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Benthic macrofauna and productivity regimes in the Barents Sea – Ecological implications in a changing Arctic

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ABSTRACT

Benthic faunal assemblages were analysed from 47 stations in the central and southern parts of the Barents Sea, together with sedimentary and water column parameters, daily ice records and modelled integrated primary productivity. Sampling spanned areas influenced by Atlantic Water (AW) to those lying under Arctic Water (ArW), and included stations with mixed water masses. Ice cover suppressed water column productivity in the northern areas. Three main faunal groups were identified, based on similarity of numerical faunal composition. The northern and southern faunal groups were separated by the northernmost penetration of AW in the bottom water and the third group, the Hopen group, was influenced by modified bank water. Faunal abundances were significantly higher within the southern faunal group relative to the northern group, but the numbers of taxa present were similar. The particularly rich fauna of the Hopen group reflected sediment heterogeneity and tight pelagic–benthic coupling. These results suggest that a retreat and thinning of the ice cover in the Barents Sea likely will result in the northern parts of the Barents Sea becoming more Atlantic in character, with a higher productivity at the sea floor.

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1. Introduction

On Arctic continental shelves, episodic pulses of fresh phytoplankton reaching the sea floor are rapidly processed by the benthos (Goody and Turley, 1990; Goody, 2002; Clough et al., 2005; McMahon et al., 2006; Sun et al., 2007; Renaud et al., 2007c). The close relationship between the structure and function of these benthic communities and the overlying primary productivity regime has been demonstrated throughout the Arctic (Northeast Water Polynya off Greenland, Ambrose and Renaud, 1995; Hobson et al., 1995; Piepenburg et al., 1997; Beaufort Sea, Carey, 1991; Renaud et al., 2007b; northern Bering and Chukchi Seas, Grebmeier and Dunton, 2000; Grebmeier et al., 2006a; Barents Sea, Piepenburg et al., 1995; Renaud et al., 2008).

Climate change may alter this generally tight relationship because the fundamental drivers of system productivity (ice cover, temperature and water mass distribution) may be affected. The extent and thickness of sea ice in the Barents Sea has decreased over recent decades, and this trend is projected to continue (ACIA, 2005), with a particularly marked

reduction expected in the summer extent of sea ice (Johannessen et al., 2004). Reduced summer sea ice increases the time period and areal extent of pelagic primary production, which may affect pelagic–benthic coupling. Pelagic grazing pressure is also higher in the absence of seasonal ice relative to ice-influenced areas in the Chukchi Sea (Lalande et al., 2007), perhaps altering sedimentation on this shallow shelf. In the Barents Sea, model results (IPCC B2 Scenario) predict a 1 °C rise in the temperature of water entering the Barents Sea and an average increase in primary productivity of 8%, mainly due to increased productivity in the northern regions over the next 50 years (Ellingsen et al., 2008). Therefore, a shift in the primary energy pathways from benthic to pelagic has been predicted for Arctic shallow seas (see Carroll and Carroll, 2003; Renaud et al., 2007a). In the Arctic, both ice algae and phytoplankton are readily consumed by the benthos (Clough et al., 2005; McMahon et al., 2006; Sun et al., 2007), but the relative and actual amounts of each reaching the seafloor may be altered due to climate change. This is because any changes in the magnitude or timing of the respective blooms would affect how much of the material is consumed by grazers. Because benthic communities in the Barents Sea are an important food source for a range of top predators such as marine mammals (e.g. bearded seals, walrus), seabirds (e.g. eider), and fish (e.g. halibut, cod), changes in pelagic–benthic coupling are likely to

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have substantial effects throughout the ecosystem (Grebmeier et al., 2006b).

The Barents Sea is a highly productive inflow shelf sea (Carmack and Wassmann, 2006), with an estimated overall average annual primary productivity of $90 \text{ g C m}^{-2} \text{ y}^{-1}$ (Sakshaug, 2004; Wassmann et al., 2005, 2006). Depending on the water mass characteristics and physical regime, between 48 and 96% of primary production in the Barents Sea is estimated to reach the sea floor (Wassmann, 1991; Carmack and Wassmann, 2006). This large range in primary productivity throughout the Barents Sea, together with the physical habitat properties, contributes to supporting rich, but quite varied, benthic communities (Wassmann et al., 2006). The community structure throughout much of the Barents Sea, has been well characterised (Brotskaya and Zenkevich, 1939; Zenkevich, 1963; Antipova, 1973, 1975; Piepenburg et al., 1995; Cochrane et al., 1998; Dahle et al., 1998; Galkin, 1998; Kröncke et al., 2000; Denisenko, 2001, 2002, 2004; Denisenko et al., 2003; Carroll et al., 2008). However, benthic community structure in the area shows large inter-annual and long-term variability (Denisenko, 2001). As with benthos anywhere, this likely is a result of fluctuations in temperature, water masses, food quality, quantity and timing, as well as biological competition and

recruitment success. In our study area, these factors are further affected by ice conditions and wind-driven current patterns (e.g. Wassmann et al., 2006), but little focused research has been carried out on such cause–effect relationships.

We investigated patterns in the abundance and composition of benthic faunal assemblages in the Barents Sea in relation to environmental factors, particularly primary productivity, ice cover and water mass. The spatial coverage of stations spanned both Norwegian and Russian sectors of the Barents Sea. Therefore, the data are also highly relevant as baseline information to evaluate human impacts on the Barents Sea from activities such as petroleum development and fisheries.

2. Methods

2.1. Hydrographic setting and sampling strategy

The sampling scheme encompassed the different hydrographic and productivity regimes of the Barents Sea. Highly productive southern areas are under strong influence from Atlantic Water (AW), are generally ice-free throughout the year, and have a deep

