

Free-living nematodes and macrobenthos in a high-latitude glacial fjord

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Abstract

Kongsfjord is an open glacial fjord on the west coast of Svalbard, where the influence of the West Spitzbergen current ameliorates the effects of high latitude (79°N). The fjord is heavily influenced by glacial discharges of meltwater, ice and till, and related environmental gradients in sediments from the glaciers to the open sea include sediment deposition, organic content and disturbance. Other factors, such as the formation and break up of sea ice, also affect benthic communities. In this study spatial patterns in nematode and macrofaunal communities, in samples collected using box-corers and van Veen grabs during a cruise in September 1997, are described, compared and contrasted. Non-parametric multivariate analyses demonstrate that there were clear differences in community structure between stations in both macrofaunal and nematode assemblages. At stations where macrofauna were sampled using both box-cores and grabs there were also significant differences between samples collected by different methods, although there is evidence that these were influenced in part by slight differences in sampling location. Some evidence of disturbance to macrofaunal assemblages in the centre of the fjord is apparent. Macrofaunal community composition varied most closely with a combination of depth and sediment C:N ratio, whereas that of nematodes varied most closely with C:N alone. Proportions of feeding groups of nematodes showed little variation along the fjord. There is no evidence of a specialised nematode assemblage inhabiting the part of the fjord subject to the heaviest deposition of sediment. The taxonomic distinctness of nematodes decreased with increasing distance from the source of disturbance. This is in contrast to studies showing that the taxonomic distinctness of nematodes tends to decrease with increasing anthropogenic stress.

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1. Introduction

Free-living nematodes are the numerically dominant group of metazoa in the majority of marine sediment ecosystems. Being in the meiofaunal size range they are

characterised by direct benthic development, with the whole of their life-cycle closely coupled to the sediment, no specific dispersal phase, and generation times very much less than one year. Warwick (1988) and Heip et al. (1988) hypothesised that aspects of their ecology might make them more sensitive to rapid changes in the environment, compared to the majority of macrofaunal organisms which often live for more than a year, and often have a planktonic phase in their life-cycle. It was further hypothesised (Warwick et al., 1990) that meiofauna are less sensitive to physical disturbance than

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macrofauna. This was followed up by experimental studies (Schratzberger and Warwick, 1998, 1999) which demonstrated, inter alia, that nematodes are sensitive to the nature, frequency and quantity of disturbance, but that different assemblages may be predisposed to disturbance. Somerfield et al. (1995) examined changes in nematode and macrofaunal community structure along a transect through a site receiving a continuous input of diverse, often organically enriched, sediments off north-west England. They concluded that nematodes were more sensitive to ongoing sediment deposition at the site, while macrobenthos reacted to events over longer periods of time. Few studies have directly compared changes in assemblage structure of free-living nematodes and macrobenthos in relation to disturbance in the field, particularly in relation to long-term natural disturbance.

There have been a number of studies of high-latitude meiofaunal and nematode communities, most addressing sympagic (e.g. Schunemann and Werner, 2005; Gradinger et al., 2005), intertidal (e.g. Urban-Malinga et al., 2004; Węśławski et al., 1997) and deep-water (e.g. Soltwedel et al., 2003; Vanreusel et al., 2000) assemblages. Kendall et al. (1997) noted low endemism in the soft-sediment fauna (macro- and meiofauna) in the region of Svalbard, and suggested that processes influencing aspects of the structure of assemblages reflect evolutionary processes outside, rather than within, the Arctic. In this study we examine inter-relationships between the community structure of free-living nematodes and macrofauna along an environmental gradient in the Kongsfjord, an open glacial fjord on the west coast of Svalbard. The influence of the West Spitzbergen current ameliorates the effects of high latitude (79°N), but the fjord is heavily influenced by glacial discharges of meltwater, ice and till. Environmental gradients in sediments from the glaciers to the open sea include sediment deposition, organic content and disturbance. Situated towards the extremity of warm Atlantic currents and near the boundary with true Arctic waters, Kongsfjord is an obvious candidate as a site for monitoring the effects of changes in earth-system components such as the thermohaline circulation and climate (Warwick et al., 2003), and despite its high-Arctic location a considerable amount of scientific research has focused on the benthos of the fjord. Comprehensive reviews of the physical environment (Svendsen et al., 2002) and aspects of the communities inhabiting it (Hop et al., 2002) exist. This study ran concurrently with a survey of larval benthic invertebrates (Fetzer et al., 2002). Other surveys of infaunal macrofauna took place in the inner basin in July 1997 (Kendall et al., 2003) and throughout the fjord in July 1997 and 1998 (Włodarska-Kowalczyk and Pearson,

2004), and of meiofaunal major taxa in July 1999 and 2000 (Kotwicki et al., 2004). This, however, is the first study of a meiobenthic taxon from the fjord which examines variation in community structure at the species level, and which examines variation in free-living nematode and macrofaunal community structure simultaneously.

The primary focus of this work is to compare changes in community structure of nematodes with changes in the community structure of macrofauna along a long-term natural gradient of disturbance. As the site itself is of interest we also describe the assemblages found in our study, compare our results with those from other studies in the area, and discuss factors relevant to the development of programmes to monitor long-term changes.

2. Methods

Samples were collected from the F.F. Jan Mayen on the 4th and 5th September 1997, during UNIS cruise AB301. A series of stations (Fig. 1; Table 1) from the open sea to the inner part of Kongsfjord were sampled. Samples were collected using a 0.25 m² Reineck box-corer and a 0.1 m² van Veen grab. Box-coring was

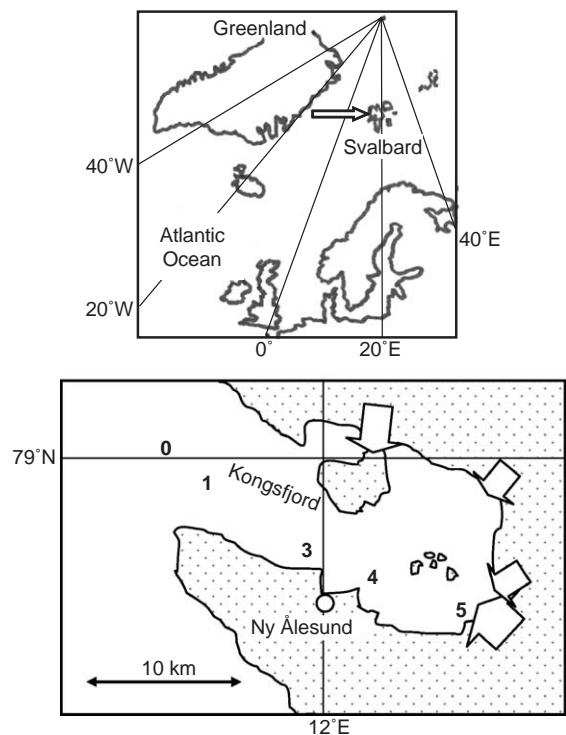


Fig. 1. Schematic maps showing the study location, Kongsfjord, on the west coast of Spitsbergen in the Svalbard archipelago, and the position of sampling stations along the fjord. Broad arrows indicate glaciers.

