

## Diversity of the arctic deep-sea benthos

Bluhm A. Bodil · William G. Ambrose Jr · Melanie Bergmann · Lisa M. Clough ·  
Andrey V. Gebruk · Christiane Hasemann · Katrin Iken · Michael Klages ·  
Ian R. MacDonald · Paul E. Renaud · Ingo Schewe · Thomas Soltwedel ·  
Maria Włodarska-Kowalczyk

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**Abstract** A benthic species inventory of 1,125 taxa was compiled from various sources for the central Arctic deeper than 500 m, and bounded to the Atlantic by Fram Strait. The inventory was dominated by arthropods (366 taxa), foraminiferans (197), annelids (194), and nematodes (140). An additional 115 taxa were added from the Greenland–Iceland–Norwegian Seas (GIN). Approximately half of all taxa were recorded from only 1 or 2 locations. A large overlap in taxa with Arctic shelf species supports previous findings that part of the deep-sea fauna originates from shelf species. Macrofaunal abundance, meiofaunal abundance and macrofaunal biomass decreased significantly with water depth. Robust diversity indices could only be calculated for the

polychaetes, for which S, ES(20), H' and Delta+ decreased significantly with water depth, and all but ES (20) decreased slightly with latitude. Species evenness increased with depth and latitude. No mid-depth peak in species richness was observed. Multivariate analysis of the Eurasian, Amerasian and GIN Seas polychaete occurrences revealed a strong Atlantic influence, the absence of modern Pacific fauna, and the lack of a barrier effect by mid-Arctic ridges. Regional differences appear to be moderate on the species level and minor on the family level, although the analysis was confounded by a lack of methodological standardization and inconsistent taxonomic resolution. Future efforts should use more consistent methods to observe temporal trends and

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B. A. Bodil (✉) · K. Iken  
School of Fisheries and Ocean Sciences,  
University of Alaska Fairbanks,  
Fairbanks, Alaska 99709, USA  
e-mail: bluhm@ims.uaf.edu

W. G. Ambrose Jr  
Department of Biology, Bates College,  
Lewiston, Maine 04240, USA

M. Bergmann · C. Hasemann · M. Klages · I. Schewe ·  
T. Soltwedel  
Alfred Wegener Institute for Polar and Marine Research,  
27570 Bremerhaven, Germany

L. M. Clough  
Department of Biology, East Carolina University,  
Greenville, NC 27858, USA

A. V. Gebruk  
P.P. Shirshov Institute of Oceanology,  
Russian Academy of Sciences,  
Moscow, Russia

I. R. MacDonald  
Florida State University,  
Tallahassee, FL 32306, USA

W. G. Ambrose Jr · P. E. Renaud  
Akvaplan-niva AS, Polar Environmental Centre,  
9296 Tromsø, Norway

M. Włodarska-Kowalczyk  
Institute of Oceanology, Polish Academy of Sciences,  
Spot, Poland

help fill the largest sampling gaps (i.e. eastern Canada Basin, depths >3,000 m, megafauna) to address how climate warming, and the shrinking of the perennial ice cover will alter deep-sea communities.

**Keywords** Diversity · Arctic · Deep sea · Abundance · Biomass · Polychaeta

## Introduction

The Arctic's central basins have been very poorly studied even compared to other deep-sea areas due to challenging sampling logistics and little obvious need for exploration. In recent decades, however, the central Arctic has received increased attention because of its shrinking sea ice cover (Stroeve et al. 2007) and, very recently, through the International Polar Year 2007–2009. Work from the last two decades has included a number of ecological and faunistic studies that have greatly advanced our knowledge of benthic processes and diversity (e.g., references in Table 1; Klages et al. 2004). In summary, these studies convey a picture of the Arctic deep sea as an oligotrophic area with steep gradients in faunal abundance and biomass from the slopes to the basins primarily driven by food availability, but with overall density and biomass broadly similar to other deep-sea areas. As in other soft sediment habitats, foraminiferans and nematodes generally dominate the meiofauna, whereas annelids, crustaceans and bivalves dominate the macrofauna, and echinoderms dominate the megafauna (see references in Table 1). In total, just over 700 benthic species were catalogued from the central basins a decade ago (Sirenko 2001).

Efforts over the last decade in the Arctic under the umbrella of the Census of Marine Life (Yarincik and O'Dor 2005) have led to descriptions of new species (e.g., Rogacheva 2007; Gagaev 2008, 2009), range extensions (MacDonald et al. 2010), an online Arctic Register of Marine Species (Sirenko et al. 2010), and an open access data base of Arctic diversity data (<http://dw.sfos.uaf.edu/arcod/>). Globally, the substantial increase of diversity research in the deep sea in the last two decades was driven by scientific curiosity, but also by the need for baseline inventories in the light of expanding deep-sea fisheries, manganese nodule exploitation, exploratory CO<sub>2</sub> deposition, petroleum exploration, tourism, and other human-induced pressures (Thiel 2003). Much of the Arctic deep-sea floor has until now experienced only a weak human footprint (but see Galgani and Lecornu 2004 for Fram Strait), but a predicted ice-free summer in the Arctic in the near future (e.g., Stroeve et al. 2007) may change that situation, thus an up-to-date inventory is urgently needed.

Several paradigms have emerged from deep-sea research in the past decades, including those of mid-depth peaks and latitudinal declines in diversity (Levin et al. 2001; Rex and Etter 2010). Much of the initial work underlying these paradigms was centered in the North Atlantic and the question remains as to whether they apply broadly to the Arctic deep basins that comprise approximately 50% of the Arctic Ocean seafloor (Jakobsson et al. 2004). The Arctic basins differ from the North Atlantic deep sea because the Arctic deep sea is: (1) largely ice-covered, (2) semi-isolated from the world oceans, (3) relatively young in age (Vinogradova 1997), and (4) experiences more pronounced seasonality in light and primary production than lower latitudes. A peak in benthic diversity at mid-depths (1,500–3,000 m) has not been observed for benthic meiofaunal nematode and macrofauna diversity in the central Arctic (Renaud et al. 2006) or for macrofauna in Fram Strait (Włodarska-Kowalczyk et al. 2004). A trend toward reduced taxonomic richness with latitude has been documented for meiofaunal nematode and macrofaunal diversity (Renaud et al. 2006), but not for other community components.

The history and semi-isolation of the Arctic basin play a role in the Arctic basin's diversity patterns (Golikov and Scarlato 1990). Originally an embayment of the North Pacific, the Arctic deep sea was influenced by Pacific fauna until ~80 million years ago when the deep-water connection closed (Marincovich et al. 1990). Exchange with the deep Atlantic began ~40 million years ago, coinciding with a strong cooling period (Savin et al. 1975). While some Arctic shelf and deep-sea faunas were eradicated by Pleistocene glaciations, other shelf fauna in the Atlantic sector of the Arctic found refuge in the deep sea and are considered the ancestral fauna of some of today's Arctic deep-sea fauna (Nesis 1984). The only present-day deep-water connection from the high Arctic to the world oceans through Fram Strait (~2,500 m) allows exchange with the Greenland and Norwegian Basins (average depth 2,000–3,000 m). Steep ridges form physical barriers within the Arctic basin: the Gakkel Ridge (shallowest depth ~2,500 m) separates the Nansen and Amundsen Basins in the Eurasian Arctic (maximum depth ~4,200 m), and the Lomonosov Ridge (~1,400 m shallowest depth) separates the Amerasian Canada and Makarov Basins (maximum depth ~3,800 m) from the Eurasian Basins (Jakobsson et al. 2004). Despite their boundary character, current evidence suggests the ridges do not form biogeographic barriers (Deubel 2000; Kosobokova et al. 2010). Several other bathymetric features such as the Yermak Plateau north of Svalbard and the Chukchi Borderlands in the Canada Basin contribute to the regional heterogeneity of the Arctic deep sea.

**Table 1** Data sources included in this article

Reference	Geographic area	Sampling year	Locations	Samples	Records (presence only)	Taxa	Polychaete taxa	Min depth (m)	Max depth (m)	Sieve size (µm)	Sample area (m <sup>2</sup> )	Total area (m <sup>2</sup> )	Gear type	Abundance	Total biomass	Taxa	Taxonomic resolution
Hasemann 2006	Fram Strait	2001, 2003	2	12	547	115	0	2,310	2,600	32	10 cm <sup>2</sup>	0.012	ROV - corer	x	x	Nem	G
Lorenz 2005	Denmark Strait	2002	10	10	263	97	0	980	2,564	125	15 cm <sup>2</sup>	0.015	Multi-corer	x		For	S
Soitwedel et al. 2009a	Yermak Plateau	1997–2006	24	72	255	89	0	635	4,268	32	10 cm <sup>2</sup>	0.072		x		Nem	G
Schewe and Soitwedel 2003	Yermak Plateau/Fram Strait	1999	14	42	237	20	0	635	3,020	32	10 cm <sup>2</sup>	0.014	Multi-corer	x		For	G
Schewe 2001	Makarov Basin, Alpha Ridge, Lomonosov Ridge	1998	6	18	54	20	0	1,270	3,170	32	10 cm <sup>2</sup>	0.006	Multi-corer	x		For	G
Włodarska-Kowalczyk et al. 2004	Svalbard	2000	8	16	344	117	47	525	2,977	500	0.1 m <sup>2</sup>	1.6	Box corer	x		All	S
Clough et al. 1997	Arctic Ocean transect	1994	18	53	315	38	23	540	4,190	250	0.015 m <sup>2</sup>	0.0795	Box corer	x	x	All	P/O, Poly S
Deubel 2000	Lomonosov Ridge, Laptev Sea	1995	67	67	1,677	283	88	510	4,170	250–500	0.25 m <sup>2</sup>	16.75	Box corer	x	x	All	S
Schnack 1998	Greenland Sea	1994/1995	15	37	567	91	49	200	2,700	300–500	0.0625 m <sup>2</sup>	2.3125	Box corer	x	x	Poly	S
Blumh et al. 2005, MacDonald et al. 2010	Canada Basin, Chukchi slope, Chukchi Borderland	2002, 2005	17	44	557	176	78	640	3,961	250	0.03–0.06 m <sup>2</sup>	3.08	Box corer	x	x	All	S
Kröncke 1994, 1998	Eurasian Basins	1991	47	163	266	136	41	560	4,478	250	0.02 m <sup>2</sup>	3.72	Box corer	x	x	All	S
Romero-Wetzel and Gerlach 1991	Norwegian Sea	1987	17		Not used	Not used	0	1,244	1,450	500	0.125 m <sup>2</sup>	1.7	Box corer	x (total)	x	N/A	-
Seiler 1999	Greenland Sea	1994–1997	19	49	Not used	Not used	0	770	3,704	300–500	0.0625 m <sup>2</sup>	4.75	Box corer	x (total)	x	N/A	-
Sirenko 2001 and online data base	Pan-Arctic	1877–1995	128	128	373	86	0	500	4,000	Not given	Not given	Not given	Various	Presence		Ech, Biv, Art	S
Carey 1977	Beaufort Sea slope	1971	12	36	485	74	60	540	3,010	1,000	0.1 m <sup>2</sup>	3.6	Grab	x		Poly, Harp	S
Sharma and Bluhm 2010	Canada Basin, Chukchi slope, Chukchi Borderland	2002, 2005	15	22	236	70	0	640	3,250	250	0.03–0.06 m <sup>2</sup>	1.2	Box corer	x		Nem	G
Soitwedel et al. 2009b	Fram Strait	1997,	5	524 photos	>84	49	ND	1,306	5,404	N/A	~1,800 m <sup>2</sup>	830	Still camera (plus trawls)	x		All	Mix
Bluhm et al. 2005	Canada Basin	2002, 2005	7	5	80	54	ND	817	2,800	7 mm (4 cod end)	N/A	Not quantified	ROV sampler, trawl	Presence		All	Mix
Rogacheva 2007 and in	GIN Seas & central	1875–2002	259	259	359	53	ND	505	4,106	not given	Not given	Not given	Various, not given	Presence		Ech, Biv	S

