



Depth gradients of benthic standing stock and diversity on the continental margin at a high-latitude ice-free site (off Spitsbergen, 79°N)

Maria Wlodarska-Kowalczuk^{a,*}, Michael A. Kendall^b, Jan Marcin Weslawski^a,
Michael Klages^c, Thomas Soltwedel^c

^a*Institute of Oceanology PAS, ul. Powstancow Warszawy 55, 81-712 Sopot, Poland*

^b*Plymouth Marine Laboratory, Prospect Place, Plymouth PL1 3 DH, UK*

^c*Alfred Wegener Institute for Polar and Marine Research, Columbusstrasse, D-27568 Bremerhaven, Germany*

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Abstract

High-latitude seas are mostly covered by multi-year ice, which impacts processes of primary production and sedimentation of organic matter. Because of the warming effect of West Spitsbergen Current (WSC), the waters off West Spitsbergen have only winter ice cover. That is uncommon for such a high latitude and enables to separate effects of multiyear-ice cover from the latitudinal patterns. Macrofauna was sampled off Kongsfjord (79°N) along the depth gradient from 300 to 3000 m. The density, biomass and diversity at shallow sites situated in a canyon were very variable. Biomass was negatively correlated with depth ($R = -0.86$, $p < 0.001$), and ranged from 61 g ww m^{-2} (212 m) to 1 g ww m^{-2} (2025 m). The biomasses were much higher than in the multiyear-ice covered High Arctic at similar depths, while resembling those from temperate and tropical localities. Species richness (expressed by number of species per sample and species–area accumulation curves) decreased with depth. There was no clear depth-related pattern in diversity measures: Hurbert rarefaction, Shannon–Wiener or Pielou. The classic increase of species richness and diversity with depth was not observed. Species richness and diversity of deep-sea macrofauna were much lower in our study than in comparable studies of temperate North Atlantic localities. That is related to geographic isolation of Greenland–Icelandic–Norwegian (GIN) seas from the Atlantic pool of species.

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*Corresponding author. Tel.: +48-58-551-72-81; fax: +48-58-551-21-30.

E-mail address: maria@iopan.gda.pl
(M. Wlodarska-Kowalczuk).

1. Introduction

Much of the published discussion on broad-scale patterns of deep-sea macrobenthic biodiversity is

based on observations made in North Atlantic between 50°N and 68°N (Rowe et al., 1991; Thurston et al., 1998; Levin and Gage, 1998; Lamshead et al., 2000). Of the few deep-sea studies that considered high latitudes, most were either qualitative or restricted to a limited number of taxonomic groups (Isopoda, Gastropoda, Bivalvia—Rex et al. (1993); asellote isopods—Svavarsson et al. (1990); isopods—Poore and Wilson, (1993); Foraminifera—Culver and Buzas, (2000); polychaetes—Dauvin et al. (1994)). It is tempting to broaden the discussion on latitudinal patterns of macrobenthic diversity towards higher latitudes. However, most of the high Arctic seas are covered with permanent ice, which strongly influences both the pelagic primary production and the processes controlling the fluxes of organic matter to the deeper layers (Bodungen et al., 1995). Such strong differences in the dynamics and patterns of energy flux impede comparisons of biodiversity with lower latitudes, since any latitudinal effect is masked by the overwhelming influence of ice cover. That was the case of the unique data of Paul and Menzies (1974), Kröncke (1994, 1998) and Kröncke et al. (2000) who reported very low density, biomass and species richness of macrofauna sampled quantitatively on the ridges and in the basins of the Arctic Ocean. These areas are covered with permanent ice, which results in very low productivity.

The seas around the west coast of Spitsbergen, the largest island in the Svalbard Archipelago are warmed by the West Spitsbergen Current (WSC) and kept ice-free despite their high latitude (76–80°N). These seas offer a unique opportunity to examine the biodiversity of a high-latitude deep water site that has only winter ice cover and hence has higher annual productivity than permanently iced locations. The lack of summer ice-cover offers researchers the opportunity to separate the effects of ice cover and latitude on benthic biodiversity.

In the present study, we describe changes in the dominant fauna, density, biomass and diversity along the depth gradient on the continental margin off west Spitsbergen and make comparisons with the results of similar studies undertaken in temperate, tropical and permanently ice-covered polar sites. We aim to separate and detect the

effects of the permanent ice cover/low productivity and the latitude on high-latitude macrobenthic standing stocks and diversity.

2. Material and methods

The study was carried on the shelf, continental slope and rise off Kongsfjord, West Spitsbergen. The area is ice-free throughout most of the year despite its high northerly position (79°N). Ice pack occurs seasonally from November to June; icebergs are common on shelf. The WSC flows northwards along the shelf break. The WSC is one of the two branches of the North Atlantic Current, the northern extension of the Gulf Stream. The Atlantic Waters of salinity exceeding 34.91 and temperature exceeding 0 °C are present down to a depth of 700–800 m (Schlichtholz and Houssais, 1999, 2002; Osinski et al., 2003). The Norwegian Sea Deep Waters of lower temperature (between –1.1 and –0.5 °C) are present from 800 to about 2000 m (Schlichtholz and Houssais, 1999, 2002). The deep Greenland Sea is occupied by the coldest water mass (temperature below –1.1 °C)—Greenland Sea Deep Water (Schlichtholz and Houssais, 1999, 2002).

