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Megabenthic commmunities in the waters around Svalbard

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Abstract Composition and distribution of megabenthic communities around Svalbard were investigated in June/July 1991 with 20 Agassiz trawl and 5 bottom trawl hauls in depths between 100 and 2100 m. About 370 species, ranging from sponges to fish, were identified in the catches. Species numbers per station ranged from 21 to 86. Brittle stars, such as *Ophiacantha bidentata*, *Ophiura sarsi* and *Ophiocten sericeum*, were most important in terms of constancy and relative abundance in the catches. Other prominent faunal elements were eunephthyid alcyonarians, bivalves, shrimps, sea stars and fish (Gadidae, Zoarcidae, Cottidae). Multivariate analyses of the species and environmental data sets showed that the spatial distribution of the megabenthos was characterized by a pronounced depth zonation: abyssal, bathyal, off-shore shelf and fjordic communities were discriminated. However, a gradient in sediment properties, especially the organic carbon content, seemed to superimpose on the bathymetric pattern. Both main factors are interpreted as proxies of the average food availability, which is, hence, suggested to have the strongest influence in structuring megabenthic communities off Svalbard.

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Introduction

The information on the composition and distribution of the benthos of the Barents Sea is currently rather unbalanced. While the mostly ice-free area south of the Polar Front has been studied relatively well (for a review see Grebmeier and Barry 1991), knowledge of the benthos of the northern high-Arctic Barents Sea, including the Svalbard Archipelago, is still scarce. Faunistic inventories around Svalbard primarily covered intertidal and sublittoral sites along the coasts of West and South Spitsbergen (Ambrose and Leinaas 1988; Kendall and Aschan 1993; Weslawski et al. 1993). On the Barents Sea shelf east of Svalbard, which is particularly difficult to reach due to the almost persistent ice cover, only a few off-shore studies were conducted on the macrofauna by Russian researchers, being summarized by Zenkevitch 1963 (basically a translation of Zenkevitch 1947), and (on the meiofauna) by Pfannkuche and Thiel (1987).

During the previous investigations in the northern Barents Sea, the bottom fauna was primarily sampled by grabs and corers. These gears are known, however, to be inadequate for collecting megafaunal organisms, i.e. mobile epibenthic or sessile endobenthic animals that are large enough to be seen in seabed images or to be caught by trawls (*sensu* Gage and Tyler 1991). These organisms, though mostly occurring with comparatively low abundances (and being, therefore, generally underestimated by corer samples), have been shown to significantly affect benthic systems, particularly in higher latitudes, because of their high biomass share (Schwinghamer 1981), their bioturbation and bioirrigation activity (Romero-Wetzel and Gerlach 1991), and their non-negligible contribution to total benthic energy turnover (Piepenburg et al. 1995).

However, ecological studies on the role of the megafauna in benthic systems should be based on a profound knowledge of faunistic community patterns, especially in less well investigated areas. We utilized the Arctic "European Polarstern Study" (EPOS) of R/V "Polarstern" in June/July 1991 (Rachor 1992) to perform a first comprehensive quasi-synoptic assessment of the megabenthos occurring in the poorly known off-shore waters around Svalbard north of the Polar Front. Our specific objectives were:

(1) to perform a faunistic inventory of the study area;
(2) to delineate faunistic zones and describe the composition of their specific species assemblages; and
(3) to relate the faunistic distribution pattern to environmental gradients.

Due to collaboration with numerous taxonomic experts, primarily from the Zoological Institute in St. Petersburg (Russia), a large proportion of the collected animals could be identified to species level. Our study therefore provides a sound data base for further, more detailed, zoogeographical analyses. Furthermore, it constitutes a framework for quantitative analyses of certain taxa (Piepenburg and Schmid 1995) and community fractions (Kendall 1996) as well as the assessment of the role of megafauna in the total benthic community respiration (Piepenburg et al. 1995). As the Arctic EPOS cruise covered areas of insufficient knowledge on pelagic productivity and its relation to the benthos, this paper is also regarded as a contribution to a better understanding of the benthic-pelagic relationships in an Arctic environment.

Materials and methods

Study area

In general, the study area is characterized by typically polar conditions, such as very low, but relatively constant, water temperatures, long-lasting ice cover and large seasonal fluctations in light regime and primary productivity (Hempel 1985). The morphology of the northwestern Barents Sea shelf is rather complex, comprising both shallow ($<$ 100 m) banks and deep ($>$ 300 m) troughs (Loeng 1989). Cold Arctic water masses ($T < 0°C$) shape the hydrography, being separated from the warmer Atlantic water masses ($T > 2°C$) of the southern Barents Sea by a sharp Polar Front at about 77°N (Fig. 1). The Arctic water enters the Barents Sea as surface water along two main routes (through the straits between Svalbard and Franz Josef Land as well as between Franz Josef Land and Novaya Zemlya), moving in a southwestward direction. This surface water inflow is probably counter-balanced by a northward transport of warmer, more saline, Arctic-Atlantic bottom water, formed at the Polar Front, through the trough system of the northern Barents Sea (Loeng 1989; Schauer 1992). There is also some evidence that morphological features, such as shallow banks and small islands (e.g. Kvitøya), cause mesoscale anti-cyclonic eddies (Loeng 1989), which would lead to downwelling phenomena and, hence, locally enhanced sedimentation.

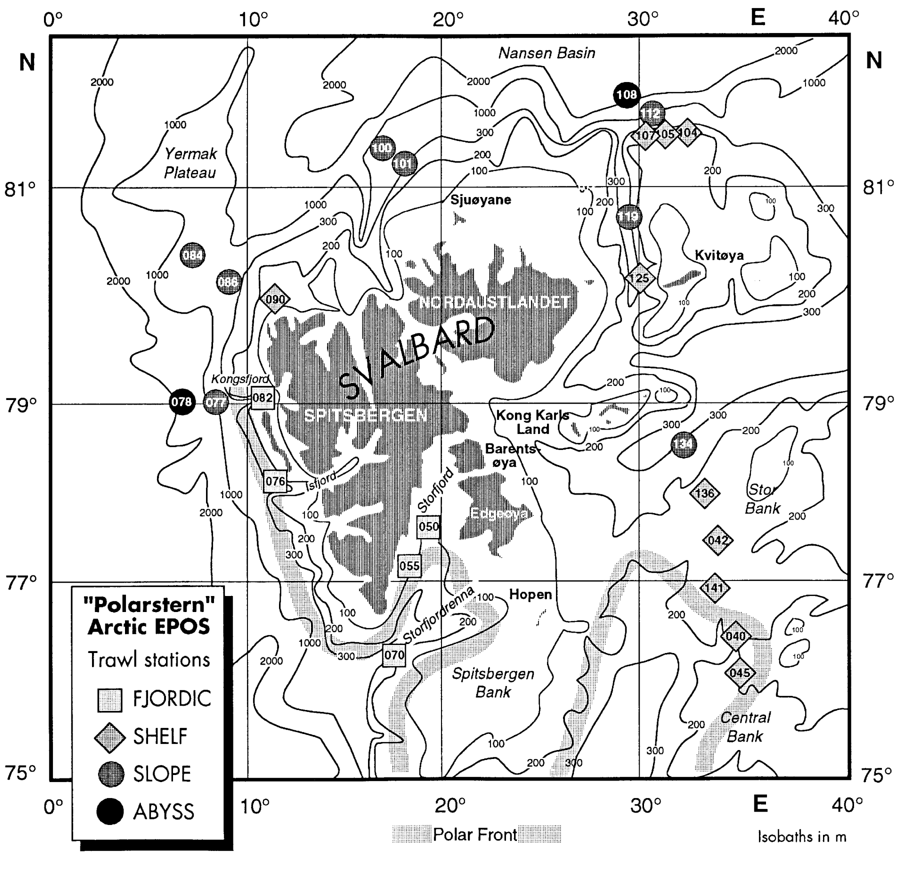


Fig. 1 Svalbard Archipelago. Trawl station map of cruise ARK VIII/2 of R/V "*Polarstern*" in June/July 1991, showing the spatial distribution of the station groups Fjordic, Shelf, Slope and Abyss

