

ORIGINAL PAPER

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Benthic faunal associations on soft substrates at Potter Cove, King George Island, Antarctica

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Abstract Associations of benthic invertebrates from Potter Cove (Antarctica) were defined from photo-transects. Density, percentage cover, species richness S' , diversity index H' , evenness index J' and mean-size estimations were studied in relation to water depth down to 30 m. A clear bathymetric pattern was evident, with two different communities at 15 and 30 m, and a transition area between 20 and 25 m. At 15 m we observed a small number of taxa (nine in total), a high percentage of bare substratum (95%), and the dominant species were pennatulids and the bivalve *Laternula elliptica*. From 20 to 30 m the dominant species was the ascidian *Molgula pedunculata* and there was a slight increase in S' , H' and J' , as well as in the mean size of individuals, especially in *M. pedunculata*, while the proportion of bare substratum showed a constant decrease with depth. Using multivariate analyses, three faunal assemblages related to depth were defined and a strong association of some species, mainly predators and opportunistic necrophages, with *M. pedunculata* was revealed. Ice impact (icebergs and anchor ice) seems to be the major regulating factor of benthic assemblages in shallow waters.

Introduction

Biological zonation patterns and changes in faunal assemblages along a bathymetric gradient in shallow

subtidal and intertidal communities have been reported worldwide by several authors (Dayton et al. 1970; Dayton 1971; Paine 1974; Witman 1987; Metaxas et al. 1994). The factors that define these patterns are mainly physical disturbances in the upper levels and biological interactions such as competition, predation, and the settlement rate of larvae of benthic organisms and their post-settlement success in the deeper levels, where highly stressing physical disturbances are not so frequent (Paine 1966, 1971; Dayton 1971; Dayton et al. 1974; Menge 1976; Menge and Sutherland 1976; Osman 1977; Buss 1981; Paine and Levin 1981; Woodin 1981; Dethier 1984; Watanabe 1984; Connell 1985; Roughgarden et al. 1985; Lewis 1986; Witman 1987; López Gappa 1989; Diaz-Castañeda et al. 1993; Edgar and Aoki 1993; Rodríguez et al. 1993).

In the Antarctic sublittoral the principal factor of physical disturbance is the impact caused by the annual formation of anchor ice in conjunction with ice scour and icebergs, producing marked zonation patterns in community structure (Dayton et al. 1969, 1970, 1974; Bellisio et al. 1972). Below the ice impact zone, biological interactions act as the main structuring force on benthic communities (Dayton et al. 1974).

Photo- and video-transects are techniques that allow the quantitative analysis of communities, providing information about habitat, abundance, percentage cover, and species associations of benthic assemblages, and that also allow a fast data acquisition in the field. However, these methods may underestimate abundances of small, cryptic and highly mobile individuals (Barthel et al. 1991; Leonard and Clark 1993; Roberts et al. 1994). In Antarctic waters, photographs have been used to define benthic assemblages (Dayton et al. 1974; Barthel et al. 1991; Barthel and Gutt 1992).

Community is the level of biological organization most extensively used for the assessment of environmental impact (Dayton 1972; López Gappa et al. 1990, 1993; Warwick 1993; Meire et al. 1994; Zmarzly et al. 1994) because benthic organisms are highly sensitive to bioaccumulation of contaminants and their diversity

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and abundance constitute a useful measure of ecosystem health (Thouzeau et al. 1991). Given this potential for disturbance to influence the benthic communities, the identification and description of macrobenthic associations are important, not only in addressing issues fundamental to ecology, but also for being the first step in the conservation of coastal ecosystems. Despite the comprehensive research carried out at Potter Cove, no study has so far described its benthic animal communities. In this study we examine the benthic associations across a bathymetric gradient on a soft bottom at Potter Cove using a photographic technique.

