

Nematode biomass and morphometric attributes as biological indicators of local environmental conditions in Arctic fjords



Katarzyna Grzelak^{a,*}, Marta Gluchowska^a, Klaudia Gregorczyk^b, Aleksandra Winogradow^a, Jan Marcin Weslawski^a

^a Institute of Oceanology, Polish Academy of Sciences, ul. Powstańców Warszawy 55, Sopot, Poland

^b Institute of Oceanography, University of Gdańsk, al. Marszałka Piłsudskiego 42, Gdynia, Poland

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ABSTRACT

Kongsfjord and Hornsund are fjords located on the west coast of the island of Spitsbergen that differ in terms of hydrographical conditions and food source availability for benthic organisms. We studied the nematode communities of these two glacial fjords with respect to their morphometric attributes (body length, width, length/width ratio) and biomass (total and individual) to evaluate whether their differences reflect differences in hydrographical and biogeochemical conditions. Sediments collected from Kongsfjord, which contained enhanced marine organic material than sediments from Hornsund, supported nematode communities exhibiting higher biomass and morphological diversity. The roles that the biochemical properties of sediments and food availability play in structuring biological communities were reflected in the wider spectrum of length/width ratio (L/W) and size spectra, with biomass dominance in the higher weight-classes observed in Kongsfjord. In this respect, the appearance of short and plump nematodes in the Kongsfjord nematode assemblage (12% of all nematodes), characterised by a L/W ratio of <12, was striking. This morphotype, which is almost absent in the Hornsund fjord (4%), is considered to be an indicator of well-oxygenated sediments with favourable food sources and may further confirm that the organic material in the Kongsfjord sediments is of higher quality. Furthermore, the homogeneity of sediment composition suggests that the morphological landscape of nematode communities are not structured by granulometry per se, as has been suggested in other studies, but rather by other environmental factors that are indirectly connected with particle size. The results of the present study provide evidence that the morphometric characteristics of nematodes are suitable for detecting differences in sediments, particularly with regard to organic matter availability.

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1. Introduction

The hydrographical regime is one of the key factors driving biodiversity patterns and ecological functioning in marine systems (Grebmeier and Barry, 1991). In particular, in fjords, which are ecosystems of a restricted geographical area, hydrodynamical complexity shapes the temporal and spatial variations of its physical and biological components (Syvitski and Shaw, 1995; Gilbert, 2000). The fjords of the west coast of Spitsbergen are representative of places with dynamic hydrographical conditions (Svendsen et al., 2002). Although located in close geographical proximity, the environmental conditions of the fjords along the west coast of Spitsbergen differ markedly due to the balance of the influx of Atlantic and Arctic waters, river run-off and glacial melt.

For example, Kongsfjord, which is located in the northwest of the island, is influenced by the northern branch of the North Atlantic warm current (West Spitsbergen Current), whereas the Hornsund fjord, which is located in the south, is to a largely influenced by cold Arctic waters flowing from the Barents Sea via the Sørkapp Current (Swartel, 1985; Weslawski et al., 1991). Differences in the cross-shelf water-mass exchanges, together with strong environmental gradients due to marine-terminating glaciers at the head of the fjords, are likely to affect the flux of organic matter and energy transport through the food web. Regulated by the interaction between hydrographical regimes, physical process, and the structure and function of the food web, organic carbon produced in the surface waters fuels the benthic system (Smetacek, 1984).

The magnitude and composition of the organic material exported to the fjords, along with the strong environmental gradient along the fjords' axis, influence a wide range of benthic patterns and processes (Piepenburg, 2005). The response of benthic communities to these processes and physical forces is reflected

* Corresponding author. Tel.: +48 587311783.
E-mail address: kgrzelak@iopan.pl (K. Grzelak).

in their structural diversity, population densities and biomasses (Włodarska-Kowalcuk et al., 2005; Kędra et al., 2010a; Ronowicz et al., 2011), not only for macrofauna but also for meiobenthic and nematode communities (Kotwicki et al., 2004; Somerfield et al., 2006; Grzelak and Kotwicki, 2012). However, for the most part, research on the structural aspects of the nematode communities has not yielded a wealth of information about functional traits, such as trophic structure or body size, which are thought to be related to important ecological functions (Losi et al., 2013a,b; Norling et al., 2007; Vanaverbeke et al., 2003).

Due to their small body size (between 32 µm and 500 µm), nematodes are in intimate contact with the sediment and are therefore directly and indirectly influenced by the physical properties of the surrounding environment (e.g., granulometry, oxygen supply). Nematodes are regarded as suitable taxa for use in environmental monitoring (Kennedy and Jacoby, 1999; Semprucci et al., 2015a) and have already been implemented in many studies examining the impacts of anthropogenic and natural physical disturbances, environmental pollution and alterations in marine ecosystems (e.g., Sherman et al., 1983; Schratzberger et al., 2009; Alves et al., 2013; Semprucci et al., 2015b). However, the morphometrics of nematodes, despite being easier to study than taxonomical analyses, do not receive adequate attention in the context of environmental impact assessments. This is an unfortunate situation, since as a result of a wide range of morphological adaptations to an interstitial lifestyle, nematodes show significant differences in body size and shape (e.g., Tita et al., 1999; Soetaert et al., 2002; Losi et al., 2013a). As was shown by Schwinghamer (1981), variation in body size is a direct adaptation to sediment particle size, and interstitial pore size is a major influence on the size distribution of sediment dwelling organisms. Subsequent research (Duplisea and Drgas, 1999; Tita et al., 1999; Duplisea, 2000) has either failed to confirm this or has yielded inconsistent results, suggesting that other biotic and abiotic factors, such as sediment water content, oxygen concentration and organic content (as a proxy of food availability), are all important in determining body size and proportions. Nematode body length and width – as well as the length-to-width ratio, a quantitative measure of nematode shape – are also considered to be useful parameters reflecting

the state of the ecosystem that they inhabit (Soetaert et al., 2002; Vanaverbeke et al., 2003, 2004; Vanhove et al., 2004; Losi et al., 2013a). Body size can be indicative of the environmental context of behavioural life histories, physiologies, and energy requirements and reflect the structural and functional aspects of the nematodes (Peters, 1983; Vanaverbeke et al., 2003; Losi et al., 2013a); that is, body size has important implications for community structure and is a useful descriptor of an ecosystem. Analysis of the biomass spectrum is an alternative but complementary approach to traditional taxonomical investigation, which can lead to a broader and more comprehensive understanding of the processes and ecological roles of species within an ecosystem than performing taxonomic distinctions and grouping organisms into taxonomical units (Kerr, 1974; Woodward et al., 2005). In addition, focusing on biomass distribution over size has the added advantage of being less time-consuming and does not require considerable expertise.

Here, we describe the morphometry of nematodes, their biomass and body shape, and characterise the length–width relationships of nematode assemblages in two Arctic fjords, the Kongsfjord and the Hornsund, with different environmental conditions. We hypothesised that the different hydrographical regimes of the Hornsund and Kongsfjord determine the quality and quantity of the organic matter flux to the seabed, which leads to differing biogeochemical properties in the sediments and, consequently, differences in the morphological characteristics of the nematodes inhabiting the two fjords.

