both microphytobenthos and detritus) are strongly enriched with values ranging between –20.3 and –13.6, although the $^{13}C/^{12}C$ ratios of sediments under algae were more heterogeneous and wider in their range (Fig. 8). All macrofauna had $^{13}C/^{12}C$ ratios that were substantially more enriched than *Phyllophora* and closer in range to the particulate organic matter associated with the sediments (Fig.8). These results strongly suggest that *Phyllophora* are not a direct food source to the benthic taxa investigated in this study (Fig. 8), especially when assuming the typical enrichment by about 1‰ of ^{13}C of a consumer relative to its food source (Fry & Sherr 1984). However, the polychaetes and crustaceans found under the drift algal accumulations all had more reduced $^{13}C/^{12}C$ ratios than those found on bare sand (Fig. 8). The species composition of polychaetes and crustaceans were more or less the same in both bare sand and under algae, and hence differences in $^{13}C/^{12}C$ ratios reflect differences in food sources rather than differences in functional feeding groups (Table 2 & 3). The N stable isotope data support these patterns; *Phyllophora* had $^{14}N/^{15}N$ ratios ranging from 0 to 2.2, while $^{14}N/^{15}N$ ratios of sediments under algae ranged from 3.1 to 6.3 and bare sediments from 4.8 to 6.1. Polychaetes and crustaceans found under the drift algal accumulations all had more reduced $^{14}N/^{15}N$ ratios than those found on bare sand. Polychaetes under algae had $^{14}N/^{15}N$ ratios ranging from 5.6 to 7.7 while polychaetes on bare sand had values ranging from 7.1 to 9.6. In comparison, crustaceans under algae had $^{14}N/^{15}N$ ratios ranging from 4.8 to 8.0, while values for crustaceans on bare sand were more enriched, ranging from 6.0 to 9.6. These results indicate that polychaetes and crustaceans under algae are feeding at a lower trophic level than those on bare sand.

Discussion

The functional role of macroalgal detritus in the coastal benthic communities of Antarctica has received only limited attention (Dunton 2001). This is especially the case with the high latitude waters of McMurdo Sound in the Ross Sea. At Cape Evans we found the red alga, *Phyllophora antarctica,* to be a conspicuous habitat feature from a few m's to more than 30 m depth. Although we did find attached *Phyllophora* plants, they were only recorded at depths of less than 15 m. From our observations and measurements down to 30 m, the vast majority of the biomass occurred as drift material with the highest biomasses recorded at the 15-25 m depth strata. It is clear that *Phyllophora* drift algae represent a significant potential carbon source in the shallow benthic communities at Cape Evans.

While the decomposition and incorporation of carbon from macroalgal detritus is rapid in temperate waters we would predict it to be slow in Antarctica. When we initiated our study in November 2001 it is very likely that the *Phyllophora* drift accumulations had been stationary in complete darkness for at least 9 months, and potentially longer. Remnants of old fast ice from winter 2000 were still in place over the study sites, and would have given protection from wave action during the 2000/01 summer. As the tidal currents are very weak at the site, these algal accumulations are likely to be redistributed only when exposed to turbulence created by wind-wave action. Nevertheless, measurements of the photosynthetic capacity of the drift algal accumulations indicated that they appeared to be in good health. In 2001, plants from the top of the accumulations were well within the range of attached plants whilst plants from the bottom of the accumulation showed signs of reduced photosynthetic capacity. In contrast, the photosynthetic capacity of the accumulations was significantly reduced in 2002 (Fig. 3).

In a companion study we showed that *Phyllophora* is extremely shade adapted with low respiration rates (Schwarz et al. in press). In the summer of 2001-2002 it was only during the two-month ice-free period that irradiance exceeded compensation enabling *Phyllophora* to grow. The low respiration rates enable *Phyllophora* to survive the winter darkness and retain photosynthetic capacity for periods of higher irradiance (Schwarz et al in press). Similarly these physiological characteristics make them well adapted to survive for extended periods of time in the constant darkness at the bottom of drift algal accumulations. The longevity of these algae is further enhanced by polyphenols which serve as protection from grazers (Amsler et al. 1999) and which are likely to enhance resistance to bacterial degradation (Ballesteros et al. 1992, Duggins & Eckman 1997). The cold temperatures of Antarctic waters further inhibit the development of anaerobic degradation at the bottom of the *Phyllophora* accumulations and we never saw any signs of hypoxia, anoxia or hydrogen sulphide associated with the accumulations which are common in temperate waters. However, the *Phyllophora* accumulations were neither very thick (about 4 cm), nor were they dense because of the thallus morphology of *Phyllophora* which probably delays (or prevents) the development of anaerobic conditions.