The study area belongs to the seasonal pack-ice zone encircling the permanently ice-covered Arctic Ocean. The actual position of the marginal ice zone, however, varies considerably between both seasons and years (Loeng 1989). River discharge and sediment load are generally lower than in other Eurasian-Arctic shelf seas (Grebmeier and Barry 1991). Seabed characteristics of the northern Barents Sea are only little known. According to Zenkevitch (1963), most of the area is covered by fine-grained brown sediment with comparatively low content of organic carbon. During the Arctic EPOS cruise, coarser sediments were found to predominate on shallow shelf banks (< 100 m) or in the sublittoral zone around islands (H. Grobe, personal communication), and seabed imaging has revealed that stones and boulders occur locally in significant quantities (Piepenburg and Schmid 1996).

Loeng (1989) reported primary production in the Barents Sea to range from 60 to 80 g C m^{-2} yr^{-1}, most of which occurs during the spring bloom. In the ice-covered region north of Svalbard, however, Strömberg (1989) estimated annual primary production rates of only about 10 g C m^{-2} yr^{-1}. The bulk of the yearly primary production in the seasonally ice-covered northern Barents Sea is assumed to take place within the marginal ice zone that crosses the area while receding during the period June/August from its winter position at the Polar Front (Wassmann et al. 1991; Strass and Nöthig 1996). Pfannkuche and Thiel (1987) found surprisingly high levels of chlorophyll in sediment samples from the continental shelf and slope northeast of Svalbard, indicating a substantial sedimentation of phytodetritus to the seabed. Summarizing Russian quantitative inventories in the deeper parts of the northern Barents Sea, Zenkevitch (1963) reported average benthos biomass to be 5–10 times lower than in the richest regions of the Barents Sea, under the Polar Front or west of Novaya Zemlya.

Data collection and analysis

Samples were collected in June/July 1991 during the ARK VIII/2 expedition of R/V "Polarstern" (see Rachor 1992 for detailed information) using an Agassiz trawl (AGT) and a commercial 140′ bottom trawl (BT). The opening of the AGT was 3 m wide and 1 m high, and its mesh size in the cod-end was 10 mm. The BT had a net opening of about 22 m (on the ground) and a cod-end mesh size of 20 mm. The along-bottom haul time was 15 min for the AGT and 30 min for the BT, with trawling speeds of about 1 knot and about 4 knots, respectively. Trawl catches were carried out at 25 stations (Table 1: 20 AGT and 5 BT hauls) at depths of 100–2100 m (Fig. 1).

The station plan focussed on the region north of the Polar Front and covered various gradients in order to foster the intended comparative community analyses, i.e. gradients in terms of seabed morphology (shelf-slope, bank-trough), large-scale hydrography (West Spitsbergen Current – "Atlantic Boundary Current" at the northern slope – Arctic shelf water), and ice regime (permanent ice cover – seasonal ice cover). Sampling was concentrated on: (1) four shelf-slope transects (Kongsfordrenna, Yermak Plateau, Sjuøyane and Nansen Basin Slope), (2) the Storfjord region, and (3) a long transect crossing the Arctic Barents Sea shelf from Kvitøyarenna in the north to the central Barents Sea south of the Stor Bank.

Megabenthic animals that were discernible macroscopically, with sizes of about 2 cm minimum, were sorted from the trawl catches directly after capture. In addition, the sediment contained in the catches (or, if necessary, a random sub-sample) was washed through a 1-mm sieve. The animals picked out of the samples and the sieve residues were fixed in a borax-buffered 4% formalin/seawater solution for further examination.

The collaboration with several taxonomic experts, primarily from the Zoological Institute of the Russian Academy of Sciences in St. Petersburg, allowed us to identify the collected animal material to species (or putative species) level for a broad range of taxonomic groups (see acknowledgements for a list of contributing experts). Though the sampling methods used were not quantitative, gross differences in the abundances of the species were evident in the catches. These differences were approximated by a four-point scale abundance code: · absent, + rare (only single specimens in the catch), + + common (10–100 specimens in the catch), and + + + abundant (> 100 specimens in the catch).

We applied a variety of multivariate analysis techniques to outline the distribution and structure of distinct megabenthic species assemblages in relation to environmental conditions. Classification and ordination procedures were used to discriminate between groups of stations with similar faunal composition (Field et al. 1982). As two trawl types with undoubtedly different catch efficiencies were employed for sampling, the faunistic resemblance between stations was measured by the qualitative Jaccard coefficient, calculated for each station pair on the basis of presence-absence data. Species that occurred at only one station as well as the few exclusively pelagic species without any relation to the benthic system, such as the fish *Mallotus villosus* and *Boreogadus saida*, were not considered in the calculation of the faunistic station resemblances, i.e. community analyses were based on a subset of 245 of the 373 species identified. For the classification of stations according to their faunistic resemblance, as illustrated by a dendrogram, we used agglomerative UPGMA (group average) clustering. Non-metric multidimensional scaling (MDS) was applied to the same resemblance data set to order the stations in a two-dimensional plot in such a way that their faunistic similarities were reflected best (Kruskal and Wish 1978). The discrimination of distinct stations groups in the cluster dendrogram and the MDS plot was, however, a subjective process, i.e. our approach involved no statistical testing of the group delimitation made (Field et al. 1982).

The relationships between the faunistic pattern (as represented by the inter-station Jaccard resemblances) and the environment (parameterized by abiotic station variables such as water depth, latitude, longitude, distances from the coast and from the shelf break, as well as hydrographical and sedimentological data) were analysed using the multivariate BIO-ENV procedure proposed by Clarke and Ainsworth (1993). This multivariate method allows the identification of a set of environmental parameters that correlates best to the biotic structure and may thus be assumed to strongly affect the communities.

Results

A total of 373 different species (including a few putative species) were collected from the AGT and BT catches, comprising 10 sponges, 19 hydrozoans, 14 actinians, 42 bryozoans, 2 brachiopods, 44 polychaetes, 60 molluscs (includng 29 gastropods and 27 bivalves), 11 pantopods, 71 crustaceans (2 cirripeds, 4 cumaceans, 6 isopods, 46 amphipods, 2 mysids and 11 decapods), 44 echinoderms (3 crinoids, 22 asteroids, 2 echinoids, 10 ophiuroids and 7 holothurians) and 44 fish (Table 2).