2. Materials and methods

2.1. Study area

Sampling was undertaken in two fjords along the west coast of Spitsbergen. Kongsfjord is an open, 26-km-long fjord located on the northwestern coast of Spitsbergen, Svalbard (12°E 79°N; Fig. 1). The fjord is divided into the outer basin, with average depths of 200–300 m, and separated from the outer basin by a chain of islands (Lovénøyane), the inner basin, with average depths of 50–60 m. Landforms around Kongsfjord were and are shaped by glacial activity, with the active tidal glacier Kongsbreen situated at the head of

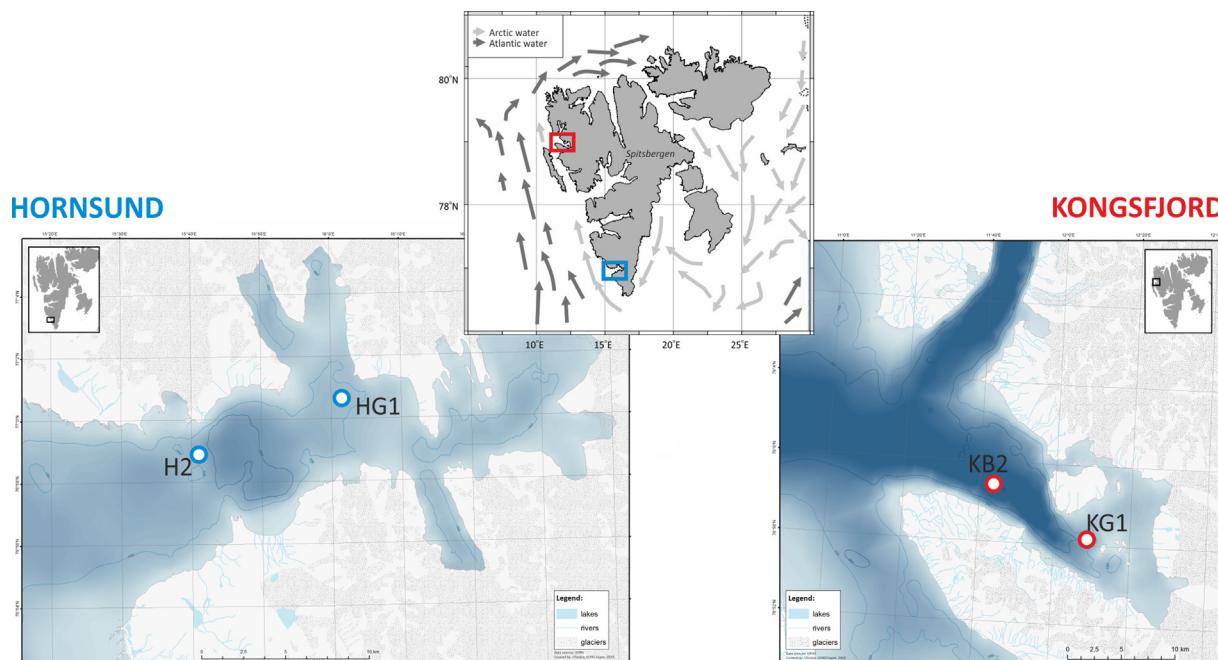


Fig. 1. Map of the Svalbard Archipelago showing the location of Hornsund and Kongsfjord and sampling stations.

Table 1

Coordinates of the sampling stations, bottom water temperature and salinity, together with the characteristics and chemical composition of the sediments: chlorophyll *a* concentration (chl *a*), organic carbon-to-nitrogen ratio (C/N), organic carbon content (C_{org}), and carbon isotopic composition values ($\delta^{13}\text{C}_{\text{org}}$); mean (min–max).

Fjord	Hornsund		Kongsfjord	
Station	HG1 (inner)	H2 (central)	KG1 (inner)	KB2 (central)
Latitude (°N)	77°00'02" N	76°58'77" N	78°55'85" N	78°58'69" N
Longitude (E)	16°05'44" E	15°42'30" E	12°08'37" E	11°42'27" E
Depth (m)	78	145	105	310
POC _{flux} (g/m ² /24 h)	3.6–5.2	0.8–1.3	12.4–13.0	2.8–4.1
Temperature (°C)	1.77	1.65	2.90	1.63
Salinity	34.7	34.8	34.8	35.0
Mean grain size (μm)	15.06 (14.0–17.2)	16.04 (12.3–18.9)	15.15 (14.2–17.2)	14.97 (14.2–15.4)
Sorting (μm)	2.89 (2.5–3.3)	3.13 (2.3–4.5)	2.54 (2.4–2.9)	2.46 (2.3–2.5)
chl <i>a</i> (μg/g)	2.13 (0.6–3.7)	0.84 (0.5–1.2)	2.09 (0.7–3.3)	1.54 (0.7–2.9)
C/N	8.24 (7.1–8.6)	9.38 (9.0–9.5)	6.09 (5.7–6.2)	8.08 (7.8–8.2)
C _{org} (%)	1.36 (1.2–1.5)	1.26 (1.1–1.3)	0.46 (0.3–0.6)	1.21 (1.0–1.4)
$\delta^{13}\text{C}_{\text{org}}$ (‰)	-24.56 (-24.9 to 24.0)	-23.86 (-24.1 to 23.8)	-22.47 (-22.6 to 22.2)	-22.16 (-22.3 to 22.0)

the fjord. Marine primary production is the main source of organic carbon (C_{org}) for the Kongsfjord system (Kuliński et al., 2014).

The 30-km-long open Hornsund fjord is the southernmost glacial fjord on the west coast of Spitsbergen (Fig. 1). As much as 70% of the Hornsund's catchment area is covered with glaciers, with thirteen of them directly entering the fjord (Błaszczyk et al., 2013) and five of the most active glaciers located in the inner, topographically isolated Brepollen basin. It has been estimated that tidewater glaciers in Hornsund retreat faster (~70 m a⁻¹ on average) than elsewhere on Svalbard (~45 m a⁻¹ on average), most likely due to local topographical conditions (Błaszczyk et al., 2013). Hornsund is homogenous in terms of trophic conditions, specifically organic carbon (C_{org}) and chlorophyll *a* (chl *a*) content in sediments (Drewnik et al., 2016).

Two sampling stations were placed in each fjord: stations HG1 and KG1 were located in the shallower, inner parts of the fjords (78 and 105 m, respectively), and stations H2 and KB2 were located in the deeper, central areas of the fjords (145 and 310 m, respectively) (Table 1 and Fig. 1).

2.2. Sampling and laboratory analyses

Samples were collected in July and August 2013 during a cruise of the R/V *Oceania* (Institute of Oceanology, Polish Academy of Sciences). Undisturbed sediment cores were collected using a Niemistö gravity corer (9-cm inner diameter). Three cores, which were obtained from separate deployments, were sampled for meiofaunal analysis using a Plexiglas tube with an inner diameter of 3.6 cm. One additional Niemistö core was collected to determine the biogeochemical parameters (chlorophyll *a*, organic carbon and total nitrogen, stable carbon isotope composition) and grain size distribution. All samples were sliced vertically into 1-cm layers, down to a depth of 5 cm. Sediment cores used for meiofaunal analyses were fixed immediately in 4% buffered formaldehyde, whereas samples used for biogeochemical analyses were frozen on-board at a temperature of -80 °C and transported to the laboratory. To assess the organic carbon sedimentation rate, double cylindrical sediment traps with diameters of 7.2 cm and lengths of 46 cm were deployed 2 m above the bottom of the fjords, following Zajączkowski (2002). Sedimentation rates were measured after a minimum of 24 h of exposure; samples were then filtered through pre-combusted and pre-weighted Whatman GF/F glass fibre filters, after which the samples were immediately frozen at -80 °C.

In the laboratory, each sediment slice intended for meiofaunal analysis was centrifuged in a solution of colloidal silica LUDOX TS50 and organisms being filtered from the supernatant using a 32-μm sieve (Vincx, 1996). All metazoan meiobenthic organisms were counted and classified at higher taxonomic levels under a stereomicroscope after staining with Bengal Rose to facilitate

identification of the organisms amongst the similarly coloured sediment grains. From one replicate, 100 nematodes (or all nematodes if fewer than 100 were present in the sample) from each sediment slice were picked out randomly and mounted in anhydrous glycerine (Seinhorst, 1959) on glass slides. Nematodes were measured individually using an image analyser (AxioCam Zeiss), with body length (*L*) being measured from head to tail (excluding filiform tails). The width of the nematodes (*W*) was measured at the thickest part of the body (Platt and Warwick, 1983).

Prior to the biogeochemical analyses, the samples of both sediments and filters were freeze-dried and homogenised. Chlorophyll *a* (chl *a*) concentrations in the sediment samples were measured using the fluorometric method (Evans et al., 1987) and a Perkin Elmer LS55 Fluorescence Spectrometer. Pigments from freeze-dried sediments were extracted from samples immersed in 90% acetone for 24 h at 4 °C. Emission at 671 nm exited at 431 nm was measured before and after sample acidification with 1 M HCl and used to calculate chl *a* concentrations in accordance with the method described by Evans and O'Reilly (1983).

