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Sublittoral epifaunal communities at Signy Island, Antarctica. II. Below the ice-foot zone

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Abstract Photographic samples were taken every 5 m along two 40 m transects on mostly rock face at Signy Island, Antarctica, during the austral winter of 1991. Dense and taxonomically rich communities of benthos occurred at most of the sublittoral study locations. These communities, however, varied significantly with substratum type, substratum profile and depth. Algae were generally the largest occupiers of space, but the area of substratum colonised by animal taxa increased whenever the profile approached vertical. Shallower than 15 m, disturbance effects, largely from ice, restricted community development to a high degree, but the frequency of disturbance at 25 m appeared to maintain high diversity by preventing domination of the assemblage by a few competitively superior taxa. Bryozoans, and to a lesser extent sponges, were the most abundant animal phyla. Among the bryozoans, species with an encrusting growth form occurred at the shallowest depths followed by encrusting massive/foliaceous species and, at 40 m, the erect flexible forms. The ratio of encrusting to erect bryozoan species changed rapidly over the 0 to 50 m depth zone, from exclusively encrusting at 0 to 5 m to approaching 1 at 50 m. The erect bryozoans studied, from the shallow sublittoral to 290 m, could be classified as encrusting massive (foliaceous), erect flexible or erect rigid forms. There was some suggestion, despite the overlap between groups and considerable intra-group variation, that encrusting massive forms were abundant in the shallowest water, followed by erect flexible forms and then erect rigid forms with increasing depth. Some species which occurred as encrusting massive/foliaceous forms in deeper water occurred mostly in encrusting form only in shallow water (< 15 m).

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Introduction

Antarctic marine benthic herbivores are subject to strong seasonal variations in food availability and disturbance (Clarke 1988; Barnes and Clarke 1994). Much of the austral year has traditionally been viewed as a period of winter starvation (Clarke 1988; Fenchel 1990) and even hibernation (Gruzov 1977) for these organisms. The growth rates of the benthic fauna so far studied have proved variable, but generally slower than equivalent temperate species (Clarke 1980; Luxmoore 1982; Arntz et al. 1995), and feeding has been little studied (Barnes and Clarke 1994). Large, sessile, benthic communities are well known from deeper locations (Bullivant 1961, 1967; Winston and Heimberg 1988). In the sublittoral the distribution of these is dependant on aspects of both substratum (Kirkwood and Burton 1988; review in Arntz et al. 1995) and ice (Dayton et al. 1970, 1974). At Signy Island in the maritime Antarctic, despite the short duration and unpredictable intensity of primary production and the typically long period of annual sea-ice cover (Whitaker 1982; Clarke et al. 1988), the benthos is diverse and abundant even in the shallow sublittoral (White and Robins 1972; Barnes 1995).

Sessile benthic communities contain several groups which are important but, at least until recently, only poorly known taxonomically (Belyaev and Ushakov 1957; Knox 1970; Kirkwood and Burton 1988; Galéron et al. 1992). Two of these groups, bryozoans and brachiopods, have recently been the subject of study at Signy Island (Peck 1989, 1992; Peck et al. 1986 a, b, 1987 a, b; Barnes 1994, 1995; Barnes and Clarke 1994; Sanderson et al 1994). In the case of bryozoans, a group particularly well represented in the Southern Ocean, this research has largely been possible through recent improvements in taxonomy (Hayward and Thorpe 1987, 1988 a, b, c, d, 1989 a, b, 1990; Hayward and Ryland 1990; Hayward 1991, 1992, 1993). The present study, complimenting a parallel more detailed study on the ice-foot zone of the intertidal (see preceding paper: Barnes 1995), addressed the distribution and abundance of benthic communities from the anchor-ice zone to 40/50 m depth. Particular attention was paid to the phylum of bryozoans. The main aims of the present study were to determine the variation with depth of the percentage cover of substratum, the taxonomic composition of the community, and the growth morphology of the bryozoans.

Materials and methods

Study site and species

The transect component of this study was undertaken at Powell Rock and Outer Island, close to the British Antarctic Survey research station at Signy Island, South Orkney Islands (60°43′S; 45°36′W) in the maritime Antarctic (see Barnes and Clarke 1994 for a fuller description of the site). SCUBA observations were also made over a similar depth range at a number of other locations within Borge Bay. Specimens from 50 m down to 290 m were obtained from bottom trawls in Outer Borge Bay, between Signy Island and Coronation Island.

