Patterns and Determinants of the Distribution and Structure of Benthic Faunal Assemblages in the Northern North Atlantic

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Abstract: The distribution and structure of zoobenthic communities have been investigated in the northern North Atlantic. The principal goal of these studies is to assess the degree to which benthic community patterns depend on and/or mediate carbon flux between the pelagic and benthic realms, as well as between seabed, sediment-water interface and benthic boundary layer. A common rationale is that these patterns integrate the impact of environmental factors over longer periods of time and reflect relatively long-lasting or predictably recurrent environmental states, thus providing clues to the relative significance of potential community determinants on a time scale of months to years. Since 1992, several meso-scale field studies have been carried out in three regions at the East Greenland continental margin between 68° N and 81° N at water depths ranging from 40 to 3,700 m. A suite of sampling methods was employed (corers, trawls, seabed imaging) to adequately probe various benthic community fractions, such as foraminifers, poriferans, macrobenthic endofauna, peracarid crustaceans and megabenthic epifauna. A depth zonation in the faunal composition, accompanied by a shift in the predominance of different feeding types and a significant decline in biomass and abundance by as much as two and three orders of magnitude was the most conspicuous general pattern detected. However, in terms of species richness, no common trend for water depth or latitude was perceivable. The general depth zonation of the macrobenthos as well as the spatial concordance of high macrobenthic abundance and biomass with relatively productive hydrographic zones, such as marginal ice zones, polynyas and anti-cyclonic gyres, provide evidence for the importance of water column processes and, hence, for subsequent food availability as major determinants for benthic assemblages and the significance of pelago-benthic coupling in the study area in general. However, for megafaunal species such as echinoderms, community patterns on a 10-km scale and the dispersion of organisms on a 100-m scale, are best explained by seafloor properties. There is no evidence of direct pelago-benthic coupling, irrespective of water depth. These contrasting findings emphasize that the relative importance of potential community determinants can change with both spatial scale and life traits, e.g. body size, mobility and feeding ecology, of the organisms considered.

Introduction

Benthic distribution and community features, such as composition, diversity and standing stock, are known to be influenced by a complex of abiotic and biotic factors (Dayton 1984). In the scientific literature, a wide variety of different – and partly interacting – parameters have been discussed in this context, e.g. water depth, habitat heterogeneity, seafloor properties, bottom-water hydrography, food availability, as well as inter- and intraspecific competition and disturbance caused by predation or burrowing activities (Gray

1981). The relative importance of these benthic community determinants strongly depends on the spatial scale considered (Dayton and Tegner 1984; Gage and Tyler 1991). Seabed attributes are most commonly suggested to be major control factors (Snelgrove and Butman 1994), but in the recent past the quantity, quality and temporal pattern of food supplies have been recognized as equally important in affecting the benthos (Dayton and Oliver 1977; Graf 1992).

With only few exceptions at hot vents (Grassle 1986) or cold seeps (Sibuet and Olu 1998), the food supply of benthic communities depends almost entirely on the flux of phytogenic organic matter from the upper euphotic layer of the water-column to the seafloor (Tyler 1995). For this fundamental relationship, the term "pelago-benthic coupling" has been coined (Hargrave 1973). The recurrent finding that food availability is a principal benthic community determinant suggests that the benthos is strongly affected by abiotic and biotic water-column processes which mediate both pelagic production and the sedimentation of organic matter to the seabed (Graf 1992). In the same manner, benthic organisms have been shown to modify particle flux in the near-bottom water layer (Thomsen et al. 1995), as well as the deposition of particles in the sediment (Graf et al. 1995) in manifold manners.

The mechanisms and effects of processes involved in pelago-benthic coupling can be investigated on various scales of time and space (Ritzrau et al. this volume). For instance, the metabolic response of micro- and meiobenthic organisms to seasonal food pulses in terms of activity and biomass has been shown to be quite rapid, i.e. occurs within days (Graf 1989). In contrast, community patterns are pronouncedly more inert in their reaction to environmental forcing, especially those of larger macro- and megabenthic organisms (Gage and Tyler 1991). The distribution and structure of assemblages integrate the impact of control factors over longer periods of time and reflect relatively long-lasting or predictably recurrent environmental states. Therefore, studies of these patterns can provide clues to the long-term effects of potential community determinants, i.e. on a time scale of months to years.

This was the basic rationale of the study of spatial patterns in benthic community distribution and structure conducted within the sub-project A3 "Benthic community patterns and particle flux" of the *Sonderforschungsbereich (SFB) 313* in the northern North Atlantic, i.e. the Greenland-Iceland-Norwegian Seas (GIN), since 1985. Various meso-scale field studies were carried out, covering a broad water depth gradient between continental shelves and abyssal plains (40 to

3,700 m) and encompassing areas in both the generally ice-free eastern GIN Seas (Vøring Plateau at approximately 68° N, western Barents Sea slope at 75° N) and the predominantly ice-covered western GIN Seas (Denmark Strait and Kolbeinsey Ridge at 68° N, East Greenland continental slope at 75° N, 79° N and 81° N, and Northeast Water Polynya at approximately 80° N). Various benthic community fractions have been investigated, such as foraminifers (Ahrens 1994; Ahrens et al. 1997; Altenbach 1992), sponges (Barthel and Tendal 1993; Witte 1994; Witte 1996; Witte et al. 1997; Witte and Graf 1996), macrobenthic endofauna in general (Romero-Wetzel 1987; Romero-Wetzel 1989a; Romero-Wetzel 1989b; Romero-Wetzel and Gerlach 1991; Schnack 1998; Seiler 1998; Thomsen et al. 1995), peracarid crustaceans, i.e. Amphipoda, Cumacea, Isopoda, Mysidacea and Tanaidacea (Brandt 1993; Brandt 1995; Brandt 1997a; Brandt 1997b; Brandt and Piepenburg 1994; Brandt et al. 1996), echinoderms (von Juterzenka 1994; Piepenburg 1997; Piepenburg 1998; Piepenburg and von Juterzenka 1994), as well as epibenthic megafauna in general (Mayer 1995; Mayer and Piepenburg 1996; Piepenburg et al. 1997; Piepenburg and Schmid 1996). The common goal of these studies is to assess the degree to which benthic communities depend on and/or mediate carbon flux between the pelagic and benthic realms, as well as between seafloor, sediment-water interface and benthic boundary layer. The primary objective of this paper is to provide a synoptic overview of the various findings and to frame general conclusions from their implications. Special emphasis is placed on the western Greenland Sea, where most of the work has been carried out since 1992.

Materials and Methods

Areas Studied

The continental margin of the western Greenland Sea, i.e. the area off eastern Greenland north of Iceland and south of the Fram Strait, is rather narrow (mostly < 100 km) and rugged, consisting of numerous shallow banks separated by trenches several hundred metres in depth (Perry and Fleming 1986). The hydrography of the region is strongly affected by the cold East Greenland Current, which transports polar surface-water (T < 0 °C, S < 34) and – primarily multi-year – sea ice from the Arctic Ocean to the south (Coachman and Aagaard 1974; Quadfasel et al. 1987). In general, the waters are ice-covered throughout the year (Wadhams
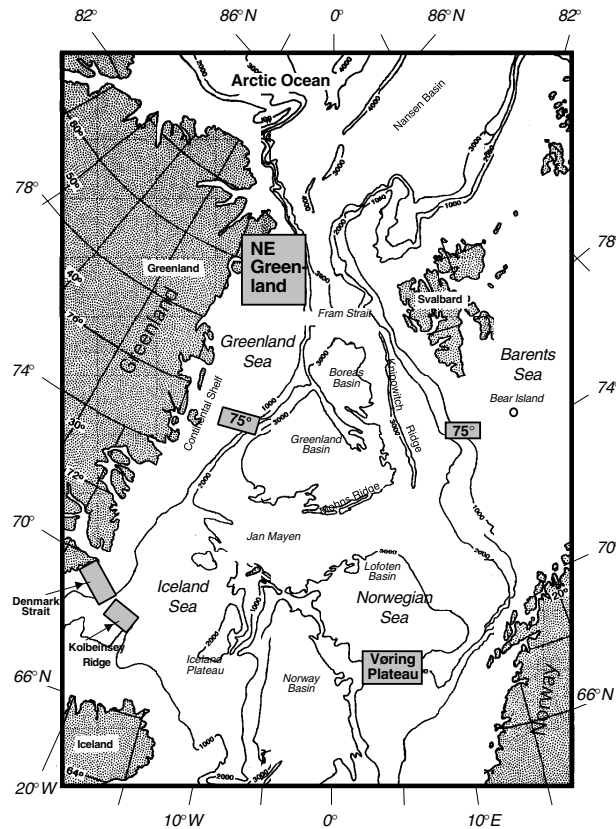
Fig. 1: Areas studied in the northern North Atlantic (Greenland-Iceland-Norwegian Seas)

