



Polychaete diversity patterns on two Arctic shelves: impacts of ice and primary production?

WILLIAM G. AMBROSE, JR.^{1,2,4}, PAUL E. RENAUD¹, SABINE K.J. COCHRANE¹, STANISLAV G. DENISENKO³ & JOFRID SKARÐHAMAR¹

¹ Akvaplan-niva, Polar Environmental Centre, N9296, Tromsø, Norway

² Department of Biology, Bates College, Lewiston, Maine 04230, USA

³ Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, St. Petersburg, 199034, Russia

⁴ Corresponding author. E-mail: wambrose@bates.edu

Abstract

We used data sets from two Arctic shelves to examine relationships between primary production (or a proxy), ice cover, and the diversity of polychaetes. Benthic samples were collected from the Northeast Water Polynya on the Northeast Greenland shelf and from the Barents Sea. Each of these areas is characterized by large differences in seasonal ice cover and primary production on a mesoscale. In addition to enumerating polychaete diversity, we also quantified the concentration of benthic algal pigments, sediment percent organic carbon, ice cover for the four years preceding sampling, and sediment grain size. In the Barents Sea, primary production was estimated from an ecosystem model. In both northeast Greenland and the Barents Sea, locations with lower primary production (Barents Sea) or proxies for primary production (benthic algal pigments: Greenland and Barents Sea), exhibited the greatest taxonomic richness. In Greenland, the area with the lowest concentration of benthic pigments had an $ES_{(201)}$ up to 30% higher than values from areas with four times more pigments. In the Barents Sea, $ES_{(201)}$ was greatest in the North under heaviest ice cover (>25% cover per year), again approximately 30% higher than in the South (<15% cover) or under the Polar Front (15–25% cover). Other factors also explained diversity: multiple regressions and Principal Component Analysis indicated that grain size, water depth and concentration of sediment organic carbon were important predictors of species diversity (Shannon-Wiener Index and Simpson's Reciprocal Index), but the results of these analyses were occasionally different from the patterns observed in the species accumulation curves or $ES_{(201)}$ values. Simpson's Index indicated that high ice-cover (and low primary production and benthic pigment) areas in the Barents Sea had greater evenness (lower dominance) than regions with higher indicators of food supply to the benthos. Low resource levels may prevent a few species from becoming very abundant and out-competing rare species. Diversity indices from northeast Greenland did not vary significantly among regions. We did not address habitat heterogeneity, but patchy distribution of food, combined with small-scale sediment heterogeneity also could enhance richness in food-poor areas. While the mechanism for the relationship between polychaete species richness and ice concentration or primary production is not clear, it does suggest that a change in polychaete diversity may need to be added to the list of possible responses of the benthos to climate-driven changes in ice cover.

Key words: Arctic, productivity, ice cover, Northeast Water Polynya, Barents Sea

Introduction

Ecologists have long been interested in the relationship between species diversity and primary

production (Rosenzweig & Abramsky 1993; Waide et al. 1999; Mittelbach et al. 2001; Gillman & Wright 2006). Despite numerous studies spawned by a renewed interest in this relationship, there is considerable controversy over the nature of the production-diversity relationship (Schmid 2002). Claims have been made that this relationship is unimodal, with the highest diversity at intermediate levels of production (Rosenzweig 1995), or linearly related, either positively (Gillman & Wright 2006) or negatively (Haddad et al. 2000). What appears more likely is that the form of the relationship is dependent on the taxonomic groups examined, scale (Waide et al. 1999; Mittelbach et al. 2001), history (Fukami & Morin 2003), level of disturbance (Kondoh 2001; Svensson et al. 2007), and the metric used to measure primary production (Thackeray 2007). In aquatic systems, the relationship does appear to be predominantly, though not exclusively, unimodal (Mittelbach et al. 2001). Many of the aquatic studies showing a unimodal relationship have examined primary production and invertebrate diversity, especially zooplankton in lacustrine systems (Dodson 1992, Dodson et al. 2000; Declerck et al. 2007).

A unimodal relationship between production and diversity is proposed for many systems because intermediate levels of production are hypothesized to favor the highest number of taxa. At low levels of production, only a few taxa can survive the limits set by low resources. As production increases, populations are larger and rarer species less prone to extinction (Huston 1994; Declerck et al. 2007). There is no consensus for the explanations of lower diversity at high production levels (Rosenzweig 1995): heterogeneity of resources may be reduced (Tilman 1982), competitive displacement may be more common (Huston 1994), and/or predation may be more intense than at lower levels (Steiner 2003). Under extreme eutrophic conditions, many aquatic species are excluded due to hypoxic or anoxic conditions on the seafloor (Pearson & Rosenberg 1978).

Tests of the productivity-diversity hypothesis involve both sampling across gradients in productivity (Rex et al. 2005) and manipulative experiments (Declerck et al. 2007). In marine systems, tests have involved sampling across the gradient of declining production accompanying an increase in water depth moving from the shelf to bathyal depths (Levin & Gage 1998; Rex et al. 2005). The one study explicitly examining the relationship between benthic diversity and primary production in the deep sea did not find a unimodal relationship and only a suggestion of increasing diversity with productivity (Glover et al. 2002). Few marine studies have examined changes in diversity across gradients on continental shelves (Brandt 1997; Starmans et al. 1999; Ellingsen 2001, 2002).

Arctic shelves offer an ideal system in which to test the productivity-diversity relationship for benthic communities for two reasons. First, annual phytoplankton production in the Arctic is directly proportional to the temporal extent of open water (Rysgaard et al. 1999), and ice cover is often variable on a mesoscale. Second, because of tight pelagic-benthic coupling, benthic biomass and community composition on Arctic shelves are, in part, a reflection of ice cover, with highest biomass associated with more ice free areas (Grebmeier et al. 1988; Ambrose & Renaud 1995; Piepenburg et al. 1997). Documented reductions in the thickness (Mclaren et al. 1992; Rothrock et al. 1999; Laxon et al. 2003) and aerial extent of sea ice (Johannessen et al. 1999, 2002; Serreze et al. 2003), and an increase in the number of ice-free days in seasonally ice-covered areas (Parkinson et al. 1999; Clarke & Harris 2003), all presumably in response to warming, have been postulated to have profound effects on the structure and function of the Arctic marine ecosystem (Gradinger 1995; Carroll & Carroll 2003; Renaud et al. 2008b). The effects of ice cover on the species diversity of benthic communities have received little attention.

We used two data sets to examine the relationships between primary productivity (or its proxy), ice cover, and the diversity of polychaetes. We chose polychaetes because they are numerical dominants in most Arctic soft-sediment shelf systems (Kendall et al. 2003), as well as world-wide

(Fauchald 1977). Further, polychaete assemblages are considered useful as environmental indicators (Giangrande et al. 2005). On the northeast Greenland shelf we sampled the area encompassed by the Northeast Water polynya, which offered the chance to sample areas of different ice cover, but otherwise generally similar depth and sediment type. The second data set was collected in the Barents Sea from the nearly ice-free Atlantic Water areas in the south, to heavily ice covered stations in Arctic Water to the north. In both areas we ask if the diversity of polychaetes varies with different ice cover and differences in water column production or a proxy for productivity, benthic pigment concentration, which may be more relevant for benthic organisms than phytoplankton production.

Materials and methods

Site descriptions. The Northeast Water Polynya (NEW) is a summer polynya off the northeast coast of Greenland (Parkinson et al. 1987). The NEW polynya varies in size among years, but lies between 77° and 81°N latitude and 5° and 15° W longitude and is bounded by the coast of Greenland on the west and the south-flowing East Greenland Current on the east. The polynya opens in the northwest corner in April or May and closes in September (Minnett et al. 1997). In some years, southern and eastern areas may experience no open water. The polynya is often centered over two shallow Banks, Ob and Belgica Banks. The larger of these two, Belgica Bank, is bounded on the north, south, and west by troughs with an average depth of 300 m and some depths exceeding 500 m. Fine sediments predominate in the trenches whereas coarse sediments characterize the banks, except in deeper depressions (Ambrose & Renaud 1995). For a more detailed description of the bathymetry and water circulation see Bourke et al. (1987) and Schneider & Budéus (1994).

The Barents Sea is a marginal sea located on the northern European continental shelf and open to the central Arctic basin to the northeast and the Norwegian and Greenland Seas to the west and covering 1.6×10^6 km² (Carmack et al. 2006). It is bounded by land on the south (continental land of Norway and Russia), east (Novaya Semlya), and north by the Svalbard and Franz-Josef Land archipelagos. The western boundary of the sea is considered to be a line between South Cape (West Spitzbergen) to North Cape (Norway) passing through Bear Island.

The bathymetry of the Barents Sea is complex. While the average depth of the sea is about 200 m, it is characterized by shallow (less than 50 m deep) banks and deeper (greater than 300 m) trenches (Wassmann et al. 2006a). The variability in depth is matched by variability in sediment grain size. In general, the deeper areas tend to be dominated by muds and fine sands, with an admixture of gravel in shallower areas, especially on the banks (Fredriksen et al. 1994).

The Polar Front is a well-known feature in the central Barents Sea (Loeng 1991; Wassmann et al. 2006a), and is the zone where relatively warm and saline Atlantic (> 0°C, > 34.8 psu) and cold, less saline Arctic (< 0°C, < 34.8 psu) water masses meet. The convergence of these two different water masses results in enriched pelagic and benthic communities (Denisenko 2002; Carroll et al. 2008), presumably due to higher vertical flux of fresh material to the sea floor (Carmack & Wassmann 2006).

Sampling. Samples from NEW were collected between June and August from the USCG vessel *Polar Sea* and the R/V *Polarstern* in 1992 (15 stations) and 1993 (13 stations) using a 0.25-m² USNEL Mark III box core (Fig. 1; Ambrose & Renaud 1995; Piepenburg et al. 1997). Macrofauna were subsampled from box cores with 8-cm-diameter x 15-cm-deep cores. Three to five replicates were taken from each box core and the contents sieved on a 500-µm-mesh sieve. Material retained on the sieve was fixed in 10% formalin, stained with Rose Bengal, and eventually sorted using a dissecting microscope at 25X magnification.

Samples from the Barents Sea (BASICC) were collected in August 2003 from the RV *Ivan Petrov* using a modified 0.1-m² van Veen grab. Five replicate samples were taken at each of 47 stations (Fig. 1). The large number of samples made the use of a box core for faunal sampling impractical and the use of a van Veen grab also made it possible to compare our results with earlier Russian studies. Sample stations were arrayed along five transects that ran from open water in the south to as far north as ice conditions would allow. The entire contents of a grab were sieved for fauna. The sampling and sample preservation procedures followed international guidelines (ISO 16665), except for the sieve type used (0.75-mm-square-mesh bag, compatible with previous Russian surveys). The different sieve mesh sizes used in NEW and BASICC mean that diversity between the two areas cannot be directly compared.

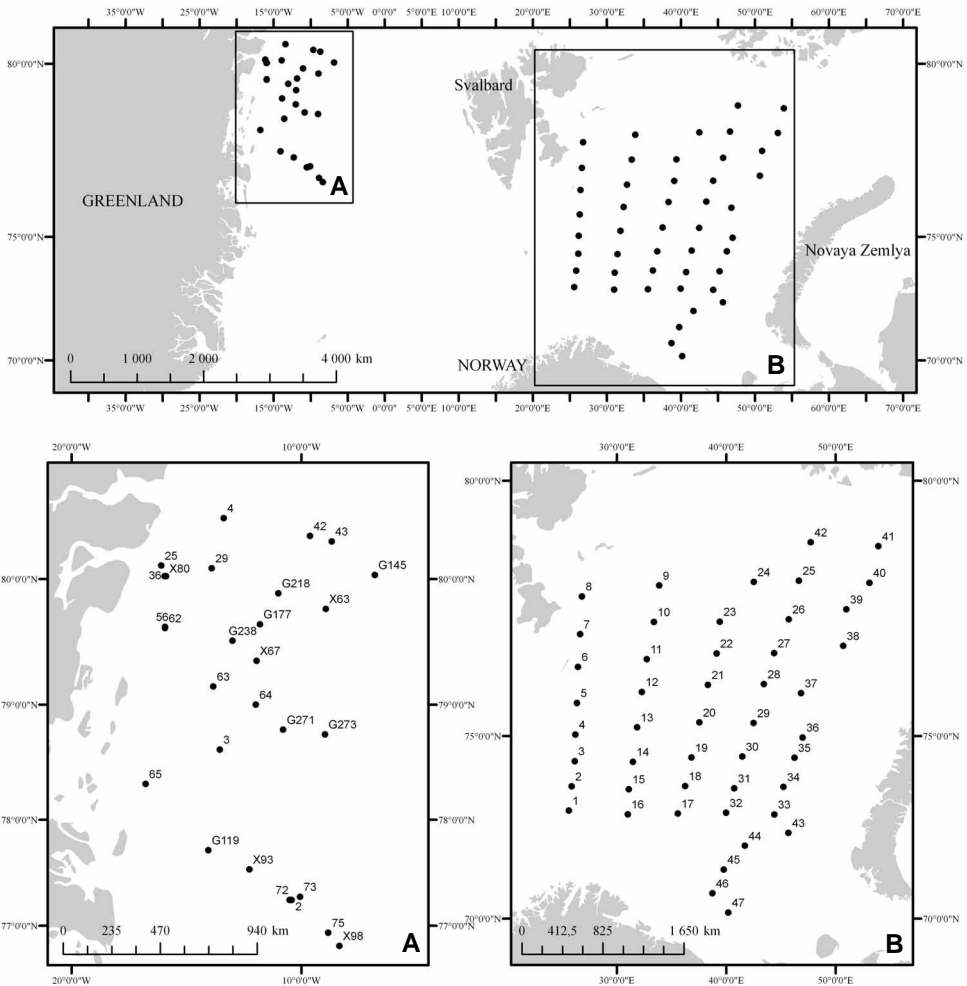


FIGURE 1. Sampling areas and station locations. A, off northeast Greenland; B, in the Barents Sea.

