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# Benthic infauna of the seasonally ice-covered western Barents Sea: Patterns and relationships to environmental forcing

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## ABSTRACT

The northwestern Barents Sea and Svalbard archipelago are influenced by both warm Atlantic and cold Arctic water masses. We investigated infaunal benthic community structure in Atlantic- and Arctic-dominated areas, and at the Barents Sea Polar Front in order to assess the patterns of variability and to examine the influence of environmental variables on benthic fauna in this region. As part of the CABANERA program, we sampled 14 stations between 2003 and 2005 for benthic infaunal community composition, density, and biomass. Stations were in offshore shelf locations with soft sediments ranging in depth from 200 to 500 m, and encompassed different water mass characteristics and a wide range of other environmental conditions. Benthic biomass averaged  $66 \text{ g WW m}^{-2}$  (range  $10\text{--}152 \text{ g WW m}^{-2}$ ), mean density was  $4340 \text{ ind. m}^{-2}$  ( $1970\text{--}7896 \text{ ind. m}^{-2}$ ), and species richness varied from  $71\text{--}192 \text{ taxa stn.}^{-1}$ . Community structure was reflective of large-scale oceanography, as stations clustered in groups related to predominant water masses. Patterns in faunal density and biomass were largely determined by sedimentary characteristics, with water temperature, depth, and annual primary production also influencing some community parameters. Organism density and species richness were 86% and 44% greater at stations located near the Polar Front, compared to stations located in either Atlantic- or Arctic-dominated water masses. This pattern is coincident with elevated primary production at the Polar Front (48% compared to Atlantic- or Arctic-dominated water), suggesting a direct link between food availability in the Barents Sea and the benthic community structure. This leads to the conclusion that benthic communities in northwestern Barents Sea region are food-limited, and strongly dependent on predictable, albeit episodic, delivery of organic matter from the water column. Climatic processes leading to long-term changes in the location of the Polar Front will therefore have impacts on community structure and function on the sea floor.

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## 1. Introduction

Benthic fauna are considered good indicators of environmental conditions. Their predominantly sessile existence and relatively long lives are characteristics amenable for detection of a time-integrated response to external forcing, either individually or collectively as a community. Thus, changes in benthic communities over time have been used as indicators of environmental changes resulting from both natural variations (Kröncke, 1995; Kröncke et al., 1998, 2001) and anthropogenic disturbances (Pearson and Rosenberg, 1978; Underwood, 1996; Carroll et al., 2003) in marine systems.

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Benthic faunal community structure is regulated through both abiotic factors, such as water depth and sediment characteristics (i.e. grain size), food availability (Gray, 1974, 1981; Snelgrove and Butman, 1994; Kendall, 1996), and biotic interactions with other fauna, including predation and competition (Peterson, 1979; Ambrose, 1984; Wilson, 1990; Olafsson et al., 1994). Animals living on the sea floor below the euphotic zone away from riverine inputs are totally reliant on material from the water column sedimenting to the sea floor for their energetic requirements (Klages et al., 2004). In the Arctic, primary production is highly variable in time and space, and benthic food supply is often in the form of episodic pulses of pelagic- and ice-related organic carbon (i.e. the spring bloom) (review in Carmack and Wassmann (2006)). Although the fate of primary production in Arctic shelf seas depends upon numerous water-column processes related to the spatial and temporal variability in both the production regime and pelagic grazers (Eilertsen et al., 1989; Wassmann et al., 1996;

Andreassen and Wassmann, 1998; Falk-Petersen et al., 1999; Carroll and Carroll, 2003), the amount and quality of this organic material reaching the sea bottom is strongly related to the overlying primary production regime. Wassmann (1991) estimated that 48–96% of photosynthesized carbon in the water column reaches the sea floor, emphasizing the coupling between pelagic and benthic systems. The result of this pelagic–benthic coupling in the short term is seasonally and locally elevated concentrations of chlorophyll and fatty acids (correlates of primary production) on the sediment surface (Bauerfeind et al., 1997; Stephens et al., 1997; Sun and Wakeham, 1999; Renaud et al., 2008a) and associated increases in benthic processing (Rysgaard et al., 1998; Gooday, 2002; Clough et al., 2005; Moodley et al., 2005; McMahon et al., 2006; Sun et al., 2007; Renaud et al., 2008a). But benthic community parameters (biomass, organism density, and diversity), which integrate over longer temporal and spatial scales such as years or even decades, have also been found to reflect the overlying primary production regime (Grebmeier et al., 1988; Highsmith and Coyle, 1990; Ambrose and Renaud, 1995; Piepenburg et al., 1997; Dunton et al., 2005).

Tight pelagic–benthic coupling seems to be particularly amplified at mesoscale features in the Arctic such as polynyas, fronts, and the marginal ice zone, where episodic but intense pulses of primary production favor export of pelagic material to the sea bottom (Hobson et al., 1995; Smith and Barber, 2007 and references therein). The Barents Sea continental shelf is bathymetrically and hydrographically complex, resulting in high spatial and temporal variability (i.e. patchiness) in the physical (Elverhøi et al., 1989; Fredriksen et al., 1994) and biological (Engelsen et al., 2002) features influencing the benthic environment. Increased biomass and density of benthic communities are associated with the summer marginal ice zone of the Barents Sea (Zenkevich, 1963; Antipova, 1975; Denisenko, 2002), but these studies have not specifically examined the influence of the more stable Polar Front region on benthic communities.

The Barents Sea shelf is key region of the Arctic, the largest of the pan-Arctic shelves and a nexus of hydrological, biological, and geological transformation and exchange processes. It is characterized by high average productivity ( $93 \text{ gC m}^{-2} \text{ yr}^{-1}$ ), and supports 49% of the total Arctic shelf primary production and vigorous geochemical cycling (Sakshaug, 2004; Wassmann et al., 2006a). Hydrologic and ecologic processes occurring in the Barents Sea affect the entire Arctic Ocean (Carmack and Wassmann, 2006). The primary production and trophic links support large populations of higher trophic levels and, including fisheries, birds, and marine mammals (Wassmann et al., 2006a).

However, in this region of the Arctic, studies of benthic community composition have been concentrated on the west coast of Svalbard (Blacker, 1957, 1965), both within the western fjords (Holte and Gulliksen, 1998; Włodarska-Kowalczyk et al., 1998; Hop et al., 2002; Kendall et al., 2003; Włodarska-Kowalczyk and Pearson, 2004; Renaud et al., 2007b) and across the shelf break in Fram Strait (Weslawski et al., 2003; Włodarska-Kowalczyk et al., 2004). Benthic faunal studies in the Barents Sea and the shelf-slope north of Spitsbergen are far less common (but see Piepenburg et al., 1995; Cochran et al., 1998; Kröncke, 1998; Kröncke et al., 2000). The most widespread studies that have been carried out in the Barents Sea were conducted by the Russians during the Soviet period (Brotskaya and Zenkevich, 1939; Zenkevich, 1963; Antipova, 1975), and only recently have become accessible to non-Russian speakers (Galkin, 1998; Denisenko, 2001, 2002, 2004; Wassmann et al., 2006a). Further, most of the benthic faunal studies in the Svalbard–Barents Sea region have been descriptive studies focused on documenting spatial patterns of species distributions or faunal community types, without investigating the external processes responsible for regulating the

observed patterns. In the present era of changing climate in the Arctic, it is essential to understand not only the composition of benthic communities, but also how they are linked to environmental processes, if we hope to be able to anticipate the consequences of climate change to these systems.

