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## Mega-epibenthic communities in Arctic and Antarctic shelf areas

Received: 22 January 1999 / Accepted: 7 June 1999

**Abstract** Mega-epibenthic shelf assemblages were investigated off Northeast Greenland and in the Weddell, Bellingshausen and Amundsen Seas in the Antarctic using underwater video. In the Arctic a total of 94 taxa represented by more than 100 000 individuals were identified. Echinoderms, particularly brittle stars, were the most important elements of the mega-epibenthic fauna on the shelf off Northeast Greenland. Multivariate analyses of the species distribution revealed a conspicuous depth zonation in which an assemblage on the shallow banks can be clearly distinguished from that in the troughs. Between these a transitional zone with a heterogeneous benthic fauna was found. Physical disturbances are supposed to be responsible for the pronounced dominance patterns observed on the shallow banks. The fauna in the troughs, which consists of more than 50% suspension feeders, is diverse but low in numbers of individuals. In the Antarctic more than 115 000 individuals belonging to 169 taxa were analyzed. Obvious faunal differences exist between the stations in the Weddell Sea and the Bellingshausen/Amundsen Seas. Assemblages of suspension feeders dominated by sponges and bryozoans are prevalent on the shelf of the eastern Weddell Sea, but almost absent in the Bellingshausen and Amundsen Seas. These assemblages seem to be restricted to areas where bottom currents provide favourable feeding conditions. However, motile deposit feeders are more abundant in both regions where there is a soft bottom substrate with presumably slow bottom currents and reduced horizontal transport of organic particles.

### Introduction

In this study, we examined the distribution and structure of epibenthic assemblages both in the Arctic and in the Antarctic. The investigation sites were situated on the continental shelves of high-polar regions, in the zone of permanent pack ice (Hempel 1985), but where coastal polynas of varying size occur in all areas during summer (Hellmer and Bersch 1985; Yevsyeyev 1990; Schneider and Budéus 1994). This meant that the ecological parameters in all areas were essentially characterized by low, but relatively constant water temperatures, permanent or persistent ice cover in winter and occasionally during the entire year, as well as strong seasonality in light regime and primary production (Hempel 1985). One of the major features distinguishing between Arctic and Antarctic ecosystems is that the Arctic is an enclosed ocean surrounded by continental landmasses with shallow (< 300 m) shelves and freshwater inflow, whereas the Antarctic is a continental landmass surrounded by a deep shelf (500 to 800 m). Since the Antarctic continent is covered by ice, very little freshwater inflow occurs. During the last 20 to 30 million years the large-scale current regime in the Southern Ocean has developed into a cold ring ocean, which is one of the most discrete and thus zoogeographically isolated marine ecosystems in the world (Dayton 1990; Arntz et al. 1994). By comparison, the glaciation of the Arctic Ocean is thought not to have taken place before the Pliocene (4 million years ago), resulting in a cold-water environment as late as the Pleistocene (2 million years ago; Bleil and Thiede 1990). Besides the profoundly different evolutionary histories, the Antarctic benthos is not generally subject to the degree of mechanical disturbance experienced by the Arctic benthos, such as bottom-feeding fish, gray whales and walruses, surface-burrowing species and ice gouging (Dayton 1990; Dayton et al. 1994). However, several authors have shown that the Antarctic benthic environment can be exposed to more physical disturbance than expected (Gallardo 1987; Arntz et al. 1994;

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Communicated by O. Kinne, Oldendorf/Luhe

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Gutt et al. 1996; Gutt and Starman 1998). Both historical and recent biological as well as physical processes influence the structure of most benthic communities (Dayton 1990). Thus, it is likely that the differences in biogeographic histories and physical factors between the two polar systems will be reflected in their community structures.

Underwater video was chosen to provide quantitative data on the epibenthic communities as a whole. The Arctic area comprised the shelf off Northeast Greenland, which consists of a system of shallow banks (< 100 m) separated by troughs with a depth > 400 m. Fine-grained sediments cover the bottom and slopes of the troughs, whereas coarser fractions predominate on the shallower banks. The Antarctic area included the deep (< 500 m), narrow shelf of the eastern Weddell Sea in the Atlantic Sector of the Southern Ocean, as well as the shelves of the Bellingshausen and Amundsen Seas in the Pacific Sector. Poorly sorted sediments were mainly found in these areas. In contrast to the Bellingshausen and Amundsen Seas, the benthos of the Weddell Sea has already been studied in some depth (Voß 1988; Galéron et al. 1992; Piepenburg et al. 1997; Gutt and Starman 1998).

The main objectives of the present study were to: (1) depict distinct assemblages using multivariate classification and ordination techniques in order to account for the faunal heterogeneity of the different areas of investigation, (2) describe the composition and biodiversity of the communities, and (3) determine environmental factors that may influence faunal composition.