Materials and methods

Investigation area

Potter Cove ($62^{\circ}14'S$, $58^{\circ}38'W$), where the Argentinian station Jubany and the Argentinian-German laboratory Dallmann are situated, is a tributary inlet close to the entrance of Maxwell Bay, one of the two big fjords of King George Island (Fig. 1). The cove is divided into a mouth and an inner part. The mouth has an area of

about 3 km^2 and is bordered by steep slopes down to 100 m to the north and by a broad intertidal platform to the southwest. Hard bottoms and macroalgae dominate this area (Klöser et al. 1994). The inner cove has an area of 1.5 km^2 , is covered by muddy and sandy sediments, and is no deeper than 50 m. The soft bottom is colonized by a diverse community of sessile animals (Klöser et al. 1994).

Investigations were carried out in the austral summer 1994/1995. Raw data were obtained from photo-transects taken at 1-m intervals along a 50-m line at particular depth profiles (15, 20, 25 and 30 m) covering 50 m^2 in total. The photographs were taken using a Nikonos V camera with a 15-mm lens and a Subtronic SF 3003 TTL strobe, both mounted on an aluminium "quadrapod" ($50 \times 50\text{ cm}$) (Kühne 1992). Samples were also taken for identification. Photographs were projected onto grids of 100 random points and the number of points underlying each organism were counted to estimate percentage cover and bare substratum. All the animals in each photograph were counted and the total number divided by the area sampled to estimate densities. A coefficient between total density and total percentage cover at each depth was calculated to estimate mean-size of individuals at different depths. The same coefficient was calculated for *Molgula pedunculata*.

Data analysis

We analysed bathymetric variation in community structure by comparing species richness (S), Shannon-Wiener diversity index (H') and evenness index (J'). These indices were calculated separately for each sample, in order to estimate means and standard deviations. The values of S , H' and J' for different depths were compared using one-way analyses of variance (ANOVA). Homogeneity of variances were tested using Cochran's C test. Cluster analyses were performed to describe the similarity among samples and the pattern of species association, using the product-moment correlation as a measure of similarity and the complete linkage method to build dendrograms. This technique provides an objective basis for revealing patterns of community structure (Witman 1985).

Results

We recorded a total of 20 taxa (Table 1), the majority being ascidians and echinoderms. A pattern of depth zonation became evident at the study site. The percentage cover and density of each species along a bathymetric gradient are shown in Fig. 2. At 15 m the situation was characterized by the low number of taxa (nine in total), the high percentage of bare substratum (95%), and the dominance of pennatulids and the bivalve *Laternula elliptica*. At 20 m there was a marked shift in community structure, the ascidian *Molgula pedunculata* becoming the dominant species. Also there was an increase in the number of taxa (12) and a decrease in the percentage of bare substratum (85%). This trend was maintained down to 25 m (14 taxa and 81% bare substratum). At 30 m the community was dominated by six ascidians: *M. pedunculata*, *Aplidium radiatum*, *Corella eumyota*, *Ascidia challengerii*, *Cnemidocarpa verrucosa* and *Pyura setosa*. Except for *Aplidium radiatum*, these species are solitary, *M. pedunculata* being the most abundant organism ($16.32\text{ individuals/m}^2$).

The highest number of taxa, 20 in total, and the lowest percentage of bare substratum (65%) were found at a depth of 30 m. The largest individuals of all species

