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Epibenthic community patterns on the continental slope off East Greenland at 75°N

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ABSTRACT: Megabenthic assemblages on the East Greenland continental slope at 75° N were surveyed at 8 locations between 190 and 2800 m depth using sea floor images taken vertically with a still camera. A total of 91 epibenthic species with 14447 individuals were identified from 422 photographs depicting 297 m^2 of the sea floor. Classification and ordination analysis defined 3 faunal zones that corresponded to different depth regions of the continental margin: shelf break, upper slope and lower slope. Megafaunal abundance was highest on the shelf (about 200 ind. m^{-2}). In the other zones, the densities were distinctly lower (15 to 30 ind. m^{-2}). Assemblages were frequently dominated by 1 or 2 species, such as the polychaete *Onuphis conchylega* at the shelf break and the sponge *Polymastia* sp. at the lower slope. The upper slope was characterized by a diverse octocoral-sponge assemblage. A statistical analysis of the correlation between megafaunal and environmental data at a 10 km scale (between stations) indicated that epibenthic distribution patterns were best explained by sea floor characteristics, whereas no evidence for a direct benthic-pelagic coupling was found, irrespective of water depth. Additionally, the within-station distribution of megabenthic organisms (100 m scale) was clearly affected by sea floor properties.

KEY WORDS: Megabenthos · Greenland · Seabed imaging Community · Distribution · Abundance · Diversity

INTRODUCTION

The western Greenland Sea is strongly influenced by cold polar water originating in the Arctic Ocean (Hopkins 1991). Therefore, its environmental conditions are generally characterized by very low but relatively constant water temperatures, long periods of ice cover, large seasonal fluctuations in light regime and low biological productivity (Hempel 1985). However, there are locations off East Greenland from which relatively rich benthic assemblages have been reported (e.g. Thorson 1933, Svarvarsson et al. 1990, Piepenburg & Schmid 1996). The western Greenland Sea has been the focus of several recent field studies carried out in the framework of the 'Sonderforschungsbereich 313' of Kiel University in Germany (Schäfer et al. 1995). One principal issue of this multidisciplinary research project was to examine the relationships between the benthic community patterns and particle flux between the euphotic water column, benthic nepheloid layer (BNL) and sea floor (Graf 1992). In a comprehensive approach, different benthic size fractions and spatio-temporal scales were investigated by various working groups (Graf et al. 1995). In this paper, special attention is directed to the epibenthic megafauna (sensu Gage & Tyler 1991). These organisms often contribute considerably to total benthic biomass (Lampitt et al. 1986) and carbon cycling (Piepenburg et al. 1995) and are supposed to have a strong impact on the micro-scale environment with, for instance, bioturbation and bioirrigation (Hüttel & Gust 1992).

Densities and distribution patterns of polar epibenthos, assessed by means of sea floor imaging, have only described selected species (e.g. Gutt 1988, Piepenburg & von Juterzenka 1994). However, the present study gives a description of the whole community because abundance and distribution patterns for all recognizable species on the seabed were consid-

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ered. The main objectives were to delineate distinct assemblages, identify key species, characterize the community in terms of diversity and abundance, and determine the combination of environmental factors which are most likely to influence faunal groupings. In addition, small-scale (i.e. within-station) distribution patterns were analysed. The study complements similar investigations on the continental margin off East Greenland at 68° N (Piepenburg & von Juterzenka 1994) and 80° N (Piepenburg & Schmid 1996).

MATERIALS AND METHODS

The area of investigation was the western Greenland Sea at 75° N, where the shelf break is approximately 200 km off the East Greenland coast (Fig. 1). In a steep descent of 20 to 65 m km^{-1}, water depths increase from 200 to 2800 m within 60 km (Weber 1989). Sea floor images were taken during the expedition ARK X/1 of RV 'Polarstern' in July 1994 at 8 stations distributed along a slope-normal and a slope-parallel transect (Fig. 1). For more details about the cruise see Fahrbach (1995). The design and operation of the camera probe used is described by Piepenburg & von Juterzenka (1994). A total of 422 colour slides (39 to 61 per station) were taken from the drifting ship (Table 1). On average, a single photograph showed 0.70 m^2 of the seabed (SD = 0.04). Different numbers of photographs taken at every station were due to technical problems. Thus, different sea floor areas were covered at each station (27.94 to 44.96 m^2). The lengths of each station transect, which depended on the ship's drift speed, were calculated from the GPS-derived positions of the first and the last picture taken. Single shots were made every 40 s. Assuming a continuous drift by the ship, the distances between photographs varied between 2 and 13 m. For convenience, stations are labelled according to their depths instead of using the ARK X/1 station numbering (Table 1).

Specimens recognizable on the slides were identified to species (if possible) under a binocular microscope (magnification 6.5 to 16×) based on taxonomic literature (Heding 1935, Wesenberg-Lund 1940, Stephensen 1943a, b, 1944, Ockelmann 1958, Grainger 1966, Tendal 1970, Hartmann-Schröder 1971, Macpherson 1971, Jensen 1974, Hayward & Ryland 1979, 1985, Paterson et al. 1982, George & Hartmann-Schröder 1985, Pethon 1989). Due to the spatial resolution of the optical system of the photo probe used, organisms as small as 0.8 cm could be detected and counted. Specimen counts were standardized to an area of 1 m^2. For doubtful cases, determination of taxa was aided by comparison with specimens collected