## Materials and methods

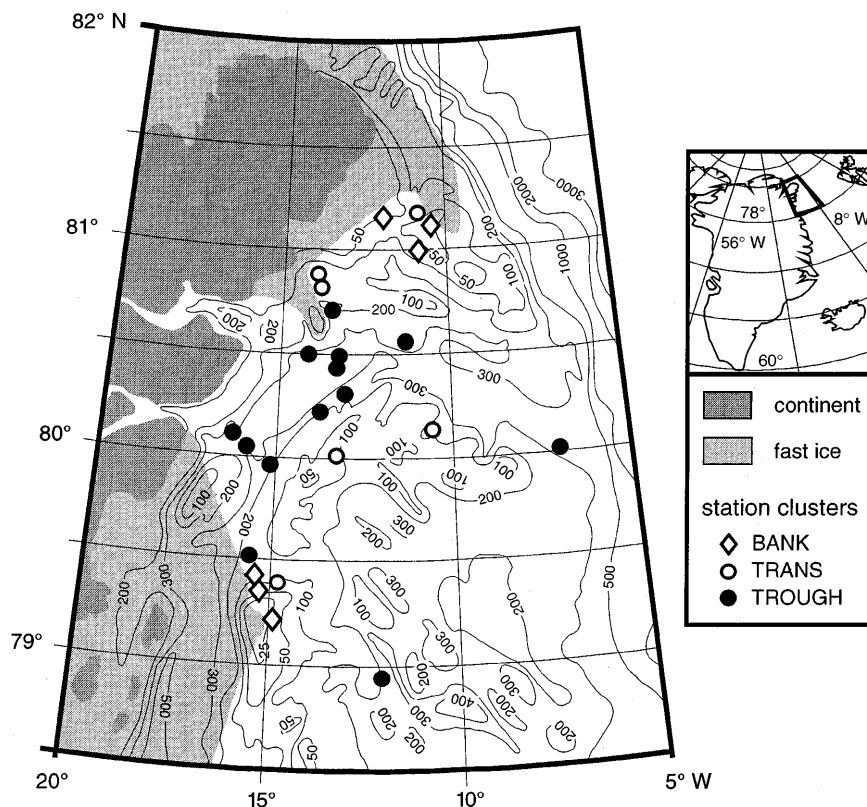
### Field sampling

The investigations were carried out aboard the German R.V. "Polarstern" during the expeditions ARK IX/2-3 (Northeast Greenland, 1993), ANT VI/3 (Weddell Sea, Antarctica, 1988) and ANT XI/3 (Bellingshausen Sea, Antarctica, 1994) (Figs. 1, 2). For cruise reports see Fütterer (1988), Hirche and Kattner (1994) and Miller and Grobe (1996). Data were collected using a remotely operated vehicle (ROV). All stations were situated either on the Arctic or on the Antarctic continental shelves at a depth of between 30 and 370 m or 140 and 550 m, respectively. Most stations comprised between 60 and 90 min of video observation of the sea floor. In order to achieve straight transects, the ROV was left suspended in mid-water and the ship allowed to drift. The transects had an average length of roughly 1 km. The width of the transects (average approximately 50 cm) was indicated by two parallel laser beams, which act as a scale on the image. Each station covered an area of between 82 and 1153 m<sup>2</sup> (average 406 m<sup>2</sup>). The optical resolution of the cameras permitted all organisms larger than 1 cm to be counted. In addition to the videos, a minimum of 100 still photographs were taken by the ROV at each station as an aid in identifying the taxa present.

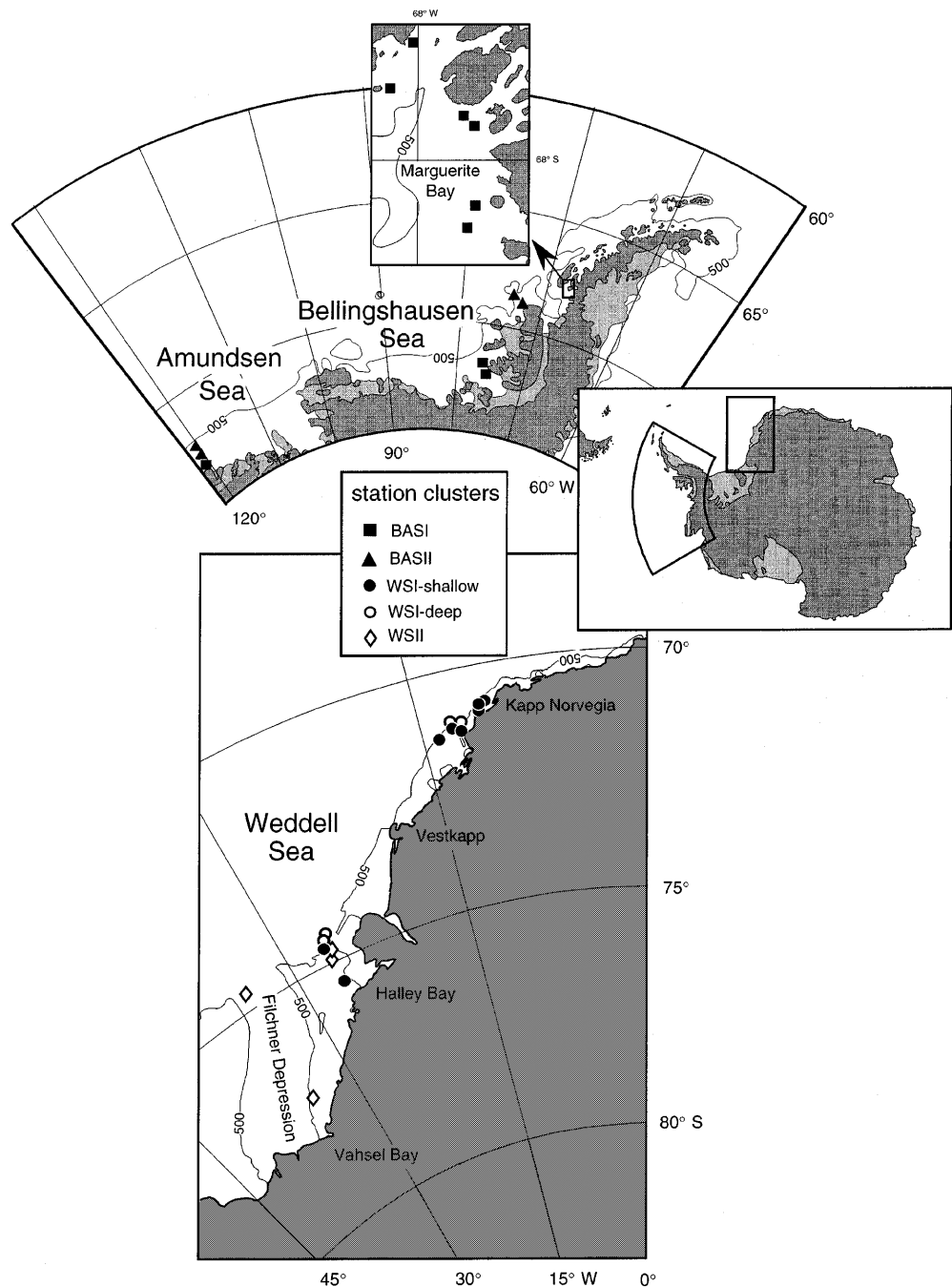
### Identification and counting

The following experts assisted in the identification of different species/taxa: V.M. Koltun (sponges), S. Grebelny (anthozoans), N.V. Slepikova (octocorals), H. Ristedt (bryozoans), S. Hain (molluscs), M. Stiller (polychaetes), F. Krapp (pycnogonoids), C. Dahm, D. Piepenburg and I. Smirnov (ophiuroids) and C. Monniot (ascidians). Virtually all visible organisms were counted, however, small encrusting forms were ignored. Wherever possible colonies were counted as single individuals (e.g. bryozoans and

**Fig. 1** Map of the stations in the Arctic (off Northeast Greenland)



**Fig. 2** Map of the stations in the Antarctic (*upper panel* Amundsen and Bellingshausen Seas; *Lower panel*, Weddell Sea)



ascidians); for other colonial taxa the percentage cover of the sea floor was multiplied by two to obtain a rough equivalent to the abundances of the other taxa. In subsequent calculations these values were treated as true abundances. Infaunal species were included when part of their body was visible. Abundances were standardized to numbers per 100 m<sup>2</sup>.

