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Intertidal meiofauna of a high-latitude glacial Arctic fjord (Kongsfjorden, Svalbard) with emphasis on the structure of free-living nematode communities

Abstract Meiofauna communities of four intertidal sites, two sheltered and two more exposed, in Kongsfjorden (Svalbard) were investigated in summer 2001 at two different tidal levels (i.e. the low-water line and close below the driftline, referred to as mid-water (MW) level). A total of seven meiofaunal higher taxa were recorded with nematodes, oligochaetes and turbellarians being numerically dominant. Mean total meiofaunal densities ranged between 50 ind. 10 cm^{-2} and 903 ind. 10 cm^{-2}. Our data showed a clear decrease in total meiofaunal densities with increasing coarseness of the sediment. Total meiofaunal biomass varied from 0.2 g dwt m^{-2} to 2 g dwt m^{-2} and, in general, was high even at low meiofaunal densities, i.e. larger interstitial spaces in coarser sediments supported larger meiofauna, especially turbellarians. The results on the vertical distribution of meiofauna contrasted sharply with typical meiobenthic depth profiles on other beaches, probably in response to ice-scouring and concomitant salinity fluctuations. Oligochaetes were the most abundant taxon, with a peak density of 641 ind. 10 cm^{-2} at Breoyane Island. They were mainly comprised of juvenile Enchytraeidae, which prohibited identification to species/genus level. Nematode densities ranged between 4 ind. 10 cm^{-2} and 327 ind. 10 cm^{-2}. Nematodes were identified up to genus level and assigned to trophic guilds. In total, 28 nematode genera were identified. *Oncholaimus* and *Theristus* were the most abundant genera. The composition of the nematode community and a dominance of predators and deposit feeders were in agreement with results from other arctic and temperate beaches. Nematode genus diversity was higher at the more sheltered beaches than at the more exposed ones. Low-water level stations also tended to harbour a more diverse nematode communities than stations at the MW level. Differences in nematode community structure between low- and MW stations of single beaches were more pronounced than community differences between different beaches and were mainly related to resources quality and availability.

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Introduction

Seashore ecosystems in the Spitsbergen archipelago are typically characterized by low abundance or even absence of macrobenthos (Węsławski et al. 1993, 1997). By contrast, Arctic intertidal meiobenthic densities cover a wide range, from 0 to more than 10,000 ind. 10 cm^{-2} (Szymelfenig et al. 1995), and are often similar to densities from more temperate locations. It has been inferred that meiofauna may thus have a prominent role in the transformation and recycling of organic matter in Arctic intertidal environments (Mokievsky 1992; Węsławski et al. 1993, 1997). However, empirical evidence for this hypothesis is lacking, and the exceptionally strong variability and patchiness observed in Arctic intertidal meiofaunal densities and community composition imply that caution is needed when drawing generalized hypotheses on the role of Arctic intertidal meiofauna.

This strong meiobenthic variability has been suggested to relate mainly to local environmental conditions like presence/absence of ice, exposure to waves, sediment composition and resource availability (Radziejewska

and Stańkowska-Radziun 1979; Szymelfenig et al. 1995; Urban-Malinga et al. 2004). However, except for a recent study of two beaches on Bear Island (Urban-Malinga et al. 2004), reports of meiobenthic distribution and community structure on Arctic beaches have generally presented little information on the abiotic environment so that links with meiofaunal communities remain largely speculative.

In this study, we describe the intertidal meiobenthic community structure of Kongsfjorden, a glacial, open Arctic fjord located on the west coast of Spitsbergen. Our objective is to better understand how the horizontal and vertical distribution of intertidal meiofauna is related to sedimentary and other environmental features in this high latitude (79°N) fjord. Special focus is on the structure of the free-living nematode communities. Their relatively short generation times, continuous reproduction, restriction to the sediment throughout their life and high diversity (with a wide range from tolerant to very sensitive species) make nematodes a suitable ecological indicator taxon for benthic environments (Platt and Warwick 1980; Heip et al. 1985; Gheskiere et al. 2004 and references therein). Hitherto, only one report (Gerlach 1965) was dedicated to nematode communities from intertidal habitats in Spitsbergen, but this was a purely taxonomic study. In the present report, we analyse the diversity and the trophic structure of nematode communities and discuss the role of the physical environment in structuring them.

Materials and methods

Study site

Kongsfjorden is a glacial, open Arctic fjord located on the west coast of Spitsbergen at 79°N, 12°E (Fig. 1). It is 20 km long and its width varies from 4 km to 10 km. The hydrology of this fjord is strongly influenced by freshwater inputs as meltwater from large tidal glaciers (Kronebreen and Kongsvegen at the head of the fjord, Conwaybreen and Blomstrandbreen on its northern coast). The concentration of suspended particulate matter in fjord waters is mainly a reflection of the activity of glaciers, which, together with meltwater, transport large quantities of inorganic particles. Sedimentation rates of suspended particulate matter are highest in the glacier's proximal inner basin (Svendsen et al. 2002 and references therein). Kongsfjorden is frozen during winter, but open and influenced by the warmer and more saline Atlantic waters during summer.

Four intertidal sites differing in sediment texture and location relative to the glaciers were selected for this study: two more exposed beaches with generally coarse sands, designated as "K" - a beach in the vicinity of the glacier Kongsvegen, and "T" - a beach in Tyskehytte; and two more sheltered beaches located opposite the glacier Blomstrandbreen, characterized by finer sands, i.e. "B" - a beach on the Breoyane Island and "N"—a

