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Comparison of nematode communities in Baltic and North Sea sublittoral, permeable sands − Diversity and environmental control

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Abstract

The structure of free-living nematode communities was investigated seasonally at two sandy locations representing typical shallow sublittoral, permeable environments of the North Sea and the Baltic Sea. At the Baltic study site the chlorophyll and organic carbon concentrations in the sediment were, on average, four times lower than at the North Sea. Highest nematode densities (1674−4100 ind. 10 cm^{-2}) and a higher number of free-living nematode genera (66) were recorded in the North Sea (Baltic: 206−1227 ind. 10 cm^{-2}, 30 genera). Despite lower salinity and lower food availability the less dense and less diverse Baltic nematode community was similar in generic composition to the North Sea community. At the North Sea site, all trophic groups according to Wieser's classification were present with omnivores/predators, dominated by *Viscosia*, prevailing and followed by epistrate-feeders. In the food-limited Baltic community, non-selective deposit feeders (mainly *Ascolaimus*, *Axonolaimus* and *Daptonema*) and omnivores/predators dominated by *Enoplolaimus* were the most abundant trophic groups while selective deposit feeders were absent or their contribution was negligible. An analysis of the vertical generic distribution revealed highest diversity of the Baltic community in deeper sediment layers, below the sediment surface affected by ripple migration and near the interface of oxic and anoxic conditions. The diversity pattern in the North Sea sediment was more variable but generally showed high diversity in the upper centimetre of the sediment. These observations suggest that food supply and sediment oxygenation are the most important factors influencing the vertical pattern of nematode generic diversity in sublittoral, permeable sands.
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1. Introduction

Sandy sediments are common in shallow sublittoral environments (Emery, 1968). They are characterized by highly diverse meiofauna communities (Heip et al., 1985; Coull, 1988; Giere, 1993) with nematodes usually representing one of the dominant taxonomic groups. The relatively large open pores of the sands provide space for foraging and shelter, and biofilms and microalgae growing on the grain surfaces represent a prolific sedimentary food source. Near the surface of the sands, the interaction of bottom flow with sediment ripples results in rapid pore water exchange and filters large volumes of water through the upper layers of the bed. In contrast to the relatively slow molecular diffusion that dominates solute transport in fine-grained, muddy sediments, the filtration process in permeable sands, which can reach several hundred liters of seawater per square meter and day (Precht and

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Huettel, 2003), transports effectively oxygen and organic particles into the sand, the latter supplying the interstitial community with diverse food of pelagic origin (e.g. planktonic algae, microzooplankton, bacteria) (Huettel et al., 1996; Huettel and Rusch, 2000). Hence, despite generally low organic matter concentrations and low standing stocks of reactants, sandy sediments are biogeochemically highly active and may play an important role in marine carbon cycles (Shum and Sundby, 1996). Nematodes are the most abundant and ubiquitous marine metazoan group. They directly or indirectly influence many processes associated with the degradation of organic matter in sediments. It is assumed that nematode communities increase energy flow, mineralization rates, enhance the recirculation of nutrients and may have an important and direct influence on the productivity of shallow waters (Platt and Warwick, 1980; Heip et al., 1982, 1985). The nematode community, thus, may play a key role in the sedimentary cycling of matter and, as phrased by Platt and Warwick (1980) any general assessment of the ecology of a given habitat is incomplete if the nematode fauna is not taken into consideration. Since nematodes combine a high diversity (a rich species pool) with short generation times they are able to respond rapidly to alterations in food supply. Because of their reproductive strategies, changes in population structure usually can be related to a change in environmental conditions.

The differences in the structure of nematode assemblages on large, horizontal scales are mainly related to differences in sediment composition, hydrodynamic conditions, salinity and food resource availability (Heip et al., 1985; Giere, 1993; Soetaert et al., 1994, 1995; Li et al., 1997; Steyaert et al., 1999, 2003; Tita et al., 2002; Somerfield et al., 2003). On the vertical scale, abiotic and biotic factors cause changes in nematode community structure over a few centimetres that are as large as those occurring over hundreds of meters on the horizontal scale (Heip et al., 1985; Steyaert et al., 2003).

The aim of this study was to compare the structure of the nematode communities at two comparable sublittoral sites located on the southern Baltic Sea (hereafter referred to as the Baltic) and the southeastern North Sea coast in order to increase our understanding of the factors that control nematode abundance, diversity and spatial distribution patterns in sands. The most prominent environmental differences between the two sites are salinity and organic matter supply. The Baltic is one of the largest brackish water areas in the world, and the associated salinity variations and ensuing osmotic stress may explain the relatively low number of macro- and meiofauna species that inhabit the sublittoral sands (Elmgren, 1978; Elmgren and Hill, 1997). The North Sea site, in contrast, is characterized by relatively constant marine salinity and copious food supply provided by the tidal water exchange and high benthic primary production.

At the Baltic and North Sea site, we analyzed the nematode communities, their trophic structure and vertical diversity patterns. Our working hypothesis was that due to the brackish conditions in the Baltic, a reduced diversity would produce a different representation of the nematodes in ecological niches equivalent to those at the North Sea site. We related the structure of the nematode communities at the two sites to the respective environmental conditions and analyzed the differences in these conditions between the sites in order to find factors explaining best the nematode diversity patterns.

This study is a part of the EU project COSA "Coastal Sediments as a Biocatalytical Filters".