Table 1 (continued)

Reference	Geographic area	Sampling year	Locations	Samples	Records (presence only)	Taxa	Polychaete taxa	Min depth (m)	Max depth (m)	Sieve size ( $\mu\text{m}$ )	Sample area ( $\text{m}^2$ )	Total area ( $\text{m}^2$ )	Gear type	Abundance	Total biomass	Taxa	Taxonomic resolution
preparation and unpublished MacDonald et al. 2010	Arctic Canada Basin, Chukchi slope, Chukchi Borderland	2005	6	2,134 photos	>141	68	ND	911	3,843	N/A	10,526 $\text{m}^2$	10,526	Still camera	x		All	Mix
Prepenburg 1988	Fram Strait	1985	3	3	125	80	ND	530	890	20 mm (10 cod end)	N/A	21,800	Agassiz trawl, still camera	x		All	S

Art Arthropoda, *Biv Bivalvia*, *Ech Echinodermata*, *For Foraminifera*, *Harp Harpacticoida*, *Nem Nematoda*, *Poly Polychaeta*, *G genus*, *O order*, *P phylum*, *S species*, *N/A not available*, *ND no data*

Besides physiography, bathymetry and tectonic history, environmental conditions shape deep-sea diversity including flow regime, sediment characteristics and energy input (reviewed in Levin et al. 2001). The bottom of the Arctic basin is filled with water originating from the North Atlantic (Rudels et al. 1994) that has a very long residence time of ~450 years in the Canada Basin (MacDonald et al. 1993). In the basins, the sediments are primarily silt and clay while ridges and plateaus have a higher sand fraction (Stein et al. 1994). Exceptions include drop stones, that provide hard substrata and enhanced habitat heterogeneity for benthic fauna (MacDonald et al. 2010; Schulz et al. 2010), and some areas of coarser sediments (Bluhm et al. 2005). Considerable inputs of refractory terrestrial organic matter from the large Russian and North American rivers characterize the organic component of the sediments from the shelves to along the slopes and into the basins (Stein and MacDonald 2004). Overall, the Arctic deep sea receives relatively low input of marine-derived organic matter, because the region is largely covered by multi-year ice, which allows only low average primary production that is highly seasonal (Wheeler et al. 1996; Gosselin et al. 1997). Consequently, carbon flux to the deep-sea floor is low (Olli et al. 2006), but in the slope areas is complemented by carbon advected from some highly productive shelves and from turbidites (Grantz et al. 1996; Cooper et al. 1999; Soltwedel 2000). In the last decade, the perennial ice cover has retreated far over the shelves and into the basins in some areas, in particular over the Chukchi Sea slope and the adjacent southwestern Canada Basin (Stroeve et al. 2007). This may have important implications for spatial patterns in carbon flux and potentially benthic diversity from the slope to deeper basins, patterns that may vary in areas of the Arctic where ice withdrawal has been different.

The goal of our paper is to synthesize information on Arctic benthic deep-sea diversity on a pan-Arctic scale based on numerical analysis of available data from mostly recent faunistic studies of the Arctic deep sea. Our specific objectives in this paper are to:

- 1 Update the benthic invertebrate taxonomic inventory of the Arctic deep sea (meio-, macro- and megabenthos) relative to the most current comprehensive list (Sirenko 2001)
- 2 Test for latitudinal and bathymetric trends in diversity, abundance and biomass in the geo-referenced data, and
- 3 Identify spatial patterns and potential distribution barriers.

## Methods

The data employed are from samples collected during a variety of expeditions largely conducted in the 1990s and 2000s, but also as early as 1875, at depths ranging from

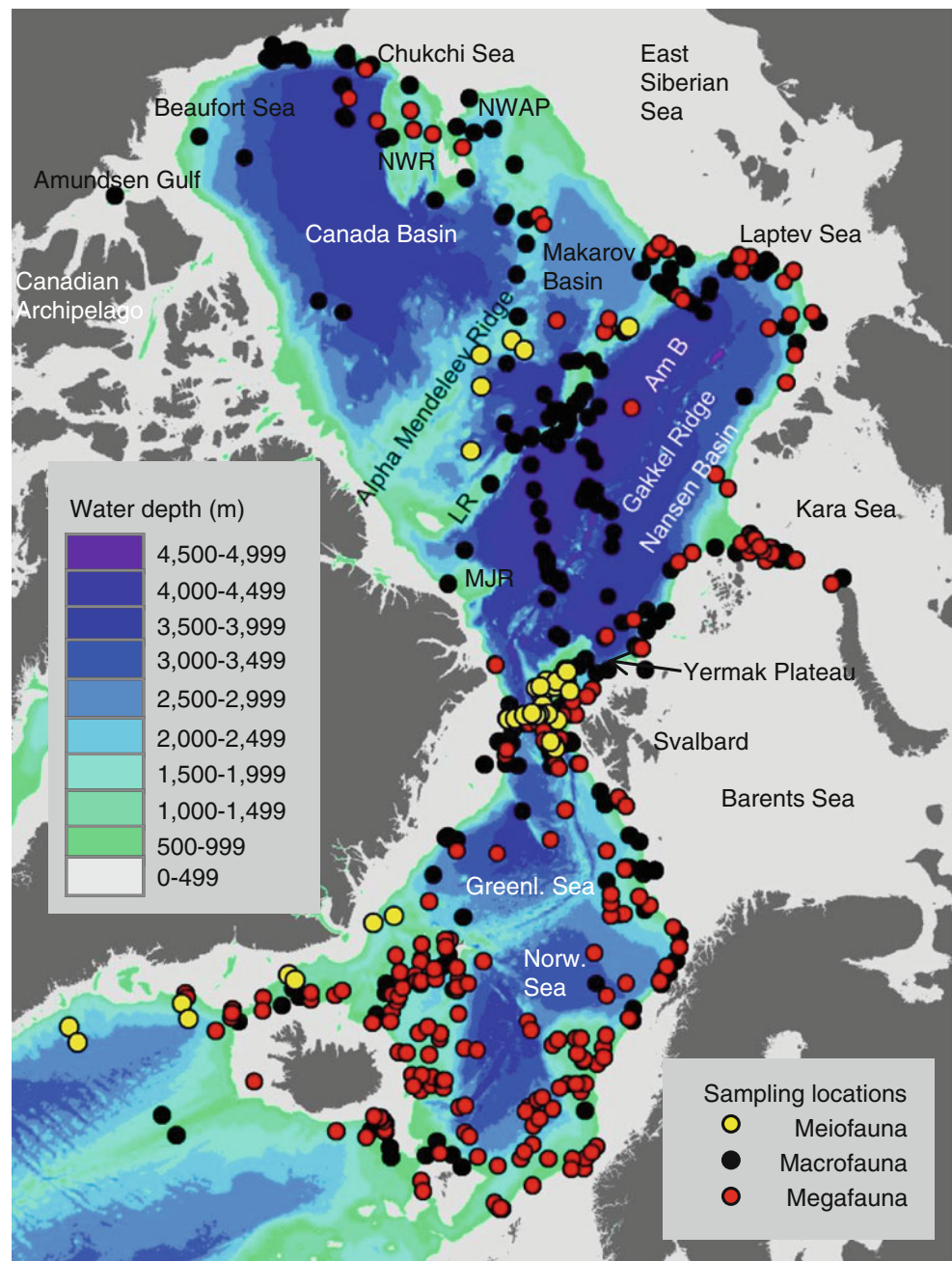
500–5,404 m (Table 1). A total of 5,775 geo-referenced records from 629 locations were compiled for meio-, macro- and megafauna with 70% in the macrofaunal size fraction. Faunal size fractions are defined as meiofauna  $>32\ \mu\text{m}$ , macrofauna  $>250\text{--}500\ \mu\text{m}$ , and megafauna typically  $>4\ \text{mm}$  and epifaunal. One ‘record’ is the occurrence of a particular taxon at a specific site with one or more individuals. Sampling gear included primarily multi-corers for meiofauna, primarily box corers for macrofauna, and trawls and camera systems for megafauna (Table 1). Sample areas of the gears used varied, as did the mesh sizes of trawls and the size of sieves used to process sediment samples (Table 1). These differences cause

inevitable biases discussed by Gage et al. (2002) that we could partly address (see below), and partly only discuss.