Table 1
Summary of location, samples collected and environmental measures at each station

| Station | 0 | 1 | 3 | 4 | 5 |
|--------------|--------------|--------|--------------|--------|--------|
| Latitude | 79°02' | 79°01' | 78°57' | 78°55' | 78°53' |
| Longitude | 11°08' | 11°22' | 11°57'–56' | 12°07' | 12°28' |
| Macrobenthos | 4 × B, 1 × G | 5 × G | 4 × B, 5 × G | 4 × B | 10 × G |
| Nematodes | 4 × B | 4 × B | 4 × B | 4 × B | 4 × G |
| Depth (m) | 301 | 363 | 290 | 133 | 80 |
| % silt/clay | 90 | 96 | 94 | 93 | 95 |
| % TOC | 1.60 | 1.80 | 0.69 | 0.44 | 0.19 |
| % TN | 0.26 | 0.30 | 0.12 | 0.09 | 0.05 |
| C:N | 6.2 | 6.0 | 5.8 | 4.8 | 3.8 |

B = box-core, G = van Veen grab.

initially the sampling method of choice but, as discussed below, the nature of the environment leads us to rely on the simpler and more robust van Veen grab at some stations. Samples for meiofaunal analysis were collected as subsamples from the surface of the sediment within the remote samplers (Somerfield et al., 2005), and samples which appeared disturbed or which failed to retain clear surface water were discarded. Each meiofaunal sample comprised 3 cores taken with a sawn-off 50 mm³ syringe to a depth of 5 cm, which were pooled (sample area 1.5 × 10⁻⁵ m²). On board the ship each sample was briefly (<1 h) fixed with 40% formalin, extracted by decantation with fresh water and flotation-extraction with Ludox TM (Somerfield and Warwick, 1996) using a 63 µm mesh, and transferred to 4% formalin for storage. Box-core and van Veen grab samples for macrofauna were sieved on deck using a large sieve-table with a 1 mm mesh, and stored in 4% formalin. Temperature and salinity measurements were taken in the near-bottom layer using a CTD (Neil Brown Mark III). Surface-scrapes from van Veen grab samples were collected for sediment analyses (one sample per station) and frozen.

In the laboratory, meiofaunal samples were slowly evaporated to anhydrous glycerol, evenly spread on microscope slides and the coverslips ringed with Bioseal (Somerfield and Warwick, 1996). Nematodes were counted and identified, under a compound microscope with conventional bright-field illumination, to species or putative species using pictorial keys (Warwick et al., 1998). Macrofauna were identified to species level using standard taxonomic keys.

Nematodes all have a similar body-form, being free-living round worms, and as such may be expected to differ functionally primarily in terms of their trophic relationships. Within the macrofauna many body-plans are evident, ranging from echinoderms to planarians. In order to compare distributions of functional types along

the fjord, therefore, we focus on the polychaete component of the macrofauna, which potentially offers a meaningful comparison with the nematodes. Polychaetes were assigned to functional groups according to their motility, feeding and bioturbation modes (Fauchald and Jumars, 1979; Pearson, 2001), and nematodes were assigned to feeding types (Warwick et al., 1998).

The percent silt/clay in sediment samples was determined by wet sieving using a 63 µm sieve to separate the coarse and fine fractions which were then dried at 95 °C and weighed. Samples for the measurement of total organic carbon and total nitrogen were pretreated with HCl to remove inorganic carbon, followed by combustion at 1800 °C and column chromatography. The N₂ and CO₂ gases were quantified using a warm-wire detector in a CHN analyser.

Data were analysed with non-parametric multivariate methods (Clarke, 1993; Clarke et al., 2005) using Primer 6. Raw abundances were dispersion-weighted to down-weight contributions to intersample similarities from species with significant underdispersion (Clarke et al., in press). Intersample similarities were calculated using an adjusted form of the Bray–Curtis similarity coefficient (Clarke et al., 2006) as some samples from the inner parts of the fjord contained low abundances and it could be assumed that these were depauperate for similar reasons. Intersample similarities were ordinated using non-metric multidimensional scaling (MDS). Formal significance tests for differences between groups of samples were addressed using 1- and 2-way ANOSIM tests, and for relationships with distance from the glaciers using RELATE 'seriation with replication' tests (Somerfield et al., 2002). Relationships between faunal and environmental variables were tested and explored using the BEST routine in BIO-ENV mode. Species contributing to differences between groups of samples were determined using 1- and 2-way SIMPER. *K*-dominance plots were constructed in order to examine changes in dominance and diversity, and differences between groups of curves were tested using ANOSIM (Clarke, 1990). In addition to numbers of species (*S*), and individuals (*N*), a univariate measure of relatedness between species (Δ^+ , Clarke and Warwick, 1998) was calculated using taxonomic hierarchies based on Lorenzen (1994) for nematodes, and Howson and Picton (1997) and the European Register of Marine Species (Costelloe et al., 2001) for macrofauna.

3. Results

The intention was to sample all stations with the box-corer, but this did not prove possible (Table 1). Stations

0 to 4 were sampled with the box-corer for meiofauna, but the macrofauna were only extracted for Stations 0, 3 and 4 before the corer collected a large drop-stone and was damaged to the extent that it could no longer be used. The remaining meiofaunal samples (Station 5) and macrofaunal samples (a single sample from Station 0, and replicate samples from Stations 1, 3 and 5) were collected using the van Veen grab.