Our study, part of the interdisciplinary Norwegian-funded CABANERA ecosystem study, examined benthic communities over a continuum of environmental conditions in the western Barents Sea. The transect spanned 75–82°N from the Atlantic-dominated water mass of the west-central Barents Sea, through the Polar Front and the Arctic water east of Spitsbergen and extended just past the Arctic Ocean shelf-break north of Svalbard. Our goals were to document general patterns of community structure over the wide range of environmental conditions in the Barents Sea as well as to understand environmental forcing of benthic community structure, rather than a focus on distributions of specific species. We placed particular emphasis on examining community structure at the Polar Front region of the Barents Sea in order to identify how benthic community parameters compared to non-Polar Front locations. To achieve this, we compared benthic community parameters and species distributions to the physical and biological characteristics of the system most likely to influence benthic communities on short and long time scales.

## 2. Materials and methods

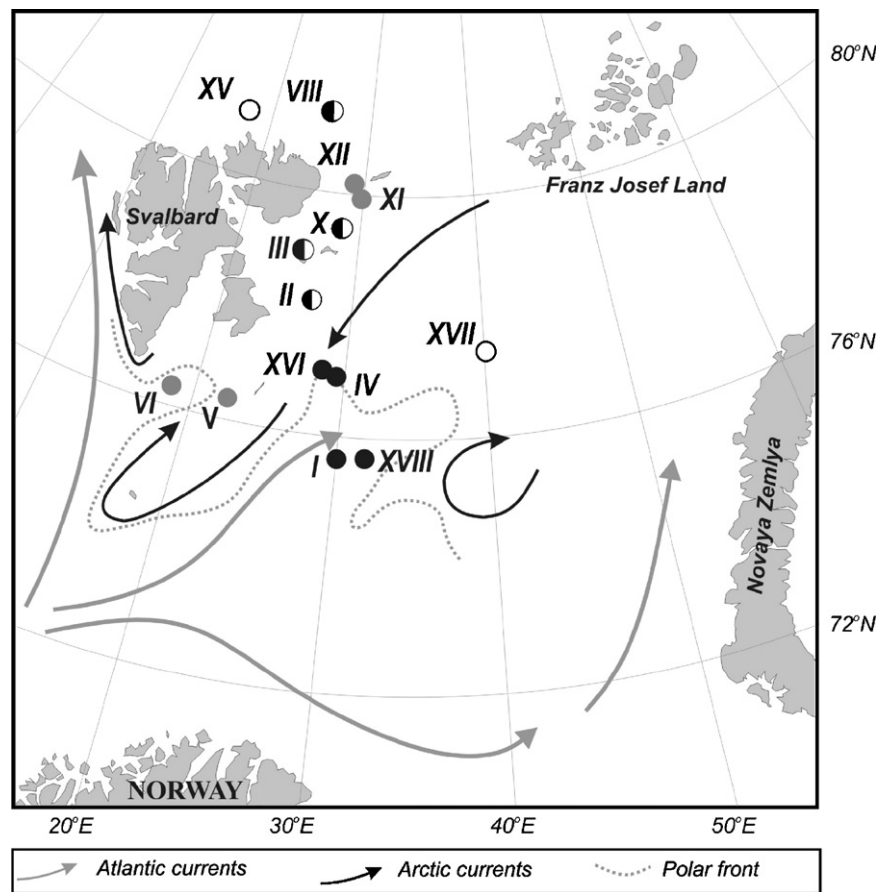
### 2.1. Study sites

Three sampling expeditions were carried out through the CABANERA program on the R/V *Jan Mayen* (University of Tromsø): 7–23 July 2003, 20 July–3 August 2004, and 18 May–5 June 2005. A total of 14 stations were sampled for benthic fauna from the western Barents Sea, north Svalbard shelf, and Nansen Basin of the Arctic Ocean (Fig. 1). The stations were oriented roughly in a transect along 30°E latitude from 75°N to 82°N, from the Atlantic-dominated water mass of the west central Barents Sea, through the Polar Front and the Arctic water east of Spitsbergen and extending just past the Arctic Ocean shelf-break north of Svalbard. Most, but not all, stations had at least some ice present at the time of sampling; ice concentrations ranged from 0% to 90% during our work at the station. All stations except XVIII were ice-covered at some point during the winter preceding sampling. The station network for the benthic sampling was similar to the pelagic stations sampled during the CABANERA field program in order to facilitate studies spanning both benthic and pelagic components (Tamelander et al., 2006; Morata and Renaud, 2008; Renaud et al., 2008a) and to provide a framework for more general inferences about the overall marine ecosystem at specific locations within the Barents Sea. But it was not always possible to conduct benthic sampling at exactly the same locations as pelagic or ice-related work (Table 1).

### 2.2. Field sampling and laboratory analyses

Samples were collected at each station with a van Veen grab ( $0.1 \text{ m}^2$ ), with lead-weighted arms and hinged, lockable, rubber-covered inspection ports. Five replicate van Veen grabs were collected sequentially with the ship held in position. Sediment in the grab from each cast was viewed on deck through inspection ports for washout, and rejected if the jaws were not fully closed, if uneven penetration was detected or if the grab was less than two-thirds full.

Samples were washed through a 0.5-mm sieve, then all material retained was fixed in 4% buffered formalin with Rose



**Fig. 1.** Map of the Barents Sea indicating the location and number of the CANABERA benthic stations. The shading of the symbols indicates station groupings according to multivariate analyses (see Results for details). Main current patterns and the location of the Polar Front is also shown. See Table 1 for the dates of sampling.

**Table 1**  
Stations sampled during the CABANERA field campaign 2003–2005

Date (YYYY.MM.DD)	Station no.	Location	Latitude °N	Longitude °E	Depth (m)
2003.07.11	I	Hopen Trench	75°40.0'	30°10.0'	345
2003.07.14–15	II	S. Kong Karlslandet	78°14.7'	27°09.7''	320
2003.07.16–17	III	E. Erik Eriksenstredet	79°01.2'	25°46.3'	198
2003.07.19	IV	Hopen Bank	77°01.1'	29°29.2'	222
2003.07.20	V	SE Storfjord	76°23.2'	22°10.4'	199
2003.07.20	VI	SW Storfjord	76°21.6'	18°21.6'	226
2004.07.25	VIII	N. Kvitøya Trench	81°16.7'	26°51.2'	503
2004.07.28	X	N. Kongkarlsland	79°26.5'	28°48.4'	303
2004.07.30	XI	NE Kongkarlsland	79°56.6'	30°17.0'	195
2004.07.31	XII	Central Kvitøya Trench	80°09.0'	29°36.0'	286
2005.05.21	XV	Questrenna Shelf	81°01.5'	18°01.1'	311
2005.05.26	XVI	N. Hopen Deep (Saddle)	77°05.2'	28°33.0'	206
2005.05.29	XVII	E. Storbanken (Central Barents Sea)	77°25.6'	40°18.3'	208
2005.05.30	XVIII	Hopen Trench	75°40.8'	31°48.7'	340

Stations are listed in chronological order of sampling. Note that in the Results section, stations are ordered in a south–north geographical orientation.