The compositions of organic carbon (C_{org}), total nitrogen (N_{tot}) and stable carbon ($\delta^{13}\text{C}_{\text{org}}$) isotopes in both the sediment and the filter samples were measured with an Elemental Analyzer Flash EA 1112 Series in combination with a Isotopic Ratio Mass Spectrometer IRMS Delta V Advantage (Thermo Electron Corp., Germany). To remove carbonates, dry and homogeneous samples were weighed into silver vials and acidified with HCl (Chang et al., 1991; Hedges and Stern, 1984). The methodology used provided satisfactory accuracy and precision (average recovery 98.5 ± 2.7%). Carbon isotopic ratios ($\delta^{13}\text{C}_{\text{org}}$) were calculated using the laboratory working pure reference gases: CO₂ was calibrated against IAEA (International Atomic Energy Agency) standards, and $\delta^{13}\text{C}$ values were reported relative to PDB (Pee Dee Belemnite). The standard deviation for replicate samples (*n* = 6) was less than 0.17‰ for $\delta^{13}\text{C}_{\text{org}}$. The ratio of C_{org} to N_{tot} is referred to as C/N and indicates the state of organic matter degradation. $\delta^{13}\text{C}$ is commonly used to distinguish between marine and terrigenous material and we used both indicators to characterise source and fate of organic material in fjords' sediments.

Analysis of grain-size distribution was conducted using a Counter Particle Size Analyser, and grain-size statistics were calculated using the geometric method of moments of GRADISTAT software (Blott and Pye, 2001). Grain size data are presented in μm.

2.3. Data analysis

Nematode individual biomass was calculated via an adjusted Andrassy's formula (1956), wherein wet weight (μg) = *L* (μm) × W² (μm)/1,600,000, and a dry-to-wet weight ratio of 0.25 was applied.

Table 2

Results of multivariate (granulometric characteristics) and univariate PERMANOVA tests for differences in environmental variables between fjords (Fj), basins (Ba) and among sediment layers (Sl); significant effect: * $p < 0.05$, ** $p < 0.001$ are indicated next to the values of PERMANOVA 'pseudo' F statistics (p-F).

Source	df	Granulometry		chl a		C/N		C _{org}		δ ¹³ C _{org}	
		MS	p-F	MS	p-F	MS	p-F	MS	p-F	MS	p-F
Fj	1	0.304	1.603	0.670	2.318	14.909	141.080**	1.144	96.255**	17.886	484.580**
Ba	1	0.028	0.147	3.697	12.790*	12.183	115.290**	0.530	44.585**	1.290	34.959**
Sl	4	0.109	0.576	2.545	8.805*	0.272	2.576	0.026	2.167	0.070	1.898
Fj × Ba	1	0.093	0.489	0.663	2.292	0.875	8.278*	0.923	77.712**	0.188	5.081
Fj × Sl	4	0.194	1.025	0.062	0.213	0.149	1.406	0.023	1.959	0.014	0.375
Ba × Sl	4	0.192	1.014	0.528	1.828	0.065	0.620	0.004	0.330	0.074	2.004
Res	4	0.190		0.289		0.106		0.012		0.037	
Total	19										

Nematode biomass spectra (NBS) were constructed following the procedure described by Vanaverbeke et al. (2003), in which the total biomass per size class (dry weight, µg) on the y-axis is plotted against the log₂ grouping of the dry weight of nematodes (µg) on the x-axis. Thus, for example, the biomass in size class 1 is the sum of the biomass of all organisms with a dry weight range of $\geq 2^1$ to $< 2^2$, which is ≥ 2 µg to < 4 µg. The measurements per cm slice were pooled per core to construct NBS to provide an entire spectrum of nematodes in the 5-cm sediment columns at each station. To facilitate comparisons of the plotted spectra, biomass of each size class was converted to a percentage of the total biomass for each station or sediment depth. For allometric attributes, geometric means next to arithmetic means were calculated, given that the distribution of nematode length, width and, therefore, the corresponding biomass are usually skewed towards smaller values.

Both univariate and multivariate non-parametric permutational ANOVA (PERMANOVA, Anderson, 2001; Anderson et al., 2008) were used to test for differences in nematode characteristics and for differences in the biogeochemical properties between the fjords and the basins. Differences in nematode abundance were tested using a 4-factor mixed model design, with the factors consisting of 'Fjord' (Fj; fixed), 'Basin' (Ba; fixed), 'Sediment layer' (Sl; fixed) and 'Core' (Co, random and nested within Fj × Ba) because different depth layers were not replicated in each core, and replicates were considered to be independent and separate from one another (Gallucci et al., 2009). Other univariate descriptors of nematode assemblages (e.g., biomass, length, width, L/W, individual biomass) and all environmental variables were analysed using a 3-factor mixed model design with the factors Fj, Ba, Sl because one replicate sample was available for each variable. All calculations of Pseudo-F and p values were based on 9999 permutations of the residuals under a reduced model, and because the samples were not replicated, the highest order interaction (the 4-way or 3-way) was included in the residual. Euclidean distance similarity was used to calculate the resemblance matrix based on untransformed data for all univariate analyses and on square-root transformed data for multivariate analysis of the sediment granulometric composition.

Based on a histogram analysis of all available L/W ratio values, we distinguished two morphotypes of nematodes (group I and group II), with the group I morphotype consisting of plump nematodes and the group II morphotype composed of longer and more slender nematodes. Given that the majority of nematodes belonged to the group II morphotype, several sub-groups were distinguished within this group based on the length and width values: in terms of length, nematodes were classified as 'short' if they measured below the first quartile ($< Q1$); 'medium', if they ranged between the first and third quartiles ($Q1-Q3$); and 'long', if they measured above the third quartile ($> Q3$); for width values, nematodes were classified as 'slender' ($< Q1$), 'medium' ($Q1-Q3$) and 'thick' ($> Q3$). The relative abundance of each morphotype and selected sub-groups in the two fjords were compared using a chi-square (χ^2) test for independence (2×2 table).

A two-sample Kolmogorov-Smirnov test and a G-test were used to determine whether the nematode L/W ratio and biomass class distribution differed significantly among stations. A Spearman correlation analysis was performed to examine the relationships between environmental factors and nematode characteristics.

All analyses were performed with PRIMER v6 and PERMANOVA+ add-on software (Clarke and Gorley, 2006; Anderson et al., 2008) and STATISTICA12 software.

3. Results

3.1. Biogeochemical characteristics of sediments

The sediments of the two fjords were composed primarily of poorly sorted, medium-grained silt (Table 1). Granulometric characteristics were homogeneous, and no differences between fjords and stations were recorded for grain size (Table 2). Granulometric distribution was also very consistent throughout the vertical profile of the sediments (Table 2).

Although the concentrations of chl a were comparable between the two fjords, significant differences were found between the basins of the fjords (Table 2), with inner basin sediments being chl a-enriched compared with those of the central basins (Table 1). At the inner basin stations, the highest chl a concentrations were measured in the sub-surface sediment layers (1–2 cm), whereas a gradual decrease in chl a values was observed in the central station sediments. Significant differences between the fjords (Fj) and the basins (Ba) were detected for other environmental parameters, including C/N, C_{org} and δ¹³C_{org}. For C/N and C_{org}, significant Fj × Ba interactions suggest that the variability in parameter values among the stations was dependent on the fjord.

Molar C/N ratio values were higher in the Hornsund fjord, with the highest values recorded at the central station (H2; Table 1). In general, sediments in the central basins had higher C/N ratio values and were significantly different from those of the inner basins. Organic carbon content (C_{org}) was also significantly higher in the Hornsund fjord (Table 2), but no differences between the inner and the central stations were recorded, in contrast to Kongsfjord, where sediments were more heterogeneous in terms of this parameter. Carbon isotopic composition (δ¹³C_{org}) of sediments varied significantly between the two fjords, with values ranging from -22.2‰ in sediments from the Kongsfjord central station to -24.6‰ in sediments collected from the inner station in Hornsund. A comparison of the C/N ratio signature with δ¹³C_{org} values reflects a predominance of marine organic matter in Kongsfjord (Fig. 2).

The flux of organic carbon (POC) to the bottom of the fjords was as much as 3 times higher in the Kongsfjord fjord than in the Hornsund fjord (Table 1), and the flux of organic particles was substantially lower in the central basins than in the inner basins (mean values 2.2 vs 8.5 g/m²/24 h, respectively).