Sediment parameters. For NEW, benthic chlorophyll *a* and phaeopigments were determined from one subcore (1.9-cm inside diameter x 2 cm deep) taken from each box core. Pigments were extracted with 10 mL of 90% acetone for 23–25 hours in the dark at -20°C and concentrations determined fluorometrically using a method based on Holm-Hansen et al. (1965). One subcore was also collected from each box core for total organic carbon analysis. After acidification with 1 N HCL to remove calcium carbonate, the sediment was dried, homogenized, and run on a Control Equipment Corporation model 440 elemental analyzer using acetanilide as a standard. One final subcore (4.0 cm x 15 cm deep) was collected for sediment grain size. Samples were processed according to procedures outlined in Folk (1980), including pipette analysis for the silt/clay fraction.

In the BASICC program, we used a 0.25-m² box core to collect undisturbed sediment samples. Sediment for pigments (chlorophyll *a* and *b*, and their degradation products—phaeopigments) was collected from the top 1 cm of sediment, which was analyzed by the Norwegian Institute for Water Research (NIVA) using HPLC. Sediment for grain size analysis was also collected from the top 1 cm of the sediment and analyses carried out by dry sieving for the coarser fraction >0.063 mm and using a Sedigraph 5000 unit to analyze the finer fraction. Pigment and grain size analyses were conducted by GeoGruppen Analyse AS, Tromsø.

Ice Data. Sea ice data was obtained from the National Snow and Ice Data Center (Cavalieri et al. 2006). This data set is generated from brightness temperature data derived from Nimbus-7 Scanning Multichannel Microwave Radiometer (SMMR) and Defense Meteorological Satellite Program (DMSP) Special Sensor Microwave/Imager (SSM/I) passive microwave data at a grid cell size of 25 x 25 km (<http://nsidc.org/data/nsidc-0051.html>). For both NEW and BASICC, the grid cell matching the position for each station was identified, and monthly mean data from these grid cells were extracted from the database. The chosen periods were: for the NEW study area from 1990 to 1993 and for the BASICC area from 2000 to 2003. These periods were chosen to cover four years of ice coverage before sampling and covered the presumed life span of many of the polychaetes. Based on these data, the average ice concentration for the peak productivity season (May–October) was computed for each year and station.

Production. For BASICC we also had an estimate of primary production at each station. Integrated water column production for each of the stations was estimated using the SINMOD coupled physical-biological ecosystem model for the Barents Sea (Slagstad & McClimans 2005; Wassmann et al. 2006b). The annual production data were extracted from the 4x4 km pixel corresponding to each station for two years (2002, 2003) using realistic climate forcing functions (Ellingsen et al. 2008), and the results were averaged.

Faunal identification. Taxonomic determination was carried out to the lowest feasible taxonomic level, and recorded without reference to Linnean ranks (see the PhyloCode at <http://www.ohiou.edu/phylocode/>), as also was done for the BASICC data in Cochrane et al. (2009). Identifications were made by S. Gagaev, Zoological Institute, Russian Academy of Sciences, St. Petersburg (BASICC), and K. Sandøy, Bates College, Lewiston, ME USA (NEW). Within some identified taxa, two or more forms were recognized but not named, due to a combination of deviation from available taxonomic descriptions, uncertain taxonomic status in the available literature, or juvenile or damaged specimens. These are marked (*) in the appended taxon list. The nomenclature used for both data sets was standardized using the World Register of Marine Species (WoRMS; <http://www.marinespecies.org/>). Although names are used consistently within each study, issues of discrepancies in identifier practices between two independent studies always remain a problem for comparative analyses. Therefore, we minimize direct comparison of taxon richness between the NEW and BASICC data sets and focus mainly on comparing the relative trends within each of the two studies. Further, we make no assumptions of polychaetes as a proxy for macrofaunal diversity (see critique in Bertrand et al., 2006).

Statistical analysis. Polychaete abundances in sub-cores from each box core were averaged in the NEW study and then box cores treated as replicates and averaged for each station. In BASICC, the data from the five van Veen grabs at each station were pooled prior to statistical analysis. We averaged (pseudoreplicate) subcores in NEW because sample sizes among box cores were different. In BASICC we had the same numbers of grabs at each station, so averaging and pooling would produce the same index values. We ran analyses on single values for each station because we are interested in differences at the station (not grab or core) level, and this is the same scale at which the environmental parameters were measured.

The ice analysis revealed differences in ice cover between the Northern Trough, Southern Trough and Bank stations in NEW, which agreed with previous studies of ice coverage in NEW (Schneider & Budéus 1995; Minnett et al. 1997), and we used these characterizations in all statistical analysis (see Table 1 for station designations).

For comparisons of the BASICC stations, we separated the stations into three zones (Northern, Southern, and Polar Front). This grouping is based on a combination of several related factors. First, a 10-year average ice concentration (1992–2001) indicates that the zones correspond to approximately >25%, <15%, and 15–25% ice cover, respectively (Denisenko 2002). Secondly, they are associated with the water masses dominant in the respective zones: Atlantic Water dominating in the south, Arctic Water in the north, and a mix in the frontal area (Cochrane et al. 2009). Finally, the Polar Front is a persistent feature in the southern/central Barents Sea, and the stations we designated as ‘front’ stations correspond to the average annual position of the front (Loeng 1991, Falk-Peterson et al. 2000). Denisenko (2002) has also used this geographic distribution of sample sites in his investigation of benthic secondary production. We compared parameters from stations among these three regions (see Table 2 for station designations).

Species accumulation curves were generated for each of the different locations (Northern Trough, Southern Trough, Bank) within NEW and North, South and Polar Front within BASICC and for all the stations combined in each study using the EstimateS package (Colwell 1997). We also used Hurlbert’s rarefaction (Hurlbert 1971) to compare diversity among regions in both NEW and BASICC. This method calculates the expected number of species in a sample of n individuals. There were insufficient numbers to calculate $ES_{(n)}$ for individual stations, so we pooled samples among areas in NEW (Southern Trough, Northern Trough, and Bank) and BASICC (North, Sound, Front). These calculations also allow us to compare our polychaete diversity with diversity in other areas of the Arctic.

Shannon-Wiener diversity index (H' , based on natural log) and Simpson’s Reciprocal Index ($1/D$) were calculated for polychaete taxa at each station for NEW and BASICC using Biodiversity Pro. Simpson’s Reciprocal Index has been shown to be more sensitive than the Shannon-Wiener Index to changes in benthic community structure (Gray 2000). We used linear regressions to explore possible relationships between depth, sediment grain size, and diversity/evenness. We also compared differences in H' and $1/D$, depth, mean grain size, organic carbon, pigment concentrations, and ice cover among stations in different geographic areas (NEW) or with different ice cover (BASICC) using ANOVA after testing for homogeneity of variances (Sokal & Rohlf 1995). When necessary, data were transformed using a log transformation and re-tested. When an ANOVA was significant, we used the post-hoc Bonferonni test to determine differences between means.

We also used a multiple step-wise regression to examine linear relationships between H' and $1/D$ and environmental variables. Variables were included in the regression only if there was a suggestion from correlation analysis that they may explain a significant portion of the variability in diversity ($p < 0.15$).

TABLE 1. Northeast Water Polynya (NEW) station information. Abbreviations: Sta. (station), lat. (N. latitude) long. (W. longitude), location (geographic designation), Depth (water in meters), B-pig. (benthic sediment pigments, chlorophyll *a* and phaeopigments), Phi (mean grain size), 1/D (Simpson's Reciprocal Index), H' (Shannon-Wiener diversity index). Samples were collected between June and August in 1992 and 1993. ND = no data.

Sta.	Lat.	Long.	Location	Depth (m)	B-Pig. mg/m ²	Ice %	TOC %	Phi	1/D	H'
2	77.25	10.42	S trough	470	12.22	60.2	ND	6.954	7.00	0.845
65	78.32	16.78	S trough	505	7.22	82.1	0.61	6.952	8.10	0.975
72	77.25	10.51	S trough	490	10.6	60.7	0.68	6.947	5.67	0.885
73	77.28	10.05	S trough	355	8.92	60.7	0.95	6.576	11.34	1.233
75	76.93	8.83	S trough	363	8.82	54.7	0.63	6.135	10.63	1.090
X93	77.54	12.26	S trough	502	1.09	65.4	0.57	6.742	8.33	0.960
X98	76.8	8.34	S trough	348	3.89	50.1	0.9	6.334	9.39	1.055
G119	77.72	14.05	S trough	378	1.39	67.9	0.55	6.534	12.16	1.193
G177	79.65	11.8	S trough	326	6.52	64.3	0.7	6.802	4.71	0.990
G145	80.03	6.8	N trough	310	8.74	43.4	ND	ND	9.84	1.116
4	80.45	13.38	N trough	315	15.14	43.4	0.71	6.648	8.47	1.124
25	80.1	16.1	N trough	310	14.82	51.8	0.61	5.499	18.14	1.434
29	80.08	13.9	N trough	180	14.11	48.5	1.45	6.102	6.54	0.924
36	80.02	15.95	N trough	152	45.62	46.8	0.46	6.397	14.79	1.233
42	80.32	9.62	N trough	440	10.14	56.5	0.71	6.913	5.25	1.000
43	80.28	8.68	N trough	316	32.63	59.3	0.97	6.852	7.35	1.125
56	79.63	15.93	N trough	285	32.56	72.9	0.95	6.803	5.01	0.986
62	79.62	15.93	N trough	176	11.98	68.6	0.56	6.445	7.41	1.141
G218	79.89	11.0	N trough	320	19.47	75.0	ND	6.195	17.81	1.420
G238	79.52	13.0	N trough	229	61.39	79.6	ND	6.862	6.85	1.356
G273	78.75	8.97	Bank	169	24.07	70.8	0.59	5.076	14.29	1.318
3	78.62	13.55	Bank	150	11.39	69.4	0.53	5.602	18.88	0.976
63	79.15	13.83	Bank	125	26.16	46.8	0.75	6.443	6.25	1.432
64	79	11.98	Bank	217	46.86	60.2	0.68	6.101	19.61	1.465
X63	79.77	8.93	Bank	201	22.55	82.1	ND	6.316	19.62	1.248
X67	79.36	11.95	Bank	241	10.09	60.7	0.88	6.437	13.44	1.064
X80	80.02	15.89	Bank	425	16.31	60.7	0.65	6.679	7.11	1.142
G271	78.79	10.79	Bank	355	ND	54.7	ND	7.065	8.54	1.047

Finally, we also used Principal Component Analysis (PCA) (Canoco ver. 4.5), a multivariate ordination method, to explore the relationships between diversity (H' and 1/D) and environmental variables. Canoco allows environmental data and, in our case, diversity data to be plotted together by treating the diversity measurements as supplemental data that do not affect the ordination. The environmental variables used in the PCA were: ice cover, benthic pigments, TOC, water depth and sediment grain size (phi for NEW and pelite for BASICC), and for BASICC we also included modeled primary production. Diversity is then plotted into the ordination without affecting the weighting of the environmental variables. While some of these parameters are likely correlated, the

relationships between any two of these parameters are far from perfect. Even the typical depth-grain size relationship does not hold well for the Barents Sea ($r = 0.19$), where many northern areas are deeper and have lower pelite content (Table 2).

TABLE 2. Barents Sea (BASICC) station information. Abbreviations: lat. (N. latitude) long. (E. longitude), loc. (location relative to long-term ice cover, North > 25% cover, South < 15% cover, PF = Polar Front, 15–25% cover), Depth (water in meters), B-pig. (benthic pigments, chlorophyll *a* and phaeopigments), Ice (percent ice cover June–September 2001–2003), TOC (total organic carbon), Pelite (percent silt and clay), Prod. (primary production), 1/D (Simpson’s reciprocal index), H' (Shannon-Wiener diversity index). Samples were collected in August in 2003.