We found significant reductions in the abundance of soft sediment macrofaunal assemblages under algae. This structuring effect was more pronounced in 2002 than in 2001, matching patterns of increasing degradation of the algal accumulations. However, there were no clear differences in the numbers or types of taxa found in bare sand or under algae. These findings contrast with studies conducted at Terra Nova Bay, which found high numbers of syllid polychaetes (*Pionosyllis* cf. *comosa*), tanaids (*Nototanais dimorphus*) and gastropods of the genus *Onoba* and *Philobrya* associated with attached *Phyllophora* (Cattaneo-Vietti et al. 2000). While we did find examples of each of these types of fauna in our study (Tables 2 and 3), with the exception of the syllid polychaete *Syllidia intermis* and the gastropod *Onoba* sp. in 2002, all were more abundant in the bare sediments than under the algae. These differences could be due to the fact that our study focused on the fauna found in sediments under drift *Phyllophora*, rather than

amongst the *Phyllophora* which would have been more comparable to the attached *Phyllophora* habitat. Qualitative samples obtained from within the drift algal accumulations indicate the presence of very diverse faunal communities. We found juvenile stages of many common benthic fauna (e.g., *Sterechinus neumayeri, Odontaster validus, Abatus* sp., *Diplasterias brucei*), suggesting that these algal accumulations may be important nursery areas. In addition, it is likely that many mobile infaunal species, especially crustaceans, colonise the drift algal accumulations from the underlying sediments or from adjacent bare sediments. Patterns of high faunal diversity associated with *Phyllophora* were reported by Dhargalkar et al (1988) in the Vestfold Hills region and by Gambi et al. (2000) in Terra Nova Bay. Gambi et al. (2000) showed that macrobenthic abundance and diversity from 2-16 m depth was strongly positively correlated with increasing biomasses of *Phyllophora*. They attributed these promotive effects to the increase in habitat complexity provided by the algae, which serve to provide shelter and habitat to macrofauna. Also in other parts of the world the *Phyllophora* genus has been associated with high faunal diversity. In the 1950's in the Black Sea, "Zernov's *Phyllophora* field" (Zaitsev 1992), formed a *Phyllophora* community which covered an area of 11 000 km^2 down to 60 m depth. Up to 120 species of invertebrates and 50 species of fish were tightly associated with this *Phyllophora* field (Zaitsev 1992). Unfortunately, this unique *Phyllophora* field had been reduced by 95% in the early 1980's due to eutrophication and the faunal communities collapsed.

Apart from providing structural complexity and refuge to benthic invertebrates, our results provide clear evidence that slowly decomposing *Phyllophora* may be an important source of carbon to higher trophic levels. The $^{13}C/^{12}C$ ratios of animals collected under drift algal accumulations were more reduced than those found on bare sand (Fig. 8) while the $^{14}N/^{15}N$ ratios of animals found under algae indicate that they feed at a lower trophic level than those on bare sand. Duggins & Eckman (1997) showed that growth of suspension feeders feeding on kelp detritus was inversely related to the total polyphenolic concentration in the aging kelp particles. Similar results were reported by Norderhaug et al. (2003) who showed that bacterial activity is crucial for making macroalgal kelp detritus available as food to amphipods and gastropods by decreasing the C:N ratio and polyphenolic content. Thus, it is likely that trophic mediation by bacteria and other microorganisms and cell necrosis has to take place before *Phyllophora* is incorporated into the benthic macrofauna. Our stable isotope results suggest that although structurally intact *Phyllophora* from the bottom of drift-algal accumulations might not be a direct food source, detritus originating from *Phyllophora* is still utilised as food. However, the large difference in ^{13}C ratios between *Phyllophora* from the bottom of the accumulation and the benthic invertebrate taxa is puzzling. A likely explanation may be found in trophic mediation processes by bacteria and meiofauna, which ages the detritus making it edible to macrofauna. An equally likely alternative hypothesis is that the animals are omnivorous and feed on multiple food sources, which is reflected in their ^{13}C signature. Thus for example, an additional but strongly enriched food source would make the consumer more enriched relative to *Phyllophora*. At Cape Evans the coralline algae, *Phymatolithon foecundum*, is abundant and a potential food source. The calcareous *Phymatolithon* has a strongly enriched ^{13}C signature, ranging from –8.8 to -6.8 ‰. Thus a diet consisting of both macroalgal species would result in a stable-carbon isotope signature most likely within the range of that measured for the benthic invertebrates in this study. On the other hand, *Phymatolithon* growing on hard substrates is not necessarily directly available to soft sediment invertebrates as food unless it occurs as detritus in the sediments.

The strong seasonality in sea ice cover and consequently the light regime in the Antarctic coastal environment mean that primary production and input of food to benthic communities is pulsed (Dayton et al. 1986, Clarke 1988). As a response, many benthic invertebrates rely on multiple food sources for survival (i.e., settling phytoplankton, settling sea ice algae, benthic diatoms, detritus and the lateral advection of re-suspended matter; Arntz et al. 1994, Brockington et al. 2001). Thus the persistence and slow degradation of *Phyllophora* detritus may serve to dampen the seasonality in food supply by providing a more consistent source of food to the benthic fauna. Macroalgal detritus clearly plays an important trophic role in Antarctic coastal waters, but the time scales for its incorporation into food web appear to be long, and very little is known about the utilisation of this resource by higher trophic levels. Factors contributing to slow degradation of *Phyllophora* include the extremely low temperatures (colder than the deep sea?), limited mechanical degradation due to low wave energy, extreme shade adaptation and low respiration rates, and secondary metabolites, which serve to protect the algae from grazers and bacterial development.