Limitations of underwater time, particularly at deeper parts of the SCUBA transect (0 to 40 m), dictated the use of photographic techniques. This in turn limited the taxonomic resolution of the study. To facilitate interpretation of these transects, and partly due to taxonomic complexity, algae were placed into three groupings: macroalgae, the coralline alga *Lithothamnion* sp., and *Hildenbrandia* sp. (see Table 1). Five animal phyla were recorded: sponges, cnidarians, brachiopods, bryozoans and urochordates (ascidians). The bryozoans, being particularly abundant, were subdivided into four morphological groups: encrusting, encrusting massive/foliaceous, erect flexible and erect rigid (see Table 2). The trawled specimens were available for taxonomic study, and various species of bryozoans are listed under these different morphological groups in the presentation of the trawling component results; the statistical comparisons were, however, largely between the morphological groups and not the individual species. Some animal taxa were present but not recorded; these included the annelids and entoprocts which, although abundant numerically, occupied comparatively negligible areas of substratum.

Transect method and analysis

The field work and analysis took place over the austral winter of 1991. At each station, photographic samples were taken every 5 m, along transect lines running from the sea ice to 40 m depth. The Outer Island 40 m transect was at the south end of the island; this is a different location from the 5 m transect at Outer Island of the preceding paper (Barnes 1995), hence the difference in profile. Five photographs were taken, each covering an area of 0.5 m^2, at every 5 m increment, using a Nikonos II underwater camera fitted with 35 mm lens and twin electronic flashguns. Photographs were taken on colour reversal film which was developed on site and projected onto a screen composed of 7700 points in a regular grid. The amount of area occupied by the base of each group was divided into the total area of the photograph to give the percentage area covered. Mean values for each taxonomic group were calculated from five replicates at each depth. The depth profile of each location was also recorded.

Trawl method and analysis

Specimens were collected and sorted from 28 trawls at depths ranging from 50 to 290 m during the austral summer of 1991/1992. An Agassiz benthic trawl was towed for bottom durations of 15 min at each location. A combination of echosounder and hydrographic charts was used to ensure that each sample came from a narrow range of depths (within 10 m of the nominal depth). This aspect of the study was solely concerned with bryozoans. Bryozoan specimens were identified, where possible, on sorting, or sent to Dr P. J. Hayward at the University College of Swansea, Wales, for identification. Species were recorded as either abundant if they were found in >2 trawls from any one depth or merely present if found in ≤2 trawls from a given depth.

Results

At both transect locations the substratum profile was a shallow slope down to ~15 m, with one small vertical ledge at each site (Fig. 1). The rock face then steepened to 25 m at Powell Rock and 35 m at Outer Island. The substratum at both sites was then characterised by shallow sloping rock and pebble rubble until about 37 m, whereafter it comprised soft sediment with occasional rock outcrops.

The taxa recorded on the SCUBA transects are listed in Table 1. Algae, particularly a coralline alga (probably *Lithothamnion* sp.) dominated the gradually sloping shallow-water component of both transects. Another coralline alga (probably *Hildenbrandia* sp.) became more abundant at ~15 m and likewise macroalgae, such that algae in general were the major occupiers of space almost throughout the transects. At the deep end of the transect (35 m and deeper), the macroalgae were the largest occupiers of space, and at 40 m macroalgae were the only algal group present. Animal phyla generally became abundant at ~15 m, although they were also locally abundant at shallower depths where vertical shelves occurred. Of these animal taxa, sponges and bryozoans were by far the largest occupiers of space, although representatives of the cnidarians, brachiopods and ascidians were also very common in places. Some animal phyla such as the annelids and entoprocts were common but only occupied relatively small areas. Other phyla such as the echinoderms, not being sessile or encrusting, were not recorded by this study despite being locally abun-

Table 1 Taxa of organisms occurring in communities surveyed by SCUBA transects at Powell Rock and Outer Island, Signy Island, Antarctica (*nr* not recorded)