1981) and thus belong to the permanent pack ice zone (Hempel 1985). Field investigations were conducted in three regions (Fig. 1).

The bottom morphology of the shelf off *northeastern Greenland* between 78° and 82° N is characterized by a system of shallow banks with water depths of < 40 to 150 m and troughs with water depths of as much as > 500 m. At depths < 100 m, temperatures are < 0 °C and salinities < 34.4. At greater depths, values are slightly higher (0.5° to 1.0 °C and 34.4 to 34.9), implying an inflow of Atlantic water masses to the shelf troughs (Budéus et al. 1997; Budéus and Schneider 1995). A geostrophic circulation of surface-water masses, indicating an anticyclonic meso-scale topography-driven gyre centred over Belgica Bank, was detected in several studies (Bourke et al. 1987; Schneider and Budéus 1994). A polynya referred to as *Northeast Water* (NEW) is a recurrent annual feature of variable size south of Nordostrundingen (Budéus et al. 1997; Schneider and Budéus 1994), extending to a size of up to 120,000 km^2 (Böhm et al. 1997) in some years. The formation and development of the polynya are controlled by a combination of various factors, including

winds, insolation, surface-water currents (Minnett et al. 1997), as well as the effect of persistent fast ice plates (Budéus et al. 1997; Schneider and Budéus 1995). It has been demonstrated that pelagic productivity is higher in the NEW Polynya than it is in surrounding ice-covered regions (Lara et al. 1994; Smith 1995; Spies 1987). In general, the transport of pelagic particles to the seabed is rapid due to low water depths in the area, but the actual temporal pattern and quality of this flux (autotrophic vs. heterotrophic origin) is strongly affected by sea-ice distribution (Ramseier et al. 1997). The abundance and grazing impact of herbivorous meso- and macrozooplankton appears to be relatively low (Ashjian et al. 1997; Ashjian et al. 1995; Hirche et al. 1994; Hirche and Kwasniewski 1997), pointing to strong pelago-benthic coupling. Rather fine-grained sediments cover the seafloor, particularly in the shelf troughs and at the continental slope (Piepenburg 1988). Coarser sediments and ice-rafted dropstones were found primarily on the shelf banks, indicating higher average bottom-water current velocities. Photographs reveal a pronounced patchiness of seabed facies at the 100-m scale, comprising areas of

uniform soft bottom as well as patches of gravel (Piepenburg 1988).

Off *eastern Greenland at 75° N*, the shelf break, i.e. the 200-m isobath, is approximately 200 km off the coastline. Within an area stretching 60 km further to the east, water depths rapidly increase in a steep descent of 2 to 6 % from 200 to 2,800 m (Weber 1989). The area studied lies under the eastern edge of the East Greenland Current and is, therefore, generally but not always ice-covered throughout the year, depending on meso-scale fluctuations in surface current regime (Wadhams 1981). The bottom-water of the shelf break and upper slope (200 to 800 m) has a temperature slightly > 0 °C, indicating the entrainment of relatively warm Atlantic Water, whereas at greater depths, Deep Water masses (T < 0 °C, S = 34.9) prevail (Coachman and Aagaard 1974). At the shelf break, the seabed is characterized by a pronounced small-scale (10 to 100 m) heterogeneity in texture and composition. At the slope, however, biotic structures provided by octocorals and sponges or a uniform soft bottom prevailed (Mayer and Piepenburg 1996).

The southern area studied comprises the *Denmark Strait* between Iceland and Greenland, as well as the *Kolbeinsey Ridge* at 67°55' N, 210 km north of the Icelandic coast. Various water masses of different origin and properties are found in the area. The northeastern part is primarily influenced by the Arctic Water of the Iceland Current, the western part by a cyclonic gyre located between the Iceland-Faeroes Ridge and the Jan Mayen Ridge, with a T–S signature intermediate between very cold but less saline Polar Water and relatively warm, fully marine (in terms of salinity) Atlantic water (Hopkins 1991). Towards the southwest, the significance of the East Greenland Current as characterized by Polar Water and permanent ice cover increases (Birgisdottir 1991; Henrich et al. 1989). During study conducted in 1992, surface-water temperatures along the Kolbeinsey Ridge transect increased from more than 1.9 °C at the westernmost station to 5 °C at the easternmost station. Bottom-water temperatures, however, varied considerably less, ranging only from −0.42 °C to −0.55 °C (Piepenburg and von Juterzenka 1994). Seabed sediments reflect surface hydrography, biogenic particle production within the water-column, the extent of ice cover and submarine volcanic activity. Coarse-grained volcanic material predominates in the ridge area (Oehmig and Wallrabe-Adams 1993), whereas fine-grained detritus from Iceland characterizes the adjacent basins (Lackschewitz and Wallrabe-Adams 1991). The carbonate content of the sediment surface, generally interpreted as indicator for water mass productivity, decreases towards the southwest (Paetsch et al. 1992). Since the late Tertiary, sedimentation rates north of Iceland have been high, probably reflecting a high input of ice-rafted material (Thiede et al. 1986).

Sampling

The basic approach of this sampling strategy was to investigate macrobenthic communities along gradients in terms of water depth, hydrography and sea-ice cover for the purpose of analysing their distribution and structure in response to different regimes of sediment composition, as well as to pelagic production, sedimentation and, hence, food supply. Within the three principal areas studied, stations were, therefore, usually distributed along transects extending from the shelf over the continental slope to the abyssal realm. During six expeditions to the Greenland Sea carried out between 1992 and 1997, (Fahrbach 1995; Hirche and Kattner 1994; Krause 1996; Mienert et al. 1998; Pfannkuche et al. 1993; Spindler et al. 1998) macrobenthic samples were obtained from 76 stations (Table 1).

A variety of sampling methods were employed (coring devices, trawled gear such as epibenthic sledge and Agassiz trawl, as well as seabed imaging) to collect quantitative information about the organisms in the various benthic community fractions under investigation.

For the study of endobenthic macrofauna, 2 to 3 replicate box cores (BC) were taken per station or, less frequently, a modified multiple corer (MUC) was employed. Sediment surface area (sub-)sampled in each core varied between 78 (MUC) and 625 cm² (BC). Core contents were sieved on a 300-μm mesh sieve and fixed with 4 % buffered formaldehyde. Macrofaunal organisms were sorted from the sediments, and individuals were identified and counted. Biomass was estimated by a combination of direct weighing, measurements of biovolume and biometric modelling (Schnack 1998; Seiler 1998).