Bengal added. Samples were transported to the Laboratory of Marine Research, Zoological Institute of the Russian Academy of Sciences, St. Petersburg (LMR-ZIN) for further processing. At LMR-ZIN, samples were rinsed in running freshwater to remove formalin and break apart any remaining sediment clumps ('clay balls'), and preserved in 70% ethanol. Animals were sorted into main phyletic groups. Taxonomic specialists from LMR-ZIN subsequently identified all individuals to species or lowest

possible taxonomic level. All identified individuals were counted and the aggregate wet weight of each species (including shells when present) was measured to 0.0005 g. Sediment granulometry, organic content, and C:N:P ratios were also determined from core samples at each faunal station (Carroll et al., 2008; Zaborska et al., 2008). Sediment pigments from selected stations were determined by fluorometry (Renaud et al., 2008a).

### 2.3. Statistical analyses

Density and biomass data from individual replicates were averaged for each station and normalized to a per  $\text{m}^2$  basis for estimation of density, biomass, and diversity measures. Prior to analyses, nematodes, ostracods, and foraminifera were eliminated from the datasets, as these groups are incompletely retained on 0.5-mm sieves, and the latter are notoriously difficult to accurately determine whether they were alive at the time of sampling.

Diversity indices (species richness, Shannon–Wiener Diversity ( $H'$ ,  $\log_2$ )) were calculated based on abundance data. Multivariate analyses were based on the Bray–Curtis similarity matrix for untransformed species density data (Bray and Curtis, 1957), and presented as an MDS plot and a cluster dendrogram of station community relatedness. Given the large geographic span and environmental gradients (water masses, ice cover, sediment types, etc.) encompassed in the study area multivariate analyses based on untransformed data, which emphasizes patterns in dominant species, were more appropriate than applying transformations that would identify changes in rarer components of the community.

Analysis of similarities (ANOSIM) (Clarke, 1993; Clarke and Warwick, 2001) on individual replicate data was conducted to first determine whether community structure of all stations were significantly different, and then to assess whether the stations located at the Polar Front were significantly different from the remaining stations. Faunal regions within the CABANERA study area were delineated by the 35% Bray–Curtis similarity level.

The location of the Polar Front was determined based on its historical location (Loeng, 1991) and the temperature and salinity characteristics at the stations during sampling (Sundfjord et al., 2007, 2008). Benthic community measures (density, biomass, species richness, species diversity ( $H'$ )), as well as modeled annual primary productivity (Slagstad et al., unpublished data; Wassmann et al., 2006b) at stations presumed to be influenced by the Polar Front were statistically compared to non-Polar Front stations using  $t$ -tests, following diagnostic tests for equal variance and data normality (none violated the assumptions necessary for using parametric analyses).

While multivariate analyses such as Principal Component Analysis would have been our preferred approach to testing for the influence of potential explanatory variables on the benthic community, missing values in the environmental variable dataset would have necessitated removing more than half the stations in the dataset, severely reducing the utility of the results from a multivariate approach. Therefore, we used correlation (Pearson) analysis to assess the relationships between the faunal and environmental variables. The environmental variables were selected from those compiled through the CABANERA program including: latitude, water depth, porosity, sediment grain size (percent sediment fraction  $< 63 \mu\text{m}$ ), TOC content, carbon accumulation rate (Carroll et al., 2008), bulk sediment accumulation rate (Zaborska et al., 2008), sediment chlorophyll (Renaud et al., 2008a), surface and bottom water masses at each station at the time of sampling (Sundfjord et al., 2007, 2008), ice cover over the previous 1 and 4 years (Cavaliere et al., 2004), particulate carbon flux at the time of sampling (Reigstad et al., 2008), and average annual primary productivity between 1998 and 2005 (model results of Slagstad et al., unpublished data; Wassmann et al., 2006b). Dependent faunal variables tested were species richness, species diversity ( $H'$ ), total faunal abundance, and total biomass. Statistical computations were carried out with Microsoft Excel, Primer 6 (Clarke, 1993; Clarke and Warwick, 2001), or Statistica (ver. 6).

## 3. Results

### 3.1. Faunal community summary parameters

A total of 30,383 organisms, covering 546 taxa, were identified in the 70 samples collected from 14 stations. Of the total taxa, 32% were polychaetes, 25% crustaceans, and 17% molluscs (Fig. 2A). The number of taxa recorded per station ranged from 71 (Stn. II) to 185 (Stn. XV), with an average of 135. Species diversity (Shannon–Wiener,  $H'(\log_2)$ ) ranged from 4.6 (Stn. 18) to 5.8 (Stn. XV) (Table 2).

Organism density ranged from 1483 (Stn. 10) to 7896 ind.  $\text{m}^{-2}$  (Stn. V), with an average of 4340 ind.  $\text{m}^{-2}$  (Table 2, Fig. 2B). The majority of organisms found were polychaetes (55%), with molluscs representing 24% of individuals and crustaceans 14% (Fig. 2B).

Biomass ranged from a low of 10 (Stn. VIII) to a maximum of 152  $\text{g m}^{-2}$  (Stn. XI), with an average of 65.5  $\text{g m}^{-2}$  (Table 2). Polychaetes also had the highest biomass of all phyletic groups (36%), followed by echinoderms (26%), and molluscs (19%) (Fig. 2C).