Sta.	Lat. (N)	Long. (E)	Loc.	Depth (m)	B-Pig. mg/m ²	Ice %	TOC %	Pelite %	Prod.		
									gC/m ² /yr	1/D	H'
1	73.1262	25.6272	South	425	0.18	0	1.76	88.9	121.3	4.13	2.573
2	73.7582	25.8763	South	459	1.08	0	1.78	65.4	100.1	19.92	3.172
3	74.3917	26.1683	PF	387	0.4	0.4	1.46	42.8	95.2	21.92	3.159
4	75.0338	26.2217	PF	218	3.63	6.3	2.39	61.6	76.6	16.85	2.36
5	75.7635	26.3607	PF	130	3.63	23.0	2.01	36.2	79.6	8.47	3.435
6	76.5562	26.4648	North	79	3.74	38.3	1.78	83.7	92.3	8.28	3.512
7	77.2343	26.6607	North	133	1.6	47.1	1.63	91.3	79.4	13.87	3.189
8	77.9773	26.8253	North	136	2.76	55.1	1.84	76.7	52.8	14.16	2.803
9	78.1858	33.8855	North	164	1.51	56.9	1.25	64.3	34.3	5.48	2.68
10	77.4792	33.3938	North	144	0.92	49.8	1.46	40.9	43	9.22	3.085
11	76.7185	32.7503	North	190	0.93	34.4	0.75	32.7	50	7.09	3.122
12	76.0102	32.3042	PF	323	3.28	14.6	2.31	82.7	56.2	7.88	2.46
13	75.2037	31.8597	PF	338	1.44	3.9	2.2	88.0	59.5	13.59	2.838
14	74.3772	31.4807	PF	260	2.12	0.02	1.77	59.3	65.8	6.85	2.983
15	73.6853	31.0980	South	374	0.48	0.01	1.71	82.0	68.3	6.50	2.885
16	73.0262	31.0103	South	279	0.51	0.01	1.26	54.6	101.2	5.29	3.184
17	73.0447	35.5818	South	224	3.17	0.1	1.75	53.8	67.8	4.65	2.86
18	73.7660	36.2557	South	245	4.66	0.9	1.29	61.9	65.3	8.03	2.578
19	74.4817	36.8368	PF	224	4.16	5.3	2.00	43.3	53.5	11.07	2.273
20	75.3193	37.5542	PF	169	4.63	11.4	2.13	35.5	46.4	7.16	2.29
21	76.1678	38.3477	PF	258	1.95	20.7	1.13	36.5	36	7.99	2.748
22	76.8392	39.1303	North	192	2.79	36.9	1.35	79.8	28.9	7.48	2.83
23	77.4857	39.4295	North	217	2.06	43.0	1.56	88.8	23	9.97	2.567
24	78.2508	42.5382	North	221	2.2	47.3	1.05	66.2	17.3	6.56	2.642
25	78.2762	46.6610	North	244	1.18	47.2	1.09	66.9	16.2	4.51	2.624
26	77.5325	45.7313	North	251	2.71	36.2	1.6	79.7	17.5	3.71	2.48
27	76.8443	44.3962	North	275	3.81	26.0	2.25	85.0	20.5	6.00	2.145
28	76.1818	43.4648	PF	342	2.96	16.6	2.16	71.5	25.5	7.39	2.157
29	75.3045	42.5082	PF	267	2.72	11.5	1.39	50.4	32	12.72	2.01
30	74.5042	41.4867	PF	208	2.73	8.4	1.31	53.4	39.7	8.63	2.287
31	73.7060	40.7472	South	295	3.56	5.1	1.68	54.0	48	9.64	2.454

.....continued

TABLE 2 (continued)

Sta.	Lat. (N)	Long. (E)	Loc.	Depth (m)	B-Pig. mg/m ²	Ice %	TOC %	Pelite %	Prod. gC/m ² /yr	1/D	H'
32	73.0647	39.9983	South	324	1.95	1.8	1.57	57.4	60.6	6.03	2.929
33	73.0217	44.4072	South	335	2.56	0.3	1.96	58.7	48.6	3.79	2.637
34	73.7415	45.2518	South	340	3.78	0.5	1.96	59.1	37.4	6.91	2.872
35	74.4757	46.2527	PF	243	4.33	3.1	0.43	17.0	31.8	5.58	2.605
36	74.9650	47.0032	PF	243	10.15	6.2	1.52	51.0	28.1	9.06	2.112
37	76.9958	50.7037	PF	349	2.66	32.3	1.45	47.4	21.1	10.93	2.404
38	77.7290	51.0025	North	225	2.11	39.5	1.69	82.2	14.7	17.72	1.879
39	78.2343	53.1197	North	305	1.11	49.7	1.07	61.3	14	11.03	2.666
40	78.8997	53.9292	North	241	1.46	51.4	1.29	69.1	11.8	6.57	2.723
41	78.9700	47.7498	North	254	3.62	54.5	0.99	67.3	12.4	5.95	3.228
42	75.9822	46.8593	North	268	2.54	49.7	2.18	41.5	15.7	9.48	2.862
43	72.5198	45.7058	South	284	3.14	15.2	1.68	52.8	49.6	6.67	2.682
44	72.1622	41.7267	South	286	2.65	0.01	2.25	80.8	60.7	10.22	2.461
45	71.4822	39.7998	South	365	1.86	0.1	2.75	76.8	64.9	4.13	2.746
46	70.7790	38.7498	South	233	0.51	0	1.2	53.7	83.7	19.92	2.74
47	70.1887	40.2060	South	145	2.5	0.02	0.47	17.4	94.7	21.92	2.934

Results

Northeast Water Polynya (NEW)

Ice conditions varied among the three regions in NEW. Between 1990 and 1993, Bank stations experienced an average 67.4% (SE= 3.5) ice cover from May–October. This value was significantly greater (Table 3) than that from either the Northern Trough (55.8%, SE= 2.9) or the Southern Trough (62.9%, SE= 3.0), which were not significantly different from each other. Though not considered in the ice coverage analysis, ice in the Southern Trough was thicker than ice on the Bank or in the Northern Trough (WGA, pers. obs.). It was not possible to sample very coarse sediment in the shallow areas of the Northeast Water Polynya using the box core; sampling was, therefore, limited to finer sediments in the deeper areas of the central Bank. This limitation had the effect of sampling similar depths and grain size in all areas (Tables 1–2).

Cores in NEW sampled approximately 2 m² and collected 1797 polychaetes representing 177 taxa (Appendix 1). The species accumulation curve shows no indication of reaching an asymptote (Fig. 2A). Individual species accumulation curves for the three regions indicated that polychaete species richness was slightly higher in the Southern Trough compared to the Bank and Northern Trough (Fig. 2B). The pooled ES₍₂₀₁₎ value for the Northern Trough was lower (53.0) than values for either the Bank (64.6) or Southern Trough stations (69.89).

While the species accumulation curves and ES₍₂₀₁₎ values suggested differences in richness among the three regions, there was no significant difference in the Shannon-Wiener diversity index, H' (Table 3). The index was slightly lower in the Southern Trough (1.025, SE= 0.044), than in the Northern Trough (1.169, SE=0.052) or the Bank (1.212, SE=0.065). There was also no difference in 1/D among areas (Table 3). The index was similar for the Northern Trough (Mean = 9.77, SE= 1.46) and Southern Trough (Mean = 8.59, SE= 0.846), but higher on the Bank (Mean = 13.48, SE=1.99).

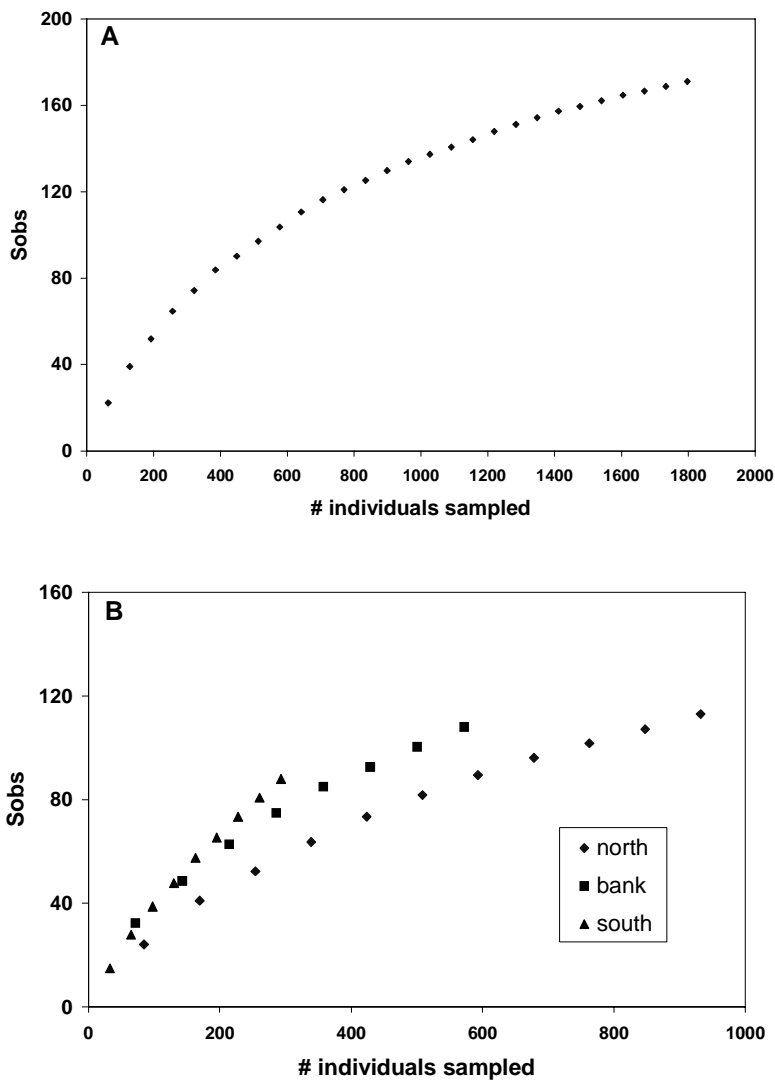


FIGURE 2. A, Species accumulation curve for polychaetes from 28 stations in the North East Water Polynya, East Greenland Shelf; B, species accumulation curves for polychaetes from three regions in the North East Water Polynya: Northern Trough, Bank, and Southern Trough.

There were differences among the three regions in physical and biological conditions. Despite our efforts to sample similar depths in each region, the mean depth of stations in the Southern Trough (415.2 m, SE=24.8) was significantly deeper than stations on the Bank (235.4 m, 36.8) or in

the Northern trough (275.2 m, SE=25.4), which were not significantly different from each other (Table 3). There was also a significant difference in the mean concentration of benthic pigments among the three regions, with the concentration of pigments in the Southern Trough (6.74 mg/m², SE= 1.4) lower by a factor of four than in the Northern Trough (24.24 mg/m², SE=5.1) and Bank (22.49 mg/m², SE=4.7), which were not significantly different from each other (Table 3). Despite the difference in depth between the stations in the Southern Trough and those on the Bank and in the Northern Trough, there were no differences in the mean grain size among these regions (Table 3).

TABLE 3. ANOVA tables for (A) NEW (NT= Northern Trough, ST = Southern Trough) and (B) BASICC (South = less than 15% ice cover over 10 years, PF = 15–25% ice cover, North = greater than 25% cover). Pair-wise comparisons between means were made using the Bonferonni post hoc test when an ANOVA was significant (Bold face; p<0.05) and differences are significant at p<0.05. NS = not significant (p> 0.05).

A.				
Variable	F-value	df	p-value	Multiple comparisons
Ice cover	3.52	2.25	p < 0.04	NT, ST < Bank
Depth	9.79	2.25	p < 0.0001	ST > NT, Bank
Benthic pigments	10.77	2.24	p < 0.0001	ST < NT, Bank
Grain size (phi)	1.46	1.46	p > 0.2 (NS)	NS
Organic carbon	0.34	2.19	p > 0.7 (NS)	NS
H' diversity	3.13	2.25	p < 0.06	NS
1/D	2.68	2.25	p < 0.08	NS
B.				
Variable	F-value	df	p-value	Multiple comparisons
Ice cover	145.6	2.44	p < 0.001	South < PF < North
Depth	7.88	2.44	p < 0.0001	South > North
Productivity	11.31	2.44	p < 0.001	South > PF, North
Benthic pigments	7.47	2.44	p < 0.05	South, North < PF
Grain size (pelite)	3.88	2.44	p < 0.03	PF < North
Organic carbon	1.23	2.44	p < 0.30	NS
H' diversity	2.15	2.44	p < 0.129	NS
1/D	3.62	2.44	p < 0.04	North > PF

For NEW, only mean grain size (p<0.001) entered the step-wise multiple regression and explained 51% of the variability in H' indicating that the Shannon index increases with an increase in grain size.

$$H' = -0.244 (\text{phi}) + 2.68$$

In the second multiple regression, benthic pigments (p<0.03) along with water depth (p<0.003) and organic carbon (p<0.03) together explained 47.6% of the variability in Simpson's Reciprocal Index (1/D):

$$1/D = -0.03 (\text{depth}) + 8.9 (\text{organic carbon}) - 0.157 (\text{B-pig.}) + 16.26$$

The first two axes of the PCA explained 62.1% of the variability in the environmental data (Fig.

3A). Diversity as measured by Shannon-Wiener (H') is strongly related to benthic pigment concentration and was negatively related to water depth and grain size (ϕ). Interestingly, the PCA indicates that ice cover was not related to benthic pigments or diversity. The results are very similar when Simpson's Index ($1/D$) is used instead of the Shannon-Wiener index.