Fig. 1 Map of Kongsfjorden and location of sampling stations (N Nordvagen, B Breoyane, T Tyskehytte, K Kongsvegen)
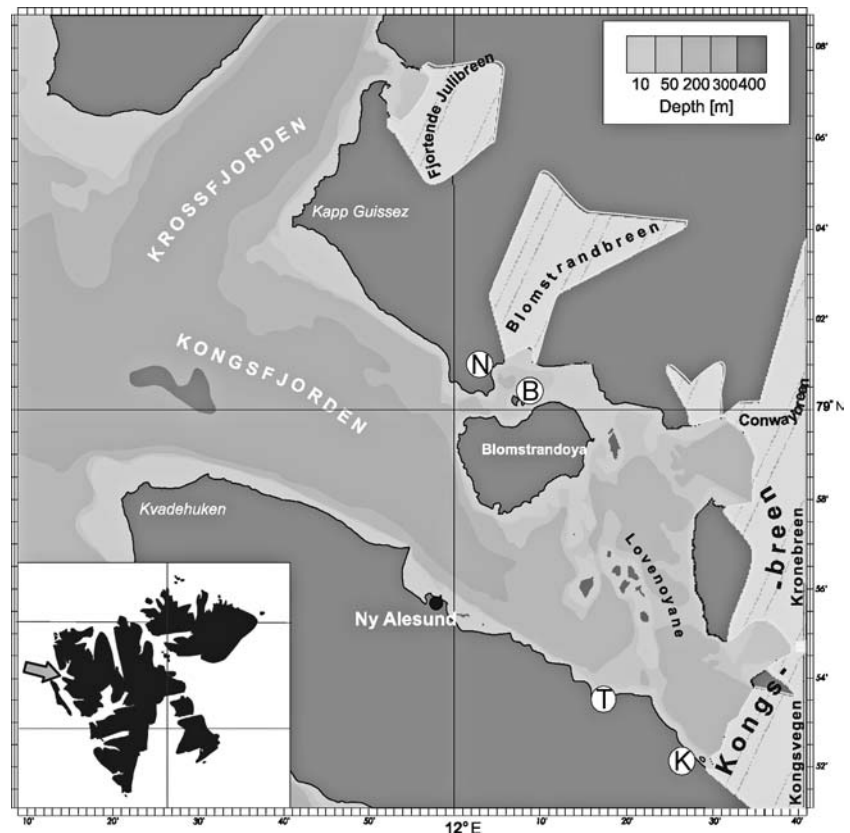
beach at Nordvagen (Fig. 1). These sites were sampled once between 2 August 2001 and 7 August 2001. Water and air temperature at the time of sampling ranged between 2.7–4.1°C and 3.2–4.3°C, respectively.

The terms "exposed" and "sheltered" are somewhat ambiguous. According to a rating system to assess the degree of beach exposure (McLachlan 1990), our study sites can all be classified as exposed: moderate to heavy wave action, reduced layers deep if present, usually no macrofaunal burrows, etc... However, considering specific local conditions we have distinguished two open beaches exposed to wind and wave action from the open fjord, and two beaches located in a bay, sheltered by cliffs and island(s) and, to an extent, separated from the open fjord waters. The presence of fine/medium sands in sheltered beaches is an indication of relatively calm conditions (McLachlan 1990). The presence of gravels in these sites mostly results from continuous cliff erosion and is not related to exposure.

Meiobenthos sampling and treatment

On each of the selected beaches, samples were collected at low tide from the low water (LW) mark and from a station close below the driftline [hereafter referred to as mid-water (MW)]. Triplicate samples for meiobenthic community structure were taken parallel to the waterline (the distance between replicates being approximately 50 cm) using Perspex cores with a surface area of 10 cm^2. The sediment was sectioned on site into four depth layers: 0–2, 2–4, 4–6, 6–10 cm. These samples were preserved with a neutral 4% formaldehyde solution. In the laboratory, all meiofaunal samples were rinsed with freshwater over a 1-mm sieve to exclude macrofauna and decanted (ten times) over a 32 μm mesh sieve. The fraction retained on this sieve was stained with Rose Bengal. Meiofauna was identified and counted to higher taxon level under a stereomicroscope. All nematodes were sorted out by hand, mounted on permanent glycerin slides following the procedure described by Vincx (1996), and identified to genus level. Classification into feeding groups used Wieser's (1953) scheme, which distinguishes four 'guilds' on the basis of mouth morphology: (1A) selective and (1B) non-selective deposit-feeders, (2A) epistrate-feeders, and (2B) predators/omnivores. Although such morphology-based 'guilds' suffer from many shortcomings and restrictions (Moens and Vincx 1997, Moens et al. 2004), the absence of empirical evidence on feeding habits of most free-living aquatic nematodes often prohibits the use of an alternative functional classification.

Mean individual biomass of meiofauna was estimated by a volumetric method. The body length and maximum width of an animal were measured under a camera lucida and body volume was calculated by assuming conversion factors specific for each taxon (Feller and Warwick 1988). Body volume was translated to wet weight (wwt) by assuming a specific gravity of 1.13 (Wieser 1960) and converted into dry weight (dwt) assuming a dry/wet weight ratio of 0.25 (Feller and Warwick 1988).

Sediment characteristics

Sediment granulometry was determined on each of three replicate samples, taken with the same type of cores as for meiofauna, to the same depth, in the vicinity of the meio-cores. Analysis was done by standard sieving. The sediment fractions were defined according to the Wentworth scale. Additional parameters like medium grain size, sorting coefficient, skewness and kurtosis were calculated according to Boggs (1987).

Three additional sediment cores, 1.13 cm^2 in surface area, were taken at each water mark to a depth of 10 cm for carbon and nitrogen content. The samples were stored frozen (at −20°C) until analysis. Total carbon, organic carbon (C_{org}) and nitrogen (N_{org}) concentrations were determined on dried samples by thermal combustion using a CHN-analyzer (Perkin Elmer 2400). Samples for C_{org} were pretreated with HCl to remove carbonates. C/N-ratios were used as a rough measure of organic matter quality.

Phytopigment concentrations (Chl$a$ and phaeopigments) were measured on three more replicate sediment samples taken to a depth of 2 cm. Sediment was processed immediately after transport to the laboratory. Pigments were extracted with 90% methanol. Phaeopigment concentrations were determined after acidification with 10% HCl. Measurements were done fluorimetrically with a Turner Design Fluorometer AU10. Chl$a$ and phaeopigment concentrations, and the Chl$a$/phaeopigment ratio were used as proxies for (freshly) deposited primary producers (macroalgae and phytoplankton) (EPA Method 445.0 1997).

Concentration of suspended particulate matter in the ambient water at each study site was estimated by filtration of 5 l of seawater on Whatman GF/C glass-fibre filters. The amount of total suspended matter in the water was determined after drying the filters at 60°C for 24 h.