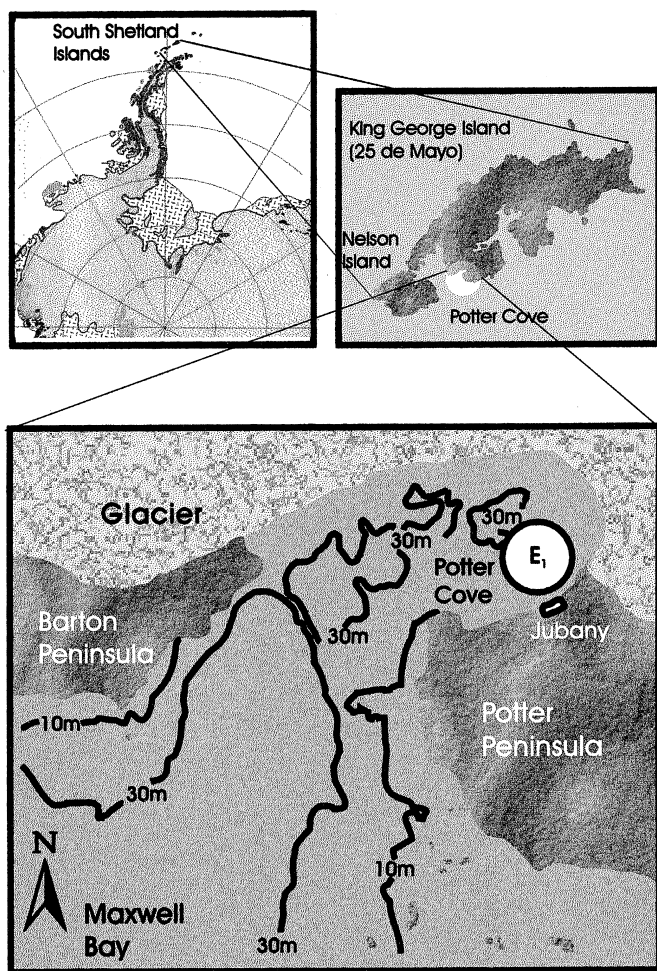


Fig. 1 Map of Potter Cove and its location at King George Island and Antarctica. Sampling station E_1 is highlighted

including *M. pedunculata* were also present at this depth, as shown by the variation of the mean size of individuals with depth (Fig. 3).

Table 1 List of taxa sampled and abbreviations used in figures

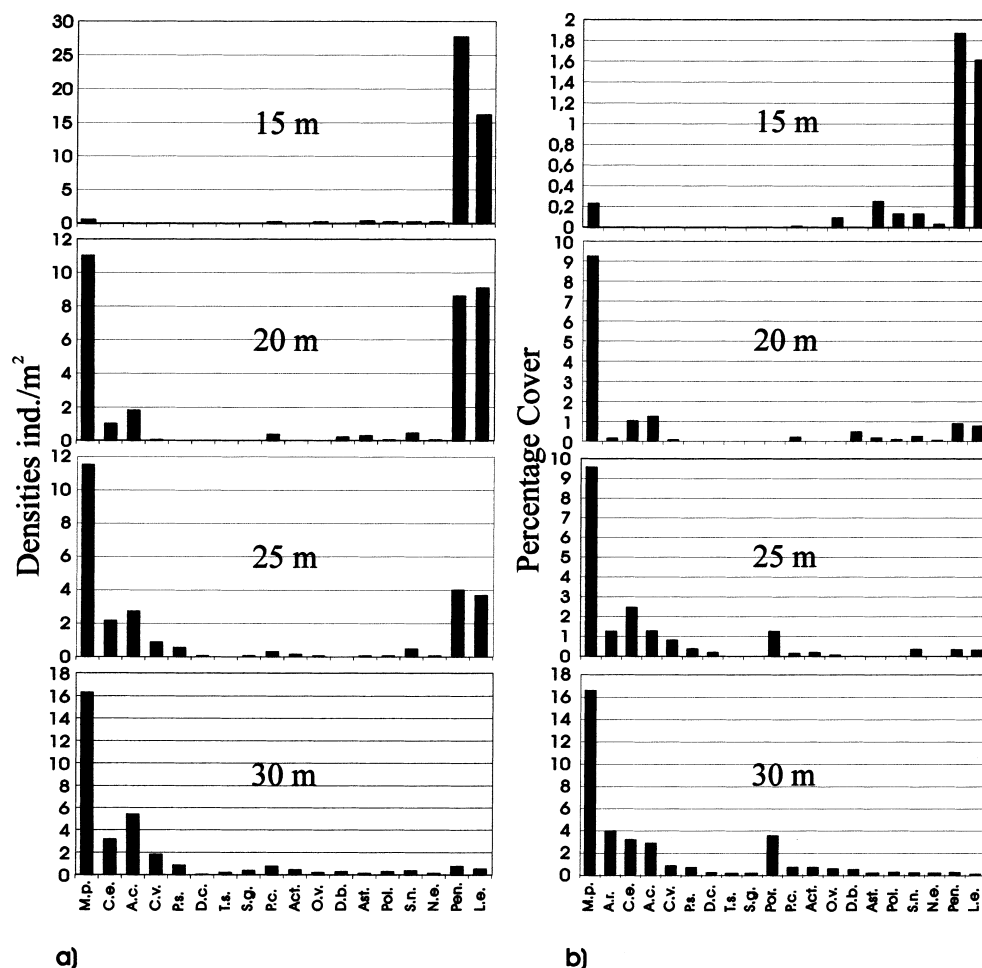
Taxa		Abbreviation
Ascidacea	<i>Molgula pedunculata</i>	M.p.
	<i>Aplidium radiatum</i>	A.r.
	<i>Ascidia challengerii</i>	A.c.
	<i>Corella eumyota</i>	C.e.
	<i>Cnemidocarpa verrucosa</i>	C.v.
	<i>Pyura setosa</i>	P.s.
	<i>Tilobrachion speciosum</i>	T.s.
	<i>Sicozoa gaimardi</i>	S.g.
Porifera	<i>Distaplia cylindrica</i>	D.c.
		Por.
Pennatulids		Pen.
Gastropoda	<i>Neobuccinum eatoni</i>	N.e.
Bivalvia	<i>Laternula elliptica</i>	L.e.
Asterioidea	<i>Diplasterias brucei</i>	D.b.
	Unidentified	Ast.
Ophiuroidea	<i>Ophionotus victoriae</i>	O.v.
Echinoidea	<i>Sterechinus neumayeri</i>	S.n.
Nemertina	<i>Parborlasia corrugatus</i>	P.c.
Actiniaria		Act.
Polychaeta		Pol.