Phyla present	Designation	Comments
Phaeophyta, Rhodophyta	"Macroalgae"	Macroalgae grouped because of taxonomic complexity
Rhodophyta	Genera *Lithothamnion* and *Hildenbrandia*	Separated from macroalgae because of growth form
Porifera	Phylum Porifera	–
Cnidaria	Phylum Cnidaria	–
Annelida	nr	Insignificant area occupied
Mollusca	nr	Mobile fauna
Entoprocta	nr	Insignificant area occupied
Brachiopoda	Phylum Brachiopoda	
Bryozoa	Morphological groups	Listed in Table 2
Echinodermata	nr	Mobile fauna
Chordata	ascidians	

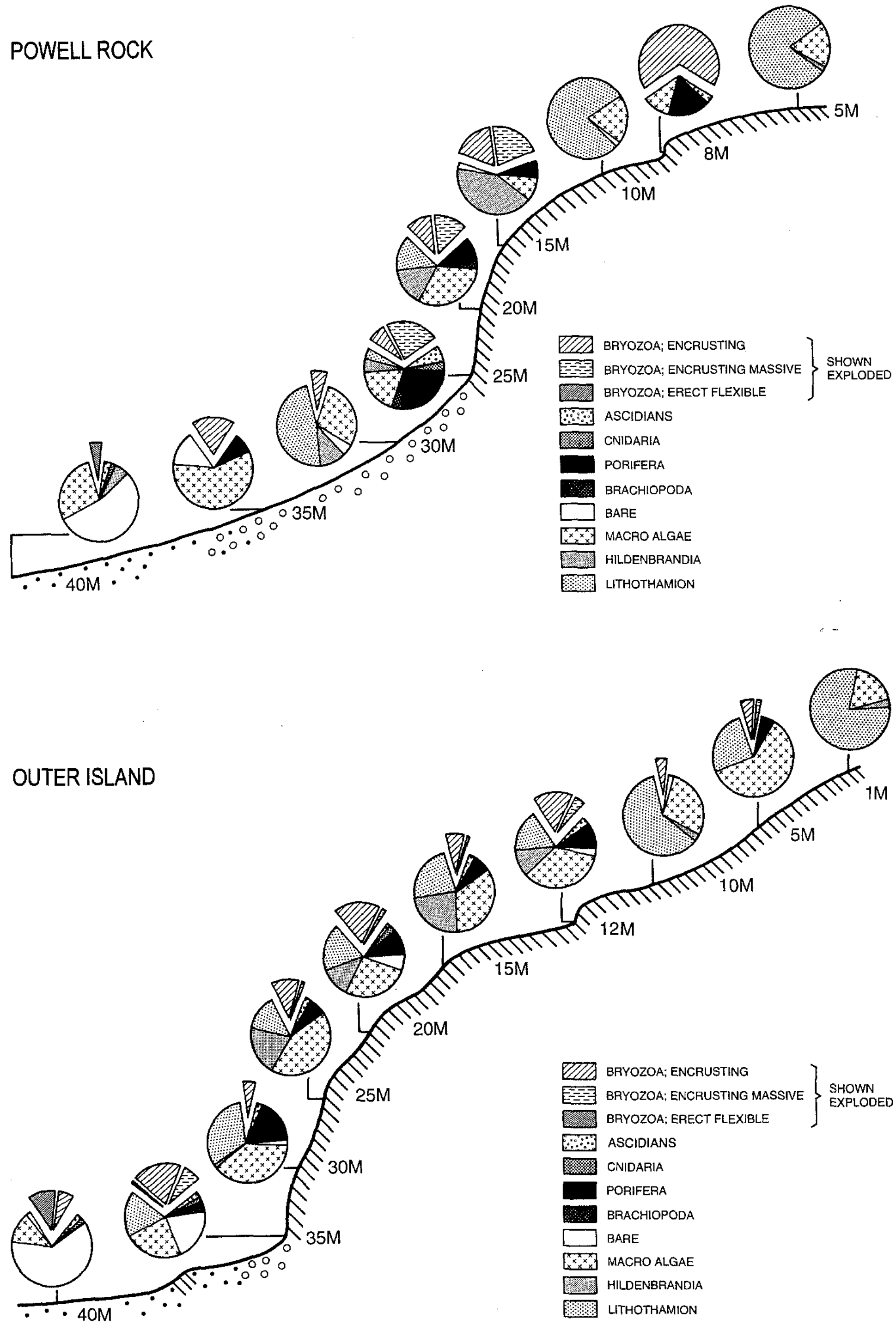

Fig. 1 Substratum profile of transect sites, with percent substratum cover by colonising benthos represented as pie charts (Substratum types: *hatching* rock face; *circles* rock/pebble rubble; *dots* sediment). Pie chart data presented as mean of five samples of percentage area of substratum occupied. Section of each pie representing the Bryozoa is shown exploded

dant on some transects. The amount of substratum void of surface colonisation increased dramatically at ~35 m, and at 40 m over half the substratum surface was uncolonised.