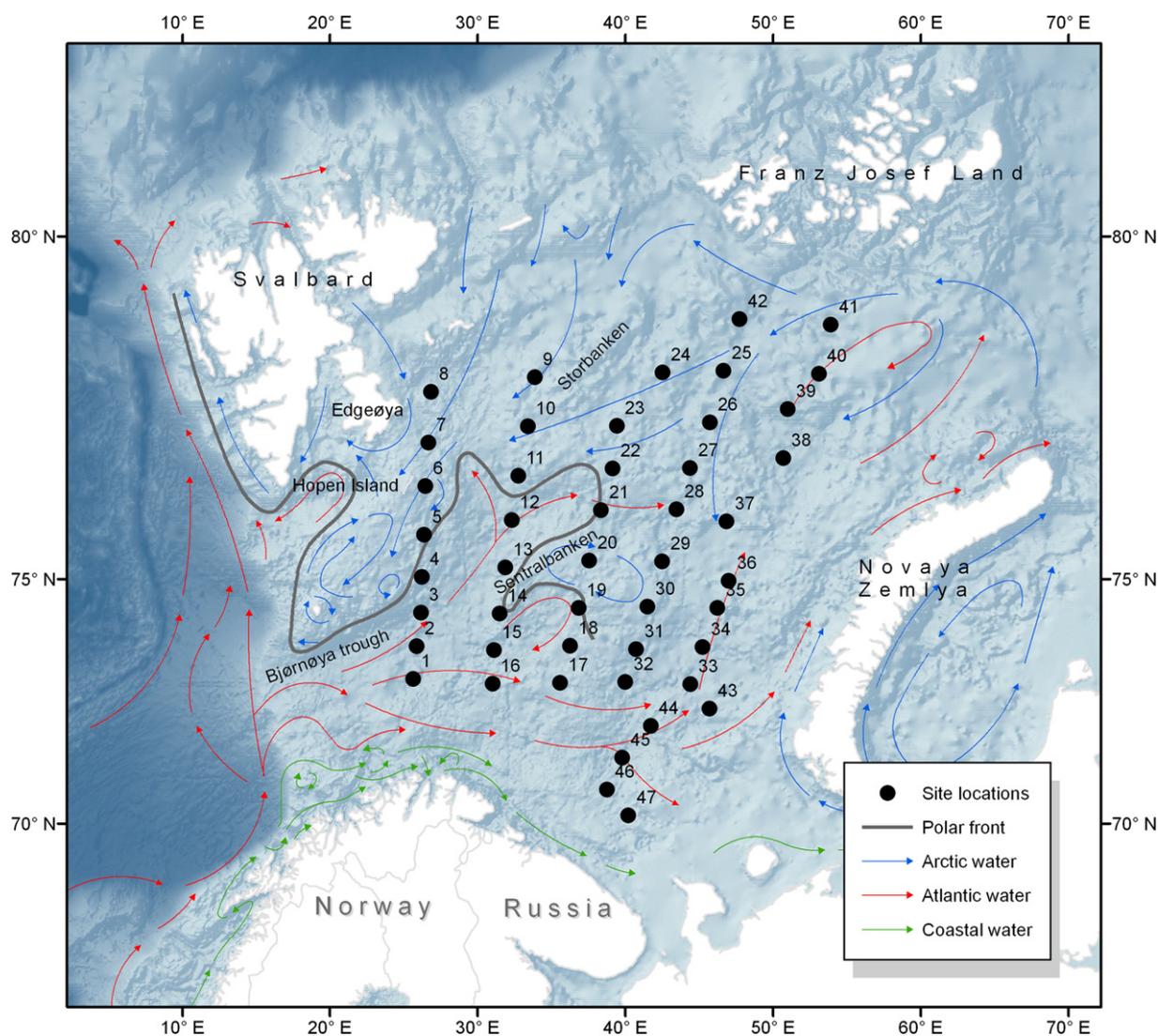


Fig. 1. Location map of the Barents Sea, showing surface currents, the average location of the Polar Front (grey line) and the sampling stations visited in this investigation. Blue arrows: Arctic Water; red arrows: Atlantic Water and green arrows: Norwegian Coastal Current. GIS files of bathymetry and surface currents kindly supplied by Harald Loeng, Institute of Marine Research, Norway.

mixed layer. Northern areas, however, are dominated by Arctic Water (ArW), and characterised by heavy ice cover throughout most of the year and low productivity. In marginal ice zone (MIZ) areas, seasonal ice-melting causes a pronounced vertical stratification, and a nutrient-rich euphotic zone develops, giving rise to an intense, but short-lived, phytoplankton bloom (Sakshaug and Skjoldal, 1989). Finally, the presence of a shifting Polar Front (PF) and strong tidal mixing over shallow banks (Nansen, 1906; Midttun, 1985; Anderson et al., 1988; Schauer, 1995), are other drivers of productivity patterns and can lead to significant spatial variability in primary production.

Samples were collected from 03–28 August, 2003, from the RV *Ivan Petrov* (VNIIOkeanologia St. Petersburg). The 47 stations sampled spanned approximately 400 000 km² of the seasonally ice-influenced central and eastern Barents Sea (Fig. 1), ranging from 79–459 m. The deepest stations in the Atlantic-influenced southwestern part were in the Bjørnøya Trough, at depths of down to 459 m. The centre of the westernmost transect was characterised by shallow waters surrounding Hopen island and northwards to Edgeøya (between 79 and 130 m depth). In the mid-northern to central part are the relatively shallow bank areas around Storbanken and Sentralbanken (between 169–224 m depth). The remainder of the stations was between 200 and 300 m depth.

Sediments were sampled using a 0.25 m² box core. Care was taken during deployment and retrieval of the equipment, to preserve an undisturbed sediment surface. Samples of the top 1 cm sediment layer were immediately frozen at –20 °C. Granulometric composition were analysed by GeoGruppen Analyse AS, Tromsø. Granulometric analyses were carried out by dry sieving for the coarser fraction >0.063 mm (after Buchanan, 1984) and by electronic particle counting of the fine fraction using a Sedigraph 5000. Pigments (chlorophyll *a* and *b*, and their breakdown products phaeophytin *a* and *b*) were analysed by the Norwegian Institute for Water Research (NIVA). Pigments were extracted from freeze-dried sediments using 90% acetone in water for 4 h. Analysis was performed according to standard methods (Wright et al., 1991; Jeffrey et al., 1997). The HPLC system consisted of a Waters HPLC equipped with a reverse phase C18 column and an online photodiode array detector (Waters 996 PDA). Pigments were detected at a wavelength of 436 nm, and identification was performed by comparing retention time and PDA spectra with standards (DHI Water and Environment, Denmark).

A 0.1 m² van Veen grab was used to sample the benthic fauna. Five replicate samples were taken at each of the 47 stations. Sampling and sample preservation procedures followed international guidelines (ISO 16665), except for the sieve size (the sieve was a 0.75 mm square mesh bag, compatible with previous Russian surveys, but stiff to reduce the specimen damage typical of soft-mesh sieves. The pore openings measured approximately 1 mm from corner to corner, therefore discrepancies in sampling between this and the 1 mm diameter round-pore sieves that are usually used in “western” surveys are likely to be minor). Fauna was identified to the lowest taxonomic level possible and individuals within each taxon were weighed, for each sample replicate. Taxon names were cross-checked against the European Register of Marine Species (ERMS; available at www.marbef.org). Macrofaunal foraminiferans, mostly *Hyperammia subnodosa*, were highly abundant at many of the sampling stations. These agglutinated forms cannot be quantified in a manner comparable with the remainder of the fauna, because they are brittle and it is difficult to determine what constitutes one individual. Therefore, they were excluded from our analyses. Likewise, nematodes, which are not sampled quantitatively using a macrofaunal mesh size, and planktonic taxa including chaetognaths and copepods, were excluded.

2.2. Sea ice cover, hydrography and primary production

Mean annual ice cover was compiled from daily ice records (% ice cover in 25 × 25 km area surrounding a station) obtained from the

National Snow and Ice Data Center (NSIDC; <http://nsidc.org/data/nsidc-0051.html>, Cavalieri et al., 2006) for each of the 47 stations for the three years prior to sampling (i.e. 2000–2003; selected as broadly representative of average lifespan of the majority of the fauna). Water column profiles of temperature and salinity were constructed for all stations using a Sensordata SD-204 CTD probe on the cruise in August 2003. These data were used to characterise water masses.

Water-column chlorophyll content was not measured due to instrument failure. Instead, we estimated the annual integrated water column productivity for each of the stations using the SINMOD hydrodynamical–chemical–biological ecosystem model for the Barents Sea (Slagstad and McClimans, 2005; Wassmann et al., 2006). The data were extracted from the model with horizontal resolution of 4 km at positions that correspond to each station for two year-runs (2002, 2003) of the model. This technique provides a more realistic estimate of the potential food supply for the benthos than a single measurement.

2.3. Data analysis

Uni- and multi-variate analyses were carried out using PRIMER version 6 (Primer-E Ltd). A measure of taxonomic richness (ES₂₀₁) was calculated using Hurlbert's (1971) modification of Sanders' (1968) rarefaction method, calculating the expected number of taxa (*S*) in a sample of 201 individuals selected at random (and without replacement) from a larger collection. Shannon–Wiener *H'* (log_e) diversity and taxonomic evenness were also calculated.

All measures of taxonomic richness or diversity are highly influenced by how the animals are identified (see Bertrand et al., 2006), and the actual numbers are of little biological relevance. For this reason, we do not attempt to compare our measures of taxon richness with other studies. Taxa are discussed without reference to Linnean ranks (see the PhyloCode at <http://www.ohiou.edu/phylocode/>).

Faunal groupings were constructed using the Bray–Curtis similarity index (group average linking). Biological and environmental variables were compared across the three main faunal regions using analysis of variance (on square-root transformed data where necessary), with Tukey's HSD post-hoc test to elucidate differences among station groups. Pearson's correlation coefficient (*r*) was calculated for the environmental variables and univariate faunal statistics (normalised data). Canonical Correspondence Analysis (CCA) was carried out on the faunal and environmental data using Canoco for Windows v.4.5 and CanoDraw for Windows 4.0 (ter Braak and Smilauer, 2002). Taxa contributing less than 1% of the total abundance were excluded. Data were square-root transformed and downweighting of rare species was applied.