3.1. Free-living nematodes

110 putative species of nematode, distributed among 83 genera, were identified in samples from Kongsfjord, of which 45 (41%) were significantly spatially clustered and therefore downweighted in multivariate analyses. Although the sampling gear, used to retrieve sediment as undisturbed as possible, differed, the size of each sample was the same. With the exception of Stations 0 and 1 ($p=0.057$) all stations were significantly different (ANOSIM Global $R=0.818$, $p<0.001$, all pairwise $p<0.05$) in terms of community structure. There was a gradient in structure (Fig. 2) from the glacier at the head

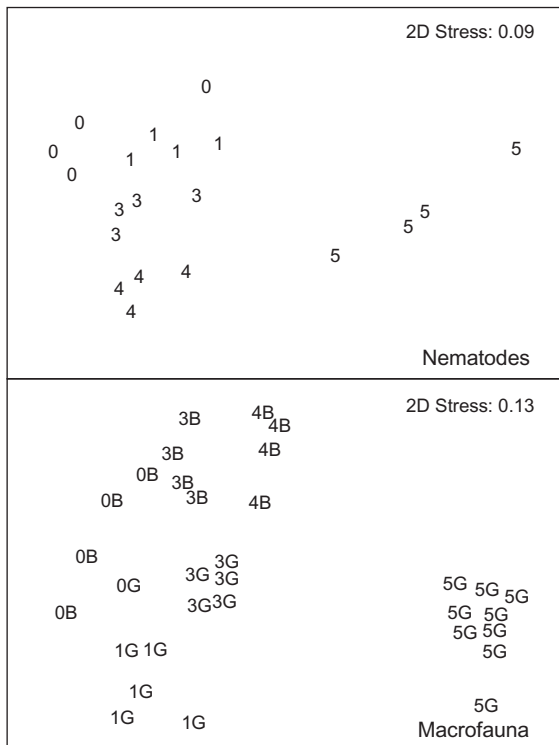


Fig. 2. Non-metric multidimensional scaling ordination plots of adjusted Bray–Curtis similarities between samples calculated from dispersion-weighted abundances of free-living nematodes and macrofauna. Numbers indicate stations. For macrofauna box-core and van Veen grab samples are indicated by B and G, respectively.

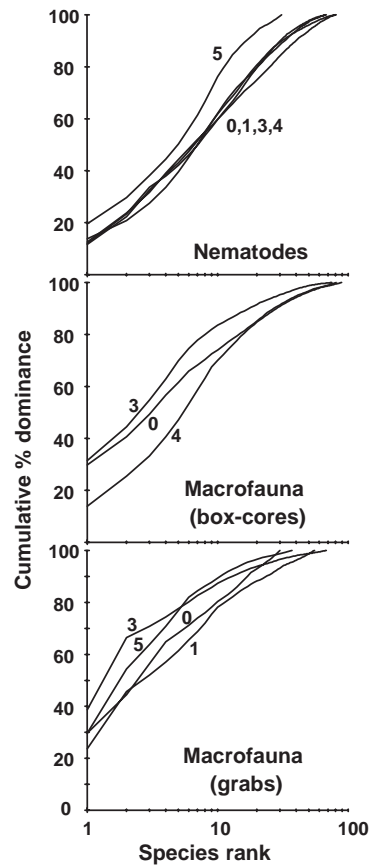


Fig. 3. *K*-dominance curves calculated using average within-station abundances of nematodes and macrofauna.

of the fjord (Station 5) to the open sea (Stations 0 and 1), confirmed by a significant ($\rho=0.664$, $p<0.001$) seriation with replication test with ranked distances from the glacier. Samples within stations had to be averaged for comparison with environmental variables, leading to a loss of power as there were only 5 stations. A single variable, the C:N ratio in the sediment, provided the closest match ($\rho=0.78$) with nematode community structure, although a correlation as high as this could have arisen by chance ($p=0.12$).

The dominance structure (Fig. 3) shows little difference between the majority of stations other than Station 5 where dominance is increased and diversity reduced, at least in some replicates. ANOSIM on intercurve distances confirms this, as the global test is significant ($R=0.457$, $p<0.001$) but the only significant pairwise tests ($p<0.029$) are between Station 5 and all other stations.

Of the 110 putative species recorded, 38 (34%) contribute to up to a cumulative 50% of dissimilarities between stations along the fjord (Table 2). There are clear differences in species composition between Stations 0