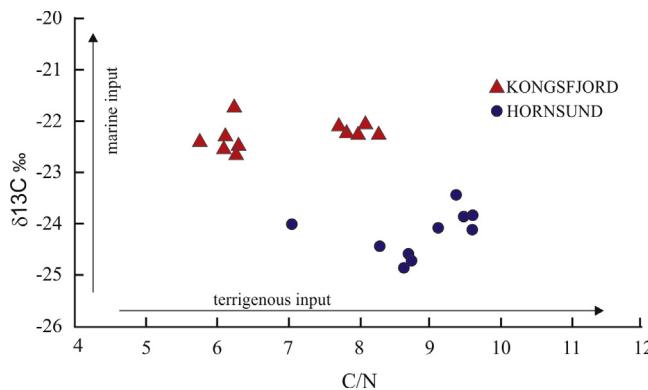


Fig. 2. Relationship between C/N ratio and $\delta^{13}\text{C}_{\text{org}}$ values indicating source and fate of organic matter in the investigated fjords.

3.2. Nematode standing stocks and morphometrics

A total of 17 higher taxa of meiofauna were recorded, including 11 in Kongsfjord and 13 in Hornsund. Nematodes were the dominant group at all stations, comprising between 89.4% and 94.2% of the total metazoan community.

Mean nematode abundance in Kongsfjord ($8384 \pm 1463 \text{ ind}/10 \text{ cm}^2$) and Hornsund ($6512 \pm 1425 \text{ ind}/10 \text{ cm}^2$) was comparable, whereas significant differences were observed between the fjord basins (Tables 3 and 4), with total nematode abundance being significantly larger in the inner basins than in the central areas of the fjords.

Higher nematode abundances in the inner part of the fjords were associated with higher chl *a* and lower C/N values in the sediments (Table 1). Significant differences in nematode density distributions between the fjords and the basins were also observed when the vertical profiles of sediments were compared (Fig. 3 and Table 4); in Kongsfjord, nematodes were more evenly distributed throughout the sediment layers, and their densities remained high as deep as 4 cm (between 270 and 800 ind/ 10 cm^2). In Hornsund,

a sharp decrease in nematode density was observed between the surface layer and the deeper layers for central station HG1, where almost 80% of the nematode community was concentrated in layer 1, whereas a more gradual decrease in nematode density was observed at the outer station H2 (Fig. 3).

Total biomass was significantly higher in the shallower areas of the inner basins than in the deeper central basins (Tables 3 and 4), and on average, biomass was markedly higher in Kongsfjord ($1278 \pm 328 \mu\text{g}/10 \text{ cm}^2$) than in Hornsund ($853 \pm 336 \mu\text{g}/10 \text{ cm}^2$) (Table 4). The vertical distribution pattern for biomass resembled that described for nematode density, with the exception of layer 3 from the inner station at Kongsfjord. At this location, station KG1, nematode density declined gradually with increasing sediment depth, but total biomass was highest in the middle of the sediment core (at 3 cm) (Fig. 3). Densities and total biomass of nematodes were, in general, significantly correlated with indicators of organic matter quality (chl *a* and C/N) (Table 5).

Almost 2000 individual nematodes were measured, averaging (geometric means) $720 \mu\text{m}$ in length and $26 \mu\text{m}$ in width, with an individual dry weight of $0.076 \mu\text{g}$ (arithmetic means: $847 \mu\text{m}$, $29 \mu\text{m}$, and $0.262 \mu\text{g}$, respectively). A broad range of nematode sizes and shapes was observed; nematode length ranged from 145 to $6204 \mu\text{m}$, and width, from 6.8 to $174 \mu\text{m}$ (for all data). The stoutest nematode, with a *L/W* ratio of 4.3, was collected from the deepest sediment layer (layer 5) at the inner station in Hornsund (HG1), whereas the most slender nematode, with a *L/W* ratio of 119, was collected from the mid-section of the sediment core (layer 3) at the Kongsfjord inner station (KG1). Nematodes in Kongsfjord were generally longer and wider than those in Hornsund, resulting in a significantly greater mean individual biomass (Tables 3 and 4). There was also greater variation in nematode individual biomass in the shallower inner basins (0.0036 – $9.4 \mu\text{g DW}$) than in the central basins (0.006 – $9.8 \mu\text{g DW}$).

The plots of the length-width relationship, which are presented in Figs. 4 and 5, revealed marked differences in nematode size between the two fjords. In general, two distinct morphological groups were distinguished, illustrated in the *L/W* ratio histogram (Fig. 4) as two clearly demarcated peaks, with the first occurring

Table 3
Mean values of nematode total abundance (mean \pm SE), total biomass, body length, width, the *L/W* ratio and individual biomass; for length, width and individual biomass, geometric means/arithmetic means are presented.

Fjord	Hornsund				Kongsfjord			
	Station		HG1 (inner)	H2 (central)	KG1 (inner)	KB2 (central)		
Abundance (ind./ 10 cm^2)			8547 ± 2107.4	4477 ± 1255.7	$11,650 \pm 196.3$	5119 ± 104.9		
Biomass ($\mu\text{g}/10 \text{ cm}^2$)			1189	517	1606	950		
Length (μm)			673.8/765.4	756.9/869.5	622.4/775.6	843.4/976.1		
Width (μm)			24.3/26.5	24.1/26.9	27.2/29.9	28.8/32.6		
<i>L/W</i>			27.7/30.9	31.3/34.0	22.8/26.8	29.2/31.6		
Ind. biomass (μg)			0.062/0.148	0.069/0.300	0.072/0.262	0.109/0.341		

Table 4
Results of univariate PERMANOVA tests for differences in nematode characteristics between fjords (Fj), basins (Ba) and among sediment layers (Sl); significant effect: * $p < 0.05$, ** $p < 0.001$ are indicated next to the values of PERMANOVA 'pseudo' *F* statistics (p-*F*).

Source	Abundance			Biomass			Length		Width		<i>L/W</i>		Ind. biomass	
	df	MS	p- <i>F</i>	df	MS	p- <i>F</i>	MS	p- <i>F</i>	MS	p- <i>F</i>	MS	p- <i>F</i>	MS	p- <i>F</i>
Fj	1	764.7	6.26	1	4913.6	11.63*	24.1	0.36	80.1	24.92**	65.1	5.00*	0.039	25.34*
Ba	1	1566.9	12.82*	1	2235.0	5.29*	459.5	6.79*	2.6	0.82	99.6	7.66*	0.037	23.93*
Sl	4	5664.3	208.85**	4	4307.7	10.19**	426.0	6.30*	19.6	6.08*	99.8	7.67*	0.043	27.32*
Fj × Ba	1	365.9	3.00	1	329.3	0.78	97.0	1.44	3.2	1.01	13.1	1.01	0.015	9.60*
Fj × Sl	4	85.6	3.15*	4	1301.8	3.08*	61.8	0.91	5.7	1.76	5.5	0.43	0.006	3.91
Ba × Sl	4	293.3	10.81**	4	403.1	0.95	40.0	0.59	8.9	2.78	9.8	0.75	0.009	5.87
Co (Fj × Ba)	8	122.1	4.50**											
Fj × Ba × Sl	4	258.4	9.52**											
Res	32	27.1		4	422.5		67.6		3.2		13.0		0.002	
Total	59			19			19		19		19		19	

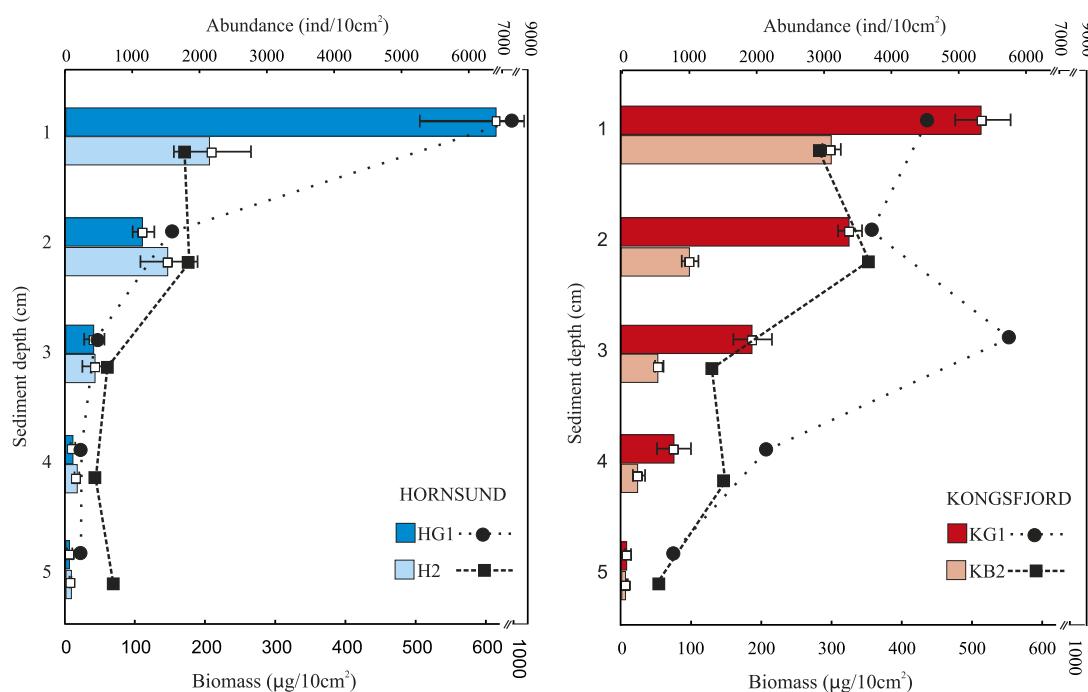


Fig. 3. Mean nematode abundance (\pm SE) (bars) and biomass (dotted lines) along the vertical profile of the sediment.