The mean species richness S' showed significant increments with depth (ANOVA; F -ratio = 10.923, $P < 0.01$), as did the mean values of H' (ANOVA; F -ratio = 14.014, $P < 0.01$) and J' (ANOVA; F -ratio = 4.624, $P < 0.01$) (Fig. 4). The mean values of S' increased steadily from 15 to 30 m, whereas H' and J' values showed two extreme situations at 15 and 30 m and a transition between 20 and 25 m, where differences were not significant (Fig. 4).

The cluster analysis performed on the samples discriminated two main groups, with three sub-groups within the first group (Fig. 5). The main groups correspond primarily to samples characterized by low and high degrees of diversity found at 15 and 30 m respectively, while samples from 20 and 25 m were present in both groups.

Cluster analysis performed on species revealed three main groups, with two sub-groups within group 1 (Fig. 6). This analysis reveals strong associations between species that define the different communities found along a bathymetric gradient. The assemblage found at 15 m was dominated by *L. elliptica* and pennatulids, whereas the assemblages having their upper limit at 20 m were characterized by the dominance of *M. pedunculata*. This latter species had a patchy distri-

Fig. 2 **a** Abundance (percent-age cover) of the taxonomic groups present at each depth profile. Unfilled columns indicate the absence of the taxon at a given depth. **b** Densities (ind./m²) of the taxonomic groups present at each depth profile. Unfilled columns indicate the absence of the taxon at a given depth



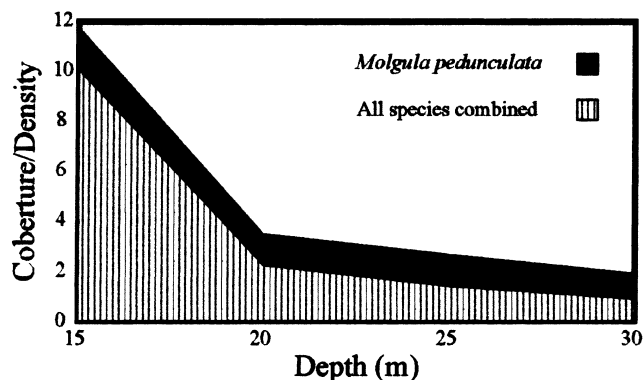


Fig. 3 Mean size estimation (percentage cover/densities) of all taxonomic groups combined and of *Molgula pedunculata* in relation to depth