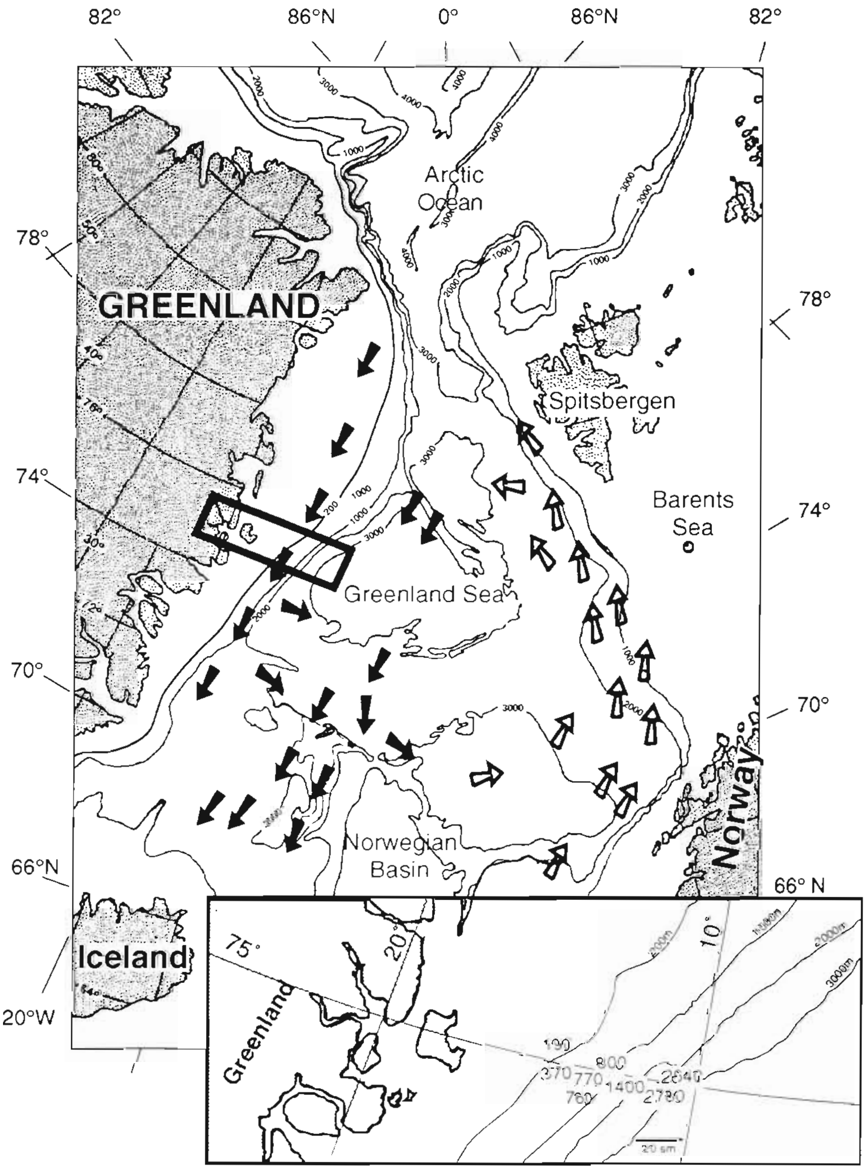

Fig. 1. Greenland Sea. Sea floor photography at 8 stations at the continental slope at 75° N. Inset: study area with station numbers of transects. Black arrows: flow of polar waters; white arrows: flow of North Atlantic waters

Table 1 Seabed photography during the Arctic expedition ARK X/1 in the western Greenland Sea in July 1994. Chlorophyll *a* (Chl *a*) concentration in surface water (10 m) and bottom nepheloid layer (BNL), phaeopigment (Phaeo) concentration in surface water (10 m) and bottom nepheloid layer (BNL); sediment type in number of stones classifications (see 'Materials and methods') and description. Station indices: diversity (*H'*) and evenness (*E*)

	Shelf Break		Upper Slope			Lower Slope		
Name:	190	370	760	770	800	1400	2640	2780
'Polarstern' Stn:	17	14	25	16	20	9	24	6
Date	21 Jul	19 Jul	27 Jul	20 Jul	23 Jul	16 Jul	26 Jul	13 Jul
Lat. (N)	75° 00'	74° 58'	74° 55'	74° 59'	75° 03'	74° 57'	74° 57'	74° 55'
Long. (W)	13° 47'	12° 58'	12° 47'	12° 39'	12° 28'	12° 25'	11° 09'	11° 07'
Depth (m)	190–197	365–377	751–776	772–775	805–807	1376–1413	2584–2699	2776–2785
Photos imaged	59	56	54	54	61	39	59	40
Area imaged (m^2)	38.2	39.3	35.7	40.9	44.9	28.1	41.7	27.9
Transect length (m)	778	519	477	104	294	435	293	728
Temperature (°C)	1.02	1.32	0.17	0.06	−0.16	−0.78	−0.98	−1.01
Salinity	34.79	34.93	34.89	34.89	34.89	34.91	34.9	34.9
Chl a_{10m} ($\mu g\ l^{-1}$)	0.22	0.03	2.23	0.95	0.62	0.89	1.84	2.5
Chl a_{BNL} ($\mu g\ l^{-1}$)	0.03	0.06	0	0.01	0.01	0.01	0	0.01
$Phaeo_{10m}$ ($\mu g\ l^{-1}$)	0.03	0.04	0.22	0.03	−0.05	−0.06	0.27	0.01
$Phaeo_{BNL}$ ($\mu g\ l^{-1}$)	0.03	0.05	0.02	0.01	0.01	0.01	0.01	0.01
Sediment type	2 (0–4) Clay-like silt	3 (3–5) Many stones	3 (0; 3) Sandy clay Sponge mats	3 (0–3) Sandy clay Sponge mats	2 (0–4) Sandy clay Sponge mats	3 (2–4) Sandy clay	0 (0) Clay	0 (0) Clay
H'	0.57	3.49	3.31	3.7	3.28	1.04	2.48	2.47
E	0.13	0.63	0.7	0.77	0.68	0.3	0.67	0.69

from Agassiz trawl catches made at the same stations. Some taxa could only be identified with the help of experts (see 'Acknowledgements'). Organisms that could not be identified to species level (e.g for the photographically similar looking sponges *Schaudinnia rosea* and *Trichasterina borealis* or the crinoids *Heliometra glacialis* and *Poliometra prolixa*) were classified by higher taxonomic levels (e.g. 'vase shaped' sponges and Crinoidea, respectively). In general, colonies of sponges, bryozoans, alcyonarians, pennatularians, and synascidiaceans were each counted as single individuals. This was not possible for the encrusting sponges *Hymedesmia paupertas*, *H. curvichela*, and *Aplysilla sulphurea*, so they are considered as presence/absence values in the species list. A special abundance estimate was conceived for the octocoral *Isidella lofotensis*, because its branches grew too densely to distinguish single colonies. A 16-square grid was spread over every slide, and each grid was counted if it had a coral coverage of more than 50%. Thus, a value of 16 indicates a completely covered sea floor, a value of 8 a half-covered one, etc. This abundance parameter is comparable to the density values of solitary species (Gutt & Starmans in press).

Community analysis is based on the mean abundances of 77 species at 8 stations. Encrusting sponges, fish, and unidentified taxa are not considered. Analyses were carried out for both stations (Q-mode) and taxa (R-mode) (Lance & Williams 1967). For R-mode computations, 58 taxa that did not reach at least 5% dominance at any of the 8 stations were excluded to minimise the bias caused by the random occurrence of rare species. 19 species were used in the analysis. Double square root transformation of abundance values was used to buffer the influence of extremely dominant species (Field et al. 1982). Prior to the R-mode analysis, abundances were in addition standardized as percentages of the total abundance of each species. Similarities between stations and taxa were computed using the Bray-Curtis coefficient (Bray & Curtis 1957). The similarity values were subjected to both classification ('complete linkage clustering'; Lance & Williams 1967) and ordination (multidimensional scaling, MDS; Kruskal & Wish 1978). The similarities of stations and taxa are depicted in a dendrogram (cluster analysis) and an ordination biplot (MDS). A low MDS stress coefficient (<0.2) indicates that the multivariate similarity pattern is represented in a 2-dimensional plot without much distortion (Clarke 1993). Delineation of station groups and species assemblages in these graphical representations of the overall similarity pattern is subjective and involved no statistical testing (Field et al. 1982).