Table 5

Spearman correlation between selected environmental variables (chl *a* – chlorophyll *a*; C/N – carbon-to-nitrogen ratio; C_{org} – organic carbon content; δ¹³C_{org} – carbon isotopic composition values) and nematode characteristics (Abund – abundance; Biom – biomass; *L* – length; *W* – width; IndB – individual biomass; *L/W* – length-to-width ratio) calculated for all data together and separately for the fjords. Only significant correlation values with $p < 0.05$ are shown; underlined values indicate $p < 0.001$.

	Abund	Biom	<i>L</i>	<i>W</i>	IndB	<i>L/W</i>
All data						
chl <i>a</i>	0.79	0.75	-0.53	ns	-0.68	-0.49
C/N	-0.46	<u>-0.59</u>	0.41	ns	ns	0.53
C _{org}	ns	ns	ns	ns	ns	ns
δ ¹³ C _{org}	ns	0.43	ns	<u>0.61</u>	ns	ns
Hornsund						
chl <i>a</i>	ns	ns	ns	ns	-0.68	ns
C/N	ns	ns	ns	ns	ns	ns
C _{org}	ns	ns	ns	0.73	ns	ns
δ ¹³ C _{org}	ns	ns	ns	ns	ns	ns
Kongsfjord						
chl <i>a</i>	<u>0.92</u>	0.81	-0.82	<u>-0.91</u>	<u>-0.90</u>	-0.65
C/N	ns	-0.60	0.71	ns	0.53	0.61
C _{org}	ns	ns	ns	ns	ns	ns
δ ¹³ C _{org}	ns	ns	ns	ns	ns	ns

at value 8 and the second between the 20 and 30, and a minimum at value 12. As such, a *L/W* ratio of 12 was used to distinguish between plump nematodes (group I), characterised by a low *L/W* ratio (*L/W* < 12), and more slender and on average longer nematodes (group II), characterised by a higher *L/W* ratio (*L/W* > 12).

Of the nematodes collected in Kongsfjord, 12% belonged to group I, whereas a significantly lower proportion – only 4% – of nematodes in Hornsund belonged to this group (χ^2 test, $\chi^2 = 14,820.1$, $p < 0.001$). Within group II, marked differences in nematode size were observed between fjords (Fig. 5).

The majority of the nematode community in Hornsund consisted of shorter and more slender forms. Their abundance was significantly higher than in Kongsfjord, where longer and thicker individuals dominated in the sediments (Table 6 and Fig. 5). Thus,

significant differences in nematode abundance from the two outermost sub-groups were observed. The shortest (<540 µm) and most slender nematodes (<19 µm) (sub-group 'short and slender') occurred in higher abundance in Hornsund, where they constituted almost 15% of the nematode community. Nematodes that belonged to the 'long and thick' sub-group (those with a body length > 1050 µm and body width > 32 µm) were twice as abundant in Kongsfjord than in Hornsund (26% and 12%, respectively). These differences are also reflected in the *L/W* ratio distribution plot (Fig. 6). The morphometric class distribution in Hornsund shifted towards smaller values than in Kongsfjord, with a peak *L/W* ratio of 19:24 (Fig. 6A and B). Individuals with such morphometric characteristics were commonly observed in the surface layer (43% of the surface assemblage) of sediments collected from the inner basin of Hornsund (HG1). In both fjords, the wider and more equally distributed spectrum of *L/W* classes in deeper sediments (2–5 cm depths) (Fig. 6A, smaller panels) suggests that the distribution of length and width of the nematodes in these layers was spread more evenly, with neither morphotype dominating. The *L/W* frequency graph also had a second, smaller peak between the ratio values of 42–46 for nematodes collected from Hornsund (Fig. 6A), reflecting the presence of slender nematodes with average lengths of 900–1000 µm. Individuals with such proportions were less common in Kongsfjord (15% vs 7% of the community, respectively). A higher abundance of longer nematodes with larger body width were observed in Kongsfjord, with 86% of nematodes exhibiting a *L/W* ratio below 40, whereas the same ratio for nematodes collected in Hornsund was 67%. Accordingly, significant differences in the spectrum of nematode *L/W* ratios were found between the fjords (Kolmogorov–Smirnov test, $p > 0.05$).

In general, apart from the width values, there was a negative correlation between allometric attributes (*L*, *L/W* ratio) and individual biomass and chlorophyll *a* concentration in the sediments of the fjords (Table 5) and a positive correlation between *L/W* ratios and C/N values. No relationship was found between nematode