#### Inventory

To present an updated inventory of the Arctic benthos in water depths  $>500\ \text{m}$ , we compiled a unique taxon list (Electronic supplemental material, Table 1) for the Arctic deep sea from the data sources in Table 1 (with locations plotted in Fig. 1) and from the column ‘‘Arctic basin’’ in Sirenko (2001). The southernmost boundary on the Atlantic side was in Fram Strait, although additional records from the sub-Arctic

**Fig. 1** The study area with symbols marking locations of data records. Some locations include full community data while others represent individual taxon occurrences only. *Am B* Amundsen Basin, *Greenl. Sea* Greenland Sea, *LR* Lomonosov Ridge, *MJR* Morris Jesup Rise, *Norw. Sea* Norwegian Sea, *NWAP* Northwind Abyssal Plain, *NWR* Northwind Ridge





Greenland–Iceland–Norwegian (GIN) Seas were included for comparison (Fig. 1; Electronic supplemental material, Table 1). This list is based on morphological identifications by a wide range of investigators including taxonomic experts and parataxonomists. Taxa identified to genus or family level were only counted towards the unique taxon list when no species-level entry of that genus or family was in the dataset, but were otherwise deleted. Taxa identified by a single investigator as, for example, *Chone* sp. A–F, were counted towards the total species number only when not represented by other species-level entries for that genus. The list was standardized to the World Register of Marine Species (WoRMS, [www.marinespecies.org](http://www.marinespecies.org)) using the match function to avoid duplication due to misspellings, synonymies or differences in taxonomic classifications. Taxon names that could not ultimately be reconciled to WoRMS were kept in the dataset if they were found in other recognized species lists such as the Integrated Taxonomic Information System ([www.ITIS.gov](http://www.ITIS.gov)) or in recent publications. The few remaining taxa (<1%) were deleted.

#### Depth and latitudinal trends and other spatial patterns

Sampling effort per region, sample size, and taxonomic resolution differed among studies (Tables 1 and 2). The highest number of records for any taxon, and the best and reasonably consistent taxonomic resolution, were available for macrofaunal polychaetes from seven datasets with a total of 1,842 taxon records from 238 locations. Therefore, diversity indices were calculated only for polychaetes, with the goal of identifying patterns in Arctic deep-sea benthic diversity. Polychaete data were analyzed using the DIVERSE routine in PRIMER-6 software based on either station means or individual replicates, dependent on data availability. Alpha diversity indices were calculated for stations containing more than two polychaete taxa, thereby excluding 66 of 238 stations and eliminating the depth stratum >4,000 m (Table 2). We examined number of taxa (S), Pielou's evenness ( $J'$ ), Shannon-Wiener diversity ( $H'$ ), and average taxonomic distinctness (Delta +). For the calculation of the expected number of taxa found in 20 randomly chosen individuals ES(20), only samples containing equal to or more than 20 polychaete specimens were included, thereby reducing the number of samples to 127, excluding most samples with small sampling area (0.015–0.03 m<sup>2</sup>) and again those samples collected at great depths (Table 2). Delta+ is based on presence/absence and describes the average distance between all pairs of species in a community sample, with this distance defined as the path length through a standard Linnean tree connecting these species. Like ES(n), Delta+ is less sensitive to sampling effort than S or  $H'$  (Clarke and Warwick 1999, 2001; Magurran

2004). The aggregation file containing the taxonomic hierarchy for calculating Delta+ was created by WoRMS. Differences in diversity indices among groups (4 basins, 15 regions, 4 depth strata, 7 investigators and 4 sample sizes; Table 2) were assessed using one-way analyses of variance with post-hoc Tukey tests (Systat version 13). Taxon accumulation curves ( $S_{\text{obs}}$ , Chao-2) by sample with 95% confidence intervals were assembled for different regions and slope, ridge and abyss using EstimateS Software (Colwell 2000).

Depth and latitudinal trends were assessed through Pearson correlations for total abundance (individuals 10 cm<sup>-2</sup> for meiofauna, individuals m<sup>-2</sup> for macrofauna; insufficient information for megafauna) and total biomass (mg C m<sup>-2</sup>; macrofauna only). Where necessary wet-weight was converted to carbon assuming 1 mg C=0.034 mg wet weight (Rowe 1983). Spatial patterns in macrofaunal abundance and biomass were produced using ArcGIS version 9.1 (ESRI) with bin sizes determined according to a Jenks' natural breaks classification scheme. This scheme chooses breaks—relatively large jumps in the data values—in the ordered distribution of values that minimize the within-class sum of squared differences. Diversity indices for the polychaete data were regressed on depth and latitude, and the residuals of the depth–latitude and the diversity index–depth relationships were regressed against each other to test for the effect of latitude on diversity independent of depth (Lambhead et al. 2001; Renaud et al. 2006). Differences and similarities in polychaete community structure among major basins, regions, depth strata, investigators, and sample sizes were assessed using non-metric multidimensional scaling (MDS), analysis of similarity (ANOSIM) and similarity of percentages (SIMPER) using PRIMER-6 software.

## Results

### Inventory

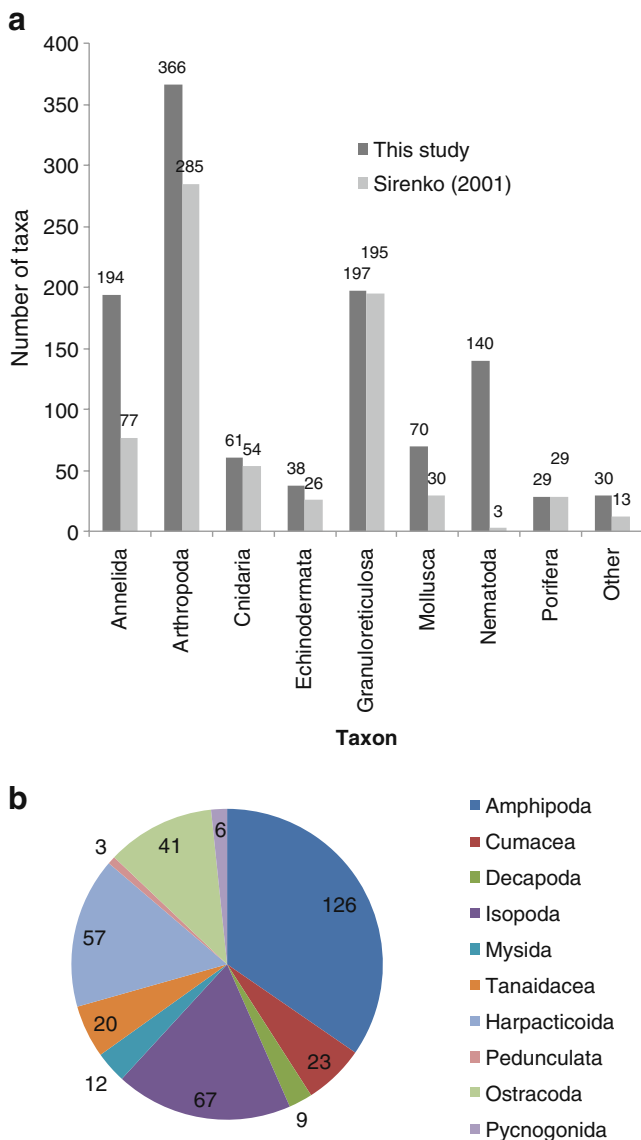
The compilation of 5,775 geo-referenced records (Table 1) yielded a total of 1,031 different taxa identified to genus or species level. The combination of these records with Sirenko's (2001) non-geo-referenced benthic deep-sea species inventory (712 taxa) yielded a total of 1,240 taxa (including GIN Seas), of which 1,125 taxa occurred only in the central Arctic (>500 m and north of 80°N in Fram Strait; Fig. 2a). Relative to Sirenko's (2001) deep-sea inventory, 413 new taxa were added to the Arctic proper through our effort. The biggest gain in species numbers relative to Sirenko (2001) were in the nematodes, annelids and arthropods (Fig. 2a). The most speciose groups were the arthropods, followed by the foraminiferans, annelids, and nematodes (Fig. 2a). Within the arthropods, amphipods were the most speciose, followed

**Table 2** Factors and number of stations therein used for comparisons of community structure (column *A*) and diversity indices (column *B* except for ES(20) for which column *C* applies) of Arctic deep-sea polychaetes

	A. Total number of polychaete samples	B. Samples with >2 polychaete taxa	C. Samples with >20 polychaete individuals
<b>Major Basins</b>			
Amerasian Basins	117	85	57
Eurasian Basins	48	25	24
North Atlantic Basins	45	45	33
Lomonosov Ridge	28	17	13
<b>Regions</b>			
Amundsen Basin	24	13	24
Amundsen Gulf	1	1	1
Beaufort Sea slope	24	24	23
Canada Basin	31	18	31
Chukchi Sea slope	21	16	21
Gakkel Ridge	2	0	0
Greenland Sea slope	29	29	24
Laptev Sea slope	16	16	0
Lomonosov Ridge	28	17	0
Makarov Basin	9	5	0
Mendeleev Ridge	12	4	0
Morris Jesup Rise	4	1	0
Nansen Basin	7	0	0
Northwind Abyssal Plain	8	7	0
Northwind Ridge	4	3	0
Svalbard slope	16	16	0
Yermak Plateau	2	2	2
<b>Depth strata</b>			
500–1000 m	58	54	50
>1,000–2,000 m	72	56	34
>2,000–3,000 m	62	47	34
>3,000–4,000 m	37	15	9
>4,000 m	9	0	0
<b>Investigators</b>			
Bluhm et al.	42	32	12
Carey	35	34	33
Clough et al.	33	9	0
Deubel	55	47	47
Kröncke	28	5	2
Schnack	29	29	21
Włodarska-K. et al.	16	16	12
<b>Sample size</b>			
0.015–0.03 m <sup>2</sup>	68	17	2
0.04–0.0625 m <sup>2</sup>	64	58	33
0.01 m <sup>2</sup>	51	50	45
0.25 m <sup>2</sup>	55	47	47

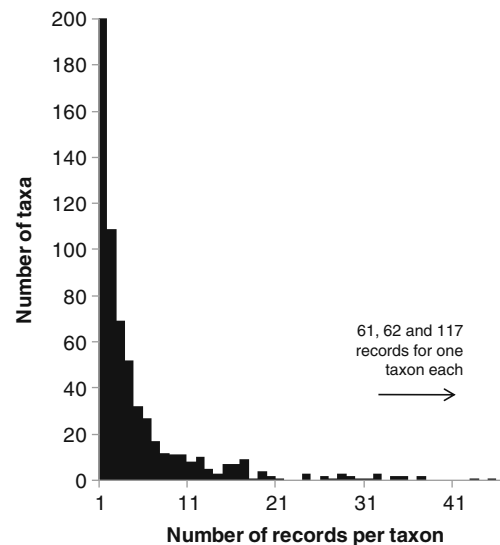
by isopods and harpacticoids (Fig. 2b). Taxa with very few species included bryozoans (1 species), echiurans (1), cephalorynchs (2), ciliophorans (1), and hemichordates (2). By number of records, the five most common species were the polychaete *Chaetozone setosa* (103 records), the scaphopod *Siphonodentalium lobatum* (62 records), the polychaete

*Myriochele heeri* (56 records), the holothuroid *Elpidia heckeri* (45 records), and the polychaete *Aricidea quadrilobata* (43 records). Within the arthropods, our most speciose group, the species with the most records were the tanaids *Akanthophoreus gracilis* (28), *Pseudospyrapus anomalus* (27), and *Pseudotanais affinis* (24).