Overall, the most prominent species (in terms of constancy of occurrence (%) and relative abundance at single stations) was the brittle star *Ophiacantha bidentata*, which occurred at 21 out of 25 stations (84%). Additional important species were the brittle stars *Ophiura sarsi* (68%), *Ophiocten sericeum* (64%) and *Ophioscolex glacialis* (52%), the bivalves *Bathyarca glacialis* (64%), *Astarte crenata* and *Yoldiella intermedia* (both 52%), the shrimps *Pandalus borealis* and *Sabinea septemcarinata* (both 60%), the sea stars *Ctenodiscus crispatus* and *Pontaster tenuispinus* (both 60%), the polychaete *Nephtys caeca* (60%), the sea urchin

Table 1 Trawl stations during Arctic EPOS (R/V "Polarstern" ARK VIII/2) in June/July 1991 (*Stat*: station numbers; *Date*: dates of sampling; positions (*Lat*: latitude, *Long*: longitude); geographic *location*; *Depth*: water depths (m); *Gear*: *AGT* Agassiz trawl, *BT* bottom trawl; *Area*: estimated swept area (m^2); *Temp*: bottom-water temperatures; *Sal*: salinities (data provided by U. Schauer, Bremerhaven; *Fines*: dry weight percentages of silt and clay; *TOC*: dry weight percentages of total organic carbon (data provided by H. Grobe, Bremerhaven). "." denotes "no data"

Stat	Date 1991	Lat N	Long E	Location	Depth (m)	Gear	Area (m^2)	Temp (°C)	Sal	Fines (% dw)	TOC (% dw)
040	23.6.	76°37′	34°51′	Stor Bank Slope	220	BT	83200	1.40	34.97	83.2	1.45
042	24.6.	77°21′	33°19′	Stor Bank	150	AGT	2800	[a]1.63	[a]34.93	.	.
045	25.6.	75°59′	34°48′	Central Bank Slope	250	BT	82300	0.13	34.96	36.1	1.40
050	27.6.	77°33′	19°05′	Storfjord	180	AGT	2700	− 1.86	35.07	86.1	2.13
055	28.6.	77°12′	18°19′	Storfjord	100	AGT	4400	− 1.38	34.69	31.5	1.75
070	29.6.	75°59′	17°10′	Storfjordrenna	320	AGT	4400	2.88	34.99	91.7	1.53
076	1.7.	78°16′	10°42′	Isfjordrenna	340	AGT	4400	0.90	34.81	.	.
077	2.7.	79°09′	7°59′	Kongsfjordrenna	960	BT	80000	2.96	35.03	.	.
078	3.7	79°00′	5°45′	Knipovich Ridge	2000	AGT	15900	− 0.96	34.91	72.2	1.02
082	5.7.	79°01′	10°48′	Kongsfjordrenna	300	AGT	3400	0.46	34.81	100.0	1.75
084	6.7.	80°19′	7°28′	Yermak Plateau	650	AGT	7400	0.02	34.91	92.7	1.17
086	7.7.	80°08′	9°49′	Yermak Plateau	550	AGT	6500	0.96	34.92	91.4	1.41
090	8.7.	80°00′	11°24′	Yermak Shelf	150	AGT	1300	2.84	34.95	4.0	0.17
100	11.7.	81°22′	17°28′	Sjuøyane Slope	850	AGT	5700	− 0.54	34.91	53.6	0.75
101	12.7.	81°12′	18°33′	Sjuøyane Slope	400	AGT	4000	1.71	34.96	85.9	1.57
104	14.7.	81°26′	31°39′	Kvitøya Slope	200	AGT	4400	1.49	34.91	28.8	0.63
105	15.7.	81°25′	31°00′	Kvitøya Shelf	240	AGT	3000	1.47	34.91	55.1	0.73
107	16.7.	81°25′	30°40′	Kvitøya Shelf	350	BT	63100	1.62	34.92	.	.
108	17.7.	81°36′	30°28′	Nansen Basin	2100	AGT	8600	− 0.79	34.98	100.0	1.41
112	19.7.	81°34′	31°10′	Kvitøya Slope	850	AGT	6300	− 0.24	34.90	87.3	1.08
119	20.7.	80°43′	29°07′	Kvitøyarenna	550	AGT	3800	0.24	34.83	94.0	1.36
125	23.7.	80°08′	30°02′	Kvitøyarenna	290	BT	.	.	.	.	.
134	24.7.	78°39′	32°09′	Stor Bank Slope	280	AGT	4300	1.62	34.90	94.1	1.26
136	25.7.	77°59′	32°58′	Stor Bank	140	AGT	3600	0.64	34.75	39.1	0.81
141	26.7.	76°57′	33°31′	Stor Bank	150	AGT	2700	1.73	34.93	.	.

[a] Data from nearby station 041, 10 km apart

Table 2 Megabenthic species in trawl catches (Abundance codes: · absent, + rare, + + common, + + + abundant)

Taxon	Station group Fjordic	Shelf	Slope	Abyss
Porifera				
Tentorium semisuberites	.	+	+ +	.
Polymastia mammillaris	+	+ +	+ +	.
Geodia sp.	.	+	.	.
Radiella sol	.	+	.	.
Caulophacus arcticus	.	.	.	+
Cladorhiza gelida	.	.	.	+ +
Tetilla polyura	.	.	+	.
Lissodendoryx comlicata	.	.	+	.
Lissodendoryx indistincta	.	+	.	.
Cornulum textile	.	+	.	.
Hydrozoa				
Hydractinia carica	.	+	.	.
Eudendrium ramosum	.	+	+	.
Eudendrium capillare	.	.	.	+
Staurophora mertensii	+	.	+	.
Modeeria rotunda	+	.	.	.
Modeeria plicatile	+	+	+	.
Rhizocaulus verticillatus	.	+	.	.
Grammaria abietina	.	+	+	+
Acryptolaria borealis	.	+	.	.
Lafoea dumosa	+	+	+	.
Lafoea grandis	.	+	.	.
Zygophylax pinnata	.	+	+	.
Abietinaria abietina	.	+	.	.
Sertularella tenella	.	.	+	.
Sertularia tenera	+	.	.	.
Halecium beani	.	.	.	+
Halecium labrosum	.	.	+	.
Halecium muricatum	.	+	.	.
Ptychogastria polaris	.	.	+	.
Anthozoa				
Alcyonaria				
Eunephthyidae spec. aff.	+ + +	+ + +	+ +	+
Pennatularia				
Umbellula encrinus	.	.	+ +	.
Actiniaria				
Tealia felina lofotensis	+ +	.	.	.
Hormathia digitata	+ +	+	+	.
Hormathia nodosa	+	.	.	.
Amphianthus aff. margaritacea	.	.	+	+ +
Allantactis parasitica	+ + +	+ +	+ +	.
Hormathiidae spec. aff.	.	+	.	.
Glandulactis spetsbergensis	+ +	+	+	.
Pycnanthus densus	.	.	+	.
Stomphia coccinea	.	+	+	.
Liponema multicornis	+	+	+	.
Cactosoma abyssorum	.	.	+	.
Edwardsia sp.	+	.	.	.
Kadosactis rosea	.	.	.	+ +
Sagartia splendens	.	.	.	+ +
Zoantharia				
Epizoanthus incrustatus	.	.	+ +	.
Sipunculida				
Phascolion strombi	+ +	+	+	.
Sipunculida spec. aff.	+	+	+	.
Plathelminthes				
Turbellaria spec. aff.	.	+	.	.
Nemertini				
Nemertini spec. aff.	+	+	+	.
Priapulida				
Priapulus sp.	+	+	+	.
Priapulus bicaudatus	.	+	.	.