2. Materials and methods

2.1. Study sites

The sampling station in the North Sea was located near the Island of Sylt (Germany) (Fig. 1) in the Wadden Sea, a shallow coastal sea with tidal flats covering about 50% of the area at low tide (Gätje and Reise, 1998). The study site is on the lee side of the island and protected from direct wave impact from the North Sea. Tides are semi-diurnal and the tidal amplitude is ca. 2 m. Seawater salinity ranges between 28 and 32 (Gätje and Reise, 1998). Samples were taken from the shallow sublittoral sand bottom situated south of List Harbour. The distance between the low water and the high water lines was app. 100 m. The Baltic sampling station was located at the tip and landward side of the Hel Peninsula separating the open sea from Puck Bay (Poland) (Fig. 1). In contrast to the North Sea site, tidal influence is minimal with a maximum tidal range of 10 cm and water level fluctuations are primarily controlled by wind induced seiches. Salinity at the study site ranged from 3 to 8. Both sites selected for this study were located at a mean water depth of 1.5 m.

2.2. Sediment characteristics

Sediment granulometry was determined on each of three replicate samples, taken with Perspex cores with an inner
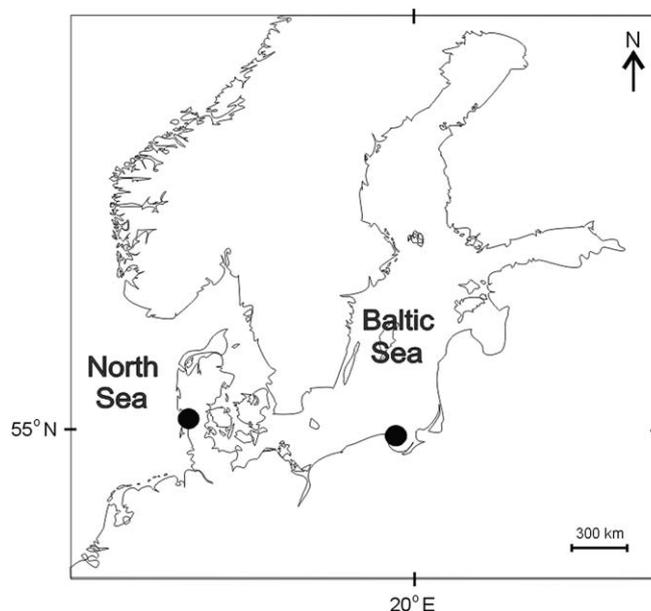

Fig. 1. Map of the investigation area. Study sites marked with black dots (Sylt — North Sea, Hel — Baltic).

diameter of 3.6 cm and a cross-sectional area of 10 cm^2. In Hel, the sediment cores were divided according to the same scheme as for meiofauna; in Sylt the cores were sliced according to the scheme: 0–5, 5–10, 10–15 cm. Granulometric analysis was done by standard dry sieving after rinsing the sediment twice with freshwater. The sediment fractions were defined according to the Wentworth scale (Buchanan, 1984). Sediment parameters (medium grain size, sorting coefficient, skewness and kurtosis) were calculated according to Boggs (1987), by means of software package GRADISTAT.

At Hel, three sediment cores of an inner diameter of 3.6 cm were taken at random for chlorophyll *a*, organic carbon and total nitrogen content determination, whereas on Sylt eight cores were taken. Cores were sliced in 1 cm steps down to a depth of 15 cm. The slices from different cores were homogenized and three subsamples of a volume of 3 cm^3 were taken for analyses of Chl *a* and C and N content. All subsamples were frozen at −20 °C and freeze dried before further analysis.

Chl *a* content was determined according to the method described by Lorenzen (1967). In Sylt, one gram of sediment of each depth centimeter was extracted with 7.5 ml acetone (90%), whereas in Hel 10 cm^3 of sediment was extracted with 20 ml acetone (90%). Samples were incubated for 24 h at 4 °C in the dark and were shaken in between to maximize extraction efficiency. Samples were centrifuged at 3600 rpm for 10 min and extinction of the fluid overlying the sediment was measured in a spectrophotometer (UVIKON XL in Sylt and BECKMAN DU-62 in Hel) at 665 and 750 nm before and after acidification with 2 drops of HCl (10%).

At Sylt, organic carbon (TOC) and nitrogen content were measured with a Thermo-Finnigan Flash EA 1112 CHN analyzer. For these measurements, 60 mg of homogenized sand was weighted into silvercups. 30 µl Millipore water and at least two times 10 µl of 6 N HCl were added to remove the carbonates. Then samples were dried for at least 4 h at 60 °C prior to the measurement.

At Hel, organic carbon and nitrogen content were measured with a Perkin Elmer CHNS/O analyzer. For the measurements 100 mg of sand was weighted and 1 ml 1 N HCL was added to remove the carbonates. Then samples were dried for 24 h at 60 °C. Prior to the measurement 50 mg homogenized sediment were put into zinc cups, 1 ml of Millipore water was added and again samples were dried at 60 °C till the constant weight.

For pore water nutrients analysis, eight cores with an inner diameter of 3.6 cm were sliced in 1 cm intervals to a depth of 15 cm. Replicate sediment slices were pooled together and the pore water blown out with nitrogen (Billerbeck et al., 2006). The pore water was filtered through 0.45 µm nylon filters and frozen until further analysis. Ammonium, phosphate, nitrate and nitrite concentrations in the pore water were measured with an autoanalyzer (AA3, Bran & Lübbe) in on-line diluted samples.