bution. It formed highly clumped bunches, with which the other species are mainly associated, especially other ascidians and predators, such as *Diplasterias brucei* (seastar), which was directly observed predating *M. pedunculata* (Fig. 7). These patches were more frequent, larger, and richer in faunal composition as depth increased. We also registered the presence of epibionts, mainly erect and encrusting bryozoans, over the most abundant solitary ascidians, while colonial ascidians showed a surface completely free of epibionts. There was a marked variation in fouling between species, *M. pedunculata* being the most fouled species, being not only colonized by bryozoans but also by other ascidians, sponges, actinians, etc. Other ascidians, however, like *Cnemidocarpa verrucosa*, *P. setosa* and *Corella eumyota* showed less fouled surfaces. *Corella eumyota* was only colonized by encrusting bryozoans, and *Ascidia chalcengeri* exhibited a surface almost free of epibionts.

Discussion

The benthic faunal organization of the soft bottom at Potter Cove and the depth zonation patterns observed down to 30 m may be explained, first of all, by the erasing action of icebergs. We have observed deep depressions in the bottom, down to 20 m, caused by icebergs. Such impacts remove all the bottom fauna over extensive areas. Moreover, anchorice formation is able to remove weights up to 25 kg (Dayton et al. 1969). Although we never observed this latter phenomenon it has been described by divers who worked during the winter season. These phenomena may be responsible for the removal of the established fauna in their area of influence, thus accounting for the low diversity and high percentage of bare substratum observed at 15 m. This situation is similar to that at McMurdo Sound described by Dayton et al. (1970, 1974). There, however, anchorice impact is the main cause of the low diversity pattern in shallow waters, and its influence extends down to 33 m. The relatively high density of *L. elliptica* at 15 m

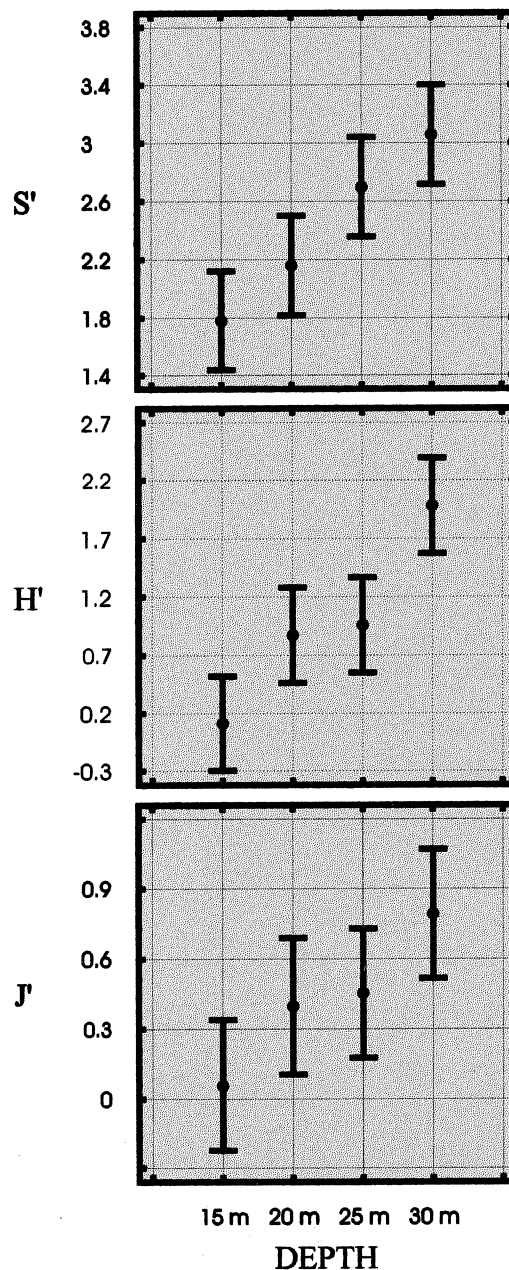


Fig. 4 Mean values of species richness S' , H' and J' in relation to depth (Scheffé intervals are represented)

may be explained by the animals' capacity to bury themselves, enabling them to avoid the ice impact. The pennatulids are also very abundant in this areas due to their high growth rates with an almost complete generation cycle in 1 year, thus acting as opportunistic species with an r-strategy (J. Kowalke unpublished data). The success of these two different strategies, one infaunal and the other opportunistic, with a rapid colonization of the disturbed space and high growth rates, supports the idea of an area highly affected by ice action.