Table 2 (continued)

Taxon	Station group Fjordic	Shelf	Slope	Abyss
Bryozoa				
Tubulipora fruticosa	.	+	.	.
Crisia eburneo-denticulata	.	.	+	.
Crisiella sp.	+	.	.	.
Lichenopora verrucaria	+	+	+	.
Disporella hispida	.	+	.	.
Alcyonidium mamillatum	.	+	.	.
A. radicellatum	.	.	+	.
A. gelatinosum anderssoni	+	+	+	.
Nolella dilatata	+	.	.	.
Eucratea loricata	+	+	+	.
Eucratea loricata arctica	.	+	.	.
Notoplites sibirica	+	.	.	.
Tricellaria ternata	+	.	.	.
Tricellaria gracilis	+	.	.	.
Hornera lichenoides	+ +	+ +	+	.
Hornera sp. nov	+	.	.	.
Diplosolen obelia arctica	.	+	.	.
Diplosolen intricarius	.	+	+	.
Retepora beaniana	.	+ +	+	.
Myriapora subgracilis	+	+ +	+	.
Myriapora coarctata	+	+	.	.
Palmicellaria skenei bicornis	.	.	+	.
Kinetoskias smitti	.	.	+	.
Cystisella saccata	+	+	.	.
Cribrilina watersi	.	+	.	.
Phylactella labiata	.	+	.	.
Smittina glaciata	+	+	+	
Parasmittina jeffreysii	.	+	.	.
Idmidronea atlantica gracillima	.	+	.	.
Porella minuta	.	+	+	.
Pseudoflustra solida	+	+	+	
Pseudoflustra sinuosa	.	+	+	.
Pseudoflustra birulai	.	+	+	.
Pseudoflustra hincksi	.	.	+	.
Sarsiflustra abyssicola	.	+	+ +	.
Securiflustra securifrons	.	+	.	.
Defrancia lucernaria	.	+	.	.
Ragionula rosacea	.	+	.	.
Cellepora nodulosa	.	+ +	+	.
Cellepora pumicosa	+	+	.	.
Cellepora canaliculata	.	+	+	.
Escharoides jacksoni	.	+	.	.
Brachiopoda				
Terebratulina retusa	+	.	.	.
Macandrevia cranium	+ +	+	.	.
Hirudinea				
Hirudinea spec. aff.	+	.	+	.
Polychaeta				
Harmothoe (*Eunoe*) *nodosa*	+ +	+ +	+	.
Gattyana cirrosa	+	.	+	.
Phyllodoce groenlandica	+	+	.	.
Nereis zonata	+ +	+	+	.
Nephtys caeca	+ +	+ +	+	.
Aglaophamus sp.	+	+	+ +	.
Glyceridae spec. aff.	.	+	.	.
Onuphis conchylega	+	+ +	+ +	.
Lumbrineris fragilis	+ +	+	+	.
Lumbrineris sp.	.	.	.	+
Laonice spirata	.	.	+	.
Laonice cf. sarsi	+	+	+	.
Prionospio cf. malmgreni	.	.	+	.
Spiochaetopterus typicus	+ + +	+	+	.
Pherusa plumosa	.	+	.	.
Brada inhabilis	+ +	+ +	.	.
Brada cf. villosa	+	+	.	.
Ophelia cf. rathkei	.	+	.	.

Table 2 (continued)

Taxon	Station group Fjordic	Shelf	Slope	Abyss
Ophelina acuminata	.	+	.	.
Capitella capitata	.	.	.	+
Maldane sarsi	+ + +	+	+ +	
Nicomache lumbricalis	+	.	.	.
Owenia fusiformis	+	.	.	.
Myriochele sp.	+	.	+	.
Pectinaria spp.	+ + +	+ +	.	.
Melinna cristata	.	.	+	.
Glyphanostomum sp.	.	.	+	.
Ampharete sp.	.	+	+	.
Amphicteis gunneri	+	.	+	.
Amphicteis sundevalli	+	.	.	.
Melinnopsis arctica	.	.	+	.
Artacama proboscidea	+	.	.	.
Pista maculata	.	.	+	.
Amphitrite cirrata	+	.	.	.
Neoamphitrite affinis	.	.	+	.
Terebellidae spec. aff.	.	+	+	.
Polycirrus medusa	.	.	+	.
Thelepus cincinnatus	.	+	+ +	.
Trichobranchidae spec. aff.	.	.	+	.
Bispira sp.	.	+	.	.
Sabellidae spec. aff.	+	+	+	+
Apomatus globifer	.	+	+	.
Protula tubularia	.	+	.	.
Serpulidae spec. aff.	.	+	+	+
Echiurida				
Echiura sp.	.	+ +	+	.
Mollusca				
Solenogastres				
Solenogastres spec. aff.	.	+	+	.
Scaphopoda				
Siphonodentalium lobatum	+	+	+	.
Gastropoda				
Chitonidae spec. aff.	.	+	.	.
Lepeta coeca	+	.	.	.
Margarites costalis sordida	+	.	.	.
Margarites sp.	.	+	.	.
Frigidoalvania jan-mayeni	.	.	+	.
Tachyrhynchus erosus	+	+	.	.
Cryptonatica clausa	+ +	+ +	+	.
Lunatia pallida	+	.	+	.
Boreotrophon truncatus	+	.	.	.
Velutina sp.	.	+	+	.
Onchidiopsis sp.	.	+	+	.
Oenopota cinerea	+	+	+	.
Oenopota pyramidalis	.	.	+	.
Propebella scalaris	.	.	.	.
Curtitoma trevelliana	.	.	+	.
Volutopsius norvegicus	+	.	.	.
Buccinum hydrophanum	+	+ +	+	.
Buccinum nivale	.	.	+	.
Admete viridula	+	.	.	.
Colus islandicus	+	+	+	.
Colus sabini	+	+	+ +	.
Colus turgidulus	.	.	+	.
Colus latericeus	+	.	.	.
Colus (Anomalosipho) altus	.	.	+	.
Mohnia parva	.	.	.	+
Turrisipho voeringi	+	+	+ +	.
Cylichna sp.	+	+	+	.
Dendronotus spec. aff.	+	.	+	.
Aldisia spec. aff.	.	+	.	.