**Fig. 2** Taxonomic composition of Arctic benthic deep-sea fauna a based on geo-referenced taxon records north of 80°N on Atlantic side compiled in this paper combined with the most complete previous inventory (Sirenko 2001) (dark bars) and based on Sirenko (2001) only (light bars), **b** for Arthropoda only (geo-referenced records from this paper combined with Sirenko 2001)

Of the geo-referenced records identified to species and genus level, nearly 50% were only found at only one or two locations (Fig. 3). In total, 601 of the geo-referenced taxa occurred from 500–<1,000 m, 425 from 1,000–<2,000 m, 267 from 2,000–<3,000 m, and 77 at  $\geq 3,000$  m, with some taxa occurring in several depth strata. The 254 taxa that only occurred deeper than 1,000 m in our dataset included recently described species such as the polychaetes *Terebellides irinae* (Gagev 2009) and *Sigambra healyae* (Gagaev 2008), and recent first records for the Arctic such as the polychaetes *Ymerana pteropoda*, and *Sosane bathyalis*



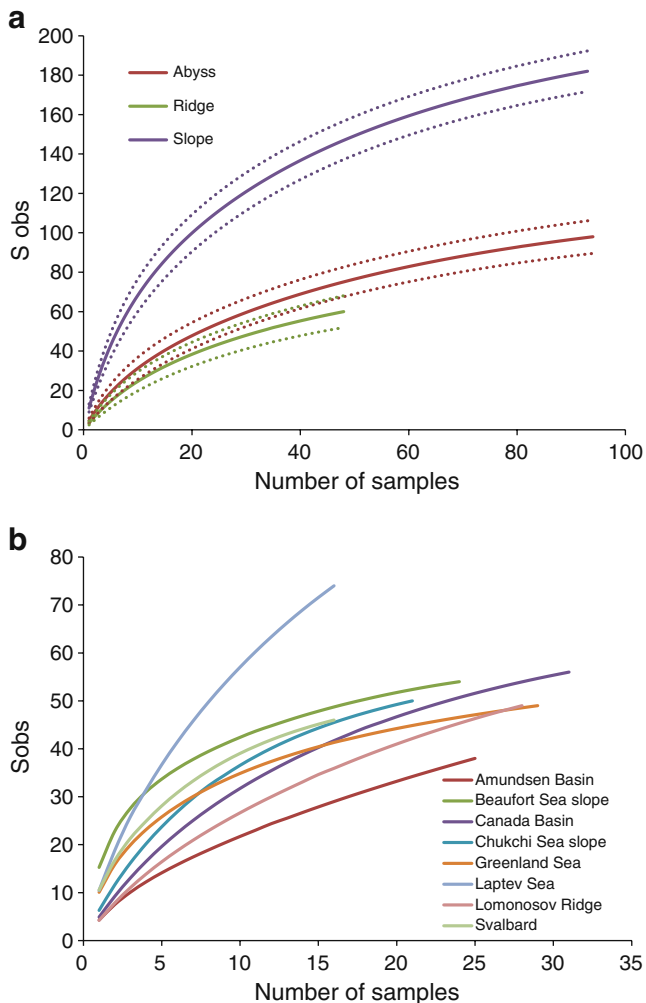
**Fig. 3** Distribution of the number of geo-referenced occurrence records per taxon (all taxonomic groups). Close to 50% of the taxa were only represented by one or two records in the dataset

(Electronic supplemental material, Table 1). The 268 taxa that only occurred shallower than 1,000 m included typical and common shelf species such as the amphipods *Ampelelisca eschrichti* and *Byblis gaimardi*, the cumacean *Dia-stylis rathkei*, the polychaetes *Phyllodoce (Anaitides) groenlandica* and *Maldane sarsi*, and the ophiuroid *Ophiura sarsii*. None of the species accumulation curves reached an asymptote (Fig. 4). The initial slope of the curves was greater for continental slope than for ridge and abyssal samples with no overlap of the 95% confidence intervals (Fig. 4a). Confidence intervals (not shown) overlapped for most regions in the species accumulation curves by region, where values were lowest for the Amundsen Basin and highest for the Laptev Sea (Fig. 4b). It is noteworthy, however, that abyssal samples typically had fewer individuals than slope samples and sampling area differed widely between studies (Tab. 1).

#### Latitudinal and depth trends

All observations encompassed large ranges. Total meiofaunal abundance for individual samples ranged from 72 to 4,673 individuals  $10 \text{ cm}^{-2}$  (Table 3). Total macrofaunal abundance and biomass for individual samples ranged from 0 to 9,848 individuals  $\text{m}^{-2}$  and from 0 to 2,810  $\text{mg C m}^{-2}$ , respectively (Fig. 5). Total megafaunal abundance in individual photographs ranged from 0.1 to 112 individuals  $\text{m}^{-2}$  with much greater overall values for HAUSGARTEN stations than Canada Basin stations (Table 3). Meiofaunal abundance, macrofaunal abundance and macrofaunal biomass were significantly and negatively correlated with water depth and latitude, despite considerable variability (Table 4).





**Fig. 4** Species accumulation curves ( $S_{\text{obs}}$ ) for Arctic deep-sea polychaete samples for **a** slope, ridge and abyssal stations, and **b** for those regions that contained 16 or more samples. Means and 95% confidence intervals (CI) are given for (a), but (CI) were omitted for (b) to enhance clarity

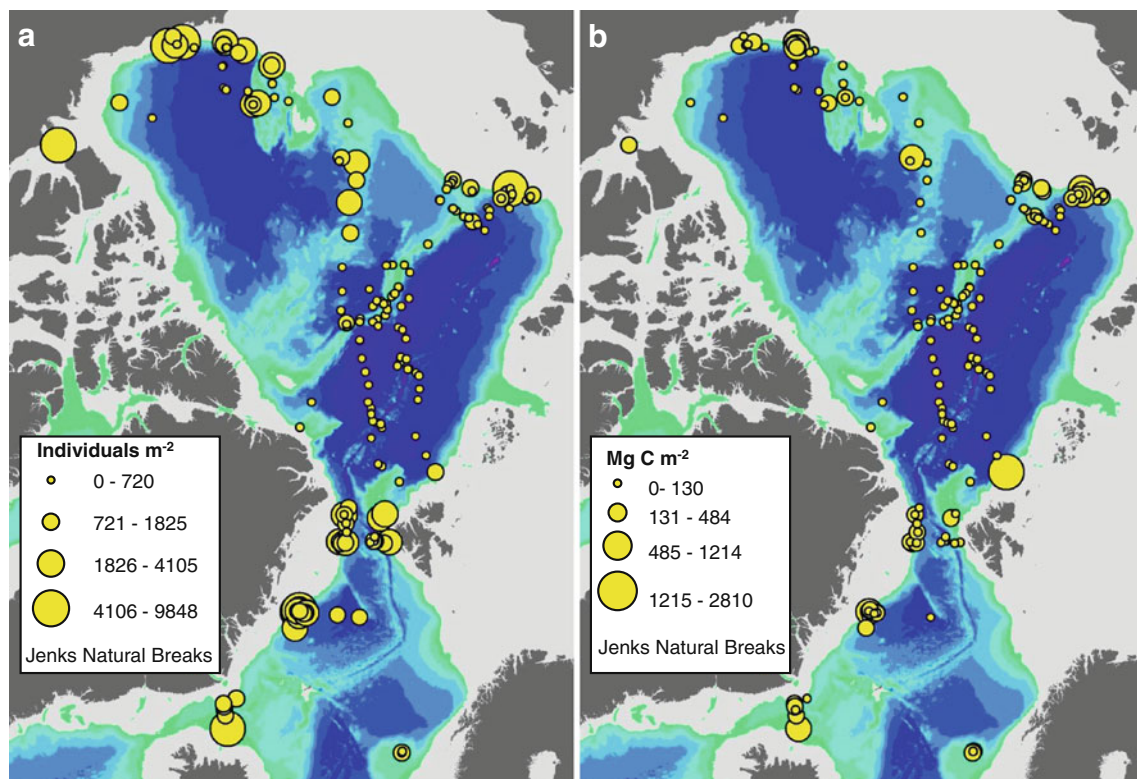
Insufficient meiofaunal biomass, megafaunal abundance and megafaunal biomass data were available to test relationships (but see Soltwedel 2000 for a larger meiofaunal data set).

For the macrofaunal polychaetes, the diversity indices  $S$ ,  $H'$ , and  $\Delta+$  significantly decreased with depth and latitude, while  $J'$  increased significantly (Table 5). Likewise, the regressions of residuals of those indices against depth on the residuals of latitude against depth were significant (i.e., depth and latitude were confounded).  $ES(20)$  significantly decreased with depth but not with latitude, and the regression of residuals of  $ES(20)$  against depth on the residuals of latitude against depth was not significant. In all significant cases, only 28% or less of the variability in the data was explained by depth or latitude, and only 16% or (much) less was explained by latitude alone (Table 5).