#### Community analysis and discriminator taxa

Abundances of taxa were summarized in separate taxa/station tables for the Arctic and Antarctic. Taxa were excluded if: (a) they occurred at more than 75% of the stations, since the omission of these taxa will only slightly affect the outcome of the analysis; or

(b) they occurred at only one station, so as to minimize the bias caused by the random occurrence of rare taxa (Field et al. 1982). Organisms which could not be fairly accurately identified were also omitted. A double square root transformation was used to weight the contribution of common and rare taxa (Field et al. 1982). Analyses were carried out for both stations (Q-mode) and taxa (R-mode) (Field et al. 1982). Similarities between stations and taxa were calculated using the Bray-Curtis coefficient (Bray and Curtis 1957). A classification (cluster analysis, complete linkage) of the similarity matrices was calculated for all stations and taxa. The multivariate similarity patterns of stations were depicted by ordination plots for multidimensional scaling (MDS, Kruskal and Wish 1978). A low MDS stress coefficient (<0.2) indicates that the multivariate similarity pattern is represented by a two-dimensional

plot without much distortion (Clarke 1993). A modified Bray–Curtis index (Clarke 1993) was used to identify discriminator taxa for each station group. In a pairwise comparison of station groups, the average contribution of each taxon  $\delta_{jk(i)}$  to the overall average dissimilarity ( $\delta_{jk}$ ) between two station groups,  $j$  and  $k$ , was computed. Good discriminator taxa contribute greatly to the average total dissimilarity between clusters but also do so consistently in inter-comparison of all stations in the two clusters, parameterized by a high quotient between  $\delta_i$  and its standard deviation  $SD(\delta_i)$ .

#### Diversity

Calculations only involved organisms which had been identified to the genus or species level. The commonly used Shannon diversity index,  $H'$  (using  $\log_e$ ; Shannon and Weaver 1964), and the Pielou evenness index,  $E$  (Pielou 1977), were determined for each station. Hurlbert's (1971) rarefaction method was used to calculate species richness. Non-parametric  $H$ -tests (after Kruskal–Wallis) were used to test the significance of differences ( $p < 0.05$ , two-tailed) among assemblages.

#### Relationship between physical and biological data

Investigation of the relationship between environmental and epibenthic distribution patterns involved recording the same four physical parameters in both the Arctic and the Antarctic, namely: water depth, longitude, latitude and distance between the station and coast (ice edge) for all areas of investigation. In addition, two further parameters were recorded for stations off Northeast Greenland (Arctic), i.e. the distance between each station and the 300 m depth contour of the trough system and the distance between the station and the eastern 300 m depth contour parallel to the continental slope. Also the distance between each station and the 500 m depth contour parallel to the continental slope was measured for the Antarctic stations. The explorative BIOENV procedure proposed by Clarke and Ainsworth (1993) was used to analyze the degree to which these parameters were related to the faunistic distribution. This method correlates the biotic pattern represented in the Bray–Curtis similarity matrix, using the harmonic Spearman rank correlation ( $\rho_s$ ), with the dissimilarities between stations computed for each of the ( $n$ ) abiotic variables alone ( $k = 1$ ), as well as for all their possible ( $k = 2, 3, \dots, n$ ) combinations. It is then possible to identify the sub-set of physical parameters that correlates best with the megabenthic distribution.

Data analysis was performed using the computer programmes PRIMER (Clarke and Warwick 1994), BioDiversity Pro (The Natural History Museum, London and Scottish Association for Marine Science, Oban) and StatView (Abacus Concepts, Inc.).

## Results

### Number of taxa

Off Northeast Greenland, a total of 94 mega-epibenthic taxa were identified comprising 101 054 individuals, including 16 sponges, 13 cnidarians, 5 bryozoans, 1 nemertean, 7 molluscs, 10 polychaetes, 3 pycnogonoids, 3 crustaceans, 17 echinoderms, 9 ascidiaceans and 10 fish species. The number of taxa per station ranged between 17 and 40 (see Table 1). In the Antarctic a total of 115 152 megabenthic specimens belonging to 169 taxa were recorded. The sponges, echinoderms and cnidarians accounted for the highest number of taxa (35, 33, 32) followed by the ascidiaceans (22), polychaetes (15), molluscs (14), crustaceans (6), hemichordates (5), bryozoans (4), brachiopods, nemerteans and pycnogonoids (1).

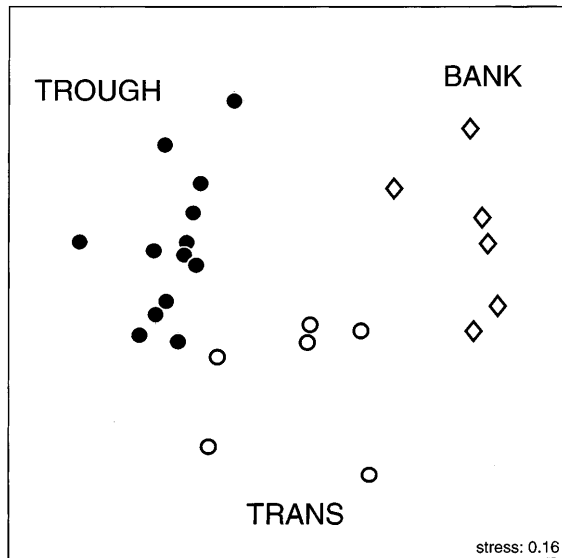
### Community analysis and structure

The 25 stations off Northeast Greenland were divided into three clusters (Fig. 1; Table 1) corresponding to distinct depth zones. Clusters were labelled according to Piepenburg and Schmid (1996a). The first station group, BANK, contained the shallow stations located on shallow shelf banks between 32 and 55 m depth. The second station group, TRANS, consisted of six stations on the slopes of the troughs. The third cluster, TROUGH, included 13 stations in the deeper parts of the troughs. The difference between BANK and TROUGH clusters was also clearly visible in the MDS-plot resulting from the ordination analysis (Fig. 3), whereas the faunal composition of the stations belonging to the TRANS cluster confirms its intermediate position between the other two more distinct clusters. Examination of the univariate measures of community structure (Table 1) showed that the number of taxa increases with depth, whereas the mean abundances decrease. The Shannon diversity index,  $H'$ , and the evenness index,  $E$ , showed no clear