In Antarctica the relationship between primary producers and consumers and the role macroalgal detritus plays in fuelling biodiversity are inextricably linked to sea ice and therefore light conditions. In McMurdo Sound (78°S) were sea ice conditions are severe, macroalgal diversity is reduced while already at the lower latitudes and the less severe sea ice conditions of Terra Nova Bay (74°S), macroalgal diversity and biomasses are higher albeit still dominated by rhodophytes (e.g. Cormaci et al. 1998, Gambi et al. 2000). At the Antarctic Peninsula the diversity is even greater with many phaeophytes, rhodophytes and chlorophytes (Dunton 2001). At these low Antarctic latitudes (64°S) several studies have investigated the decomposition processes (e.g. Reichardt & Dieckmann 1985, Fischer & Wiencke 1992, Brouwer 1996) and trophic role (Dunton 2001) of macroalgae. These studies show that especially phaeophytes degrade relatively fast and enter the detrital food web. For example, Dunton (2001) showed that kelp detritus composed 60-70% in the diet of omnivorous polychaetes and 30-40% in the diet of omnivorous amphipods in the coastal waters of the

Antarctic Peninsula. Similarly, Fischer & Wiencke (1992) showed that phaeophytes made a strong contribution to the total organic carbon pool at 2000 m depth in the King George Basin. Similarly, Snelgrove et al. (1996) provided evidence that phaeophyte detritus can play an important role contributing to high deep-sea macrofuanal diversity. In temperate coastal areas, macroalgal detritus, especially phaeophytes has been shown to have profound influences on coastal benthic communities as they can provide important habitat and structural complexity to the seafloor thereby increasing diversity and fuelling productivity (e.g. Vetter 1995, Vetter & Dayton 1998, Norkko et al. 2000, Okey 2003). However, degradation in these areas can be fast with subsequent local disturbance effects on the underlying benthic community due to anaerobic decomposition (e.g. Thrush 1986b, Norkko & Bonsdorff 1996 a,b, Okey 2003). Thus, the ecological role of *Phyllophora* reported in this study is in stark contrast to the often rapid decomposition and incorporation into the food web reported for phaeophytes from lower Antarctic latitudes and temperate waters. This study has begun to investigate the role of *Phyllophora antarctica* in structuring Antarctic macrofaunal communities, but further research is needed to gauge the role different primary producers have in fuelling coastal benthic communities.

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Figure legends

Figure 1. Map of the study site, Cape Evans, in McMurdo Sound in Antarctica

Figure 2. The depth distribution and biomass of drifting and attached *Phyllophora* at Cape Evans in 2001. 0 = no attached algae recorded.

Figure 3. The photosynthetic yield (Fv/Fm) of drift algae at the top and the bottom of the accumulations in 2001 and 2002. The dotted lines indicate the range of photosynthetic yield of healthy, attached plants. Values are the mean ± standard error.

Figure 4. The net difference in photosynthetic yield (Fv/Fm) between the drift algal accumulations (the top and the bottom) and the minimum value recorded for attached *Phyllophora*. Values are the mean ± standard error.

Figure 5. Sediment chlorophyll *a* and phaeophytin in bare sediments and under algal accumulations. Values are the mean ± standard error. * = significaantly different ($p<0.05$).

Figure 6. The number of taxa and individuals per core in bare sediments and under algal accumulations in 2001, 2002 and both years combined Values are the mean ± standard error. * = significaantly different ($p<0.05$).

Figure 7. Non-metric Multidimensional scaling ordinations (MDS) showing differences in macrobenthic community structure in bare sediments (B) and under algae (UA) in 2001 and 2002. The dotted circle circumscribes the bare sediment samples (B).

Figure 8. The range in $\delta^{13}C$ values of attached and drifting *Phyllophora*, sediments and fauna found in bare sediments and under drift algal accumulations.

Table 1. Habitat types and sediment characteristics at Cape Evans in 2001. Habitat types are measured as percent cover from five video transects at 18 to 21 m depth. Sediment characteristics were determined from five cores obtained in bare sediment patches along transects 1, 2 and 3. Values are the mean (± standard error). Chl *a* = Chlorophyll *a*.

	Transect					
Habitat (% cover)	*T1*	*T2*	*T3*	*T4*	*T5*	*All*
Phyllophora *drift*	28.9 (6.2)	12.3 (1.3)	39.0 (7.5)	40.3 (7.0)	28.1 (6.6)	29.7 (5.0)
Bare rock / Crustose algae	16.7 (4.8)	51.1 (5.0)	21.4 (4.4)	31.8 (6.7)	13.8 (4.6)	27.0 (6.8)
Coarse sediment with detritus	55.3 (6.8)	37.3 (5.7)	39.6 (7.3)	27.8 (7.2)	57.7 (8.3)	43.4 (5.6)