The material presented in this paper has been collected by various expeditions along the 79°N line of latitude along a depth gradient from 300 to 3000 m (Fig. 1). It includes samples taken from R.V. *Oceania* in 1999 and 2000, and R.V. *Polarstern* in 1991 and 2000 (ARK XVI). As the stations were named differently at different cruises, in our study, we name the stations after their depths (Table 1). The samples taken from R.V. *Oceania* were collected with a 0.1 m² van Veen grab. On R.V. *Polarstern* cruises, the sediments were collected by taking 0.1 m² subsamples to a depth of 20 cm from a 0.25 m² box-corer. The grab and box-corer were lowered gently to the sea bottom to minimize bow-wave which can wash away the surficial sediments (Blomqvist, 1991; Bett et al., 1994).

The shallow samples (300–400 m) were taken in Kongsfjordrenna, a submarine canyon that extends from shallow water to 400 m cutting the shelf and entering the outer part of Kongsfjord. At

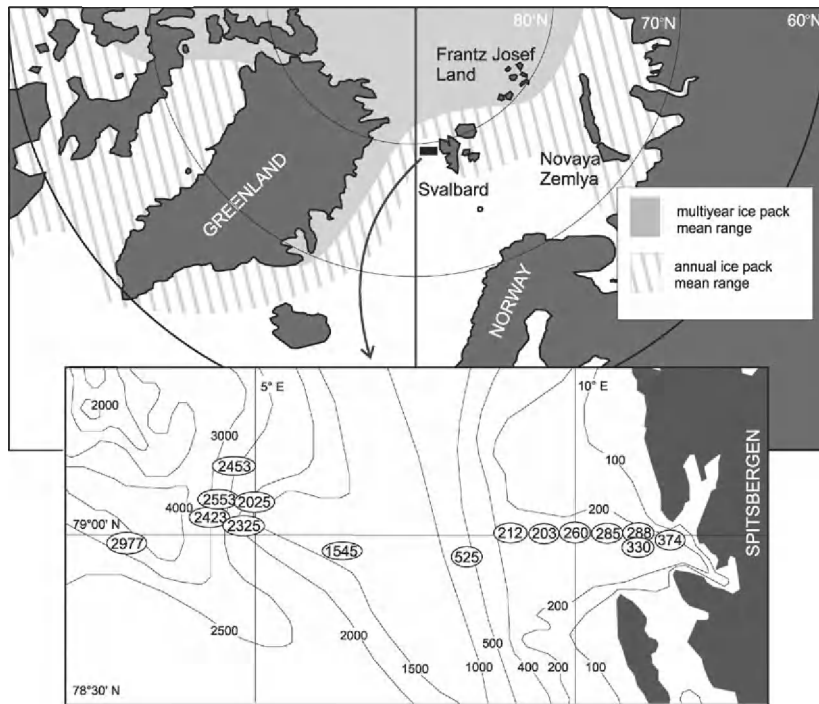


Fig. 1. Location of sampling area and sampling stations.

Table 1
The geographical position, depth, number of samples and sediment type at sampling stations

Depth (m)/ station name	Cruise/cruise station name	Longitude	Latitude	No. samples	% Clay	% Silt	% Sand	% Gravel	Sediment type
374	O99-sh1	11 30°E	79 00°N	1	—	—	—	—	*Sand and gravel
288	O99-sh2	11 00°E	79 00°N	1	—	—	—	—	*Sand and gravel
285	O99-sh3	10 30°E	78 59°N	1	—	—	—	—	*Sand and gravel
260	O99-sh4	9 59 E	79 00°N	1	—	—	—	—	*Sand and gravel
203	O99-sh5	9 30°E	79 00°N	1	—	—	—	—	*Sand and gravel
212	O99-sh6	9 00°E	79 00°N	1	—	—	—	—	*Sand and gravel
337	EPOS-88	10 45°E	79 01°N	4	—	—	75.0	—	Sand
330	O00-B3	11 00°E	79 00°N	3	—	—	—	—	*Sand and gravel
525	ARKXVI-263	8 28°E	78 55°N	2	3.5	3.1	61.5	31.9	Sand and gravel with stones
1545	ARKXVI-267	6 46°E	78 54°N	2	45.0	37.5	17.6	0.0	Silty-sandy clay
2025	ARKXVI-188	4 14°E	79 09°N	2	37.8	42.5	19.7	0.0	Sandy-clayey silt
2325	ARKXVI-275	4 19°E	79 05°N	2	36.4	31.8	31.7	0.0	Silty-sandy clay
2423	ARKXVI-276	4 09°E	79 05°N	2	28.1	45.7	26.2	0.0	Sandy-clayey silt
2453	ARKXVI-151	4 19°E	79 18°N	2	27.5	57.7	14.8	0.0	clayey silt
2553	ARKXVI-254	3 59°E	79 05°N	2	46.9	34.2	15.6	3.2	Silty-sandy clay
2977	ARKXVI-189	3 00°E	79 00°N	2	22.5	61.0	16.5	0.0	Sandy-clayey silt

— Is the missing data, *the description based on field notes. Cruises: O99, O00— R.V. *Oceania* 1999, 2000.

station 337, the four samples were from four separate box corers. At ARK XVI stations the two samples were sub-sampled from a single box-core taken at each station. They are pseudo-replicates (see Hurlbert, 1984) and do not increase the number of degrees of freedom available for statistical testing.