In the transition area, between 20 and 25 m, the ice impact may have lower occurrence and intensity than in shallower areas, being limited to the phenomenon of the

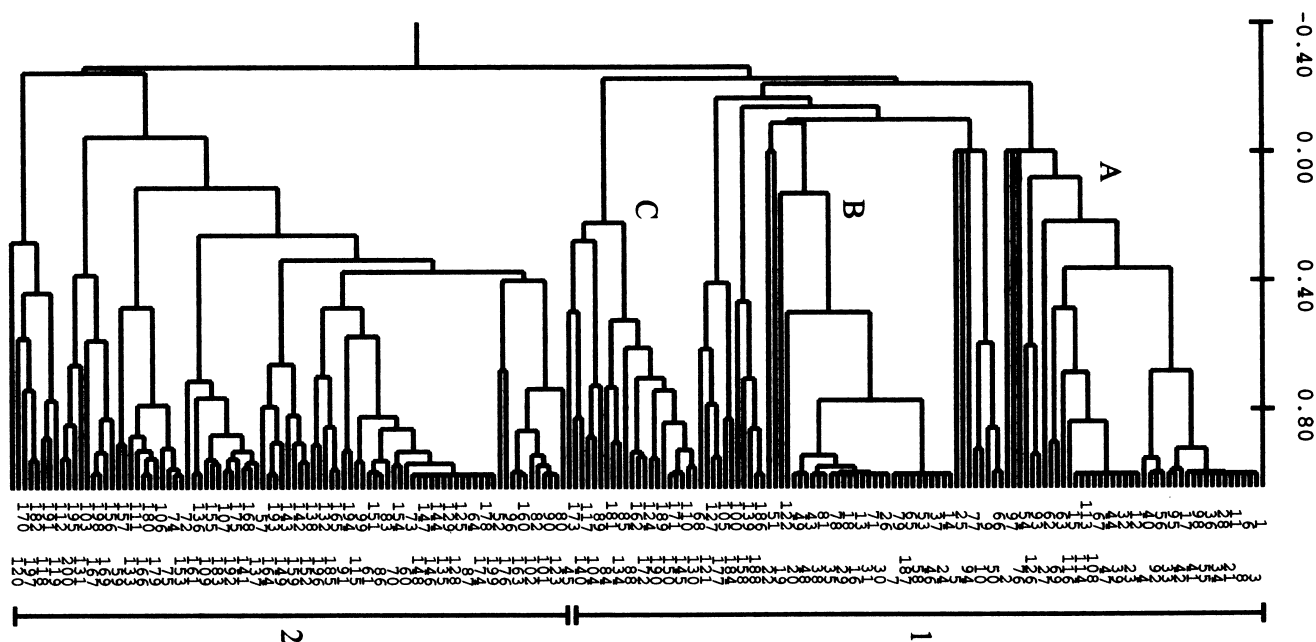


Fig. 5 Samples clustered by product moment correlation using the complete linkage method. Clusters 1A and 1B mainly grouped 15-m samples. All clusters include 20-m samples but they are best represented in group 1. The 25-m samples were evenly distributed in all the clusters, but had a higher representation in cluster 2. The 30-m samples were mainly represented in cluster 2

entrance of big icebergs into the cove, producing local effects of biomass removal. At this point, there is a change in community structure, with a reduction in pennatulids and infaunal species densities and the ascidian *M. pedunculata* being the dominant organism. This ascidian was distributed in patches with which other species were associated. Probably this occurs because the substrate is one of the more restrictive conditions determining the settlement and distribution of ascidians. Its larval life is usually very short, so the scarcity of a viable area for settlement is an important limiting factor for species dispersion (Monniot 1965). *M. pedunculata* could act by increasing the available surface, thus providing suitable substrate for the settlement for other species and enriching habitat heterogeneity.