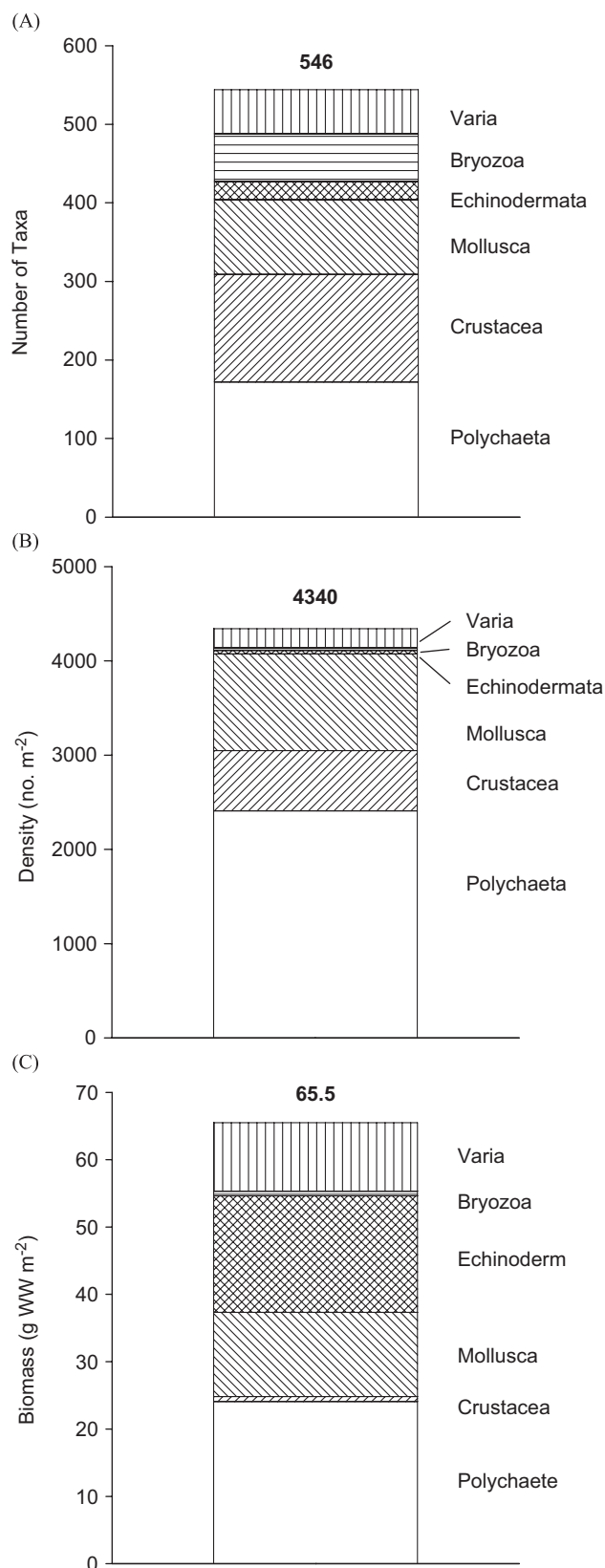
### 3.2. Spatial patterns

When stations were ordered by latitude, a distinct spatial pattern emerged (Fig. 3). Density increased from the southernmost stations in Atlantic water (Stns. I, XVIII) to their highest levels ( $\sim 8000 \text{ ind. m}^{-2}$ ) at the Polar Front stations (Stns. V, VI, IV, XVI). Stations further north in the core of the Arctic water (Stns. II, III, X) had macrofaunal densities around  $2000 \text{ ind. m}^{-2}$ , while the northernmost stations (Stns. XI, XII, XV, VIII) had organism densities of  $\sim 2500\text{--}6000 \text{ ind. m}^{-2}$ , intermediate between the highest values at the Polar Front stations and the lowest values from the Arctic-water stations.

Multivariate relationships based on Bray–Curtis similarity are revealed through an MDS plot and cluster dendrogram (Fig. 4). These distinguished three primary clusters of stations, delineated at 30–50% similarity. The first cluster ('Hopen') included stations I, XVIII, IV, XVI; the second ('Storfjord/Kvitøya') contained V, VI, XI, XII; and the third ('Kong Karls Land'), stations II, III, VIII, X. Two stations did not cluster with the remainder of stations: Station XVII, located well east of the main transect in the central Barents Sea, and station XV, which was well west of the main transect on the north Svalbard shelf-slope (Fig. 4). The MDS plot also suggests that Stn. I is rather more independent from the Hopen cluster than indicated in the cluster dendrogram. Meanwhile, Stn. IV, which is solidly grouped in the Hopen cluster in the dendrogram, is suggested by the MDS to be reasonably closely related to the Storfjord/Kvitøya cluster. ANOSIM indicated that all stations were significantly different from one another (Global  $R = 0.947$ ,  $p < 0.008$  for all), but also that density-based composition of the most dominant species did not differ at the Polar Front compared to the remainder of stations (Global  $R = -0.108$ ,  $p > 0.74$ ).

Several benthic community parameters were higher at stations situated at the Polar Front compared with those elsewhere in the study area (Table 3). Density and species richness were significantly elevated, by 86% and 44%, respectively, at the Polar Front compared to the rest of the stations ( $t$ -test,  $p < 0.05$ ). Shannon–Wiener diversity followed the same trend, though the relationship was statistically significant only at  $\alpha = 0.10$  ( $t$ -test,  $p < 0.07$ ). Biomass was 16% higher at the Polar Front stations, yet this difference was not statistically significant ( $t$ -test,  $p > 0.70$ ) (Table 3). Finally, average annual primary production was 48% higher for the Polar Front sites than for the others ( $t$ -test,  $p < 0.01$ ).





**Fig. 2.** Stacked bar chart showing a summary of community variables from all 14 stations combined and the relative composition of the six main taxonomic groups. (A) Number of taxa, (B) density (no. m<sup>-2</sup>), (C) biomass (g WW m<sup>-2</sup>). Those interested in actual values can contact the lead author.

### 3.3. Dominant species

The most abundant species at all stations combined was *Mendicula ferruginosa*, a thyasirid bivalve, which comprised 11.9% of all animals identified (Table 4). *M. ferruginosa* was one of the 10 most abundant species in each station cluster (the most abundant at two of the three clusters), and was present at each of the 14 stations. The polychaete *Maldane sarsi* was the second most abundant taxon, representing 5.8% of the overall animal abundance, followed in order by the polychaetes *Spiochaetopterus typicus*, *Galathowenia oculata*, *Heteromastus filiformis*, and *Spiophanes kroeyeri*. The nuculanid bivalve *Yoldiella solidula* and polychaetes *Paraninoe minuta*, *Scoloplos acutus*, and *Minuspio ciffiera* complete the 10 most abundant taxa.

The 10 most abundant taxa differed substantially between the three different groupings of stations: Hopen and Storfjord/Kvitøya station groups shared five of the same abundant taxa, Storfjord/Kvitøya and Kong Karls Land station groups shared four abundant taxa, and Hopen and Kong Karls Land station groups shared only three of the 10 most abundant taxa (Table 4). The Hopen cluster had five dominants not shared by any other cluster, including *S. typicus*, which was the most abundant taxon (14.1%) at the southernmost stations east and south of Hopen, but was not a dominant at any other station groups. There were four and six unique dominants in the Storfjord/Kvitøya and Kong Karls Land cluster group's, respectively (Table 4).

The species accounting for the highest biomass percentage at all stations combined (14.9%) was the bivalve *Astarte crenata*. *A. crenata* was one of the most dominant taxa in all three regions and represented up to 22% of total biomass (in the Kong Karls Land station cluster) (Table 5). *S. typicus* was the second biomass-dominant overall (14.4%), and represented 31.5% of the total biomass at the southernmost stations east of Hopen, though considerably less in the more northern stations. The mud star, *Ctenodiscus crispatus*, had the third greatest biomass, with 11.4% of total biomass across all regions, and one of only three taxa (*A. crenata* and *S. typicus* being the others) that occurred as biomass-dominants in all the station groups. The echinurid, *Echiurus echiurus*, was fourth overall (6.5%) and contributed the most biomass at the stations near Kong Karls Land (29.3%), while the holothuroid, *Ekmania barthi*, was fifth overall (5.2%) and contributed up to 14.9% of the total biomass of the Storfjord/Kvitøya station group. The Storfjord/Kvitøya station group had the most distinct biomass-dominants, with five taxa not shared with any other region, while the Hopen and Kong Karls Land groups had three and two unique dominants, respectively.