Sponges and peracarid crustaceans were sampled with an Agassiz trawl (AGT) and an epibenthic sledge (EBS) (Brandt and Barthel 1995; Voß 1987). Both trawled gears were hauled over the ground for 10 to 20 min. at a mean velocity of 1 kn (Barthel and Tendal 1993; Brandt 1993; Brandt 1995). As the distances sampled varied, abundance was standardized to 1,000-m haul length (i.e. using the unit 'ind. 1,000 m⁻¹'). Samples were decanted through a 300-μm screen and preserved in 4 % buffered formaldehyde solution before being transferred to 70 % ethanol

Table 1: Cruises to the Greenland Sea from 1992 to 1997. Sampling: C – coring by box or multiple corer; T – trawling by epibenthic sledge or Agassiz trawl; I – seabed imaging; # – number of stations

Vessel/Cruise/Leg	Year	Region	Depths [m]	Sampling	#	Cruise report
Meteor 21/5	1992	Kolbeinsey Ridge	830–1100	T, I	5	Pfannkuche et al. (1993)
Polarstern ARK IX/2+3	1993	NE Greenland	40–800	C, T, I	40	Hirche and Kattner (1994)
Polarstern ARK X/1	1994	Greenland 75° N	190–2780	C, T, I	8	Fahrbach (1995)
Polarstern ARK XI/2	1995	NE Greenland	180–1970	C	7	Krause (1996)
Meteor 36/3	1996	Denmark Strait	390–1570	C	7	Mienert et al. (1998)
Polarstern ARK XIII/1	1997	NE Greenland	350–3500	C	3	Spindler et al. (1998)
		Greenland 75° N	200–3700	C	6	

after 2 days. Further sample processing followed the methods already outlined in previous papers (Brandt 1993; Brandt 1995; Brandt and Barthel 1995).

For an assessment of epibenthic megafaunal abundances, series of underwater photographs (UWP), each depicting approximately 1 m^2 of the seabed, were taken along transects of approximately 100- to 600-m lengths from the drifting ship. For details on the camera system used and its operation see Piepenburg and von Juterzenka (1994). Megabenthic organisms were counted on each photograph. The average counts per station were raised to abundance figures (ind. m^{-2}) using the mean area covered by each photograph taken along a given station transect. Biomass was computed by combining mean abundances, body size frequencies and size-mass relationships obtained from specimens sampled by AGT or EBS (Piepenburg 1997).

For ease of comparison, all biomass figures were converted to organic carbon using conversion factors given in the literature (Brey et al. 1988; Lampitt et al. 1986; Rowe 1983; Salonen et al. 1976; Wacasey and Atkinson 1987).

Data Analysis

A variety of classification and ordination techniques (Clarke and Warwick 1994; Field et al. 1982; Piepenburg and Piatkowski 1992) was applied to species-station abundance data to identify distinct groups of stations with similar faunal composition for each of the community fractions considered. In case of low station numbers, such groups were discerned on the basis of well-pronounced environmental and concurrent faunal gradients. *Per definitionem*, these faunal zones were inhabited by distinct macrobenthic assemblages and are, therefore, regarded as natural units for which averages of diversity and stock size can be meaningfully computed.

To identify principal community determinants, the biotic patterns distinguished in these macrobenthic data

sets were related to information about the environment. For both seabed and water-column parameters, data were available through interdisciplinary cooperation within the *SFB 313* or the shipboard scientific parties of the various expeditions. For instance, the percentage of silt and clay, i.e. sediment grain size $\leq$ 63 µm, in surgical sediments was used to parameterize sediment granulometry. Bottom-water temperature and salinity characterized water mass. The concentration of chloroplastic pigments in the sediment, organic carbon content and carbon-nitrogen ratios were used as proxies of the quality and quantity of potential food for the benthos. Sediment-oxygen demand quantified the activity of the sediment communities. Water-column pigment concentrations parameterize the current stock of the ultimate pelagic food source for the benthos. Water-column "nitrate depletion", i.e. nitrate concentrations, inversely scaled by being subtracted from the regional maximum concentration, was used as a proxy of export production despite the potential for results to be confounded by multiple source water signatures (Piepenburg et al. 1997).

In addition to the environmental parameters used in the above-mentioned papers and theses, an alternative proxy of potential food supply to the benthos which parameterizes both the magnitude of its primary source, that is, the largely sea-ice controlled pelagic production of organic matter and its vertical flux out of the euphotic zone, and its depth-dependent decay during further descent in the water-column was computed for the present synopsis. The euphotic carbon source was estimated using an empirical model (Ramseier et al. 1999) which, based on data derived from sediment trap measurements and remotely sensed ice parameters, provided flux values of organic carbon at 500 m water depth as a function of the ambient ice regime (ice concentration, duration of ice cover and distance from the ice edge) for the years 1985–1996. To account for the general decrease of vertical particle flux with water depth during sedimentation to the

seafloor as caused by decomposition, grazing and other processes, a modified exponential function (Martin et al. 1987) was applied. The proxies obtained by this approach are certainly only gross estimates of the actual food supply in absolute terms. Nevertheless, they are assumed to mirror rank differences in carbon flux to the seabed between stations with sufficient fidelity.

Various approaches were applied to explore the degree to which macrobenthic community traits are related to the environment. The most straightforward approach is to interpret the general spatial concordance in the distribution of biotic and environmental patterns (Brandt 1995). A Spearman rank correlation analysis of the interrelationships among these environmental variables and macrobenthic bulk parameters, such as species diversity or total abundance and biomass, was applied to identify the potentially relevant determinants of benthic community patterns (Piepenburg 1997; Schnack 1998). In a strictly explorative approach involving no inferential testing, the resulting heterogeneous pattern of positive and negative associations among the variables was further examined using correlation-based principal component analysis (Piepenburg et al. 1997). At a multivariate level, i.e. regarding the faunal composition of macrobenthic assemblages, two non-parametric statistical approaches were used: (a) the permutation-based ANOSIM procedure (Clarke and Green 1988) examines whether there are significant differences among pelagically defined provinces in terms of their benthic faunal composition, thus providing evidence for the significance of pelago-benthic coupling at a meso-scale spatial level; (b) the multivariate BIO-ENV correlation technique (Clarke and Ainsworth 1993) identifies the set of environmental factors which best correlates with macrobenthic faunal composition and may, therefore, be assumed to strongly affect the macrobenthic communities studied.

Results and Discussion

First, the findings obtained by *SFB 313* studies are briefly communicated for the various community fractions to establish a sound basis for the subsequent synopsis.

Foraminifera

The large-scale distribution of benthic foraminiferan assemblages in the abyssal Greenland and Norwegian Sea features a pronounced depth zonation (Altenbach 1992). This influence is also discernible in a shift of the relative importance of various feeding types. With increasing depth and subsequently decreasing carbon flux, suspension-feeding species gradually became more important than debris feeders, and at greatest depths and fluxes < 1.5 g C m^{-2} a^{-1} opportunistic species, which can feed on all kinds of nutrient sources and survive with a very sporadic food supply predominate. On the northeastern Greenland shelf, in the region influenced by the NEW Polynya, 61 foraminiferan species were identified from a total of 19 stations at depths of 170 to 490 m (Ahrens 1994; Ahrens et al. 1997). Multivariate analyses of abundance data suggest that foraminiferan communities fall into two major faunistic zones: the polynya proper in the north and the predominantly ice-covered Belgica Trough to the south. Abundances and biomass in surficial sediments, ranging from 97,000 to 507,000 ind. m^{-2} and from 0.1 to 0.3 g C m^{-2}, were comparable to ice-free deep-sea regions of the Norwegian Sea. Distribution, composition and biomass were correlated with sediment pigment and ATP content, with maxima occurring in the northern shallow polynya region, suggesting a general dependence on food availability.