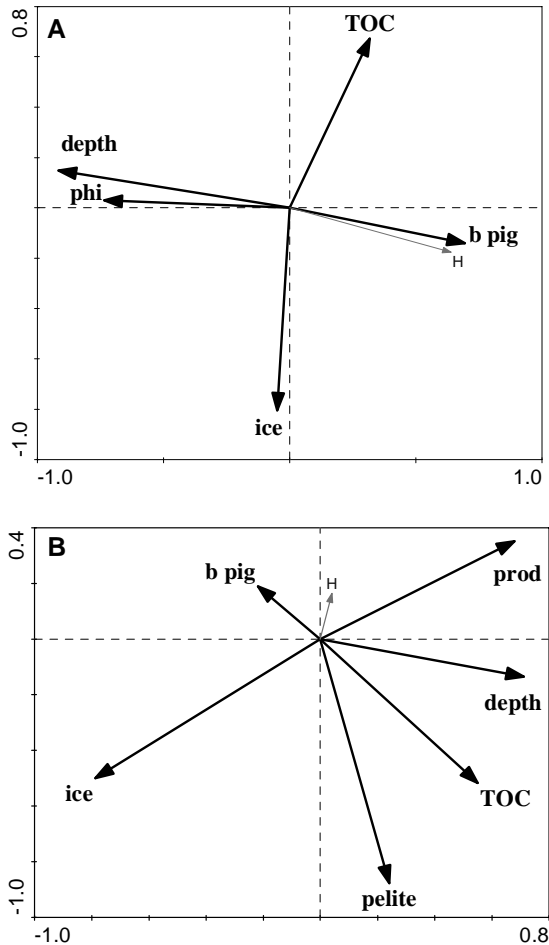


FIGURE 3. Graphical representation of the results of the Principle Components Analysis for (A) NEW and (B) BASICC environmental variables. The Shannon-Wiener diversity index (H') was entered as a supplemental variable in each analysis and is indicated by a grey vector. The first two axes explain 62.1% and 57.6% of the variability in the data for NEW and BASICC respectively.

BASICC

May through October ice conditions for 2001–2003 agreed with the longer-term ice data and other parameters used to classify stations in BASICC. Southern stations had a mean ice coverage of 1.6% ($SE=1.0$) for May to October in the four years preceding the study, while Northern stations had an average of 44.9% ($SE= 2.1$) coverage and Polar Front stations had a mean ice coverage of 10.9% ($SE=2.4$). Mean ice cover was significantly different ($p<0.001$) among all areas (Table 3).

Grab sampling covered approximately 24 m² at the 47 BASICC stations and collected a total of 36,240 individual polychaetes from 158 taxa (Appendix 1). The species accumulation curve for all BASICC stations showed no indication of reaching an asymptote (Fig. 4A). More polychaete species were collected from the 17 Northern stations under heavier ice cover compared to areas with less ice for a similar number of individuals sampled (Fig. 4B). For Northern stations, 125 species were collected for 6,765 individuals compared to 115 species for 11,746 individuals from Southern stations and 123 species for 17,729 individuals from stations under the Polar Front. The calculation of $ES_{(201)}$ revealed the greatest richness of polychaetes under the heaviest ice cover in the North ($ES_{(201)} = 53.3$) compared to $ES_{(201)}$ values of 42.4 and 38.9 for Southern and Polar Front regions, respectively.

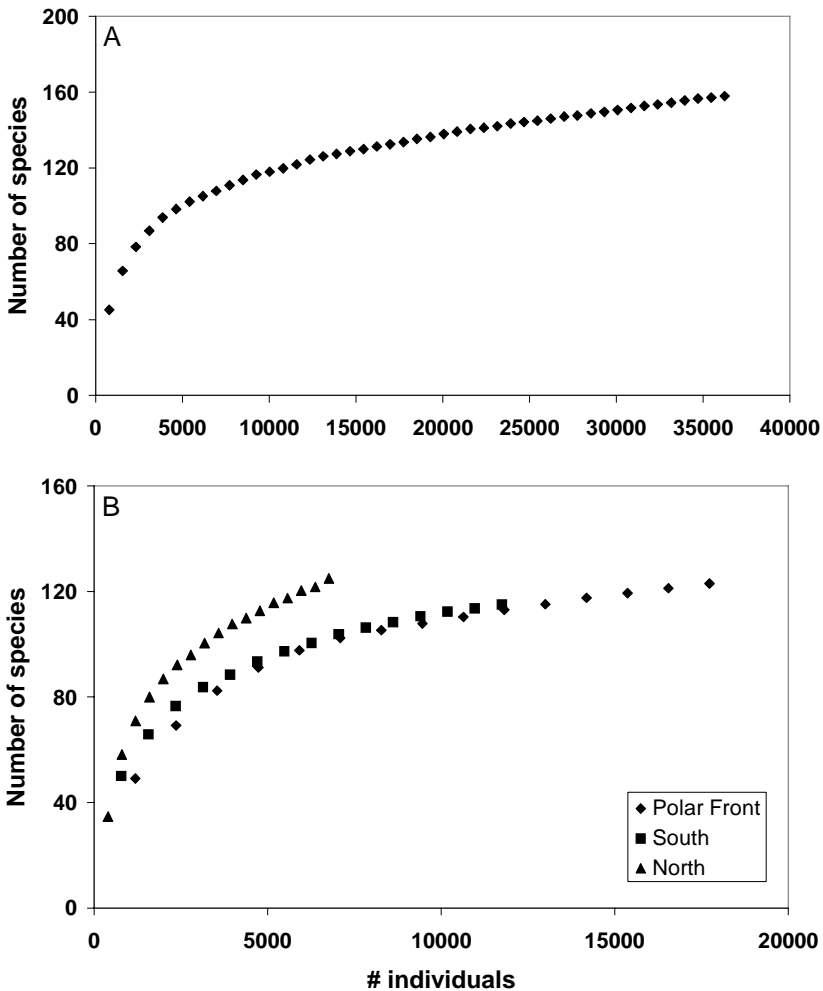


FIGURE 4. A, Species accumulation curve for polychaetes from 47 stations sampled as part of the BASICC project in the Barents Sea; B, species accumulation curves for polychaetes from three regions (North, Polar Front, and South) in the BASICC project area (see Table 2 for designations).

Even though the species accumulation curves suggested greater species richness in areas with the greatest ice cover, there was no significant difference in H' among areas (Table 3). Mean H' was very similar between Northern (2.767, SE=0.097), Polar Front (mean = 2.781, SE=0.058), and Southern regions (mean=2.541, SE= 0.197). There was, however, a significant difference in 1/D among regions (Table 3). The Northern region with more ice had a significantly higher index (Mean = 11.06, SE= 1.09) than the Polar Front region (Mean = 7.15, SE = 1.09) while the index (Mean = 9.22, SE= 0.91) in the South was not significantly different from either of the other two regions.

There were differences in the depth of stations ($p < 0.001$) and the percent fine sediment (pelite) among the regions (Table 3). Northern stations were significantly shallower (mean depth = 208.2 m, SE= 14.7) compared to Southern stations (Mean=307.5, SE=20.9) while Polar Front stations had a mean depth of 263.9 m (SE=18.5) which was not significantly different for the other two areas. Northern stations also had a greater proportion of pelite (fine sediment) (Mean=69.3%, SE=4.2) than Polar Front stations (Mean= 51.8%, SE= 4.6), while fine sediment was not significantly different between these two regions and the Southern stations (Mean=61.2%, SE=4.4).

Differences in the concentration of benthic pigments among the regions were marginally significant (Table 3). There was no difference in benthic pigment concentration between the Southern and Northern stations (mean=2.17, SE=0.36, and 2.18, SE=0.23, respectively), but these concentrations were less than at the Polar Front stations (mean= 3.39, SE=0.564). This marginal difference in benthic pigments was not reflected in the amount of total organic carbon among the regions, which was not significantly different and varied over a small range from 1.46% at stations in the north to 1.71% at stations under the Polar Front (Tables 2–3).

Productivity among the three regions was significantly different (Table 3). Southern stations from the area had significantly higher mean annual productivity (mean=71.48, SE=6.14) than stations from the Polar Front (mean= 48.80, SE=5.73) or the North (mean=31.99, SE=5.86).

For BASICC, only productivity and ice cover entered the multiple regression, and explained 48.6% of the variability with p -values for both predictors significant at 0.001.

$$H' = 0.019 (\text{prod}) + 0.001(\text{ice}) + 2.18$$

The results were similar for the multiple regression with 1/D, with 43.4% of the variability in 1/D explained:

$$1/D = 0.112 (\text{prod}) + 0.149 (\text{ice}) + 5.72$$

p -values for both variables were less than 0.0001.

The first two axes of the PCA explained 57.6% of the variability in the data (Fig. 3B). The Shannon-Wiener diversity index (H') was most closely associated with benthic pigments, as in NEW, and with modeled primary productivity. The diversity vector, however, is small, indicating that the first two axes of the ordination based on environmental variables do not explain much of the variation in diversity. As in NEW, there was no relationship between benthic pigments and ice cover, but modeled primary productivity is highly negatively correlated with ice cover. We also included Simpson's Reciprocal Index (1/D) in PCA for each area and the results were very similar to H' .

Appendix 2 shows the 10 numerically dominant and frequently occurring taxa at each of the three locations for the Northeast Water Polynya (NEW) and the Barents Sea (BASICC) data sets. The overall top dominant taxa comprised 15.6–20.2 % of the total individuals present in the NEW area, and 9.9–23.5 % in the BASICC area. At the NEW Northern trough and Bank locations, only four of the numerically most abundant taxa also were among the most frequently occurring (present at 80% or more of the stations). For the Southern trough, none of the taxa were present at more than 78% of the stations.

Discussion

Polychaete species richness patterns on the continental shelves of the Barents Sea and of northeast Greenland indicated that these two communities were distinct, but may well be structured by similar processes. While neither shelf area came close to reaching asymptotes on their respective species accumulation curves, and total polychaete richness was similar, it took 10 times the area and 20 times the number of individuals sampled to achieve similar taxon richness in BASICC as for NEW. Mechanistically, however, they were remarkably similar in that regions with lower primary productivity (Barents Sea) or proxies of primary productivity (benthic pigments, Northeast Greenland and Barents Sea), and highest ice concentration (both sites) exhibited the greatest taxonomic abundance as indicated by both species accumulation curves and $ES_{(201)}$.

In support of NEW and the Barents Sea having distinct community compositions, only *Maldane sarsi* was a numerical dominant at all locations in both datasets. Four taxa were dominant across all the NEW locations: *Prionospio cirrifera*, *M. sarsi*, *Aricidea quadrilobata*, and *Eclysippe vanelli*. All of these taxa display some extent of vertical particle transport or diffusive mixing behavior (see Pearson 2001). For BASICC, *Spiophanes kroeyeri*, *Galathowenia oculata*, *Spiochaetopterus typicus*, and *Heteromastus filiformis* were common dominants, all of which all of which are “conveyor-belt” particle transporters. *Prionospio cirrifera*, which was among the overall dominants at all the NEW locations, was dominant only at the Northern location in BASICC. Conversely, *Heteromastus filiformis* and *Galathowenia oculata*, which were dominant at all BASICC locations, were dominant only at the NEW North and Bank locations, respectively. *Chaetozone setosa* dominated at the NEW North and Bank locations, reminiscent of the BASICC Polar Front location, which was dominated by unidentified species of *Chaetozone*.

There is striking similarity in species richness on Arctic shelves, although it appears to be a little lower in the Laptev and Beaufort Seas than in other areas (Curtis 1975; Stewart et al. 1985; Grebmeier et al. 1989; Kendall & Aschan 1993; Kendall 1996; Włodarska-Kowalczyk et al. 1998; Sejr et al. 2000; Sirenko 2001; Steffens et al. 2006; Renaud et al. 2007a). Considering polychaetes alone, of 796 taxa recorded from all the Russian Arctic seas, a total of 341 records were from the Barents Sea, 181 and 174 from the Chukchi Sea and Kara Sea, respectively, whereas only 114 are recorded from the Laptev Sea (Zoological Institute, St. Petersburg Census of Marine Life project; available at www.zin.ru/projects). In fjords, the estimated number of species for 201 individuals ranges from 28 in Svalbard to 52 in Greenland. The range of $ES_{(201)}$ values in our study also varied by approximately a factor of two: 53–70 in NEW and 39–53 in BASICC. An $ES_{(201)}$ value calculated for only polychaetes is not directly comparable to one calculated for an entire community, but compared to the few other Arctic studies that have calculated $ES_{(201)}$, it appears that shelf communities are, perhaps not surprisingly, more diverse than fjord communities.

Diversity indices, as opposed to species richness, incorporate both richness and dominance (or its opposite, evenness). Only Simpson’s reciprocal index ($1/D$) was significantly different among regions and only in the Barents Sea (Table 3). A lower $1/D$ index indicates greater dominance, in this case where food supply (benthic pigments) is the greatest (Polar Front), and greater evenness where food supply is lowest (North). Primary productivity did not differ significantly between the North and the Polar Front, although it was more than 50% greater at the Polar Front than in the North. These results are consistent with the general picture of the Polar Front region in the Barents Sea as one of enhanced vertical flux of fresh phytodetritus, but not necessarily higher primary productivity (Wassmann et al. 2006).