All samples were sieved through 0.5-mm sieve and fixed with buffered formaldehyde. All individuals were identified to the lowest possible taxonomic level and enumerated. The animals, excluding samples taken at station 337, were grouped by phylum and weighed.

The full list of taxa from the samples taken from R.V. *Oceania* and a partial list of material collected during the 2000 R.V. *Polarstern* cruise have already been published by Weslawski et al. (2003) while data for the samples from station 337 were included in Kendall (1996).

The species abundance data were subjected to multivariate analyses following double square root transformation. Bray Curtis similarities were calculated and presented as a dendrogram (based on group average clustering) and an nMDS ordination.

Species richness and species diversity were estimated. Species richness is the total number of species in a given area. Species diversity is the number of species in a given number of individuals and takes into account both species richness and evenness (e.g. Magurran, 2004).

We have expressed species richness as number of species per sample, and by the use of species–area accumulation plots. The species diversity was measured using the Hurlbert index (Hurlbert, 1971) calculated for 50 individuals and Shannon–Wiener \log_e -based index. The Pielou index (J) was calculated as a measure of the evenness.

3. Results

The multivariate analyses distinguished four groups of samples (Fig. 2):

- samples taken on the edge of shelf or in Kongsfjordrenna at depths shallower than 370 m (referred to as SHELF),

- samples taken on the slope at 500 m (SHALLOW SLOPE),
- samples taken on the slope at 1500 m (DEEP SLOPE),
- samples taken deeper than 2000 m (RISE).

The SHELF fauna was dominated by polychaetes—*Prionospio cirrifera*, *Cossura longocirrata*, *Lumbrineris* sp., *Leitoscoloplos* sp. and *Chaetozone* group (Table 2). Polychaete species dwelling in tubes—*Maldane sarsi*, *Clymenura polaris*, *Myriochele oculata* and the ophiuroid *Ophiura robusta* were also characteristic. The tube-dwelling polychaetes *Terebellides stroemi* and *Spiochaetopterus typicus* accounted for about 1% of individuals in this group.

On the slope, the most abundant species were bivalves—the protobranch *Yoldiella lucida* at 500 m and the thyasirid *Thyasira dunbari* at 1500 m. These were accompanied by several species of crustaceans and ophiuroids as well as the polychaetes—*Exogone verugeta*, *Heteromastus filiformis*, *Chone paucibranchiata* at 500 m, and species of *Aricidea*, *Paranionis/Paradoneis* and *Myriochele fragilis* at 1500 m.

The RISE group was dominated by polychaetes—*Myriochele heeri*, *M. fragilis* and *Paranionidae*. The identity of species of the genus *Myriochele* changed with depth: *M. oculata* occurred on the shelf, *M. fragilis* on the deep slope, and *M. fragilis* and *M. heeri* at the deepest stations.

In the Kongsfjordrenna (SHELF), the density of animals was very variable—ranging from 78 ind. 0.1m^{-2} at station 337 to 724 ind. 0.1m^{-2} at station 285. The mean density for the SHELF was 290.2 ind. $0.1\text{m}^{-2} \pm 218$ SD. The mean density in the SLOPE samples was lower at 194.3 ind. $0.1\text{m}^{-2} \pm 65$ SD. In the group RISE, the mean density of macrofauna was very low, averaging 64.6 ind. $0.1\text{m}^{-2} \pm 24$ SD.

The abundance of macrofauna decreased with depth (Fig. 3, $R = -0.66$, $p = 0.001$). Biomass also decreased with depth (Fig. 4; $R = -0.86$, $p < 0.001$). The equation of semi-log regression of biomass versus depth was: \log_{10} biomass = $1.61 - 0.0013$ [depth] ($R = -0.90$).