Table 2 (continued)

Taxon	Station group Fjordic	Shelf	Slope	Abyss
Bivalvia				
Leionucula belloti	+ +	+	+	.
Leionucula corticata	.	+	.	.
Nuculana pernula	+ +	+	.	.
Yoldia hyperborea	+ +	.	.	.
Yoldiella intermedia	+	+ +	+ +	.
Yoldiella lenticula	+	+	.	.
Yoldiella lucida	.	+	+	.
Musculus niger	+	.	.	.
Dacrydium vitreum	.	+	.	.
Bathyarca glacialis	+ + +	+	+ +	+
Bathyarca pectunculoides	+	.	+ +	.
Chlamys islandica	+	+ +	.	.
Arctinula greenlandicus	+	+	+	.
Cyclopecten imbrifer	.	+	.	.
Thracia myopsis	.	.	+	.
Ciliatocardium ciliatum	+ +	+	+	.
Astarte crenata crenata	+ +	+ +	+	.
Astarte acuticostata	.	+	+ +	.
Astarte montagui striata	+ +	.	+	.
Astarte borealis placenta	+	.	+	.
Thyasira sp.	.	.	+	+
Macoma calcarea	+	+	.	.
Mya truncata	+	.	.	.
Hiatella arctica	+	+ +	.	.
Panomya arctica	.	+	.	.
Cuspidaria arctica	+	+	+ +	.
Cuspidaria subtorta	.	+	+	.
Cephalopoda				
Rossia sp.	+	+ +	+	+
Bathypolypus arcticus	+	+	+	.
Pantopoda				
Nymphon cf. gracilis	.	+	.	.
Nymphon stroemi	+	+	+	.
Nymphon sluiteri	.	.	+	.
Nymphon grossipes	+	.	.	.
Nymphon elegans	.	+	.	.
Nymphon sp.	.	+ +	+	.
Nymphon hirtipes	+ +	+ +	+	.
Boreonymphon abyssorum	+	+ +	+ +	.
Boreonymphon ossiansarsi	.	.	+	.
Colossendeis proboscidea	.	+	+	.
Colossendeis angusta	.	.	+	+
Crustacea				
Cirripedia				
Balanus balanus	+	+	.	.
Scalpellum sp.	.	.	+	+
Cumacea				
Diastylis goodsiri	+ +	.	+	.
Diastylis spinulosa	+	+	.	.
Diastylis lepechini	+	.	.	.
Campylaspis spec. aff.	+	.	.	.
Isopoda				
Calathura brachiata	.	+	+ +	.
Saduria sabini	+	+	+	+
Saduria megalura	.	.	.	+ +
Munnopsurus giganteus	+	.	+	.
Eurycope sp.	.	.	+	.
Gnathia stygia	.	.	+	.
Amphipoda				
Ampelisca eschrichti	+ +	+	.	.
Haploops tubicola	+	+	.	.
Haploops cf. sibirica	.	.	+	.
Haploops spp.	.	+	+	+
Byblis longicornis	.	+	.	.

Table 2 (continued)

Taxon	Station group Fjordic	Shelf	Slope	Abyss
Byblis gaimardi	.	+	+	.
Ampeliscidae spec. aff.	.	.	+	.
Amphilochus sp.	.	.	+	.
Amphilochidae spec. aff.	.	.	+	.
Anonyx nugax	+	+	+	.
Tmetonyx cicada		+	.	.
Lepidepecreum umbo	+	.	+	.
Socarnes bidenticulatus	.	+	.	.
Socarnes sp.	.	+	.	.
Lysianassidae sp. 1	.	+	+	.
Lysianassidae sp. 2	.	+	+	.
Stegocephalus inflatus	+	+ +	+	.
Stegocephalopsis ampulla	.	+	.	.
Epimeria loricata	+	+	+	.
Amathillopsis spinosa	.	.	+	.
Paramphithoe hystrix	+	+	+	.
Cleippides quadricuspis	.	.	+	+
Rhachotropis aculeatus	+	+ +	.	.
Rozinante fragilis	.	.	+	.
Eusirus cuspidata	.	.	+	.
Eusirus longipes	.	.	+	.
Eusirus sp.	.	.	+	.
Unciola leucopis	+	.	+	.
Unciola cf. planipes	.	.	+	.
Neohela monstrosa	+	+	.	+
Corophiidae spp.	.	.	+	.
Acanthostepheia sp.	+	+	+	.
Aceroides latipes	.	.	+	.
Oediceratidae spec. aff.	+	.	+	.
Idunella cf. aequicornis	.	.	+	.
Liljeborgia fissicornis	.	.	+	.
Liljeborgia sp.	.	.	+	.
Melita dentata	.	.	.	+
Podoceridae spec. aff.	+	.	.	.
Dulichia macera	.	.	+	.
Phoxocephalidae spec. aff.	.	.	+	+
Metopa cf. borealis	.	.	+	.
Ischyrocerus sp.	.	.	+	.
Pardaliscidae spec. aff.	.	.	+	.
Tiron spiniferum	.	+	+	.
Austrosyrrhoe fimbriatus	.	.	+	.
Mysidacea				
Parerythrops spectabilis	.	.	+	.
Pseudomma roseum	.	.	+	.
Decapoda				
Spirontocaris spinus	+	.	+	.
Lebbeus polaris	+	+ +	+	.
Bythocaris leucopis	.	.	+ +	+ +
Pandalus borealis	+ +	+ + +	+ +	
Hymenodora glacialis	.	.	+	+ +
Pasiphaea tarda			+	+
Sabinea septemcarinata	+ +	+ + +	+	.
Sclerocrangon ferox	.	+ +	+ +	.
Sclerocrangon cf. boreas	.	+	+	.
Hyas sp.	+ +	+	.	.
Pagurus pubescens	+ +	+	.	.
Echinodermata				
Crinoidea				
Bathycrinus carpenteri	.	.	.	+ +
Heliometra glacialis	+ +	+ +	+	.
Poliometra prolixa	.	+	.	.
Asteroidea				
Ctenodiscus crispatus	+ + +	+ +	+ +	.
Pontaster tenuispinus	.	+ +	+ +	.
Bathybiaster vexillifer	.	.	+	+
Leptychaster arcticus	.	+	+	.

Table 2 (continued)

Taxon	Station group Fjordic	Shelf	Slope	Abyss
Ceramaster granulatus	.	+	.	.
Hippasteria phrygiana	.	+	.	.
Tremaster mirabilis	.	+	.	.
Poraniomorpha bidens	.	+	+	.
Poraniomorpha hispida	.	+	+	.
Poraniomorpha tumida	.	+	+	.
Korethraster hispidus	.	+ +	.	.
Pteraster sp. 1	.	+ +	+	.
Pteraster sp. 2	.	+	.	.
Pteraster obscurus	.	+ +	.	.
Hymenaster pellucidus	.	+	+ +	+
Henricia spp.	+	+ +	+	.
Lophaster furcifer	.	+	.	.
Solaster spp.	+	+	+	.
Icasterias panopla	+	+ +	+	.
Urasterias lincki	+	+	+	.
Leptasterias sp. 1	.	+	.	.
Leptasterias sp. 2	.	+	.	.
Echinoidea				
Strongylocentrotus pallidus	+	+ +	+	.
Pourtalesia sp.	.	.	+	+ +
Ophiuroidea				
Gorgonocephalus spp.	+	+ +	+ +	.
Ophioscolex glacialis	+	+ +	+	.
Ophiacantha bidentata	+ + +	+ + +	+ +	.
Ophiopholis aculeata	+	+ + +	+	.
Ophiopus arcticus	.	+	.	.
Amphiura sundevalli	+	+	.	.
Ophiocten sericeum	+ + +	+ +	+ +	.
Ophiura sarsi	+ +	+ + +	+ +	.
Ophiura robusta	+	+	.	.
Ophiopleura borealis	.	+ +	+ +	
Holothuroidea				
Cucumaria cf. frondosa	+	.	.	.
Psolus sp.	.	+ +	.	.
Elpidia glacialis	.	.	.	+
Myriotrochus rinkii	+ +	+	.	.
Eupyrgus scaber	+ +	.	.	.
Ekmania spec. aff.	.	+	.	.
Molpadia sp.	+	+ +	+ +	.
Ascidiacea				
Ascidiacea spec. aff.	.	+ +	+	.
Pisces				
Raja radiata	+	+	.	.
Raja hyperborea	.	.	+	.
Mallotus villosus	.	+ + +	.	.
Macrourus berglax	.	.	+	.
Boreogadus saida	+	+ + +	+	.
Gadus morhua	+	+	.	.
Melanogrammus aeglefinus	.	+	.	.
Gaidropsarus argentatus	.	+	+	.
Sebastes mentella	+	+ +	+	.
Artediellus atlanticus	.	+ +	+	.
Gymnocanthus tricuspis	+	.	.	.
Icelus bicornis	+	+	.	.
Triglops murrayi	.	+	.	.
Triglops nybelini	+	+ +	+	.
Cottunculus microps	.	+	+	.
Leptagonus decagonus	+	+ +	+	.
Eumicrotremus spinosus	.	+	.	.
Liparis gibbus	+ +	+	+	.
Liparis fabricii	+	+	.	.
Careproctus sp. 1	.	.	+	.
Careproctus sp. 2	.	.	+	.
Careproctus sp. 3	.	+	.	.