### 3.4. Relationship to environmental variables

Correlation analysis revealed the importance of both sedimentary and biological parameters in explaining the four community parameters. Sedimentary characteristics, compared to other environmental variables, were most strongly related to each of the four community measures, emphasizing the intimate relationship between fauna and their sedimentary environment.

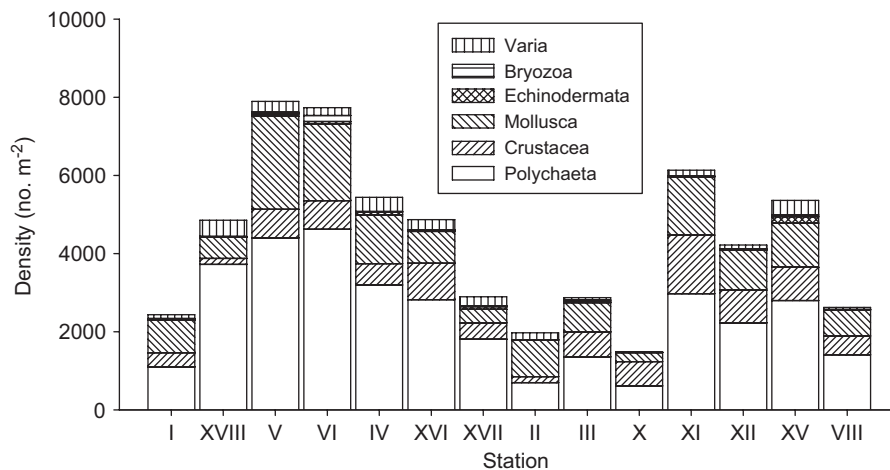
Density, species richness, and Shannon Wiener diversity were most strongly related to grain size, and biomass was best correlated with porosity (Table 6). The organic carbon content of the sediment, which often covaries with grain size, was also strongly correlated with the number of taxa and diversity. Sediment chlorophyll concentration was correlated with abundance and number of taxa. The only non-sedimentary variables that were significantly correlated with the community parameters were bottom water temperature and water depth (correlated with

**Table 2**

Summary of community parameters for the stations sampled during the CABANERA field campaign 2003–2005

Station no.	Depth (m)	No. species	Density (no. m <sup>-2</sup> )	Biomass (g WW m <sup>-2</sup> )	Diversity ( <i>H'</i> )
VIII	503	107	2619	10	5.1
XV	311	185	5359	30	5.8
XII	286	148	4219	50	5.2
XI	195	141	6135	152	5.1
X	303	74	1483	43	4.7
III	198	117	2869	138	5.3
II	320	71	1970	11	4.9
XVII	208	137	2895	37	5.4
XVI	206	164	4865	70	5.8
IV	222	164	5438	88	5.4
V	199	172	7896	48	5.2
VI	226	192	7734	85	5.3
XVIII	340	103	4852	83	4.6
I	345	115	2432	71	4.8

Stations are ordered in a north–south geographical orientation. See Table 1 for the sampling dates of each station.

**Fig. 3.** Stacked bar chart showing faunal density (no. m<sup>-2</sup>) at stations oriented from south to north and the relative composition of the six main taxonomic groups.

biomass), and modeled annual primary production at each station (density). Latitude, surface water temperature, ice cover, carbon flux, and sediment or carbon accumulation were not significantly correlated to any benthic community parameter.