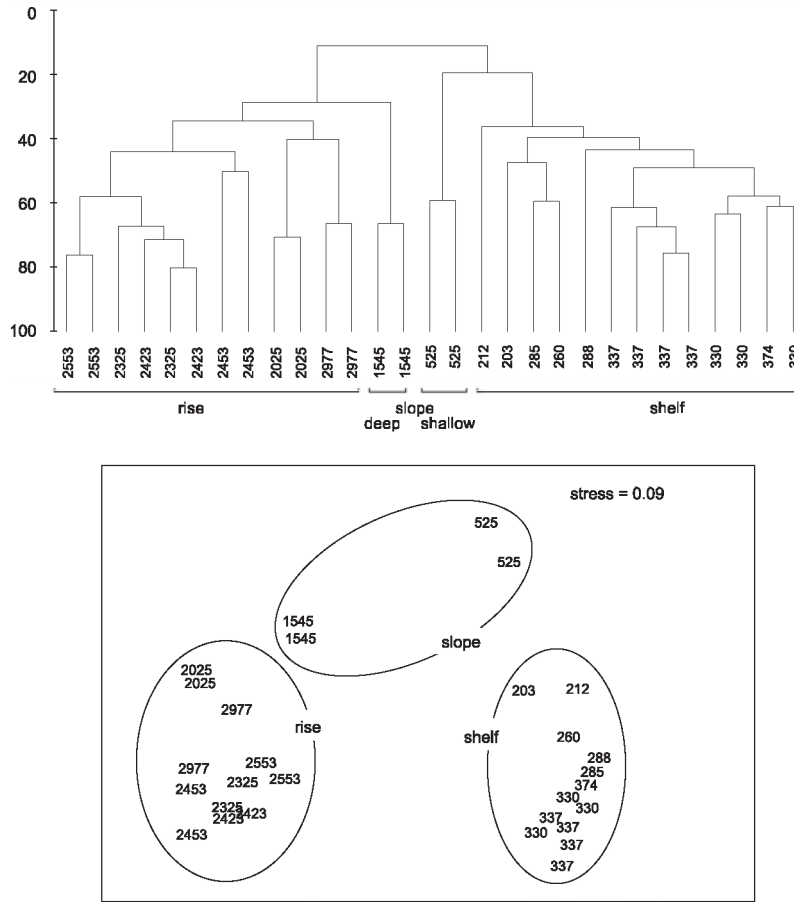


Fig 2. Dendrogram and MDS plot of Bray-Curtis similarities of double-root transformed data of species abundance in samples.

The biomass at SHELF stations in Kongsfjordrenna varied from 20.2 g ww(wet weight) m⁻² (station 330) to 61.0 g ww m⁻² (station 212). It was less variable in RISE samples varying from 1.1 g ww m⁻² (station 2025) to 6.0 g ww m⁻² (station 2977). The mean values for groups of samples were as follows: SHELF—38.7 ± 14.5 g ww m⁻², SLOPE—20.9 ± 14.7 g ww m⁻², RISE- 2.2 ± 1.5 g ww m⁻².

The species richness decreased with depth (Fig. 5, *R* = -0.74, *p* < 0.001). In Kongsfjordrenna, it ranged from 15 species per sample at station 337 to 59 species per sample at station 260 (Fig. 5). The highest value, 62 species per sample, was at station 525. At stations below 1500 m, there were no more than 20 species in a single sample. When the species-area accumulation curves were com-

pared (Fig. 5) the curve of SLOPE samples was the steepest, but this conclusion should be viewed with caution as it is derived from only four samples. The curve of the SHELF group was much higher and steeper than the curve for RISE, which was lower and flatter (Fig. 5).

There was no clear depth-related trend in species diversity measures (Fig. 6). This is a pattern that, at least in part, reflects the strong spatial variability in species richness among the shallowest group of samples. None of the species diversity measures used showed a significant correlation to depth (Fig. 6). ES (50) ranged from 10 (station 374) to 27 (station 525). Shannon-Wiener index was the highest on station 525 (3.54), the lowest on station 2025 (1.46). The Pielou index was the least