The initial picture from the study of richness and diversity indices, then, suggests higher richness in areas of lower food supply. Cochrane et al. (2009) found higher macrofaunal diversity and

evenness, but lower faunal abundance, in areas with high ice cover and lower annual primary production. Total infaunal abundance and polychaete biomass have also been found to correlate positively with benthic pigments in NEW (Ambrose & Renaud 1995; Piepenburg et al. 1997). When only the southern and western Barents Sea is considered, diversity patterns are different from the present results: species richness and abundance is positively correlated with benthic chlorophyll in the Barents Sea (Carroll et al. 2008). These results suggests that some taxa, most likely including some polychaete species, respond to food inputs at the population level by increasing in numbers (and perhaps size), and that benthic pigments are a good measure of food supply for what is largely a deposit-feeding polychaete assemblage. Long-lived Arctic benthos, thus, integrate the productivity signal from the pelagic zone, with consequences for richness and diversity patterns.

Multivariate analysis (PCA) from both BASICC and NEW yielded similar results. Both showed no relationship between H' (or $1/D$) with ice cover or TOC, and both also indicated a negative relationship between diversity and grain size (higher diversity in coarser sediments). The food-supply variables primary production and benthic pigments (BASICC) and benthic pigments (NEW) were positively correlated with diversity, though the relationship was weak in BASICC (Fig. 3).

Using benthic pigments as a proxy for production, however, is valid only if the samples are representative of relative differences in *annual* deposition of food. Since Arctic benthic fauna are capable of rapid consumption of fresh organic material when it reaches the seafloor (McMahon et al. 2006; Renaud et al. 2007b, 2008a), this prerequisite may not be satisfied for all our sampling stations in each shelf area. Unsynchronized peaks in primary production among stations in the region result in our sampling probably missing the annual pulse of material to the benthos at some sites by sampling either too early or too late. While we were able to identify strong patterns in benthic pigments among regions in NEW (4-fold higher in Northern Trough and Bank compared to Southern Trough) and BASICC (a 60% difference), it is likely that ours is only a rough estimate of relative productivity differences. The PCA from BASICC highlights this, as modeled annual production and one-time measurements of benthic pigments were uncorrelated (Fig. 3B)

Studies of polychaete diversity in the deep sea have found weak evidence for an increase in diversity with productivity in the abyssal Pacific (Glover et al. 2002), a positive correlation between polychaete diversity and meiobenthic abundance, a food proxy, along a shelf to deep sea transect in the Gulf of Mexico (Haedrich et al. 2008), and a parabolic response, highest diversity at intermediate levels of productivity, in the tropical northeast Atlantic (Cosson-Sarradin et al. 1998). Patches of deep-sea sediment enriched with food have been found to support higher densities but lower diversity than unenriched patches (Snelgrove et al. 1992). Levin et al. (2001) suggest that food input, bottom flow, bottom- water oxygen levels, sediment heterogeneity, and ecological disturbance are the five most important factors determining deep-sea benthic diversity. It is likely, therefore, that a suite of biotic and abiotic factors contribute to diversity patterns in soft sediments (Glover et al. 2002).

In shallow water and on shelves there is often only a weak relationship between natural food enrichment and species diversity (see review by Quijón et al. 2008). Surprisingly few studies have experimentally examined the relationship between quality and quantity of phytodetritus and soft-sediment community structure in shallow water and shelf systems. At 20 m depth on a boreal shelf, Quijón et al. (2008) found a decrease in diversity in response to experimental addition of phytodetritus, but the response was short lived and seasonally dependent. The rapid utilization of fresh phytodetritus at high latitudes (e.g., Renaud et al. 2008a) may make it hard to examine the relationship between diversity and food on a small scale; larger mesoscale patterns of diversity and food input may provide a clearer picture.

Results from multiple regressions indicate that other environmental variables are important in

explaining diversity patterns on the two Arctic shelves we studied. In NEW, half of the very low among-station variability in H' was explained by sediment grain size (higher diversity where coarser sediments were found), and this result was supported by the PCA (Fig. 3A). For BASICC, the regressions indicated that diversity was positively correlated with both ice cover and productivity, a finding that contradicts earlier results and the general understanding of the system as having higher productivity under the lowest ice cover regime (Wassmann et al. 2006a). It is important to understand, however, that these regressions are not based on regions, but on individual stations, and that components entering the regression need not correlate with each other. For example, the two different components of H' , richness and evenness, may be influenced by separate factors (ice cover and productivity, respectively), even though these factors may be unrelated or negatively related to each other.

The importance of sediment parameters to benthic community structure is well described (Gray 1974, 1997; Pearson & Rosenberg 1978). The manner in which fauna are impacted by sediment characteristics varies, but factors such as depth, grain size, organic carbon, and bottom currents are often strongly intercorrelated (but see comment above regarding the lack of a strong relationship between depth and % pelite in the Barents Sea stations). In Arctic waters, metazoan diversity has been shown to be either invariant (Weissappel & Svavarsson 1998; Renaud et al. 2006), negatively correlated with depth (Bluhm et al. 2005), peaking at intermediate depths (Kröncke 1994) or reduced in shallow water (Steffens et al. 2006). Most Arctic studies of benthic diversity, however, examined patterns over a much wider depth range than our sampling in NEW and BASICC.

Few hypotheses have been posited to explain Arctic benthic diversity patterns, however. Grebmeier et al. (1989) attributed differences in diversity among areas in the Northern Bering and Chukchi Seas to differences in food supply, sediment heterogeneity, and temperature. They found lower H' diversity under the more productive water masses, but also higher diversity where there was warmer water and more heterogeneous sediment. In studies of Young Sound, East Greenland (Sejr et al. 2000) and Spitzbergen fjords (Włodarska-Kowalczyk et al. 1998; Włodarska-Kowalczyk et al. 2007), patterns of diversity do not appear to be related to any specific environmental factor; though habitat heterogeneity is often invoked as a causative factor it is rarely quantified. Finally, Renaud et al. (2006) suggest that unspecified ecological factors may be driving diversity patterns in macrofaunal communities along a transect from the shelf to the North Pole.

Diversity patterns, where they can be documented, appear to be difficult to explain. Disturbance from iceberg scour has been implicated in determining large-scale patterns in polychaete assemblages in the Antarctic (Kröger & Rowden 2008), but there is no evidence of physical disturbance from recent iceberg scour in photographs taken at the depth of our stations on the Greenland shelf (Piepenburg & Schmid 1996; pers. obs.), and the modern icebergs in the Barents Sea are not large enough to scour at the depths we sampled. Instead, our results suggest food supply (a proxy of primary production on these Arctic shelves) and sediment characteristics may be important in determining richness and diversity patterns of polychaetes. Richness is highest at the lowest levels of productivity on both the Greenland shelf and in the Barents Sea. Low resource levels may prevent a few species from becoming very abundant and out-competing rare species, as suggested by increased dominance and reduced $1/D$ indices in BASICC, and cited increases in abundance under areas of higher pelagic production in NEW. Habitat heterogeneity was not addressed by our study, but patchy distribution of food, combined with small-scale sediment heterogeneity, could also enhance richness. While the mechanism(s) for higher polychaete species richness under greater ice concentration or lower productivity is not clear, it does suggest that a change in polychaete diversity may need to be added to the list of possible changes to the benthos as a consequence of climate change induced changes in ice cover (Renaud et al. 2008b).

Acknowledgements

This work was supported by grants from the National Science Foundation (DPP-91-13756) under the Arctic Systems Science Initiative, the Research Council of Norway (contract 152798/730), Norsk Hydro (contract 5341794), Akvaplan-niva and the Zoological Institute, St. Petersburg (ZIN). We thank Ingrid Ellingsen for providing model output for productivity data, Rune Palerud and Chris Emblow for fauna database work, the latter also for creating the station maps. We are grateful for the tireless efforts on our behalf by the crews and offices of the USCG *Polar Sea*, RV *Polarstern*, and the RV *Ivan Petrov*. Laboratory assistance was provided by S. Gagaev, P. Martin, B. Orlando, K. Sandøy, D. Syster, K. Yarborough, and ZIN staff. We would also like to thank our colleagues and collaborators for their insights. In particular, we want to acknowledge the late John Gray for many stimulating discussions about benthic species diversity over coffee. We would also like to thank three anonymous reviewers whose suggestions markedly improved our work. This publication is contribution no.MPS-09008 of MarBEF, within the responsive mode program “ArctEco” (see www.marbef.org).

References

- Ambrose, W.G., Jr. & Renaud, P.E. (1995) Benthic response to water column productivity: evidence for benthic-pelagic coupling in the Northeast Water Polynya. *Journal of Geophysical Research*, 100 (C3), 4411–4421.
- Bertrand, Y., Pleijel, F. & Rouse, G.W. (2006) Taxonomic surrogacy in biodiversity assessments, and the meaning of Linnaean ranks. *Systematics and Biodiversity*, 4, 149–159.
- Brandt, A. (1997) Abundance, diversity and community patterns of epibenthic- and benthic-boundary layer peracarid crustaceans at 75° N off East Greenland. *Polar Biology*, 17, 159–174.
- Bluhm, B.A., MacDonald, I.R., Debenham, C. & Iken, K. (2005) Macro and megabenthic communities in the high Arctic Canada Basin: initial findings. *Polar Biology*, 28, 218–231.
- Bourke, R.H., Newton, J.L., Paquette, R.G. & Tunncliffe, M.D. (1987) Circulation and water masses of the East Greenland shelf. *Journal of Geophysical Research*, 92, 6729–6740.
- Carmack, E.C. & Wassmann, P. (2006) Food webs and physical–biological coupling on pan-Arctic shelves: Unifying concepts and comprehensive perspectives. *Progress in Oceanography*, 71, 446–477.
- Carmack, E., Barber, D., Christensen, J., Macdonald, R., Rudels, B. & Sakshaug, E. (2006) Climate variability and physical forcing of the food webs and the carbon budget on panarctic shelves. *Progress in Oceanography*, 71, 145–181.
- Carroll, M. & Carroll, J. (2003) The Arctic seas. In: Black, K.D. & Shimmield, G.B. (Eds.), *Biogeochemistry of Marine Systems*. Blackwell, Oxford, pp.127–156.
- Carroll, M.L., Denisenko, S.G., Renaud, P.E. & Ambrose, W.G. Jr. (2008) Benthic in-fauna of the seasonally ice-covered western Barents Sea: Patterns and relationships to physical forcing. *Deep-Sea Research II*, 55, 2340–2351.
- Cavalieri, D., Parkinson, C., Gloersen, P. & Zwally H.J. (1996, updated 2006) *Sea ice concentrations from Nimbus-7 SMMR and DMSP SSM/I passive microwave data*. Boulder, Colorado USA: National Snow and Ice Data Center. Digital media.
- Clarke, A. & Harris, C. M. (2003) Polar marine ecosystems: major threats and future change. *Environmental Conservation*, 30, 1–25.
- Cochrane, S.J., Denisenko S.G., Renaud P.E., Emblow C.S. & Ambrose W.G., Jr. (2009) Benthic fauna and productivity regimes in the Barents Sea - ecological implications in a changing Arctic. *Sea Research*, 61(4), 222–233.
- Colwell, R. K., (1997) EstimateS: Statistical estimation of species richness and shared species from samples,