#### 4. Discussion

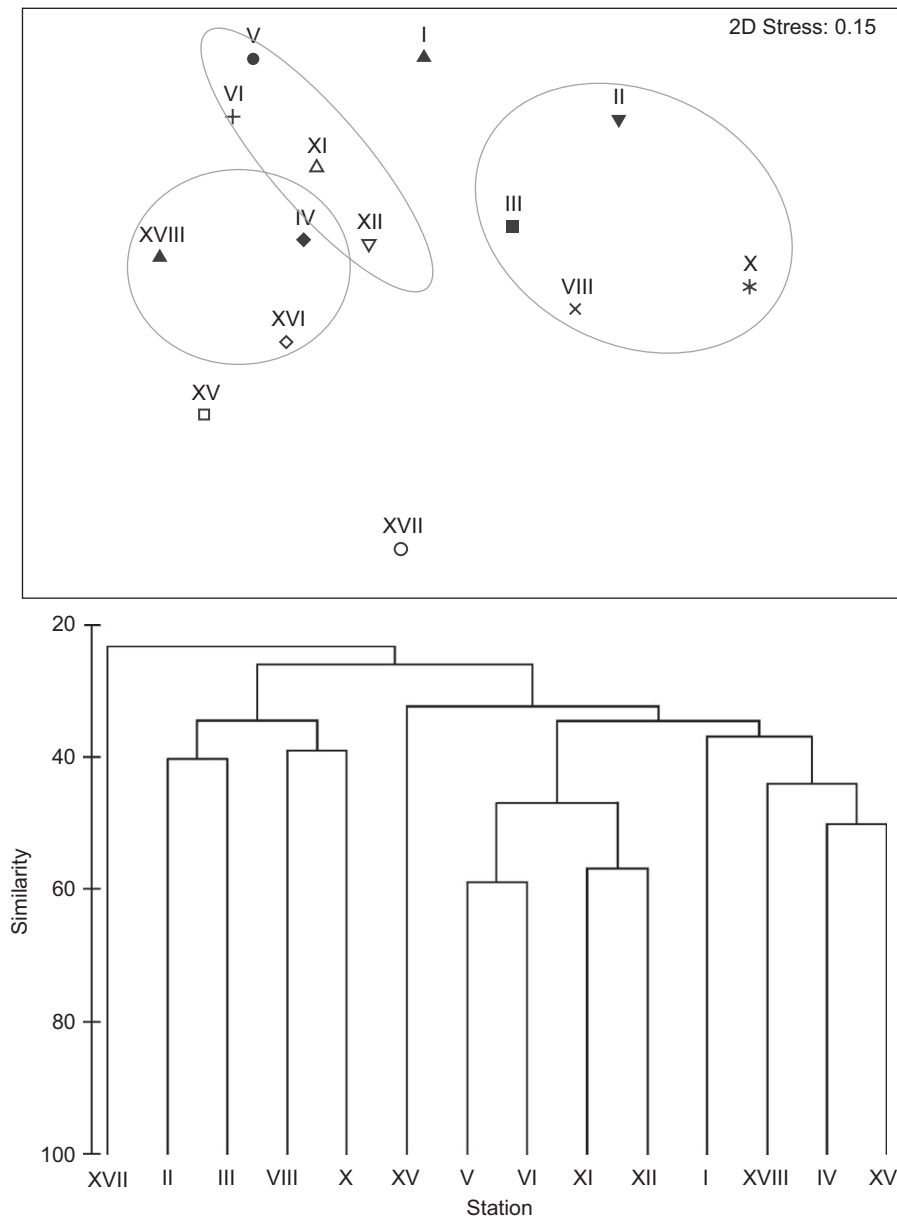
##### 4.1. Faunal patterns

The stations sampled in this study of the soft-sediment habitats of the western Barents Sea had an average infaunal biomass of 66 g WW m<sup>-2</sup>, although biomass and density were both highly variable among stations. Soft sediments in the deeper areas of the Barents Sea are low-current depositional areas, consistently dominated by deposit-feeding taxa, many of which are small. In fact, polychaetes are the dominant organisms in our survey (55% individuals, 36% biomass; Tables 3 and 4), and represent a much higher percent composition than they have in previous, larger-scale studies of the Barents Sea (i.e. Zenkevich, 1963; Antipova, 1975; Galkin, 1998; Denisenko, 2001, 2004; Denisenko and Tytov, 2003, review in Wassmann et al. (2006a)). This discrepancy likely results from our station selection of soft-sediment habitats between 200 and 500 m. Sampling only in these deeper areas excluded the bank areas that make up nearly

45% of the Barents Sea and can support extremely high benthic biomass (>1000 g WW m<sup>-2</sup>) (Cochrane et al., 1998, Carroll, unpublished data). Grab sampling is inefficient at sampling larger organisms living on top of the sediment surface (brittle stars, sea cucumbers, and mobile crustaceans such as crabs) that tend to be more common in shallower areas. These organisms may dominate biomass in high-flow erosional habitats of Arctic shelves (Piepenburg et al., 1995), and can process large quantities of organic matter (Piepenburg et al., 1995; Renaud et al., 2007a). Although some epifaunal species (*Ophiacantha bidentata*, *Ophiopholis aculeata*) were present in the biomass dominants list (Table 4), epifauna are undoubtedly more abundant than appear from our dataset.

##### 4.2. Spatial patterns: regional scale

Despite large inter-station variation in both density and biomass, a pattern emerges with relatively lower abundance in the far south, middle, and far north, with distinctly higher abundance in the south-central and north-central stations (Fig. 3). The Atlantic and Polar Front stations had relatively consistent biomass of 50–90 g m<sup>-2</sup>, and the Arctic water stations in the middle of the transect were <40 g m<sup>-2</sup> (Table 2). In the northernmost stations, biomass was highly variable, from 10 to



**Fig. 4.** Multidimensional scaling plot (top panel) and cluster analysis (bottom panel) based on the Bray-Curtis Similarity matrix for benthic station density at the CABANERA stations. Clusters of >35% similarity are used for grouping stations within the region, and groups are shown with ovals in the MDS plots, except for station I (discussed in text).

**Table 3**  
Results of one-way ANOVA testing for differences in faunal community parameters at stations located at or near the Polar Front (PF, *n* = 4) and the remainder of benthic stations (*n* = 10) in this study

Community parameter	Mean PF stations (S.D.)	Mean non-PF stations (S.D.)	d.f.	<i>t</i> -statistic	<i>p</i> -value
Density	6483 (1556)	3483 (1557)	12	−3.256	0.007
Biomass	72.8 (18.3)	62.5 (49.3)	12	0.397	0.698
Species richness	173 (13.2)	120 (34.6)	12	2.934	0.013
Diversity ( <i>H'</i> )	5.44 (0.23)	5.06 (0.34)	12	2.001	0.071
Annual primary productivity	96.1 (18.4)	64.8 (15.8)	12	3.208	0.008

Average annual primary productivity was modelled between 1998–2005 (data from Wassmann et al., 2006b; Slagstad et al., unpublished data).

150 g m<sup>−2</sup>, reflecting a complex bathymetry and hydrography north of Kong Karls Land. In this region of Olga Strait, there is a canyon there is a horizontal delineation of water masses with Arctic water on the surface overlaying an Atlantic layer occurring from about 150 m to the bottom. Tidal forcing leads to large gradients in turbulent mixing over small scales (Sundfjord et al.,

2008). Thus, there is an environmental situation with abundant ice, a primary production regime characteristic of Arctic waters, yet advection of Atlantic waters near the bottom where the benthic communities exist. Given this complex external situation, it is not surprising that there is great variability in abundance and biomass as well as community structure.

**Table 4**

Percentage dominance of the 10 most common species (in bold) based on density at all stations and different station groups

Species	All (14)	Hopen (4)	Storfjord/Kvitøya (4)	Kong Karls Land (4)
<i>Mendicula ferruginosa</i> (B)	<b>11.9</b>	<b>11.0</b>	<b>14.5</b>	<b>11.3</b>
<i>Maldane sarsi</i> (P)	<b>5.8</b>	<b>3.1</b>	<b>10.1</b>	0.5
<i>Spiochaetopterus typicus</i> (P)	<b>5.2</b>	<b>14.1</b>	1.8	1.5
<i>Galathowenia oculata</i> (P)	<b>4.1</b>	<b>2.3</b>	<b>7.1</b>	1.0
<i>Heteromastus filiformis</i> (P)	<b>4.0</b>	<b>5.8</b>	<b>4.3</b>	<b>2.8</b>
<i>Spiophanes kroeyeri</i> (P)	<b>3.5</b>	<b>4.5</b>	<b>2.1</b>	<b>3.6</b>
<i>Yoldiella solidula</i> (B)	<b>3.0</b>	1.5	<b>4.2</b>	<b>5.7</b>
<i>Paraninoe minuta</i> (P)	<b>2.3</b>	1.2	<b>4.3</b>	0.8
<i>Scoloplos acutus</i> (P)	<b>1.8</b>	1.6	<b>2.6</b>	0.8
<i>Minuspio cirrifera</i> (P)	<b>1.7</b>	1.4	0.9	<b>3.0</b>
<i>Pholoe assimilis</i> (P)	1.6	<b>3.5</b>	1.1	0.3
<i>Leucon nathorsti</i> (C)	1.3	<b>2.9</b>	0.2	<0.1
<i>Nephasoma diaphanes</i> (P)	1.4	<b>2.0</b>	0.3	0.7
<i>Lumbrineris tetraura</i> (P)	0.6	<b>2.0</b>	0	0
<i>Frigidoalvania janmayeni</i> (G)	1.3	0.4	<b>2.3</b>	1.6
<i>Lumbriclymene cylindrica</i> (P)	0.8	<0.1	<b>1.9</b>	0
<i>Thyasira equalis</i> (B)	1.0	0.2	0.5	<b>4.9</b>
<i>Ophelina cylindrica</i> (P)	0.9	0.5	<0.1	<b>4.8</b>
<i>Ektonodiastylis nimia</i> (C)	0.7	0.1	0.2	<b>4.1</b>
<i>Maldane arctica</i> (P)	0.8	0.2	0.5	<b>3.0</b>
<i>Levinsonia gracilis</i> (P)	1.1	0.5	1.4	<b>2.8</b>

Station groupings are based on the cluster analysis and Bray–Curtis similarity matrix: Hopen (Stns. I, IV, XVI, XVIII), Storfjord/Kvitøya (Stns. V, VI, XI, XII) and Kong Karls Land (Stns. II, III, VIII, X). Parentheses in the category groups indicate the number of stations.