The richest and most diverse community was found at 30 m (Fig. 4). Ice impact is very unlikely here, since there is a natural barrier in the mouth of the cove, a sill at 28–30 m, which prevents the entrance of large icebergs that could affect the faunal communities. Thus, the highly stressing physical factors should have less influence here than in the upper levels, whereas biological interactions such as predation, competition, settlement rate of larvae of benthic organisms, and post-settlement success may be the main structuring forces determining community structure. This hypothesis is supported by the larger size of the individuals compared to those of the upper levels (Fig. 3), which may indicate a long development time. Moreover, ascidians are considered to be successful competitors and also rank very highly in a hierarchical classification among other organisms in numerous ben-

thic associations (Osman 1977; Quinn 1982; Russ 1982; Sebens 1986; Turon 1990). Ascidians, therefore, dominate in less disturbed areas where biological interactions become the most relevant factor. The dominant ascidian *M. pedunculata* presents a long stalk that allows fixation on a relatively small surface, while the rest of the body remains over the bottom avoiding possible overgrowth from other species; this kind of structure represents an advantageous adaptation for benthic competition. However, substrate competition could be an important factor mainly limited to patches of *M. pedunculata*, where animal density is higher. The cluster analysis revealed a strong association of the starfish *D. brucei* and the nemertean *Parborlasia corrugatus*, besides other ascidians species, with *M. pedunculata*. *D. brucei* is an important predator that was observed several times preying on *M. pedunculata*. *Parborlasia corrugatus* is probably a opportunistic necrophage, as are many other Antarctic benthic organisms (Arnaud 1970), which feeds on ascidians already killed by *D. brucei*. This suggests that *M. pedunculata* constitutes not only increasing habitat heterogeneity for the settlement of other species but also constitutes a good prey and food source for predators and necrophagous species.

Although the competitive abilities of ascidians and their abundance in Antarctic waters (Monniot and Monniot 1983) were already known, this is the first report about an Antarctic benthic community dominated by this group and with high animal densities (Fig. 2). However, in McMurdo Sound the ascidian density was markedly lower, e.g. 0.04 individuals/m² for *Cnemidocarpa verrucosa* (McClintock et al. 1991) with the community dominated by sponges (Dayton et al. 1974) as in many other Antarctic benthic communities (Barthel and Gutt 1992).

Another point of interest was the presence of epibionts; these were mainly encrusting and erect bryozo-