**Table 1** Northeast Greenland, station groups. For each station cluster, number of stations investigated, names of dominant taxa as well as median values (ranges in parentheses) of water depth (m), total number of taxa per station, mean abundance (no. 100 m<sup>-2</sup>), number of taxa per station used for the diversity calculations,

Hurlbert rarefaction [ $E(S_n)$ ; no. species for  $n = 100$ ], Shannon diversity ( $H'$ ) and evenness ( $E$ ) are given. Asterisks indicate significant differences among station groups (Kruskal–Wallis  $H$ -tests,  $p < 0.05$ )

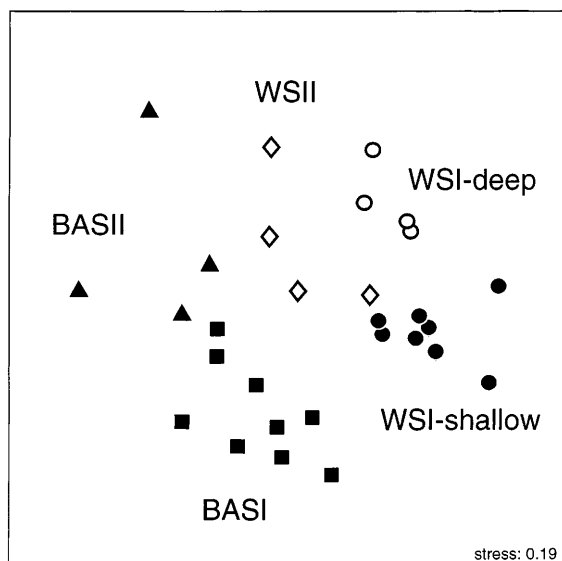
	BANK	TRANS	TROUGH
No. stations	6	6	13
Depth	49 (32–55)	101 (62–186)	266 (119–376)
Taxa (total)	22 (19–26)	30 (17–36)	31 (19–40)
Dominant taxa	<i>Arcturus</i> cf. <i>hastiger</i> <i>Ophiacantha bidentata</i> Bryozoa spp.	<i>Ophiocten sericeum</i> <i>Psolus phantapus</i> Sabellidae sp. 2	<i>Ophiacantha bidentata</i> Ophiuroidea spp. <i>Ophiocten sericeum</i>
Abundance	71.8 (24.1–137.4)	68.7 (40.8–125.6)	35.5 (4.3–99.6)
Taxa (diversity)*	14 (12–17)	21 (11–26)	23 (14–30)
$E(S_{100})^*$	6.09 (4.63–7.85)	7.69 (4.80–9.21)	10.19 (7.82–19.28)
$H'^*$	1.14 (0.65–1.62)	1.06 (0.53–1.79)	1.81 (1.38–2.62)
$E^*$	0.44 (0.26–0.60)	0.34 (0.22–0.60)	0.58 (0.46–0.78)



**Fig. 3** Plot of the multidimensional scaling (Arctic). Different symbols (see Fig. 1) indicate affiliation to faunistic station groups according to cluster analysis.

pattern although they were highest for the TROUGH stations. A similar pattern was discernible when Hurlbert's richness estimator [ $E(S_{100})$ ] was calculated, with highest values for the TROUGH stations whereas, once again, the TRANS and BANK assemblages did not differ significantly from each other.

In the Antarctic, four station clusters were identified. The MDS ordination showed a gradient between the stations, rather than distinct groups (Fig. 4). However, it did reveal a separation of the Weddell Sea stations (WSI and WSII) from the Bellingshausen and Amundsen Sea stations (BASI and BASII). Furthermore, it can be seen



**Fig. 4** Plot of the multidimensional scaling (Antarctic). Different symbols (see Fig. 2) indicate affiliation to faunistic station groups according to cluster analysis.

that the WSI stations fell into two further groups with the shallower samples (WSI-shallow) being distinct from the deeper ones (WSI-deep). The number of taxa per station varied markedly among the assemblages (Table 2). In the Weddell Sea, the median values ranged from 41 in the WSI-deep cluster to 73 for the WSI-shallow stations, whereas in the Bellingshausen and Amundsen Seas the difference between BASI and BASII (44 and 37, respectively) was not significant. The highest values for the Shannon diversity index ( $H'$ ) and the richness estimator [ $E(S_{100})$ ] were calculated for the Weddell Sea clusters WSII and WSI-shallow. The clusters WSI-deep, BASI and BASII had intermediate values with medians ranging from 1.60 to 1.95 and 10.50 to 14.70 for  $H'$  and  $E(S_{100})$ , respectively. Apart from the generally high degree of evenness found for WSII, indicating a more even distribution of individuals among the taxa, the values for the other assemblages ranged broadly (Table 2).

#### Discriminator taxa and faunal composition

Off Northeast Greenland the isopod *Arcturus* cf. *hastiger* was the most typical species found in the BANK cluster. It was often seen on the stalked ascidian *Pyura ovifera*, which was another species characteristic of the BANK stations (Table 3). The TRANS stations were dominated by the brittle star *Ophiosten sericeum* (47%), which acted as a good discriminator, distinguishing this cluster from the other two. *Cerianthus* spp. and Pycnogonidae spp. as well as Sabellidae sp. 1 served as good key taxa for separating the BANK and TROUGH clusters (Table 3). The brittle star *Ophiopleura borealis*, the blue encrusting sponge *Hymedesmia* spp., two groups of polychaetes and the fish *Artediellus atlanticus* best characterized the TROUGH community (Table 3).

In the Antarctic the synascidians *Synoicum* spp., the sea stars *Henricia* spp. and the sponge *Isodictya* sp. 2 were found to be typical of the Weddell Sea cluster WSI (Table 4). A comparison of the sub-clusters WSI-shallow and WSI-deep showed that five of the six taxa, which contributed most to the discrimination between these two station groups, were more abundant within the cluster WSI-shallow (Table 5). For the WSI-deep assemblage only one characteristic taxon, the deep-sea octocoral *Umbellula* spp., was found. The holothuroids of the family Psolidae and the hemichordates Pterobranchia sp. 3 were the best discriminators of the cluster WSII (Table 4). Neither of them were found at any of the Bellingshausen or Amundsen Sea stations. The tube-dwelling sea anemone *Ceriantharia* sp. 5, the solitary ascidian *Cnemidocarpa verrucosa*, the bryozoan *Campoplex tricornis* and the benthic siphonophoran *Rhodalia miranda* were all typical of the BASI, whereas the holothurian *Bathyploes rubipunctatus* characterized the cluster BASII (Table 4).