3. Results

3.1. Sediment granulometry and benthic pigments

Most of the sediments were composed of glacio-marine blue-grey clay, with an overlying layer of fine flocculent material. The finest sediments were found in the northwest and at the deep, southwestern corner of the sampling area (Table 1, sts. 7 and 1; 91% and 89% mud [silt + clay fractions], respectively). Muddy areas were also found between Hopen and the Sentralbanken (sts. 6, 12, 13) as well as east of Storbanken (sts. 23, 27) and st. 38 in the northeast. The sediment in the shallow southeastern area (st. 47) and mid-way along the easternmost transect (st. 35), was mainly a fine/very fine sand mixture. The coarsest sediments, with approximately 25% gravel, were found close to Hopen and on the Sentralbanken (sts. 5 and 20, respectively). The remaining stations comprised more or less equal proportions of mud and sand.

In general, benthic pigment values ranged from 2–4 μg g⁻¹ dry weight, with lowest values (<0.5 μg g⁻¹ dry weight) at sts. 1, 3 and 15

Table 1
Selected characteristics at the sampling stations.

Station	Depth	Latitude	Longitude	Bottom temp.	Ice cover	PrP	Mud	Benthic pigments	S	N	J'	ES (201)	H' (log _e)
1	425	73.13	25.63	2.3	0	134	89	0.18	119	1200	0.70	51	3.34
2	459	73.76	25.88	1.3	0	119	65	1.08	92	547	0.71	56	3.19
3	387	74.39	26.17	0.6	0	114	43	0.40	143	1293	0.78	65	3.85
4	218	75.03	26.22	0.8	6	101	62	3.63	152	1828	0.63	52	3.15
5	130	75.76	26.36	−1.0	23	92	36	3.63	191	1477	0.78	76	4.10
6	79	76.56	26.46	−0.6	38	106	84	3.74	179	2607	0.79	70	4.08
7	133	77.23	26.66	−1.3	47	81	91	1.60	126	1295	0.81	62	3.92
8	136	77.98	26.83	−1.3	55	56	77	2.76	114	660	0.83	66	3.93
9	164	78.19	33.89	−0.7	57	37	64	1.51	101	595	0.79	59	3.63
10	144	77.48	33.39	−0.6	50	50	41	0.92	114	1090	0.82	62	3.88
11	190	76.72	32.75	1.1	34	59	33	0.93	134	1339	0.74	60	3.65
12	323	76.01	32.30	−0.1	15	62	83	3.28	96	960	0.65	46	2.99
13	338	75.20	31.86	−0.1	4	84	88	1.44	112	1330	0.72	52	3.40
14	260	74.38	31.48	−0.8	0	89	59	2.12	188	2395	0.73	67	3.81
15	374	73.69	31.10	1.4	0	98	82	0.48	102	726	0.71	55	3.29
16	279	73.03	31.01	0.8	0	118	55	0.51	138	1062	0.81	68	3.99
17	224	73.04	35.58	0.4	0	90	54	3.17	165	2985	0.65	52	3.34
18	245	73.77	36.26	−1.2	1	87	62	4.66	139	2332	0.69	53	3.42
19	224	74.48	36.84	−1.2	5	72	43	4.16	125	2148	0.61	45	2.97
20	169	75.32	37.55	−0.8	11	61	36	4.63	157	1837	0.62	51	3.13
21	258	76.17	38.35	−0.3	21	47	37	1.95	160	2162	0.70	58	3.56
22	192	76.84	39.13	−0.7	37	36	80	2.79	82	419	0.83	59	3.66
23	217	77.49	39.43	−0.8	43	30	89	2.06	78	453	0.79	54	3.44
24	221	78.25	42.54	−0.4	47	23	66	2.20	118	1044	0.76	59	3.63
25	244	78.28	46.66	−0.4	47	22	67	1.18	114	833	0.77	60	3.62
26	251	77.53	45.73	−0.4	36	24	80	2.71	74	467	0.79	49	3.41
27	275	76.84	44.40	−0.4	26	29	85	3.81	55	330	0.77	45	3.09
28	342	76.18	43.46	−0.6	17	37	72	2.96	69	604	0.72	42	3.07
29	267	75.30	42.51	−0.7	11	44	50	2.72	118	2164	0.64	41	3.04
30	208	74.50	41.49	−1.1	8	56	53	2.73	96	2149	0.62	36	2.81
31	295	73.71	40.75	−1.0	5	70	54	3.56	82	914	0.76	45	3.34
32	324	73.06	40.00	−0.8	2	85	57	1.95	85	1158	0.78	47	3.47
33	335	73.02	44.41	−0.5	0	75	59	2.56	72	905	0.75	40	3.19
34	340	73.74	45.25	−0.4	0	60	59	3.78	75	815	0.77	46	3.32
35	243	74.48	46.25	−0.4	3	46	17	4.33	153	2245	0.71	59	3.56
36	243	74.97	47.00	−0.6	6	40	51	10.15	111	1921	0.64	44	3.04
37	349	77.00	50.70	−0.6	32	21	47	2.66	103	1535	0.70	48	3.26
38	225	77.73	51.00	−0.8	39	20	82	2.11	39	322	0.70	31	2.58
39	305	78.23	53.12	−0.4	50	22	61	1.11	76	402	0.83	56	3.59
40	241	78.90	53.93	−0.8	51	17	69	1.46	69	203	0.89	69	3.77
41	254	78.97	47.75	−0.7	55	17	67	3.62	102	488	0.84	67	3.90
42	268	75.98	46.86	−0.6	50	21	42	2.54	135	975	0.80	65	3.91
43	284	72.52	45.71	−0.2	15	32	53	3.14	111	910	0.72	55	3.37
44	286	72.16	41.73	−0.5	0	75	81	2.65	73	586	0.77	47	3.28
45	365	71.48	39.79	−0.2	0	84	77	1.86	77	880	0.74	43	3.21
46	233	70.78	38.75	−0.5	0	102	54	0.51	141	1813	0.69	56	3.43
47	145	70.19	40.21	2.5	0	106	17	2.50	163	2017	0.74	59	3.75

Depth (m); latitude and longitude (degrees); bottom temperature (°C); ice cover (%; average 2000–2003); PrP: modelled integrated water column productivity ($\text{g C m}^{-2} \text{y}^{-1}$), average of 2002 and 2003 values; mud (%; sum of silt + clay fractions); benthic pigments ($\mu\text{g/g}$ dry weight); S: number of taxa; N: number of individuals (0.5 m^2 sampling area); J': Pielou's index of faunal evenness; ES₂₀₁: expected number of taxa from a sample of 201 individuals and H': Shannon–Wiener diversity index.

(Table 1), which were influenced purely by Atlantic Water. The highest value for benthic pigments ($10.15 \mu\text{g g}^{-1}$ dry weight), more than double that at any other station, was found at Station 36. Here phaeophytin-*a* contributed only 25% of the chlorophyll-*a* + phaeophytin-*a* total (compared with an average of $48\% \pm 16$ at the other stations), indicating a recent settlement of fresh material not yet utilised by the benthos.