Porifera

The composition and distribution of sponge assemblages have been studied in the abyssal Norwegian and Greenland Sea at water depths of 2,000 to 3,300 m (Barthel and Tendal 1993). 19 species were recorded, most of which were new to the area. A core association of 8 regularly occurring species distributed in the entire deep Norwegian and Greenland Seas was identified. The most abundant species, the demosponge *Thenea abyssorum*, which has been used as a character species for high Arctic areas (Paul and Menzies 1974), comprised more than 50 % of the individuals of all taxa caught at many stations (Witte, unpubl. data).

Crustacea Peracarida

Peracarid crustaceans were investigated in all three major areas studied in the western Greenland Sea: at the Kolbeinsey Ridge (Brandt 1993; Brandt and Piepenburg 1994), at the continental margin of eastern Greenland at 75° N (Brandt 1997a), and off northeastern Greenland (Brandt 1995; Brandt et al. 1996). In total, more than 60,000 specimens of peracarid crustaceans were collected from 33 epibenthic sledge catches obtained (Brandt 1997b). In addition to polychaetes and bivalves, peracarid crustaceans were the most abundant macrofaunal animals in each of the areas

studied. Off NE Greenland, in the region of the NEW Polynya at water depths between 45 and 517 m, the peracarid fauna was dominated by Cumacea (relative abundance of 31%), followed by Amphipoda (28%), Isopoda (25%), Mysidacea (12%) and Tanaidacea (3%). Total peracarid abundance was highest at 280 m with approximately 16,000 ind. 1,000 m^{-1} and decreased to approximately 5,000 ind. 1,000 m^{-1} at depths < 100 m and approximately 30 ind. 1,000 m^{-1} at 500 m depth. On the continental slope at 79° N, at depths of 200 to 1,800 m, Cumacea were again the most numerous taxon (33%), followed by Isopoda (28%), Amphipoda (21%), Mysidacea (12%) and Tanaidacea (6%). The highest total abundance (35,738 ind. 1,000 m^{-1}) was reported from the deepest station at 1,800 m. At 75° N, along a transect ranging from 300 to 2,700 m depth, Isopoda were most frequent (51%), followed by Amphipoda (27%), Cumacea (14%), Tanaidacea (4%) and Mysidacea (3%). Total abundance was highest at 1,525 m (23,000 ind. 1,000 m^{-1}), being 70% higher than at the deepest station at 2,700 m and even 340% higher than at the shallowest station at 300 m. On the Kolbeinsey Ridge, at depths between 830 and 1,100 m, Isopoda and Amphipoda were most abundant, followed by Cumacea and Tanaidacea. Mysidacea were very rare. There were pronounced differences between the eastern and western ridge flanks in faunal composition, diversity and abundance (Brandt and Piepenburg 1994). Total densities were highest on the eastern flank at 940 m (approximately 6,100 ind. 1,000 m^{-1}) and decreased rapidly to values of approximately 100 ind. 1,000 m^{-1} towards both the west and greater depths.

Macrobenthic Endofauna

The macrobenthic fauna of the East Greenland continental margin was investigated in all three major areas studied (Schnack 1998; Seiler 1998), with special emphasis on polychaetes (Schnack 1998). Stations were located on four down-slope transects across the continental shelf break at 81° N (350 to 3,400 m depth), 79° N (200 to 2,000 m), 75° N (200 to 3,700 m) and at 68–69° N (280 to 1,200 m), as well as on a parallel-slope transect along the 2,000 m isobath between 79° N and 80°30' N. In total, 75 box corer sub-samples (0.0625 m^2) and 6 multicorer samples from 31 stations were analysed. The taxonomic spectrum comprised Porifera, Brachiopoda, Sipunculida, Nemertini, Priapulida, Aplacophora, Bivalvia, Gastropoda, Polychaeta, Acari, Crustacea, Ophiuroidea and Holothuroidea. The polychaete fauna consisted mainly of Atlantic zoo-

geographic elements and was characterized by a low number of species. From all samples, a total of 81 species was identified. Species numbers per station decreased with depth and were generally low compared with more temperate areas, such as in the NE-Atlantic Rockall Trough (Paterson and Lambshead 1995) or the Irish Sea (Mackie et al. 1997). Multivariate statistics revealed a depth zonation with 3 distinct polychaete assemblages at shelf (200 to 400 m), mid-slope (800 to 1,400 m) and deep stations (> 1,400 m) for the two down-slope transects along 75° N and 79° N. On the continental shelf between 75° N and 79° N, the assemblages were similar in composition. With increasing water depth the similarity between transects decreased. Stations from the parallel-slope transect at 2,000 m depth were quite different in faunal composition from those of the down-slope transects.

Megabenthic Epifauna

Epibenthic megafauna was investigated in three areas by means of seabed photography and concomitant trawl or sledge catches: in the NEW area at 54 stations at depths between 40 and 770 m (Piepenburg and Schmid 1996), on the continental slope at 75° N at 8 stations at depths ranging from 190 to 2,800 m (Mayer 1995; Mayer and Piepenburg 1996), and at the Kolbeinsey Ridge along a 34-km-long cross-ridge transect at 67°55' N at depths of 830 to 1,100 m (von Juterzenka 1994; Piepenburg and von Juterzenka 1994).

In the NEW area, 10 epibenthic species were quantitatively analysed on a total of 2,358 photographs. Multivariate analyses of megabenthic species distribution revealed a distinct depth zonation. Shallow shelf banks (< 150 m), characterized by coarse sediments, numerous stones and boulders as well as by negative bottom-water temperatures, housed a rich epifauna (30 to 340 ind. m^{-2}, 0.9 to 5.2 g C m^{-2}) strongly dominated (80 to 98% by numbers) by the brittle stars *Ophiocten sericeum* and *Ophiura robusta*. On the bank flanks sloping to the shelf troughs (100 to 580 m), finer sediments prevailed, stones were rare, and bottom-water temperatures were positive due to the inflow of Atlantic water. Compared to bank sites, total epibenthic abundances were roughly ten times and total biomass about four times lower. In deep shelf depressions as well as at the continental slope (200 to 770 m), stones were completely lacking and sediments very fine. Epibenthic abundance and biomass were one to two orders of magnitude lower than on the banks.

On the East Greenland continental slope at 75° N, a total of 91 epibenthic species with 14,447 individuals

were identified from 422 photographs depicting 297 m^2 of the seafloor. Using classification and ordination analyses, three faunal zones were distinguished which correspond to different depth regions of the continental margin: shelf break (190 to 370 m), upper slope (760 to 800 m) and lower slope (1,400 to 2,800 m). Megafaunal abundance was highest on the shelf (approximately 200 ind. m^{-2}). In the other zones, densities were distinctly lower (30 to 40 ind. m^{-2} and 15 to 20 ind. m^{-2}). The assemblages at the shelf break and on the lower slope were dominated by single species, such as the polychaete *Nothria conchylega* (synonymous with *Onuphis conchylega*) and the sponge *Polymastia* sp. In contrast, the upper slope was characterized by a diverse octocoral-sponge assemblage.

On the Kolbeinsey Ridge, only the brittle star fauna was analysed in quantitative terms. Only five species were found, and only one species, *Ophiocten gracilis*, occurred with densities of more than 1 ind. m^{-2}. Ophiuroid distribution was characterized by differences between ridge slopes. In general, densities were significantly higher on the eastern slope, where the highest mean abundance per station of *O. gracilis* was 497 ind. m^{-2}. Except for one station, a distinct patchiness on the 100-m scale was obvious in its spatial distribution. Small settling stages with disc diameters < 1 mm accounted for up to 98 % of the population of *O. gracilis* near the ridge top, but the abundance of these small specimens decreased with depth to only 6 % on the eastern slope foot. Highest total biomass (0.06 g C m^{-2}) was found on the deep eastern slope, where adult *O. gracilis* with disc diameters > 4 mm were most abundant (56 ind. m^{-2}).

Synopsis

Summarizing the various investigations, the depth zonation of benthic assemblages was the most conspicuous spatial pattern throughout the areas studied, whereas latitudinal differences were – within the geographical range covered – noticeably less pronounced. However, there were differences among community traits and faunal groups in the clearness of this pattern.