Data analysis

Meiofaunal densities between beaches were compared using the non-parametric Kruskal-Wallis test; a posteriori pairwise comparisons followed Conover's (1980) procedure. An exploratory correlation analysis of meiofauna and sediment characteristics was performed using Spearman rank correlation. Analyses were performed using the STATISTICA software package (StatSoft 2002). The Shannon-Wiener diversity index (H'log^e) was calculated to express nematode diversity. Nematode community analysis (using the genus abundance data) was performed on double root transformed data using the PRIMER software package (Version

5.2.4.). Bray-Curtis similarities were calculated. Ordination [non-metric multidimensional scaling (MDS)] and classification (using group-average linking) of samples were performed. Groups of samples were distinguished based on the resultant dendrogram and MDS plot.

Results

Sediment characteristics

Table 1 and Fig. 2a show the main sediment characteristics at all study sites. The extremes in terms of sediment composition are the beaches at Breoyane (B) and Tyskehytte (T), dominated by medium and very coarse sand fractions, respectively. Sediments at Nordvagen (N) and at Kongsvegen (K) were dominated by the coarse sand fraction, however, the proportions of fine and medium sand at Nordvagen were much higher than at Kongsvegen. Sediment granulometry differed significantly between LW and MW stations at all our study sites. Except for the beach at Tyskehytte, the finer sediment fractions were always more prominent at the MW level than at the LW level; the opposite was true for the coarser sediment fractions. By contrast, MW level sediments at Tyskehytte were dominated by coarser sediment fractions. Gravel was an important sediment fraction in Tyskehytte only (up to 28% at the MW level). The sediment was moderately sorted at all our study sites.

Concentrations of organic carbon varied from 0.07–0.09% at Nordvagen to 0.15% at Breoyane (MW station) (Table 2). Organic nitrogen concentrations were always low, ranging from 0.01 to 0.02%. The highest concentrations of Chl$a$ were found at the two more sheltered sites (B and N) (up to 0.25 mg m^{-2}) and the lowest at Kongsvegen (K) (0.04–0.07 mg m^{-2}) (Table 2). Chl$a$ values were always lower at the LW level when compared to the MW level. The opposite trend was observed for phaeopigment concentrations.

The amount of suspended particulates in the ambient sea water reflected the distances of our study sites from the glaciers and ranged between 11 (Tyskehytte) and 20 (Kongsvegen) mg dwt/l (Table 1).

Meiofaunal densities and biomass

Mean total meiofaunal densities ranged between 50 ind 10 cm^{-2} at Tyskehytte (LW) and 903 ind. 10 cm^{-2} on Breoyane Island (MW) (Table 3, Fig. 2b). In general, the more exposed beaches (T and K) had lower meiofaunal densities than the more sheltered ones (B and N). A total of seven meiofaunal higher taxa were recorded (Oligochaeta, Turbellaria, Nematoda, Gastrotricha, Harpacticoida, Bivalvia, Halacaroidea) with nematodes, oligochaetes and turbellarians being numerically dominant. The number of taxa per station varied little: between three and six.

Table 1 Physical characteristics of the study sites

Study site	Geographic position	Beach width (m)	Beach slope (°)	Water suspension content (mg/l)	Water salinity (PSU)	Water mark	Phi (Φ)	So	Sk	Ku	Silt (%)	Very fine sand (%)	Fine sand (%)	Medium sand (%)	Coarse sand (%)	Very coarse sand (%)	Gravel (%)
B	79°00′716″N 012°02′005″E	15	3	18.5	30	LW	1.1	1.0	−0.7	4.0	0.0	0.3	14.7	53.5	19.1	4.9	7.5
						MW	1.6	0.6	0.0	5.5	0.0	0.5	24.6	65.2	9.0	0.4	0.4
N	79°00′118″N 012°05′046″E	15	2.5°	18.0	30	LW	0.5	0.9	0.2	3.6	0.0	0.2	5.3	23.5	47.0	20.4	3.6
						MW	1.0	0.8	0.2	4.0	0.0	0.3	11.4	43.1	40.0	4.9	0.3
K	78°52′783″N 012°23′508″E	17	2°	20.15	32	LW	0.1	0.8	0.2	5.4	0.0	0.3	1.8	8.3	57.2	23.9	8.5
						MW	0.4	1.0	0.6	7.8	0.1	0.6	4.7	19.6	50.0	17.2	7.9
T	78°53′453″N 012°13′856″E	15.5	3.5°	11.15	25	LW	0.0	0.9	0.2	4.7	0.0	0.3	1.6	8.7	48.0	25.3	16.2
						MW	−0.4	1.0	0.8	4.5	0.0	0.6	2.1	2.6	35.4	30.7	28.6

The results on granulometric characteristics are arithmetic means
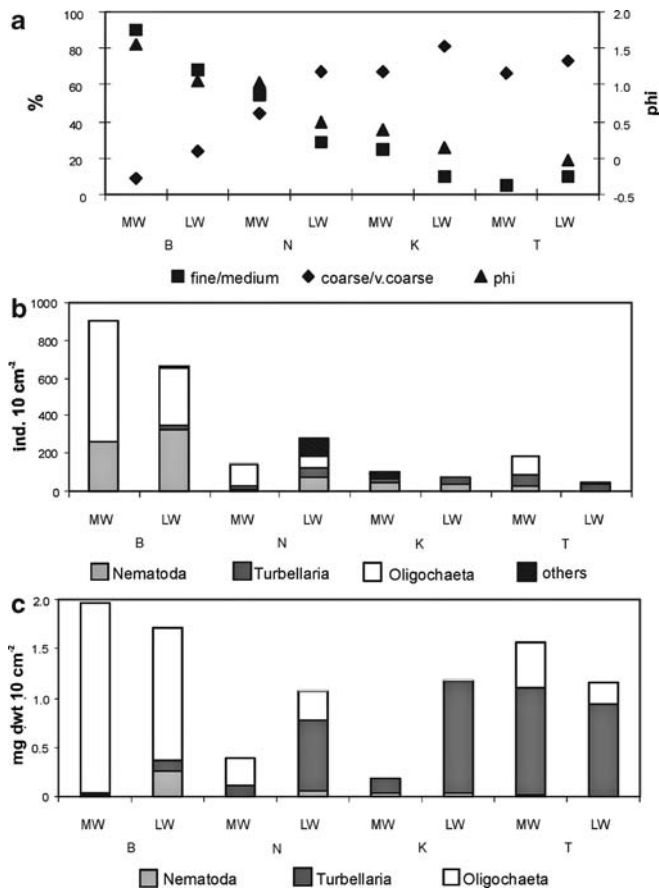*So* sorting index, *Sk* skewness, *Ku* kurtosis