### Spatial patterns: polychaetes

The community structure of macrofaunal polychaetes differed little among major basins, depth strata or sample sizes, with global  $R$  values from 0.10–0.27, although larger differences were found for some of the pairwise comparisons (ANOSIM; Table 6; Fig. 6a). Specifically, the community structure in samples from >4,000 m depth was different from the shallowest samples, and the Greenland Sea, Svalbard and Beaufort Sea slope samples differed greatly from other regions (Table 6). The community structure was significantly different among regions and investigators, with intermediate global  $R$  values of 0.41 and 0.46, respectively (ANOSIM; Fig. 6a, b; Table 6). It must be noted that all investigator teams, except Clough et al., studied only one particular region (Table 1). Dissimilarities of the polychaete fauna among pairs of regions with the highest  $R$  statistic (Table 6) were over 95% (SIMPER). The most similar regions in terms of their polychaete fauna were the Greenland Sea slope and Svalbard (22%), Svalbard and the Laptev Sea slope (13%), and Svalbard and the Lomonosov Ridge (13%). Within-region similarity was highest for the Beaufort Sea slope and Svalbard (both 49%) and the Greenland Sea slope (41%). SIMPER analysis showed that the separation by investigator was partly caused by differing taxonomic resolution, for example taxonomic identification as *Terebellidae*, could have been the same species identified by another investigator as *Terebellides* sp. or a third investigator as *Terebellides stroemi*. We, therefore, repeated the analysis on the family level. This reduced the number of taxa for analysis from 224 to 46. In this case, the separation of polychaete community structure by regions and by investigators was much smaller (Global  $R=0.27$ ,  $p<0.001$  in both cases; Fig. 6c, d) and remained minor by major basins and depth strata (Global  $R=0.06$  and  $R=0.15$ , respectively,  $p<0.001$  in both cases).

When stations containing less than 3 polychaete taxa were excluded,  $S$  ranged from 3 to 41 for individual stations,  $ES(20)$  ranged from 2.9 to 12.1,  $J'$  ranged from 0.3 to 1,  $H'$  ranged from 0.4 to 3.0, and  $\Delta+$  ranged from 77.8 to 100 (means and SD in Fig. 7 and 8). Basin-wide patterns showed significant differences for  $ES(20)$ ,  $J'$ ,  $H'$ , and  $\Delta+$  with differences primarily due to higher values in the North Atlantic (except for  $J'$ ) compared to the Amerasian deep sea (Fig. 7). Regional differences were significant for all indices except for  $\Delta+$  and were primarily due to high values for the Greenland Sea ( $ES(20)$  and  $H'$ ), higher  $S$  or lower  $J'$  values for the Beaufort Sea slope, and low values for the Northwind Ridge ( $ES(20)$ ,  $J'$ ,  $H'$ ). Differences among depth strata were significant for  $S$ ,  $J'$  and  $H'$  with highest and lowest values for 500–1,000 m samples ( $S$  and  $J'$ , respectively), and lowest values for deep samples ( $H'$ ). Differences among investigators were significant for all indices except  $\Delta+$ ,



**Fig. 5** Distribution of total macrofaunal abundance and biomass in the Arctic deep sea with highest values found generally along the slopes. The legend of the depth contours is in Fig. 1

and were primarily due to particularly high  $S$  and low  $J'$  values for Carey, and high values for Schnack (ES(20),  $H'$ ) (Fig. 8). Effects of sample size were significant for  $S$ , ES(20) and  $J'$  and were due to highest  $S$  and lowest  $J'$  for 0.1 m<sup>2</sup> samples and highest ES(20) values for 0.04–0.0626 m<sup>2</sup> samples. For four of five groupings, Delta+ was not significantly different.

## Discussion

### Taxonomic patterns

Our taxonomic inventory increased the number of Arctic deep-sea species relative to the most recent list (Sirenko 2001) by more than 400 taxa (and by more than 500 if GIN Seas are included). This increase occurred mostly in the nematodes, annelids and arthropods (Fig. 2). While Sirenko acknowledged that nematodes had poor representation in his list, large gains in annelids and arthropods arise largely because they are the most speciose metazoans in his list, and in most soft-bottom habitats around the world. Nonetheless, we know that our inventory remains incomplete based on the lack of an asymptote in the species-accumulation curves (Fig. 4), the poor sampling

coverage in the study area, and the likelihood that datasets not included in our analysis contain additional taxa (e.g., Paul and Menzies 1974; Vanreusel et al. 2000). A reasonable estimate of the actual total number of Arctic benthic deep-sea species can be obtained from the polychaete species-accumulation curves. The Chao-2 estimate for polychaetes from the species-accumulation curve was  $282 \pm 19$  (mean  $\pm$  SD). Polychaetes represented 17% of all species in our list, so assuming other groups in the inventory are equally incomplete then we would predict a total of  $\sim 1,660$  species;  $\sim 420$  more than currently in our list. Alternatively, Chao-2 estimated 56 (=25%) more species than  $S_{\text{obs}}$ , and adding 25% to all species gives 310 more species for a total of 1,550. These estimates all assume that we have adequately and representatively sampled the heterogeneity present in the Arctic basin. This is probably not the case: for example, the sampling locations were rather unevenly distributed with particularly large gaps on the eastern side of the Canada Basin, and at depths  $>3,000$  m (Fig. 1). Increased sampling in these areas is expected to yield higher total species richness estimates. The number of currently known polychaete taxa may be lower in the Arctic deep sea than in other deep-sea basins of similar size (Table 7), although comparability of the referenced studies is

**Table 3** Abundance and biomass values for Arctic deep-sea meio-, macro- and megafauna

Size fraction	Depth category (m)	Abundance (individuals m <sup>-2</sup> )					Biomass (mg C m <sup>-2</sup> )				
		Mean	SD	Min	Max	<i>n</i>	Mean	SD	Min	Max	<i>n</i>
Meiofauna	All depths	1,242 <sup>a</sup>	1,160	72	4,673	86	Data not taken				
	500–1,000	1,385 <sup>a</sup>	944	243	3,305	12					
	>1,000–2,000	1,226 <sup>a</sup>	983	113	3,955	24					
	>2,000–3,000	1,729 <sup>a</sup>	1,414	116	4,673	30					
	>3,000–4,000	453 <sup>a</sup>	530	72	1,743	14					
	>4,000	435 <sup>a</sup>	389	86	1,094	6					
Macrofauna	All depths	937	1,227	0	9,848	257	140	272	0	2,810	253
	500–1,000	2,295	2,057	56	9,848	44	436	569	18	3,061	44
	>1,000–2,000	840	708	8	953	93	157	172	1	953	92
	>2,000–3,000	791	694	8	2,767	55	116	694	1	2,810	55
	>3,000–4,000	271	385	0	1,741	46	19	31	0	130	44
	>4,000	104	60	4	250	19	10	11	1	37	18
Megafauna	All depths	28/2.1	19	4	112	5(225)/6(2,134)	Data not taken				
	500–1,000	6.8	6.5	0	36	1(153)					
	>1,000–2,000	35/0.1	14/0.1	14/0	112/1.3	2(104)/1(283)					
	>2,000–3,000	11/3.2	5/1.7	4/0	25/9.8	2(107)/2(855)					
	>3,000–4,000	0.9	0.5	0	2.8	2(260)					
	>4,000	35	3	30	40	1(14)					

Only two datasets were available for megafauna abundances, which differed greatly between the HAUSGARTEN area and the Canada Basin (in italics), hence their data are presented separately. Sample size (*n*) for megafauna is given as the number of stations, with the number of photographs per station in parentheses

<sup>a</sup> Individuals 10 cm<sup>-2</sup>

complicated by differences in habitat area, depth range, and other methodological differences.

Of the commonly recorded Arctic benthic deep-sea taxa, several are widely distributed, eurybathic species also found on the Arctic and GIN Seas shelves such as the polychaete *Myriochele heeri*, the tanaid *Pseudotanaeis*

**Table 4** Pearson correlations of meiofaunal and macrofaunal abundance and macrofaunal biomass versus depth and latitude, respectively

Correlation	Pearson's correlation coefficient	<i>n</i>	<i>p</i>
Abundance meiofauna × depth	−0.213	86	0.049
Abundance macrofauna × depth	−0.428	229	<0.001
Biomass macrofauna × depth	−0.449	247	<0.001
Abundance meiofauna × latitude	−0.622	86	<0.001
Abundance macrofauna × latitude	−0.481	229	<0.001
Biomass macrofauna × latitude	−0.368	247	<0.001

*affinis*, and the asteroid *Pontaster tenuispinus* ([www.iobis.org](http://www.iobis.org)). This distribution demonstrates the strong influence of the Arctic shelf fauna (see discussion below) on the deep sea: a comparison of our list with a parallel shelf benthos effort showed that ~60% of the macro- and megabenthic deep-sea species are shared with the Arctic shelves (Piepenburg et al. 2010). Other common Arctic deep-sea benthic taxa also dominate in other areas of the world's deep sea, for example the well-studied NE Atlantic Rockall Trough (Pain et al. 1982; Tyler et al. 1982; Billett et al. 2001). Examples include elasipodid sea cucumbers, represented in our dataset by the comparatively small species *Elpidia heckeri* and *Kolga hyalina*, and the sea stars *Bathybiaster vexillifer* and *Pontaster tenuispinus*. The ability of many elasipodids to take advantage of sedimentation events, and their fine trophic niche partitioning (Roberts et al. 2000; Iken et al. 2001), apparently contribute to the success of this group. Isopods and amphipods, taxa that are particularly speciose and widespread in other deep-sea areas including the Antarctic (Brandt et al. 2004), were relatively speciose in the Arctic deep sea as well. It is notable that both these groups had a high degree of

**Table 5** Relationships between diversity indices, depth and latitude (*Lat.*) and of diversity index–depth residuals (*Resid.*) and latitude–depth residuals

Regression	$R^2$	<i>p</i> value
S × Latitude	0.219	<0.001
S × Depth	0.279	<0.001
Resid. S–depth × resid. Lat.–depth	0.149	<0.001
ES <sub>(20)</sub> × Latitude	<u>0.003</u>	<u>0.519</u>
ES <sub>(20)</sub> × Depth	0.133	<0.001
Resid. ES <sub>(20)</sub> –depth × resid. Lat.–depth	<u>0.011</u>	<u>0.127</u>
H'log <sub>e</sub> × Latitude	0.195	<0.001
H'log <sub>e</sub> × Depth	0.253	<0.001
Resid. H'log <sub>e</sub> –depth × resid. Lat.–depth	0.126	<0.001
J' × Latitude	0.179	<0.001
J' × Depth	0.025	0.015
Resid. J'–depth × resid. Lat.–depth	0.164	p<0.001
Delta+ × Latitude	0.192	<0.001
Delta+ × Depth	0.171	<0.001
Resid. Delta+ × resid. Lat.–depth	0.131	<0.001

Non-significant regressions are underlined

rareness, with only one species of each found at more than 10 locations. The lack of epibenthic sled samples in our dataset is perhaps an underlying cause of the patchy and incomplete crustacean spatial patterns, since this gear

efficiently samples the epi- and suprabenthic amphipods and isopods (Brandt et al. 2004).