Table 2 (continued)

Taxon	Station group Fjordic	Shelf	Slope	Abyss
Careproctus spp.	+	+	+	.
Paraliparis bathybius	.	.	+	+
Gymnelus retrodorsalis	.	+	.	.
Lycenchelys kolthoffi	.	+	.	.
Lycodes esmarkii	.	.	+	.
Lycodes eudipleurostictus	+	+	+ +	.
Lycodes frigidus	.	.	.	+
Lycodes pallidus	+	+ +	+	.
Lycodes reticulatus	.	+	.	.
Lycodes rossii	+	+	.	.
Lycodes seminudus	.	+	+	.
Lycodes squamiventer	.	.	+	.
Lycodes vahlii gracilis	+	+	.	.
Lycodonus flagellicauda	.	.	+	.
Lycodonus sp.	.	.	+	.
Anisarchus medius	+	.	.	.
Leptoclinus maculatus	.	+	.	.
Lumpenus lampretaeformis	+ +	+	.	.
Anarhichas minor	+	+	.	.
Hippoglossoides platessoides	+ +	+ +	+	.
Hippoglossus hippoglossus	.	+	.	.
Reinhardtius hippoglossoides	.	+	+ +	.

Strongylocentrotus pallidus (52%), and the fish *Sebastes mentella* (60%, all juvenile), *Hippoglossoides platessoides* (64%), *Leptagonus decagonus* (60%), *Triglops nybelini* (52%) and *Boreogadus saida* (48%). A group of species occurring at relatively many stations, but mostly only in small numbers, encompassed eunephthyid alcyonarians (76%), nemertines (72%), the sea cucumber *Molpadia* sp. (64%), as well as the sea star *Henricia* spp. (52%).

By classification and ordination techniques, four station groups were discriminated in terms of faunistic composition: both the dendrogram (Fig. 2a) and the MDS plot (Fig. 2b) revealed a conspicuous separation of the two deep-sea stations (station group called Abyss in the following) from all the others. The faunistic differences between the remaining stations were less pronounced. Seven stations, located at the continental slope off North Spitsbergen and the slopes of deep shelf troughs of the Barents Sea (Fig. 1), were combined in the group designated as Slope. Because of its position in the MDS plot (Fig. 2b) and its depth (960 m), stn. 077 was also allocated to this group. The remaining stations were divided into two groups: five catches carried out near the Spitsbergen coast, either in the Storfjord (stns. 050, 055) or in shelf troughs that are geomorphologically related to fjords, were combined in a group called Fjordic, and nine stations on shelf banks in the eastern part of the study area were fused in a group named Shelf (Fig. 1). Stn. 090 was allocated to the Shelf group because of its depth (150 m) and its position in the MDS plot (Fig. 2b).