3.2. Ice and water masses

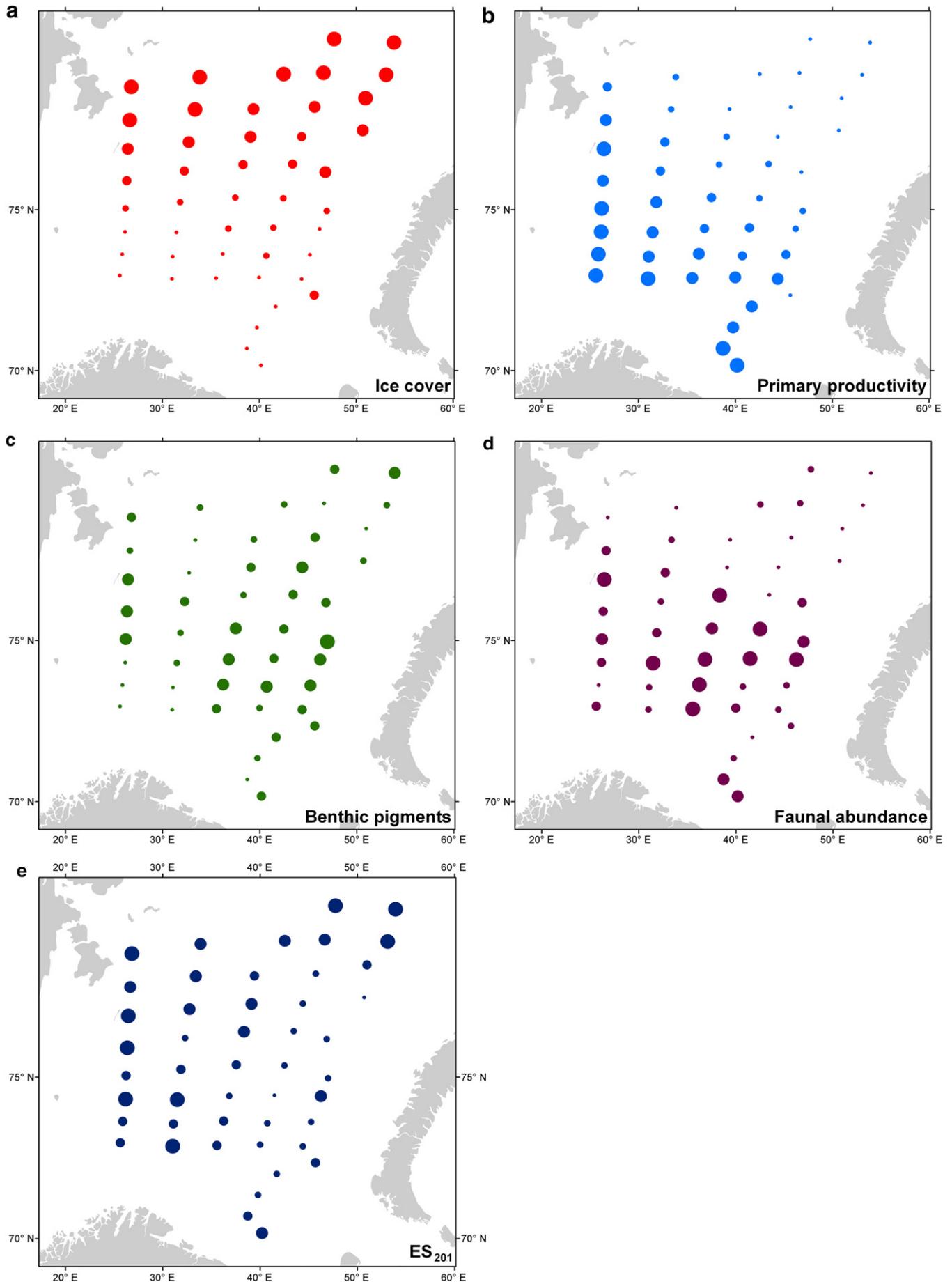
3.2.1. Ice conditions

Between 2000 and 2003, all stations were ice-free during August and September, with the exception of the very northeastern corner (st. 41), which still was under ice during the first week in August 2003 (data from NSIDC; Table 1). Averaged over the three year period, the heaviest annually-averaged ice cover (between 40 and 57%) occurred at 11 stations located in the north of the sampling area (sts. 7, 8, 9, 10, 23, 24, 25, 39, 40, 41 and 42). October was ice-free in 2000 and 2001, and in 2002 the area was ice-free

already in July. Between 2000 and 2003, maximal ice cover generally occurred during February–April in the northernmost parts, although heavy ice cover was already attained in January and remained until June. The southwestern and southeastern areas, on the other hand, were entirely ice-free during the three year period. Ice conditions were relatively similar during 2000–2002 (although 2002 was reported as a record low-ice year, see Serreze et al., 2003), but 2003 was a heavier-ice year, e.g. Stations 31 and 32 had around 65 and 30% ice cover in March, respectively, as opposed to none during the previous years.

3.2.2. Water mass distributions

Water mass characterisations at each station generally agreed with known hydrographic patterns (Loeng, 1991; Fig. 1). The northern stations (bordered to the south by 8, 10, 25 and 39) were dominated by Arctic Water (ArW; bottom temperatures down to $-0.3 \text{ }^\circ\text{C}$, salinities around 34.4–34.6). Most of the stations to the south of this border were variously influenced by Atlantic Water (AW; temperature around



1 °C at bottom to 5 °C on surface and salinity around 34.9). The four southwestern-most stations (1, 2, 15 and 16) had AW throughout the water column, but most had AW in the bottom layers, ArW in the mid-to upper layers and a surface layer of melt water up to 30 m depth in the northern and central areas.

The northeastern stations 39, 40, 41 and 42 showed some transitional characteristics; with a mixture of transformed (strongly cooled and diluted) Atlantic water, and some Barents Sea Water (BSW; temperature <0 °C, salinity around 34.8–35) influence was seen along the easternmost transect. Stations 19, 20, 30 and 31, on and around the Sentralbanken, were characterised by ArW, and sts. 5, 6, 7 and to some extent also st. 8, around and to the north of Hopen Island, had modified ArW (mixed with meltwater; bottom salinity down to 34.0). Norwegian Coastal Water (NCW; temperature around 3–4 °C and salinity around 34.9) predominated at st. 47 in the southeastern corner of the sampling area (Fig. 3).

Water mass identifications were supported by data on the relative proportions of calanoid copepods (*Calanus finmarchicus*, *C. hyperboreus* and *C. glacialis*) across the sampling area (L. Kiel Jensen, Akvaplan-niva, pers. comm.). *C. finmarchicus* is of Atlantic origin, *C. glacialis* is present on Arctic shelf areas, and *C. hyperboreus* originates from the deep waters in the Polar Basin (reviewed in Søreide et al., 2008).

3.2.3. Modelled primary productivity

Modelled spatial patterns of integrated primary production across the sampling area were similar in 2002 and 2003 ($r = 0.93$), but values were on average 37% lower in 2003 than 2002. Overall, the highest production (98–134 g C m⁻² y⁻¹) occurred in the primarily Atlantic-dominated southwestern corner of the sampling area, and in the shallow, tidally mixed waters near Hopen and Edgeøya, as well as st. 47 in NCW. Lowest productivity (7–21 g C m⁻² y⁻¹) occurred at the northeastern AW-dominated stations (sts. 38, 40, 41 and 42). Intermediate productivity occurred in the ArW–AW mixed area (91 and 51 g C m⁻² y⁻¹, respectively).

3.3. Faunal composition

3.3.1. General faunal characteristics

The highest faunal abundances occurred within the southern half of the sampling area; sts. 17, 14, 18, 35, 29, 21, 30, 19 and 47, in decreasing order (ranging from 2985 to 2017 ind. per 0.5 m²). Station 6, at Hopen, also supported a high faunal abundance (2607 ind. per 0.5 m²) (Table 1). Lowest abundances occurred at sts. 40, 38, 27, 39, 22, 23, 26 and 41, all located within the northeastern part of the sampling area, ranging from 202 to 487 ind. per 0.5 m².

Polychaete worms were numerically dominant (65%), followed by molluscs (21%), crustaceans (6%) and echinoderms (4%) (Fig. 2). Abundance patterns of polychaetes mirrored that of the entire community, with highest abundances (between 1000 and 2000 ind. per 0.5 m²) at stations in the central part of the sampling transects (sts. 30, 19, 21, 35, 20, 4, 14, 36, 29, 37, 6), the southern part of the middle transect (sts. 17, 18), and along the Russian coast (Sts. 46, 47). Lowest polychaete abundances (<200 ind. per 0.5 m²) occurred at the northern stations 38, 40, 27, 26, 39 and at the southwestern station 2.