Table 2
Summary of SIMPER results

| Station | 0 | | 1 | | 3 | | 4 | | 5 |
|---|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| Nematodes | 48% | 39% | 49% | 43% | 53% | 42% | 60% | 18% | 43% |
| <i>Daptonema minuta</i> | 11 | > | 6 | > | 2 | | | | |
| <i>Pomponema</i> sp. | 6 | > | 0 | | | | | | |
| <i>Chromadorella</i> sp. | 6 | > | 1 | | | | | | |
| <i>Paramonohystera</i> sp. | 6 | > | 1 | | | | | | |
| <i>Dorylaimopsis</i> sp. | 8 | > | 3 | < | 9 | > | 4 | > | 0 |
| <i>Terschellingia longicaudata</i> | 6 | > | 4 | < | 7 | > | 3 | | |
| <i>Halanonchus</i> sp. | 3 | > | 0 | | | | | | |
| <i>Pareudesmoscolex</i> | 1 | < | 3 | > | 2 | | | | |
| <i>Halalaimus</i> sp. 1 | 3 | > | 2 | < | 4 | > | 4 | > | 0 |
| <i>Halichoanolaimus</i> sp. | 2 | > | 1 | | | | | | |
| <i>Metadesmolaimus</i> sp. 1 | 4 | > | 1 | | | | | | |
| <i>Aegialoalaimus</i> sp. | 3 | > | 1 | | | | | | |
| <i>Theristus</i> sp. | 3 | > | 1 | | | | | | |
| <i>Daptonema</i> sp. 1 | 3 | > | 2 | > | 1 | | | | |
| <i>Prochromadorella</i> cf. <i>attenuata</i> | 2 | > | 0 | < | 2 | | | | |
| <i>Comesa vitia</i> | | | 0 | < | 3 | < | 4 | > | 0 |
| <i>Paracanthonchus</i> cf. <i>longicaudatus</i> | | | 0 | < | 3 | | | | |
| <i>Comesa</i> sp. 2 | | | 0 | < | 3 | | | | |
| <i>Halalaimus</i> sp. 2 | | | 1 | < | 3 | | 4 | > | 0 |
| <i>Desmoscolex</i> sp. 1 | | | 1 | > | 3 | > | 3 | | |
| <i>Diplopeltula</i> sp. 2 | | | 2 | > | 2 | | | | |
| <i>Terschellingia</i> cf. <i>distalamphida</i> | | | 0 | < | 2 | | | | |
| <i>Tricoma</i> sp. | | | 1 | < | 2 | | 3 | > | 0 |
| <i>Camacolaimus</i> sp. | | | 0 | < | 2 | | | | |
| <i>Dichromadora</i> sp. | | | 0 | < | 1 | | | | |
| <i>Anticoma</i> sp. | | | 2 | > | 1 | | | | |
| <i>Actinonema</i> sp. | | | 0 | < | 2 | | | | |
| <i>Calomicrolaimus</i> sp. | | | 0 | < | 2 | < | 9 | > | 1 |
| <i>Paraspaerolaimus</i> sp. | | | 1 | < | 2 | | | | |
| <i>Microlaimus</i> sp. 1 | | | | | 0 | < | 15 | > | 3 |
| <i>Leptolaimus</i> sp. 1 | | | | | 1 | < | 11 | > | 1 |
| <i>Desmoscolex</i> sp. 2 | | | | | 2 | < | 10 | > | 0 |
| <i>Rhabdodemanis</i> sp. | | | | | 0 | < | 5 | > | 0 |
| <i>Cervonema</i> sp. | | | | | 1 | < | 5 | > | 0 |
| <i>Sabatieria punctata</i> | 5 | | 4 | | 4 | < | 8 | > | 1 |
| <i>Geomonhystera</i> sp. | | | | | 1 | < | 4 | | |
| <i>Campylaimus</i> sp. | | | | | 1 | < | 3 | | |
| <i>Quadricoma</i> sp. | | | | | 0 | < | 2 | | |
| <i>Thalassomonhystera</i> sp. | | | | | | | | | 2 |
| Macrofauna | 37% | 22% | 46% | 25% | 39% | 29% | 43% | 9% | 49% |
| <i>Golfingia margaritacea</i> | 4 | > | 0 | | | | | | |
| <i>Spiophanes kroyeri</i> G | 0 | < | 3 | > | 3 | > | 0 | | |
| <i>Nephtys ciliata</i> G | 2 | < | 4 | > | 1 | | | | |
| <i>Lumbrineris mixochaeta</i> B | 2 | > | 0 | < | 2 | | | | |
| <i>Spiochaetopterus typicus</i> G | 0 | < | 2 | > | 1 | | | | |
| <i>Chaetozone setosa</i> B | 2 | > | 0 | < | 1 | < | 3 | > | 0 |
| <i>Diplocirrus hirsutus</i> | 2 | > | 0 | | | | | | |
| <i>Praxillella gracilis</i> | 0 | < | 2 | > | 1 | | | | |
| <i>Phascolion strombus</i> | 1 | > | 0 | | | | | | |
| <i>Myriochele oculata</i> B | 2 | > | 2 | < | 7 | > | 4 | > | 0 |
| <i>Euchone papillosa</i> B | 2 | > | 1 | < | 4 | < | 9 | > | 0 |
| <i>Bathyarca glacialis</i> B | 1 | < | 2 | > | 1 | | | | |
| Nemertea B | 1 | > | 0 | < | 1 | < | 3 | > | 0 |
| <i>Lanassa venusta</i> B | 1 | > | 0 | | 1 | < | 6 | > | 0 |

Table 2 (continued)

| Station | 0 | | 1 | | 3 | | 4 | | 5 |
|---|-----|-----|-----|-----|-----|-----|-----|----|-----|
| Macrofauna | 37% | 22% | 46% | 25% | 39% | 29% | 43% | 9% | 49% |
| <i>Propebela reticulata</i> | 1 | > | 0 | | | | | | |
| <i>Neoamphitrite groenlandica</i> | 0 | < | 1 | | | | | | |
| <i>Arrhis phyllonyx</i> | 1 | > | 0 | | | | | | |
| <i>Maldane sarsi</i> G | | | 0 | < | 2 | > | 1 | | |
| <i>Heteromastus filiformis</i> B | | | 0 | < | 2 | > | 2 | > | 0 |
| <i>Eudorella emarginata</i> B | | | 0 | < | 2 | < | 3 | > | 1 |
| <i>Prionospio cirrifer</i> B | | | 0 | < | 2 | > | 0 | | |
| <i>Laonice cirrata</i> | | | 0 | < | 1 | | | | |
| <i>Amphicteis gunneri</i> | | | 0 | < | 1 | | | | |
| <i>Thyasira dunbari</i> | | | 0 | < | 1 | < | 7 | > | 1 |
| <i>Terebellides stroemi</i> | | | | | 0 | < | 4 | > | 0 |
| <i>Yoldiella lenticula</i> | | | | | 1 | < | 4 | > | 3 |
| <i>Lumbriclymene minor</i> | | | | | 0 | < | 2 | | |
| <i>Macoma</i> sp. | | | | | 0 | < | 2 | | |
| <i>Cuspidaria subtorta</i> | | | | | 0 | < | 2 | | |
| <i>Laphania boeckii</i> B | | | | | 1 | < | 2 | > | 0 |
| <i>Nuculana pernula</i> | | | | | 0 | < | 2 | | |
| <i>Ciliatocardium ciliatum</i> | | | | | 0 | < | 2 | | |
| <i>Anobothrus gracilis</i> | | | | | 0 | < | 2 | | |
| <i>Yoldiella</i> sp. (<i>nana/solidula</i>) | | | | | | | 1 | < | 7 |
| <i>Capitella</i> sp. B | | | | | | | | | |
| <i>Leitoscoloplos</i> sp. B | | | | | | | | | |
| <i>Eteone longa</i> B | | | | | | | | | |
| <i>Pholoe assimilis</i> B | | | | | | | | | |
| <i>Spio filicornis</i> B | | | | | | | | | |
| <i>Microclymene acirrata</i> B | | | | | | | | | |

Average dispersion-weighted abundance of taxa of nematodes and macrofauna contributing to Bray–Curtis similarities (%) within (bold) and between (<, >) consecutive stations in a 1-way analysis. A cut-off of 50% was applied. Among macrofaunal taxa, those contributing to up to a cumulative 50% similarity (of a total 31% similarity) between sampling gears in a 2-way analysis are indicated by: B, those with higher abundances in box-core samples; G, those with higher abundances in grab samples.

to 4, while Station 5 is generally characterised by reduced abundances of species found at other stations.