The faunistic zones were compared with regard to total epibenthic abundance and diversity. The Shannon index (Shannon & Weaver 1963) was used to indicate diversity. Evenness was determined by the Pielou index (Pielou 1977). The SIMPER procedure of Clarke (1993) was used to identify 'discriminator species' for each faunistic zone. In a pairwise comparison between station groups, the contribution of each species to the discrimination is parameterised by its average species-specific dissimilarity (δ_k) or its proportion (%) to the average total dissimilarity value (δ). If a species is found at consistently different abundances throughout both groups, the standard deviation SD(δ_k) of its dissimilarity (δ_k) is low. Species with high δ_k and low SD(δ_k) are called 'discriminator species'.

To investigate the relationship between environment and epibenthic distribution patterns, 9 environmental parameters were recorded at each station. Water depth, temperature and salinity, as well as chlorophyll *a* and phaeopigment concentrations, were fluorometrically measured in both surface (i.e. in 10 m depth) and bottom water (i.e. 10 m above seabed) with CTD casts (Holm-Hansen et al. 1965). For seabed classification, sediment composition was described from box core samples taken at the same stations (A. Kohly pers. comm.). In the photographs, the presence of sponge spiculae mats was registered, as well as the number and size of stones on the sediment surface, and indications of endobenthic organisms ('Lebensspuren'), such as molluscs' siphons and tracks, were counted. Seabed categories were defined with regard to quantity and sizes of stones: (0) no stones, (1) less than 10 stones smaller than 5 cm, (2) more than 10 and less than 50 stones smaller than 5 cm, (3) more than 50 stones smaller than 5 cm, (4) stones bigger than 5 cm, and (5) more than 5 stones bigger than 5 cm. For large epibenthic organisms, we regard these seabed traits to be ecologically more important than sediment parameters (e.g. grain size) that are commonly used to describe the physical characteristics of the sea floor. The epibenthic distribution patterns were related to the environmental data by means of the BIO-ENV procedure proposed by Clarke & Ainsworth (1993). This explorative method correlates the biotic pattern (represented by the faunistic station resemblance matrix), using the weighted Spearman (or harmonic) rank correlation (ρ_H), with the dissimilarities between stations computed for each of the (n) abiotic variables alone ($k = 1$) as well as for all possible ($k = 2, 3, ..., n$) combinations of them. It is then possible to identify the subset of environmental parameters which correlates best with (and, thus, may influence most) the distribution of the epibenthic assemblages.

All community analyses were performed using the computer program PRIMER (Clarke & Warwick 1994).

The small-scale spatial dispersions of each species (i.e. the distribution of individuals along the photographic station transects) were described by Fisher's index (Gray 1984). The significance of departure from the expected random distribution (dispersion coefficient, DC = 1) was tested by a 2-tailed χ^2 statistic. An aggregated dispersion is indicated by DC > 1, whereas a DC < 1 is evidence for a uniform dispersion.

RESULTS

Species

At 8 stations, a total of 91 mega-epibenthic species with 14 447 individuals were identified (Appendix 1), including 17 sponges, 13 cnidarians, 3 bryozoans, 1 brachiopod, 7 molluscs, 2 polychaetes, 2 pantopods, 12 crustaceans, 26 echinoderms, 2 ascidiaceans, and 4 fish species. The number of species per station, ranging between 22 and 47 (see Fig. 4a), was not significantly correlated with the area covered by the photographs (Spearman's rank correlation = 0.61, p = 0.10).

Community analysis

The analysis of faunistic station resemblances classified the 8 stations into 3 station groups or categories (Fig. 2a, b) which corresponded to distinct depth zones. The first category, 'Shelf Break', contained the shallow Stns 190 and 370. The second category, 'Upper Slope', comprised Stns 770, 800, and 760. These stations housed the most similar epifauna. The third category, 'Lower Slope', consisted of Stns 1400, 2640, and 2780. Stn 1400 was distinctly different from all other stations but had the highest relative similarity to the deep Stns 2640 and 2780.

The 19 numerically dominant species were allocated to 5 assemblages (I–V; Fig. 3a, b). Species assemblage V contained mostly species that were not very abundant but occurred in all depth zones (Table 2). The species of assemblage I preferred the 'Upper Slope' whereas assemblage IV encompassed typical shelf species and assemblage III species characteristic for the 'Lower Slope' (Table 2). *Polymastia* sp. exhibited a very special distribution pattern. It dominated the 'Lower Slope' Stn 1400 but occurred at the 'Upper Slope' and the deeper stations as well (Table 2).

Community structure

At the 'Shelf Break' Stns 190 and 370, 22 and 47 species, respectively, were observed (Fig 4a). At Stn 190, the highest epibenthic densities were registered

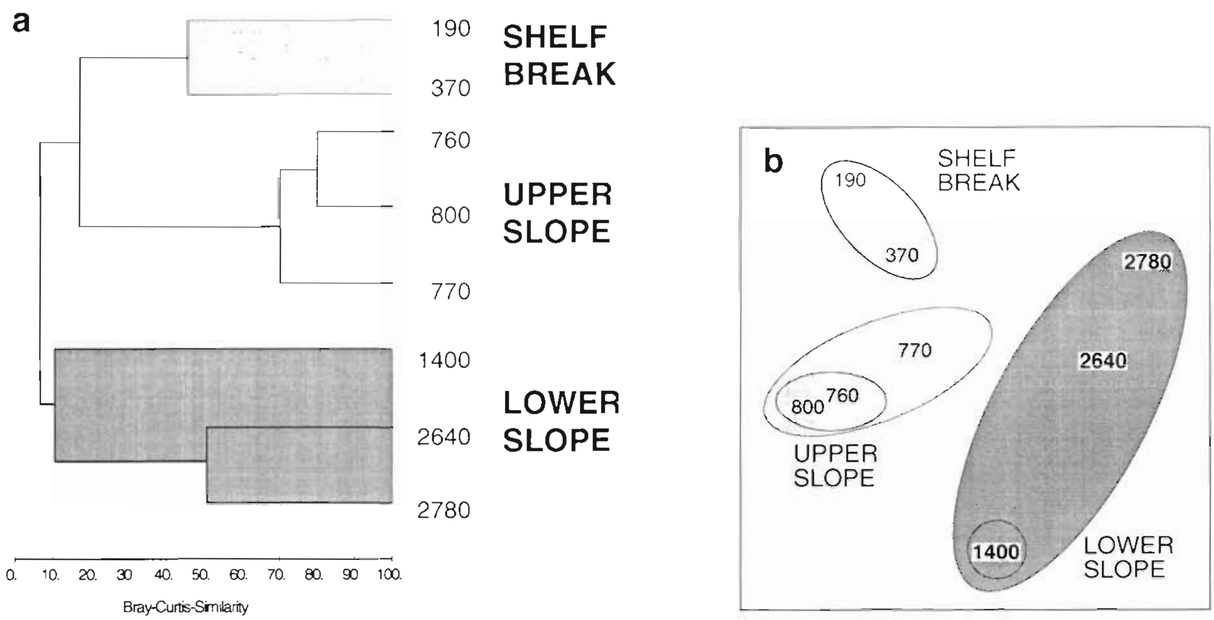

Fig. 2. Station similarities. Results of classification and ordination analysis. (a) Cluster dendrogram; (b) multidimensional scaling plot, stress coefficient = 0.04. Grouping of stations according to cluster analysis is indicated by different shadings