Molluscs showed less variation, but the highest abundances (>500 ind. per 0.5 m²) occurred at station 29, immediately east of the Storbanken, and sts. 17 and 18 in the southern part of the middle transect. Lowest abundances (<100 ind. per 0.5 m²) occurred at the northeastern sts. 22, 40 and 41, and the southeastern sts. 34, 43 and 45. Stations 14 and 17 in the south contained the highest numbers of Crustacea (around 500 ind.), whereas the lowest numbers (<20 ind.

per 0.5 m²) occurred at sts. 40 and 33. The highest abundance of echinoderms (348 ind. per 0.5 m²) occurred at Station 5, just south of Hopen, and lowest abundances (8 or fewer ind. per 0.5 m²) were at the northern and northeastern sts. 23, 39, 40 and 41. In the southwestern corner and around the Sentralbanken, up to around 65 and 140 ind. per 0.5 m² were found, respectively, but otherwise echinoderms were sparse (less than 30 ind. per 0.5 m²).

A total of 660 taxa were recorded from the 47 stations. Only one taxon, the small bivalve *Thyasira gouldii*, was present at all stations; its close relative, *Mendicula ferruginosa*, was present at all but one station. Of the 660 taxa, only 24 were present at more than three-quarters of the sampling stations and 69 were present at more than half the stations. Taxonomic richness ranged from 39 at station 38 in the northeast to 191 at st. 5, just south of Hopen (Table 1). None of the far northern stations were among the ten most taxon-rich stations, and the easternmost stations generally contained the lowest numbers of taxa. Stations 5 and 6, around Hopen, ranked highest in terms of faunal diversity (H') and richness, whereas st. 38 ranked lowest. Interestingly, and in contrast to simple numbers of taxa, many northern stations were among those with the highest H' diversity (including sts. 8, 7, 42, 41, 10). Also high in diversity were sts. 16, 3 and 14 in the southwestern part of the sampling area. Station 19, in the Storbanken area, and which had a high number of individuals, was among the three least diverse stations, as a result of low evenness.

The 15 most common taxa are listed in Table 2 in terms of both abundance and frequency of occurrence. The tubicolous polychaete *Spiochaetopterus typicus* was particularly abundant in the relatively sandy sediments around the Sentralbanken (sts. 17–21) and also at station 14 to the west and several scattered locations in the eastern to southeastern part of the sampling area (for example sts. 14, 35 and 46). The second overall dominant, *Galathowenia oculata*, also a tubicolous polychaete, was most abundant in the central part of the sampling area (more than 500 ind. per 0.5 m² at sts. 4, 19, 29 and 36 and between 200 and 350 ind. per 0.5 m² at sts. 18, 30, 35 and 37, and also at the south-eastern sts. 46 and 47).

3.3.2. Faunal groupings

Multivariate analysis of community structure delineated three station groupings (Fig. 3). The two Hopen stations separated out at 20% similarity and contained an average of 2042 (± 799) individuals per 0.5 m² within an average of 185 (± 8.5) taxa. Almost equally abundant at the two Hopen stations were annelids and bryozoans (37% and 33%, respectively), followed by molluscs and echinoderms (both 10%). Crustaceans and “diverse” taxa comprised 7% and 2%, respectively. At approximately 35% similarity level, the northern station group was composed of 11 stations (sts. 8, 9, 10, 22, 23, 24, 25, 39, 40, 41 and 42), and had an average of 651 (± 295) ind. per 0.5 m² within an average of 100 (± 21) taxa. The fauna mostly was comprised of annelids (56%), molluscs (18%) and crustaceans (14%). Bryozoans and echinoderms comprised 4% and 2% of the fauna, respectively, and the remaining 6% were from “diverse” taxa including sipunculids. Most of the remaining stations comprised the southern faunal group, which had an average of 1420 (± 681) ind. per 0.5 m² within an average of 115 (± 34) taxa. The fauna was characterised primarily by annelids (65%), molluscs (20%) and echinoderms (9%). Table 2 shows the most abundant taxa at each of the three groups.

The Hopen group (sts. 5, 6) was less than 25% similar to the other stations. The Hopen and southern groups had significantly higher faunal abundances and than the northern group ($F = 9.08$, $p < 0.0006$, Fig. 4a), and the Hopen group had a significantly higher taxonomic richness than both the northern and southern faunal groups ($F = 5.07$,

Fig. 2. Graphic representation of selected results at the sampling stations; a) average ice cover during the period July 2002–August 2003; values from 0–57%, b) modelled integrated water column productivity; averaged for 2002–2003; values from 17–134 g C m⁻² y⁻¹, c) sum of chlorophyll-*a* and phaeophytin-*a* measured in sediments in August 2003; values from 0.18–10 µg/g dry weight, d) faunal abundance in August 2003; values from 203–2985 individuals per 0.5 m² and e) the ES₂₀₁ index.

Table 2

List of the overall most abundant (averaged for 0.5 m²) and most frequently occurring taxa within each of the faunal groups.

		Ind. 0.5 m ²	% occurrence
<i>Northern group</i>			
Polychaeta	<i>Spiophanes kroeyeri</i>	53	100
Polychaeta	<i>Myriochele heeri</i>	45	100
Polychaeta	<i>Prionospio cirrifera</i>	39	100
Bivalvia	<i>Mendicula ferruginosa</i>	24	100
Polychaeta	<i>Scoletoma fragilis</i>	21	91
Bivalvia	<i>Yoldiella solidula</i>	19	100
Bivalvia	<i>Astarte crenata</i>	19	100
Bivalvia	<i>Thyasira gouldi</i>	17	100
Polychaeta	<i>Galathowenia oculata</i>	17	91
Polychaeta	<i>Spiochaetopterus typicus</i>	16	100
Sipunculida	<i>Nephasoma d. diaphanes</i>	14	91
Polychaeta	<i>Heteromastus filiformis</i>	14	91
Ostracoda	<i>Ostracoda</i>	13	82
Amphipoda	<i>Harpinia mucronata</i>	13	91
Polychaeta	<i>Aglaophamus malmgreni</i>	13	91
Polychaeta	<i>Aphelochaeta marioni</i>	12	100
Polychaeta	<i>Ophelina cylindricaudata</i>	11	100
Bryozoa	<i>Alcyonidium</i>	8	91
Bivalvia	<i>Dacrydium vitreum</i>	5	91
Bivalvia	<i>Cuspidaria arctica</i>	3	91
Polychaeta	<i>Aricidea nolani</i>	3	91
<i>Southern group</i>			
Polychaeta	<i>Spiochaetopterus typicus</i>	202	100
Polychaeta	<i>Galathowenia oculata</i>	165	94
Bivalvia	<i>Mendicula ferruginosa</i>	108	100
Polychaeta	<i>Heteromastus filiformis</i>	71	100
Polychaeta	<i>Paraninoe minuta</i>	51	94
Polychaeta	<i>Maldane sarsi</i>	50	97
Polychaeta	<i>Spiophanes kroeyeri</i>	45	82
Bivalvia	<i>Yoldiella solidula</i>	43	100
Polychaeta	<i>Chaetozone</i>	23	82
Bivalvia	<i>Thyasira gouldi</i>	21	100
Polychaeta	<i>Scoloplos acutus</i>	20	97
Bivalvia	<i>Yoldiella lenticula</i>	18	79
Bivalvia	<i>Yoldiella intermedia</i>	17	82
Amphipoda	<i>Haploops tubicola</i>	16	61
Sipunculida	<i>Nephasoma d. diaphanes</i>	15	91
Polychaeta	<i>Aphelochaeta marioni</i>	15	94
Bivalvia	<i>Dacrydium vitreum</i>	13	85
Polychaeta	<i>Myriochele heeri</i>	12	85
Polychaeta	<i>Scalibregma inflatum</i>	11	85
Polychaeta	<i>Terebellides stroemi</i>	11	94
Aplacophora	<i>Aplacophora</i>	7	94
<i>Hopen group</i>			
Bryozoa	<i>Hippothoa divaricata arctica</i>	159	100
Ophiuroidea	<i>Ophiura robusta</i>	146	100
Bryozoa	<i>Reussina impressa</i>	136	100
Bryozoa	<i>Electra crustulenta arctica</i>	81	100
Polychaeta	<i>Chone murmanica</i>	75	50
Polychaeta	<i>Chaetozone</i>	55	100
Bivalvia	<i>Leionucula tenuis</i>	50	100
Bivalvia	<i>Macoma calcarea</i>	48	100
Polychaeta	<i>Paraninoe minuta</i>	43	100
Polychaeta	<i>Scoloplos acutus</i>	42	100
Bryozoa	<i>Escharella klugei</i>	40	50
Amphipoda	<i>Melitidae</i>	39	50
Ophiuroidea	<i>Ophiocten sericeum</i>	39	50
Polychaeta	<i>Scalibregma inflatum</i>	38	100
Polychaeta	<i>Aphelochaeta marioni</i>	31	100
Bivalvia	<i>Thyasira gouldi</i>	28	100
Polychaeta	<i>Pholoe assimilis</i>	27	100
Polychaeta	<i>Galathowenia oculata</i>	24	100
Bryozoa	<i>Porella obesa</i>	24	100
Bryozoa	<i>Escharella ventricosa</i>	24	100
Polychaeta	<i>Maldane sarsi</i>	21	100
Polychaeta	<i>Terebellides stroemi</i>	21	100

Bold type indicates taxa which were both most numerically abundant and frequently occurring.