Table 2
The dominant taxa in groups of samples

	Shelf <i>n</i> = 140		Shallow slope <i>n</i> = 80		Deep slope <i>n</i> = 36		Rise <i>n</i> = 48	
	<i>A</i>	<i>D</i>	<i>A</i>	<i>D</i>	<i>A</i>	<i>D</i>	<i>A</i>	<i>D</i>
<i>Prionospio cirrifera</i>	68.1	23.5						
<i>Cossura longocirrata</i>	51.3	17.7						
<i>Lumbrineris</i> sp.	36.4	12.5	1.5	0.6	13.0	9.1	1.9	3.0
<i>Leitoscoloplos</i> sp.	29.6	10.2						
<i>Chaetozone</i> group	22.3	7.7	1.5	0.6	2.0	1.4	2.6	4.0
<i>Levinsenia gracilis</i>	10.1	3.5	2.5	1.0				
<i>Myriochele oculata</i>	4.4	1.5						
<i>Ophiura robusta</i> (E)	3.0	1.0	2.5	1.0	1.0	0.7		
<i>Maldane sarsi</i>	2.8	1.0	4.0	1.6				
<i>Heteromastus filiformis</i>	8.4	2.9	7.5	3.0	0.5	0.4		
<i>Chone paucibranchiata</i>	1.9	0.7	11.5	4.7				
<i>Nicomache</i> sp.	0.9	0.3	10.0	4.1				
<i>Yoldiella lucida</i> (B)	0.5	0.2	22.0	8.9				
<i>Nothria conchylega</i>	0.3	0.1	9.0	3.7				
<i>Exogone cf. verugera</i>			21.0	8.5				
<i>Leucon nathorsti</i> (C)			12.5	5.1				
<i>Tanaidacea</i> sp B (C)			9.5	3.9				
<i>Tanaidacea</i> sp A (C)			10.5	4.3	2.5	1.8	2.6	4.0
<i>Ophiura</i> juv. (E)			7.5	3.0	6.5	4.6		
<i>Thyasira dunbari</i> (B)	0.1	0.0	0.5	0.2	32.0	22.5	0.1	0.1
<i>Capitellidae</i> nd	1.8	0.6	0.5	0.2	4.0	2.8		
<i>Ilyarachnidae</i> nd (C)			5.0	2.0	4.5	3.2	0.2	0.3
<i>Oedicerotidae</i> nd (C)			5.0	2.0	3.5	2.5		
<i>Aricidea</i> spp.			1.0	0.4	24.0	16.8	0.3	0.4
<i>Myriochele fragilis</i>			0.5	0.2	5.0	3.5	10.5	16.3
<i>Paraonis</i> sp./ <i>Paradoneis</i> sp.					8.0	5.6	6.2	9.5
<i>Sipunculida</i> nd	0.5	0.2			4.5	3.2	3.3	5.0
<i>Notomastus</i> sp.					0.5	0.4	4.6	7.1
<i>Haustoriidae</i> nd (C)							2.1	3.2
<i>Yoldiella</i> sp. (B)					1.5	1.1	1.9	3.0
<i>Myriochele heeri</i>	0.2	0.1					16.7	25.8

The 10 most numerous taxa in each group are listed. Bold letters indicate the top species in the group. *A*—mean density in a group (ind./0.1 m²), *D*—dominance (%), *n*—number of species found in the group. The taxa listed are mostly Polychaeta. Other taxa: C—Crustacea, B—Bivalvia, E—Echinodermata.

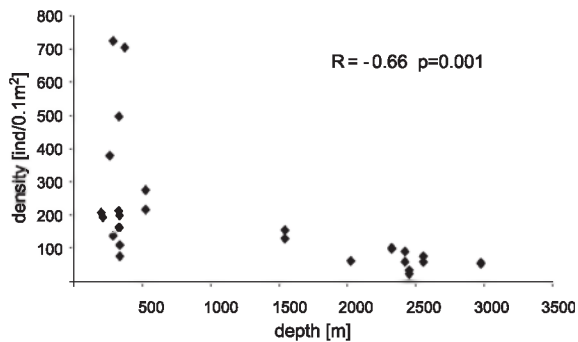


Fig. 3. Density of macrofauna (ind./0.1 m²) in relation to depth.

variable and varied from 0.54 (station 330) to 0.93 (station 2453).

4. Discussion

Both the abundance and biomass of the benthic fauna are much greater off Kongsfjord than in the Arctic Ocean proper (Table 3). Kröncke (1994, 1998) and Paul and Menzies (1974) reporting on the deep-sea fauna in Amundsen Basin, Nansen Basin and the Lomonosov and Alpha Ridges, observed very low faunal abundance and biomass,

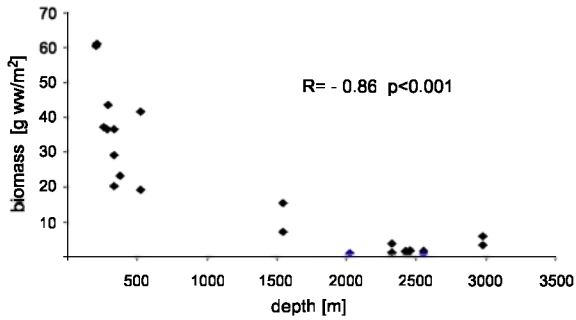


Fig. 4. Biomass of macrofauna (g ww/m^2) in relation to depth.

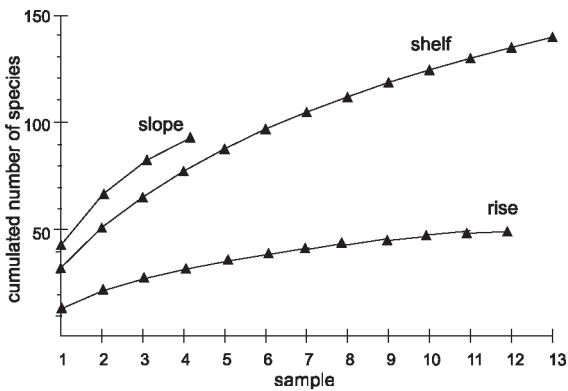
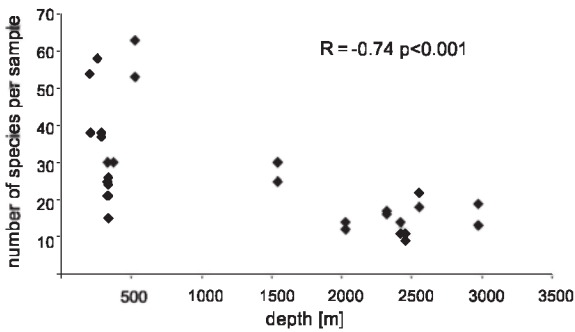


Fig. 5. Species richness expressed in number of species per sample and species–area accumulation curves for groups of stations.

except at a small number of stations where there was a mass occurrence of sponges.