Animal groups were the largest occupiers of space in only a few locations, and at these locations, bryozoans constituted the major proportion. The bryozoan component of the SCUBA transects were divided into three broad morphological groups: encrusting species dominated by *Beania erecta* Waters, encrusting massive/foliaceous species dominated by *Arachnopusia inchoata* Hayward & Thorpe and *Lageneschara lyrulata* (Calvet), and erect flexible species dominated by *Alloeflustra tenuis* (Kluge) and *Nematoflustra flagellata* (Waters). The encrusting group constituted an important proportion of the bryozoans from the shallowest locations at which the phylum occurred down to 35 m. The encrusting massive group was much more abundant at Powell Rock than Outer Island, and at both sites was found only on the steeper areas of rock face. In contrast, the erect flexible group was abundant only at 40 m on the sediment substratum, where it was the largest

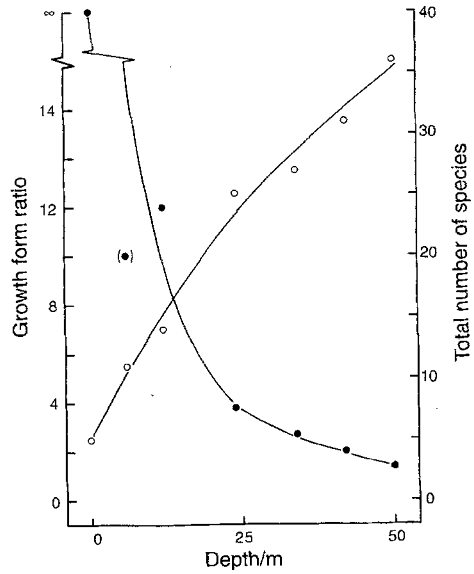

Fig. 2 Ratio of encrusting and encrusting massive/foliaceous to erect (flexible and rigid) cheilostome Bryozoa and number of species as a function of depth from 0 to 50 m [● ratios of total numbers of species found at these depths at all study locations in Borge Bay; (●) single specimen of one erect species known from unusually shallow location; ○ total numbers of cheilostome species found at these depths at all study sites]. Data points for 50 m depth were taken from trawl data

Table 2 Bryozoans, grouped according to colony growth form, recorded by transects (0 to 45 m using SCUBA) and by trawls (50 to 290 m)

Growth form of bryozoans	Transect (0–45 m)	Trawl (50–290 m)
Encrusting	+	
Encrusting massive	+	+
Erect flexible	+	+
Erect rigid		+

occupier of space, not only of the bryozoan groups but also of all the animal phyla.

Variation of bryozoan morphology with depth

In both SCUBA transects, the shallowest occurring bryozoan morphology was encrusting forms, followed with increasing depth by encrusting massive/foliaceous and finally erect flexible forms. The ratio of encrusting (including encrusting massive/foliaceous forms) to erect species was calculated from this study together with data collected from the parallel companion study (Barnes 1995) and incidental SCUBA observations. This ratio showed a striking variation with depth (Fig. 2). The outlying point at 6 m depth was due to a single colony of an erect species at one location. One species (*Arachnopusia inchoata*) changed classification between 12 and 24 m: it was of predominantly encrusting form in shallow water but exhibited predominantly erect morphology in deeper locations.