Although multivariate analyses detect a significant gradient in community structure along the fjord, univariate analyses (Fig. 4) tend not to, although numbers of individuals (N) and species (S) are clearly lower at Station 5. Average taxonomic distinctness (Δ^+), however, shows a smooth and significant increasing trend going from the open sea towards the innermost parts of the fjord ($R^2 = 0.8141$, $\nu = 18$, $p < 0.001$). A randomisation test (Fig. 5), however, shows that the values for all replicates, with the exception of 2 from Station 0, lie within the confidence funnel and as such are behaving as if the assemblages are random subsets from the complete list of nematodes found in the survey. The two that fall below the funnel are from a station at one end of the gradient, and it has already been demonstrated that there is a gradient in Δ^+ along the fjord.

3.2. Macrofauna

167 taxa were identified, distributed among 21 classes in 15 phyla. Of these, 63 taxa (38%) were significantly

clustered and therefore downweighted in subsequent multivariate analyses. There were significant differences in macrofaunal community structure (Fig. 2) between stations sampled with box-cores (ANOSIM $R = 0.653$, $p < 0.001$) and grabs ($R = 0.953$, $p < 0.001$), and a significant relationship between macrofaunal community structure and distance along the fjord (RELATE $\rho = 0.842$, $p < 0.001$). A 2-way ANOSIM confirms the significant differences between stations ($R = 0.906$, $p < 0.001$) and also shows that differences between samples collected by different gears were significant ($R = 0.691$, $p = 0.006$).

As with the nematodes, samples within stations had to be averaged for comparison with environmental variables, leading to a loss of power. The best match ($\rho = 0.891$) was with a combination of depth and the C:N ratio in the sediment, and this was significant ($p = 0.044$).

Of the 167 taxa recorded, 34 (20%) contribute up to a cumulative 50% of dissimilarities between stations along the fjord (Table 2). Although there are clear differences in species composition between Stations 0 to 4,

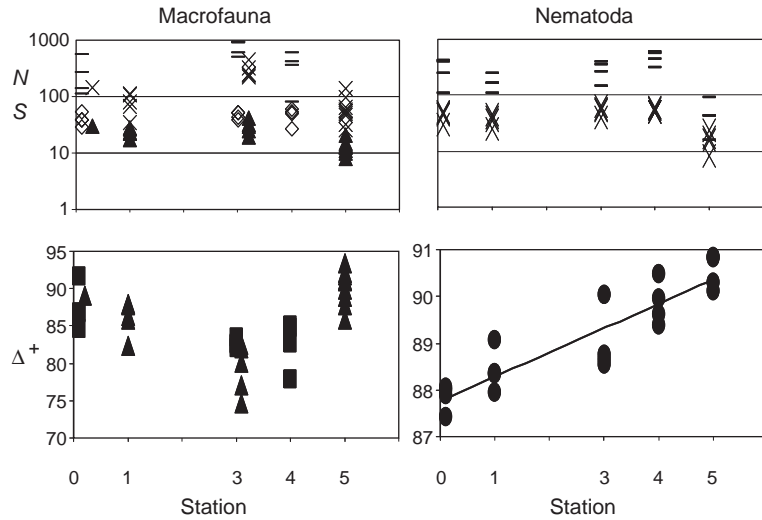


Fig. 4. Univariate measures N (number of individuals), S (number of species), and Δ^+ , calculated for macrofauna (box-cores and van Veen grabs) and free-living nematodes. For macrofauna, values for grab samples (0.1 m^2) are indicated by dashes for N and diamonds for S , and for box-cores (0.25 m^2) by crosses for N and triangles for S . Values of Δ^+ of macrofauna in grabs are indicated by triangles, and in grabs by squares. For nematodes (sample area $1.5 \times 10^{-5} \text{ m}^2$) dashes indicate values of N , and crosses of S , and circles indicate values of Δ^+ . The trendline is significant (see text).

Station 5 is generally characterised by reduced abundances of species found at other stations and high abundances of protobranchs in the genus *Yoldiella*.

Among macrofaunal taxa at stations sampled using both gears *Spiophanes kroyeri*, *Spiochaetopterus typicus* and *Maldane sarsi* were more abundant in grab samples (Table 2). As expected, given the larger samples collected, several species occurred in greater numbers in box-core samples (Table 2), but by no means all species.

ANOSIM on intercurve distances for K -dominance curves derived from all samples shows a significant difference between sampling gears ($R=0.618$, $p<0.001$), box-core samples being more diverse and less dominated. For samples collected by box-cores differences in diversity-dominance structure between stations (Fig. 3) were significant (Global $R=0.340$, $p<0.047$) although pairwise tests failed to achieve significance at $p=0.05$. For samples collected by grab, however, differences between stations were more marked (Global $R=0.701$, $p<0.001$, all pairwise tests $p<0.025$ except those with Station 0 where there were insufficient replicates), and there is evidence of a gradient of decreasing diversity and increasing dominance from Stations 0 and 1 to Stations 3 and 5 (Fig. 3).