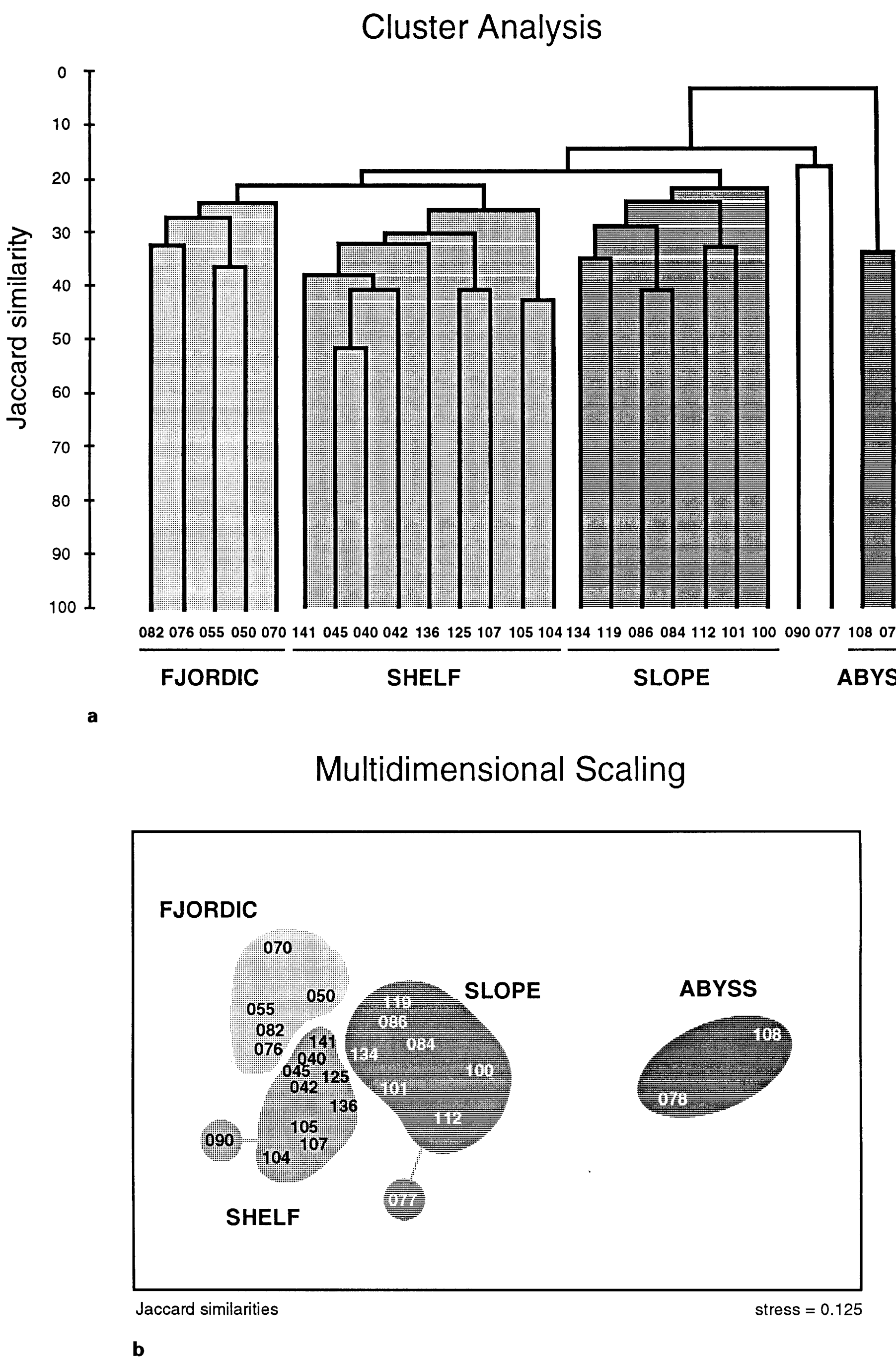
Fjordic

At the 5 stations at depths ranging from 100 to 340 m, 167 species were found (Table 2). Species numbers per catch ranged between 43 and 75. Most important species were the polychaetes *Spiochaetopterus typicus*, *Maldane sarsi*, *Nephtys caeca* and *Pectinaria* spp., the bivalves *Leionucula belloti*, *Nuculana pernula*, *Ciliatocardium ciliatum*, *Bathyarca glacialis* and *Nicania montagui*, the sipunculid *Phascolion strombi*, the sea star *Ctenodiscus crispatus*, as well as the brittle stars *Ophiacantha bidentata* and *Ophiocten sericeum*. Among the 36 Fjordic character species (i.e. species caught exclusively in this zone), only the bivalves *Yoldia hyperborea* and *Nicania montagui* were constant or numerically important.

Shelf

The 10 catches carried out at shelf locations mainly east of Svalbard in depths between 100 and 340 m yielded 231 species, with 66 being charcteristic for this station group (Table 2). The species numbers in the catches ranged from 42 to 86. Brittle stars predominated, primarily *Ophiacantha bidentata*, *Ophiopholis aculeata* and *Ophiura sarsi*. In addition, the brittle star *Ophiocten sericeum*, the shrimp *Pandalus borealis*, and the feather star *Heliometra glacialis* were numerically important, but less constant. Among the character species, only

Fig. 2a, b Trawl stations. Results of classification and ordination analyses, both based on between-station Jaccard similarities, calculated from the presence-absence data of 245 species that occurred in at least two trawl catches **a** Cluster dendrogram (UPGMA linkage), **b** MDS plot (grouping of stations according to cluster analysis is superimposed)



Ophiopholis aculeata, *Artediellius atlanticus* and *Icasterias panopla* occurred frequently in this zone.

Slope

At 8 stations, located at the continental slope in depths ranging from 280 to 960 m, 219 megabenthic species were caught (Table 2). The numbers of species per station ranged from 45 to 75. The echinoderms *Ophiacantha bidentata*, *Ophiocten sericeum* and *Pontaster tenuispinus*, as well as the zoanthid cnidarian *Epizoanthus incrustatus*, eunephthyid alcyonarians, and the bivalve *Bathyarca glacialis*, dominated the catches. A total of 59 species were found exclusively in the Slope group, and all except *Molpadia* sp., *Urasterias linki* and *Epizoanthus incrustatus* were rare.

Abyss

Only 36 species were found at the 2 abyssal stations (2000 m: 25 species; 2100 m: 21 species). The catches were dominated by the sponge *Cladorhiza gelida*, the

Table 3 BIO-ENV analysis of the relation between the megabenthos distribution and environmental factors (Combinations of environmental variables, *k* at a time, yielding the harmonic rank correlation ρ_H (given in parentheses) between the faunistic and abiotic resemblance data sets (17 stations both) for each *k*. *Bold type* indicates the combination with maximum ρ_H. *TOC*: Total Organic Carbon (%dw) in surficial sediments, *FINE*: proportions of silt and clay (%dw) in surficial sediments, *DEP*: water depth (m), *TEMP*: bottom-water temperature (°C), *SAL*: bottom-water salinity, *LAT*: geographical latitude, *LON*: geographical longitude, *COA*: distance (km) from the nearest coastline, *SHE*: distance (km) to the nearest shelf break (200-m isobath) of the Barents Sea, either at the northern slope (towards the Arctic Ocean) or at the western slope (towards the Greenland Sea). The variables *DEP*, *FINE* and *COA* were log-transformed)

k	Environmental variable combinations (ρ_H: harmonic rank correlation)								
1	DEP (0.60)	TEMP (0.19)	TOC (0.14)	FINE (0.08)	LAT (0.05)	COA (0.00)	LON (− 0.01)	SAL (− 0.13)	SHE (− 0.24)
2	**DEP, TOC** (0.61)	DEP, TEMP (054)	DEP, FINE (0.52)	DEP, LAT (0.51)	DEP, COA (0.45)	DEP, SAL (0.37)	DEP, SHE (0.28)	TOC, TEMP (0.27)	...
3	DEP, TOC, TEMP (0.56)		DEP, TOC, LAT (0.55)		DEP, TOC, LEN (0.51)		DEP, FINE, TEMP (0.50)		...
4	DEP, TOC, TEMP, LAT (0.52)		DEP, TOC, TEMP, LON (0.51)		DEP, TOC, LAT, LON (0.50)		DEP, TOC, FINE, TEMP (0.50)		...
5	DEP, TOC, TEMP, LAT, LON (0.51)		DEP, TOC, TEMP, LAT, FINE (0.48)		DEP, TOC, TEMP, LAT, LON (0.47)		...		
6	DEP, TOC, TEMP, FINE, LAT, LON (0.49)		DEP, TOC, TEMP, LAT, LON, COA (0.44)		DEP, TEMP, FINE, LAT, LON, COA (0.42)		...		
..	..								

sea anemones *Amphianthus* aff. *margaritacea*, *Kadosactis rosea* and *Sagartia splendens*, the cirriped *Scalpellum* sp., the shrimps *Bythocaris leucopis* and *Hymenodora glacialis*, and the feather star *Bathycrinus carpenteri*. A total of 13 species occurred exclusively in the deep-sea catches, including *Cladorhiza gelida*, *Kadosactis rosea*, *Sagartia splendens*, *Saduria megalura*, *Bathycrinus carpenteri*, and the fish *Lycodes frigidus*.

The MDS plot (Fig. 2b) suggests that the spatial distribution of the megabenthos was primarily characterized by a conspicuous depth zonation: the principal MDS gradient (horizontal axis) was significantly correlated with water depth (Spearman's rho: $\rho = 0.831$). The distribution of the stations along the vertical MDS axis, being distinctly less well pronounced, was significantly correlated with organic carbon content of surficial sediments (TOC) ($\rho = 0.794$). This pattern indicates that the largely bathymetric pattern was superimposed by a gradient in the TOC, a factor which itself was not correlated with depth ($\rho = -0.047$).

This pattern of the relationship between the distribution of megabenthic animals and the abiotic environment was corroborated by the multivariate BIO-ENV analysis (Table 3). Water depth was shown to have the highest affinity to the overall faunistic resemblance structure (harmonic rank correlation $\rho_H = 0.60$), and all other factors were of distinctly less importance. The combination of depth and TOC yielded a slightly higher correlation ($\rho_H = 0.61$), and the inclusion of more environmental factors lessened the match between the biotic and abiotic pattern. The combination of depth and TOC (with the former factor being more important) was therefore identified as the subset of environmental variables that "best explained" the faunistic distribution.