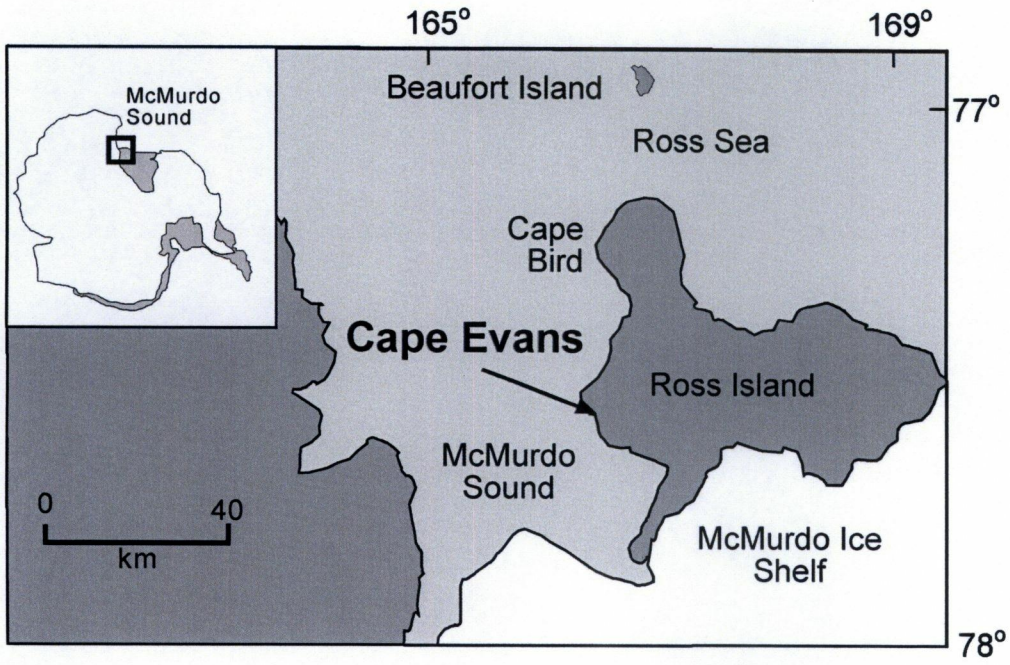
Sediment characteristics	*T1*	*T3*	*T5*
Grain size (%)			
-gravel (> 2000 µm)	12.6 (3.1)	4.3 (1.3)	6.1 (1.9)
-coarse sand (500-2000 µm)	77.1 (2.8)	81.0 (1.6)	80.1 (1.5)
-medium sand (250-500 µm)	6.2 (1.0)	9.0 (0.9)	7.3 (0.5)
-fine sand (62.5-250 µm)	2.8 (0.5)	3.4 (0.5)	3.1 (0.5)
-silt (3.9-31 µm)	1.3 (0.2)	2.2 (0.5)	3.3 (0.6)
-clay (< 3.9 µm)	-	-	0.1 (0.0)
Organic content (%)	0.7 (0.0)	0.6 (0.1)	0.9 (0.1)
Chlorophyll *a* (µg g sediment^{-1})	2.4 (0.8)	2.8 (0.8)	4.1 (0.9)
Phaeophytin (µg g sediment^{-1})	7.4 (1.2)	10.2 (1.8)	16.4 (5.3)
Chl *a* : Phaeophytin ratio	0.32	0.27	0.25

Table 2. The average number of individuals per core of the ten most frequently occurring macrobenthic taxa in bare sediments and under algae in 2001 and 2002. Values are the mean (± standard error).

Taxa	2001		2002	
	Bare sediment	*Under algae*	*Bare sediment*	*Under algae*
?Nematode type A)	36.1 (14.0)	16.3 (9.2)	113.0 (94.9)	0.0 (0.0)
Nototanais sp. (tanaidacea)	25.3 (13.0)	13.9 (4.8)	78.2 (48.6)	33.8 (19.1)
Austrosignum grande (isopoda)	7.3 (1.8)	4.0 (1.6)	47.2 (29.9)	10.0 (3.0)
Stenetriidae (isopoda)	1.5 (0.6)	1.7 (0.8)	3.4 (2.0)	6.8 (5.1)
Heterophoxus videns (amphipoda)	2.0 (0.4)	2.5 (0.6)	6.2 (4.1)	0.4 (0.4)
Myodocopida (ostrocoda)	5.0 (3.8)	1.2 (0.7)	3.8 (3.6)	2.4 (2.4)
Ostracoda	1.5 (1.0)	1.4 (0.6)	3.0 (2.5)	0.6 (0.4)
Syllidia inermis (polychaeta)	6.5 (1.6)	2.9 (0.8)	0.4 (0.4)	2.4 (1.5)
Onoba sp. (gastropoda)	4.7 (2.9)	2.9 (1.0)	1.8 (0.9)	2.0 (1.3)
Gastropod 2	0.6 (0.5)	1.5 (0.6)	2.6 (2.1)	0.6 (0.4)

Table 3. Results from SIMPER analysis depicting the most important taxa driving the observed differences in macrobenthic community composition between bare sediment and under algae in 2002. These 18 taxa explain 75.6 % of the observed differences in community composition.

Taxa	*Average abundance core^{-1}*		*Contribution (%)*	*Cumulative contribution (%)*
	Bare sediment	*Under algae*		
Nematode type A	112.8	0.0	12.1	12.1
Gnathia calva (isopoda)	2.0	1.8	4.9	17.0
Nebulacea sp. (?)	2.0	0.0	4.8	21.8
Heterophoxus videns (amphipoda)	6.2	0.4	4.5	26.3
Stenitriidae (isopoda)	3.4	6.8	4.5	30.8
Oligochaeta	14.2	11.8	4.4	35.2
Syllidia inermis (polychaeta)	0.4	2.4	3.9	39.1
Nototanais sp. (tanaidacea)	78.2	33.8	3.8	42.9
Onoba sp. (gastropoda)	1.8	2.0	3.6	46.5
Nematoda sp. 2	3.4	1.2	3.6	50.1
Austrosignum grande (isopoda)	47.2	10.0	3.5	53.6
Gastropoda sp. 2	2.6	0.6	3.3	56.9
Hessionidae (polychaeta)	0.8	0.8	3.3	60.2
Myodocopidae (ostracoda)	3.8	2.4	3.2	63.4
Orchmenella franklini (amphipoda)	1.4	0.0	3.1	66.5
Eulagisca sp (polychaeta)	0.8	1.0	3.1	69.6
Acarina (mite)	1.6	0.4	3.0	72.6
Ostracoda	3.0	0.6	3.0	75.6