The faunal composition on a rough taxonomic level differed considerably among the stations off Northeast Greenland, in the Bellingshausen and Amundsen Seas

and in the Weddell Sea (Fig. 5). Echinoderms, particularly the ophiuroids *Ophiacantha bidentata* and *Ophioc-ten sericeum*, strongly dominated the stations off Northeast Greenland (see also Table 1), whereas on the shelf of the Weddell Sea, sponges predominated. The abundant groups were most evenly distributed in the Bellingshausen and Amundsen Seas. Echinoderms, anthozoans and bryozoans were most common, whereas sponges composed only 2% of the total abundance (see also Table 2).

### Relationship between physical and biological data

Off Northeast Greenland, six environmental variables were originally recorded. According to the recommendation of Clarke and Ainsworth (1993), the distance between the station and the eastern 300 m depth contour parallel to the continental slope was omitted because of the good correlation ( $r = 0.96$ ) with longitude. The highest value for the correlation between physical and biological data was found for the combination of water depth and latitude ( $\rho_s = 0.48$ ; Table 6). The highest correlation for single variables were water depth ( $\rho_s = 0.39$ ) and latitude ( $\rho_s = 0.33$ ).

For the Antarctic, none of the pairwise combinations of the five environmental variables showed a very high degree of correlation. All environmental variables were log-transformed ( $\ln = \log_e$ ) to convert the data to an approximately normal multivariate distribution (Clarke and Ainsworth 1993). The correlation analysis revealed that neither one single parameter nor a combination of variables showed any relationship with the megabenthic distribution (Table 7).

## Discussion

Analysis of the benthic species distribution revealed a conspicuous depth zonation off Northeast Greenland in which the benthic assemblage of the shallow banks could be clearly distinguished from that of the deeper parts of the troughs. Similar bathymetric zonation patterns in the same area have been reported for the megafauna, epifauna and selected species (Piepenburg 1988; Piepenburg and Schmid 1996a; Piepenburg et al. 1997). Our results show that the deeper stations tend to have high numbers of taxa but low abundances, whereas the shallow stations showed a distinctly opposite trend. The combined effects of these differences in the distribution pattern and the high species dominance on the shallow shelf banks resulted in an increasing diversity with depth.

The BANK stations were characterized by coarse sediments and a large number of stones. In general, such a well-structured environment is supposed to offer suitable substrata for different species and, thus, increase diversity. However, our results indicate a comparatively

**Table 2** Antarctic, station groups. For each station cluster, number of stations investigated, names of dominant taxa as well as median values (ranges in parentheses) of water depth (m), total number of taxa per station, mean abundances (no. 100 m<sup>-2</sup>), number of taxa per station used for the diversity calculations, Hurlbert rarefaction [ $E(S_n)$ ]; no. of species for  $n = 100$ ], Shannon diversity ( $H'$ ) and evenness ( $E$ ) are given. Asterisks indicate significant differences among station groups (Kruskal-Wallis  $H$ -tests,  $p < 0.05$ )

	WSI-shallow	WSI-deep	WSII	BASI	BASII
No. stations	8	4	4	9	4
Depth	311 (175–417)	479 (427–538)	454 (412–555)	202 (171–476)	415 (328–561)
Taxa (total)	73 (44–75)	41 (34–50)	59 (36–73)	44 (34–61)	37 (23–51)
Dominant taxa	<i>Rossella antarctica</i> <i>Stylocordyla borealis</i> (s) <i>Gorgonaria</i> spp. 14.6 (10.9–130.6) 56 (32–59) 17.54 (7.64–21.68) 2.33 (0.59–2.53) 0.57 (0.14–0.62)	<i>Melicerita obliqua</i> <i>Corymorpha microrhiza</i> <i>Dendrochirotrida</i> spp. 12.7 (6.7–32.2) 26 (20–36) 11.85 (8.89–16.82) 1.63 (0.97–1.98) 0.48 (0.30–0.53)	<i>Achlyonice violaceuspidata</i> <i>Synoicum</i> spp. <i>Psolidae</i> spp. 6.0 (5.4–14.8) 45 (24–57) 22.99 (19.66–25.07) 2.77 (2.30–2.98) 0.70 (0.68–0.73)	<i>Melicerita obliqua</i> <i>Ceriantharia</i> sp. 5 <i>Gorgonaria</i> spp. 5.9 (4.0–48.6) 30 (20–46) 14.70 (7.03–19.27) 1.95 (0.62–2.47) 0.53 (0.19–0.71)	<i>Penigone vignioni</i> <i>Corymorpha microrhiza</i> <i>Notocrangon antarcticus</i> 5.9 (3.5–10.8) 23 (9–23) 10.50 (6.68–19.19) 1.60 (0.64–2.38) 0.49 (0.24–0.65)
Abundance					
Taxa (diversity)*					
$E(S_{100})^*$					
$H'$					
$E^*$					

**Table 3** Northeast Greenland, average abundances (no. 100 m<sup>-2</sup>) of the discriminator taxa calculated by comparing the station groups (according to Clarke 1993) [ $\delta_i$  average contribution from the  $i$ th taxon to the overall dissimilarity ( $\delta$ ) between station groups;  $SD(\delta_i)$  standard deviation]

Comparison	Taxa	Average abundance			$\delta_i$	$\delta_i/SD(\delta_i)$
		BANK	TRANS	TROUGH		
BANK vs TRANS $\delta = 72.34$	<i>Ophiocten sericeum</i>	0.0	598.4		7.72	2.47
	<i>Arcturus</i> cf. <i>hastiger</i>	215.5	136.0		3.98	1.65
	<i>Cerianthus</i> spp.	0.5	33.6		2.34	1.60
	<i>Pyura ovifera</i>	13.5	0.6		1.93	1.57
	Pycnogonidae spp.	0.1	1.6		1.27	1.52
BANK vs TROUGH $\delta = 80.34$	<i>Arcturus</i> cf. <i>hastiger</i>	215.5		0.0	5.63	3.22
	<i>Ophiopleura borealis</i>	0.0		65.5	3.93	2.12
	Serpulidae spp.	0.1		47.2	3.68	3.11
	<i>Pyura ovifera</i>	13.5		0.0	2.49	2.32
	Sabellidae sp. 1	0.1		10.8	2.45	2.07
TRANS vs TROUGH $\delta = 66.98$	<i>Ophiocten sericeum</i>		598.4	78.6	4.94	1.74
	Sabellidae sp. 2		140.5	10.1	2.82	1.35
	Serpulidae spp.		1.0	47.2	2.59	1.86
	<i>Hymedesmia</i> spp.		1.0	17.9	1.99	1.35
	<i>Artediellus atlanticus</i>		0.3	2.2	1.40	1.85