Zoogeography

From all three areas studied, 288 peracarid species from 152 genera and 59 families were identified (Brandt 1997b). 38 genera were very frequent and showed a wide zoogeographic range. They were sampled during each expedition, comprising 22 species

of Isopoda, 7 species of Cumacea, 3 species of Amphipoda and Mysidacea, each, and 2 species of Tanaidacea. 60 genera are eurybathic, occurring at least over a depth range of 1,000 m, some even from the shelf down to 2,681 m depth. Only 10 genera are stenobathic, occurring only in the deep sea.

Among the brittle stars sampled and/or photographed in the Greenland Sea, there were no species new to science or the area studied (Piepenburg 1997; Schnack 1998). However, the discovery of the bathyal species *Ophiocten gracilis* at the Kolbeinsey Ridge (Piepenburg and von Juterzenka 1994) suggests that it should be added to current lists of echinoderms occurring in Arctic waters (Anisimova 1989; Smirnov 1994a). In accordance with previous reports, only few endemic Arctic species were found while the majority of the brittle stars species were widespread boreal Arctic species (Piepenburg 1997).

About a third of the polychaete species also belonged to this zoogeographic category, while the remaining two thirds were even more widely distributed species in the Arctic as well in boreal waters of both the Atlantic and Pacific Oceans (Schnack 1998). Some species were even cosmopolitan, whereas no endemic Arctic species were found at all. A similar zoogeographic composition of polychaete assemblages has been reported from most sub-Arctic and Arctic seas (Bilyard and Carey 1980; Holthe 1978).

Generally, findings for polychaetes, peracarid crustaceans and brittle stars corroborate the notion of a comparatively young age and low degree of zoogeographic isolation of Arctic regions such as the western Greenland Sea (Dunbar 1977; Dunton 1992; Knox and Lowry 1977; Smirnov 1994a; Svavarsson et al. 1993).

Diversity

Overall, there is no consistent latitudinal or bathymetric trend for species richness throughout the entire study area. For peracarid crustaceans in total, for instance, there is no significant relationship for depth or latitude (Brandt 1997b). Only for Amphipoda separately, species numbers decreased slightly with depth whereas for Isopoda the opposite trend was discernible. A similar bathymetric pattern was also reported from the Norwegian Sea (Dahl et al. 1976) but not for the amphipod fauna off northern Iceland (Weisshappel and Svavarsson 1998). This may be attributed to changes in sediment structure with depth (Brandt 1993) and/or the general appearance of the taxa in the course of the evolution of Eumalacostraca (Schram 1981). The species richness of polychaete fauna on the East Greenland

margin, in addition to being lower than in boreal regions, also declined significantly along the depth range of 200 to 2,700 m (Schnack 1998). Findings for both peracarid crustaceans and polychaetes do not, thus, support the notion of somewhat elevated species richness at bathyal depths of 2,000 to 3,000 m (Rex 1981; Rex 1983) or of relative high species richness in abyssal biotopes in general (Gage and Tyler 1991; Grassle 1989; Grassle and Maciolek 1992; May 1992). Rather, these results corroborate recently formulated criticism challenging the general validity of the latter paradigm for the deep sea (Gray 1994; Gray et al. 1997).

Twelve brittle star species were identified in the three areas studied (Piepenburg 1997). It should be noted that the total number of ophiuroid species inhabiting all Arctic seas – including the Siberian shelf seas influenced by Pacific water masses – ranges between only 15 (Smirnov 1994a) and 22 (Anisimova 1989) and is, thus, rather low, especially compared to Antarctica, from where more than 100 species have been reported (Smirnov 1994b). A comparative case study shows, however, that various diversity parameters (species richness, Shannon diversity, evenness) of the ophiuroid fauna of the eastern Weddell Sea (Antarctica) were significantly higher at both local and regional scales than off northeastern Greenland (Arctic), while those of the assemblages inhabiting the southern Weddell Sea shelf and shelf trenches were not (Piepenburg et al. 1997). As many species are phylogenetically more closely related in the Weddell Sea than off Greenland, the Antarctic assemblages also did not differ significantly from those distinguished in the Greenland Sea in terms of "taxonomic diversity" and "taxonomic distinctness" (Warwick and Clarke 1995). These findings indicate that the paradigm of a pronounced Arctic-Antarctic diversity difference may be an overgeneralization, at least with regard to the brittle star fauna and to regional/local scales (Piepenburg 1997).

Distribution

A pronounced depth zonation in the distribution of benthic assemblages is consistent across the various benthic community groups and areas investigated at the continental margin of eastern Greenland. Generalizing the different results, three principal zones can be distinguished:

- 'shelf' (< 400 m),
- 'slope' (800 to 2,000 m),
- 'deep sea' (> 2,000 m).

For some regions these major zones were more finely partitioned. On the shelf off NE Greenland, for instance, megabenthic assemblages on shallow banks (< 100 m) and in shelf troughs (200 to 500 m) differed significantly in faunal composition (Piepenburg et al. 1997). For polychaetes and peracarid crustaceans, however, faunal contrasts between a northern and southern area of the NEW Polynya were more pronounced than any bathymetric pattern (Ambrose and Renaud 1995; Brandt 1995). In the area studied at 75° N, upper and lower slope assemblages were discerned for both megabenthos (Mayer 1995) and macrobenthos (Schnack 1998; Seiler 1998). However, this differentiation was not as distinct as that between shelf and slope. Special distribution patterns were observed for submarine ridges and plateaus, such as the Kolbeinsey Ridge, where the differences detected between the ridge slopes are most likely related to meso-scale hydrography (Brandt 1993; Piepenburg and von Juterzenka 1994). For foraminifers and polychaetes, the bathymetric zonation of faunal assemblages was shown to be accompanied by a shift in the predominance of various feeding types (Altenbach 1992; Schnack 1998).

A gross but consistent depth zonation in the distribution of various benthic community fractions along the entire continental margin studied is a general phenomenon (Gage and Tyler 1991), although the boundaries of these zones vary among regions and faunal groups (Carney et al. 1983) on a global scale. It is well known, for instance, that bathymetric faunal change is more pronounced for megabenthos (Haedrich et al. 1980) than for endobenthic polychaetes (Grassle et al. 1979; Rex 1981).

Abundance, Biomass and Potential Carbon Demand

Despite a pronounced small-scale (i.e. within-station) patchiness discernible for most faunal groups investigated, it is evident that the depth zonation of benthic fauna is generally accompanied by a clear decline in benthic standing stock with water depth. This trend is, however, not consistent across all faunal groups.

Both photographic inventories and trawl catches clearly show that, in general, epibenthic communities at the Greenland continental margin are dominated by brittle stars (Piepenburg 1998). In shelf assemblages (< 100 m), *Ophiocten sericeum* was by far most important in terms of abundance and biomass. At greater depths (100 to 400 m), *Ophiacantha bidentata* prevailed. Slope assemblages (400 to 1,000 m) were characterized by *Ophiopleura borealis* and *Ophioscolex glacialis*. On the shelf (< 100 m), as well as on the

eastern Kolbeinsey Ridge (800 to 1,100 m), dense brittle star beds forming high standing stocks of up to several hundred ind. m^{-2} and up to several grams organic carbon m^{-2} were recorded (Piepenburg 1997). These stock figures are among the highest observed in northern seas, being in the same order of magnitude as those reported for ophiuroid mass occurrences in sublittoral and bathyal habitats of non-polar regions (Piepenburg 1997). Sub-dominant taxa, such as sea urchins, sea cucumbers and bivalves, reached only about a tenth of ophiuroid abundance and half of ophiuroid biomass. Within the dense brittle star beds, the specimens showed a pronounced non-random dispersion on the 1–100-m scale, most likely caused by the heterogeneity of the seabed (presence of dropstones etc.). Overall, ophiuroid abundances decreased significantly with water depth from a maximum at approximately 50 m over roughly three orders of magnitude to lowest values at approximately 800 m (Piepenburg 1997). Such a negative trend with depth was also obvious for biomass, albeit with a decline over roughly two orders of magnitude not as pronounced as for abundance (Piepenburg 1997). A similar exponential biomass gradient was reported for the invertebrate megabenthos from 500 to 4,100 m on the continental slope of the Porcupine Bight at 50 to 52° N in the northeastern Atlantic Ocean (Lampitt et al. 1986).