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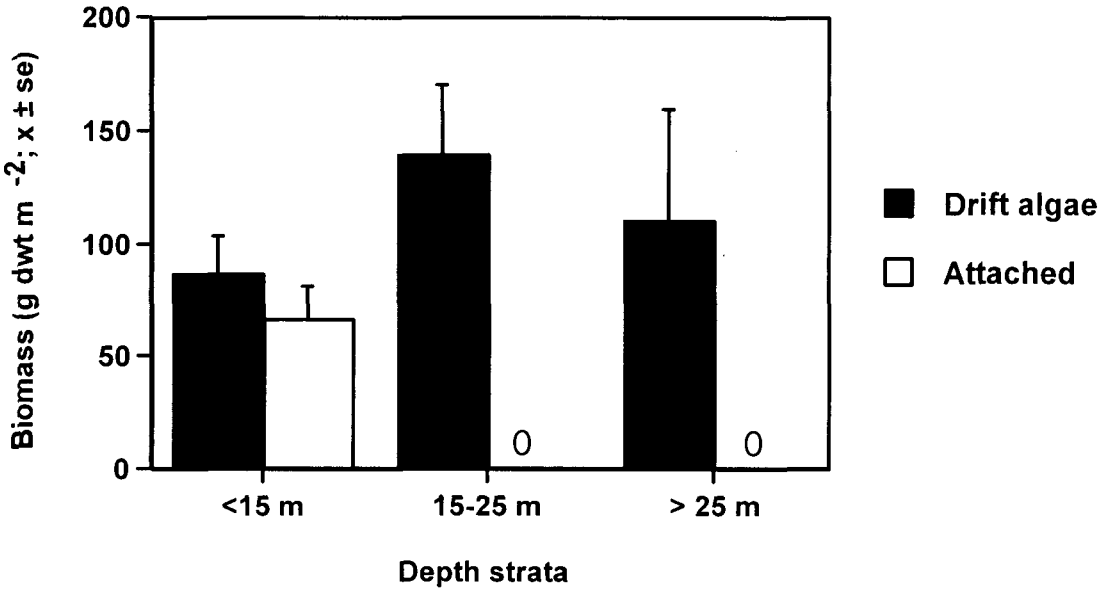

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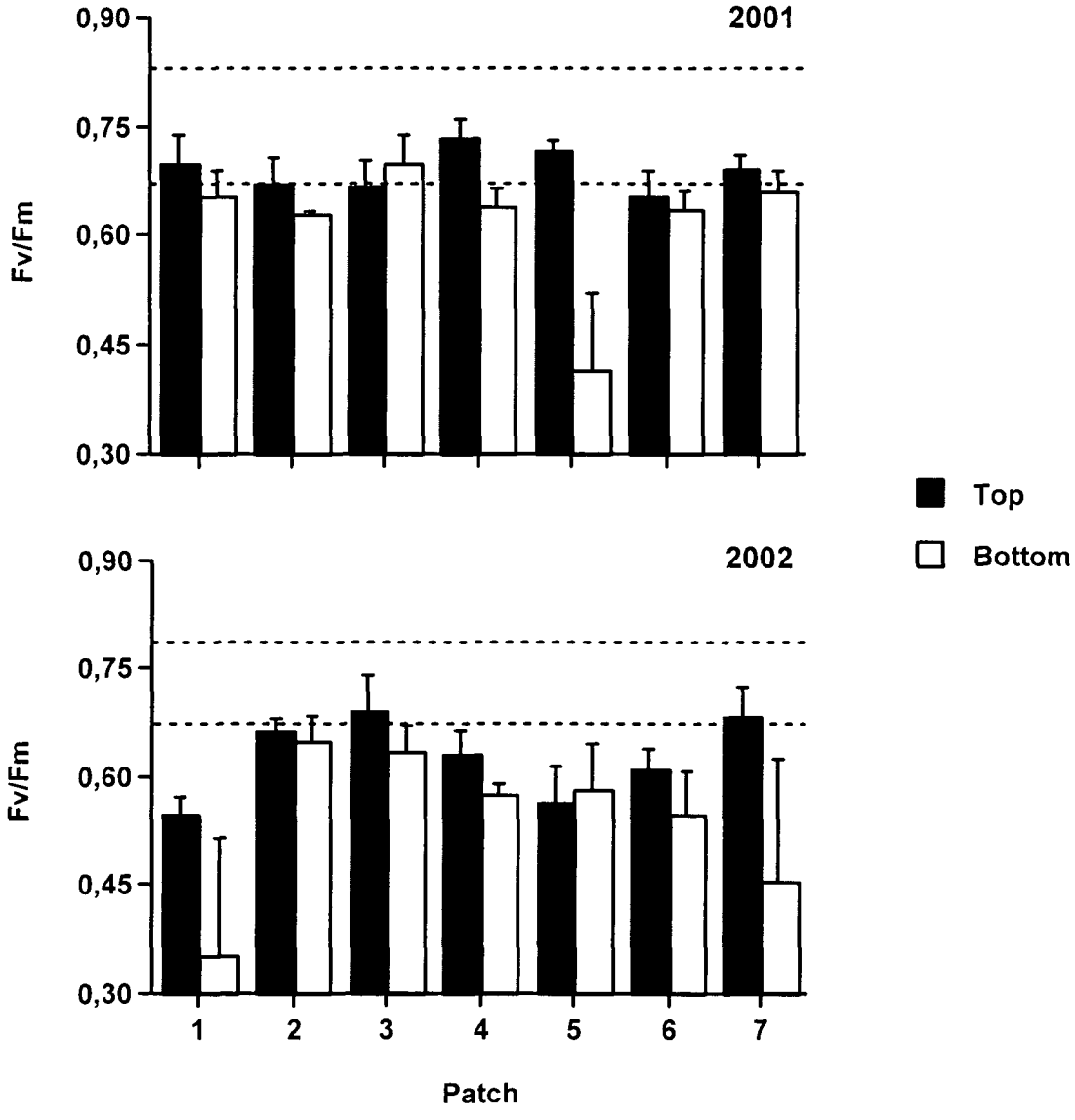