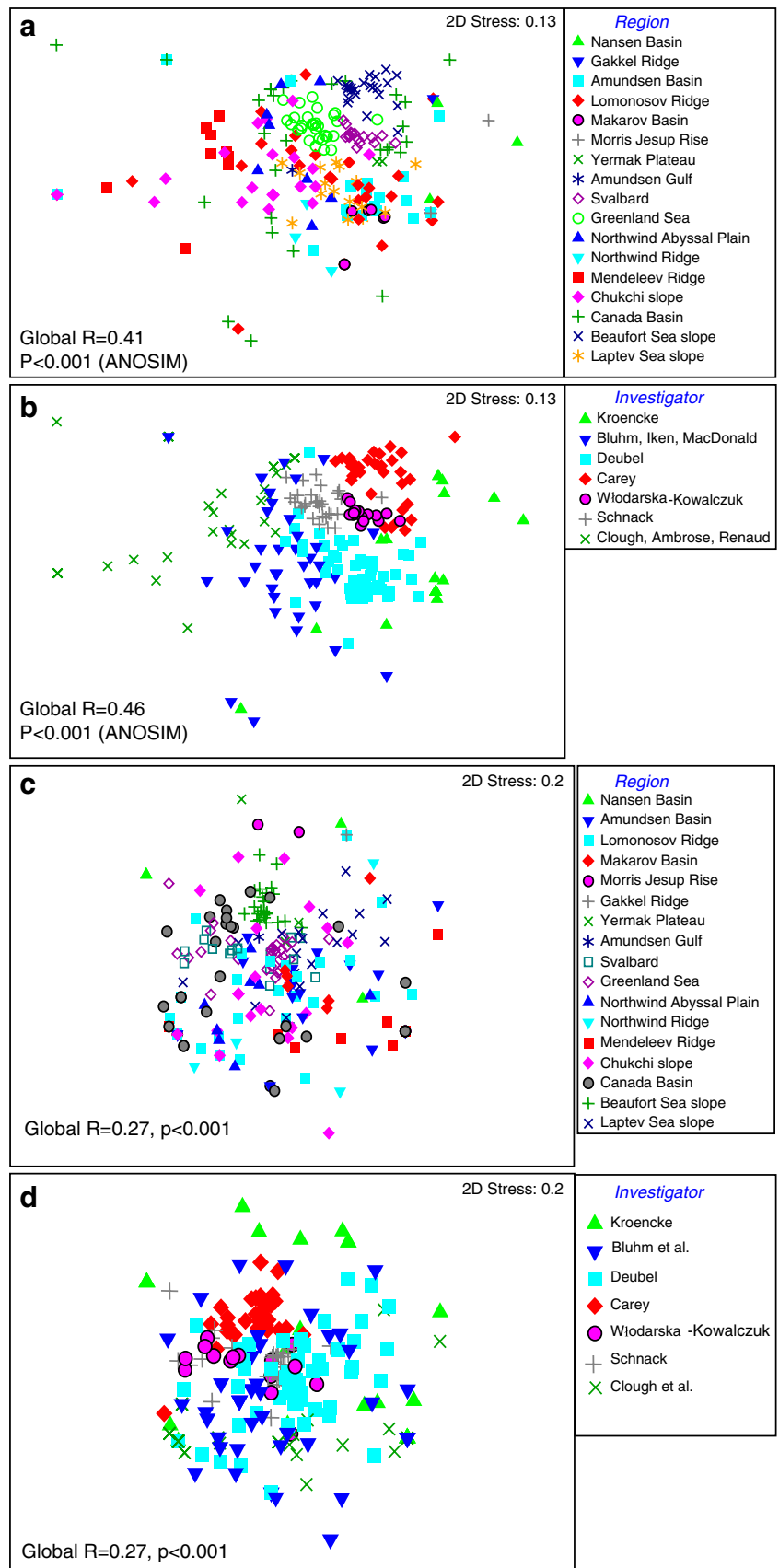
Several phyla previously found to be species poor in the Arctic deep sea continue to be classified as such based our

**Table 6** Analysis of similarity (ANOSIM) for the entire polychaete community based on presence/absence data

Group	<i>R</i> Statistic	Significance level
Major basins	<b>0.10</b>	<b>&lt;0.001</b>
Lomonosov Ridge, North Atlantic	0.81	<0.001
Regions	<b>0.41</b>	<b>&lt;0.001</b>
Lomonosov Ridge, Beaufort Sea	0.96	<0.001
Lomonosov Ridge, Svalbard	0.88	<0.001
Lomonosov Ridge, Greenland Sea	0.96	<0.001
Beaufort Sea, Svalbard	0.98	<0.001
Beaufort Sea, Greenland Sea	0.98	<0.001
Beaufort Sea, Chukchi slope	0.70	<0.001
Beaufort Sea, Laptev Sea	0.95	<0.001
Greenland Sea, Laptev Sea	0.86	<0.001
Depth strata	<b>0.11</b>	<b>&lt;0.001</b>
>4,000 m, 500–1,000 m	0.56	<0.001
Investigator	<b>0.46</b>	<b>&lt;0.001</b>
Carey, Włodarska-Kowalczyk	0.88	<0.001
Carey, Schnack	0.93	<0.001
Sample size	<b>0.27</b>	<b>&lt;0.001</b>

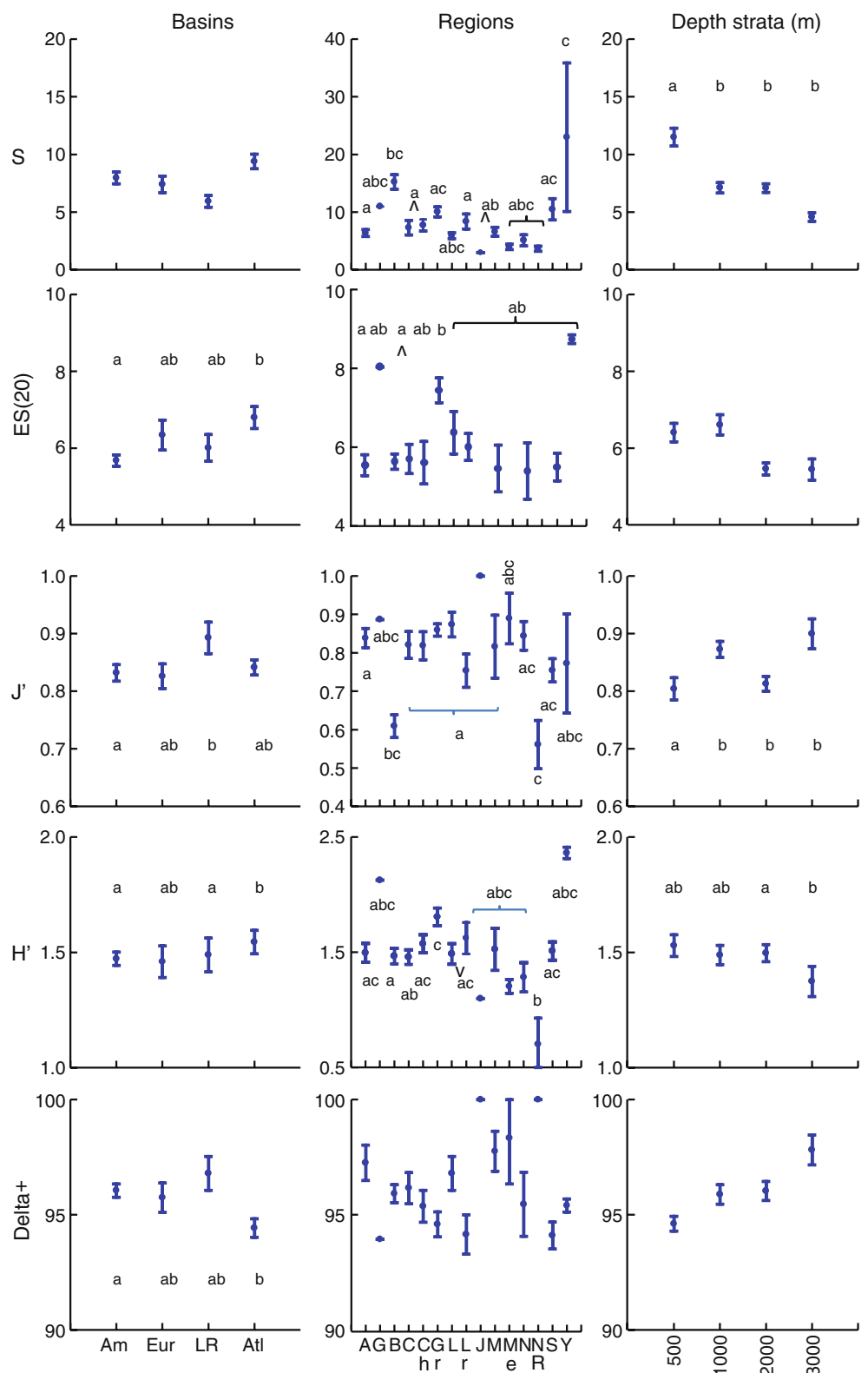
Significant results for Global *R* (in bold) and pairwise comparisons (only where  $R > 0.7$ ,  $p < 0.05$  and for regions containing >15 samples)

**Fig. 6** Multidimensional Scaling plots of Arctic deep-sea polychaete communities by species (**a, b**) and families (**c, d**) and color-coded by region (**a, c**) and investigator (**b, d**)