Even though it is situated at 79°N , the sea bed off west Spitsbergen receives high inputs of organic matter. The absence of ice in summer is crucial for pelagic production and sedimentation.

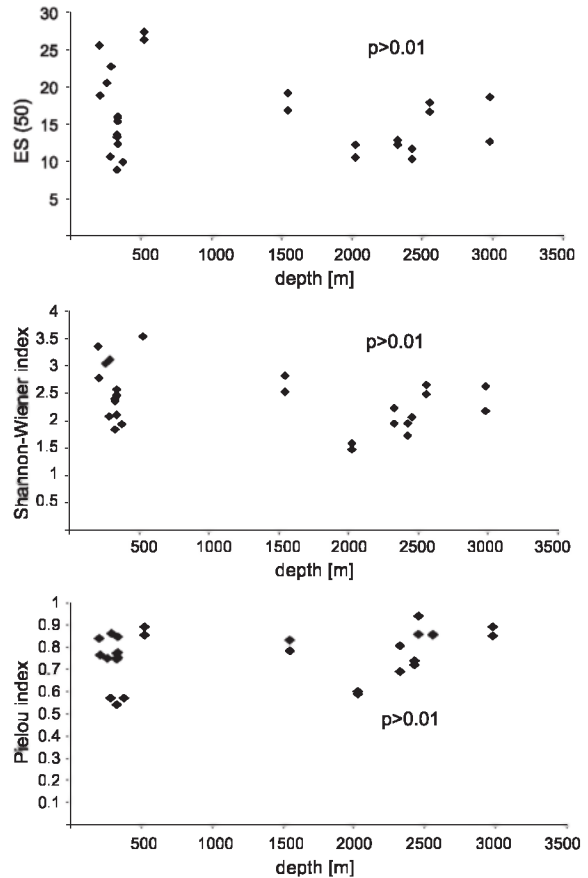


Fig. 6. Species diversity expressed in Hurlbert rarefaction index for 50 individuals (ES (50)), Shannon–Wiener ($\log(e)$) and Pielou evenness index.

von Bodungen et al. (1995) compared sites with and without summer ice cover in GIN (Greenland-Icelandic-Norwegian) Seas. They found similar levels of primary production, but higher sedimentation rates of POC in sites not covered by multiyear ice. In sites not covered by permanent ice, the timing of primary production and the vertical transport of organic matter were found to be driven by the activity of pelagic grazers rather than by the hydrographic conditions that controlled ice-covered areas (von Bodungen et al., 1995). The sedimentation of fecal pellets instead of phytoplankton cells was observed off Kongsfjord by Andreassen et al. (1996). In addition to vertical sedimentation, the

Table 3

Densities (D (ind./m²)) and biomass (B (g ww/m²)) of macrofauna at different geographical sites in High Arctic and northeastern Atlantic arranged by latitude

Reference, sampling device, sieve size	Region, latitude		Down to 500 m	500–2000 m	2000–3000 m	3000 m and deeper
<i>Paul and Menzies (1974)</i>	Alpha Cordillera,			(1000–2000 m)	(2000–2500 m)	
Mini-LUBUS corer, 0.149 mm	84–86°N	D		64–453	5–194 (514)	
		B		0.05–1.40	0.06–2.94 (16.06)	
<i>Kröncke (1994)</i>	High Arctic,			(1018–1867 m)	(2035–2609 m)	(3047–4478 m)
Box corer, 0.5 mm	82–90°N	D		50–475	50–200	50–475
		B		0.05–2.35	0.1–1.1	0.05–1.77 (41.4)
	81°N				(2950 m)	
		D			950	
		B			82.65	
<i>Kröncke (1998)</i>	High Arctic			(1072–1614 m)	(2531 m)	(3838–4347 m)
Box corer, 0.5 mm	82–89°N	D		150–1550	150	50–550
		B		0.09–3.44	0.15	0.02–0.71
	Yermak Plateau		(560 m)	(888 m)		
	80°N	D	3000	1200		
		B	5.82	2.97		
<i>This study</i>	Off Spitsbergen,		(203–374 m)	(525–1545 m)	(2025–2997 m)	
Box corer/van Veen 0.5 mm	79°N	D	780–7240	1300–2750	230–1000	
		B	20.2–61.0	7.5–41.6	1.1–6.0	
<i>Gage (1979)</i>	Rockall Trough			(1800–2000 m)	(2500–2900 m)	
Box corer, 0.42 mm	55–58°N	B		3.72–10.24	3.08–4.08	
<i>Flach (pers. comm.)</i>	Goban Spur,		(208–231 m)	(607–1457 m)	(2182–2256 m)	(3648–4470 m)
box corer	49°N	D	4785–7980	2882–6169	1413–1655	542–648
0.5 mm		B	33.3–71.2	1.6–51.2	2.3–4.0	2.4–3.2 (15.4)
<i>Galeron et al., 2000</i>	Off Mauritania,			(1600–2100 m)	(3110 m)	(4640 m)
box corer, 0.25 mm	18–21°N	D		3984–5432	1708–1840	204–232
		B		2.9–4.1	1.2–2.2	0.05

lateral transport of organic matter is very important on the Barents Sea shelf (von Bodungen et al., 1995).