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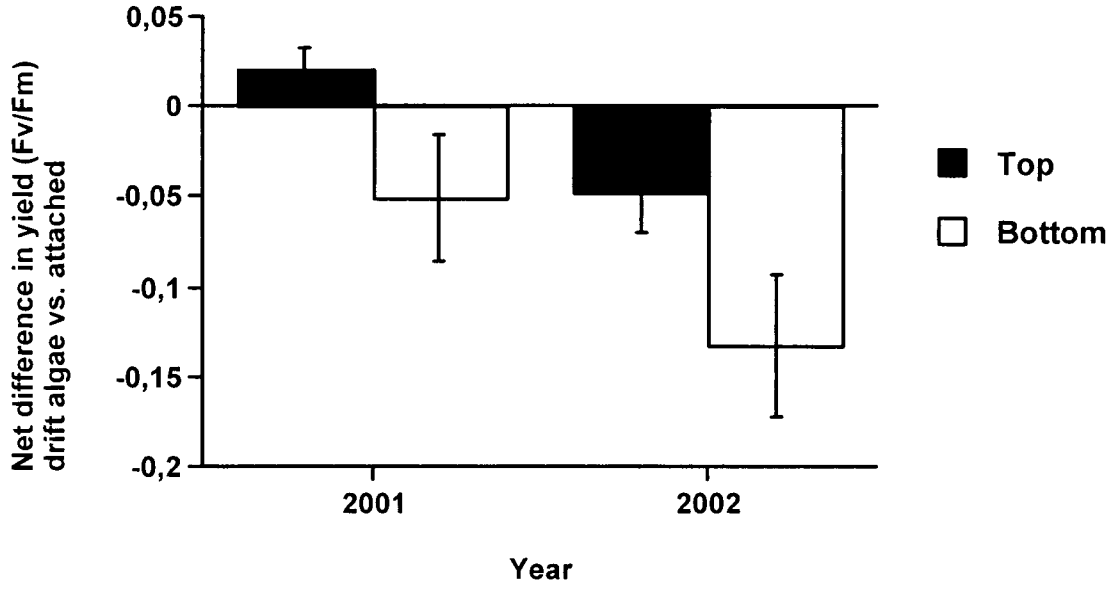

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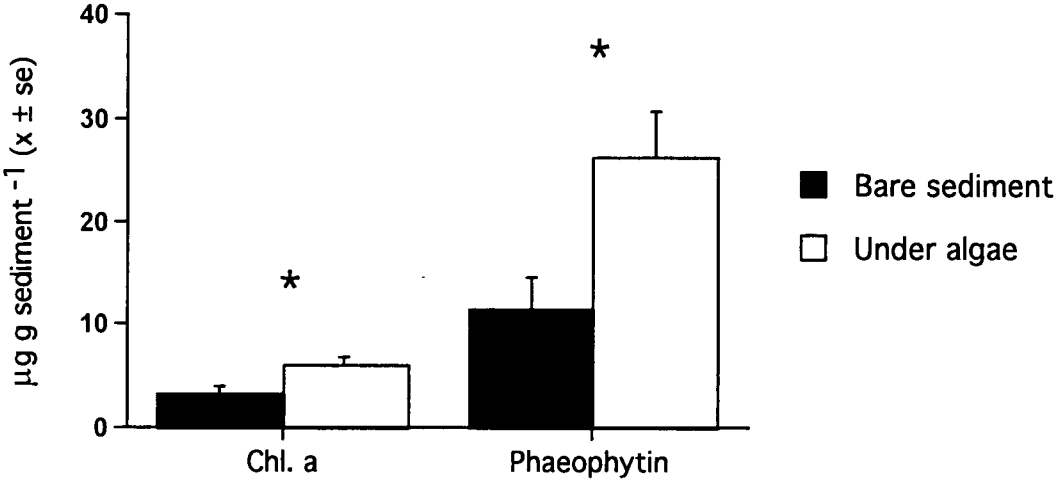