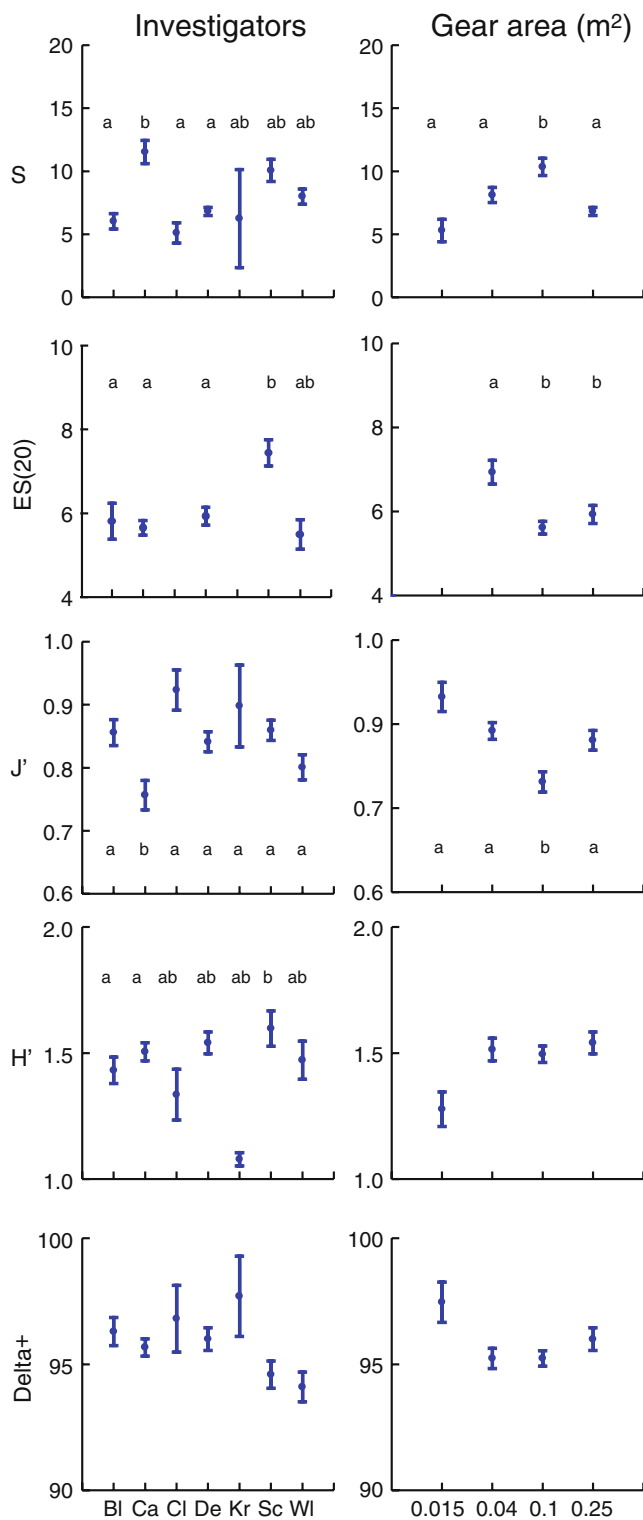


**Fig. 7** Means ( $\pm$ SE) of diversity indices S, ES(20), J', H', and Delta+ by major basins, regions, and depth strata for Arctic deep-sea polychaete communities. Significant differences are indicated by letters. ES(20) was calculated only for samples that contained 20 or more polychaete individuals which reduced the number of regions relative to the other diversity indices. A Amundsen Basin, Am Amerasian Arctic, Atl North Atlantic, B Beaufort Sea, C Canada Basin, Ch Chukchi Sea slope, Eur Eurasian Arctic, G Amundsen Gulf, Gr Greenland Sea, J Morris Jesup Rise, L Laptev Sea slope, Lr Lomonosov Ridge, M Makarov Basin, Me Mendelev Ridge, N Northwind Abyssal Plain, NR Northwind Ridge, Sv Svalbard slope, YP Yermak Plateau. Depth strata: 500 500–1,000 m, 1000 >1,000–2,000 m, 2000  $\pm$ 2,000–3,000 m, 3000  $\pm$ 3,000 m



dataset. Some taxa are species poor throughout the world's oceans such as the echiurans with ~160 species worldwide and 2 of those in the Arctic (Murina, unpublished), and the priapulids with 18 species globally and a high portion of

those (4) in the Arctic (Adrianov, unpublished). In contrast, more than 300 species of bryozoans occur on Arctic shelves (Sirenko 2001; Kuklinski, personal communication) and reports on encrusting fauna, including bryozoans, on drop



**Fig. 8** Means ( $\pm$ SE) of diversity indices S, ES(20), J', H', and Delta+ by the confounding factors, investigators and sample size for Arctic deep-sea polychaete communities. Significant differences are indicated by letters. ES(20) was calculated only for samples that contained 20 or more polychaete individuals which reduced the number of gear sampling size. Bl Bluhm et al., Ca Carey, Cl Clough et al., De Deubel, Kr Kroencke, Sc Schnack, Wl Włodarska-Kowalczyk et al. Gear sample size categories: 0.015 0.015–0.03 m<sup>2</sup>, 0.04 0.04–0.0625 m<sup>2</sup>, 0.1 0.1 m<sup>2</sup>, 0.25 0.25 m<sup>2</sup>

stones in the Greenland Sea (Schulz et al. 2010) suggest our list under-represents bryozoans and probably other taxa from this poorly sampled habitat. Within the arthropods, crabs were absent altogether from our dataset as is typical for the high-latitude deep sea. The scarceness of large organisms or organic falls (from phyto-detritus to whales) may also limit the occurrence of large scavengers in these areas.

That about half of all taxa in our dataset were recorded from only one or two locations agrees with the global observation that deep-sea communities have a high proportion of rare species compared to shelf communities (Glover et al. 2002; Rex and Etter 2010). The high level of rareness and endemism (estimated at 50–80% in the Arctic deep sea - Vinogradova 1997) may be overestimated because of the relatively low sampling intensity. However, other deep-sea areas in the Atlantic, including Porcupine Abyssal Plain (4,800 m), Rockall Trough permanent station (2,900 m) and Cap Verde Abyssal Plain (4,800 m), also have high rareness values of over 60% (G. Paterson, personal communication). The large proportion of rare taxa hinders elucidation of the Arctic basin's relationships to the Atlantic and Pacific deep sea and its species dispersal pathways (Vinogradova 1997). However, the minor separation of the polychaete community structure between the Arctic and North Atlantic basins supports the common view that the modern Arctic deep-sea fauna is closely related to the modern North Atlantic abyssal fauna (e.g., Filatova 1957). Modern Pacific elements are rare, but it is noteworthy that some fauna is secondarily Atlantic and originally Pacific (Golikov and Scarlato 1990). The modern Arctic fauna is thought to be young, of Pleistocene age (Guryanova 1970), and the invasion by benthic organisms from the North Atlantic to higher latitudes is probably still occurring (Guryanova 1938). Repeated invasions of shelf fauna are thought also to be an origin of Arctic deep-sea fauna (e.g., Andriashev 1953) and the relatively high number of species shared with the Arctic shelves in our data set (60% of the deep-sea fauna) supports this interpretation.

**Depth and latitudinal trends**

Meiofaunal abundance, macrofaunal abundance and macrofaunal biomass in our study decreased with water depth. This result agrees with a well-documented global trend (Rex et al. 2006; Wei et al. 2011), although some bias was introduced into our analysis by the different mesh sizes used (see Gage et al. 2002 for effects of different mesh sizes on abundance and biomass estimates). The decrease in abundance was greater for macro- than meiofauna, corroborating previous findings of an average decrease in metazoan size with depth (Thiel 1975; Rex and Etter 2010) and the consequent increasing importance of small

**Table 7** Polychaete species richness determined for different deep-sea areas

Region	Area (m <sup>2</sup> )	Depth range (m)	Polychaete taxa	Sieve size (μm)	Reference
Arctic Basin slopes and abyss	26.4+	500–4,190	194	250–1,000	This study
NW Atlantic slope	21	1,500–2,500	385	300	Grassle and Maciolek 1992
Porcupine Abyssal Plain	1.25	4,800	101	300–1,000	Glover et al. 2001
Northeast Pacific slope and abyss	6.8	550–3,100	382	300	Hilbig and Blake 2006
Central Pacific abyss I	19.25	4,800–5,100	183	300	Glover et al. 2002
Central Pacific abyss II	2.94	4,300–4,800	177	300	Glover et al. 2002
Antarctic, deep Weddell & Scotia Seas	1.94	1,138–5,194	90	300–500	Hilbig 2004

organisms (Pfanckuche and Soltwedel 1998; Rex et al. 2006). Abundance and biomass decreases with depth are linked to decreasing food availability as both primary production and lateral input from the shelves drop (Gosselin et al. 1997; Rex et al. 2006). In the Arctic, the increase in depth roughly coincides with an increase in latitude and, hence, increased seasonality in primary production and thickness and persistence of the ice cover exacerbate the depth effect. Nevertheless, the overall range of macrofaunal abundance (0–9,848 ind m<sup>-2</sup>, mostly below 4,000 ind m<sup>-2</sup>) in the depth range considered falls within the lower end of values for the temperate and sub-Arctic North Atlantic (50–55,000 ind m<sup>-2</sup>, but mostly <4,000 ind m<sup>-2</sup>). The same holds true for macrofaunal biomass: 0–2.8 g C m<sup>-2</sup> but mostly <1 g C m<sup>-2</sup> in the Arctic deep sea versus <0.01–50 g C m<sup>-2</sup> but mostly <4 g C m<sup>-2</sup> in the North Atlantic (Levin and Gooday 2003). Meiofaunal abundances in our data set (72–4,673 ind m<sup>-2</sup>) also did not generally differ from those at temperate eastern Atlantic locations in the same depth range (20–2,604 ind m<sup>-2</sup>; Soltwedel 2000; Levin and Gooday 2003). More detailed comparisons and discussion of depth trends and sampling-related caveats can be found in Soltwedel (2000) and Levin and Gooday (2003).

Like abundance and biomass, the diversity indices *S*, *H'*, and *Delta+* also decreased with latitude and depth, but the decrease was generally quite small. *ES*(*n*), an index less dependent on sampling effort than *S* and *H'*, did not significantly decrease with latitude. Globally, more pronounced latitudinal clines in diversity than we have recorded were found in different habitats and taxa (e.g., Rex et al. 1993; Boucher and Lambshead 1995; Hillebrand 2004; but see Renaud 2009). Evolutionary and ecological causes that have been proposed for these gradients focus primarily around energy and history (Rohde 1992; Jablonski et al. 2006). Our observations fit with the global trend that diversity tends to be low at low production regimes (the central basins) and higher at intermediate production levels (Arctic shelves and Greenland/Norwegian Basins) (reviewed in Waide et al. 1999; Levin et al. 2001;

see also Whitman et al. 2008). The small to moderate decrease of several diversity indices with latitude, however, and the lack thereof for *ES*(20), as well as the high variability at similar latitudes, all suggest that variability in total energy input is only of minor importance. Comprehensive exploration of latitudinal diversity gradients and their underlying cause(s) are probably best restricted to consistently collected data that extend beyond the regional scale (Renaud et al. 2009 and unpubl.). Hopefully, our data set will contribute to such future evaluations of latitudinal gradients in the global deep sea.