Macrobenthic abundance (biomass), averaged for different depth zones across all three regions studied, was approximately 5,000 ind. m^{-2} (0.55 g C m^{-2}) at shelf stations at 200 to 400 m, approximately 2,000 ind. m^{-2} (0.20 g C m^{-2}) at mid-slope stations at 800 to 1,400 m, and approximately 1,800 ind. m^{-2} (0.13 g C m^{-2}) at 2,700 m (Schnack 1998). These values are in the same order of magnitude as those reported from other continental margins in comparable latitudes and depths (Dahl et al. 1976). On the continental slope of the western Barents Sea at 75° N at 1,340 m depth, for instance, macrobenthic abundances varied between 557 and 1,052 ind. m^{-2} (Ambrose and Renaud 1995; Brinkhurst 1991; Kendall 1996; Thomsen et al. 1995), and on the Vøring Plateau off Norway at approximately 67° N at depths of 1,200 to 1,500 m depth, macrobenthic biomass ranged between 0.03 and 0.45 g C m^{-2} (Romero-Wetzel and Gerlach 1991). The mean macrobenthic abundance and biomass of the entire East Greenland continental margin investigated decreased exponentially with water depth (Schnack 1998). However, such a clear bathymetric trend was not observed for macrobenthic biomass at 75° N when examined separately (Schnack 1998). At 79° N, macrofauna and polychaetes analysed from box corer samples showed a completely different depth pattern than that of peracarid crustaceans in EBS catches (Brandt and Schnack in press). Macrofaunal abundance decreased clearly from approximately 7,000 ind. m^{-2} at 200 m to approximately 2,000 ind. m^{-2} at 800 m and approximately 800 ind. m^{-2} at 2,000 m depth. Polychaetes clearly dominated the shelf communities. However, their relative percentages decreased with water depth while those of Peracarida increased simultaneously.

The general decrease of benthic standing stock with water depth is not only recognizable for most faunal groups investigated but also for data sets pooled across taxa and regions. Summarizing the biomass results of the community fractions for which quantitative data are available, it is evident that both mega-epibenthic and macro-endobenthic biomass decreases significantly with water depth along the depth range investigated (40 to 1,100 m and 190 to 3,700 m) (Fig. 2). The depth-related biomass decline, however, is more pronounced for the megabenthos ($\rho = -0.888$, n = 59, P < 0.0001) than for the macrobenthos ($\rho = -0.622$, n = 32, P = 0.0005). It should also be noted that this general bathymetric trend may partly be breached, as the high benthic standing stock observed on the eastern Kolbeinsey Ridge (Fig. 2) emphasizes.

Macro- or megabenthic species are known to contribute considerably to total benthic biomass (Haedrich and Rowe 1977). Moreover, they strongly affect the structure of benthic food webs (Lampitt et al. 1986) and the micro-scale environment, as well as exchange processes at the sediment-water interface, by bioturbation and bioirrigation (Hüttel and Gust 1992; Smith et al. 1993). The finding of high standing stocks of some species, such as sponges and brittle stars, in the area studied suggests that they are also important in the benthic oxygen and carbon cycle. However, their oxygen uptake as well as, by implication, their mineralization and demand for organic carbon is difficult to assess. The major reason for this is that their total respiration is not included in benthic community oxygen consumption figures commonly derived from sediment core incubations and must be estimated separately by combining information concerning their abundance, size distribution and mean individual respiration rates (Piepenburg et al. 1995; Smith 1983). Using this approach, the dense brittle star beds occurring on the shelves off eastern Greenland are estimated to remineralize up to approximately 0.005 g C m^{-2} d^{-1}. Applying appropriate production and assimilation efficiencies, their extrapolated carbon demand is assessed to total at 0.01 g C m^{-2} d^{-1} (Piepenburg 1997). On the shelf banks of the northwestern Barents Sea,
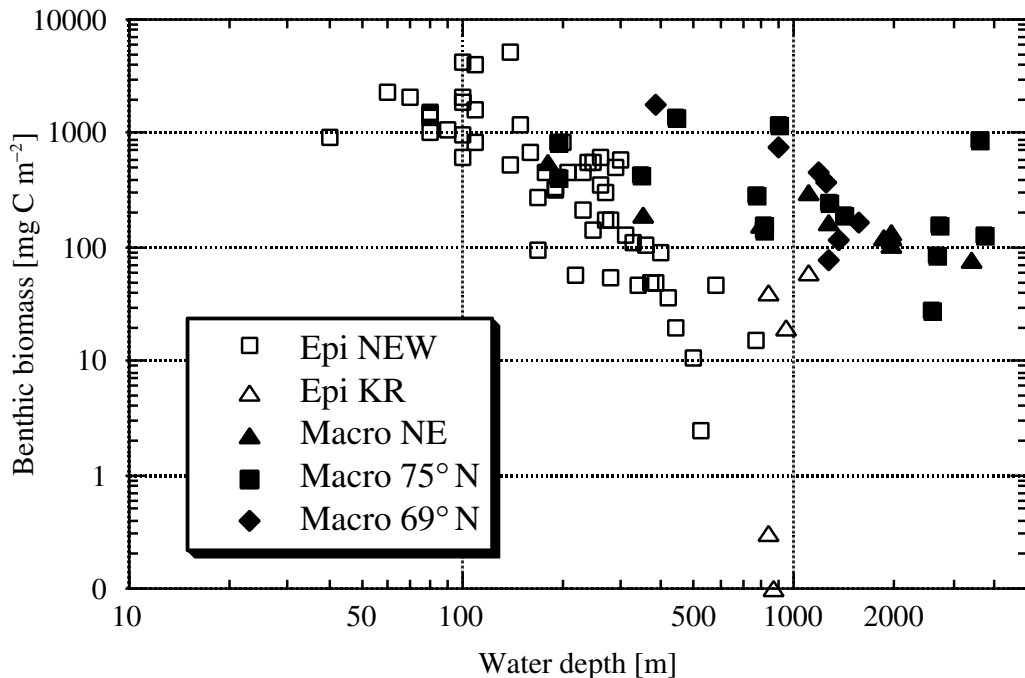
Fig. 2: Benthic biomass in relation to water depth. Epi NEW – Epibenthos *Northeast Water Polynya*; Epi KR – Epibenthos Kolbeinsey Ridge; Macro NE – Macrobenthos off northeastern Greenland (79° to 81° N); Macro 75° N – Macrobenthos off eastern Greenland at 75° N; Macro 69° N – Macrobenthos in the Denmark Strait (69° N)

ophiuroid carbon demands are assessed to be even higher, reaching maximum values of 0.02 g C m^{-2} d^{-1} (Piepenburg et al. 1995). The macrobenthic assemblages off eastern Greenland were computed to utilize 0.001 to 0.03 g C m^{-2} d^{-1} (Seiler 1998). Sponges in the Greenland Sea have been shown to be responsible for as much as 20 % of sediment community oxygen demand (Witte and Graf 1996), in addition to contributing as much as 10 % to particle input by the deposition of fine, laterally advected material (Witte et al. 1997). These results imply that macro- and megabenthic assemblages represent important pathways in the partitioning of benthic oxygen flux and significantly affect the energetics of benthic systems in the Greenland Sea. They provide additional evidence that models and budgets for benthic carbon dynamics (Ritzrau et al. this volume; Schlüter et al. this volume) need to be amended to adequately account for the contribution of abundant megabenthic organisms such as sponges and brittle stars (Piepenburg et al. 1975).