$p < 0.02$). Station 38 was an outlier, with less than 20% similarity to any other station, and contained 322 individuals per 0.5 m² and 49 taxa.

3.3.3. Faunal and environmental relationships

The deepest stations were those influenced purely by Atlantic Water, so depth was positively correlated with bottom temperature and negatively with ice cover (Table 3). Modelled integrated water column productivity was negatively correlated with ice cover and positively with faunal abundance and richness. Benthic pigments were positively correlated with abundance and negatively with evenness (all significant correlations at $p < 0.05$).

The southern faunal group stations as a whole were significantly deeper than the northern and Hopen faunal group stations ($F = 8.34$, $p < 0.0009$), with less ice cover ($F = 51.0$, $p < 0.0001$). There were no significant differences in benthic pigment concentrations or mud content among the station groups. The data for abundance, number of taxa and primary productivity violated Levene's test for heterogeneity of variance so abundance and richness data were transformed by taking the square root of the values, and productivity data were fourth-root transformed before analysis. The Hopen and southern stations had significantly higher modelled primary productivity than the northern stations ($F = 18.7$, $p < 0.0001$, Fig. 4b).

A canonical correspondence analysis (CCA) showed ice, mud, modelled integrated water column productivity (PrP), benthic pigments (Chl-*a* + Phaeo) and depth to have a significant relationship ($r = > 0.005$) with the faunal composition at the sampling stations (Fig. 5). There was a strong negative association between PrP and ice cover. A cloud of stations containing the entire northern faunal group appears on the top and right-hand side of Fig. 5, associated with heavy ice cover and low productivity. These stations also were relatively muddy and of rather intermediate depths. Towards the lower part of the plot are most of the southern stations, which generally were associated with greater depth and also higher water column productivity. Stations 1, 2 and 3 appear at the centre of the plot because they are the deepest, but also have the least ice cover and the highest productivity. To the far right of the plot are the shallowest stations 5 and 6, which comprise the Hopen Group. Among the taxa that most explain the variance in the faunal distributions are the polychaetes *Prionospio cirrifera*, *S. typicus* and the brittle star *Ophiura robusta*, which were among the three most abundant taxa at the northern, southern and Hopen groups, respectively.

4. Discussion

Primary productivity (modelled) and ice cover clearly strongly influence the distribution and abundance of infauna in the Barents Sea. We found significant differences in the structure of the benthic assemblages in the northern compared to the southern regions of our study area. These differences appear to be related most strongly to the almost inverse relationship between estimated productivity and ice cover between the two regions. Both of these factors are predicted to be affected by global warming and the resulting reduction in ice cover. In this study, depth was not associated with lowered integrated water column productivity, because the deepest stations were located in the most productive Atlantic water masses. Conversely, the shallowest stations were located on a gravelly bank area, supporting a characteristic fauna and a high habitat-related diversity, but because of heavy ice cover in the area, the actual annual estimated productivity was not higher than in adjacent areas.

In marginal ice zone (MIZ) areas, seasonal ice-melting causes a pronounced vertical stratification, and a nutrient-rich euphotic zone develops, giving rise to an intensive phytoplankton bloom (Sakshaug and Skjoldal, 1989). Much of this material reaches the sea floor before it is consumed by zooplankton (reviewed in Carmack and Wassmann, 2006), and this pulse of fresh material reaching the benthos is thought to have a profound effect on benthic community structure in the

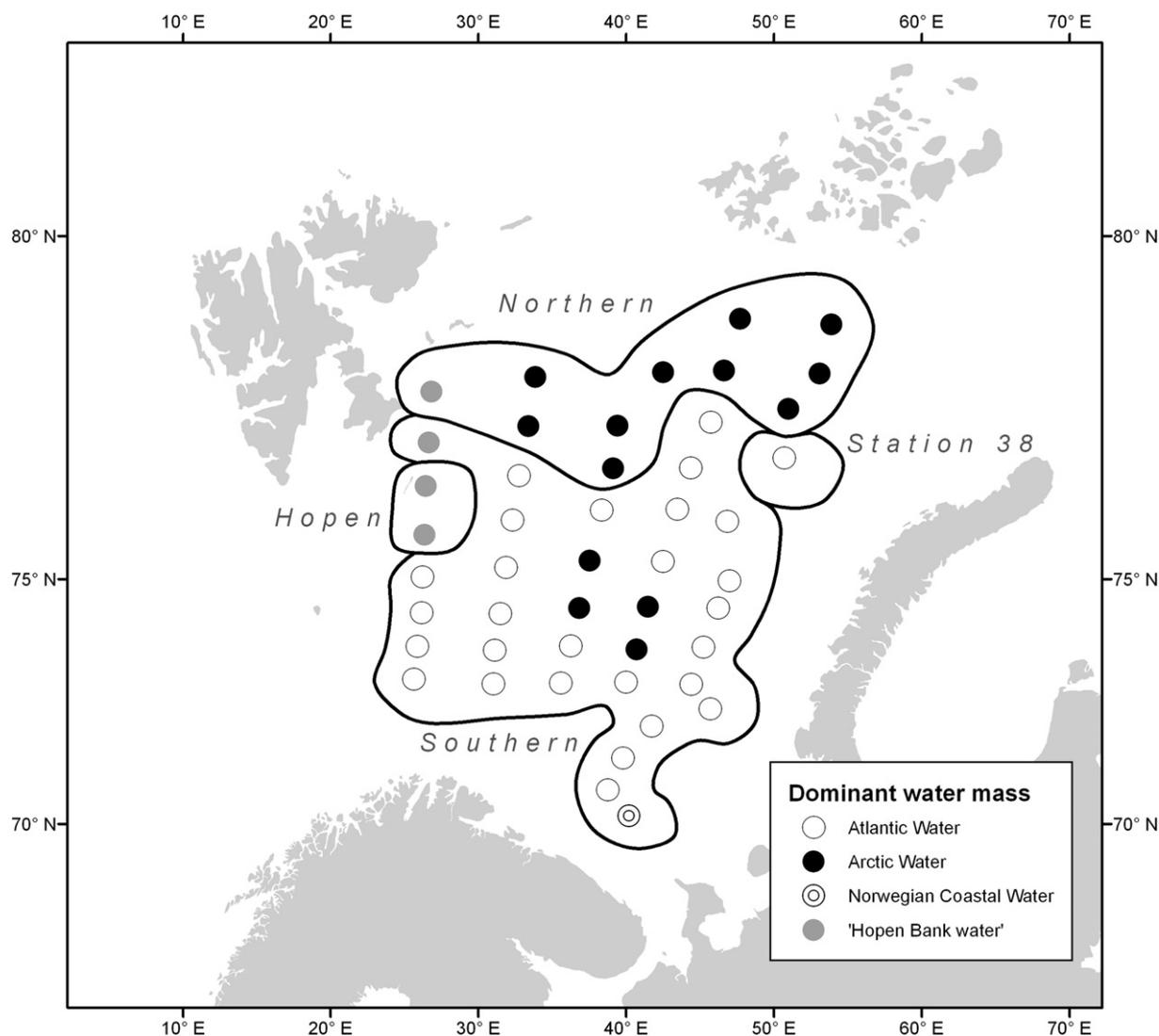


Fig. 3. Faunal groups (based on 35% similarity) and dominant water mass characteristics at the sampling stations. Note at most of the stations characterised as Atlantic Water (AW), there was some influence of Arctic Water (ArW) in the mid to upper water layers. Purely AW was only seen in the far south-western corner. In the north-eastern corner, and along the easternmost transect, there were various mixes of cooled and diluted water of Atlantic origin, combined with both ArW and Barents Sea Water (BSW).