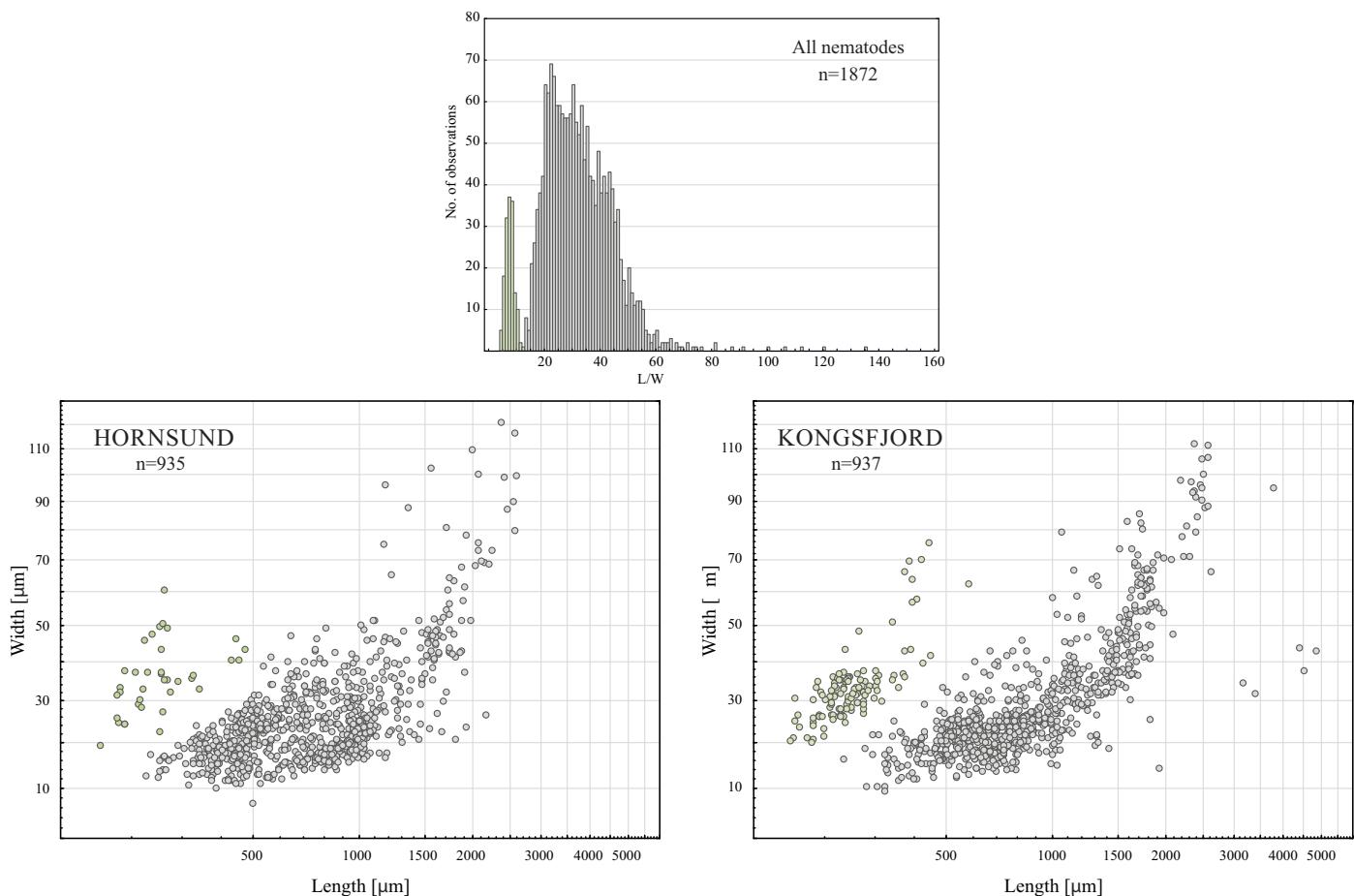


Fig. 4. Morphological diversity of Spitsbergen nematodes. Upper graph: L/W histogram for all available data; lower graphs: L/W relationship plots (log scale) for the fjords. Colouration is a function of L/W ratio values: $L/W < 12$ – green (group I), $L/W > 12$ – grey (group II). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

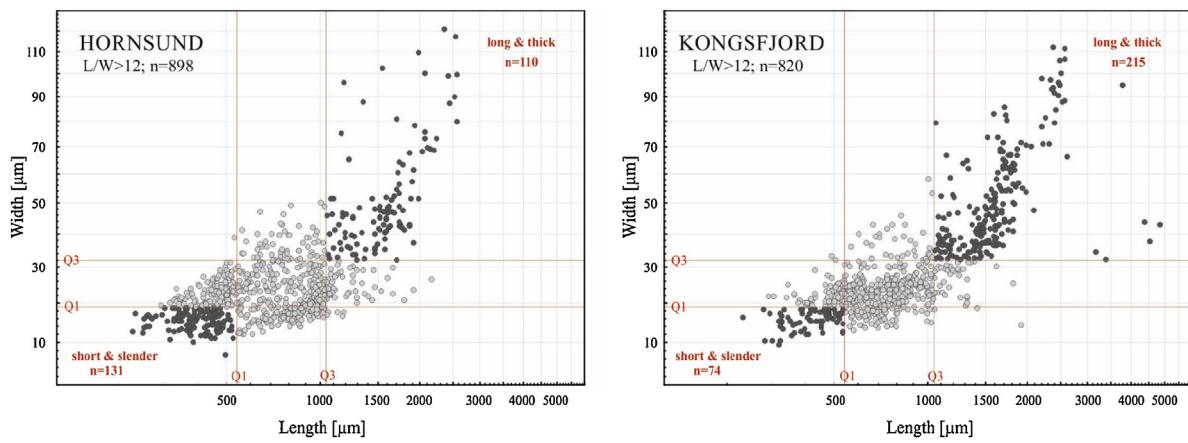


Fig. 5. Length–width relationship plots (log scale) for group II ($L/W > 12$) nematodes, with indications for the first and third quartiles (Q1, Q3).

morphometrics and sediment composition (not shown in Table 5).

Nematode biomass spectra showed different distribution patterns between the fjords (Fig. 7A, G-test, $p < 0.05$), with a unimodal size-spectra distribution for Kongsfjord and a bimodal distribution for Hornsund. A shift in body size (weight) towards a higher abundance of larger individuals at Kongsfjord was observed,

with a single peak in size class 1. In this fjord, 41% of the total biomass was composed of organisms in size classes 1 and 2. In Hornsund, biomass was distributed more evenly among size classes, and differences between size classes were less obvious than in Kongsfjord. Observed biomass peaks (in size classes –3 and 1) in Hornsund were smaller, and organisms from those classes made up 13% and 16%, respectively, of the total biomass. ‘Long

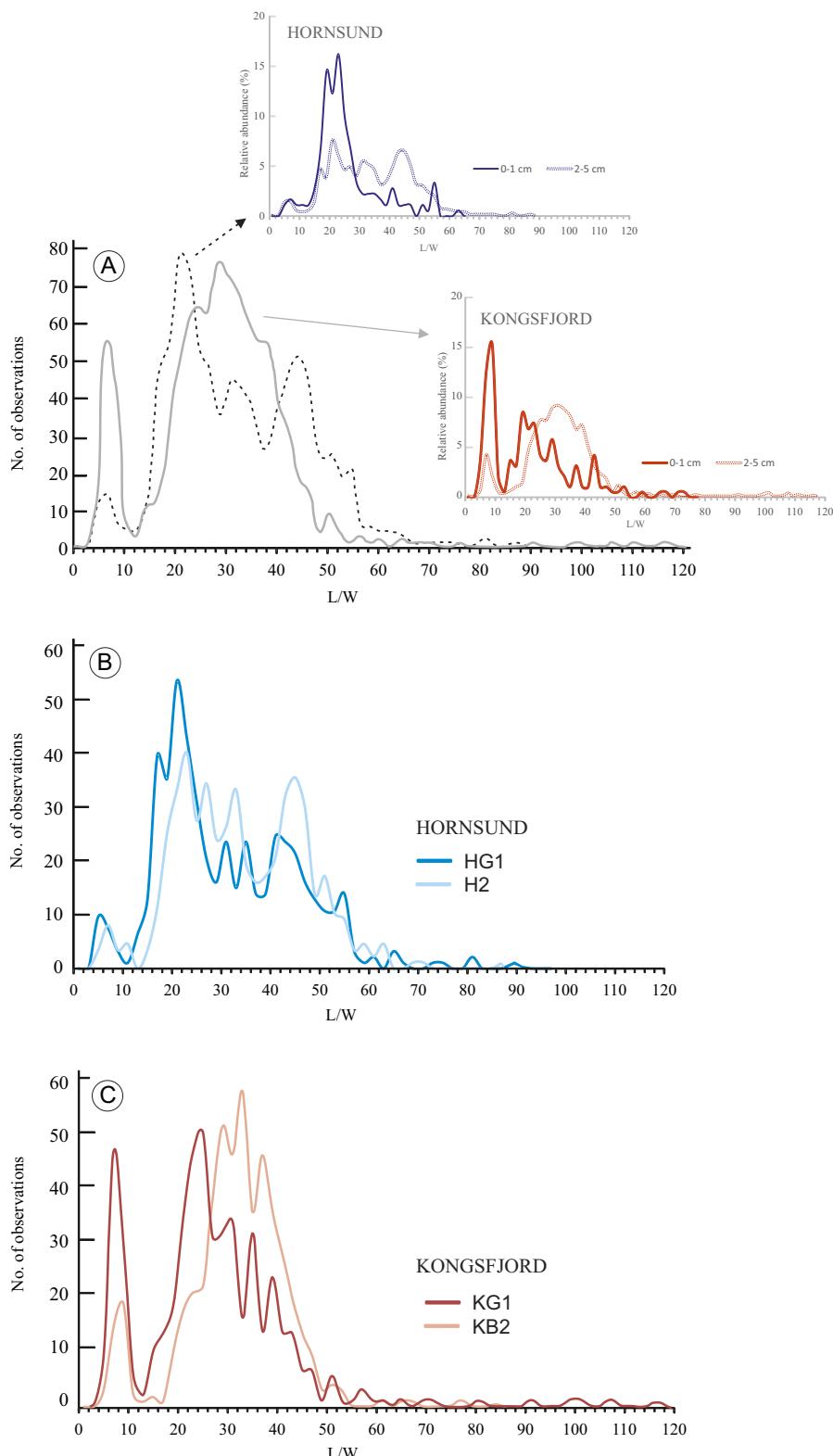


Fig. 6. Length/width ratio distribution plots for nematode assemblages for (A) Hornsund and Kongsfjord (large plot), for the surface layer (0–1 cm) and at lower depths (2–5 cm), separately in both fjords (smaller panels) – due to the high disproportion in the number of measurements for the surface layer and deeper depths, the relative abundance of nematodes in L/W classes is presented; (B) Hornsund central and outer basin; (C) Kongsfjord central and outer basin.

and thick' nematodes (Fig. 5) and commonly observed nematodes with L/W ratios roughly between 25 and 35 had a high impact on total biomass in Kongsfjord, especially below surface layers (see Fig. 6A and C), as did 'short and stout' nematodes in surface layer

(Fig. 6A), belonging mainly to size class –4. This is clearly evident when the biomass spectra within sediments collected from the Kongsfjord stations are compared (Fig. 7C): the biomass of plump nematodes, which were highly abundant at the inner station KG1,

Table 6

Relative contribution of nematode sub-groups distinguished based on length and width values within group II ($L/W > 12$), together with the results of the χ^2 test.