The continuous decrease in most diversity indices with water depth is in contrast to a considerable body of literature that documents a peak in diversity (mostly species richness) at mid-depths around 1,500–3,000 m (summarized in Rex and Etter 2010). Most data sources underlying this paradigm are from the Atlantic, but a peak in isopod diversity was also found at 3,000 m in the Antarctic (Brandt et al. 2004). In the Arctic, the known species richness does not appear to follow this pattern: the number of (macro- and megafaunal) species on the shelves is ~2600 with a predicted total number of 3,900–4,700 (Piepenburg et al. 2010), thus at least double the number we assembled and predicted for the bathyal and abyssal areas. Other authors also describe a lack of a mid-depth peak of diversity in the deep Norwegian Sea (Dauvin et al. 1994; Levin et al. 2001), the central Arctic (Deubel 2000; Renaud et al. 2006) and the Canada Basin (Bluhm et al. 2005). Nonetheless, in the Eurasian Arctic deep sea, a mid-depth peak occurs for macrofauna (Kröncke 1998) and an increase occurs with depth for Foraminifera (Wollenburg and Kuhnt 2000).

Different causes are conceivable for the apparent differences in depth-related patterns between the deep Arctic and Atlantic. Firstly, the Arctic deep sea is heavily under-sampled relative to the Arctic shelves, so the true species richness in the bathyal might indeed rival that on the shelves. Secondly, the presence of Pacific species adds to the species richness of the modern Amerasian Arctic shelf fauna (Dunton 1992). In contrast, the Arctic deep-sea fauna is isolated from the deep Pacific, and the rather stenobathic

Pacific Arctic shelf fauna does not penetrate into bathyal depths (Dahl 1972; Bilyard and Carey 1980; Nesis 1984) like the eurybathic Atlantic Arctic shelf fauna does. Thirdly, it is conceivable that influences thought to enhance diversity such as high sediment heterogeneity, intermediate biotic disturbance, food availability and flow strength levels, and high bottom water oxygen concentrations (reviewed in Levin et al. 2001) may prevail on the Arctic shelves rather than the slopes. Nevertheless, some factors known to decrease diversity, such as low salinity, also prevail on the shelves (Cusson et al. 2007). These latter possibilities require a detailed environmental evaluation that is beyond the scope of this paper. Until mechanisms responsible for generating spatial and depths patterns of diversity are more clearly defined and tested, reasons for the presence or lack of bathyal peaks in Arctic diversity remain elusive.

#### Basin-wide and regional patterns or sample bias

On the basin-scale, our multivariate analysis of the polychaete fauna supports previous findings that the prominent Lomonosov Ridge does not cause major or abrupt differences in faunal community composition between the Amerasian and Eurasian basins (Koltun 1964; Deubel 2000; Kosobokova et al. 2010). Gaps in the ridge and the circulation regime bringing Atlantic deep water all the way into the Canada Basin apparently support sufficient larval dispersal to connect communities on either side of the ridge. The absence of Pacific influence on the modern Arctic deep-sea fauna (see above) contributes to this relative similarity of the (polychaete) fauna on a pan-Arctic scale when one discounts the high fraction of poorly-characterized rare species. Of the species originating in the GIN Seas, one might suspect that species with long-lived pelagic stages capable of long-distance dispersal might be dominant, a hypothesis we propose should be tested in the future.

While community structure varied little on a basin-scale, several diversity indices did significantly differ, with higher values for ES(20), higher H', and lowest Delta+ in the GIN Seas samples versus the Amerasian Basins, and intermediate levels for the Eurasian Basins (Fig. 7). This pattern has previously been attributed to submergence of slope and shelf species to greater depths in the Greenland and Norwegian Seas than in the central Arctic basins, rather than to higher numbers of true deep-sea species (Vinogradova 1997). In addition, the overlap of boreal and Arctic faunas in the GIN Seas may add to the observed pattern. Lowest S, ES(20) and H' in the Amerasian Basin compared to both the Eurasian and GIN Basins may reflect a decreasing extent of species immigration from the Atlantic towards the Amerasian Arctic. Compared to the Atlantic basins south

of the GIN Seas, species richness in Arctic and sub-Arctic basins is thought to be lower because of the relative geographic isolation (Dahl 1972; Dauvin et al. 1994). The faunal patterns in the basins suggest that evolutionary history rather than present ecological factors appear to shape the large-scale diversity patterns.

On the regional scale of individual sub-basins, slopes and ridges, some differences were apparent from the multivariate analysis and the comparison of diversity indices of the polychaete fauna. Differences among investigators, however, often coincided with these regional differences, making it difficult to separate study bias from true regional patterns, and illustrating the importance of reliable taxonomic identification to species level (Fig. 6). We illustrate this using the largest regional difference in the polychaete community based on the multivariate analysis: between the Beaufort Sea slope and many other regions including the nearby Chukchi Sea slope. Like the remaining Arctic deep sea, the Beaufort Sea slope is dominated by Atlantic–boreoarctic species and endemics, and characterized by the absence of Pacific–boreoarctic species (Bilyard and Carey 1980). Identifying the taxa that separated the Beaufort Sea slope from the other regions (data not shown) revealed three types of species: (1) species that only occurred on the Beaufort Sea slope, or only in the combined areas of the Beaufort Sea slope and the adjacent Canada Basin, (2) species that occurred in comparatively high abundances on the Beaufort Sea slope and in lower abundances in other regions, and (3) species that we consider 'artificially different' from other regions, because of taxonomic problems.

Taxa groups 1 and 2 may reflect real spatial differences, albeit with limitations. The first group included, for example, *Capitella capitata* and *Sigambra tentaculata*. The observation of *Sigambra tentaculata* in the deep Beaufort Sea, rather than their typical distribution in shallow waters of California, suggests these records belong to the closely related species *Sigambra healyae*, recently described from the Canada Basin (Gagaev 2008). *Capitella capitata*, although only found in the Beaufort Sea slope samples in our dataset, may be of limited value as a discriminating species among regions because it consists of at least six sibling species with minor morphological differences (Grassle and Grassle 1976). The third group included, for example, *Lumbrineris minuta*, while all other investigators identified specimens from this genus as *Lumbrineris* sp., which can induce artificial differences among regions. Differences in sieve size between studies also added to artificial differences between regions (see Gage et al. 2002 for extensive discussion of sieve size effects on diversity estimates). The above examples, and the rather small separation of regional communities on the family level, suggest that the regions are overall only at

most modestly different in polychaete community structure. This implies a common species pool consisting of deep-sea and shelf taxa. In contrast to the basin-scale discussed above, environmental and ecological factors may be more likely to explain regional differences within basins than evolutionary ones, since the former vary on smaller scales.

#### Summary and outlook

Our study documented a larger number of Arctic benthic deep-sea species than previously recorded (>1,100 versus ~700 a decade ago), and predicts the addition of at least several hundred more with continued sampling effort. Globally-documented decreases of abundance and biomass with depth were confirmed for Arctic meio- and macrofauna. For the polychaete fauna, a decrease of four diversity indices with latitude and depth was significant but minor, and non-significant for latitude for ES(20). There was no indication of a mid-depth peak in any of the diversity indices employed. We found no separation of the polychaete fauna by the Lomonosov or other ridges, but a high connectivity of the central Arctic to the North Atlantic (GIN Seas) and Arctic shelf faunas, with very limited contemporary connectivity to the Pacific fauna. Regional differences exist but are probably minor, although confounded by sampling inconsistencies.

The distribution of taxon occurrences compiled in this paper and in other publications shows that the largest sampling gaps in Arctic deep-sea invertebrate benthos exist >3,000 m, on the eastern side of the Canada Basin, and in the megafauna fraction. Not surprisingly, our study also showed that lack of consistency in sampling gear and taxonomic resolution pose problems for pan-Arctic comparisons, possibly masking actual patterns and even producing artificial ones. We recommend that future efforts consider filling the above gaps and use standardized sampling gear with a large surface area and/or sufficient replication to capture true local diversity. A standardized sieve size of 250  $\mu\text{m}$  for macrofauna is recommended because of the small size of traditional macrofauna taxa in the deep sea. Small polychaetes and other prominent taxa are neglected if larger sieves sizes were used. The ideal methodology would be a size fractionation of 250  $\mu\text{m}$ , 500  $\mu\text{m}$  and 1 mm to allow fuller comparison with studies using these alternate sieve sizes.

The data compiled here, while incomplete, will be useful as a baseline for assessing future changes. It is difficult to predict whether abundance and biomass will increase or decrease in the Arctic deep sea in the coming decades. If overall pelagic-benthic coupling were to remain constant, one might predict an increase in abundance and biomass. This prediction is based on the shrinkage in multi-year ice-cover (Stroeve et al. 2007), the predicted increase in pelagic primary production

in the central Arctic (Anderson and Kaitin 2006), and the higher deep-sea biomass in Arctic regions lacking perennial sea ice (Włodarska-Kowalczyk et al. 2004). Perhaps more likely, however, is a *decrease* in carbon flux to the deep-sea floor with a subsequent decrease in abundance and biomass of deep-sea fauna, because of increased retention and recycling of organic matter in the water column (Carroll and Carroll 2003). In terms of diversity, a reasonable prediction of future change is even more difficult, because (1) it is unclear if and how much the carbon flux to the Arctic deep-sea floor will change, and (2) the unimodal distribution of the productivity-diversity relationship found in many studies does not seem to be generally applicable (e.g., Glover et al. 2002). The relationship between productivity and diversity such as studied for the Canadian Arctic shelves (Whitman et al. 2008) remains an open question in the Arctic deep sea. The extreme seasonality associated with high latitude will obviously remain, and will continue to produce different conditions for the high Arctic deep-sea fauna from those in the global deep sea. Ongoing environmental changes in the Arctic set in motion the opportunity for a large-scale “experiment”. Repeated long-term sampling in areas of extreme loss of the perennial ice cover should monitor variability and change. Additional long-term deep-sea Arctic observatories like the unique HAUSGARTEN in Fram Strait (Soltwedel 2005) should also be implemented, particularly on the Pacific side on the Chukchi Sea slope.

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