Determinants of Community Distribution and Structure

The interpretation of these findings, concerning the issue as to which factor from a host of potential determinants ranging from food availability to seabed properties and bottom-water hydrography to biotic interactions or life-history traits is of greatest significance in controlling benthos distribution patterns, is complex. The most prominent pattern in this data, the depth zonation of benthic assemblages and the exponential decline of benthic standing stock across shelves and slopes to the abyss, is a common phenomenon in Nordic seas (Curtis 1975). In fact, similar bathymetric patterns have recurrently been detected in numerous studies for different latitudes, different depth ranges and different benthic taxa (Brey and Clarke 1993; Haedrich et al. 1980; Lampitt et al. 1986; Rowe et al. 1974; Stewart 1983). The actual cause – or causes – of this ubiquitous pattern are difficult to assess. Any zonation observed must very likely be viewed as the result of several direct and indirect processes operating on various spatial and temporal scales (Carney et al. 1983).

The gradient most directly related to water depth, that is, increasing hydrostatic pressure, is known to be accompanied by specific physiological responses of the organisms (Somero et al. 1983). However, its direct effect on community patterns can be ruled out in this case, as the depth range covered was too narrow (Somero 1990). Biotic interactions, such as compe-

tition (Menge and Sutherland 1987) and predation (Dayton and Hessler 1972), or life-history traits (Giangrande et al. 1994; Olafsson et al. 1994), may also be conceived as potential control agents of benthos distribution and standing stock. For instance, brittle star populations are thought to be strongly affected by predation, based on paleoecological evidence (Aronson and Sues 1987). According to this hypothesis, dense beds of epibenthic brittle stars carpeting the seafloor with hundreds to thousands of individuals per square metre can only evolve and persist if predation pressure is low. Ophiuroid mass occurrences which are characteristic for many paleozoic and mesozoic facies are presumed to be mainly caused by the general scarcity of efficient durophagous predators, such as modern teleost fish or decapod crustaceans, which did not radiate until the Cenozoic era (Aronson 1989). Similarly, abundant brittle star populations found nowadays are primarily reported from biotopes in which potential predators are comparatively rare, such as continental slopes (Fujita and Ohta 1989; Fujita and Ohta 1990) and Arctic shelves (Piepenburg 1997). This finding can be interpreted as evidence for the general significance of predation as an effective top-down control agent. Interspecific competition for limited resources, such as food or space, is another biotic determinant which may explain benthic composition and standing stock (Dayton 1984). However, the actual significance of biological factors remains poorly understood since they cannot, as a matter of principle, be investigated by a 'mensurative non-manipulative' approach (Hurlbert 1984) as applied in these field studies.

The findings presented here suggest that large-scale benthic composition and standing stock in the Greenland Sea are primarily affected by two factor complexes: food availability and seabed properties. Both are known to be strongly related to water depth, hydrodynamics and various processes of particle transport, such as turbidity plumes, Taylor columns and internal waves (Fohrmann et al. this volume). There is a general inverse relationship between sedimentation rates and water depths which is well documented (Martin et al. 1987; Suess 1980). This explains the influence of the latter parameter on the quality and quantity of organic carbon reaching the seafloor and, hence, food supply for the benthos (Graf 1992). In energy-limited systems, such as the deep sea or polar seas, food supply has repeatedly been proposed as the prime agent controlling meio-, macro- and megabenthic biomass, since it is more important than physiological adaptations, biological interactions or com-

petition for space (Aldred et al. 1979; Grebmeier and Barry 1991; Hessler and Jumars 1974; Lampitt et al. 1986; Rowe et al. 1974).

Most, but not all, of the results presented here are consistent with this chain of arguments, pointing to a general significance of pelago-benthic coupling for the benthos of the Greenland Sea:

• Well-pronounced depth zonation, for instance, as well as spatial concordance in the distribution of high macrobenthic standing stocks with hydrographic features, such as marginal ice zones, polynyas and gyres, suggest that water-column processes strongly influence benthic community patterns (Piepenburg 1997).

• A case study in the NEW Polynya implies more stringently, particularly for foraminifers, polychaetes and peracarid crustaceans, that both (univariate) abundance and (multivariate) faunal composition of benthic assemblages are related to meso-scale patterns in hydrography and ice cover (Ambrose and Renaud 1995; Piepenburg et al. 1997). These are known to control primary production, particle sedimentation and ultimately food supply to the benthos as well (Grebmeier and Barry 1991). Evidence for the significance of the input of organic carbon is also available for a shorter time scale (weeks to months) than that reflected in benthic community patterns. For instance, both the stable isotope and lipid composition of macrobenthic organisms collected in the NEW area imply that a considerable portion of their food consists of freshly sedimented pelagic material (Graeve et al. 1997; Hobson et al. 1995). Such a dependence is further emphasized by studies of biochemical composition (Gallagher et al. 1998).

• The spatial distribution, faunal and trophic composition as well as biomass of foraminiferan assemblages in the deep basins of the GIN Seas (Altenbach 1992; Sarnthein and Altenbach 1995) and on the northeastern shelf of Greenland (Ahrens et al. 1997) are primarily governed by the magnitude of organic carbon flux to the seabed and, hence, nutrient concentration near the seafloor, strongly suggesting a general dependence on food availability.

• The seasonal reproductive pattern of the deep-sea sponge *Thenea abyssorum* is related to the seasonally pulsed food supply, a finding that further underpins the concept of generally close pelago-benthic coupling in the GIN Seas (Witte 1994; Witte 1996).

• The factors which probably cause the diversification of peracarid community structures observed in various areas studied in the Greenland Sea range from food
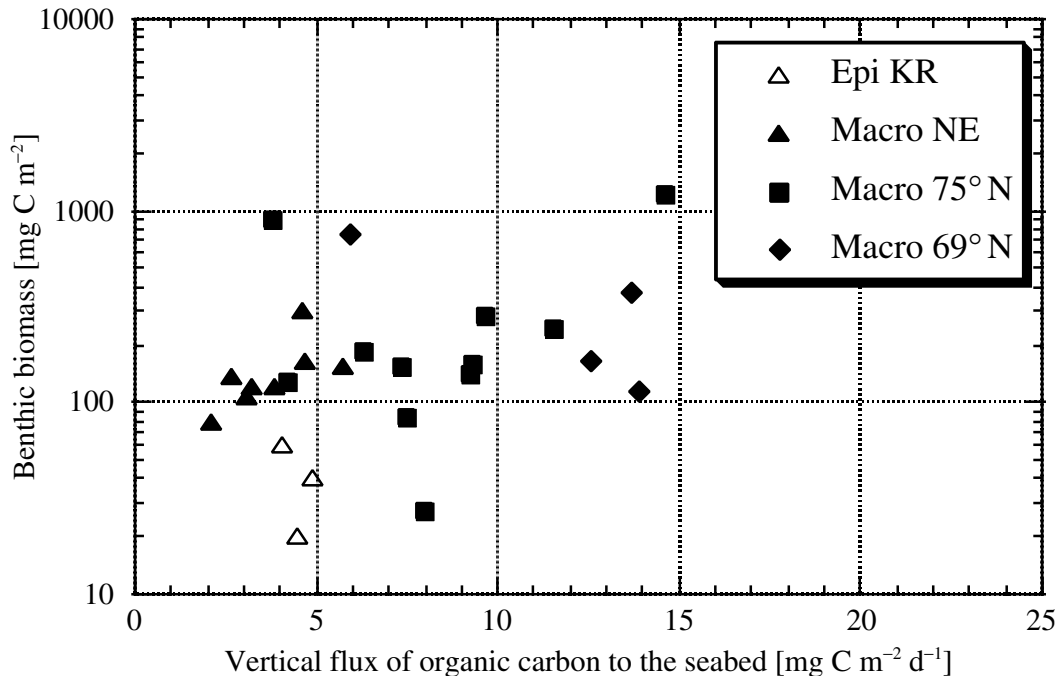
Fig. 3: Benthic biomass in relation to proxies of vertical organic carbon flux to the seabed, estimated according to Martin et al. (1987) and Ramseier et al. (1999). Epi KR – Epibenthos Kolbeinsey Ridge; Macro NE – Macrobenthos off northeastern Greenland (79° to 81° N); Macro 75° N – Macrobenthos off eastern Greenland at 75° N; Macro 69° N – Macrobenthos in the Denmark Strait (69° N)

availability over substrate or hydrographical qualities to interspecific competition (Brandt 1997b). For the peracarid assemblages in the NEW area, however, the first factor is thought to be of major importance (Brandt 1995).