- Version 5. User's Guide and Application. Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA. <http://viceroy.eeb.uconn.edu/estimates>.
- Cosson-Sarradin, N., Sibuet, M., Paterson, G.L.J. & Vangriesheim, A. (1998) Polychaete diversity at tropical Atlantic deep-sea sites: environmental effect. *Marine Ecology Progress Series*, 165, 173–185.
- Curtis, M. A. (1975) The marine benthos of Arctic and sub-Arctic continental shelves. *Polar Record*, 17, 595–625.
- Declerck, S., Vanderstucken, M., Pals, A., Muylaert, K. & De Meester, L. (2007) Plankton biodiversity along a gradient of productivity and its mediation by macrophytes. *Ecology*, 88, 2199–2210.
- Denisenko, S. G. (2002) Zoobenthos and ice distribution in the arctic seas. *Proceedings of the Zoological Institute of the Russian Academy of Sciences*, 296, 39–46.
- Dobson, S. (1992) Predicting crustacean zooplankton species richness. *Limnology and Oceanography* 37, 848–856.
- Dobson, S. I., Arnott, S. E. & Cottingham, K. L. (2000) The relationship in lake communities between primary productivity and species richness. *Ecology*, 81, 2662–2679.
- Ellingsen, I.H., Delpadado, P., Slagstad, D. & Loeng, H. (2008) Impact of climatic change on the biological production of the Barents Sea. *Climatic Change*, 87, 155–175.
- Ellingsen, K. E. (2001) Biodiversity of a continental shelf macrobenthos soft-sediment community. *Marine Ecology Progress Series*, 218, 1–15.
- Ellingsen, K. E. (2002) Soft sediment benthic biodiversity on the continental shelf in relation to environmental variability. *Marine Ecology Progress Series*, 232, 15–27.
- Falk-Peterson, S., Hop, H., Budgell, W.P., Hegseth, E.N., Korsnes, R., Løyning, T.B., Ørbæk, J.B., Kawamura, T. & Shirasawa, K. (2000) Physical and ecological processes in the marginal ice zone of the northern Barents Sea during the summer melt period. *Journal of Marine Systems*, 27, 131–159.
- Fauchald, K. (1977) The polychaete worms. Definitions and keys to the orders, families and genera. *Natural History Museum of Los Angeles County, Science Series*, 28, 1–188.
- Folk, R. L. (1980) Petrology of Sedimentary Rocks. Hemphill, Austin, Texas, USA, 185 pp.
- Fredriksen, K. R., Bjelvin, T. A. & Holm, J. P., (1994) Sediment distribution map Barents Sea. Geogruppen AS Report, 9434.01.01, Tromsø, Norway.
- Fukami, T. & Morin, P. K. J. (2003) Productivity-biodiversity relationships depend on the history of community assembly. *Nature*, 424, 423–426.
- Giangrande, A., Licciano, M. & Musco, L. (2005) Polychaetes as environmental indicators revisited. *Marine Pollution Bulletin*, 50, 1153–1162.
- Gilliman, L. N. & Wright, S. D. (2006) The influence of productivity on the species richness of plants: a critical assessment. *Ecology*, 87, 1234–1243.
- Glover, A.G., Smith, C.R., Paterson, G.L.J., Wilson, G.D.F., Hawkins, L. & Shearer, M. (2002) Polychaete species diversity in the central Pacific abyss: local and regional patterns, and relationships with productivity. *Marine Ecology Progress Series*, 240, 157–170.
- Gradinger, R. (1995) Climate change and biological oceanography of the Arctic Ocean. *Philosophical Transactions of the Royal Society of London*, 352, 277–286.
- Gray, J.S. (1974) Animal-sediment relationships. *Oceanography and Marine Biology; An Annual Review*, 12, 223–261.
- Gray, J.S. (1997) Gradients in marine biodiversity. In: Ormond, R.F.G., Gage, J.D. & Angel, M.V. (Eds.) *Marine Biodiversity*. Cambridge University Press, Cambridge, pp. 18–34.
- Gray, J. S. (2000) The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf. *Journal of Experimental Marine Biology and Ecology*, 250, 23–49.
- Grebmeier, J. M., McRoy, C. P. & Feder, H. M. (1988) Pelagic-benthic coupling on the shelf of the northern Bering Sea and Chukchi Seas. I: Food supply, source, and benthic biomass. *Marine Ecology Progress Series*, 51, 253–268.
- Grebmeier, J.M., Feder, H.M. & McRoy, C.P. (1989) Pelagic-benthic coupling on the self of the northern Bering and Chukchi Seas. II. Benthic community Structure. *Marine Ecology Progress Series*, 51, 253–268.

- Haddad, N. M., Haarstad, J. & Tilman, D. (2000) The effects of long-term nitrogen loading on grassland communities. *Oecologia*, 124, 73–84.
- Haedrich, R.L., Devine, J.A. & Kendall, V.J. (2008) Predictors of species richness in the deep-benthic fauna of the northern Gulf of Mexico. *Deep-Sea Research II*, 55, 2650–2656.
- Holm-Hansen, O., Lorenzen, C. J., Holmes, R.W. & Strickland, J. D. (1965) Fluorometric determination of chlorophyll. *Journal de Conseil International pour L'exploration de la mer*, 30L, 3–15.
- Hurlbert, S. H. (1971) The nonconcept of species diversity: a critique and alternate parameters. *Ecology*, 52, 577–586.
- Huston, M. A. (1994) *Biological diversity: the coexistence of species on changing landscapes*. Cambridge University Press., U.K., 708 pp.
- Johannessen, O. M., Shalina, E. V. & Miles, M. W. (1999) Satellite evidence for an Arctic sea ice cover in transformation. *Science*, 286, 1937–1939.
- Johannessen, O. M., Bengtsson, L. & Miles, M. W. (2002) Arctic climate change: observed and modeled temperature and sea ice variability. *Nansen Environmental and Remote Sensing Center Technical Report*, 218, 3–22.
- Kendall, M. A. (1996) Are arctic soft-sediment macrobenthic communities impoverished? *Polar Record*, 16, 393–399.
- Kendall, M.A. & Aschan, M. (1993) Latitudinal gradients in the structure of macrobenthic communities: a comparison of arctic, temperate and tropical sites. *Journal of Experimental Marine Biology and Ecology*, 172, 157–169.
- Kendall, M.A., Widdicombe, S. & Weslanwski, J.M. (2003) A multi-scale study of the biodiversity of the benthic infauna of the high-latitude Kongsfjord, Svalbard. *Polar Biology*, 26, 383–388.
- Kondoh, M. (2001) Unifying the relationships of species richness to productivity and disturbance. *Proceedings of the Royal Society B: Biological Sciences*, 268, 269–271.
- Kröncke, I. (1994) Macrobenthos composition, abundance and biomass in the Arctic Ocean along a transect between Svalbard and the Makarov Basin. *Polar Biology*, 14, 519–529.
- Kröger, K. & Rowden, A.A. (2002) Polychaete assemblages of the northwestern Ross Sea shelf: worming out the environmental drivers of Antarctic macrobenthic assemblage composition. *Polar Biology*, 31, 971–989.
- Laxon, S., Peacock, N. & Smith, D. (2003) High interannual variability in sea ice thickness in the Arctic region. *Nature*, 425, 947–950.
- Levin, L. A. & Gage, J.D. (1998) Relationships between oxygen, organic matter and the diversity of bathyal macrofauna. *Deep Sea Research Part II: Topical Studies in Oceanography*, 45, 129–163.
- Levin, L. A., Etter, R. J., Rex, M. A., Gooday, A. J., Smith, C. R., Pineda, J., Stuart, C. T., Hessler, R. R. & Pawson, D. (2001) Environmental influences of regional deep-sea species diversity. *Annual Review of Ecology and Systematics*, 32, 51–93.
- Loeng, H. (1991) Features of the physical oceanographic conditions in the Barents Sea. *Polar Research*, 10, 5–18.
- Mclaren, A. S., Walsh, J. E., Bourke, R. H., Weaver, R. L. & Wittmann, W. (1992) Variability in sea-ice thickness over the north-pole from 1977 to 1990. *Nature*, 358, 224–226.
- McMahon, K. W., Ambrose, W. G., Jr., Johnson, B. J., Sun, Ming-Yi, Lopez, G. R., Clough, L. M. & Carroll, M. L. (2006) Benthic community response to ice algae and phytoplankton in Ny Ålesund, Svalbard. *Marine Ecology Progress Series*, 310, 1–14.
- Minnett, P. J., Bignami, F., Böhm, E., Budéus, G., Galbraith, P. S., Gudmandsen, P., Hopkins, T. S., Ngram, G. G., Johnson, M. A., Niebauer, H. J., Famseier, R. O. & Schneider, W. (1997) A summary of the formation and seasonal progression of the Northeast Water Polynya. *Journal of Marine Systems*, 10, 79–85.
- Mittelbach, G. G., Steiner, C. F., Scheiner, S. M., Gross, K. L., Reynolds, H. L., Waide, R. B., Wilig, M. R., Dodson, S. I. & Gough, L. (2001) What is the observed relationship between species richness and productivity. *Ecology*, 82, 2381–2396.
- Quijón, P.A., Kelly, M.C. & Snelgrove, P.V.R. (2008) The role of sinking phytodetritus in structuring shallow-water benthic communities. *Journal of Experimental Marine Ecology and Biology*, 366, 134–145.

- Parkinson, C. L., Cavalieri, D. J., Gloersen, P., Sawlly, H. J. & Comsio, J. C. (1999) Arctic sea ice extents, areas, and trends 1978–1996. *Journal of Geophysical Research*, 104, 20837–20856.
- Pearson, T.H. (2001) Functional group ecology in soft-sediment marine benthos: the role of bioturbation. *Oceanography and Marine Biology, An Annual Review*, 39, 233–267.
- Pearson, T.H. & Rosenberg, R. (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology, An Annual Review*, 16, 229–311.
- Piepenburg, D. & Schmid, M.K. (1996) Distribution, abundance, biomass, and mineralization potential of the epibenthic megafauna of the Northeast Greenland shelf. *Marine Biology*, 125, 321–332
- Piepenburg, D., Ambrose, W. G., Jr., Brandt, A., Renaud, P. E., Ahrens, M. J. & Jensen, P. (1997) Benthic community patterns reflect water column process in the Northeast Water Polynya (Greenland). *Journal of Marine Systems*, 10, 467–482.
- Renaud, P. E., Ambrose, W. G., Jr., Vanreusel, A. & Clough, L. M. (2006) Meiofaunal and macrofaunal diversity in the Arctic Ocean. *Journal of Experimental Marine Biology and Ecology*, 300, 297–306.
- Renaud, P.E., Włodarska-Kowalczyk, M., Trannum, H., Holte, B., Węślawski, Cochrane, S., Dahle, S. & Gulliksen, B. (2007a) Multidecadal stability of benthic community structure in a high-Arctic glacial fjord (van Mijenfjord, Spitzbergen). *Polar Biology*, 30, 295–305.
- Renaud, P. E., Riedel, A., Michel, C., Morata, N., Gosselin, M., Juul-Pedersen, T. & Chiuchiolo, A. (2007b) Seasonal variation in benthic community oxygen demand: A response to an ice algal bloom in the Beaufort Sea, Canadian Arctic? *Journal of Marine Systems*, 67, 1–12.
- Renaud, P. E., Morata, N., Carroll, M. L., Denisenko, S.G., & Reigstad, M. (2008a) Pelagic-benthic coupling in the western Barents Sea: processes and time-scales. *Deep-Sea Research II*, 55, 2372–2380.
- Renaud, P. E., Carroll, M. L. & Ambrose, W. G., Jr. (2008b) Effects of Global Warming on Arctic Sea-Floor Communities and its Consequences for Higher Trophic Levels. In: Duarte, C. M. (Ed.), *Impacts of Global Warming on Polar Ecosystems*. Fundación BBVA, Bilbao, pp. 139–175.
- Rex, M. A., Crame, J. A., Stuart, C. T. & Clarke, A. (2005) Large-scale biogeographic patterns in marine mollusks: a confluence of history and productivity? *Ecology*, 86, 2288–2297.
- Rosenzweig, M. L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge, UK, 458 pp.
- Rosenzweig, M. L. & Abramsky, Z. (1993) How are diversity and productivity related? In: Ricklefs, R.E. & Schluter, D. (Eds.), *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, University of Chicago Press, pp. 52–65.
- Rothrock, D. A., Yu, Y. & Maykut, G. A. (1999) Thinning of the Arctic sea-ice cover. *Geophysical Research Letters*, 26, 1–5.
- Rysgaard, S., Nielsen, T. & Hansen, B. W. (1999) Seasonal variation in nutrients, pelagic primary production and grazing in a high-Arctic marine ecosystem, Young Sound, Northeast Greenland. *Marine Ecology Progress Series*, 179, 13–25.
- Schneider, W. & Budéus, G. (1994) The north east water polynya (Greenland Sea), *Polar Biology*, 4, 1–9.
- Schneider, W. & Budéus, G. (1995) On the generation of the Northeast Water Polynya. *Journal of Geophysical Research*, 100, 4269–4286.
- Schmid, B. (2002) The species richness-productivity controversy. *Trends in Ecology & Evolution*, 17, 113–114.
- Sejr, M.K., Hense, K.T. & Rysgaard, S. 2000. Macrobenthic community structure in a high-arctic East Greenland Fjord. *Polar Biology*, 23, 792–801.
- Serreze, M. C., Maslanik, J. A., Scambos, T. A., Fetterer, F., Stroeve, J., Knowles, K., Fowler, C., Drobot, S., Barry, R. G. & Haran, T. M. (2003) A record minimum arctic sea ice extent and area in 2002. *Geophysical Research Letters*, 30(3), 1110.
- Sirenko, B.I. (Ed.) (2001) *List of Species of Free-Living Invertebrates of Eurasian Arctic Seas and Adjacent Deep Waters*. Russian Academy of Sciences, St. Petersburg, Russia, 131 pp.
- Slagstad, D. & McClimans, T. A. (2005) Modeling the ecosystem dynamics of the Barents sea including the marginal ice zone: I Physical and chemical oceanography. *Journal of Marine Systems*, 58, 1–18.