**Table 4** Antarctic, average abundances (no. 100 m<sup>-2</sup>) of the discriminator taxa calculated by comparing the major station groups (according to Clarke 1993) [ $\delta_i$  average contribution from the  $i$ th taxon to the overall dissimilarity ( $\delta$ ) between station groups;  $SD(\delta_i)$  standard deviation]

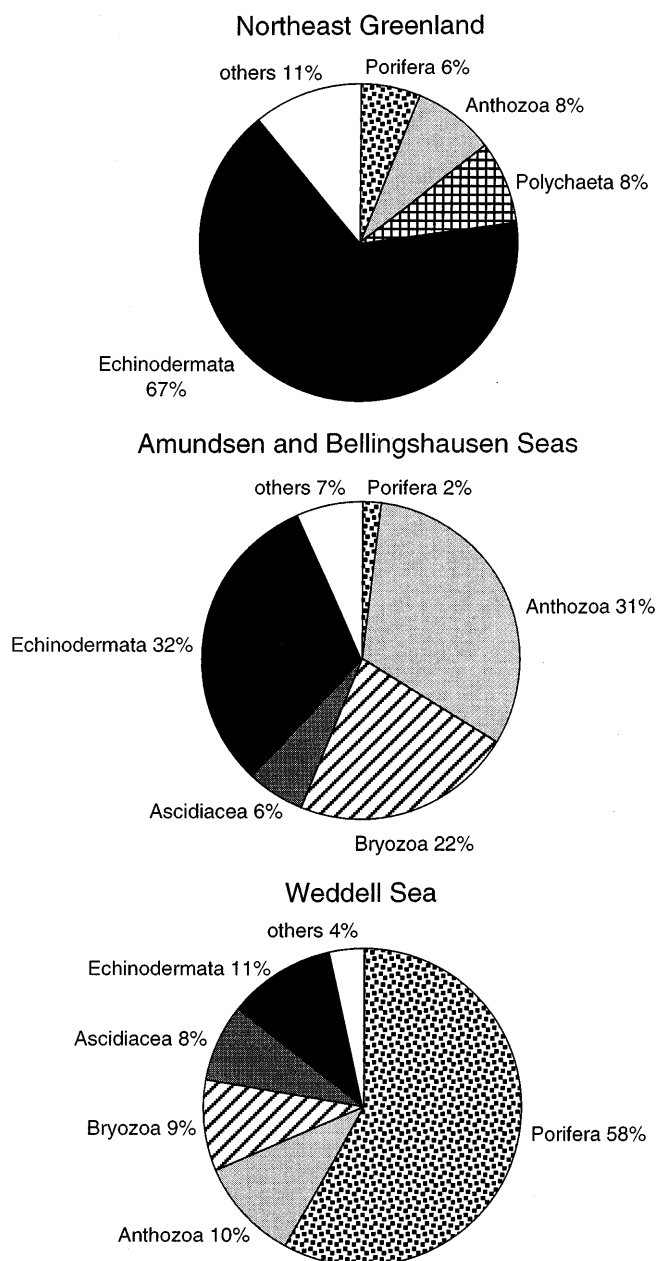
Comparison	Taxa	Average abundance				$\delta_i$	$\delta_i/SD(\delta_i)$
		WSI	WSII	BASI	BASII		
WSI vs BASI $\delta = 73.76$	<i>Melicerita obliqua</i>	174.5		160.5		3.53	1.82
	<i>Ceriantharia</i> sp. 5	0.0		75.1		2.57	1.81
	<i>Synoicum</i> spp.	60.2		0.2		1.66	1.76
	<i>Rossella nuda</i>	16.1		0.5		1.18	2.05
	<i>Henricia</i> spp.	2.4		0.0		1.04	1.87
BASI vs BASII $\delta = 72.66$	<i>Cnemidocarpa verrucosa</i>			5.1	0.0	2.19	2.03
	<i>Camptoplites tricornis</i>			8.1	0.2	2.16	2.00
	<i>Rhodalia miranda</i>			1.4	0.0	1.60	2.08
	<i>Bathyplores rubipunctatus</i>			0.0	0.4	1.43	5.59
	<i>Ctenocidaris</i> spp.			2.1	1.1	1.07	1.81
WSI vs BASII $\delta = 78.64$	<i>Rossella nuda</i>	16.1			0.2	1.71	1.75
	<i>Pista</i> spp.	15.5			0.3	1.51	1.72
	<i>Isodictya toxophila</i>	1.6			0.0	1.36	2.20
	<i>Isodictya</i> sp. 2	1.2			0.0	1.03	1.83
	<i>Bathyplores rubipunctatus</i>	0.5			0.4	0.92	2.20
WSII vs BASI $\delta = 70.29$	Psolidae spp.		26.1	0.0		2.17	2.70
	Pterobranchia sp. 3		7.2	0.0		1.74	3.33
	<i>Pista</i> spp.		7.0	0.7		1.64	2.50
	<i>Pseudostichopus mollis</i>		1.3	0.0		1.26	3.16
	<i>Corymorpha</i> spp.		1.4	0.0		1.18	3.38
WSI vs WSII $\delta = 66.78$	<i>Notocrangon antarcticus</i>	0.0	5.1			1.41	3.83
	<i>Pseudostichopus mollis</i>	0.6	1.3			0.90	2.27
	<i>Henricia</i> spp.	2.4	0.1			0.83	1.64
	Pycnogonidae spp.	1.1	6.0			0.70	1.63
	<i>Isodictya</i> sp. 2	1.2	0.1			0.68	1.56
WSII vs BASII $\delta = 75.89$	Psolidae spp.		26.1		0.0	2.58	2.71
	Pterobranchia sp. 3		7.2		0.0	2.08	3.13
	<i>Polymastia invaginata</i>		1.2		0.0	1.53	2.81
	<i>Bathyplores rubipunctatus</i>		0.0		0.4	1.15	3.76
	Pycnogonidae spp.		6.0		0.5	1.11	3.97

low diversity in these areas. Piepenburg and Schmid (1996a) also found the highest species dominance at stations between 40 and 150 m water depth, with the

isopod *Arcturus hastiger* and the sea urchin *Strombocentrotus* spp. as dominant taxa. The shallow areas are presumably subject to different types of disturbances,