Fig. 2 Sediment characteristics (integrated values of fine/medium and coarse/very coarse sand contribution) (**a**) and mean total meiobenthis densities (**b**) and biomass (**c**) with a contribution of the dominant taxa

Oligochaetes were the most abundant taxon, with a peak density of 641 ind. 10 cm^{-2} at Breoyane Island (MW) but extremely low densities at Kongsvegen (LW, ≤ 1 ind. 10 cm^{-2}). They were mainly comprised of juvenile Enchytraeidae, which prohibited identification to species or even genus level. The highest nematode densities (up to 327 ind. 10 cm^{-2}) were again noted at Breoyane Island where together with oligochaetes they comprised more than 90% of the meiofaunal community. Nematoda along with Turbellaria and Bivalvia were numerically dominant at Kongsvegen. At

Tyskehytte, Turbellaria and Oligochaeta together comprised more than 80% of the meiobenthos density, nematodes reaching only low densities (4 ind. 10 cm^{-2} and 30 ind. 10 cm^{-2}, respectively, at LW and MW). Gastrotrichs were limited to a single study site–Nordvagen (N, LW) where this group reached average densities up to 89 ind. 10 cm^{-2} (i.e. 30% of the total meiofaunal density). Harpacticoida were noted in very low densities (a maximum of 4 ind. 10 cm^{-2}) (T, MW). Bivalvia were recorded at two study sites only, in Kongsvegen (K, MW) (30 ind. 10 cm^{-2}) and in Nordvagen (N, LW) (6 ind. 10 cm^{-2}). A few individuals of Halacaroidea were recorded in Tyskehytte (LW) (< 2 ind. 10 cm^{-2})

In general, an increase of total meiofaunal density with sediment depth was observed at the LW level and an opposite trend was recorded on the upper beach. Oligochaetes reached highest densities in the upper 4 cm of the sediment (50–94% of their total density). No clear vertical patterns of nematode and turbellarian densities were observed (Table 3).

Total meiofaunal biomass varied from 0.2 (K, MW) to 2 mg dwt 10 cm^{-2} (B, MW). On Breoyane Island, oligochaetes constituted up to 78 (LW) and 98% (MW) of the total meiofaunal biomass; at Nordvagen (MW) they were responsible for 70% of total meiofaunal biomass. Turbellarians were the most important component of total biomass at all other stations (from 62% at Nordvagen [LW] to 96% at Kongsvegen [LW]) (Fig. 2c).

Spearman rank correlations indicated that percentages of fine, medium and (very) coarse sand were important factors controlling meiofaunal abundance on our study sites (Table 4).

Nematode community

In total, 28 nematode genera were identified (Table 5). *Oncholaimus* and *Theristus* were the most abundant genera. Their highest densities were recorded at Breoyane Island. *Oncholaimus* was most abundant at the LW level (on average 138 ind. 10 cm^{-2} at Breoyane, i.e. 59% of the total nematode density), *Theristus* at the medium water level (on average 153 ind. 10 cm^{-2} at Breoyane, i.e. 80% of the total community). At other sites, *Theri-*

Table 2 Environmental characteristics at the study sites (means and standard deviations)

Study site	Water mark	C_{org} %	N_{org} %	C/N ratio	Chl$a$ (mg/m^{-2})	Phaeo (mg/m^{-2})	Chl$a$/Phaeo ratio
B	LW	0.094 ± 0.055	0.022 ± 0.011	4.96	0.158 ± 0.125	0.521 ± 0.350	0.393
	MW	0.146 ± 0.090	0.016 ± 0.010	10.59	0.248 ± 0.132	0.186 ± 0.116	1.411
N	LW	0.089 ± 0.066	0.022 ± 0.018	4.69	0.227 ± 0.025	0.946 ± 0.045	0.354
	MW	0.068 ± 0.037	0.017 ± 0.014	4.64	0.249 ± 0.189	0.289 ± 0.249	0.951
K	LW	0.117 ± 0.095	0.014 ± 0.008	9.69	0.046 ± 0.080	0.093 ± 0.150	0.491
	MW	0.107 ± 0.110	0.018 ± 0.012	6.90	0.070 ± 0.140	0.101 ± 0.185	0.716
T	LW	0.105 ± 0.095	0.024 ± 0.015	5.08	0.087 ± 0.023	0.310 ± 0.027	0.551
	MW	0.104 ± 0.080	0.023 ± 0.020	5.25	0.162 ± 0.016	0.129 ± 0.009	1.450

Table 3 Mean densities (ind. 10 cm^{-2}) and number of meiobenthic taxa in vertical and horizontal beach profiles