The bathymetric gradient of biomass away from the Kongsfjord is clearly evident and similar to those observed in other regions. Rowe (1983) compiled the published data of biomass in 709 samples located all over the world from shallow shelf to the deep sea (down to below 10 000 m) and calculated a semilog biomass vs. depth regression: $\log \text{biomass} = 1.25 - 0.00039(\text{depth})$. In our study, the slope (-0.0013) of the regression is greater than in Rowe's equation, i.e. the biomass declines faster with increasing depth than the average values for the world ocean. However, a faster decline in biomass might be an artefact related to the location of shallow sites in a canyon. The biomass in canyons may be higher than in adjacent

non-canyon areas (Vetter and Dayton, 1998) due to enhanced flux of organic matter in the form of big algae drifts (Harrold et al., 1998) or of small organic matter particles (Monaco et al., 1990; Griggs et al., 1969). The biomasses of the fauna within the depth ranges of 500–2000 and 2000–3000 m were similar to values reported by Flach (Elsina Flach, pers. comm.) for the Goban Spur situated at 49°N in North-West Approaches, by Gage (1979) for the Rockall Trough at 55–58°N and by Galeron et al. (2000) for a eutrophic tropical site at 19–21°N off Mauritania (Table 3).

In contrast to biomass, the way in which patterns of species richness and species diversity change with depth in studied area, differed significantly from those that have been recorded in temperate waters.

The number of species per sample off Kongsfjord decreased with depth. In contrast, at the temperate site of the Goban Spur, the number of species per sample showed a parabolic pattern with a maximum at around 2000 m, also the species–area accumulation curves were steepest for fauna at 2000–3000 m (Flach and de Bruin, 1999). In our study the species–area accumulation curve for deep (2000–3000 m) fauna was the least steep and seemed to begin to reach an asymptote. In contrast, the species–area accumulation curve plotted for similar number of samples taken at 300–370 m did not show any signs of leveling off. This difference suggests a smaller species pool in off Kongsfjord deep waters compared to shallow waters, which is contrary to patterns observed in temperate site at the Goban Spur.

The measures of species diversity that include a component that relates to the abundance of individuals as well as species richness, failed to show the same clear pattern with depth as did species richness. We did not observe the parabolic pattern of species diversity often reported in lower latitude deep waters. A parabolic pattern of species diversity was described by Rex (1981, 1983) for polychaetes, gastropods, cumaceans and bivalves in western North Atlantic, by Paterson and Lamshead (1995) for polychaetes in the Rockall Trough and by Levin and Gage (1998) for bathyal macrofauna from various localities from North Atlantic, eastern Pacific and Indian Ocean. At the Goban Spur, the species diversity expressed by Hurlbert and Shannon–Wiener indices as well as the Pielou evenness increased along the depth gradient from 200 to 4000 m (Flach and de Bruin, 1999).

Off Kongsfjord, diversity is very variable at the shallow sites. The higher rate of species accumulation on the shelf and slope indicates a heterogeneous fauna, presumably a consequence of greater environmental heterogeneity at sampling sites situated in a submarine canyon.

The fauna of the canyons can have lower and more variable diversity (Gage et al., 1995) than the fauna of adjacent non-canyon areas at the same depth. The depression of diversity is related to highly unstable sedimentary conditions in canyons—where there can be strong bottom currents

related to internal waves as well as to unpredictable events such as storms, turbidity currents and massive slumps of sediment causing broad-scale resuspension and redeposition (Tyler, 1995; Rowe, 1972). There are no direct measurements of sedimentary processes in Kongsfjordrenna, however, the composition of macrofauna suggests that the sediments are relatively stable and the physical disturbance intensity low. The macrofauna was dominated by a spionid polychaete *Prionospio cirifera*. This species dwells in tubes built of mud grains and feeds on detritus particles, which are collected with use of ciliated palps (Fauchald and Jumars, 1979). Other dominant tube-dwelling polychaetes include *Myriochele oculata*, *Maldane sarsi* and *Clymenura polaris*. The tube-dwelling polychaetes both stabilize sediment and are sensitive to sediment instabilities (e.g. Fager, 1964). Their dominance in Kongsfjordrenna suggests a relatively low level of sedimentary disturbance compared to other canyons.