2.3. Nematode sampling and treatment

Sampling took place in August and November 2003 and in February and May 2004. Three replicate sediment samples were taken using Perspex cores with an inner diameter of 3.6 cm and a cross-sectional area of 10 cm^2. The sediment cores were sliced into seven depth layers: 0–1, 1–2, 2–3, 3–4, 4–5, 5–10, 10–15 cm and the slices were preserved with a neutral 4% formaldehyde solution. In the laboratory, samples were rinsed through a 1 mm mesh to remove macrofauna and shells, and subsequently the water overlying the sample was decanted onto a 32 µm mesh sieve. After resuspending the sediment and decanting the overlying water 10 times, the fraction retained on the 32 µm sieve was stained with Rose Bengal and meiofauna in the sample was counted and identified to higher taxon levels under a stereomicroscope.

The first 100 nematodes from each sample were sorted out at random by hand, mounted on permanent glycerin slides following the procedure described by Vincx (1996), and identified to genus level using the pictorial keys by Platt and Warwick (1983, 1988), Warwick et al. (1998), and relevant taxonomic literature (Blome, 1974, 1982). Classification into feeding groups used Wieser's (1953) scheme, which distinguishes four 'guilds' on the basis of mouth morphology: (1A) selective and (1B) non-selective deposit-feeders, (2A) epistrate-feeders, and (2B) predators/omnivores.

Most indices of species diversity are dependant on the sample-size and on the number of analysed specimens (Sanders, 1968; Hill, 1973; Soetaert and Heip, 1990). As a fixed number of individuals within each sample was identified, several different diversity indices were calculated in order to compare species richness and diversity between samples. Diversity was expressed as the N_1 diversity index (Hill, 1973), which is a normalization of the Shannon–Wiener index H and is recommended by Heip et al. (1988) for meiofaunal assemblages. The rarefaction index ES (x) (Expected number of Species), which provides an estimated number of species/genera present in a population of x individuals, was used as recommended by Sanders (1968) and Hurlbert (1971). This diversity measure is independent on sample size (the number of genera identified). Two knots, 30 and 100, were used because in Sylt all samples were 100 or more (hence ES(100)), but in Hel many samples were of smaller size, requiring a cut of 30 to allow comparisons between sediment layers. Moreover, Margalef's species-richness diversity index (d), which is a measure of the number of species present for a given number of individuals (Clarke and Warwick, 1994) was calculated. All diversity indices were calculated with the software package PRIMER (version 5).

Kruskal–Wallis test was applied to test the null hypothesis that there were no significant differences of diversity indices between different sediment layers. These analyses were performed using the software package Statistica (StatSoft, version 6). Furthermore, non-parametric multivariate techniques included in PRIMER (version 5) were used for statistical analyses of the communities. To cope with varying sample size data were standardized prior to multivariate analyses. Hierarchical cluster analysis was performed on the abundance data in the integrated sediment column. Analyses were performed on untransformed, square- and fourth-root transformed nematode abundance data (in the integrated sediment column) in order

to detect the effects of the study site on the dominant and rarer genera, respectively and on presence/absence data to detect the effect on species composition. Similarities between samples were calculated using the Bray-Curtis similarity coefficient. Group average linking was applied. Two-way crossed ANO-SIM (Clarke, 1993) was used to test for differences between study sites and seasons. The relationship between multivariate assemblage structure and environmental variables were analysed using the BIO-ENV procedure, which aimed to select variables explaining best the structure of the nematode community. Data plots were analysed prior the BIO-ENV procedure in order to exclude highly correlated environmental variables. Analysis was performed using normalised abiotic data (values for each variable had their mean subtracted and were divided by their standard deviation) and the Spearman rank correlation method.

3. Results

3.1. Sediment characteristics

Median particle size ranged between 305–348 μm in Sylt and 268–387 μm at Hel (Table 1, Fig. 2). Medium sand was the dominant sediment fraction at both study sites (74–85% in Sylt and 53–79% in Hel). The silt content of the sediment was higher in Sylt (up to 0.1–0.7% *vs.* 0.0–0.3%, respectively). Sediments were moderately well sorted at both locations.

Concentrations of organic carbon in the Sylt sediment varied from 0.18–0.28% in the upper one sediment centimeter to 0.06–0.11% in the deepest sediment layer (10–15 cm) (Fig. 3). These values were much higher than the organic carbon content measured in Hel: 0.03–0.06% (Table 2). Organic nitrogen concentrations in Sylt ranged from 0.04% in surface layer to 0.01% in the deeper layer while the nitrogen concentrations in Hel were below the detection limits of the analyzer (<0.005%).

Chl *a* content in the upper 1 cm was, on average, five times higher in the North Sea (256.4 ± 27.3 mg m^{-2}) than in the Baltic sediment (52.1 ± 22.5 mg m^{-2}). The highest concentrations in Sylt were noted in May (up to 283.5 mg m^{-2} in the

upper one centimeter; Fig. 3). In the Baltic, Chl *a* content was measured only on a few occasions (Table 2).

Pore water nutrients concentrations were measured in all months studied apart from August in Hel. Diagrams presenting the vertical changes of nutrients concentrations in the sediment at both study sites are shown in Figs. 3 and 4.

Water temperatures at the time of study at Hel were 19.3 °C, 8.6 °C, 1.8 °C, 9.9 °C in August, November, February and May respectively, whereas at Sylt 15.5 °C, 6.0 °C, 4.0 °C and 11.0 °C, respectively. Measurements performed at Sylt showed that interstitial temperatures at the sediment surface were equal to overlying water temperatures.