Study site		Sediment depth (cm)	Nematoda $N \pm SD$	Turbellaria $N \pm SD$	Oligochaeta $N \pm SD$	Harpacticoida $N \pm SD$	Others $N \pm SD$	Total abundance $N \pm SD$	Number of taxa
B	LW	0–2	23.0 ± 3.6	4.7 ± 4.2	95.3 ± 85.3			123.0 ± 84.8	
		2–4	19.3 ± 8.1	3.0 ± 1.7	120.3 ± 18.5			142.7 ± 18.6	
		4–6	71.0 ± 29.5	6.0 ± 10.4	76.3 ± 45.2	0.7 ± 0.6		154.0 ± 77.6	
		6–10	213.7 ± 30.9	7.7 ± 5.0	17.0 ± 0.0	2.3 ± 4.0		240.7 ± 34.5	
		0–10	327.0 ± 19.2	21.3 ± 9.6	309.0 ± 57.4	3.0 ± 4.4		660 ± 36.1	4
	MW	0–2	56.3 ± 4.5		291.7 ± 163.4	0.3 ± 0.6		348.3 ± 162.0	
		2–4	90.7 ± 44.8		246.3 ± 89.3			337.0 ± 134.0	
		4–6	41.0 ± 10.1		74.3 ± 55.6			115.3 ± 61.0	
		6–10	73.0 ± 11.8	1.0 ± 1.0	28.7 ± 17.4			102.7 ± 9.3	
		0–10	261.0 ± 36.0	1.0 ± 1.0	641.0 ± 116.5	0.3 ± 0.6		903.3 ± 135.0	4
N	LW	0–2	8.7 ± 2.1	10.0 ± 9.5	6.7 ± 5.9		4.7 ± 3.1	30.0 ± 13.5	
		2–4	15.7 ± 3.8	17.3 ± 7.5	24.7 ± 4.7		8.0 ± 10.4	65.7 ± 6.4	
		4–6	13.7 ± 6.0	5.7 ± 2.5	17.7 ± 3.8		41.0 ± 34.0	78.0 ± 31.3	
		6–10	43.0 ± 15.4	7.0 ± 6.2	14.0 ± 4.6	2.0 ± 2.0	35.0 ± 27.8	107.0 ± 38.4	
		0–10	81.0 ± 14.2	40.0 ± 18.4	63.0 ± 11.3	2.0 ± 2.0	94.7 ± 68.4	281 ± 60.0	6
	MW	0–2	1.3 ± 0.5	1.7 ± 1.7	77.3 ± 1.5			80.3 ± 0.6	
		2–4		6.7 ± 0.6	28.3 ± 25.7			36.0 ± 26.9	
		4–6	2.0 ± 1.0	6.7 ± 1.2	4.0 ± 3.0			12.7 ± 4.5	
		6–10	2.7 ± 2.1	9.3 ± 3.8	2.3 ± 1.5			14.3 ± 3.5	
		0–10	7.0 ± 3.6	24.3 ± 3.1	112.0 ± 29.5			143 ± 33.9	3
K	LW	0–2	4.7 ± 4.6	11.3 ± 7.4		1.0 ± 0.0		17.0 ± 9.8	
		2–4	14.3 ± 14.0	3.0 ± 2.6	0.3 ± 0.6	0.3 ± 0.6		18.0 ± 12.3	
		4–6	6.0 ± 5.3	11.3 ± 8.5	0.3 ± 0.6	0.7 ± 1.2		18.3 ± 13.4	
		6–10	9.0 ± 4.0	19.3 ± 13.4				28.3 ± 14.6	
		0–10	34.0 ± 15.5	45.0 ± 3.0	0.7 ± 0.6	2.0 ± 1.7		81.7 ± 13.3	4
	MW	0–2	9.3 ± 10.1	8.7 ± 1.2		0.7 ± 0.6	26.0 ± 11.8	44.7 ± 21.0	
		2—4	13.3 ± 8.4	2.3 ± 0.6		0.7 ± 0.6	2.0 ± 3.5	18.3 ± 7.1	
		4–6	14.7 ± 7.0	1.7 ± 1.5			2.7 ± 4.6	19.0 ± 12.1	
		6–10	15.0 ± 8.2	3.7 ± 1.5				18.7 ± 8.5	
		0–10	52.3 ± 16.2	16.3 ± 2.3		1.3 ± 0.6	30.7 ± 10.1	101 ± 26.3	4
T	LW	0–2		11.7 ± 1.5		0.7 ± 0.6	0.3 ± 0.6	12.3 ± 2.1	
		2–4		5.7 ± 3.5	2.0 ± 1.0	0.3 ± 0.6		8.0 ± 4.0	
		4–6	1.3 ± 2.3	6.7 ± 3.8	4.3 ± 0.6	0.3 ± 0.6		12.7 ± 3.5	
		6–10	2.7 ± 3.8	7.3 ± 8.7	5.3 ± 1.56	1.0 ± 1.0	1.3 ± 0.6	16.7 ± 7.0	
		0–10	4.0 ± 3.0	31.3 ± 5.1	11.7 ± 2.1	2.3 ± 0.6	1.7 ± 0.6	49.7 ± 8.4	5
	MW	0–2	0.3 ± 0.6	9.3 ± 5.0	61.3 ± 28.4	0.3 ± 0.6		71.3 ± 24.2	
		2–4	2.0 ± 2.0	32.3 ± 8.3	30.0 ± 31.2			64.3 ± 35.6	
		4–6	5.0 ± 4.6	11.0 ± 1.0	2.3 ± 1.2	0.3 ± 0.6		18.7 ± 4.2	
		6–10	22.7 ± 25.0	2.7 ± 0.6	3.7 ± 0.6	3.3 ± 3.5		32.3 ± 30.4	
		0–10	30.0 ± 19.7	55.3 ± 12.4	97.3 ± 32.6	4.0 ± 4.0		187 ± 24.3	4

stus was only present in low densities, while *Oncholaimus* also dominated at Nordvagen and in the coarser sediments at Kongsvegen. Other abundant genera were *Neochromadora* and *Chromadorina*. *Rhabditis* was abundant (38 ind. 10 cm^{-2}) in only one replicate at a single station (Tyskehytte, MW, 6–10 cm), where it

Table 4 Summary of Spearman rank correlation for meiofauna variables and environmental parameters

Abundance	Md	So	Fs	Ms	Cs	VCs	Gr	Chl$a$	Chl$a$/phaeo
Total	$r = 0.77$*	–	$r = 0.92$***	$r = 0.83$**	$r = -0.82$**	$r = -0.73$*	–	–	–
Nematoda	–	–	$r = 0.72$*	–	$r = -0.87$**	–	–	–	–
1A	–	–	–	–	–	–	0.83*	–	–
1B	0.77*	−0.83*	0.87**	0.78*	−0.75*	−0.75*	–	0.79*	–
2A	–	–	–	–	–	–	–	–	–
2B	–	–	–	–	0.71*	–	–	–	−0.86**
Turbellaria	–	–	–	–	$r = 0.86$**	–	–	–	–
Oligochaeta	$r = 0.86$*	–	$r = 0.95$***	$r = 0.83$**	$r = -0.74$*	$r = -0.78$*	–	–	–
Biomass									
Total	–	–	–	–	–	–	–	–	–
Nematoda	–	–	–	–	–	–	–	–	–
Turbellaria	$r = -0.71$*	–	$r = -0.74$*	$r = -0.79$*	–	$r = 0.88$**	–	–	–
Oligochaeta	$r = 0.73$*	–	$r = 0.89$**	$r = 0.81$**	$r = -0.84$**	–	–	–	–