- Snelgrove, P.V.R., Grassle, J.F. & Petrecca, R. (1996) Experimental evidence for aging food patches as a factor contributing to high deep-sea macrofaunal diversity. *Limnology and Oceanography*, 41, 605–514.
- Sokal, R. R. & Rohlf, F. J. (1995) *Biometry*. 3rd edition. W. H. Freeman and Co., San Francisco, USA, 887 pp.
- Starmans, A., Gutt, J. & Arntz, W.E. (2002) Mega-epibenthic communities in Arctic and Antarctic shelf areas. *Marine Biology*, 135, 269–280.
- Steffens, M., Piepenburg, D. & Schmid, M.K. (2006) Distribution and structure of macrobenthic fauna in the eastern Laptev Sea in relation to environmental factors. *Polar Biology*, 29, 837–848.
- Steiner, C. F. (2003) Keystone predator effects and grazer control of planktonic production. *Oikos*, 101, 569–577.
- Stewart, P.L., Pocklington, P. & Cuniak, R. (1985) Distribution, abundance and diversity of benthic macroinvertebrates on the Canadian continental shelf and slope of southern Davis Strait and Ungava Bay. *Arctic*, 38, 281–291.
- Svensson, J.R., Lindegarh, M., Siccha, M., Molis, M., Wahl, M. & Pavia, H. (2007) Maximum species richness at intermediate frequencies of disturbance: consistency among levels of productivity. *Ecology*, 88, 830–838.
- Thackeray, S. J. (2007) Crustacean zooplankton species richness and productivity: to what extent do the conclusions depend on the choice of metrics. *Oikos*, 116, 6714–6728.
- Tilman, D. (1982) *Resource Competition and Community Structure*. Princeton University Press, Princeton, New Jersey, USA, 296 pp.
- Waide, R. B., Willing, M. R., Steiner, C. F., Mittelbach, G., Gough, L., Dodson, S. I. & Juday, G. P. (1999) The relationship between productivity and species richness. *Annual Review of Ecology and Systematics*, 30, 257–300.
- Wassmann, P., Reigstad, M., Haug, T., Rudels, B., Carroll, M. L., Hop, H., Gabrielsen, G.W., Falk-Petersen, S., Denisenko, S. G., Arashkevich, E., Slagstad, D. & Pavlova, O. (2006a) Food webs and carbon flux in the Barents Sea. *Progress in Oceanography*, 71, 232–287.
- Wassmann, P., Slagstad, D., Wexels Riser, C. & Reigstad, M. (2006b) Modeling the ecosystem dynamics of the Barents Sea including the marginal ice zone: II Carbon flux and interannual variability. *Journal of Marine Systems*, 59, 1–24.
- Weisshappel, J.B.F. & Svavarsson, J. (1998) Benthic amphipods (Crustacea: Malacostraca) in Iceland waters: diversity in relation to faunal patterns from shallow to intermediate deep Arctic and North Atlantic Oceans. *Marine Biology*, 131, 133–143.
- Wlodarska-Kowalczyk, M., Weslawski, J. M. & Kotwicki, L. (1998) Spitzbergen glacial bays-macrofauna. *Polar Biology*, 20, 66–73.
- Wlodarska-Kowalczyk, M., Sicinski, J., Gromisz, S., Kendall, M.A. & Dahle, S. (2007) Similar soft-bottom polychaete diversity in Arctic and Antarctic marine inlets. *Marine Biology*, 151, 607–616.

APPENDIX 1.

Polychaete taxa collected from the East Greenland Shelf (NEW) and the Barents Sea (BASICC), recorded without reference to Linnean ranks (see Methods). Records of inclusive taxa refer to specimens which could not be identified to a lower level in a consistent manner between the two datasets, for either practical or taxonomic reasons. Taxa within which two or more forms were recognized, but not named are indicated with an *.

Taxon	Author	Location
<i>Abyssoninoe hibernica</i>	(McIntosh, 1903)	BASICC
<i>Aglaophamus</i>	Kinberg, 1865	NEW
<i>Aglaophamus malmgreni</i>	(Théel, 1879)	BASICC, NEW
<i>Amage auricula</i>	Malmgren, 1866	BASICC, NEW
<i>Ampharete</i>	Malmgren, 1866	BASICC, NEW
<i>Ampharete borealis</i>	(Sars, 1856)	BASICC
<i>Ampharete finmarchica</i>	(M. Sars, 1864)	BASICC, NEW
<i>Ampharete goesi</i>	Malmgren, 1866	BASICC
Ampharetidae*	Malmgren, 1866	BASICC, NEW
<i>Amphicteis gunneri</i>	(M. Sars, 1835)	BASICC, NEW
<i>Amphitrite groenlandica</i>	Malmgren, 1866	BASICC
<i>Anobothrus gracilis</i>	(Malmgren, 1866)	BASICC, NEW
<i>Anobothrus laubieri</i>	(Desbruyères, 1978)	BASICC, NEW
<i>Aphelochaeta marioni</i>	(de Saint Joseph, 1894)	BASICC
<i>Apistobranchnus tullbergi</i>	(Théel, 1879)	BASICC
<i>Apomatus</i>	Philippi, 1844	NEW
<i>Apomatus globifer</i>	Théel, 1878	BASICC
<i>Aricidea abranchiata</i>	Hartman, 1965	NEW
<i>Aricidea hartmani</i>	Strelzov, 1968	BASICC, NEW
<i>Aricidea nolani</i>	Webster & Benedict, 1887	BASICC
<i>Aricidea quadrilobata</i>	Webster & Benedict, 1887	BASICC, NEW
<i>Aricidea</i> *	Webster, 1879	NEW
<i>Artacama proboscidea</i>	Malmgren, 1866	BASICC, NEW
<i>Asychis biceps</i>	(M. Sars, 1861)	BASICC
<i>Augeneria algida</i>	(Wirén, 1901)	BASICC
<i>Axionice maculate</i>	(Dalzell, 1853)	BASICC
<i>Axiothella catenata</i>	(Malmgren, 1865)	NEW
<i>Bispira crassicornis</i>	(Sars, 1851)	BASICC
<i>Brada granulose</i>	Hansen, 1882	BASICC
<i>Brada villosa</i>	(Rathke, 1843)	BASICC
<i>Braniella</i>	Hartman, 1965	NEW
<i>Bushiella (Jugaria) quadrangularis</i>	(Stimpson, 1854)	BASICC
<i>Bylgides</i>	Chamberlin, 1919	BASICC
<i>Bylgides groenlandicus</i>	(Malmgren, 1867)	BASICC
<i>Bylgides promamme</i>	(Malmgren, 1867)	BASICC
<i>Capitella capitata</i>	(Fabricius, 1780)	BASICC
Capitellidae	Grube, 1862	NEW
Chaetopteridae*	Audouin & Milne-Edwards, 1833	NEW

.....continued

APPENDIX 1 (continued)

Taxon	Author	Location
<i>Chaetopterus</i>	Cuvier, 1827	NEW
<i>Chaetozone</i>	Malmgren, 1867	BASICC
<i>Chaetozone setosa</i>	Malmgren, 1867	BASICC, NEW
<i>Chitinopoma serrula</i>	(Stimpson, 1854)	BASICC
<i>Chone duneri</i>	Malmgren, 1867	BASICC, NEW
<i>Chone infundibuliformis</i>	Krøyer, 1856	BASICC
<i>Chone murmanica</i>	Lukasch, 1910	BASICC
<i>Chone paucibranchiata</i>	(Krøyer, 1856)	NEW
<i>Chone perseyi</i>	Zenkevitch, 1925	BASICC
<i>Chone*</i>	Krøyer, 1856	NEW
<i>Circeis armoricana</i>	Saint-Joseph, 1894	BASICC
<i>Circeis spirillum</i>	(Linnaeus, 1758)	BASICC
Cirratulidae	Ryckholt, 1851	NEW
<i>Cirratulus</i>	Lamarck, 1801	BASICC, NEW
<i>Cirratulus cirratus</i>	(O.F. Müller, 1776)	NEW
<i>Cirrophorus branchiatus</i>	Ehlers, 1908	BASICC
<i>Cirrophorus*</i>	Ehlers, 1908	NEW
<i>Clavodorum</i>	Hartman & Fauchald, 1971	NEW
<i>Clymaldane</i>	Mesnil & Fauvel, 1939	NEW
<i>Clymenura polaris</i>	(Théel, 1879)	BASICC
<i>Cossura longocirrata</i>	Webster & Benedict, 1887	BASICC, NEW
<i>Diplocirrus</i>	Haase, 1915	NEW
<i>Diplocirrus glaucus</i>	(Malmgren, 1867)	BASICC
<i>Diplocirrus longisetosus</i>	(Marenzeller, 1890)	BASICC
<i>Dipolydora coeca</i>	(Oersted, 1843)	BASICC
<i>Dipolydora quadrilobata</i>	(Jacobi, 1883)	BASICC
Dorvilleidae	Chamberlin, 1919	NEW
<i>Enipo torelli</i>	(Malmgren, 1866)	BASICC
<i>Ephesiella macrocirris</i>	Hartman & Fauchald, 1971	NEW
<i>Erinaceusyllis erinaceus</i>	(Claparède, 1863)	NEW
<i>Eteone</i>	Savigny, 1818	NEW
<i>Eteone flava</i>	(Fabricius, 1780)	BASICC, NEW
<i>Eteone longa</i>	(Fabricius, 1780)	BASICC, NEW
<i>Eteone spetsbergensis</i>	Malmgren, 1865	BASICC
<i>Euchone</i>	Malmgren, 1866	NEW
<i>Euchone analis</i>	(Krøyer, 1865)	BASICC, NEW
<i>Euchone papillosa</i>	(Sars, 1851)	BASICC, NEW
<i>Eulalia viridis</i>	(Johnston, 1829)	BASICC
<i>Eunoe nodosa</i>	(M. Sars, 1861)	BASICC
<i>Eusyllis blomstrandii</i>	Malmgren, 1867	BASICC
<i>Exogone (Exogone) naidina</i>	Örsted, 1845	BASICC
Exogoninae	Langerhans, 1879	NEW

.....continued

APPENDIX 1 (continued)

Taxon	Author	Location
<i>Flabelligera affinis</i>	M. Sars, 1829	BASICC
Flabelligeridae	Saint-Joseph, 1894	NEW
<i>Galathowenia oculata</i>	(Zachs, 1922)	BASICC
<i>Gattyana cirrhosa</i>	(Pallas, 1766)	BASICC
<i>Glycera capitata</i>	Örsted, 1843	BASICC
<i>Glyphanostomum pallescens</i>	(Theel, 1879)	BASICC, NEW
<i>Grubianella klugei</i>	(Pergament, Chlebovitch, 1964 in Chlebovitch, 1964)	BASICC
<i>Haploscoloplos</i>	Monro, 1933	NEW
<i>Harmothoe</i>	Kinberg, 1856	BASICC
<i>Harmothoe aspera</i>	(Hansen, 1878)	BASICC
<i>Harmothoe imbricata</i>	(Linnaeus, 1767)	BASICC
<i>Harmothoe impar</i>	(Johnston, 1839)	BASICC
<i>Harmothoe rarispina</i>	(M. Sars, 1861)	BASICC
Hesionidae	Sars, 1862	NEW
<i>Heteromastus filiformis</i>	(Claparède, 1864)	NEW
<i>Heteromastus filiformis</i>	(Claparède, 1864)	BASICC
<i>Jasmineira elegans</i>	Saint-Joseph, 1894	NEW
<i>Jasmineira schaudinni</i>	Augener, 1912	NEW
<i>Lanassa nordenskiöldi</i>	Malmgren, 1866	BASICC
<i>Lanassa venusta</i>	(Malm, 1874)	BASICC
<i>Laonice</i>	Malmgren, 1867	NEW
<i>Laonice cirrata</i>	(M. Sars, 1851)	BASICC
<i>Laphania boeckii</i>	Malmgren, 1866	BASICC, NEW
<i>Leaena</i>	Malmgren, 1866	NEW
<i>Leaena ebranchiata</i>	(M. Sars, 1865)	BASICC
<i>Levinsenia gracilis</i>	(Tauber, 1879)	BASICC
<i>Lumbriclymene minor</i>	Arwidsson, 1906	BASICC
Lumbrineridae*	Malmgren, 1867	NEW
<i>Lumbrineris fragilis</i>	(O.F. Müller, 1766)	BASICC, NEW
<i>Lumbrineris impatiens</i>	Claparède, 1868	NEW
<i>Lumbrineris magnidentata</i>	Winsnes, 1981	NEW
<i>Lumbrineris scopa</i>	Fauchald, 1974	NEW
<i>Lumbrineris</i> *	Blainville, 1828	NEW
<i>Lysilla loveni</i>	Malmgren, 1866	BASICC
<i>Lysippe labiata</i>	Malmgren, 1866	BASICC, NEW
<i>Macrochaeta</i>	Grube, 1850	BASICC, NEW
<i>Maldane arctica</i>	Detinova, 1985	BASICC
<i>Maldane sarsi</i>	Malmgren, 1865	BASICC, NEW
Maldanidae*	Malmgren, 1867	BASICC, NEW
<i>Marenzelleria arctica</i>	(Chamberlin, 1920)	BASICC
<i>Marenzelleria wireni</i>	Augener, 1913	BASICC

.....continued

APPENDIX 1 (continued)