3.2. Nematode communities

The highest total nematode densities, integrated over the upper 15 cm of the sediment, were recorded in the North Sea, with maximum average abundances of 4104 ind. 10 cm^{-2} in May and minimum abundances (1674 ind. 10 cm^{-2}) in August. In contrast, the highest nematode densities in the Baltic site (1227 ind. 10 cm^{-2}) were noted in August and the lowest in February and May (206 and 311 ind. 10 cm^{-2}, respectively) (Table 3).

A total of 73 nematode genera were recorded at the two study sites (66 and 30 nematode genera in Sylt and Hel, respectively), 23 genera were common to both sites. Four genera recorded in Hel and 18 genera recorded in Sylt were rare (found only in 1–2 samples).

Viscosia was the dominant genus of the North Sea assemblage (Table 4). Percentage contribution of *Viscosia* was relatively uniform seasonally and constituted 32 to 43% of the total nematode community. *Monoposthia* was the second most abundant genus; its peak density was noted in August when this genus constituted 14.7% of the community. In Hel, *Ascolaimus*, *Enoplolaimus*, *Daptonema* and *Dichromadora* were the dominant genera. Together these four genera constituted 69% to 78% of the community, but the dominance structure within this group changed seasonally. Nematodes belonging to the terrestrial order *Dorylaimida* were recorded in Hel on one occasion in May.

In Sylt, predators/omnivores (2B) and epistrate feeders (2A) were the most abundant feeding strategies (73–88% of the community; Fig. 5). At the Baltic location, non-selective deposit-feeders (1B) and predators/omnivorous nematodes (2B) were the dominant nematode trophic groups (together 60–86% of the community). Selective deposit feeders (1A) were more important in the North Sea than at the Baltic, both in terms of abundance (3–7% *vs.* 0.3–0.5% of the community, respectively) and diversity (12 *vs.* 2 genera, respectively). Epistrate feeders constituted the most diverse trophic group at both sites (11 and 26 genera in Hel and Sylt, respectively). The trophic structure of the North Sea community did not change significantly over the year, whereas in the Baltic the contribution of deposit feeders gradually increased towards May.

Two-way crossed ANOSIM showed significant differences in nematode community structure between Hel and Sylt (study

Table 1
Median grain size (μm) at both study sites (arithmetic means)

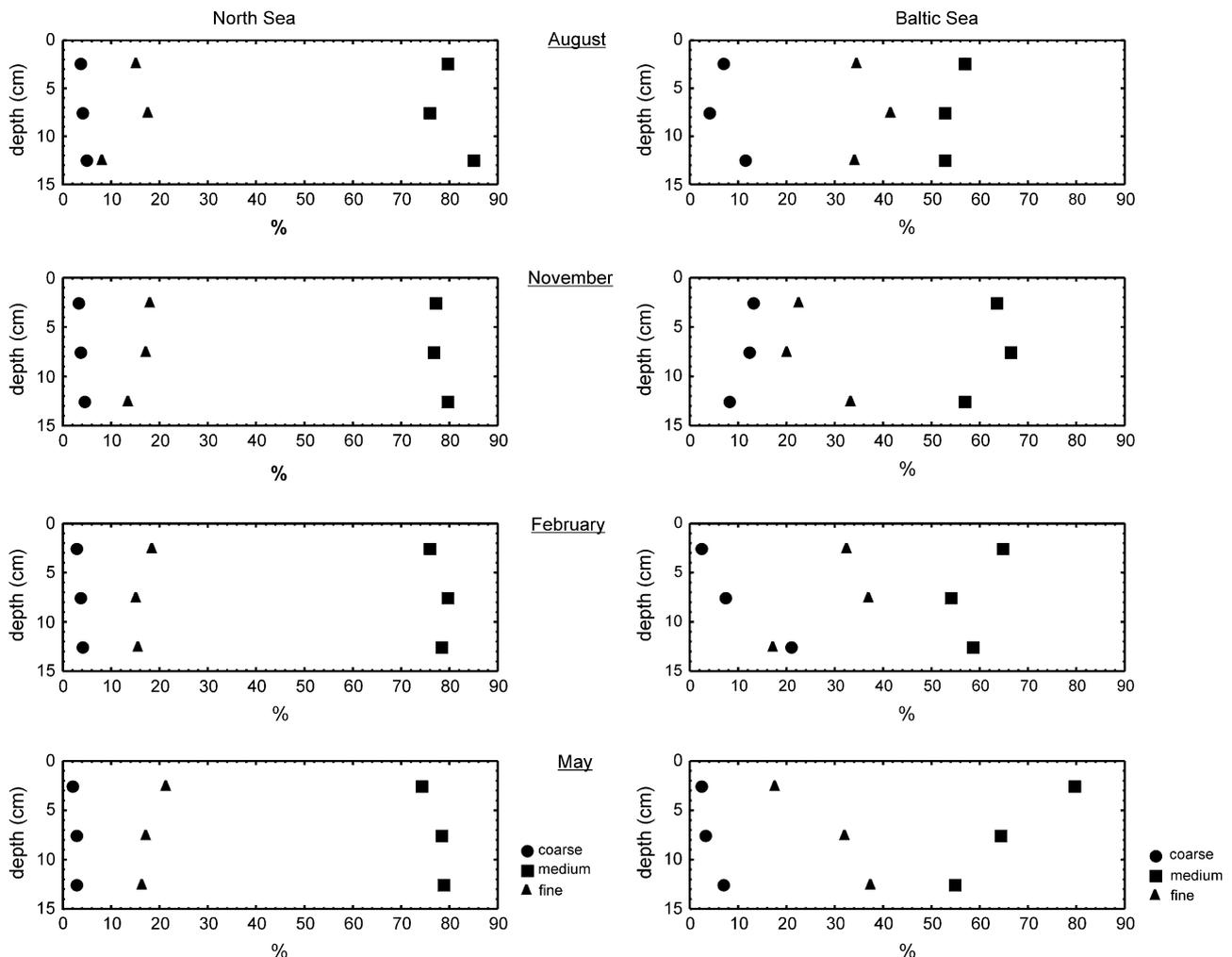| Month	Sediment depth (cm)	North Sea	Baltic Sea
	0–5	335.8	285.1
VIII	5–10	321.5	268.0
	10–15	348.3	293.8
	0–5	319.6	321.4
XI	5–10	324.1	329.0
	10–15	339.6	289.4
	0–5	318.2	283.4
II	5–10	335.0	281.4
	10–15	331.0	386.6
	0–5	305.8	324.8
V	5–10	323.0	284.9
	10–15	322.9	279.8