Md mean diameter, *So* sorting, *Fs* fine sand, *Ms* medium sand, *Cs* coarse sand, *VCs* very coarse sand, *Gr* gravels. No correlation was found between environmental variables and meiofaunal abundance and biomass
*$0.01 < P < 0.05$; **$0.001 < P < 0.01$; ***$P < 0.001$

Table 5 List of the nematode genera, their proportions (%), trophic groups and Shannon-Wiener index values (means and SD)

Genus	Trophic group	Breoyane Iseland		Nordvagen		Tyskehytte		Kongsvegen	
		LW (n = 327)	MW (n = 261)	LW (n = 81)	MW (n = 7)	LW (n = 4)	MW (n = 30)	LW (n = 34)	MW (n = 53)
Oncholaimus	2B	59.1	1.1	67.9	38.9	100	10.6	57.9	86.8
Theristus	1B	14.2	81.0	9.3	44.4		18.2		
Neochromadora	2A	6.3		2.5			1.5	24.6	11.6
Enoplolaimus	2B	1.1		6.2	5.6			14.0	
Rhabditis	1B	0.3		1.2			57.6		
Chromadorita	2A	9.5	0.2	3.7				3.5	
Chromadorina	2A	1.0	8.4	3.7					
Paracanthonchus	2A	2.0	3.0	0.6			1.5		
Ascolaimus	1B	3.3		0.6	5.6				
Paracyatholaimus	2A	0.1	1.0				4.5		
Bathylaimus	1B				5.6				
Diodontolaimus	1A		1.8						
Araeolaimus	1A	0.9	0.8						
Prochromadorella	2A	0.1	0.2						
Chromaspirinia	2B								
Parachromadorita	2A	1.0					3.0		
Monhystera	1B		0.2						
Onyx	2B								
Axonolaimus	1B						1.5		
Sabatieria	1B								0.8
Chromadora	2A	0.1		1.2					0.8
Microlaimus	2A	0.9		0.6					
Desmolaimus	1B		0.2						
Metachromadora	2A		0.2						
Prochromadora	2A		0.5				1.5		
Geomonhystera	1B		0.2	0.6					
Plectus				0.6					
Eudorylaimus				1.2					
Shannon diversity H'(loge)		0.58 ± 0.03	0.36 ± 0.04	0.57 ± 0.08	0.95 ± 0.006	0	0.66 ± 0.26	0.82 ± 0.11	0.46 ± 0.14

n mean total nematode numbers

constituted 57% of the community. Other nematode genera were noted in very low numbers (<2%). The freshwater/terrestrial genera *Plectus* (K, MW) and *Eudorylaimus* (B, MW) were found occasionally.

The most diverse communities in terms of the number of nematode genera were those on Breoyane Island (15 and 14 genera at LW and MW, respectively) and at Nordvagen (14 genera at the LW level). At other sites the number of nematode genera ranged between 1 (T, LW) and 9 (T, MW). *Chromadoridae* were the most diverse family (7 spp.). Shannon diversity index (H') ranged between 0 (T, LW) and 1.39 (B, LW) and at all stations, apart from Tyskehytte, was higher at the LW level compared to the mid water level (Table 5).

The distribution of feeding groups is shown in Table 5. Predators/omnivores, mainly represented by *Oncholaimus*, were the most abundant group at all study sites, except at the MW station on Breoyane Island and at Tyskehytte, where deposit feeders were more abundant.

Multivariate analysis (MDS) based on the genus composition distinguished four main groups of stations (Fig. 3) and illustrated that nematode community composition was mainly related to the location on the beach slope. In general, LW stations were separated from MW stations on the MDS-plot, with the exception of the MW station at Kongsvegen, which is grouped with other LW stations.

Discussion

Meiofaunal densities, biomass and taxonomic composition

Hitherto, studies on intertidal meiobenthic communities in Spitsbergen have all concentrated on more southern locations. The single report from Kongsfjorden, Virgohamna and Grahuken (Gerlach 1965) constituted a taxonomic study of nematode communities. Our total mean meiofaunal densities in Kongsfjorden (50–903 ind. 10 cm^{-2}) are mostly within the ranges reported for those more southern locations, and similarly display extremely high among-site variability (Radziejewska and Stańkowska-Radziun 1979; Mokievsky 1992; Szymelfenig et al. 1995; Urban-Malinga et al. 2004). Higher densities have occasionally been reported: up to and exceeding 1,000 ind. 10 cm^{-2} (Szymelfenig et al. 1995), up to 1,039 ind. 10 cm^{-2} with a single record of 4,092 ind. 10 cm^{-2} (Radziejewska and Stańkowska-Radziun 1979), and up to of 903 ind. 10 cm^{-2} (average of three replicates; highest value for a single replicate: 1,045 ind.

Fig. 3 Multidimensional scaling (MDS) ordinations of samples using group-average linking of Bray-Curtis similarities calculated on double-root transformed nematode genera abundance data
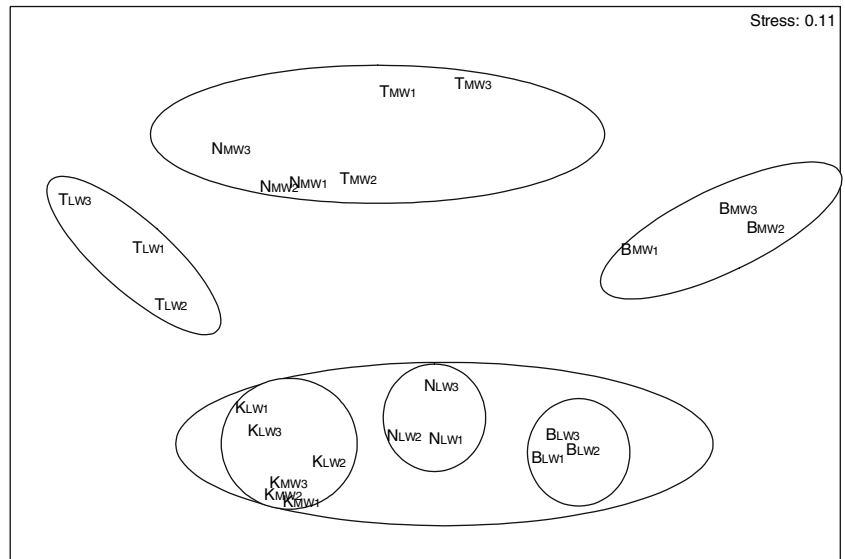
10 cm^{-2}) at Breoyane (this study). Caution is needed when comparing different studies because of the differences in depth penetration of sampling. However, the heterogeneous depth distribution of meiobenthos hampers a standardization of published densities to a fixed volume of sediment.