Although multivariate analyses detect a significant gradient in macrofaunal community structure along the fjord, univariate analyses (Fig. 4) tend not to. As would be expected, numbers of individuals and species tend to be lower in grab samples than in box-core samples, and the numbers of species are reduced at Station 5. Average taxonomic distinctness (Δ^+) does not show a monotonic relationship with distance, and appears to be reduced in the central parts of the fjord (Stations 3 and 4). A

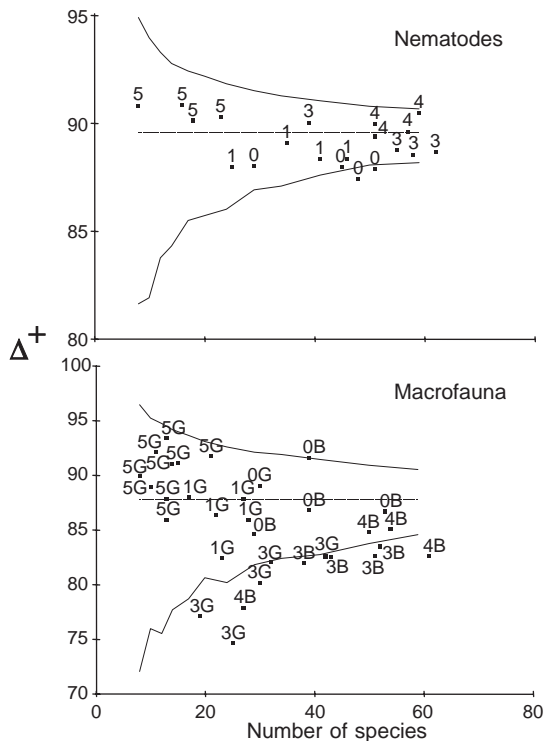


Fig. 5. Sample values of Δ^+ and probability funnels from randomisation tests using complete species lists from this study.

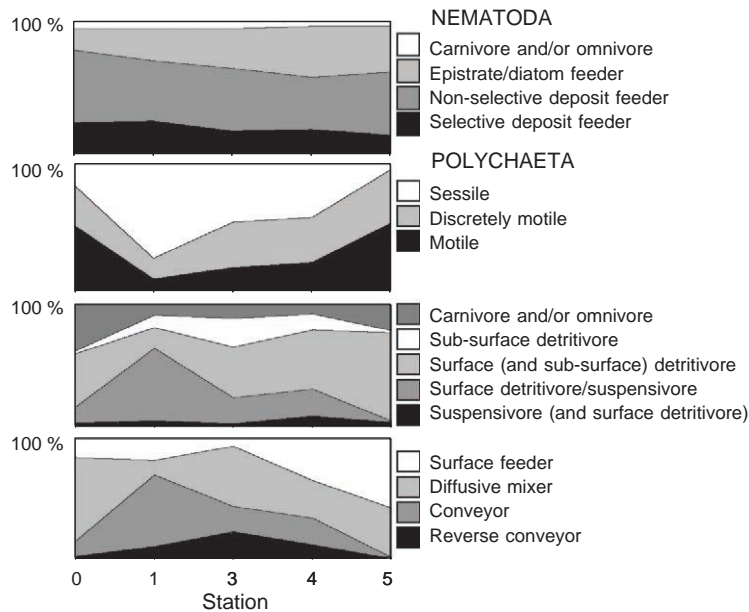


Fig. 6. Variation in proportions of individuals among functional groups of nematodes and polychaetes along Kongsfjord.

randomisation test (Fig. 5) shows that species in macrofaunal assemblages at Station 3, and in some replicates from Station 4, are significantly more closely related to each other than expected by chance. There is no evidence that this relates to sampling methods.

3.3. Functional groups

It is readily apparent (Fig. 6) that functional groups among polychaetes are not distributed evenly along the fjord, and neither does the functional composition of the polychaete assemblage change in an ordered fashion with distance from the glacier. Stations at the mouth of the fjord (0) and close to the glacier (5) are similar in terms of their functional composition, dominated by motile surface-feeding detritivorous diffusive mixers. In between, assemblages go from being dominated by sessile surface-feeding detritivore/suspensivores at Station 1 to a more even mix of functional types at Stations 3 and 4. Among the nematodes there is little evidence of change in the functional (trophic) composition of the assemblage along the fjord.

4. Discussion

There are clear and significant changes in both free-living nematode and macrofaunal assemblages with increasing distance from the Kongsbreen, which correlate to some extent with the organic content (C:N ratio) of the sediment. Patterns in the community structure of

free-living nematodes tend to show a gradual and smooth change in structure with distance along the fjord. The picture for macrofauna is somewhat clouded by the fact that differing sampling gears had to be employed, but it appears that changes in community structure are neither as smooth nor as ordered.

It was unfortunate that circumstances demanded that different sampling gears be used at different stations. It is well known that different samplers produce differing samples for a number of reasons (Somerfield and Clarke, 1997), ranging from the area and depth of penetration into the sediment, the degree of disturbance to that sediment during and after operation of the sampler at the seabed, disturbance during retrieval, and degree of loss of overlying water. Subsampling meiofauna from a grab is not generally recommended as a reliable method (Somerfield et al., 2005), and subsampling from a box-corer is not very much better (Somerfield and Clarke, 1997). It should be noted, however, that a midicorer was also deployed during this survey to sample larval invertebrates (Fetzer et al., 2002) and different problems arose, requiring subsamples from the van Veen grab to be used to characterise some stations (0 and 5). The grab used had sealed hatches, samples were discarded if the overlying water was absent or discoloured, the cohesive nature of sediment at the majority of stations made them amenable to sampling with the grab, and sampling conditions were ideal. These facts lead us to believe that samples are at least to some extent comparable, and although the influence of sampling gear on the data cannot be removed it does not

invalidate the broad findings of this study. Among macrofaunal taxa at stations sampled using both gears *S. kroyeri*, *S. typicus* and *M. sarsi*, all tubicolous polychaetes, were more abundant in grab samples. None of these species is likely to be dislodged by bow-wave effects and the latter two may penetrate deep within the sediment and so might be expected in higher abundances in box-cores. Among species more abundant in box-core samples are also several tubicolous polychaetes such as *Euchone papillosa*, *Myriochele oculata*, *Prionospio cirrifera*, *Spio filicornis* and *Microclymene acirrata*. Thus there appears to be no clear relationship between a species being more abundant in one sampling gear or the other and its size or general ecology. We conclude that, although the size of samples may influence abundances, an important factor may also be a high degree of benthic patchiness. Samples collected in slightly different places, from a slowly drifting ship for example, may collect different species as a result of this patchiness (Somerfield and Gage, 2000) whatever gear is used. While different samplers may collect various components of the benthic fauna with different degrees of certainty or accuracy, two out of three samplers failed at some stations, and one was destroyed. Only one, the simplest, operated at all stations.