Fig. 2. Percentage contribution of dominating sediment fractions (coarse, medium and fine sand) in the vertical sediment profile at both study sites.

site: $R = 1$, $p = 0.1\%$ at all transformations; season: $R = 0.7$, $p = 0.1\%$ on non-transformed, square- and fourth-root transformed data, $R = 0.5$, $p = 0.1\%$ on presence/absence data). Hierarchical cluster analysis clearly separated both study sites, however the similarity on the Bray-Curtis similarity scale was increasing with an increase of the effect of the study site on the rarer genera (similarity of 15% on untransformed data, 30% – square-root, 40% on fourth-root transformed data). The highest similarity between Hel and Sylt nematode communities (45%) was noted on presence/absence data (Fig. 6).

3.2.1. Vertical profiles

The vertical distribution of nematodes in the North Sea changed seasonally. In spring and summer, the highest nematode density was found in the upper one sediment centimetre (a maximum of 1800 ind. 10 cm^{-2} noted in May) and densities decreased towards the deeper layers (Fig. 7). In the colder months (November, February) the highest nematode concentrations were recorded in deeper layers. An opposite pattern was observed at the Baltic location, where the highest nematode abundances in colder months were noted in the upper

2–3 centimetres. In August and May the vertical distribution of nematodes was more uniform (Fig. 7).

In general, the highest nematode diversity in the North Sea occurred in the upper one centimetre of the sediment (Fig. 8). An exception was the vertical pattern observed in May with the highest diversity indices noted in the deepest sediment layers. Diversity decreased with depth in colder months, whereas an opposite pattern was noted in August and May. Apart from August, Kruskal–Wallis test showed significant differences ($p < 0.05$) with respect to the variation in diversity with sediment depth. According to the results of BIO-ENV (Table 5) the best correlations were found with organic carbon content and ammonium concentrations, an exception was February when C/N ratio and ammonium concentration made the best combination explaining the vertical structure of the community.

The diversity pattern observed in the Baltic was characterised by an increase of diversity indices from the surface of the sediment to a depth of 3–5 cm followed by a decrease towards deeper sediment layers. Apart from May, the differences in diversity measures along the sediment depth in the Baltic were statistically significant in all months studied (Kruskal–Wallis
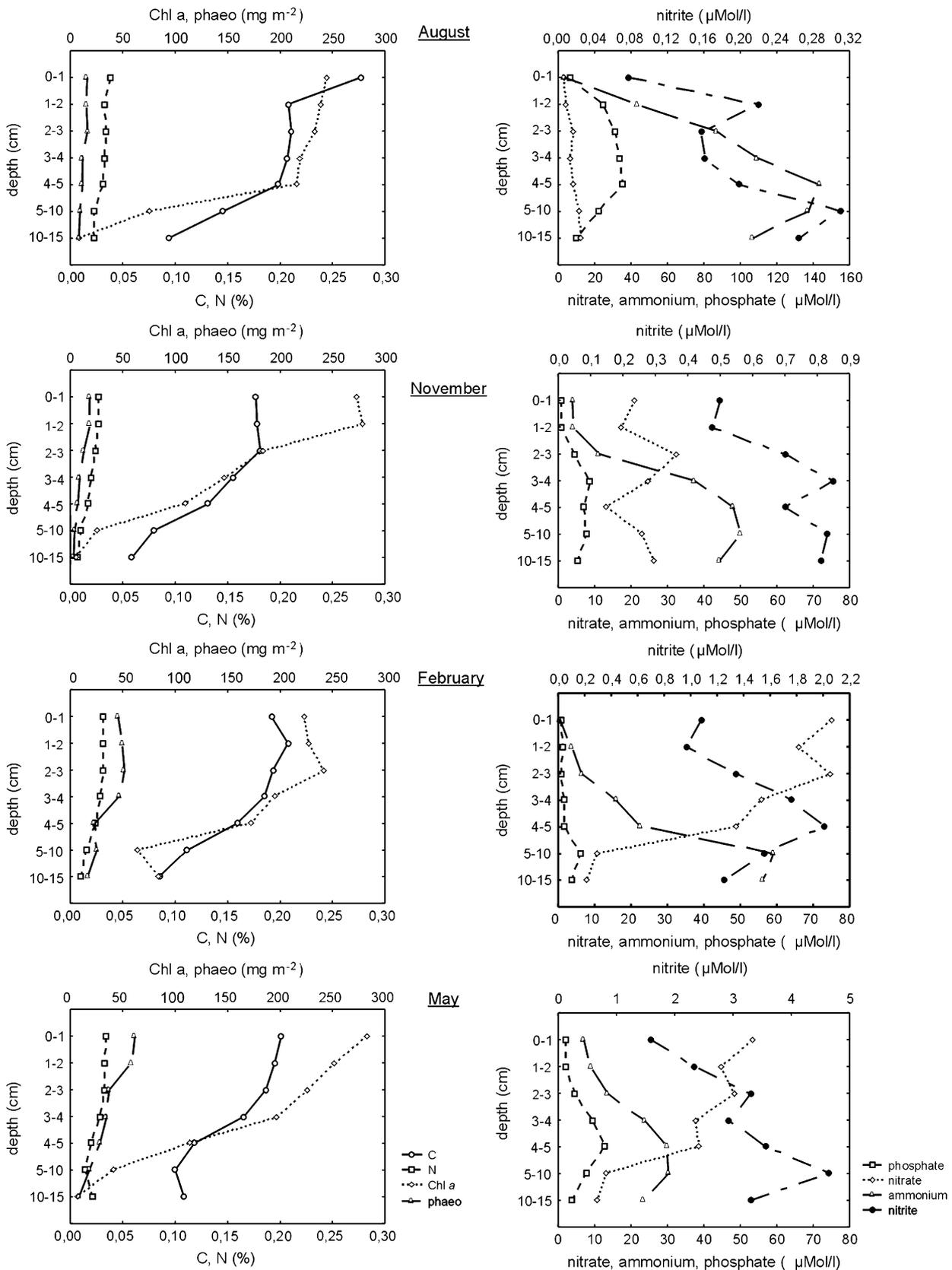
Fig. 3. Vertical distribution of organic carbon, nitrogen, chlorophyll a, phaeopigments and pore water nutrient concentrations in sublittoral sediments near the Island of Sylt (North Sea) (different scales on X axes).