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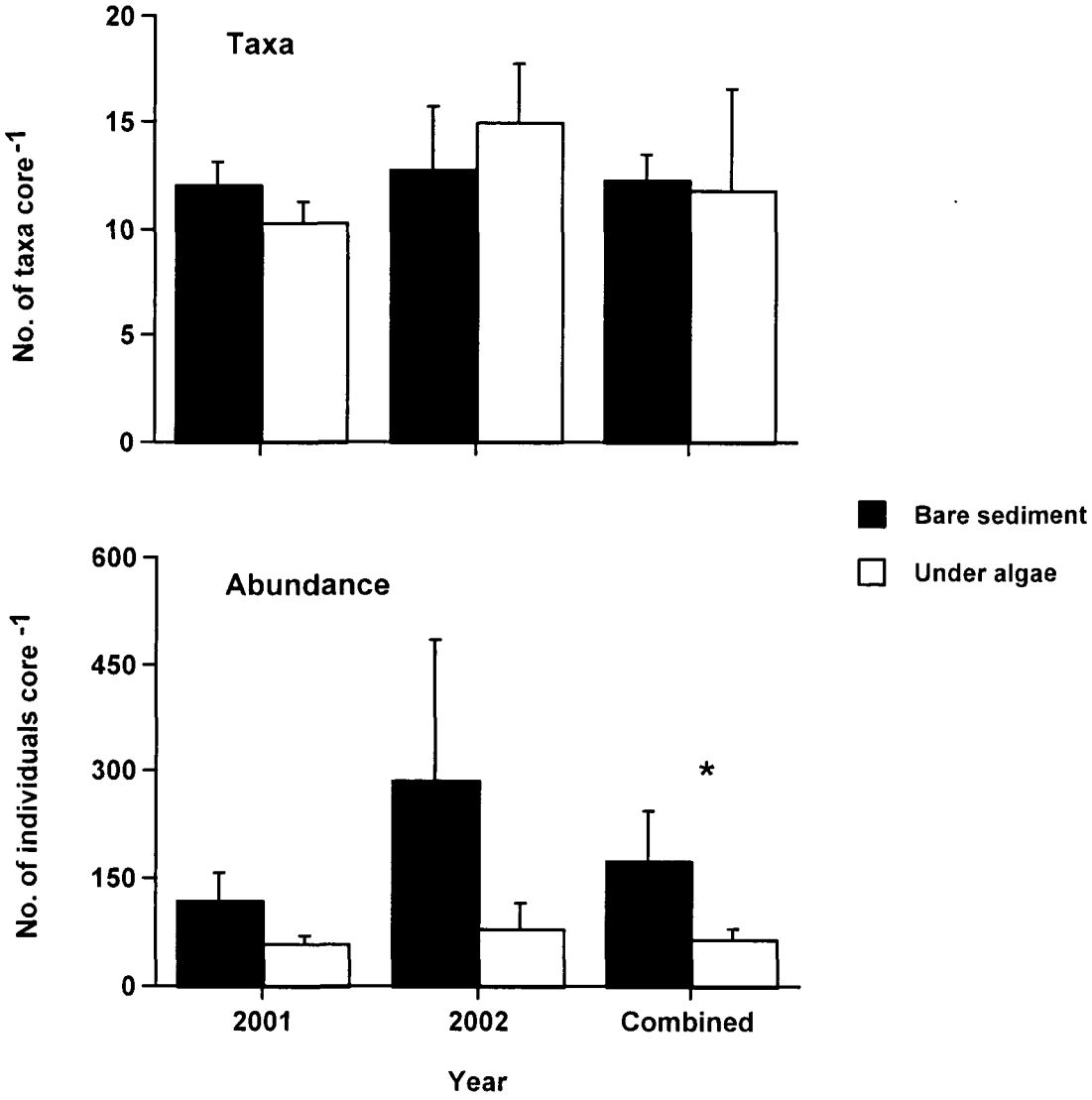

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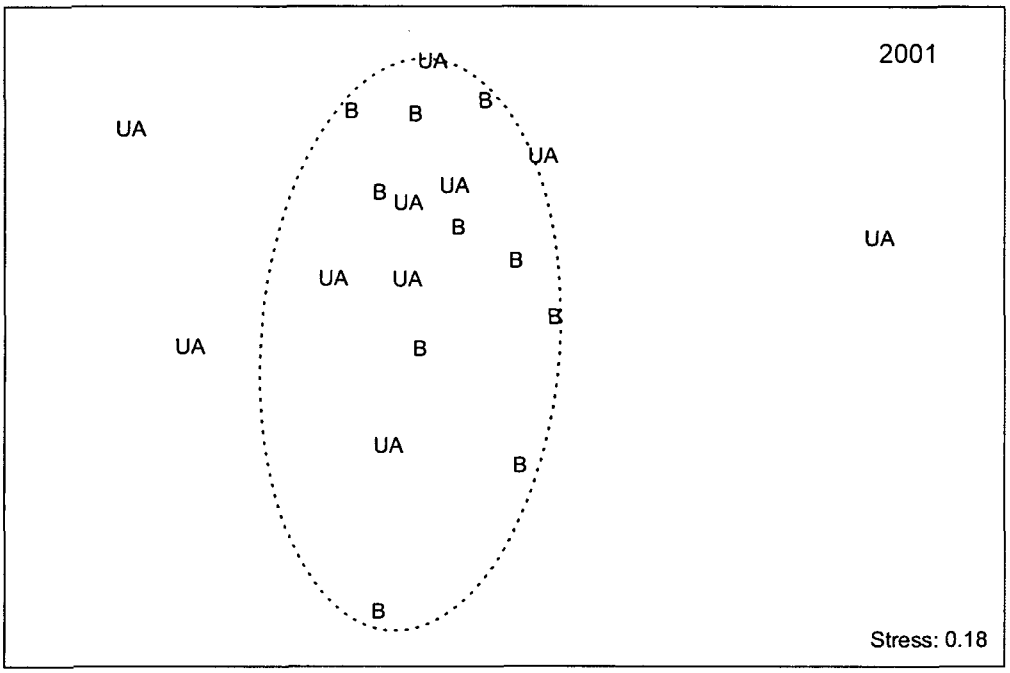