Barents Sea, in particular an elevated biomass (Denisenko, 2004). We found no clear patterns in faunal abundance or diversity related to the MIZ, but analyses of biomass from this study, in relation to long-term historical data on benthos and ice distribution are ongoing (Denisenko et al., in preparation).

The relationship between primary productivity, or a proxy for productivity (e.g. benthic pigments), and benthic community structure has been documented across the Arctic. The amount of food reaching the seafloor on Arctic shelves is positively correlated with benthic abundance and biomass, with richer benthic communities supported by more potential food (Grebmeier et al., 1988; Ambrose and Renaud, 1995; Piepenburg et al., 1997; Carroll et al., 2008). Tight pelagic–benthic coupling means that highest biomasses are usually associated with more ice free areas. The relationship between productivity and both infaunal diversity and evenness is not as clear or as well studied as between productivity and abundance. In the western Barents Sea, Carroll et al. (2008) found a positive relationship between benthic pigments and infaunal diversity, while in the Chukchi Sea the pattern appears to be the opposite (Grebmeier et al., 1989). This may be due to the Chukchi Sea being considerably shallower than the Barents Sea (30–50 m instead of 150–400 m deep). Difficulty sampling the shallower areas of the Barents Sea due to the presence of very coarse sediments results in the two

studies not sampling comparable habitats. In both the Northeast Water Polynya (Northeast Greenland) and the Barents Sea, locations with lower primary production exhibited the greatest taxonomic richness of polychaetes (Ambrose et al., in press).

In our study, the northern faunal group was characterised by a relatively low faunal abundance and low taxon dominance, giving a generally high relative faunal diversity. Within the southern group, the faunal abundance showed some variation across the area, but on average was 48% higher than that of the northern group. The border between the northern and southern groups approximately corresponds with the northeastern limit of AW penetration (Figs. 1 and 3). This difference in water mass influenced the amount of ice cover between the two areas. Northern, ArW-influenced stations averaged 49% ice cover during the period 2000–2003, whereas the AW-influenced southern group stations showed a latitudinal gradient from almost no ice in the south to just under 40% in the northernmost part, but an average of less than 10%. There was also a clear gradient in modelled estimates of integrated water-column productivity, strongly inversely correlated with ice cover. The deepest, ice-free, AW-influenced areas in the southwest supported the highest productivity, whereas the most heavily Arctic Water (ArW) – and Barents Sea Water (BSW) – influenced area in the northeast was the least productive. Our

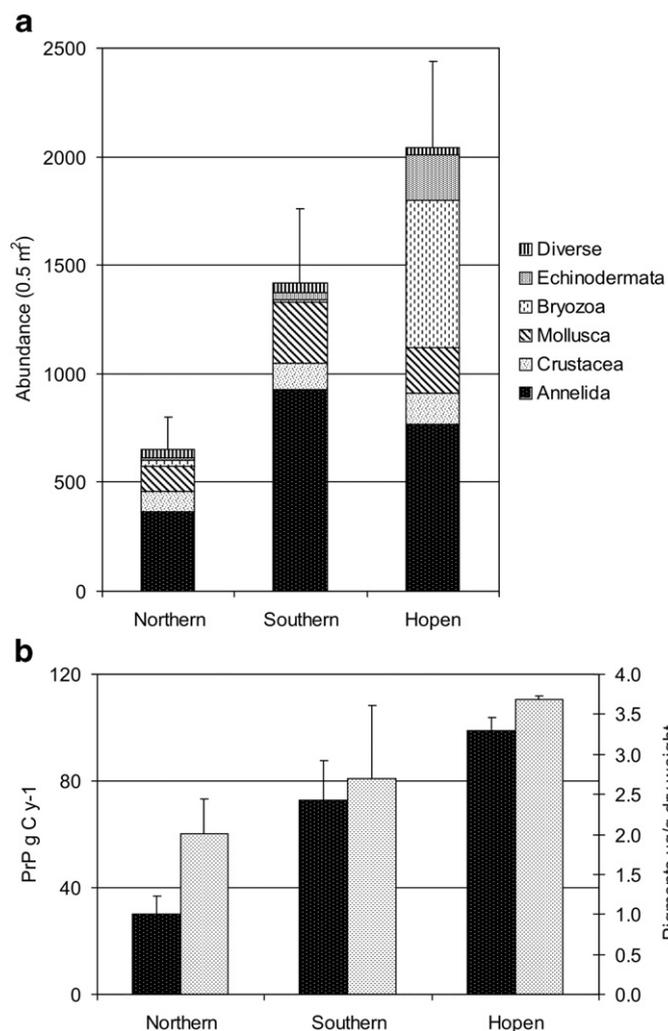


Fig. 4. Comparison of the three faunal groups in terms of a) Faunal abundance and relative contribution of the major taxa and b) modelled integrated water column productivity (PrP; dark bars) for averaged for 2002 and 2003 and benthic pigments (sum Chl-a and Phaeo-a; light bars). Error bars show standard deviations of the mean; those in a) refer to overall station abundances, not individual taxa. Despite apparent trends being similar in the two variables, PrP was significantly higher in the Hopen and southern stations relative to the northern stations ($P < 0.0001$) whereas there were no significant differences for pigments ($P > 0.3$).

findings of low faunal abundance in areas of heavy ice therefore agree with other studies in the Barents Sea in concluding that in northern parts, the fauna is food-limited and largely dependent on short bursts of food material reaching the bottom during the annual ice-melting

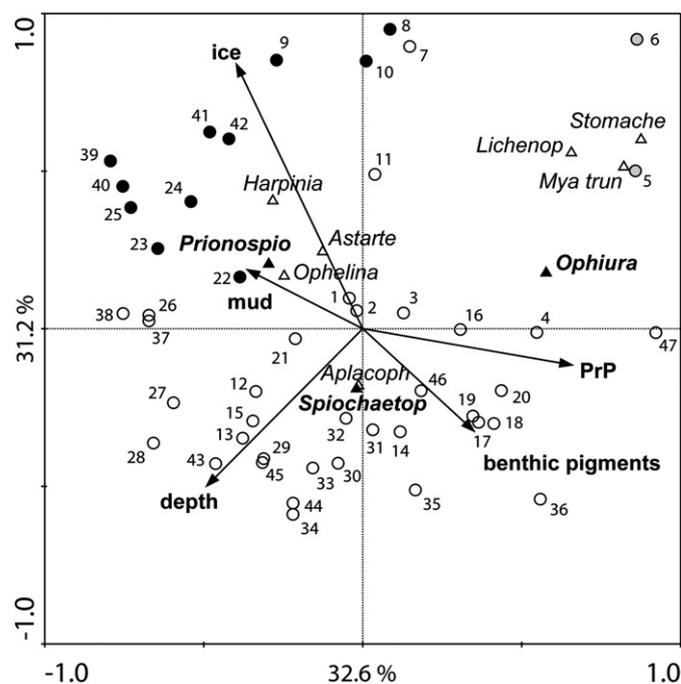


Fig. 5. Canonical Correspondence Analysis (CCA) showing the stations in relation to the environmental variables that significantly explain the faunal distributions, together with taxa for which at least 40% of the variance is explained on the first two canonical axes; bold type indicates those dominant at the three faunal groups. Station symbols relate to faunal groupings (filled black circles: northern faunal group, open black circles: southern faunal group and filled grey circles: Hopen stations). The % variance explained by the first two canonical axes is given on each axis; the length of variable vectors is proportional to its explanatory strength on axes 1 and 2. Full taxon names are as follows: Bryozoa: *Lichenopora crassiuscula*, *Stomachetosella*, Crustacea: *Harpinia mucronata*, Echinodermata: *Ophiura robusta*, Mollusca: *Aplacophora*, *Astarte montagui*, *Mya truncata*, Polychaeta: *Ophelina cylindricaudata*, *Prionospio cirrifera*, *Spiochaetopterus typicus*.

period (e.g. Zenkevich, 1963; Piepenburg et al., 1995; Carroll et al., 2008).