Table 2
Organic carbon and chlorophyll *a* content in the vertical sediment profile in the Baltic site

Month	Depth (cm)	C_{org} (%)	Chl *a* (mg m^{-2})
VIII	0−1	0.05	69.77
	1−2	0.03	
XI	0−1	0.04	59.61
	1−2	0.05	99.03
II	0−1		26.78
	2−3		25.26
	3−4		28.87
	4−5		26.06
	5−10		85.40
	10−15		12.96
V	0−1	0.05	
	1−2	0.05	
	2−3	0.06	
	3−4	0.06	
	4−5	0.05	
	5−10	0.04	
	10−15	0.03	

test, $p < 0.05$). Due to very low nematode densities in Hel in February (minimum density of 3 ind. 10 cm^{-2}), diversity indices based on this data cannot be compared with diversity measures from other seasons.

Analyses of the vertical genera distribution and vertical community structure will be presented in a separate paper by Urban-Malinga et al. (in prep.).

4. Discussion

4.1. Nematode densities and diversity

In general, nematode densities recorded in Hel (206−1227 ind. 10 cm^{-2}) agree with results of Haque et al. (1997) who found on average 473−1089 nematodes 10 cm^{-2} in sandy littoral sediments of the Gulf of Gdańsk. Also the number of nematode genera (30) lies within the range of results reported from other sandy areas of the Baltic Sea: 35 genera in the Pomeranian Bay (Rokicka-Praxmajer and Radziejewska, 2002), 24 genera in the Gulf of Riga (Pallo et al., 1998), and 27 genera in the Gulf of Gdansk (Drgas, pers. comm.).

Only a few studies address the nematode community structure in shallow sublittoral sands of the North Sea. Most studies were related to deeper sediments. Nematode densities recorded by Gheskiere et al. (2004) in coastal sands at the low water level of a sandy beach (2784 ind. 10 cm^{-2}) corresponds to our counts in Sylt (1674−4104 ind. 10 cm^{-2}). Abundances in deeper subtidal sediments are usually lower, e.g. 1000 ind. 10 cm^{-2} (Vincx et al., 1990), 141−622 ind. 10 cm^{-2} (Steyaert et al., 1999), 187−785 ind. 10 cm^{-2} (Vanaverbeke et al., 2000), 200−600 ind. 10 cm^{-2} (Vanaverbeke et al., 2004).

Nematode abundances in the Hel and Sylt sublittoral sands were lower than those reported from muddy sediments, but the number of nematode genera was higher. This agrees with general trends discussed in Platt and Warwick (1980) and Heip et al. (1982, 1985). Abundances noted by Jensen (1984) in

coastal Baltic mud ranged between 1200 and 1500 ind. 10 cm^{-2}, but the number of nematode genera (12) was lower than the record of 30 genera in our study. Hendelberg and Jensen (1993) found very high nematode densities (1700−8900 ind. 10 cm^{-2}) and only 23 species. Juario (1975) recorded in very fine subtidal sand of the North Sea 47 nematode genera (v. 66 genera in our study) and densities in the range 3047−5261 ind. 10 cm^{-2}. Steyaert et al. (1999) noted 56 nematode species in muddy subtidal of the North Sea.