Erect forms were abundant in the trawled material, whilst encrusting forms were virtually absent. This was partly a sampling artefact, as trawling would have collected erect forms preferentially, although the trawled biota suggested that the substrata encountered were mostly soft sediments, where encrusting species would be rare. The 33 erect species found were grouped into three morphological categories; encrusting massive, erect flexible, and erect rigid. The third of these morphological categories was recorded from trawled material but not from the SCUBA transect (Table 2). Of these 33 species, 8 were classified as abundant (present in >2 trawls at any depth), whilst 3 species were only recorded at one location. These trawl data have been combined with information obtained from SCUBA in the range 0 to 45 m to provide an overall picture of bryozoan distribution (Fig. 3). There were no trawls spanning the depth range 230 to 290 m, although species found at both 230 and 290 m are joined by a continuous line in Fig. 3. *Carbasea ovoidea* (Busk), shown as occurring shallower than other erect flexible species, was represented by only a single colony at <18 m.

Discussion

Distribution and abundance of phyla from 0 to 40 m

Benthos other than algae was scarce shallower than 12 to 15 m, although the degree of substratum colonised shallower than 12 to 15 m was ≃99% (Fig. 1). From 15 to 30 m, a number of taxa were abundant and the colonisation level of the substratum remained high, although both number and abundance of taxa and the fraction/percentage of substratum occupied decreased rapidly to 40 m. Little is known of the zone immediately below 30 m in Antarctic waters (Arntz et al. 1994), which is considered too deep for routine SCUBA diving but too shallow for ship-based trawling work. Sponges and their predators were characteristic at this depth in similar areas studied in McMurdo Sound (Dayton et al. 1974). Between 30 and 40 m in both SCUBA transects and other studied areas of this depth at Signy Island, the substratum changed from hard rock to predominantly soft sediment. Determination of zonation within this deeper region was not possible because of the difficulties of separating the effects of substratum type, profile and depth.

Along the course of the transect, the orientation of the hard substratum profile of both Powell Rock and Outer Island changed considerably. Coralline algae tended to dominate upward-facing rock, particularly in the shallow locations, but the presence of a steeper or vertical slope, as seen at 12 m at Outer Island and 8 m at Powell Rock, respectively, resulted in a dramatic shift in balance from coral-