(214 ind. m^{-2}), about 8 times higher than at Stn 370 (Fig. 4b). The low evenness values at Stn 190 indicated that 1 species (*Onuphis conchylega*) strongly dominated (Table 1). At the stations of the 'Upper Slope', between 28 and 30 species were identified (Fig. 4a). The total abundances of epibenthic organisms at each station varied between 28.6 and 41.3 ind. m^{-2} (Fig. 4b). No species was dominant at any station, and evenness values were high (Table 1). Altogether 12 and 15 species belonged to the 'Lower Slope' Stns 2780 and 2640, respectively (Fig. 4a). The total abundance (14.4 to 22.1 ind. m^{-2}) was lowest here (Fig. 4b). Low diversity and evenness values at Stn 1400 denote the dominance of the sponge species *Polymastia* sp. (Table 1).

The importance of specific taxonomic groups was different at each station (Fig. 4c). Sponges were most

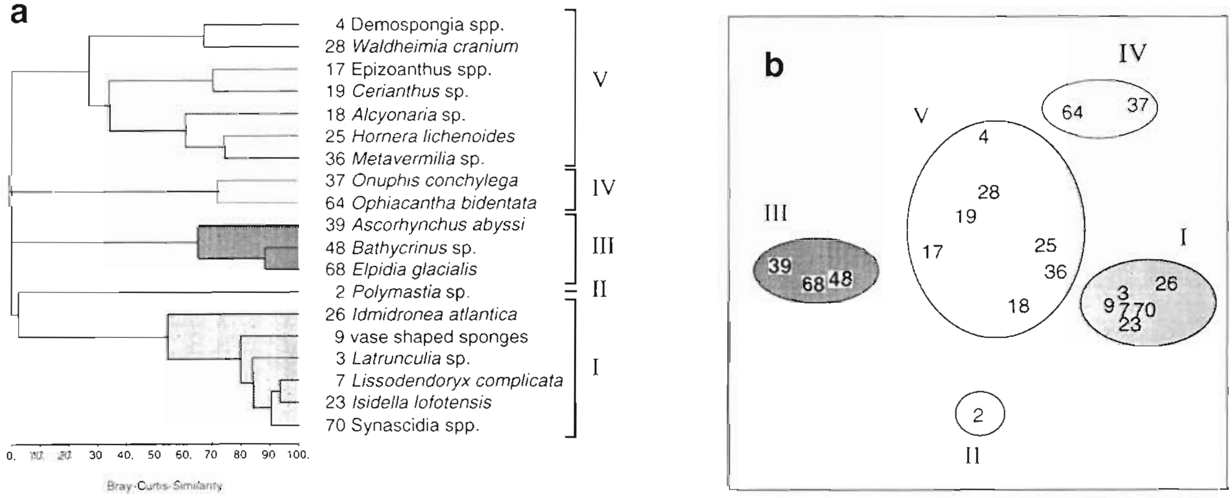

Fig. 3. Species similarities. (a) Dendrogram depicting classification of 19 epibenthic species of the East Greenland slope according to their similarity in spatial distribution. Five species groups were arbitrarily delineated from the dendrogram; numbers indicate specific species. (b) Multidimensional scaling plot of epibenthic species occurring on the East Greenland continental slope after multidimensional scaling (stress coefficient = 0.09). Species groups I, II, III, IV and V refer to similarity structure and numbers represent specific species depicted in (a)

Table 2. Community table of 19 epibenthic species occurring at any of the 8 stations with more than 5% contribution to total abundances. Stations are ordered according to depth. Values (percentages after standardizing relative species abundances by species; bold type indicates values >50%) express the focus of each species occurrence. Species groups refer to the similarity structure depicted in the dendrogram in Fig. 3a

Group	Species	Shelf Break		Upper Slope			Lower Slope		
		190	370	760	770	800	1400	2640	2780
V	Demospongia spp.		**100.0**						
	Waldheimia cranium	8.9	**67.1**		10.8				13.2
	Epizoanthus spp.		28.7	1.9	7.1			33.8	28.5
	Cerianthus sp.	6.7	38.1		9.4			44.7	1.1
	Alcyonaria sp.		27.3		35.3	1.1	36.4		
	Hornera lichenoides	2.9	46.4	5.1	25.6	12.9	7.1		
	Metavermilia sp.		30.9	12.4	42.7	13.3		0.7	
IV	*Onuphis conchylega*	**99.8**	0.2						
	Ophiacantha bidentata	**72.1**	27.9						
III	*Ascorhynchus abyssi*								**100.0**
	Bathycrinus sp.						0.7	33.8	**65.5**
	Elpidia glacialis							23.3	**76.7**
II	*Polymastia* sp.			1.0	1.0	0.3	**96.7**	0.9	
I	*Idmidronea atlantica*		1.4	10.7	12.6	**75.3**	0.0		
	Vase shaped sponges		8.0	32.3	21.0	35.8	2.9		
	Latrunculia sp.	4.8	2.3	26.7	36.1	30.1			
	Lissodendoryx complicata		0.6	32.1	30.8	36.5			
	Isidella lofotensis			26.4	34.5	39.1			
	Synascidia spp.			23.2	30.9	45.8			

dominant at the 'Upper Slope' and at Stn 1400 of the 'Lower Slope', whereas on the shelf echinoderms and polychaetes predominated. Echinoderms were also dominant at the 'Lower Slope' below 2000 m. Anthozoans and crustaceans were common over the whole depth range.

Indications of endobenthic life ('Lebensspuren'), such as siphons and holes of infauna, were detected at all stations except at Stns 1400 and 2780. There was no depth-related trend. In total, 86% of the slides from Stn 190, 11% of the slides from Stn 370 and 17% of the slides from the 'Upper Slope' stations indicated endobenthic life. At Stn 2640, signs of infauna were present at each picture.

Discriminator species

The errant polychaete *Onuphis conchylega*, the brittle stars *Ophiacantha bidentata* and *Ophiocten sericeum* and the brachiopod *Waldheimia cranium* characterized the 'Shelf Break' community (Table 3). The octocoral *Isidella lofotensis* and the sponge *Lissodendoryx complicata* were discriminators of the 'Upper Slope' (Table 3). The crinoid *Bathycrinus* sp., the holothuroid *Elpidia glacialis* and the sponge *Polymastia* sp. were typical species of the 'Lower Slope' (Table 3).

Correlation between environmental and faunal data

Prior to the actual BIO-ENV analysis, we looked at the interrelationships among the environmental variables (Table 1). Only water depth and bottom-water temperature were significantly correlated ($r = -0.95$, Bonferroni-corrected $p < 0.05$). According to the recommendation of Clarke & Ainsworth (1993), one of the correlated parameters, water depth, was omitted in the subsequent analysis.