Our data strongly suggest that sediment composition is the principal factor controlling meiofaunal densities in the Kongsfjorden intertidal. Breoyane and Nordvagen, e.g. are both sheltered sites, located close to each other, at very similar distances from the glacier, and are subject to similar wave action. Moreover, phytopigment concentrations suggest that food resource availability on these beaches is very similar. Nevertheless, Breoyane beach, with relatively high fractions of fine and medium sand, supported much higher meiofauna densities, oligochaetes and nematodes in particular being more abundant than at Nordvagen. In general, our data show a clear decrease in total meiofaunal densities with increasing coarseness of the sediment. More specifically, there seems to be a 'critical threshold' in coarseness (40% contribution of coarse/very coarse sand fraction) and in the finer sand fraction (50% contribution of fine/ medium sand fraction), which corresponds in our study to a median grain diameter of 500 μm (1 phi), and which separates high meiofaunal density stations from low-density ones. An increase of the coarseness accompanied by a decrease of finer sand resulted in a decrease in meiofaunal densities, in agreement with previous studies illustrating that grain size and sediment sorting are the main factors controlling density and structure of meiofaunal communities in beach sediments (Jansson 1967, Eleftheriou and Nicholson 1975, Henning et al. 1982, Gourbault et al. 1995, 1998, Hooge 1999).

Meiofaunal biomass in the Kongsfjorden intertidal ($0.2-2.0$ g dwt m^{-2}) was higher than elsewhere at Spitsbergen: $0.07-0.60$ g dwt m^{-2} (Szymelfenig et al. 1995; Węsławski et al. 1999), $0-0.4$ g dwt m^{-2} Węsław-

ski et al. 1997) or in temperate beaches: $0.02-0.5$ g dwt m^{-2} (Munro et al. 1978). Oligochaetes contributed importantly to the high biomass ranges in Kongsfjorden but were absent or rare in the cited studies. Interestingly, with the exception of two MW stations (Nordvagen and Kongsbreen), meiofaunal biomass in Kongsfjorden was high even at low meiofaunal densities, i.e. larger interstitial spaces in coarser sediments supported larger meiofauna, especially turbellarians.

In accordance with other data from Spitsbergen, Nematoda and Turbellaria were the dominant meiofaunal taxa in our study, both in terms of density and biomass. Harpacticoid copepods, however, were much less abundant than in previous studies: a maximum of 4 ind. 10 cm^{-2} versus up to 110 ind. 10 cm^{-2} in southern and western Spitsbergen (Szymelfenig et al. 1995). The high abundance of oligochaetes is unusual and has not been described before from arctic intertidal sites. Maxima up to 30 ind. 10 cm^{-2} were reported from the southern coast of Spitsbergen (in 5 cm long sediment cores, Szymelfenig et al. 1995) and up to 140 ind. 10 cm^{-2} in Bellsund, West Spitsbergen (in 20 cm long sediment cores, Radziejewska and Stańkowska-Radziun 1979), compared to a maximum of 641 ind. 10 cm^{-2} in the present study. Oligochaetes from the family Enchytraeidae are typical for the intertidal, supralittoral and wrack zone of sandy beaches. Their occurrence is mainly related to the ambient sediment and its food content with decomposing seaweeds often at the basis of high enchytraeid densities (Giere 1975, Giere and Pfannkuche 1982, and references therein). Indeed, we observed large amounts of *Fucus* detritus at the MW level where highest enchytraeid abundances were found.

Gastrotrichs were limited to a single station (Nordvagen, $47-173$ ind. 10 cm^{-2}), in accordance with previous work from southern and western Spitsbergen reporting gastrotrichs in no more than 10% of the samples from Bellsund (Radziejewska and Stańkowska-

Radziun 1979) and in none of 119 stations studied by Szymelfenig et al. (1995). In Bellsund, one sample, characterized by a large input of organic matter, contained high densities of gastrotrichs (more than 300 ind. 10 cm^{-2}) (Radziejewska and Stańkowska-Radziun 1979). By contrast, our gastrotrich-containing Nordvagen site was characterized by a comparatively low organic carbon content but a relatively high Chl$a$ content, suggesting resource quality rather than quantity to be of relevance. Interestingly, no gastrotrichs were recorded in deeper sediments of Kongsfjorden (Kotwicki et al. 2004). The scattered occurrence of gastrotrichs in the intertidal while being absent in the subtidal may indicate that they are transported on incoming phytodetritus and temporarily bloom on it.

Differences in meiofaunal density and taxon composition between and within (low-water level vs. MW level) sampling stations in Kongsfjorden may also be indicative of communities in different stages of (re)colonization. Arctic intertidal areas are subject to ice-scouring from sea ice, smaller icebergs (Hop et al. 2002) and growlers (small iceberg fragments, typical in the intertidal of this fjord). The associated physical (sediment turnover and erosion) and osmotic (lowered salinity) stress strongly impacts Arctic intertidal macrofauna (Pugh and Davenport 1997) and potentially also meiofauna composition and distribution patterns. Information on the effect of ice-scouring on intertidal meiofaunal communities is, however, lacking. In general, we observed an increase of total meiofaunal density with sediment depth at the low-water level and an opposite trend on the upper beach. This contrasts sharply with typical meiobenthic depth profiles on beaches (Jansson 1968; McLachlan et al. 1977; Coull 1988; Olafsson 1991), including beaches at Bjornoya Island (Urban-Malinga et al. 2004). There, highest meiofauna concentrations were at or near the sediment surface at the low-water level but deeper at the upper beach, mainly as a result of desiccation. Indeed, in contrast to the Kongsfjorden stations, growlers and icebergs are largely lacking on Bjornoya, and we suggest that the aberrant depth distribution of meiobenthos in our Kongsfjorden stations is linked to ice-scouring.