Hitherto, the coexistence of closely related species and higher nematode diversity in sandy sediments was attributed to higher heterogeneity and the availability of more microhabitats in sand as compared to mud (Heip and Decraemer, 1974; Platt and Warwick, 1980; Heip et al., 1982). This heterogeneity *sensu* Heip and Decreamer can be explained by the open, porous structure of sandy sediments and the three-dimensional biogeochemical zonation resulting from advective pore water flows. These flows increase the interfacial area between oxic and anoxic zones, accumulate particles of similar size and surface characteristics in confined layers and pump nutrients to the surface and oxygen into deeper sediment zones (Huettel et al., 1996; Huettel and Webster, 2000; Huettel and Rusch, 2000). The ensuing complex spatial distribution pattern of oxygen, organic matter, bacteria, benthic microalgae and sulfide (Huettel et al., 2003; Franke et al., 2006) provides a multitude of microniches with different biogeochemical characteristics that support more diverse nematode communities in permeable sands than in mud. In turn, nematodes affect the heterogeneity and microniches in the sediment through their grazing activities, movement through the pore space, mucus production and nutrient release.

A total of 100 nematode genera were found by Blome (1982, 1983) in a transect extending from the supralittoral to the sublittoral at a sandy beach about 400 m north from our sampling site at the island of Sylt. *Monoposthia*, *Viscosia*, *Spirinia* and *Paracanthonchus* − the dominant genera at the deepest station studied by Blome − also were among the dominant genera at our sublittoral site. Likewise, the generic composition of the nematode community at Hel is typical for the brackish areas (Heip et al., 1985). Thorson (1957) defined 'isocommunities' or 'parallel-level bottom communities' as those that use the niches provided by similar habitats by the same genera, thus representing ecological parallels or parallel animal communities. According to Gheskiere et al. (2005) the 27% genus similarity (Bray-Curtis similarity scale) fully supports the existence of isocommunities for the upper sandy beaches of the Baltic and Mediterranean. Although, the differences in community structure between Baltic and the North Sea observed in the present study were significant as showed by ANOSIM, the relatively high similarities in genus composition (up to 45%) must be emphasized. The Baltic community is impoverished in terms of the number of nematode genera when compared to the North Sea but the generic composition suggest that, despite lower salinity and poorer food conditions, these communities remain parallel systems.

Due to its brackish nature, the Baltic has relatively simple benthic ecosystems (has fewer plant and animal species than
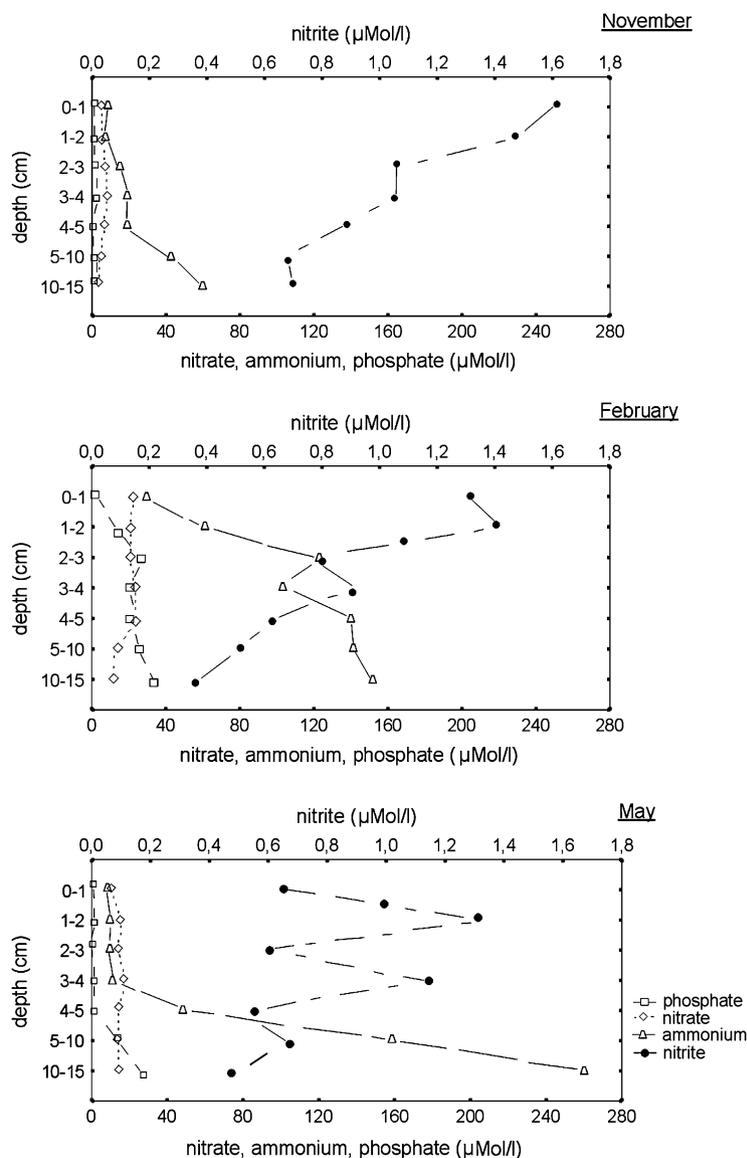
Fig. 4. Vertical distribution of pore water nutrients concentrations in sublittoral sediments at Hel (Baltic).