**Table 5** Antarctic, average abundances (no. 100 m<sup>-2</sup>) of the discriminator taxa calculated by comparing the minor station groups (according to Clarke 1993) [ $\delta_i$  average contribution from the  $i$ th taxon to the overall dissimilarity ( $\delta$ ) between station groups;  $SD(\delta_i)$  standard deviation]

Comparison	Taxa	Average abundance		$\delta_i$	$\delta_i/SD(\delta_i)$
		WSI-shallow	WSI-deep		
WSI-shallow vs WSI-deep $\delta = 65.11$	<i>Rossella nuda</i>	23.6	1.2	1.42	2.36
	<i>Cinachya antarctica</i>	4.9	0.1	1.14	1.99
	<i>Notocidaris</i> spp.	4.4	0.2	0.89	1.79
	Pterobranchia sp. 2	3.3	0.1	0.83	1.78
	<i>Umbellula</i> spp.	0.5	2.4	0.80	1.67
	<i>Cnemidocarpa verrucosa</i>	2.1	0.0	0.81	2.24



**Fig. 5** Overall proportions of the dominant higher taxa for the three areas of investigation

e.g. by wave action, feeding activities of marine mammals (Nerini and Oliver 1983; Johnson and Nelson 1984; Oliver et al. 1985) and ice gouging (Barnes et al. 1984; Woodworth-Lynas et al. 1991; Gutt et al. 1996; Conlan et al. 1998), resulting in a more fluctuating environment and, consequently, in assemblages with a high species dominance and low diversity, where opportunistic species dominate. Feder et al. (1994) also indicated that differences in faunal diversity found in the Chukchi Sea are not related to differences in sediment sorting, but rather to environmental stress.

The seabed at the TROUGH stations was predominantly a soft bottom sediment, which indicates low currents close to the substrate and low disturbance levels. More stable environmental conditions at greater depths in the troughs lead to assemblages with a more even distribution of individuals across the range of species, resulting in higher diversity, albeit with lower abundances. These lower abundances can be explained by a reduced food supply, since water depth can be regarded as a rough inverse measure of the particle sedimentation rate (Suess 1980) and, thus, of food availability. However, more than 50% of the individuals in the TROUGH cluster were suspension feeders. Moreover, the sponges *Geodia* spp. and *Schaudinina* spp. occurred in high numbers at one station in the southern Norske Trough. This finding shows that the megabenthos in the deeper part of the troughs is not dissociated from water column processes and indicates an at least temporarily high nutrient supply reaching the sea floor via either direct sedimentation or lateral advection. Ritzrau (1994) reported values of particulate organic carbon of between 29.4 and 136.0  $\mu\text{g l}^{-1}$  and current velocities between 6.4 and 21.0  $\text{cm s}^{-1}$  in the near bottom water at depths between 186 and 404 m. It is known that, particularly in polar waters, a high proportion of organic carbon actually reaches the benthos by lateral advection (Graf 1992; Feder et al. 1994).

The TRANS stations differed considerably in community structure, with all the above-mentioned sediment types being present. There was no pronounced similarity in fauna between these stations. They apparently belong to a transitional zone between the BANK and TROUGH assemblages with no distinct characteristics. The ophiuroid *Ophiosten sericeum* and the sea cucumber



**Table 6** Northeast Greenland, results of the calculation of the relationship between the biological and physical sets of data. Combinations of environmental variables,  $k$  at a time, yielding the highest rank correlation  $\rho_s$  between the biological and physical data

$k$ Spearman rank correlation; best combination of variables					
1	Depth 0.39	LAT 0.33	DT 0.26	LON 0.05	DI -0.22
2	<b>Depth, LAT</b> <b>0.48</b>	LAT, DT 0.42	Depth, DT 0.40	Depth, LON 0.30	–
3	Depth, LAT, DT 0.47	Depth, LAT, LON 0.36	LAT, LON, DT 0.28	–	–
4	Depth, LAT, LON, DT 0.36	Depth, LAT, DI, DT 0.30	–	–	–
5	Depth, LAT, LON, DI, DT 0.28	–	–	–	–

sets for each  $k$ . Bold type indicates the best combination (maximum  $\rho_s$ ) [*Depth* water depth; *LAT* latitude; *LON* longitude; *DI* distance between the station and coast (ice edge); *DT* distance between the station and the 300 m contour of the trough system]

**Table 7** Antarctic, results of the calculation of the relationship between the biological and physical sets of data. Combinations of environmental variables,  $k$  at a time, yielding the highest rank correlation  $\rho_s$  between the biological and physical data sets for each

$k$ Spearman rank correlation; best combination of variables					
1	LON 0.20	LAT 0.08	DS 0.02	Depth -0.02	DI -0.08
2	LAT, LON 0.20	LON, DS 0.14	LAT, DS 0.13	Depth, LON 0.13	–
3	LAT, LON, DS 0.22	Depth, LAT, LON 0.17	LAT, LON, DI 0.16	–	–
4	Depth, LAT, LON, DS 0.20	LAT, LON, DI, DT 0.16	–	–	–
5	Depth, LAT, LON, DI, DT 0.15	–	–	–	–

$k$  [*Depth* water depth; *LAT* latitude; *LON* longitude; *DI* distance between the station and coast (shelf ice); *DS* distance between the station and the 500 m depth contour (continental slope)]

*Psolus phantapus* were the only species to occur in larger numbers at the TRANS stations. As a consequence, the shallowest station of this cluster at 70 m depth bore a high resemblance to the BANK stations, while the deepest station (186 m) showed a distinct similarity to the TROUGH cluster.