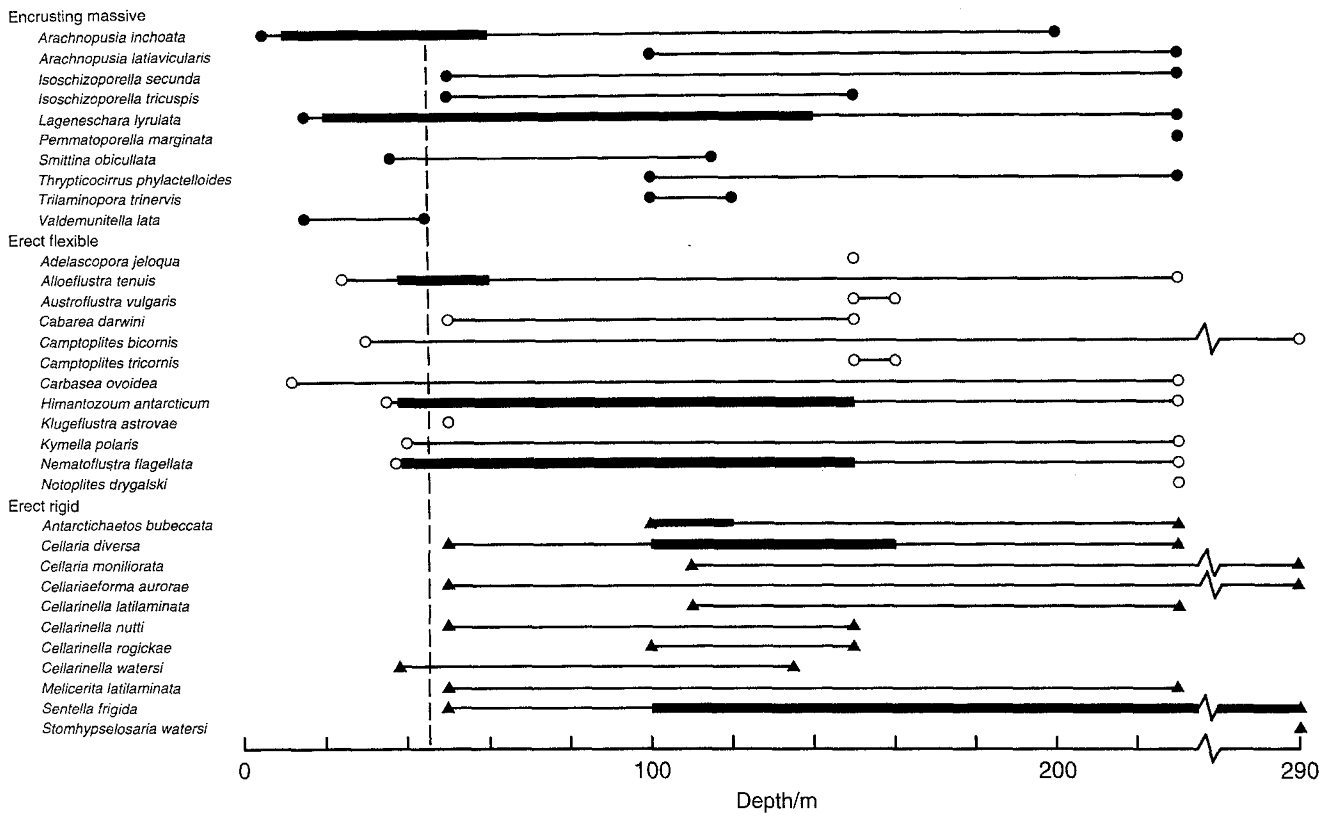

Fig. 3 Depth distributions of 33 erect cheilostome species of Bryozoa from 0 to 290 m. Species grouped into three morphological forms (● encrusting massive; ○ erect flexible; ▲ erect rigid; *filled bars* abundance; *lines* presence). Dashed line separates 0 to 45 m data from observations and collections using SCUBA, and 50 to 290 m data from 28 discrete benthic trawls

line algae to animal taxa. The colonising biota at the 1 and 5 m locations of the two transects was very different from that of three transects at Signy Island which covered this depth range with similar substrata types but with vertical profiles (Barnes 1995). Small changes in profile produced large changes in taxonomic composition and abundance within the 5.5 m range covered by the other study. Although there were some affects of profile on taxonomic composition and abundance below 15 m depth in the present study, these were small: relatively large variations in profile produced smaller changes in biota. This would suggest that the influence of profile on epifaunal composition is at its greatest in the shallower locations. Profile affects both the amount of light reaching the substratum and also the frequency and degree of damage by floating ice. Both of these factors will be more pronounced at shallow locations, as ambient light and the frequency of ice scour decrease with depth. As a result, light-dependent algae dominate the shallow upward-facing substratum and light-independent animal groups dominate the shallow vertical substratum.

Major changes in community composition with substratum orientation are well known from non-polar latitudes, particularly from a number of recent rocky, shallow, subtidal studies on the coast of New England (Steneck 1978, 1986; Garwood et al. 1985; Sebens 1986 a, b; Ojeda and Dearborn 1989). Such studies have similarly documented domination by coralline algae on inclined (and horizontal) shallow rock and by encrusting fauna on vertical or overhanging rock. There are fewer studies of hard substratum communities in deeper water (or what has been termed the circalittoral see Logan et al. 1984; Logan 1988) below the infralittoral (0 to 14 m). Circalittoral communities of the Bay of Fundy were described by Logan (1988) as being dominated by encrusting fauna irrespective of rock orientation.

In this study, the influence of depth may be separated from that of profile by comparing the communities at locations of different depths but similar profiles [the vertical hard substratum at the Powell Rock and Outer Island 25 m sites with those at 8 m at Powell rock and the three 5.5 m surveys (see Barnes 1995)] to separate depth and profile. Whilst the two 25 m locations were characterised by a number of abundant phyla, the shallow locations were dominated by bryozoans. Observations of the overgrowth hierarchy during this study and others (Barnes 1995) have revealed that bryozoans were overgrown by most other animal phyla on contact. Perhaps the higher disturbance frequency by ice at 5 to 8 m restricts community development to a greater degree than that at 25 m. Large areas of substratum at 15 to 25 m were occupied by competitively weak taxa (that is, taxa that were usually overgrown at contact points with other taxa). This suggested the possibility that the disturbance frequency of the 15 to 25 m study sites was instrumental in maintaining the high level of faunal diversity, as has been suggested for deep-sea benthos (Dayton and Hessler 1972) and proposed as a general hypothesis of diversity (Grime 1973; Connell 1978; Huston 1979).