The BIO-ENV comparison between the faunal and environmental data revealed that of all the single variables, temperature showed the highest affinity to the megabenthic distribution, followed by sediment type and salinity (Table 4). The faunal patterns were even better correlated to a combination of temperature and sediment type ($\rho_H = 0.69$), whereas an inclusion of more variables yielded lower ρ_H values.

Small-scale spatial distribution patterns

In most cases (130 of 211), epibenthic organisms were randomly distributed along photographic transects. In 81 cases, evidence for a patchy dispersion was found; no species showed a uniform distribution (Fig. 5a). The relationship between mean abundance

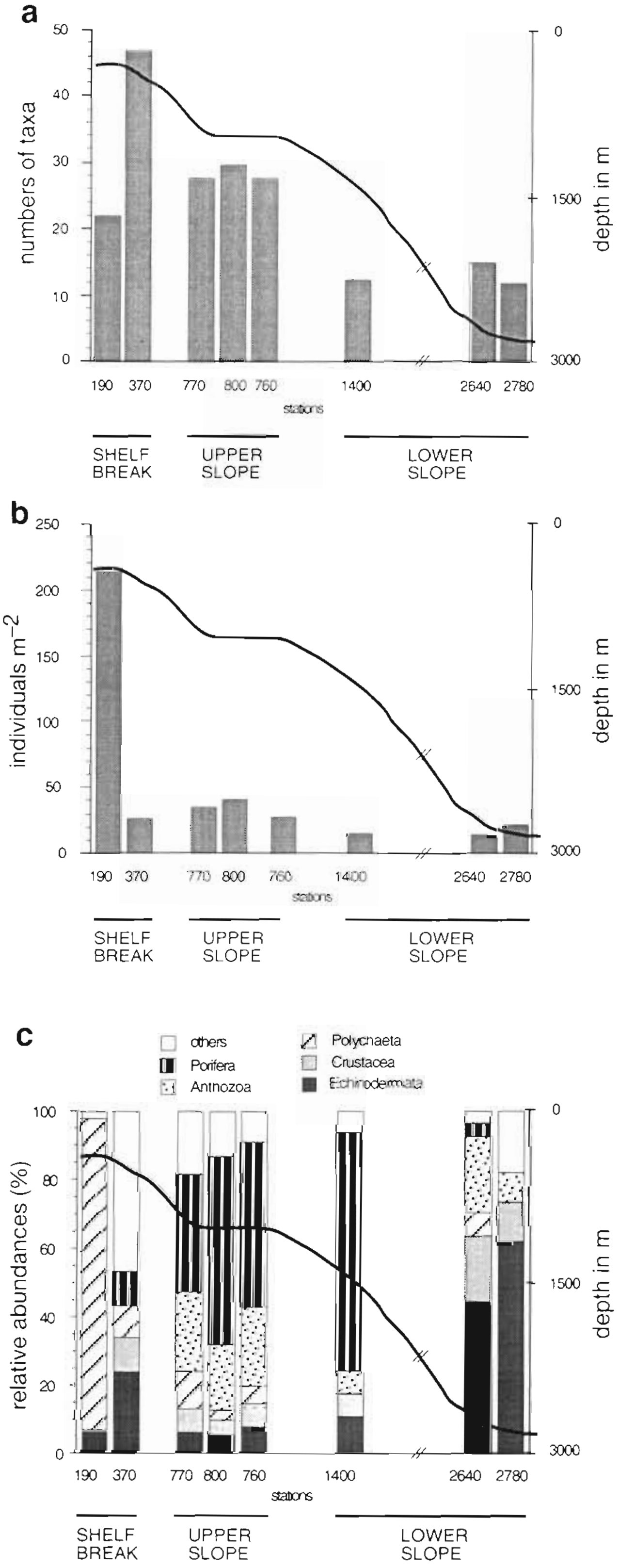

Fig. 4. Spatial dispersion of taxa along the depth gradient of the East Greenland continental slope. (a) Number of species, (b) abundance, (c) faunistic composition of major taxonomic groups. Black line symbolizes the continental slope

and dispersion pattern was not very pronounced, albeit statistically significant (Fig. 5a: Spearman rank correlation $\rho = 0.4$, $p = 0.0001$). The most abundant species, *Onuphis conchylega*, occurred in pronounced patches (Fig. 5b: DC = 10.26). The other typical shelf species, the brittle stars *Ophiocten sericeum* and *Ophiacantha bidentata*, were also patchily distributed along the transects, however, at distinctly lower abundances (Fig. 5c and Fig. 5d, respectively). The most typical species of the 'Lower Slope', *Elpidia glacialis* and *Bathycrinus* sp., occurred in similar densities. However, while specimens of the first species were slightly aggregated (Fig. 5e: DC = 1.55, $p < 0.05$), the latter was randomly dispersed (Fig. 5f: DC = 1.30, $p > 0.05$).

DISCUSSION

Methods

Sea floor imaging is commonly considered to be the best method to quantitatively investigate epibenthic assemblages (Holme & McIntyre 1984). However, small individuals on the slides may have been overlooked, especially at the 'Upper Slope' stations where corals and sponges covered large parts of the sea floor. In general, all organisms recognized on the images were arbitrarily classified as being 'epibenthic' even though some species, e.g. *Cerianthus* sp., are partially within the sediment and forage at the sediment-water interface (Jensen 1992).

The photographs on which our analysis was based were taken in a 15 d period during the Arctic summer (13 to 27 July 1994). Therefore, the samples only reflect benthic conditions for part of the summer and might be biased due to fluctuations over an entire summer period. The communities of large and rather immobile benthic organisms on which we focused are known to be comparatively stable, however (Dayton 1990).

Zonation

We found that the composition of the epibenthic assemblages on the continental slope off East Greenland at 75° N exhibited a clear depth zonation. A similar pattern was also reported from the continental margin off Northeast Greenland at 80° N (Piepenburg & Schmid 1996), and in general, depth zonation is a common benthic distribution feature of continental slopes (Carey & Ruff 1977, Haedrich et al. 1980, Hecker 1990, Horikoshi et al. 1990, Dayton et al. 1994, Gutt & Starmans in press).