Sandy beach meiofauna likely faces trade-offs between stress (sediment desiccation, scouring) avoidance and resource availability. On the upper beach slopes in Kongsfjorden, conditions are such that it may be beneficial for the meiofauna to stay at or near the sediment surface. The surface sediment layers in our upper beach stations were dominated by oligochaetes, organisms typical for transition zones and probably well adapted to environmental fluctuations (Giere and Pfannkuche 1982; McLachlan 1995). Alternatively, sandy beach meiofauna may display vertical migration behaviours (McLachlan 1995; McLachlan et al. 1977), but these are poorly documented for oligochaetes. On the other hand, the low air temperatures in the Arctic (3.2–4.3°C during the period of this study), the presence of glaciers and permafrost might effectively render sediment desiccation a less important threat. By contrast, the higher densities of meiofauna in deeper layers at the low water stations may well reflect recent effects of scouring by growlers. In addition to physical disturbance, melt water input from growlers may cause sudden local changes in osmotic pressure in the sediment. Osmotic stress adversely affects motility (Forster 1998) and fitness (Moens and Vincx 2000a, b) of nematodes and probably other meiofauna. Sudden salinity fluctuations may hamper the nematodes' ability of vertical migration. Indeed, the increase in meiofaunal densities with sediment depth at the LW level was most pronounced in nematodes.

Nematode community structure

Comparisons of diversity between different studies are difficult due to differences in sample size, sampling intensity and beach type. Hence, the comparisons below should be cautiously interpreted. Gerlach (1965) recorded a total of 43 nematode genera in an extensive study of the nematode fauna of various intertidal habitats at Spitsbergen (Kongsfjorden, Isfjorden, Grahuken, Virgohamna). Twenty-five of these genera were from sandy-gravel beaches (nine different beaches in total). We identified 28 nematode genera. All except *Diodontolaimus*, *Prochromadorella*, *Parachromadorita*, *Prochromadora*, *Onyx*, *Axonolaimus*, *Bathylaimus*, *Metachromadora* and *Geomonhystera* were also recorded by Gerlach (1965). With the exception of *Bathylaimus*, all these genera were found in low abundance ($< 2\%$ of the community) in our study. Gerlach (1965) recorded two freshwater genera in the intertidal at Kongsfjorden: *Plectus* and *Dorylaimus*, and we found *Plectus* and *Eudorylaimus* in samples from Nordvagen (LW). Genus diversity per station (1–15) and the dominance of the genera *Theristus* and *Oncholaimus* are also in good agreement with the results obtained by Gerlach (1965). Nematode genus diversity recorded on two beaches at Bjornoya (sampled at low-, mid- and high-water level) was much lower, but community composition was nevertheless similar to what we found in the present study (Urban-Malinga et al. 2004). Except for *Dichromadora* and *Viscosia*, all genera recorded from Bjornoya were also found in the present study. The total number of nematode genera in Kongsfjorden was considerably lower than in more extensively studied temperate beaches [e.g. 60 (Sharma and Webster 1983), 65 (Gheskiere et al. 2004), 48 (Nicholas and Hodda 1999)]; however, there are similarities in terms of nematode community composition (Platt and Warwick 1980; Blome 1983; Sharma and Webster 1983; Nicholas and Hodda 1999; Gheskiere et al. 2004). The numerical dominance of Xyalidae and Oncholaimidae is in accordance with the results of Nicholas and Hodda (1999) and Gheskiere et al. (2004).

Nematode genus diversity was higher at the more sheltered beaches of Breoyane and Nordvagen (MW) than at the more exposed sites of Tyskehytte and Kon-

gsvegen. Except for Tyskehytte, low-water level stations also harboured more diverse nematode communities than MW level stations. With the exception of the beach at Kongsvegen, differences in nematode community structure between low- and MW stations of single beaches were more pronounced than community differences between different beaches. Which driving forces, then, could be responsible for these differences?

The fauna in Arctic beaches, especially in glacial fjords, is faced with frequent physical disturbance by ice scouring and strong osmotic stress (freshwater outflow from the glacier and melting of growlers resulting in episodic salinity drops). In this respect, a higher diversity in more sheltered beaches may reflect a less severe disturbance regime, while it is tempting to relate a higher diversity at the low-water compared to the MW level to salinity fluctuations. The ability to overcome salinity fluctuations is a factor determining the horizontal distribution of nematodes in littoral habitats, species from the upper shore demonstrating greater capacity to osmoregulate and/or tolerate periods of raised body water content (Forster 1998).

Non-selective deposit feeders such as *Theristus* were more abundant in sheltered beaches when compared with exposed ones and were positively correlated with fine sediment content. Selective deposit feeders, by contrast, constituted a high percentage of the nematode community only at the medium water level in Tyskehytte. Their contribution at other stations was very low. Predatory nematodes represented mainly by *Oncholaimus*, constituted a dominant group at all the study sites (see also Platt and Warwick 1980; Nicholas and Hodda 1999; Gheskiere et al. 2004 for comparable results from other sandy beaches) except the two medium-water stations in Tyskehytte and Breoyane. These sites were characterized by high-quality fresh organic matter input as indicated by the highest Chl *a*/phaeopigment ratio. This may explain their high relative abundance of deposit feeders, but since oncholaimid nematodes are known to aggregate in organically enriched sites (Lorenzen et al. 1987; Prein 1988), it is surprising that *Oncholaimus* was rare at these two stations. In fact, the dominance of predators at the low-water level is at variance with the results from other beaches, where predators have mainly been found associated with the driftline (Gheskiere et al. 2004). The higher genus diversity at the more sheltered beaches may be linked to (micro)habitat heterogeneity (Platt and Warwick 1980). Sediments at these more sheltered sites are also fuelled by mineral suspension from the glacier's melting water and may thus offer additional niches for nematodes.

It is well known that large quantities of macroalgae are deposited along the Arctic coast (Węsławski et al. 1993), however, there is still a general paucity of information about the pathways of decomposition of this material. Meiofauna can be important in this process through modification of detrital quality (Tenore et al. 1977) and/or stimulation of mineralization rates of macroalgal detritus (Findlay and Tenore 1982; Alke-

made et al. 1992; Lillebø et al. 1999). In view of the low biomass and density of macrobenthos, the ecological role played by meiobenthos in the Arctic intertidal may be relatively more important than elsewhere (Mokievsky 1992; Węsławski et al. 1997). Currently, however, our understanding of the true roles of meiofauna in organic carbon utilization and turnover in the Arctic is hampered by lack of knowledge on their food sources and metabolic activities.

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