Discussion

Because of the type of sampling gear used, the megafauna covered by our study was not benthic *sensu strictu*. This conclusion is particularly evident for the list of fish species, which includes, in addition to truly benthic species, also some forms that are known to be benthopelagic (*Gadus morhua*, *Melanogrammus aeglefinus*, *Sebastes mentella*), pelagic (*Mallotus villosus*) or kryopelagic (*Boreogadus saida*). Consequently, the highly motile pelagic fish were excluded from the community study. The other, less motile fish species, however, were kept in the analyses. Given their largely benthic lifestyle, we considered them as functional parts of the megabenthic assemblages, and their mobility can be assumed to be negligible in view of the spatial scale of our study (distances between stations, extent of faunistic zones distinguished, depth range covered). Another critical point of our study was the catch efficiencies, which can be assumed to differ to an unknown degree between the two gears employed (at least for motile megafauna such as fish) as well as between stations, depending of the type of seabed, current velocities etc. Therefore, we confined our community analyses to presence-absence data, thus minimizing the sensitivity of our study to bias possibly introduced by the differences in sampling efficiency.

For the northern Barents Sea, a total of 70 fish species had been reported until 1991. Our catches yielded 44 species of 29 genera and 14 families (plus *Benthosema glacialis* from a pelagic net catch as well as eggs of *Raja fyllae* that were not found in the catches), approximately two-thirds of the total ichthyofauna known for this area. The knowledge of the composition of the invertebrate benthic communities has not been greatly increased since Zenkevitch (1963) summarized the results of the Russian investigations in the 1930s and 1940s. According to these studies, the fauna is characterized by echinoderms, primarily brittle stars such as *Ophiopleura borealis* and *Ophiacantha bidentata*, as well as the sea cucumber *Molpadia* sp. These species were also found in our trawl catches but, as a refinement of Zenkevitch's geographical distribution pattern, a conspicuous depth zonation in the northern Barents Sea is obvious.

The megafauna of both deep-sea stations (group Abyss) was distinctly different from that of lower depths. The faunistic resemblance between the 2 catches was, however, not very pronounced: only 10 of the 25 and 21 species, respectively, occurred at both stations (Jaccard similarity = 28%), e.g. dominant species such as the deep-sea shrimps *Bythocaris leucopis* and *Hymenodora glacialis* as well as the feather star *Bathycrinus carpenteri* and the fish *Lycodes frigidus*. Shallower stations, though some of them were even further apart from each other, exhibited a closer faunistic affinity. The deep-sea station west of Spitsbergen (stn. 078 in the mostly ice-free, "Atlantic" eastern Greenland Sea) had a higher resemblance to the slope assemblages than the station north of Nordaustlandet (stn. 108 in the mostly ice-covered Nansen Basin of the Arctic Ocean proper). Stn. 078 was discriminated from stn. 108 by, for example, peracarid species (*Saduria megalura*, *Haploops* sp., *Neohela monstrosa*), the sea star *Bathybiaster vexillifer* and the deep-water Arctic liparid fish *Paraliparis bathybius*. *P. bathybius*, however, is known from the area north of Svalbard as well, and its absence from our catches is probably stochastic. Typical faunal elements at stn. 108 were the shrimp *Pasiphaea tarda*, the infaunal sea urchin *Pourtalesia* sp. and the sea cucumber *Elpidia glacialis*. *Elpidia glacialis* is known as a cosmopolitan, extremely eurybathic deep-sea form but its main distribution area is the Arctic Ocean (Hansen 1975). In general, the detritivorous genus *Elpidia* is reported to exhibit an affinity to canyon or trough habitats characterized by a relatively high input of potential food (Hansen 1975). The occurrence of *Elpidia glacialis* and the relatively high TOC (stn. 108: 1.41%, stn. 078: 1.02%) may thus indicate favourable average food conditions at this location, due hypothetically to the intermittent inflow of organic matter derived from sedimenting ice-edge blooms and/or from Arctic-Atlantic water advected from the northern Barent Sea shelf through Kvitøyarenna. Further research will demonstrate to what extent the assemblages of our two deep-sea stations are similar to the true Arctic abyssal megabenthic communities (which are not properly known at the moment) or to what degree the fauna of the deep central Arctic Ocean may differ from the fauna of the deeper parts of the Greenland Sea.

Species numbers were highest in catches from offshore shelf banks (group Shelf) and from the sites in the upper bathyal zone (group Slope). Furthermore, the numbers of species restricted to these station groups were higher than in the other groups. In both assemblages, epibenthic brittle stars were the dominant faunal elements. These species are probably primarily carnivorous, but they are also known to be able to utilize a variety of nutrient sources, and are thus highly adapted to environments with variable food supply (Warner 1982). The occurrence of suspension-feeding sponges in fairly high abundances at certain slope stations may indicate an at least temporarily high nutrient load in the benthic boundary layer, originating from either direct sedimentation or lateral advection.

The fauna at the Fjordic stations was less diverse than that of the outer shelf – a common phenomenon in many littoral habitats (Gade 1986). In terms of megabenthic composition, the influence of the fjords could be traced down to the shelf troughs extending from the fjord valleys. The numerically most important species, all of them polychaetes, as well as the characteristic bivalve species, are known as typical faunal elements on mud and muddy sand (Hartmann-Schröder 1971; Bernard 1979). This finding corresponds well to the predominance of fine sediments at the fjord stations (Table 1). TOC contents were also relatively high, indicating an elevated input of organic matter, presumably from the adjacent land. All four important polychaete species exhibit – as many polychaetes – a cosmopolitan distribution, but are also known to be widespread in the Arctic (Hartmann-Schröder 1971). The characteristic bivalve species are described as Arctic or panarctic (Bernard 1979). The two cottid fish species, which were abundant at slope and shelf stations, were absent (*Artediellus atlanticus*) or rare (*Triglops nybelini*) at the near-shore stations. In contrast to our findings, however, von Hofsten (1919) reported *Artediellus atlanticus* to be common in the Isfjordrenna down to depths of 400 m.

According to our results, the pattern in the faunistic composition of megabenthic assemblages off Svalbard was largely explained by water depth and probably also the organic carbon content of sediments. Other factors, such as bottom-water properties or sediment texture, were apparently less important. Water depth can be regarded as a gross inverse measure of the particle sedimentation rate (Suess 1980) and TOC as a proxy of the average flux of organic matter to the seabed. Even though many of the species considered by our study cover a broad range of lifestyles and feeding modes (most of them do not feed directly on sediment TOC), our findings may be interpreted as indicative that the large-scale distribution of megabenthos is primarily affected by average food availability and, thus, ultimately by the patterns of sedimentation of organic matter produced in the water column. These, in turn, are largely controlled by surface hydrography and ice cover. Accordingly, our results are in agreement with those of Grebmeier et al. (1989) and Brandt (1995) who reported a similar relationship between water column processes and faunistic benthic community structures for the macrobenthos in the Bering Sea and peracarid crustaceans off Northeast Greenland, respectively.

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