Table 3. Median abundances of the discriminator species calculated by comparing the major station groups (according to Clarke 1993). δ_k: average dissimilarity; SD(δ_k): standard deviation; %: contribution of each species to discrimination of station groups

Comparison	Species	Median abundances (ind. m^{-2}) Shelf Break	 Upper Slope	 Lower Slope	δ_k	SD (δ_k)	%
Upper Slope - Shelf Break	*Onuphis conchylega*	96.76	0.02		5.02	4.29	7.50
	Isidella lofotensis	0.00	5.70		3.39	0.55	5.07
	Ophiacantha bidentata	2.69	0.00		2.81	0.79	4.20
	Lissodendoryx complicata	0.05	5.23		2.80	1.11	4.18
	Ophiocten sericeum	3.87	0.01		2.48	1.59	3.71
	Waldheimia cranium	6.17	0.59		2.34	1.38	3.49
Upper Slope - Lower Slope	*Isidella lofotensis*		5.70	0.00	4.90	0.35	5.88
	Lissodendoryx complicata		5.23	0.00	4.82	0.39	5.78
	Bathycrinus sp.		0.00	3.57	3.68	1.51	4.41
	Latrunculia sp.		1.35	0.00	3.42	0.17	4.10
	Synascidia sp.		1.16	0.00	3.28	0.33	3.94
	Metavermilia sp.		1.65	0.02	2.96	0.85	3.55
	Elpidia glacialis		0.00	2.75	2.85	2.19	3.42
Shelf Break - Lower Slope	*Onuphis conchylega*	96.76		0.00	7.72	6.43	9.05
	Ophiacantha bidentata	2.69		0.00	3.92	1.32	4.59
	Ophiocten sericeum	3.87		0.00	3.88	2.35	4.55
	Bathycrinus sp.	0.00		3.57	3.53	1.67	4.14
	Waldheimia cranium	6.17		0.71	3.20	1.81	3.74
	Elpidia glacialis	0.00		2.75	2.74	2.28	3.20
	Polymastia sp.	0.00		3.74	2.52	2.80	2.96

The directly depth-related water pressure, though probably important in a physiological sense (Somero 1990), is very unlikely to have a strong effect on the ecological zonation of the megafauna. There are other more plausible indirectly depth-related causes such as food availability and trophic structure (Haedrich et al. 1980) or effects of boundaries (Pineda 1993). In our study, faunal distribution patterns were most strongly correlated with a combination of bottom-water temperature and seabed type, whereas the other mea-

Table 4. Result of calculation of the relationship between the megabenthic distribution and environmental factors. Combinations of environmental variables, k at a time, yielding the harmonic rank correlation ρ_H between the faunistic and environmental data sets (8 stations each) for each k (for $k > 1$, only combinations with $\rho_H > 0.4$ are given). **Bold** type indicates the best combination (maximum ρ_H). t: temperature in °C; sed: sediment type; S: salinity; chl a_{10m}: chlorophyll concentration in 10 m water depth; chl a_{BNL}: chlorophyll concentration in bottom water; phaeo$_{10m}$: phaeopigments concentration in 10 m water depth; phaeo$_{BNL}$: phaeopigment concentration in bottom water; sps: sponge spicules

k	Spearman harmonic rank correlation; best combination of variables							
1	t 0.53	sed 0.44	S 0.33	chl a_{10m} 0.17	phaeo$_{BNL}$ 0.08	chl a_{BNL} −0.02	sps −0.03	phaeo$_{10m}$ −0.24
2	**t, sed** **0.69**	S, sed 0.50	t, S 0.46	.	.	.	.	..
3	t, S, sed 0.66	t, sed, chl a_{10m} 0.60	t, sed, phaeo$_{BNL}$ 0.52	.	.	..	.	.
4	t, S, sed, chl a_{10m} 0.61	t, sed, chl a_{10m}, phaeo$_{BNL}$ 0.51	t, S, sed, phaeo$_{BNL}$ 0.49	..	.	..	.	.
5	t, sed, chl a_{10m}, chl a_{BNL}, phaeo$_{BNL}$ 0.48	t, S, sed, chl a_{10m}, phaeo$_{BNL}$ 0.46	.	.	..	...	.	.
6	t, S, sed, chl a_{10m}, chl a_{BNL}, phaeo$_{BNL}$ 0.43	...		..	.	...	.	.
7	t, S, sed, sps, chl a_{10m}, chl a_{BNL}, phaeo$_{BNL}$ 0.33	.	..	.	.		.	.