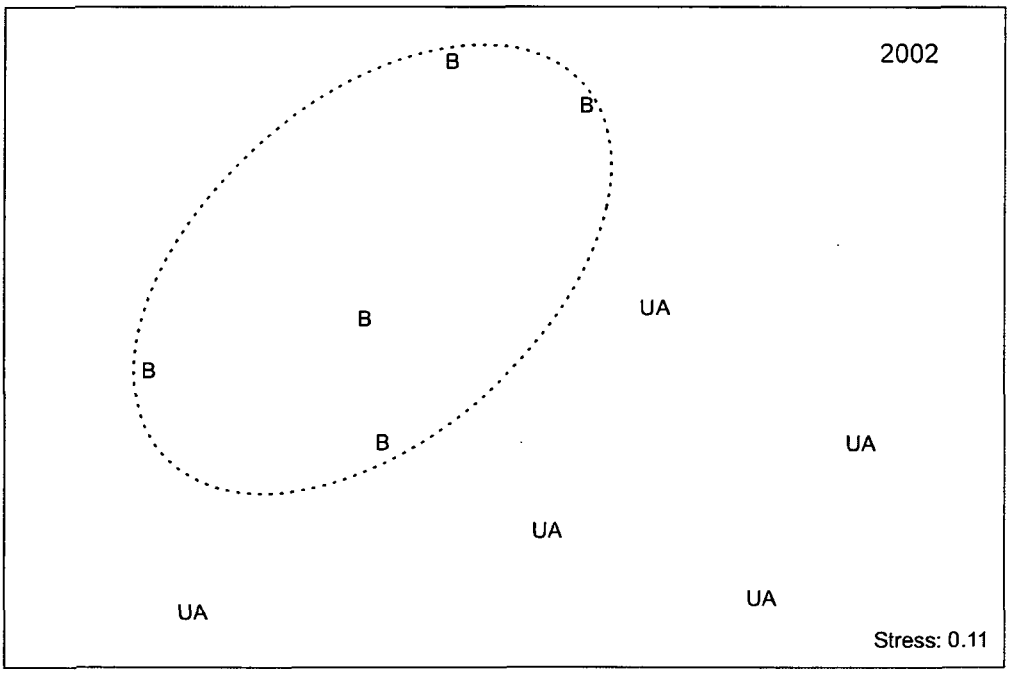

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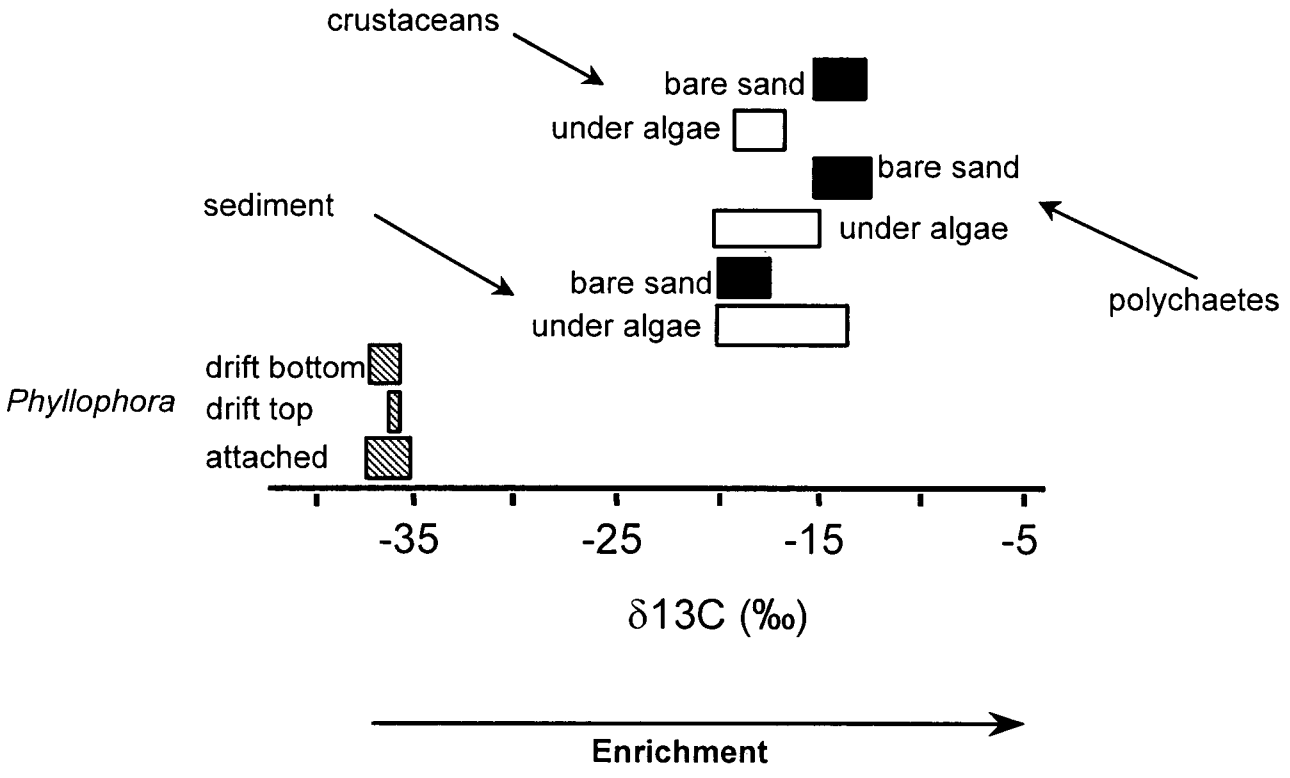

Fig. 8. Norkko et al.