• For the macrobenthos at the continental margin of eastern Greenland, BIO-ENV correlation analysis shows that distribution and composition are mainly related to water depth, whereas there is no general correlation between community patterns and sediment parameters such as grain size, organic carbon content, C:N ratio or chl *a* content (Schnack 1998). However, not depth *per se* but depth-related factors such as hydrography and the temporal and spatial heterogeneity of particle sedimentation are thought to be most important.

• Likewise, the benthic distribution observed at the Kolbeinsey Ridge is interpreted to largely reflect a cross-ridge gradient in terms of hydrographic regime and, hence, the probable pattern of food supply for the benthos (Brandt 1993; Piepenburg and von Juterzenka 1994).

In contrast to all these findings which point to the importance of food availability, multivariate analyses of correlation between megafaunal and environmental data at 75° N and in the NEW area indicate that epi-

benthic distribution patterns on a 10-km scale, i.e. between stations, as well as the within-station dispersion of organisms, i.e. on a 100-m scale, may best be explained by seafloor properties (Mayer and Piepenburg 1996; Piepenburg et al. 1997). On these spatial scales, evidence for a direct pelago-benthic coupling is not convincing, irrespective of water depth. Moreover, investigations of the spatial distribution of particle composition and microbial activity in the benthic boundary layer of the NEW area strongly suggest that pelago-benthic coupling is not a direct vertical relationship (Ritzrau and Thomsen 1997).

To synoptically test the importance of food availability and sediment composition across mega- and macrobenthic assemblages and different study areas, benthic biomass was related to (a) proxies of particle flux to the seafloor (estimated for stations deeper than 500 m and using the approach outlined in the Materials and Methods section), and (b) sediment granulometry parameterized by the relative proportion of fine materials (silt and clay). In these data sets, the parameters of particle flux and sediment grain composition were not significantly correlated (Spearman rank correlation $\rho = 0.241$, n = 21, P = 0.280). It was evident, however, that the benthic bulk parameter biomass was closer related to particle flux (Fig. 3) than to sediment grain
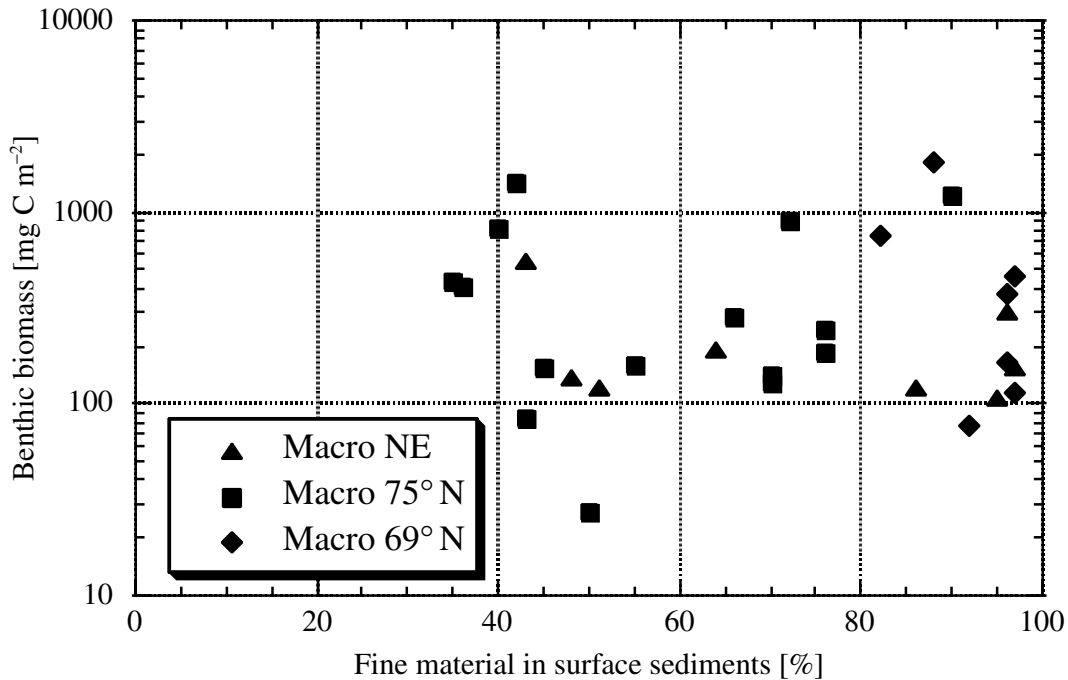
Fig. 4: Benthic biomass in relation to the relative proportion of fine material (silt and clay) in surface sediments. Macro NE – Macrobenthos off northeastern Greenland (79° to 81° N); Macro 75° N – Macrobenthos off eastern Greenland at 75° N; Macro 69° N – Macrobenthos in the Denmark Strait (69° N)

size (Fig. 4), though admittedly neither correlation was significant ($\rho = 0.371$, n = 28, P = 0.054 and $\rho = -0.108$, n = 29, P = 0.562).

In summary, various findings corroborate the notion that the availability of organic material, besides biotic interactions, primarily affects benthic biomass and abundance, while historical and physical factors, such as sediment grain size, determine the faunal composition of benthic communities (Dayton 1990).

Conclusions

The synoptic view of various results from field investigations on benthos distribution patterns presented in this paper leads to the following major conclusions:
• A depth zonation in faunal composition, accompanied by a shift in the predominance of different feeding types and a significant decline of as much as two and three orders of magnitude in biomass and abundance is the most conspicuous general pattern found.
• However, there is no consistent clear latitudinal or bathymetric trend for variations in species richness.
• For some species, e.g. sponges and brittle stars, quite high standing stocks with considerable contri-

butions to total benthic biomass are documented, suggesting that these groups strongly affect the structure of benthic food webs and exchange processes at the sediment-water interface.
• Estimations of organic carbon demands of such abundant benthic populations provide evidence that current models of benthic carbon flow, which are exclusively based on measurements of sediment oxygen demand (SOD), must amended to adequately account for the additional contribution of macro- and megabenthic organisms.
• Most of the findings concerning benthic community patterns are interpreted as evidence of the importance of water-column processes and, hence, food availability for the benthos as a determinant of benthic assemblages in the Greenland Sea, thus stressing the significance of pelago-benthic coupling in general in the areas studied.
• However, for some species, such as megafaunal echinoderms, community patterns on a 10-km scale, as well as dispersion of organisms on a 100-m scale, are best explained by seafloor properties, suggesting that processes related to pelago-benthic coupling are of less importance for this community fraction and at these spatial scales.

• The complex interpretation of these results emphasizes that the relative importance of interacting community determinants may vary among different spatial scales and faunal groups with different body size, mobility, or feeding ecology.

Acknowledgments

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