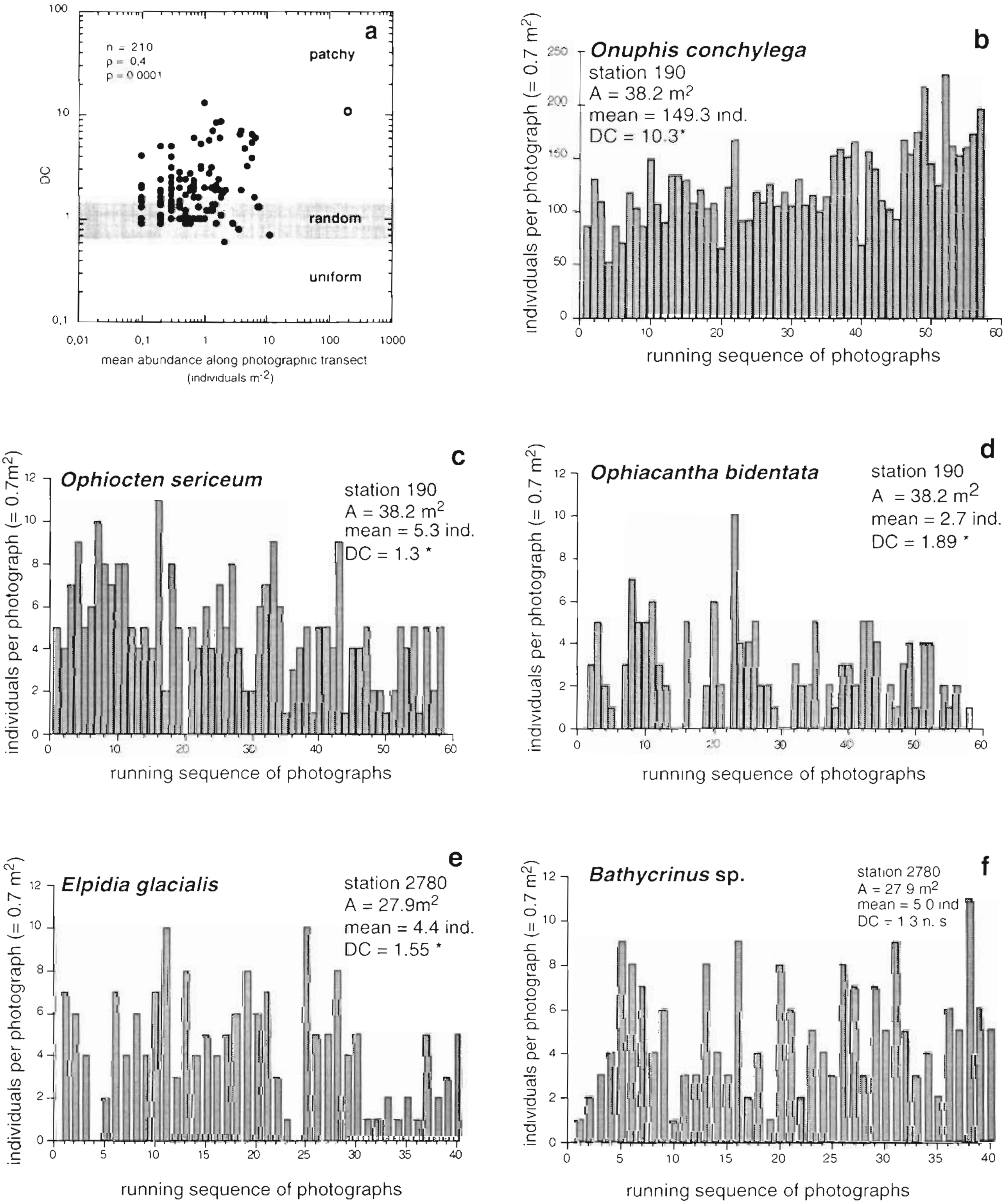

Fig. 5. (a) Dispersion coefficients (DC) versus mean densities; shaded area marks random distribution (DC = 1, $p > 0.05$) (**o**) *Onuphis conchylega*. Spatial distribution of the most common species of each depth's grouping. (b) Polychaete *Onuphis conchylega* along the transect at Stn 190, (c) the brittle stars *Ophiocten sericeum* at Stn 190; (d) *Ophiacantha bidentata* at Stn 190; (e) crinoid *Bathycrinus* sp. at Stn 2780, (f) holothurian *Elpidia glacialis* at Stn 2780. A: total area imaged, mean: mean number of individuals per photograph; DC: dispersion coefficient (χ^2 test of DC = 1 level of significance: n.s. $p > 0.05$; $^*p \leq 0.05$)

sured environmental parameters (salinity as well as pigment concentrations in the surface and bottom water) were of less significance. Temperature differed among stations with only 2°C at maximum (Table 1). Though this difference can have serious physiological impacts on the level of individuals, especially for cold-stenothermic species (Rakusa-Suszczewski 1980, Clarke 1983), we assume that it does not have a direct effect on the ecological zonation. Temperature, being highly correlated to water depth, is a signature of distinct water masses that occurred at different depths at the East Greenland slope (Arctic Surface Water, Arctic Intermediate Water, and Deep Water; Hopkins 1991). For that reason, temperature was found to be related to the depth-zonated faunal distribution. Of all environmental parameters measured, seabed type (described by number of stones; Table 1) is left as probably the most important factor directly influencing the megabenthic distribution as it was also reported, for instance, by Haedrich et al. (1975) and Hecker (1990) from the slope off New England (USA).

Community structure

The 'Shelf Break' stations differed considerably in sea floor characteristics (Table 1) and benthic community structure (Appendix 1, Fig. 4). At Stn 370, many stones (>50 stones per photograph) formed a habitat-rich biotope colonized by numerous species, offering suitable settlement substrates for e.g. sponges and bryozoans. At Stn 190, the sediment surface was less covered by stones, and in some pictures stones were even absent. The lower substrate heterogeneity probably explains the lower species diversity but also the high abundances of *Onuphis conchylega*, a polychaete that apparently avoids stony substrates (Hartmann-Schröder 1971). Molluscs were not very abundant in our samples, whereas Thorson (1933) reported them to dominate epibenthic communities off East Greenland. However, these investigations were confined to fjords and covered different kinds of marine biotopes.

In contrast to the 'Shelf Break' stations, the samples from the 'Upper Slope' were very similar in sea floor type and diversity (Table 1) as well as faunal composition (Fig. 4c) probably because depths were similar and distances between stations were small (Stns 770 to 760: 300 m; Stns 770 to 800: 900 m; Stns 800 to 760: 1000 m; all distances ± 150 m error due to GPS precision). Because distinct megabenthic species assemblages typically cover areas on a 100 to 1000 m scale (Barthel & Gutt 1992), we assume that the same assemblage was sampled at the 'Upper Slope' stations. The seabed at all stations was characterized by abrupt changes between patches of soft bottom, colonized by epibenthic species of assemblage V as well as infaunal organisms, and dense sponge spicule mats. These discontinuities were even seen in single photographs. Sponge spicule substrates strongly influence benthic distribution patterns because they provide settlement surfaces (Barthel & Tendal 1993). In our study area, they were colonized by a high-diversity octocoral-sponge association (assemblage I) which in turn offered habitats for other species. The anthozoan *Amphianthus* sp. as well as crinoids were often seen on octocoral branches. The thick network of suspension-feeding species provided shelter for crustaceans and other small animals. For an Antarctic benthos assemblage that was also strongly dominated by suspension-feeding organisms providing a 3-dimensional habitat for many other species, Bullivant (1961) coined the term 'multistoried association'. Thus, distinct species assemblages, associated with different substrates, were found in the same zone and even at the same location.

At the 'Lower Slope', the 1400 m station differed from the deeper stations considerably, mainly in terms of the seabed type (Table 1) and the presence of the sponge *Polymastia* sp. (Appendix 1). One of the most difficult problems for sponges is settling on soft bottom (Barthel & Tendal 1993). At Stn 1400, stones provided settlement substrates for *Polymastia* sp., a eurybathic sponge genus that was probably represented by several morphologically similar species (D. Barthel pers. comm.). Echinoderms, such as the typical deep-sea species *Bathycrinus* sp. and *Elpidia glacialis*, were dominant, especially at the deeper stations. In general, echinoderms are able to exploit different foraging strategies, a capability which is advantageous in biotopes with spatially and seasonally changing food availability (Haedrich et al. 1980, Taghon & Greene 1992, von Juterzenka 1994) such as deep-sea locations.

Benthic-pelagic coupling

Quality and quantity of organic food supply, reaching the sea floor via either vertical sedimentation or lateral advection, have been recognized to strongly affect the benthos (Graf 1989, Grebmeier & Barry 1991, Dayton et al. 1994). However, in our study pigment concentrations in the benthic nepheloid layer, commonly regarded as a parameter of input of organic matter to the benthos, were not as important for the benthic zonation as seabed properties, probably because they were generally rather low and did not vary much among stations.

The BIO-ENV correlation between the surface water pigment concentrations and the benthic distribution patterns was also not very pronounced, i.e. we did not find evidence for a direct benthic-pelagic coupling at the megabenthic community level, irrespective of water depth. However, this finding does not imply that the megabenthos is decoupled from water column processes. A test of this hypothesis was not the main objective of our study and, therefore, our methodological approach was not adequate in terms of temporal and spatial extent of sampling, number of variables measuring organic input, etc. to address this issue.

Furthermore, it is known that more organic matter actually reaches the benthos by lateral advection than by vertical sedimentation (Graf 1992), particularly in polar seas where benthic assemblages are assumed to be mainly nourished by allochthonous organic carbon imported from adjacent, more productive areas (Feder et al. 1994a, b).

It is commonly accepted that primary production in polar waters is strongly affected by ice cover (Smith & Sakshaug 1990). Due to the small extent of our study area (stations were only 60 km apart at maximum), the seasonal and interannual variations in ice cover are generally the same at all stations (Parkinson et al. 1987) and, therefore, the autochthonous carbon production can be assumed to be quite similar.