Size and shape of nematodes	Hornsund	Kongsfjord	Horn vs Kongsf	
	(%)	(%)	χ^2	p
Length				
Short ($<Q1 = \leq 540 \mu\text{m}$)	30.62	19.15	30.00	<0.001
Medium ($Q1-Q3 = 540-1050 \mu\text{m}$)	50.45	50.24	0.01	0.934
Long ($>Q3 = \geq 1050$)	18.93	30.61	180.93	<0.001
Width				
Slender ($<Q1 = \leq 19 \mu\text{m}$)	30.40	18.78	30.99	<0.001
Medium ($Q1-Q3 = 19-32 \mu\text{m}$)	50.56	49.51	01.9	0.665
Thick ($>Q3 = \geq 32 \mu\text{m}$)	19.04	31.71	36.58	<0.001
Length and width				
Short and slender	14.59	9.02	12.62	0.0004
Medium and slender	15.70	9.51	17.15	<0.001
Long and slender	0.11	0.24	0.01	0.936
Short and medium	15.48	9.76	12.62	<0.001
Medium and medium	28.51	35.61	9.95	0.002
Long and medium	6.57	4.15	4.92	0.027
Short and thick	0.56	0.37	0.05	0.821
Medium and thick	6.24	5.12	0.99	0.320
Long and thick	12.25	26.22	54.54	<0.001

is visualised as a first biomass mode in size class –4. Biomass increased again from class –1, reaching the second biomass mode in size class 0, and then decreased through the higher size classes. A similar distribution pattern of nematode size was observed at the central station KB2 (G-test, $p > 0.05$), although at this location, the distribution was shifted towards larger size classes. A smaller peak in biomass was observed at size class –1, whereas individuals belonging to size class 2 had a greater contribution to biomass. Biomass spectra for the Hornsund stations were more gradual than those of Kongsfjord. Small biomass peaks were observed for size classes –3 and 1 at the inner station HG1. The distribution of individuals among size classes was most homogenous in sediments collected from the central station H2, in which the distribution spectra did not show any class-size peaks (Fig. 7B). Elevated biomass values were spread over size classes 0–3. Differences between the Hornsund stations were most pronounced in the middle part of the spectrum, at size class 0, where a marked decrease in biomass was noted at station HG1, in contrast to station H2.

4. Discussion

The overall dimensions (27 km length \times $\sim 8-10$ km width) and sediment compositions of the two fjords are highly similar (Tables 1 and 2). Both are typical glacier fjords, each featuring several tidewater glaciers along their shorelines. Kongsfjord receives an enhanced inflow of Atlantic waters (e.g., Cottier et al., 2005), however, which makes its waters slightly warmer and more saline than those of Hornsund (Table 1). The advected water masses physically control and drive biological components of both pelagic and benthic systems; as such, although similar in many respects, Kongsfjord and Hornsund differ in several aspects of their pelagic (Weslawski et al., 1991; Wiktor and Wojciechowska, 2005; Piwosz et al., 2009) and benthic communities (Kędra et al., 2010a,b, 2013; Grzelak and Kotwicki, 2012; Włodarska-Kowalcuk et al., 2012). The results of our study show that the morphology and biomass of nematodes differed between the two glacial fjords. The clear division of nematode size and shape, both at the larger spatial scale (between fjords) and at the scale of the basins within the fjords, indicates that the morphological attributes of nematode assemblages are useful in demonstrating differences in the environmental conditions of the fjords. The structure of spatially related allometric measurements was especially strong in nematodes collected from

Kongsfjord, wherein the central fjord nematode community was markedly different from the community in the inner area of the fjord.

Based on investigated environmental parameters it can be assumed that differences in nematode densities, biomass and morphometric characteristics between fjords most likely reflect differences in the flux of organic material to the seafloor and in the biochemical properties of the sediments. Due to the high homogeneity of sediment composition, granulometry and sediment type were not the factors governing patterns of allometric attributes of nematodes, although previous studies have shown that particle size and heterogeneity are important factors in determining nematode body size (Steyaert et al., 1999; Tita et al., 1999; Fleeger et al., 2011; Semprucci et al., 2013). In contrast, our results highlighted the importance of food availability and sediment biochemistry, factors that are, at most, indirectly related to granulometric variables. Sedimentary organic carbon content differed significantly between the fjords (Table 2), and the quantity of organic matter varied between study sites. Moreover, the quality of organic matter seemed to differ; a mean total core C/N ratio of 6.1 at the inner station KG1 in Kongsfjord typically reflects marine organic matter (Redfield et al., 1963). This ratio was higher (8.1) at the central station KB2, indicating the presence of more degraded phytoplanktonic material, but together with stable isotopic values suggests that the sediments of Kongsfjord contained higher quality organic matter than those of Hornsund (Table 2 and Fig. 3). Research had previously demonstrated the high contribution of autochthonous organic matter in the surface sediments in Kongsfjord (Winkelmann and Knies, 2005; Kuliniński et al., 2014). The area around Hornsund is an important breeding site for several bird species and supports some of the largest seabird colonies (mostly little auks) in south-western Spitsbergen (Wojczulanis-Jakubas et al., 2008), which may lead to a greater contribution of terrestrial organic material in the waters of Hornsund than in Kongsfjord. Koziorowska et al. (2016) have recently confirmed domination of terrestrial organic carbon over that of marine origin in Hornsund. Therefore, compared with more refractory material from terrigenous origin being present in Hornsund, a higher $\delta^{13}\text{C}_{\text{org}}$ signature and a lower C/N ratio in Kongsfjord indicate that the fjord receives a higher input of carbon of marine origin, which can be used more efficiently by benthic fauna (e.g., Ingels et al., 2011a). Total nematode abundance and its vertical distribution in the sediment profiles appear to confirm this relationship: nematodes in Kongsfjord were more abundant,