The benthic communities in the Barents Sea therefore appear largely to be influenced by the spatial extent of AW penetration into the bottom water. Bottom water distributions are relatively stable in relation to the more variable surface water such that the ArW/AW boundary is reflected in the faunal communities. In transitional areas, however, where the water masses are strongly modified, such as around Hopen and along the easternmost transect parallel with Novaya Zemlya, the overall productivity regime, as dictated by ice conditions, is of greater importance in determining faunal structure than water mass type. Therefore, the importance of integrated water column processes, primary productivity in particular, in determining benthic community structure should not be overlooked.

Table 3
Pearson's correlation coefficients for selected variables.

	Depth	Bottom temp	Ice cover	PrP	Mud	Benthic pigments	S	N	J'	ES (201)	H' (loge)
Depth	1.00										
Bottom temp	0.37	1.00									
Ice	-0.48	-0.37	1.00								
PrP	0.19	0.52	-0.68	1.00							
Mud	0.19	-0.11	0.21	-0.03	1.00						
Sediment pigments	-0.24	-0.35	-0.13	-0.23	-0.18	1.00					
S	-0.40	0.18	-0.19	0.47	-0.52	0.07	1.00				
N	-0.29	0.03	-0.44	0.40	-0.49	0.31	0.78	1.00			
J'	-0.15	-0.14	0.60	-0.25	0.25	-0.35	-0.25	-0.61	1.00		
ES (201)	-0.36	0.10	0.37	0.15	-0.18	-0.25	0.59	0.05	0.57	1.00	
H' (loge)	-0.38	0.02	0.40	0.12	-0.15	-0.28	0.49	0.00	0.71	0.93	1.00

Bold type indicates statistically significant correlations ($p < 0.05$). Abbreviations as for Table 1.

The Hopen stations supported 63% and 39% greater faunal abundances than both northern and southern faunal groups, respectively. High abundances and taxonomic richness at these stations is likely a function of the sediment heterogeneity. The Hopen stations have gravelly sediments mixed with mud and are influenced by shallow, tidally mixed water. They show both high faunal abundance as well as dominance by taxa typical for coarse sediments, such as brittle stars and encrusting organisms such as bryozoans. This area does not have higher productivity than the AW area in terms of annual water column productivity, but the rich fauna here may be a result of stronger currents supplying more food for the abundant suspension feeders present (see Sundfjord et al., 2007).

Benthic pigment concentration is one of the more reliable factors found to reflect benthic community structure and function on Arctic shelves (Ambrose and Renaud, 1995; Piepenburg et al., 1997; Dunton et al., 2005; Renaud et al., 2007b), and it usually is considered to be a proxy for water column productivity. There was a general trend for concentrations of sediment pigments to mirror spatial patterns in modelled productivity (Figs. 2 and 4), although the association was not statistically significant. The lack of a strong relationship between benthic pigments and productivity most likely is a result of the moving “productivity window” (Falk-Petersen et al., 2000; Hegseth and Sundfjord, 2008). Analysis of phytoplankton communities revealed a strong latitudinal gradient in timing of the spring bloom (K. Rokken Iversen/E. Nøst Hegseth, University of Tromsø, pers. comm.): the northern stations were still in bloom while the southern stations showed advanced post-bloom characteristics. Sampling some stations early in the seasonal phytoplankton cycle meant that we sampled before much of the annual productivity reached the seafloor. In this situation, primary production may be a better measure than benthic pigments for assessing the relationship between productivity and fauna. Neither type of measurement, however, considers the potential differences in export to the benthos, which probably also will vary geographically and temporally due to different zooplankton populations and advective processes present across the range of our sampling domain (e.g. Wassmann et al., 2006).

The northern, more food-limited stations showed a lowered faunal abundance and higher evenness relative to the more productive southern stations, which generally had higher abundances, but also higher dominance. This response of the benthic assemblages in the Barents Sea to differences in food supply is similar to that of lower latitude communities to organic enrichment. The classic response of infaunal communities to an increase in organic is an increase in abundance and a decrease in evenness resulting in a decrease in diversity (Pearson and Rosenberg, 1978). Considering that the differences in organic input among our stations are far less than typically is the case in studies of benthic organic enrichment, it is interesting that the same pattern prevails.

The distribution and structure of the faunal groups shown here generally are in agreement with the previously identified “northern” and “central” biocenoses in the Barents Sea (Brotskaya and Zenkevich, 1939; Zenkevich, 1963). The northern biocenosis was reported to be dominated in biomass by echinoderms, followed by molluscs, and with a lesser representation of annelids and other taxa. The southern biocenosis was dominated in almost equal proportions by molluscs, annelids and echinoderms, with lower amounts of crustaceans and other taxa. The more important role of annelids and low representation of echinoderms in our survey likely are explained by differences between numerical abundance versus biomass. Despite this inherent bias, some similarities in the station groupings remain. The Arctic bivalve *Astarte crenata* is one of the dominants in our northern faunal group, as it was in the previously described northern biocenosis. Our southern faunal group and the central biocenosis (Brotskaya and Zenkevich, 1939) share a dominance of the polychaetes *S. typicus*,

Maldane sarsi and *Galathowenia* (previously *Myriochele*) *oculata*. Most of the other taxa reported from the biocenoses (generally high-biomass low-abundance) also were present in our corresponding faunal groups, although not amongst the dominants.

Despite differences in faunal composition between the northern and southern areas, there was no typical Arctic fauna at the northern stations. Many of the taxa that were common at the northern stations also occurred at the southern stations, though their relative abundances in the two areas were different (Table 2). A few rare taxa (e.g. *Maldane arctica*) were unique to northern stations and may indicate Arctic conditions, but it is not possible to characterise a community as Arctic based on the dominants present. The lack of a typical Arctic fauna may make it more difficult to detect the impact of climate change without in-depth analysis of infaunal community composition.

Mesoscale oceanographic features have been found to influence benthic community structure in a variety of shelf habitats (Creutzberg et al., 1984; Josefson and Conley, 1997; Dewicke et al., 2002). In the western part of the Barents Sea, Carroll et al. (2008) found higher faunal density and taxon richness at stations located near the Polar Front (PF) relative to stations on either side. Our results suggest a similar pattern in the western part of the sampling area where the PF is relatively well-defined and stable (Loeng, 1991; Loeng and Drinkwater, 2007). Some of the stations close to the PF did not have the highest production, yet they supported some of the highest faunal abundances. This may support the hypothesis that it is not a high overall water column productivity that impacts the benthos in frontal or ice-edge areas, but enhanced food quality as a result of tighter pelagic–benthic coupling (see Carmack and Wassmann, 2006).

Our results indicate that the amount and timing of primary productivity, ice cover, and water mass distributions have a large impact on benthic communities on Arctic shelves. These drivers are likely to be altered by climate change. In the Barents Sea, a northward retreat of the area heavily influenced by ice, and a corresponding increase in primary productivity, likely will cause the northern area of low faunal abundance to shift even farther north towards the Polar Basin. Because current and historical studies characterise this northern fauna as having low biomass, such a shift will result in an overall increase in benthic biomass in the northern parts of the Barents Sea. A northern shift in the penetration of AW likely will make the area more similar in faunal structure and ecosystem function to the central and southern parts of the Barents Sea. The Barents Sea today supports an intensive commercial fishery, especially for cod, saithe and capelin, and a potential climate-driven increase in their harvestable areas is of obvious social and economic interest.

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