The free-living nematode community inhabiting muddy soft sediments in Kongsfjord along most of its length is in many ways typical for a boreal coastal embayment. Dominant genera are *Dorylaimopsis*, *Terschellingia*, *Halalaimus* and *Sabatieria*. Along the fjord a range of species from various families contribute to differences between stations, but overall the assemblage, while clearly structured, is relatively homogeneous in comparison with the macrofauna. It is notable, however, that the majority of species are deposit feeders, and epistrate feeders such as chromadorids tend to be restricted to outer parts of the fjord. The epistrate feeders dominant towards the inner fjord are species with very small buccal cavities (e.g. *Calomicrolaimus* sp. 1, *Microlaimus* sp. 1), which are probably bacterial, rather than diatom, feeders. Schratzberger and Warwick (1999) and Schratzberger et al. (2000, 2004) found chromadorids to decline in control microcosms kept in the dark without addition of organic matter. The winter in Kongsfjord is long and dark. No studies have been made of microphytobenthos in Kongsfjord (Hop et al., 2002) but it is likely that extreme intra-annual variations, in daylength and turbidity (Svendsen et al., 2002) for example, make it an unreliable food source for organisms which have relatively short generation times.

Glaciers transport some 2 Mt y^{-1} of sediment into the fjord, of which the main bulk is deposited close to the glacier front. Accumulation rates of 20 kg $m^{-2} y^{-1}$

close to Kongsbreen (Svendsen et al., 2002) lead to increases in sediment depth of up to 15 cm y^{-1} (Elverhøi et al., 1983), most of which is deposited in the summer. In glacial bays such intense deposition of mineral material forms unconsolidated, labile, sediments. The material is not compacted, water is trapped within it, and a layer of very dense suspension overlies the bottom (Dyer, 1989). Few studies have addressed meiofaunal responses to intense and accumulating deposition of uncontaminated fine sediment containing no organic matter. A dense effluent of brine and clays from a potash mine reduced meiofaunal populations in the vicinity of the outfalls off the northeastern coast of England (Somerfield et al., 1993), and studies of changes in meiobenthic communities along a gradient from a red mud (bauxite waste) discharge in deep water in the Mediterranean found that all taxa were absent close to the discharge (Vitiello and Vivier, 1974; Vivier, 1978). Nematodes may migrate vertically in response to sediment deposition, although rates are low in silty sediments (Maurer et al., 1986; Schratzberger et al., 2000), and the continual vertical migration required to maintain position would place significant metabolic demands on organisms living in this zone. Despite their lack of a planktonic dispersal stage, adaptations against resuspension, and poor swimming ability, interstitial meiofaunal species are regularly found in the water column and dispersal of meiofauna has been ascribed primarily to water-column processes including passive erosion (Schratzberger et al., 2004). The build-up of fine sediments close to the glacier is in part attributed to a process whereby very fine sediments in glacial outflows flocculate and sink on contact with saline waters, and are then carried back to the glacier front by in-flowing compensation currents (Syvitski et al., 1987). The nematodes found, in low abundances, living at Station 5 were a random subset of the nematodes from the fjord as a whole, most closely related to the assemblage at Station 4. Thus it is possible that the community close to the glacier is made up of individuals brought there by the same currents that capture the fine sediment from adjacent areas within the fjord. Whether the populations are maintained there by in situ reproduction, or are made up of individuals that only survive for a short while but are continually replaced, is an open question.

Very little is known of seasonal changes in the benthos of Kongsfjord. For obvious reasons the majority of samples have been collected in the short summer period (July–September). This happens to be when glacial inputs are at their highest, and environmental gradients resulting from glacial processes are at their most obvious. For this reason the majority of studies

have interpreted observed patterns in communities in relation to environmental effects of the glaciers. While such effects, particularly gradients in turbidity and sedimentation, are clearly of major importance it should not be forgotten, however, that other processes and inputs vary along the fjord at different times of year and may impinge on benthic communities. For much of the year, for example, the glaciers are not melting and the inner parts of the fjord are covered by sea ice. Although there is no systematic monitoring of sea ice in Kongsfjord, it is known that there is high inter-annual variability in the position of the ice-edge and the timing of melting and break up (Svendsen et al., 2002). The inner part of the fjord usually becomes ice-covered in December to January, and the ice-cover generally melts or breaks up between April and July. As the ice freezes brine is formed, and sinks to the seabed. Little detail is known about increases in salinity associated with ice formation in Kongsfjord, although it is known that winter-cooled water (WCW), with $T < -0.5$ °C and $S > 34.4$ psu, can occupy isolated depressions in the inner fjord throughout the year (Svendsen et al., 2002). Nematodes were found to be absent from a sublittoral brine lake in the vicinity of a natural brine seep at 72 m depth in the Gulf of Mexico (Powell et al., 1982), and it is not impossible that the combination of brine formation, decreased hydrodynamism and lack of primary production causes meiofauna to disappear entirely from parts of the inner basin in winter.

In 1997 the inner part of the fjord was completely covered by fast ice until the onset of melt, with the ice-edge near the Lovénøyane in May (Svendsen et al., 2002), in the vicinity of Station 4. Much of the production from spring phytoplankton blooms at retreating ice-edges may sink to the bottom with little grazing by zooplankton, supporting abundant benthic communities (Lovvorn et al., 2005). Components in the freshly depositing cells may be important for successful reproduction by benthic invertebrates, but the communities are generally sustained by bacteria, which break down and rework the settled phytoplankton. Although limited studies in Kongsfjord suggest that only a minor component of the spring bloom sinks from the water column (Hop et al., 2002), a characteristic of later open-water blooms rather than ice-edge blooms (Lovvorn et al., 2005), the rich meiofaunal and macrofaunal assemblages at Station 4 suggest a considerable flux of material to the seabed. Nematode species such as *Sabatieria punctata*, which is often abundant in organically enriched sediment, and bacterial feeders such as *Leptolaimus* sp. 1 and *Desmoscolex* sp. 2, occur in high numbers as do large numbers of filter- and deposit-feeding macrofaunal

organisms including *M. oculata*, *E. papillosa*, *Lanassa venusta*, *Terebellides stroemi*, *Thyasira dunbari* and *Yoldiella lenticula*.