Taxon	Author	Location
<i>Mediomastus</i>	Webster, 1879	NEW
<i>Mediomastus fragilis</i>	Rasmussen, 1973	NEW
<i>Melinna cristata</i>	(M. Sars, 1851)	BASICC, NEW
<i>Melinna elisabethae</i>	McIntosh, 1918	BASICC
<i>Melinnopsis</i>	McIntosh, 1885	NEW
<i>Melinnopsis annenkovae</i>	(Ushakov, 1952)	NEW
<i>Melinnopsis arctica</i>	(Annenkova, 1931)	NEW
<i>Micronephthys minuta</i>	(Théel, 1879)	BASICC
<i>Myriochele</i>	Malmgren, 1867	NEW
<i>Myriochele heeri</i>	Malmgren, 1867	BASICC, NEW
<i>Myriochele oculata</i>	Zachs, 1922	NEW
<i>Mystides</i>	Théel, 1879	BASICC
<i>Mystides borealis</i>	Théel, 1879	BASICC
<i>Neopolynoe paradoxa</i>	(Storm, 1888)	BASICC
Nephtyidae	Grube, 1850	NEW
<i>Nephtys</i>	Cuvier, 1817	BASICC
<i>Nephtys ciliata</i>	(Müller, 1776)	BASICC, NEW
<i>Nephtys paradoxa</i>	Malm, 1874	BASICC
<i>Nephtys pente</i>	Rainer, 1984	BASICC
<i>Nereididae</i>	Johnston, 1865	NEW
<i>Nereimyra</i>	Blainville, 1828	BASICC, NEW
<i>Nereis pelagica</i>	Linnaeus, 1758	BASICC
<i>Nereis zonata</i>	Malmgren, 1867	BASICC
<i>Nicolea zostericola</i>	Örsted, 1844	BASICC
<i>Nicomache</i>	Malmgren, 1865	NEW
<i>Nicomache (Loxochona) quadrispinata</i>	Arwidsson, 1906	BASICC
<i>Nicomache (Loxochona) trispinata</i>	Arwidsson, 1906	NEW
<i>Nicomache lumbricalis</i>	(Fabricius, 1780)	BASICC
Nicomachinae	Arwidsson, 1907	NEW
<i>Nothria conchylega</i>	(Sars, 1835)	NEW
<i>Nothria hyperborea</i>	(Hansen, 1878)	BASICC
<i>Notomastus</i>	Sars, 1850	NEW
<i>Notomastus latericeus</i>	Sars, 1851	BASICC
<i>Notoproctus oculatus</i>	Arwidsson, 1906	BASICC, NEW
Onuphidae*	Kinberg, 1865	NEW
<i>Ophelina acuminata</i>	Örsted, 1843	BASICC
<i>Ophelina cylindricaudata</i>	(Hansen, 1878)	BASICC, NEW
Orbiniidae	Hartman, 1942	NEW
<i>Owenia fusiformis</i>	Delle Chiaje, 1844	BASICC
Oweniidae	Rioja, 1917	NEW
<i>Paradexiospira (Spirorbides) vitrea</i>	(Fabricius, 1780)	BASICC
<i>Paramphinome jeffreysii</i>	(McIntosh, 1868)	BASICC

.....continued

APPENDIX 1 (continued)

Taxon	Author	Location
<i>Paramphitrite birulai</i>	(Ssolowiew, 1899)	BASICC
<i>Paranaitis wahlbergi</i>	(Malmgren, 1865)	BASICC
<i>Paraninoe minuta</i>	(Théel, 1879)	BASICC
<i>Paraonella nordica</i>	Strelzov, 1968	BASICC
Paraonidae	Cerruti, 1909	NEW
<i>Paraonis</i>	Cerruti, 1909	NEW
<i>Pectinaria (Cistenides) hyperborea</i>	(Malmgren, 1866)	BASICC
Pectinariidae	Quatrefages, 1866	NEW
<i>Petaloproctus tenuis</i>	(Théel, 1879)	BASICC
<i>Pherusa arctica</i>	Støp-Bowitz, 1948	BASICC
<i>Pherusa plumosa</i>	(Müller, 1776)	BASICC
<i>Pholoe assimilis</i>	Örsted, 1845	BASICC
<i>Pholoe minuta</i>	(Fabricius, 1780)	NEW
<i>Pholoe*</i>	Johnston, 1839	NEW
<i>Phyllodoce</i>	Savigny, 1818	BASICC
<i>Phyllodoce (Anaitides) groenlandica</i>	Oersted, 1842	BASICC
Phyllodocidae	Williams, 1851	NEW
<i>Pionosyllis compacta</i>	Malmgren, 1867	BASICC
<i>Polycirrus</i>	Grube, 1850	NEW
<i>Polycirrus arcticus</i>	Sars, 1865	BASICC, NEW
<i>Polycirrus fedorovi</i>	Jirkov & Leontovich in Jirkov, 2001	BASICC
<i>Polycirrus medusa</i>	Grube, 1850	BASICC, NEW
<i>Polycirrus norvegicus</i>	Wollebaek, 1912	NEW
<i>Polydora*</i>	Bosc, 1802	NEW
Polynoidae*	Kinberg, 1856	NEW
<i>Polyphysia crassa</i>	(Örsted, 1843)	BASICC
<i>Praxillella gracilis</i>	(M. Sars, 1861)	BASICC
<i>Praxillella praetermissa</i>	(Malmgren, 1865)	BASICC
<i>Praxillura longissima</i>	Arwidsson, 1906	BASICC, NEW
<i>Prionospio cirrifer</i>	Wirén, 1883	BASICC, NEW
<i>Prionospio*</i>	Malmgren, 1867	NEW
<i>Proclea graffi</i>	(Langerhans, 1880)	BASICC, NEW
<i>Proclea malmgreni</i>	(Ssolowiew, 1899)	NEW
<i>Protodorvillea kefersteini</i>	(McIntosh, 1869)	BASICC
<i>Pseudopolydora antennata</i>	(Claparède, 1869)	BASICC
<i>Pseudopotamilla reniformis</i>	(Müller, 1771)	BASICC
<i>Pseudoscalibregma parvum</i>	(Hansen, 1878)	BASICC
<i>Pterolysippe vanelli</i>	(Fauvel, 1936) sensu Eliason, 1955, emend	NEW
<i>Pygospio elegans</i>	Claparède, 1863	BASICC, NEW
<i>Rhodine</i>	Malmgren, 1865	NEW
<i>Rhodine gracilior</i>	Tauber, 1879	BASICC
Sabellidae	(Malmgren, 1867)	NEW

.....continued

APPENDIX 1 (continued)

Taxon	Author	Location
<i>Samythella neglecta</i>	Wollebaek, 1912	NEW
<i>Scalibregma inflatum</i>	Rathke, 1843	BASICC, NEW
Scalibregmatidae	Malmgren, 1867	NEW
<i>Schistomeringos</i>	Jumars, 1974	NEW
<i>Scolelepis korsuni</i>	Sikorski, 1994	BASICC
<i>Scolelepis matsugae</i>	Sikorski, 1994	BASICC
<i>Scoloplos (Scoloplos) armiger</i>	(Müller, 1776)	BASICC
<i>Scoloplos acutus</i>	(Verrill, 1873)	BASICC
Serpulidae	Rafinesque, 1815	NEW
<i>Sosanopsis wireni</i>	Hessle, 1917	BASICC, NEW
<i>Sphaerodoridium fauchaldi</i>	Hartmann-Schröder, 1993	BASICC
<i>Sphaerodoropsis</i>	Hartman & Fauchald, 1971	NEW
<i>Sphaerodoropsis minuta</i>	(Webster & Benedict, 1887)	BASICC, NEW
<i>Sphaerodoropsis philippi</i>	(Fauvel, 1911)	BASICC
<i>Sphaerodorum gracilis</i>	(Rathke, 1843)	BASICC
<i>Spio arctica</i>	(Söderström, 1920)	BASICC
<i>Spio armata</i>	(Thulin, 1957)	BASICC
<i>Spiochaetopterus typicus</i>	M. Sars, 1856	BASICC, NEW
Spionidae	G.O. Sars, 1872	NEW
<i>Spiophanes kroeyeri</i>	Grube, 1860	BASICC, NEW
Spirorbidae	Pillai, 1970	NEW
Syllidae*	Grube, 1850	BASICC
<i>Syllides</i>	Örsted, 1845	BASICC
<i>Syllides longocirratus</i>	(Örsted, 1845)	NEW
<i>Syllis armillaris</i>	(O.F. Müller, 1776)	BASICC
<i>Syllis cornuta</i>	Rathke, 1843	NEW
<i>Syllis</i> *	Lamarck, 1818	NEW
Terebellidae	Malmgren, 1865	NEW
<i>Terebellides stroemi</i>	Sars, 1835	BASICC, NEW
<i>Terebellides williamsae</i>	Jirkov, 1989	BASICC
<i>Tharyx</i> *	Webster & Benedict, 1887	BASICC, NEW
<i>Thelepus cincinnatus</i>	(Fabricius, 1780)	NEW
<i>Trichobranthus glacialis</i>	Malmgren, 1866	BASICC

APPENDIX 2.

List of the 10 numerically dominant taxa recorded from the East Greenland Shelf (NEW) and the Barents Sea (BASICC), recorded without reference to Linnean ranks (see Methods). Abundances expressed as % of total polychaete individuals at the stations. Frequency expressed as % of stations within the location containing the taxa (bold type indicates taxa with >80% frequency of occurrence).

NEW				BASICC			
North Trough	Taxon	Abund.	Freq.	North	Taxon	Abund.	Freq.
Spionidae	<i>Prionospio cirrifera</i>	20.2	100	Spionidae	<i>Spiophanes kroeyeri</i>	9.9	71
Maldanidae	<i>Maldane sarsi</i>	17.1	82	Oweniidae	<i>Myriochele heeri</i>	8.2	82
Paraonidae	<i>Aricidea quadrilobata</i>	7.5	36	Spionidae	<i>Prionospio cirrifera</i>	7.4	88
Ampharetidae	<i>Eclysippe vanelli</i>	6.3	91	Oweniidae	<i>Galathowenia oculata</i>	5.0	76
Maldanidae	Maldanidae	5.5	73	Chaetopteridae	<i>Spiochaetopterus typicus</i>	4.6	82
Cirratulidae	<i>Tharyx</i>	4.2	64	Capitellidae	<i>Heteromastus filiformis</i>	4.3	82
Cirratulidae	<i>Chaetozone setosa</i>	3.8	73	Sabellidae	<i>Chone murmanica</i>	3.9	35
Capitellidae	<i>Heteromastus filiformis</i>	1.8	55	Cirratulidae	<i>Aphelochaeta marioni</i>	3.9	88
Onuphidae	<i>Onuphis conchylega</i>	1.6	18	Lumbrineridae	<i>Scoletoma fragilis</i>	3.9	71
Pholoidae	<i>Pholoe</i>	1.5	55	Maldanidae	<i>Maldane sarsi</i>	2.9	47
Bank	Taxon	Abund.	Freq.	Front	Taxon	Abund.	Freq.
Spionidae	<i>Prionospio cirrifera</i>	15.6	100	Oweniidae	<i>Galathowenia oculata</i>	21.9	93
Paraonidae	<i>Aricidea quadrilobata</i>	7.2	88	Chaetopteridae	<i>Spiochaetopterus typicus</i>	21.3	100
Cirratulidae	<i>Tharyx</i>	6.8	50	Capitellidae	<i>Heteromastus filiformis</i>	9.4	100
Cirratulidae	<i>Chaetozone setosa</i>	6.5	63	Lumbrineridae	<i>Paraninoe minuta</i>	6.7	100
Ampharetidae	<i>Eclysippe vanelli</i>	6.1	100	Maldanidae	<i>Maldane sarsi</i>	5.0	100
Maldanidae	Maldanidae indet.	5.6	100	Spionidae	<i>Spiophanes kroeyeri</i>	4.4	80
Maldanidae	<i>Maldane sarsi</i>	3.5	75	Cirratulidae	<i>Chaetozone</i>	3.1	87
Onuphidae	<i>Onuphis conchylega</i>	2.6	63	Orbiniidae	<i>Scoloplos acutus</i>	2.5	100
Maldanidae	<i>Praxillura longissima</i>	2.6	63	Pholoidae	<i>Pholoe assimilis</i>	1.2	87
Oweniidae	<i>Galathowenia oculata</i>	2.3	63	Nephtyidae	<i>Aglaophamus malmgreni</i>	1.1	100
Southern Trough	Taxon	Abund.	Freq.	South	Taxon	Abund.	Freq.
Paraonidae	<i>Aricidea quadrilobata</i>	19.5	78	Chaetopteridae	<i>Spiochaetopterus typicus</i>	23.5	100
Ampharetidae	<i>Eclysippe vanelli</i>	8.5	56	Oweniidae	<i>Galathowenia oculata</i>	12.4	100
Spionidae	<i>Prionospio cirrifera</i>	5.5	44	Maldanidae	<i>Maldane sarsi</i>	5.5	100
Cirratulidae	<i>Tharyx</i>	5.1	44	Spionidae	<i>Spiophanes kroeyeri</i>	5.2	87
Maldanidae	Maldanidae indet.	4.8	11	Capitellidae	<i>Heteromastus filiformis</i>	4.8	100
Syllidae	<i>Typosyllis</i>	3.1	22	Lumbrineridae	<i>Paraninoe minuta</i>	4.0	87
Maldanidae	<i>Maldane sarsi</i>	2.7	44	Amphinomidae	<i>Paramphinome jeffreysii</i>	2.8	93
Ampharetidae	Ampharetidae	2.7	33	Cirratulidae	<i>Aphelochaeta marioni</i>	2.5	87
Lumbrineridae	<i>Abyssoninoe scopae</i>	2.7	22	Sabellidae	<i>Chone murmanica</i>	2.5	87
Syllidae	<i>Ehlersia cornuta</i>	2.0	22	Maldanidae	<i>Maldane arctica</i>	2.3	60