Key to species groups: B, Bivalvia; C, Crustacea; G, Gastropoda; P, Polychaeta.

**Table 5**

Percentage dominance of the 10 most common species (in bold) based on biomass at all stations and different station groups

Species	All (14)	Hopen (4)	Storfjord/Kvitøya (4)	Kong Karls Land (4)
<i>Astarte crenata</i> (B)	<b>14.9</b>	<b>12.7</b>	<b>14.9</b>	<b>21.9</b>
<i>Spiochaetopterus typicus</i> (P)	<b>14.4</b>	<b>31.5</b>	<b>8.2</b>	<b>2.4</b>
<i>Ctenodiscus crispatus</i> (As)	<b>11.4</b>	<b>12.6</b>	<b>9.8</b>	<b>12.2</b>
<i>Echiurus echiurus</i> (E)	<b>6.5</b>	<0.1	0	<b>29.3</b>
<i>Ekmania barthi</i> (H)	<b>5.3</b>	<0.1	<b>14.4</b>	0
<i>Molpadia arctica</i> (H)	<b>3.5</b>	<b>2.1</b>	0	<b>15.7</b>
<i>Nephtys ciliata</i> (P)	<b>3.4</b>	<b>1.8</b>	<b>6.0</b>	<b>2.6</b>
<i>Maldane sarsi</i> (P)	<b>2.9</b>	0.9	<b>6.8</b>	0.2
<i>Asyschis biceps</i> (P)	<b>2.7</b>	<0.1	<b>6.4</b>	<0.1
<i>Cerianthus lloydii</i> (An)	<b>2.5</b>	<b>7.1</b>	0.2	0
<i>Gersemia</i> sp. (Cn)	1.9	<b>5.3</b>	0.1	<b>1.1</b>
Ascidacea spp. (T)	0.7	<b>2.0</b>	0	0
<i>Golfingia margaritacea</i> (S)	0.9	<b>1.7</b>	0	0.3
<i>Aglaophamus malmgreni</i> (P)	1.1	<b>1.9</b>	0.2	<b>1.3</b>
<i>Ophiacantha bidentata</i> (Op)	1.5	0.4	<b>2.9</b>	0.6
<i>Nephtys paradoxa</i> (P)	1.2	0.5	<b>2.3</b>	<b>0.8</b>
<i>Ophiopholis aculeata</i> (Op)	1.0	0.5	<b>1.7</b>	0
<i>Maldane arctica</i> (P)	0.3	<0.1	0.1	<b>1.3</b>

Station groupings are based on the cluster analysis and Bray–Curtis similarity matrix: Hopen (Stns. I, IV, XVI, XVIII), Storfjord/Kvitøya (Stns. V, VI, XI, XII), and Kong Karls Land (Stns. II, III, VIII, X). Parentheses in the category groups indicate the number of stations.

Key to taxonomic groups: An, Anthozoa; As, Asteroidea; B, Bivalvia; Cn, Cnidaria; E, Echiuroidea; H, Holothuroidea; Op, Ophiuroidea; P, Polychaeta; S, Sipunculida; T, Tunicata.

The station pattern that emerges based on similarity of community structure suggests three primary groups of stations that cluster together based on water masses (Figs. 1 and 4). The first cluster (I, XVIII, IV, XVI) is located in the core of the eastern branch of Atlantic water entering the Barents Sea from the west. The second cluster contains stations in Storfjord (V, VI) and in the trench between Nordaustlandet and Kvitøya (XI, XII) (Fig. 1). While these stations are widely separated geographically, they are all influenced by similar water mass characteristics. Both are affected by the subsurface jet of the West Spitsbergen Current (WSC), which flows northward along the west coast of Svalbard and then turns to the east and then south following the shelf break around Nordaustlandet (Sundfjord et al., 2008). Thus, both locations experience Arctic surface water underlain by a deeper tongue of Atlantic water > 150 m (Fig. 1).

The third cluster (Stns. II, III, VIII, X) is composed of three stations in the core of the Arctic water (II, III, X) of the western Barents Sea as well as the northernmost station in the study area (VIII). Station VIII, although occurring in the same trench system as stations in the second cluster, is located at the extreme shelf-slope break to the Arctic Ocean. It is deeper than any other station we sampled (> 500 m), and its proximity to the Arctic Ocean basin at the head of a broad submarine canyon likely subjects it to hydrodynamic conditions more characteristic of Arctic water masses. This group of stations is characterized by comparatively depauperate communities. The Arctic affinities of these stations are evident in the fauna. The dominants list of this cluster lacks the polychaetes *S. typicus* and *M. sarsi*, both often abundant in Atlantic waters. Instead, we find *Maldane arctica*, an Arctic species (Kröncke, 1998), in high densities at these stations.



**Table 6**  
Pearson correlation coefficients (*r*-values) relating benthic community parameters, density, biomass, species richness, and species diversity to various potential explanatory variables

	Density (no. m <sup>-2</sup> )	Biomass (g WW m <sup>-2</sup> )	No. of taxa	Diversity ( <i>H'</i> )
Latitude	−0.28	−0.18	−0.11	0.18
Water depth (m)	−0.48	<b>−0.58*</b>	−0.48	−0.43
Porosity (1–10 cm) <sup>(1)</sup>	−0.23	<b>−0.66*</b>	−0.44	<b>−0.67**</b>
Grain size (% < 63 μm) <sup>(1)</sup>	<b>−0.62*</b>	−0.07	<b>−0.81***</b>	<b>−0.83***</b>
Total organic carbon (%) <sup>(1)</sup>	−0.38	−0.02	<b>−0.58*</b>	<b>−0.78**</b>
Material accumulation rate (g m <sup>2</sup> yr <sup>-1</sup> ) <sup>(2)</sup>	−0.27	−0.10	−0.15	0.22
Carbon accumulation rate (g m <sup>2</sup> yr <sup>-1</sup> ) <sup>(1)</sup>	−0.34	−0.19	−0.41	−0.29
Sediment chlorophyll (0–2 cm) <sup>(3)</sup>	<b>0.68*</b>	0.16	<b>0.69*</b>	0.60
Ice cover (past year) <sup>(4)</sup>	−0.36	−0.02	−0.37	−0.15
Ice cover (past 4 years) <sup>(4)</sup>	−0.38	−0.12	−0.34	0.05
Water mass surface <sup>(5)</sup>	0.01	−0.32	0.16	0.46
Water mass bottom <sup>(5)</sup>	0.30	<b>0.62*</b>	0.14	0.03
POC flux (at 90 m) <sup>(6)</sup>	0.28	0.02	−0.23	−0.47
Annual primary productivity <sup>(7)</sup>	<b>0.56*</b>	0.12	0.34	−0.08

The levels of the significant correlations are \**p* < 0.05, \*\**p* < 0.01, \*\*\**p* < 0.001. Significant correlations are shown in bold.