Small-scale distribution

The depth zonation of benthic assemblages along a continental slope is a large-scale (10 to 100 km) distribution pattern. It is overlaid by a patchiness on a 10 to 100 m scale (Hecker 1990) which is usually measured by coefficients discriminating uniform, random and aggregated dispersion. Generally, the dispersion pattern is related to mean abundance (Jumars & Ekman 1983), but this relationship was not very evident, though statistically significant, in the present investigation. Many species that were not abundant occurred in patches. Several factors, such as environmental heterogeneity caused by different substrates (Gray 1984), social behaviour (Gutt & Piepenburg 1991), reproduction biology (Woodin 1976, 1978) or stochastic processes (Jumars & Ekman 1983), have been suggested to control small-scale patchiness. Although the factors causing the distribution patterns cannot be inferred from the dispersion coefficients, seabed imaging allows an undisturbed *in situ* view of benthic habitats and may provide clues to possible cause-effect relationships. For instance, in our photographs taken at the shelf break, the polychaete *Onuphis conchylega* did not occur on stony substrates. Aquarium observations showed that this errant species, which bears a heavy tube made of coarse particles, avoids climbing over stones. Its very patchy dispersion at Stn 190 essentially reflects the distribution of stones on the bottom.

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Appendix 1. Species-station table. Species abundances in ind. m^{-2} [a]Encrusting sponges presence (%); [b]*Isidella lofotensis* in degree of coverage; [c]species used in community analysis. (Appendix continued overleaf)

Major taxonomic group	Species	Station 190	370	760	770	800	1400	2640	2780
Sponges	Porifera spp.			3.8	4.0	11.8		0.5	
	Demospongia sp.[c]		2.0						
	Geodia mesotriaena[c]			0.5	0.3	0.2			
	Geodia phlegraei[c]		0.1	0.9	0.3	0.7			
	Polymastia sp.[c]			0.1	0.1	0.4	11.0	0.1	
	Tentorium semisuberites[c]								0.1
	Phakellia bowerbanki[c]		0.1						
	Latrunculia sp.[c]	0.2	0.1	1.2	1.6	1.3			
	Lissodendoryx complicata[c]		0.1	5.7	4.9	5.8			
	Aplysilla sulphurea[a]				9%	16%			
	Hymedesmia paupertas[a]		9%	33%	44%	5%	3%		
	Hymedesmia curvichela[a]		9%	39%	44%	15%	3%		
	Encrusting sponges[a]	7%	9%	10%	44%				
	Hexactinella sp.[c]						0.1		
	Vase shaped sponges		0.4	1.5	1.0	1.7	0.1		
	Aphrocallistes sp.			0.1		0.7			

Appendix 1 (continued)

Major taxonomic group	Species	Station							
		190	370	760	770	800	1400	2640	2780
Cnidarians	Hydrozoa sp. I[c]				0.1				
	Hydrozoa sp. II[c]				0.2				
	Hydrozoa sp. III[c]		0.1						
	Atolla sp. af.[*]	0.8	0.7						
	Actiniaria sp. I[c]								0.1
	Actiniaria sp. II[c]						0.4		
	Cerianthus sp.[c]	0.2	1.4		0.3			1.6	0.4
	Epizoanthus sp.[*]		1.4	0.9	0.3			1.6	1.4
	Alcyonaria sp.[*]		0.5		0.7	0.2	0.7		
	Amphianthus sp.[c]		0.8	0.6	0.7	0.3			
	Actinernus nobilis[c]		0.4	0.6		0.7			
	Isidella lofotensis[b,c]		4.5	5.9	6.7				
	Pennatularia spp.[c]		0.3						
Bryozoans	*Hornera lichenoides*[c]	0.1	2.9	0.2	1.1	0.6	0.3		
	Idmidronea atlantica[c]		0.3	0.2	0.3	1.6			
	Sertella beaniana[c]		0.2	0.6	0.3	0.3			
Brachiopods	*Waldheimia cranium*[c]	1.4	1.9		1.8				2.1
Platyhelminthes	Turbellaria ?	0.5			0.5		0.4		
Molluscs	*Colus* sp.[c]	1.0	0.1	0.3	0.2	0.7	0.2	0.4	0.8
	Colus lachesis[c]					0.2	0.1		
	Arctinula greenlandica[c]								0.9
	Bathypolypus arcticus[c]		0.3						
	Rossia glaucopis[c]		0.3						
	Ommatostrephes todarus[c]			0.3					
Polychaetes	Serpulidae sp.[c]					0.2		0.5	
	Metavermilia sp.[c]		2.2	0.9	3.9	1.0		0.5	
	Onuphis conchylega[c]	214.0	0.3	0.6					
Pantopods	*Nymphon* sp.[c]	0.2						0.5	
	Ascorhynchus abyssi[c]								1.9
Crustaceans	*Saduria sabini*[c]							0.2	
	Mysidacea spp.	0.8			0.1		0.4	0.7	0.1
	Metaerythrops sp.[c]		0.5	0.1		0.3			
	Gammarida sp.[c]		0.1	0.6		0.1		0.5	0.4
	Haligrades sp.[c]		0.2	0.7	1.2	0.3	0.7	0.2	0.1
	Epimeria loricata[c]		0.3		0.1				
	Stegocephalus inflatus[c]		0.3						
	Sabinea sp.[c]		0.3						
	Decapoda[c]	0.1	0.9	0.5	1.0	1.1		0.7	
Echinoderms	Crinoidea spp.[c]	0.4	0.2	0.2	0.3	0.3			
	Bathycrinus sp.[c]						0.7	3.6	7.1
	Asteroidea spp.		0.8	0.6	0.5	0.7			
	Poraniomorpha bidens[c]								0.4
	Hymenaster pellucidus[c]			0.3				0.7	
	Henricia sp.[c]	0.2	0.3	0.3	0.5	0.4			
	Pteraster pulvillus[c]		0.5			0.2			
	Pteraster obscurus[c]		0.1						
	Pedicellaster typicus[c]		0.5						
	Korethraster hispidus[c]			0.3					
	Solaster papposus[c]						0.7		
	Urasterias linki[c]		0.3						
	Icasterias panopla[c]	0.3	0.1						
	Gorgonocephalus spp.[c]		0.3	0.6	0.7	0.4			
	Amphiura sundevalli[c]		0.5						
	Ophiacantha bidentata[c]	3.9	1.5						
	Ophiopholis aculeata[c]	0.1	0.3						
	Ophiura sarsi[c]	0.3	0.3						
	Ophiopus arcticus[c]	0.8				0.4			
	Ophiocten sericeum[c]	7.5	0.2		0.2				
	Ophiopleura borealis[c]	0.1	0.1						
	Strongylocentrotus droebachiensis[c]	1.2	0.4				0.4		
	Elpidia glacialis[c]							1.9	6.3
	Molpadia arctica[c]							0.2	
Ascidians	Synascidia sp.[c]			0.8	1.8	1.6			
	Ascidiacea sp.[c]		0.3						

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