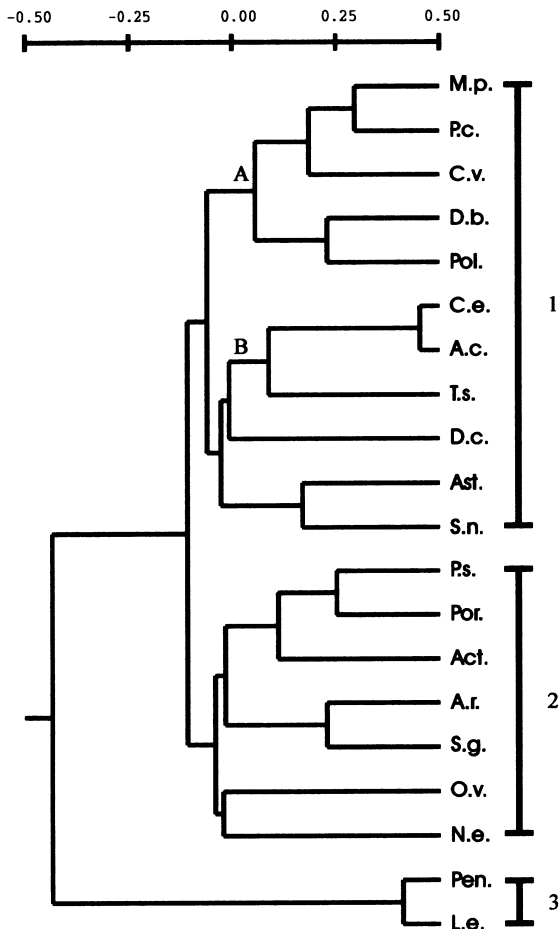


Fig. 6 Species clustered by product moment correlation using the complete linkage method. Cluster 1 (the largest unit) groups mainly those species found below 20 m. Cluster 1A included the most abundant species, *M. pedunculata*, its main predator, the asteroid *Diplasterias brucei* and the opportunistic necrophagous *Parborlasia corrugatus*. Cluster 1B included the other ascidian species that are associated with *M. pedunculata* and other asteroids, as well as the echinoid *Sterechinus neumayeri*. Cluster 2 was defined by those species mainly present at 30 m, except for the ophiuroid *Ophionotus victoriae* and the gastropod *Neobuccinum eatoni*, which were present in shallower waters too. Cluster 3 included only two taxa, which also defined the community at 15 m; the bivalve *Laternula elliptica* and pennatulids

ans, which are important members of epibiotic communities in sublittoral Antarctic assemblages (Barnes and Clarke 1995). Bryozoans colonized the most abundant solitary ascidians and showed a marked degree of fouling between ascidian species. This variation might suggest the presence of some antifouling mechanism in the less fouled species (Davis et al. 1989; McClintock et al. 1991; Teo and Ryland 1995).

In conclusion, in shallow waters up to 15 m the principal factors determining community structure are physical, mainly the ice action. However, in deeper waters up to 30 m the increase in size of the individuals, together with higher species richness and a higher degree of physical predictability, suggest that the faunal assemblages observed at this depth are in a more stable

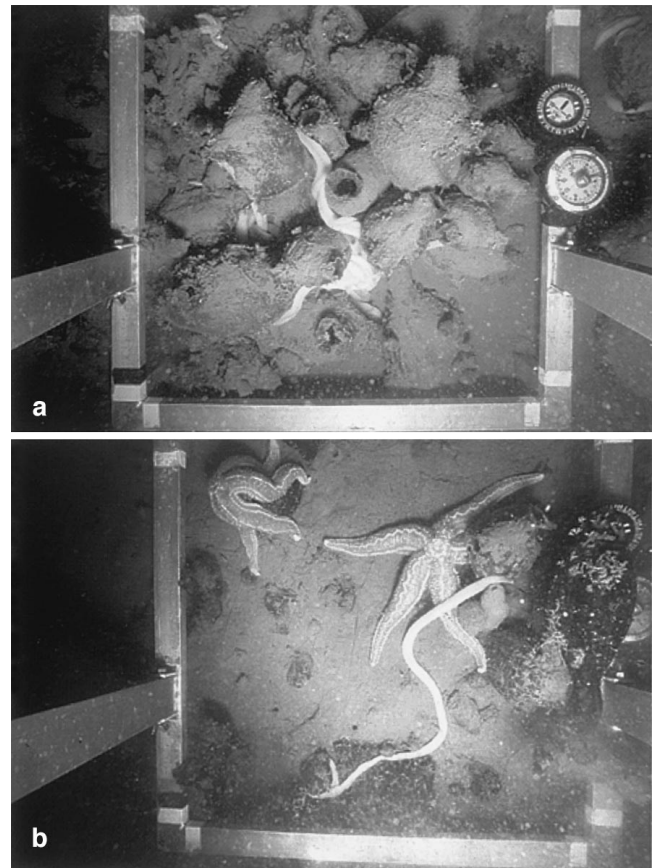


Fig. 7 **a** A highly clumped patch of *Molgula pedunculata*. Also shown are others members of the community like *Parborlasia corrugatus* and the tetrapod with the depth gauge and the compass attached. **b** *Diplasterias brucei* preying on *Molgula pedunculata*

situation than at 15 m, in an environment less affected by destructive events like ice impact, and are mainly regulated by biological interactions.

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