Zonation with depth was also noted on other substrata such as sediment: at several locations within Borge Bay, the substratum was dominated by soft sediment from 4 to 48 m, but the surface was virtually uncolonised by superficial fauna at depths shallower than 35 m depth. Substratum type, therefore, had the largest affect on taxonomic composition and abundance of colonising biota, but within a given substratum profile and depth were important factors, as was also found in macrobenthos studies of the Davis Sea (Kirkwood and Burton 1988).

Distribution and abundance of bryozoans from 0 to 50 m

At nearly all locations of this study, irrespective of substratum type, profile and depth , bryozoans were the largest occupiers of space of all the animal phyla. Such levels of abundance or area dominance by bryozoans have rarely been described from the sublittoral of other latitudes, with the exception of cryptic habitats such as caves (Harmelin 1985, 1986) or the undersurface of coral heads (Jackson 1979). The proportion of area occupied, the morphological group, and the species dominating within bryozoans, all changed with substratum type, profile and depth. *Arachnopusia inchoata* was abundant in encrusting form in shallow water and as large foliaceous forms in deeper water. Mechanical damage from wave and current action may have been largely responsible for a shift in the type of surviving morphology with depth rather than an actual shift of growth morphology with depth. At certain locations, encrusting species occurred as shallow as the intertidal (Barnes unpublished data), encrusting massive species were common on hard substrata at 15 m and deeper, and erect species became abundant at 35 m and deeper. At Borge Bay, Signy Island, the ratio of encrusting to erect species approached unity by 50 m (Fig. 2). The number of species over this depth range was 36 at 50 m compared with just 5 recorded in the intertidal zone. Much of this increase in numbers of species with depth reflects the increasing numbers of erect species. Thus, even where bryozoans were very abundant at 40 m and deeper, the amount of substratum surface covered was small compared with hard substrata. Within the study sites, the largest area occupied by bryozoans relative to other biota was the shallow, vertical, hard substrata between 5 and 8 m.

Distribution and abundance of erect bryozoans from 0 to 290 m

The separation of the erect cheilostome bryozoan species into morphological groups (Fig. 3) is very useful for broad comparisons, although obviously conclusions must be treated with an element of caution because of: (1) differences in technique – observation and collection using SCUBA over 0 to 45 m and trawling from 50 to 290 m; (2) the bias of trawling – not all benthic species are equally likely to be represented in the material collected.

Many of the erect species, of all morphologies, occurred over much of the depth range encompassed by this study (Fig. 3). These results suggest that the encrusting massive/foliaceous forms occurred and became abundant at the shallowest locations, but were scarcer at the deeper locations than the erect flexible forms. The latter, as a group, had a similar distribution pattern but were abundant at shallower depths than the rigid erect species. The erect form of growth, whilst possibly conveying advantages over encrusting forms in feeding, competition and substratum utilisation (Cheetham 1971; Jackson 1979; Grosberg 1981), encounters the problem of resistance to water flow (review by McKinney and Jackson 1991, pp 167–189). Most erect bryozoan species occurring in environments likely to experience higher flow rates are flexibly erect, although this study showed some encrusting massive/foliaceous species occurring in shallower locations. This is because these species (e.g. *Arachnopusia inchoata*) grow mostly in the encrusting form at depths shallower than 15 m. Only one small community of a single rigid erect species, *Cellarinella watersi* Calvet, was found shallower than 50 m (Barnes personal observation), but species of this morphological type are abundant in many of the deeper Antarctic shelf locations studied (Winston 1983; Winston and Heimberg 1988).

Conclusions

Dense benthic communities may occur in very shallow Antarctic waters and taxonomically rich communities at depths >15 m. The change in frequency of disturbance with profile and depth probably accounts for most of the variation in hard-substratum communities at these localities. The principal faunal component, in terms of area colonised, in this depth range are bryozoans. Although antarctic bryozoans are overgrown by most other faunal elements, the frequency of disturbance (largely by ice) and recolonisation results in the faster colonising bryozoans occupying most of the available area. The dominant morphologies of bryozoans change with increasing depth (at the study locations this was also linked with a change from hard to soft substratum) from the predominantly encrusting form through a variety of erect morphologies. There is a very high degree of overlap within these forms, and some species change their growth form with depth.

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