Sources: (1) Carroll et al. (2008), (2) Zaborska et al. (2008), (3) Renaud et al. (2008b), (4) Cavalieri et al. (2004), (5) Sundfjord et al. (2007, 2008), (6) Reigstad et al. (2008), (7) Wassmann et al. (2006b), Slagstad et al. (unpublished data).

The coincidence of community-structure patterns and influence of predominant water masses, suggests that infaunal communities in the Barents Sea region are structured, on a multivariate level, by large-scale hydrography. These results mirror those of Piepenburg et al. (1997), who found that the structure of a wide variety of benthic fauna, from foraminiferans to megabenthic epifauna in the Northeast Water polynya (E. Greenland), were highly correlated with water-column variables. The relationship we document between benthic community structure and water masses represents evidence that pelagic and benthic systems in the Barents Sea are coupled on a regional scale.

#### 4.3. Spatial patterns: mesoscale

While the three station clusters show the importance of biogeographic-scale processes, the variability within a cluster suggests that smaller-scale processes may be responsible for differences in some of the community parameters. This is probably particularly important in a heterogeneous region such as the Barents Sea, with highly variable bathymetry and a complex oceanographic and sedimentological setting. On Arctic shelves, food-supply indicators (sediment phytopigments) and physical characteristics of the sediment (the depth correlates of grain size, porosity, organic carbon content) have been shown to be important in describing spatial patterns in community parameters (Grebmeier and McRoy, 1989; Ambrose and Renaud, 1995; Piepenburg et al., 1997; Grant et al., 2002; Schmid et al., 2006; Grebmeier et al., 2006a, b). These studies often note the important influence of mesoscale features of enhanced productivity, such as the increased productivity associated with polynyas, in contributing to areas of elevated density, biomass, and diversity.

The CABANERA benthic stations transit the Polar Front in the Barents Sea (Fig. 1). The Polar Front is a well-known feature in the central Barents Sea (Loeng, 1991; Wassmann et al., 2006a), and defined as the zone where Atlantic (>0 °C, >34.8 psu) and Arctic (<0 °C, <34.8 psu) water masses meet. The four stations that appear to be influenced by the Polar Front (IV, V, VI, XVI) showed 88% greater faunal density, nearly 50% higher species richness, and a higher diversity (*H'*) compared to the other 10 stations (Table 3). Biomass shows a more equivocal pattern; while it is on average 16% greater at the Polar Front stations compared to the rest of the station network, this difference has no statistical strength due to the high within-region variability in the non-Polar

Front stations (Table 3). In particular, non-Polar Front Stns. XI and III have biomasses of 138 and 152 g m<sup>-2</sup>, respectively (Table 2), suggesting that a conflagration of local factors can result in locally high biomasses anywhere in the Barents Sea. However, if medians are used rather than means in order to reduce the influence of measurements at the tails of the distributions, the biomass difference becomes more apparent: 78 g m<sup>-2</sup> at the Polar Front vs. 47 g m<sup>-2</sup> at the other stations.

Enhanced benthic fauna in the Polar Front region has been observed in large-scale surveys of the Barents Sea (Zenkevich, 1963; Antipova, 1975; Denisenko, 2002) and other Polar Regions (Curtis, 1975). This phenomenon may be ascribed to elevated food delivery to the sea floor, since fronts or other mesoscale features such as polynyas and marginal ice zones often represent areas of higher primary production, poor retention of primary production in the surface waters, and therefore enhanced vertical flux of carbon (Denisenko et al., 2006; Carmack and Wassmann, 2006; Wassmann et al., 2006a). At the CABANERA Polar Front stations, primary production was 48% greater than at non-Polar Front stations (Table 3), suggesting a direct link between frontal processes controlling primary production and benthic abundance. Faunal density was significantly (positively) correlated with primary production; and both density and species richness showed a significant positive correlation with sediment chlorophyll (Table 6). Sediment pigment concentration was available from only one Polar Front station (Stn. XVI), where it had the second highest value of the dataset (Renaud et al., 2008a). So this pigment-faunal relationship is not possible to test quantitatively in the present study, but in other studies it has been the most reliable indicator of parameters related to both benthic infaunal structure (Ambrose and Renaud, 1995; Piepenburg et al., 1997; Dunton et al., 2005) and function (e.g. sediment respiration: Clough et al., 2005; Renaud et al., 2008a). This suggests that mesoscale oceanographic features may influence benthic communities via their effects on food supply.

#### 4.4. Integration over temporal scales

Many benthic fauna on high-latitude shelves are long-lived and relatively sessile, with the consequence that community parameters such as abundance and biomass reflect a time-integrated response compared to more transient pelagic signals. This has led to benthic communities (Beukema, 1992; Kröncke,

1995; Kröncke et al., 1998, 2001; Tunberg and Nelson, 1998; Grebmeier et al., 2006b; Renaud et al., 2007b) and individual aspects thereof (Witbaard et al., 1994; Witbaard, 1996; Schöne et al., 2005; Ambrose et al., 2006) being used as indicators of environmental change over decades or longer. Our results suggest that the Polar Front may be responsible for a multi-year signal of food supply to the sea floor that is reflected in benthic community parameters (Tables 3 and 6). In addition, oceanic current patterns lead to regional faunal structure (Figs. 1 and 4). Thus, long-term response of the benthos is evident on multiple spatial scales, reflecting both ecological (food supply, sediment characteristics) and evolutionary (biogeographical patterns) processes.

Certainly, not all responses of Arctic benthos to environmental forcing occur on long time scales. Episodic pulses of food are at once a quantitative resource enhancement for a food-limited system and a qualitative change in food composition, and the benthos collectively has been shown to respond to food inputs within hours to days (Rysgaard et al., 1998; Gooday, 2002; Moodley et al., 2005; McMahon et al., 2006; Sun et al., 2007). Tamelander et al. (2006), using stable isotopes, noted variability in the link between pelagic processes and Barents Sea benthic food webs. Stable isotopes integrate over weeks to months, depending on the turnover time of the tissues in the organisms studied. Timing of sampling relative to food pulses, then, may be reflected in the strength of dependence of benthic food webs on pelagic inputs. These results were echoed by Renaud et al. (2008a), also from the CABANERA project, suggesting that the benthic processing of carbon was closely timed with food inputs to the sea floor and pelagic carbon flux, and that benthic processes and stock-turnover vary on characteristic time scales, both long- and short-term.

It appears, then, that benthic community structure in the Barents Sea integrates long-term variability (on multiple scales), while infaunal community function (e.g. carbon cycling, food-web interactions) may respond on shorter time scales. Interestingly, some of the drivers of these processes on different scales may be the same (e.g. food supply). This may not be surprising considering how function is linked to structure in many communities, but has implications for patterns of community response to changes in these drivers due to, for example, climate change. Increased Atlantic water influence, leading to an expansion and northward displacement of the seasonal ice zone in the Barents Sea (see Carmack and Wassmann, 2006) could result initially in changes in carbon processing, but within several years these results may extend to community structure, with feedback for sedimentary processes and food web structure (see Renaud et al., 2008b).

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