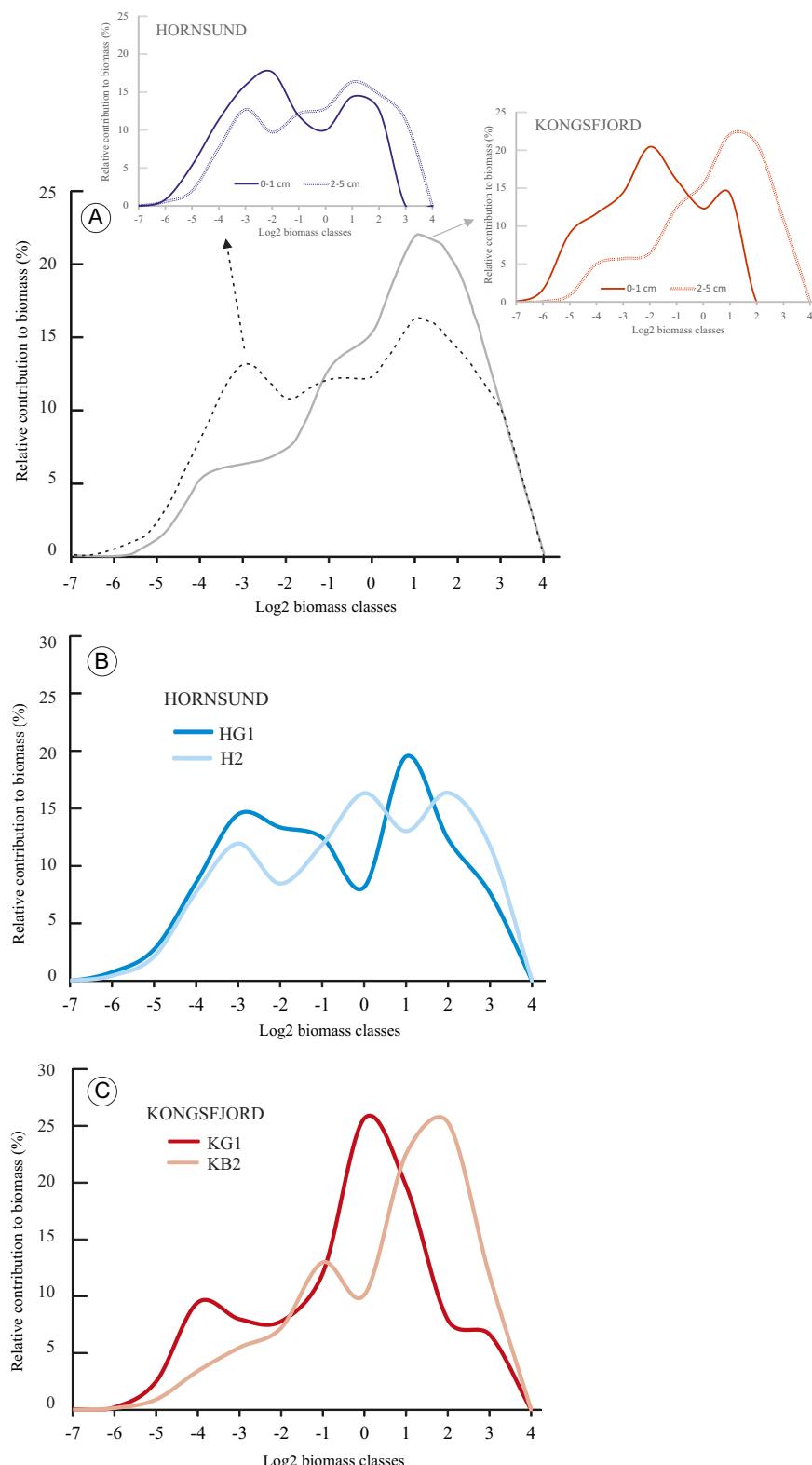


Fig. 7. Biomass spectra for nematode assemblages for (A) Hornsund and Kongsfjord (large plot), for the surface layer (0–1 cm) and at lower depths (2–5 cm), separately in both fjords (smaller panels); (B) Hornsund central and outer basin; (C) Kongsfjord central and outer basin.

penetrated deeper and were more evenly distributed within the sediment layers than nematodes in Hornsund. Relatively high concentrations of chl *a* in the deeper sediment layers, together with low organic carbon burial and high mineralisation rates (Kuliński et al., 2014), may indicate enhanced food availability and oxygenation

through the sediment profile, influencing microhabitat space for small-sized biota (Jorissen et al., 1995; Soetaert et al., 2002). Unpublished data from L. Kotwicki (IOPAN, Poland) demonstrate that oxygen penetrates deeper in Kongsfjorden sediments what confirm importance of the balance between food availability and oxygen

concentrations for meiofauna distribution within the sediment column. Vertical distribution of meiofaunal organisms in the sediment is also linked with other biotic and abiotic factors such as density/biomass of microorganism or hydrodynamic conditions (Montagna et al., 1989; Steyaert et al., 2003), among which interactions with other benthic biota are very important. The engineering activities of macrofaunal organisms – for example, bioturbation and bioirrigation – stimulate mineralisation and enhance the supply of oxidants to sediments, which in turn facilitate the presence of meiofauna in deeper part of sediment (Braeckman et al., 2010, 2011; Urban-Malinga et al., 2014). One such engineering organism may be the tube-dwelling polychaetes (e.g., *Maldane sarsi*) that are commonly observed in the inner and central basins of Kongsfjord (Włodarska-Kowalcuk and Pearson, 2004; Włodarska-Kowalcuk et al., 2005).

The availability and quality of organic matter directly alters the total and individual biomass of nematodes. The lower biomass and consequent reduction in metabolic efficiency of nematode assemblages in Hornsund are well-illustrated by the size spectra data, which shows biomass dominance in the smaller weight-classes, as well as a narrower *L/W* spectrum, compared with nematodes in Kongsfjord. The graphic distribution of *L/W* shows that nematodes are generally larger in Kongsfjord. Differences between fjords are in accordance with observations from other studies, where the prevalence of less suitable trophic conditions for nematode assemblages favours organisms of smaller body sizes (Udalov et al., 2005; Ingels et al., 2009) and opportunistic species and genera that can tolerate a wide spectrum of environmental conditions (Bongers et al., 1991). The decrease in body size with impoverished conditions is attributed to a lower maintenance cost for small organisms because food limitation prevents the higher energy consumption required by larger individuals (Thiel, 1975). Our results generally agree with this hypothesis, but with some important clarifications: for Spitsbergen fjords of comparable depths and granulometric composition of sediments, the quality of the organic matter is of prime importance. However, it should also be noted that in both fjords, nematode size was negatively correlated with chlorophyll *a* concentration. Bigger nematodes with higher *L/W* ratios (e.g. *Dorylaimopsis*, *Sabatieria*) were found in the deepest sediment layers but are not directly altered by pigment concentration availability (Soetaert and Heip, 1989; Soetaert et al., 2002). Such individuals are characterised by higher mobility and are therefore less dependent on the prevailing environmental conditions, hence the rightward shift of biomass modes and peaks in *L/W* ratio size classes for sub-surface sediment depths (Figs. 6A and 7A).

Environmental differences between the fjords were not only reflected in the differences in the *L/W* spectrum of the nematodes but also by the markedly lower occurrence of short, stout nematodes (defined by *L/W* ratio < 12) in the Hornsund assemblage. Although a detailed description of the nematode communities is outside the scope of this paper and will be discussed elsewhere, in the Spitsbergen fjords, this group was composed exclusively of members of the Desmoscolecidae family. The abundance of short and wide nematodes is thought to be limited mainly by oxygen availability (Soetaert et al., 2002), given that oxygen uptake capacity decreases with greater body width. For this reason, nematodes of this morphology are typically found in the surface layer and are assumed to be essentially surface-dwelling organisms (e.g., Portnova et al., 2011; Neira et al., 2013). Protrusions such as desmams and their large body width provide protection; thus, they do not need to migrate deeper into sediments to avoid predators. However, the presence of these types of nematodes in deeper sediment layers in the sediments in Kongsfjord indicates that favourable environmental conditions enhance the locomotor activities of this group and confirms the efficient oxygen penetration in Kongsfjord sediments. Moreover, Desmoscolecidae have a very minute buccal

cavity and thus can feed only on very small, bacteria-sized particles. Bacterial growth and density are stimulated by higher temperatures and enhanced input of organic material (e.g., Boetius et al., 2000), and, combined with high oxygen concentrations, such conditions likely explain the higher levels of bacterial activity in surface sediment layers in Kongsfjord than in Hornsund (A. Ammeryk, MIR, Poland, pers. comm), thereby providing more suitable food sources for Desmoscolecidae. The high abundance of small and stout nematodes in Kongsfjord provides further support that for this morphotype, a pulsed food supply and input of high quality organic material are advantageous (Soetaert et al., 2002; Vanaverbeke et al., 2004).

Morphometric attributes of nematode assemblages proved to be sensitive in detecting elevations of organic matter input and its content in the sediment. More intensive recycling of organic matter and the better sedimentary conditions in Kongsfjord were reflected in the sizes and shapes of nematodes. In particular, larger body width, higher individual biomass, and a size-spectrum pattern that features conspicuous peaking at higher values indicate preferential sediment settings for nematode assemblage in Kongsfjord. It is likely that environments with higher heterogeneity favour more morphologically diverse communities. Well-pronounced responses of nematodes to environmental variables confirm their functional adaptation to environmental conditions (Vanaverbeke et al., 2003, 2004; Losi et al., 2013a) and show that biomass and size spectra are not conservative features, as has been suggested in some studies (Duplisea and Hargrave, 1996; Schratzberger et al., 2004). Distinct forms of stress, as natural physical or human induced disturbance markedly affect morphometric characteristics and biomass spectra of nematodes (Vanaverbeke et al., 2003; Losi et al., 2013a). Present study shows that functional differences in nematode communities may also be detected in habitats with minor or negligible disturbance effect. Nematode size and shape most likely reflected differences in quality of organic material at investigated sites that likely is connected with different sources of sedimentary organic matter in the fjords. Measurements of nematode body size and dimensions may provide additional important ecological information about potential niches for colonisation, ecological resilience and supplement community composition data (Giere, 2009).

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