The distribution of shelf megabenthos off Northeast Greenland, however, could be explained by water depth alone, but also similarly by a combination of water depth and latitude. The fairly high correlation of the biological pattern with latitude does not primarily reflect a pronounced north-to-south gradient but more the effect of conspicuous differences in the dominant taxa of the BANK cluster. The three northern stations were dominated by the sea urchin *Strongylocentrotus* spp., whereas at the three stations in the south the isopod *Arcturus* cf. *hastiger*, the brittle star *Ophiacantha bidentata* and the alcyonarian *Gersemia* spp. predominated.

In contrast, none of the measured environmental variables were highly correlated with the faunal distribution in the Antarctic, which indicates that there is a less pronounced depth zonation on the high Antarctic shelf compared to the Arctic. Due to the circumantarctic current system creating similar conditions in the waters all around the continent, the distribution of the benthos is regarded to be circumpolar (Hedgpeth 1971; Knox and Lowry 1977; Richardson and Hedgpeth 1977).

However, our analysis revealed a geographic zonation in the composition of the megabenthos. Despite a pronounced meso-scale patchiness, distinct assemblages were distinguished both in the Weddell and in the Bellingshausen and Amundsen Seas.

Numbers of taxa and abundances were highest for the Weddell Sea cluster WSI-shallow. The fauna at these stations was strongly dominated by suspension feeders, to which all key species belonged. At some stations the sea floor was completely covered by sponges, bryozoans and gorgonians as has also been shown by video observations at 200 m depth close to the Syowa station (69°S; 39°E) by Hamada et al. (1986). Some assemblages were strongly dominated by single taxa (e.g. the sponges *Rossella racovitzae*, *R. antarctica* and *Stylocordyla borealis*). These dominance patterns result in low values for diversity at otherwise diverse stations. The fauna at the WSI-deep stations was less diverse than that of the shallow stations. Furthermore, differences concerning the dominant taxa were discernible. Sponges, mainly glass sponges, were rare. Patchily distributed bryozoans characterized the WSI-deep stations. Due to megabenthic composition, the WSI-deep assemblages may be considered as impoverished WSI-shallow communities. The situation is different at the WSII stations in the southern part of the investigation area where a soft bottom substrate prevails, indicating slow bottom

currents and presumably reduced horizontal transport of organic particles. This has led to a different composition with motile deposit feeders, such as the holothurians *Achlyonice violaecuspida* and *Pseudostichopus mollis*, being more abundant. The WSII cluster had intermediate values for numbers of taxa and abundances which were comparable to WSI-deep stations. However, the more even distribution of individuals among the taxa led to the highest overall diversity values.

Our findings agree with results recently published by Gutt and Starman (1998) on the megabenthos of the same area, which also show a gradient from suspension feeder dominated assemblages to those with higher numbers of detritus feeders. Similar distribution patterns were also described for the entire macrobenthos based on trawl sampling (Voß 1988), as well as for shrimps (Gutt et al. 1991), holothurians (Gutt 1991) and fish (Gutt et al. 1994; Hubold 1992).

In contrast to the Weddell Sea, the benthos of the Bellingshausen and Amundsen Seas was virtually unknown prior to these investigations. The two relatively heterogeneous station groups were discriminated according to their megabenthic composition. However, the ordination showed no distinct geographical or depth zonation between the clusters, but rather a gradient. The majority of the BASI stations were situated in Marguerite Bay. Sponges were rare and bryozoans patchily distributed at low abundances. Thus, these assemblages lacked the pronounced three-dimensional structure reported for the rich communities in the Weddell Sea by Gutt and Schickan (1998). However, drop-stones were fairly abundant, providing a substratum for a variety of sessile species. In between the bryozoan patches and stones the prevailing soft bottom sediment was colonized by motile deposit feeders and semi-infaunal organisms, such as the Ceriantharia. A thick layer of phytodetritus deposited on the sediment was visible at some stations, indicating slow bottom currents and, thus, a reduced horizontal transport of organic particles in these areas. In the BASII cluster, motile detritivorous taxa were the dominant faunal elements of the generally poor benthos. Of the 54 taxa present at the BASII stations, 46 were found at the stations of the BASI cluster as well, and only the holothurian *Bathyplores rubipunctatus* served as a discriminator taxon for the BASII cluster. These findings indicate that the megafauna of the cluster BASII may be regarded as an impoverished BASI assemblage.

In essence, our study of the megabenthos confirms what has often been speculated (White 1984; Hempel 1985; Picken 1985), namely that large shelf areas in the Antarctic are dominated by a variable proportion of sessile suspension feeders, mainly sponges, bryozoans, ascidians and anthozoans. However, on an intermediate spatial scale a considerable degree of patchiness is due to the changing composition of the sessile species or by a regionally more dominant motile fauna. Echinoderms, mainly the motile ophiuroids and sea urchins, are most abundant off Northeast Greenland, as has been similarly reported for other Arctic regions (Curtis 1975; Carey

1991; Piepenburg and Juterzenka 1994; Piepenburg and Schmid 1996b, 1997; Piepenburg et al. 1996; Bluhm et al. 1998). Sessile animals, however, even sponges and cnidarians, can reach local densities which have been described as being typical of the Antarctic (Bullivant 1967; Koltun 1969; Dayton et al. 1974; Barthel and Gutt 1992; Gutt and Koltun 1995; Gutt and Starman 1998).

The comparison of dominance patterns between and within both polar regions, in combination with the spatial distribution of assemblages, can contribute to a verification of some general ecological hypotheses. Sanders' (1968) "stability-time" hypothesis seems to be rather applicable to the deeper arctic assemblages on different spatial scales (station, assemblage). In accordance with this hypothesis we observed a low local (alpha-) diversity in the shallower areas as an effect of a supposed high level of disturbance. The same data support the "intermediate disturbance" hypothesis (Connell 1978) in combination with the "patch dynamics" concept (Pickett and White 1985), because for a larger area an overall more equal dominance pattern (high beta-diversity) was observed (see also Starman and Gutt 1999). In the Antarctic, apparently both stable conditions and a certain degree of fluctuation in ecologically significant environmental parameters or their effects (Arntz et al. 1994; Gutt et al. 1996) seem to be the main reasons for the rich and diverse epifaunal assemblages. However, the driving forces resulting in the clear differences between assemblages which are dominated by sessile and motile life forms have yet to be discovered.

**Acknowledgements** We would like to thank all colleagues mentioned in the "Materials and methods" section for species identification and W. Dimmler (ROV supply) for technical assistance. This is Publication No. 1612 of the Alfred Wegener Institute, supported by a grant from the Deutsche Forschungsgemeinschaft (DFG No. Gu 390/1-2).

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