Patterns in numbers of individuals and species, or in dominance, were not informative in this study although *K*-dominance curves, which utilise elements of both dominance and diversity structure, did prove more useful. Taxonomic distinctness theoretically offers some advantages (Clarke and Warwick, 1998; Leonard et al., 2006), specifically its independence of sampling effort and requirements for reference conditions, but in this study patterns were not consistent. The average taxonomic distinctness of nematode species increased towards the glacier, running counter to expectation as previous studies have shown values for nematodes to decrease with increasing (albeit anthropogenic) stress. Values of the index for macrobenthos did not vary smoothly along the perceived major environmental gradient in the fjord, and were significantly lower than expectation at Station 3, and to a lesser extent at Station 4. Station 3 is close to the settlement of Ny Ålesund, and we cannot discount the possibility that macrobenthic communities in the vicinity are showing symptoms of stress, although it is impossible to say what may be the cause. Although discharges of nutrients and oil near the settlement have been recorded in the past, these are unlikely to have impacted on the benthos at 290 m. During cruise AB301 samples for analyses of PAHs, THC, PCBs and pesticides were taken at Stations 0, 1, 3 and 5 (Olsson et al., 1998). With the exception of PAH all contaminant concentrations were low and in agreement with levels elsewhere in Arctic waters. Although Σ PAHs were elevated, similar concentrations are found in other fjords around Svalbard, and are probably a result of leakage and erosion from coal deposits on land and at sea.

The majority of studies which describe patterns in marine macrobenthic communities use information on the distribution of adult organisms, often sampled on a single occasion. The physical environment in Kongsfjord undergoes intense seasonal (and inter-annual) variation (Svendsen et al., 2002), and while the majority of macrobenthic organisms live for at least a year, and many for several years, seasonal changes must occur in the macrobenthos. Fetzer et al. (2002) found that the distribution of recently settled juvenile macrobenthic organisms was very heterogeneous, indicating that the distribution of adult organisms is, at least in part, determined by processes associated with dispersal and settlement. They found a close correlation between larval abundance and the carbon content of the sediment, largely driven by larvae of deposit-feeding

polychaetes. It should be noted, however, that many of these are the smaller species in the macrobenthic community which tend to reproduce annually, that this study identified a correlation between adult occurrence and C:N in the sediment, and many species have reduced or absent planktonic stages (Kendall et al., 1997). Thus it is difficult to know whether patterns in abundance of recently settled juveniles are driven by the distribution of adults, patterns in abundance of adults are driven by the distribution of settling juveniles, or both are driven by environmental gradients operating on one, the other, or both.

Previous studies (Hop et al., 2002; Włodarska-Kowalczyk and Pearson, 2004) recognised two major communities within the macrobenthos in Kongsfjord. One in the inner part of the fjord, dominated by small surface dwelling detritivores including *T. dunbari*, *Yoldiella* species and *Chone paucibranchiata*, with low species turnover (Kendall et al., 2003), and one throughout the outer fjord, characterised by *Heteromastus filiformis*, *M. sarsi*, *Levensenia gracilis*, *Lumbrineris* and *Leitoscoloplos* species among others, and divisible into three associations. Our survey was more limited in spatial extent (sample coverage) than those reported by Włodarska-Kowalczyk and Pearson (2004), but in essence supports the general picture of a change in community structure, in the region of Station 4, from an inner assemblage dominated by *Yoldiella* species to one characterised by larger, often tube-dwelling, polychaetes. It is noticeable, however, how few of the species regarded by Włodarska-Kowalczyk and Pearson (2004) as characterising different zones within the fjord were found to be significant components of the fauna in this study. Few species characterise more than one station, and only *M. oculata*, *E. papillosa* and *Y. lenticula* characterise three. Why the species found to be important in determining similarities within, and differences between, stations in this study, and those considered to be important in characterising large areas in Włodarska-Kowalczyk and Pearson's (2004) study, do not match may in part depend on the spatial scale of sampling and the analytical methods employed. Although seasonal patterns may play a part some of these species may be large and long-lived, and the influence of patchiness must be important. As previously mentioned, Kendall et al. (2003) found patchiness to be low in the inner basin. Along the rest of the fjord sharp gradients in depth and hydrodynamics, the heterogeneous supply of larvae (Fetzer et al., 2002), and the sporadic occurrence of drop-stones, are all factors which could contribute to benthic patchiness.

The benthic fauna of Kongsfjord is relatively well known in comparison with the majority of the Arctic,

and the fjord is an obvious candidate as a site for monitoring the effects of changes in the thermohaline circulation and climate (Warwick et al., 2003). The question is, however, how such monitoring may be implemented. Assuming a focus on benthic communities, this study has highlighted several factors which should be taken into consideration. Sampling may be difficult, and although samples may be considered less than ideal a simple robust sampling method is likely to produce results. The benthos is patchy, and samples collected in slightly different places, at different times, may collect different species as a result of this patchiness whatever gear is used. Focusing a long-term monitoring programme on stations which are revisited on regular occasions may, therefore, be problematic and a protocol which examines broad changes among widely distributed samples is likely to be preferable. Simple univariate measures of community structure (densities, numbers of species) are not particularly informative, and prone to bias by a range of factors including sampling methods. Average taxonomic distinctness (Δ^+), with its associated randomisation test, may be worth considering. Although there are issues concerning the relationship between taxonomic subdivisions and the relatedness of species (Ellingsen et al., 2005) randomisation tests in this study showed that nematode samples, however collected and from whatever part of the fjord, fell within expected values. Although values for macrofauna from certain parts of the fjord fell below expected values, there may be reasons for this which warrant further investigation. For much of the fjord, however, values fell within the expected range even though samples were of different sizes and collected using different methods. The regional pools on which the randomisation tests are based would need refining over a period of years, but it is likely that a substantial change in the numbers of stations falling out with expectation would indicate structural and functional changes in the ecosystem of the fjord. The method only relies on species lists, and as such simple methodologies, which could be applied by a range of investigators, may be developed.

For reasons outlined in the Introduction it may be expected that meiofauna react to environmental change over shorter time periods than macrofauna. It is likely, therefore, that meiofauna will be more sensitive to within-year variation whereas macrofauna react to environmental changes integrated over longer periods. As such it is worth considering a monitoring programme that considers both elements. Whichever animals are chosen, and however they are sampled, it is clear that despite considerable effort there is still much to learn

about factors affecting benthic distributions in Kongsfjord, and carefully designed baseline studies (to include inter- and intra-annual and spatial variability) are recommended.

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