At deep bathyal depths off Kongsfjord, the species richness was lower than at the Goban Spur. At depths 2000–3000 m only 40 species were found in 0.6 m², while at the Goban Spur a total of 197 species were found at depths between 2182 and 2254 m in 0.8 m², and over 152 species at depths between 3673 and 3648 m in 0.8 m² (Flach and de Bruin, 1999). A measure used frequently for species diversity comparisons is the Hulbert index calculated for 100 individuals. We did not calculate this measure for our 0.1 m² samples, because the numbers of individuals were smaller than 100 in most of the deeper samples. However, when the data for pairs of subsamples cut from the same box-core were aggregated, then ES(100) could be calculated. The values calculated fell below those for the Goban Spur (Table 4). Shannon–Wiener indices were also higher at the Goban Spur (over 3.5 at depths deeper than 1500 m) compared to our study (1.5–3). Similarly values of ES(51) calculated for Polychaeta off Kongsfjord were lower than values reported by Paterson and Lamshead (1995) for a lower latitude North Atlantic deep locality (Rockall Trough, Table 4).

Roy et al. (1998) found that the only parameter that correlates with diversity on Pacific and

Table 4

Hurlbert rarefaction index values for 100 individuals (ES(100)) for macrofauna off Kongsfjord (present study) and in Goban Spur (Flach and de Bruin, 1999) and for 51 (ES(51)) individuals for Polychaeta off Kongsfjord (present study) and in Rockall Trough (Paterson and Lamshead, 1995)

	500–1000 m	1000–2000 m	2000–3000 m
<i>ES (100) for macrofauna</i>			
off Kongsfjord (79°N)	43 (525 m)	27 (1545 m)	14–22 (2025–2977 m)
Goban Spur (49°N)	45 (670 m)	50–51 (1034–1425 m)	54–62 (2182–3673 m)
<i>ES (51) for Polychaeta</i>			
off Kongsfjord (79°N)	22 (525 m)	11 (1545 m)	7–10 (2025–2977 m)
Rockall Trough (55–57°N)	25 (601 m)	25–31 (1062–1800 m)	19–24 (2875–2900 m)

Atlantic shelves is sea surface temperature. They hypothesised that “sea surface temperature is probably linked to diversity through some aspects of productivity”. As the distribution of fluxes and composition of organic matter in the deep sea is still very poorly known, the standing crop biomass of the fauna is still the most reliable indication of the availability of food (Rex, 1981). Rowe et al. (1991) have found a significant positive correlation of macrofauna biomass and POC flux. In our study, the biomass was comparable to similar temperate sites, while the species richness and species diversity was much lower. That indicates that diversity was decoupled from productivity and might be limited by the available species pool rather than the available food.

The species pool of the deep-sea fauna in Greenland–Icelandic–Norwegian Seas is limited by the low age of these basins and their present environmental conditions as well as by the isolation from the Atlantic pool of species by the Greenland–Iceland–Faeroe Ridge. The quaternary glaciation at high latitudes of Northern Atlantic destroyed the shallow-water fauna by the direct impact of glacial ice and deep-sea fauna due to low oxygen concentrations in bottom layers (Svavarsson et al., 1993). The isolation of the deep water northern seas fauna has resulted in the absence of certain genera common in the North Atlantic as it was shown for deep-sea isopods by Svavarsson et al. (1993). The high endemism and strong isolation of Norwegian and Greenland Seas fauna was shown for amphipods (Dahl, 1979), molluscs (Bouchet and Waren, 1979) and asteroids (Sibuet, 1979). Bouchet and Waren (1979) supposed that in

addition to the effects of age and isolation, the homogeneity and absence of geographic isolating barriers within the Arctic abyssal area could result in low species richness.

The decoupling of latitudinal gradients in diversity from gradients in solar energy fluxes, water temperature and related productivity is supported by the hemispheric asymmetries in diversity gradients. In the studies of Rex et al. (1993, 1997), the diversity of bivalves, isopods and gastropods was highest in the tropical North Atlantic and decreased towards the Norwegian Sea, while the gradients in the southern Atlantic were less pronounced. Poore and Wilson (1993) who found the isopod species diversity decreasing with increasing latitude in the North Atlantic, failed to find a similar pattern on the southern hemisphere. Similarly Brey et al. (1994) did not observe the decrease of the deep-sea bivalves, gastropods and isopods polewards while comparing tropical sites and Weddel Sea.

Our study is a first attempt to address the issues of the effects of latitude and the multiyear ice cover on standing stocks and diversity by studying summer ice cover free Arctic site. We synthesise the data coming from several expeditions, as it is the only material available at the moment. Certainly there is a need for more considered sampling campaign in that region.

5. Conclusions

The macrofaunal biomass at a high-latitude ice-free deep-sea site off Kongsfjord, west Spitsbergen,

was much higher than those found for central basins of the Arctic Ocean covered by multi-year ice cover and thus exhibiting a much lower productivity. At the same time it was comparable to data from lower latitudes. The species richness and species diversity of off Kongsfjord deep fauna was clearly lower than at lower latitudes. These findings suggest that latitudinal differences in diversity may not necessarily result from differences in primary production and subsequent organic matter fluxes to the seafloor. We conclude that the low diversity of northern North-Atlantic is preliminary determined by the limited pool of species available, resulting from the geophysical properties and history of the region.

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