fully marine areas) (Elmgren, 1978; Elmgren and Hill, 1997). However, comparisons of benthic and pelagic carbon flow models of Baltic and North Sea ecosystems showed unexpectedly high similarities between the two systems (Elmgren and Hill, 1997 and references therein). Elmgren and Hill concluded that as long as major functional groups are present,

a simple, low-diversity ecosystem may be, in terms of flows of organic carbon, functionally almost equivalent to a high-diversity ecosystem, although the rates are lower. Measurements performed during this project showed that the pathways of carbon flow were similar at both study sites, but the magnitude of the fluxes was about 3 to 4 times lower in the Baltic than in the North Sea (Cook, pers. comm.). This is in line with about 4-fold lower phytobenthos biomass and carbon content of the sediment at the Hel site. The relationship between biodiversity and ecosystem functioning is currently the focus of a debate and research effort. A number of manipulative experiments have been performed in terrestrial ecosystems (Hector et al., 1999; Kinzig et al., 2001; Loreau et al., 2001) and only a limited number of studies addressed marine systems (Gessner et al., 2004 and references therein). As stated by Elmgren and Hill (1997) the ''simple'' ecosystems of the Baltic Sea

Table 3
Mean total nematode densities (ind. 10 cm^{-2}) in the integrated sediment column (0–15 cm)

Month	North Sea N ± SD	Baltic Sea N ± SD
VIII	1674 ± 136	1227 ± 409
XI	3204 ± 1120	1144 ± 141
II	2235 ± 1333	206 ± 181
V	4104 ± 483	311 ± 96

Table 4

List of the nematode genera at both study sites and their proportions (%). The most abundant genera (>2% of the community) are in bold

Genus	Trophic group	North Sea				Baltic Sea			
		August	November	February	May	August	November	February	May
Adoncholaimus	2B					**2.3**	**3.5**	**3.3**	**1.1**
Ascolaimus	1B	**1.3**	**1.9**	**3.8**	**2.5**	**32.9**	**19.8**	**25.8**	**14.8**
Axonolaimus	1B	**1.5**	**1.5**	**2.2**	**2.7**	**4.9**	**8.9**	**8.6**	**7.9**
Bathylaimus	1B		**5.0**	**11.6**	**9.5**	**2.8**	**1.2**	**1.0**	**0.4**
Bolbolaimus	2B				0.2				
Calomicrolaimus	2A	0.4	0.1	0.6	0.9	0.8	0.1	0.3	0.1
Camacolaimus	2A	0.5	1.0	0.8	0.2				
Choniolaimus	2A			1.0	0.2				
Chromadora	2A		0.4	1.2	0.5				
Chromadorella	2A		0.2	0.6	0.5	0.5			
Chromadorina	2A	0.4	0.1	0.6	0.5				1.8
Chromadorita	2A	1.7	0.6	0.5	0.2	**3.4**	**5.4**	**8.9**	**3.5**
Chromaspirina	2A	**6.2**	**0.9**	**4.9**	**5.3**				
Cobbia	2A	0.5	1.0	0.2					
Comesa	2A				0.3				
Cyartonema	1A	0.1							
Daptonema	1B	**5.3**	**3.4**	**3.5**	**1.3**	**2.7**	**12.0**	**14.8**	**54.5**
Dichromadora	2A	**5.8**	**3.9**	**3.3**	**1.3**	**18.7**	**9.4**	**8.7**	**5.5**
Ditlevsenella	2B			0.2	0.5				
Dorylaimoidea									0.4
Echinodesmodora	2A	0.5							
Eleutherolaimus	1B				0.2				
Euchromadora	2A	1.0	0.7	0.4	0.3				
Enoploides	2B			0.5					
Enoplolaimus	2B		0.2		0.5	**23.9**	**29.8**	**2.1**	**3.7**
Eumorpholaimus	1B					1.2	0.7	0.5	1.1
Eurystomina	2B			1.0	0.2				
Filitonchus	1A		0.5						
Gammanema	2B					0.2			
Gonionchus	2A				0.6				
Karkinochromadora	2A	**1.8**	**4.9**	**4.7**	**2.0**				
Leptolaimus	1A				0.1				
Leptonemella	1A	0.1			0.9				
Metachromadora	2B	**2.2**	**4.8**	**2.7**	**8.6**	0.7	1.0		0.4
Microlaimus	2A	**1.6**	**1.3**	**4.1**	**4.3**	0.6	0.1		
Molgolaimus	1A				0.5				
Monoposthia	2A	**14.7**	**9.5**	**8.1**	**6.5**		0.2		0.2
Monhystera	1B							0.6	0.3
Morlaixia	1A							0.5	
Namanema	1A			0.4	0.3				
Nannolaimus	1A	0.5			0.5				
Neochromadora	2A	0.2	0.2	0.2	0.8	**1.3**	**5.0**	**1.5**	**2.2**
Neotonchus	2A				0.5				
Odontophora	1B	0.7	0.1	0.3	0.4				
Oncholaimus	2B	**2.0**	**1.2**	**0.6**	**0.9**	1.4	0.5	1.3	0.1
Onyx	2B	0.6		0.5	0.6				
Oxystomina	1A	0.2	0.5						
Paracanthonchus	2A	**2.3**	**3.1**	**2.3**	**7.9**	1.4	0.4	0.5	0.3
Parachromadorita	2A		0.5	0.5	0.2		**0.7**	**2.6**	**0.1**
Paradesmodora	2A	0.6			0.2				
Paralinhomoneus	1B			0.4	0.7				
Paramesacanthion	2B		0.5						
Pareurystomina	2B	0.7							
Pontonema	2B		0.6						
Polygastrophora	2B	**2.9**	**6.8**	**3.7**	**0.6**		0.1		0.3
Prochromadora	2A				0.2		0.3		0.2
Prochromadorella	2A	1.9	1.7	0.9	0.7				
Promonhystera	1B		0.5		0.8				
Pseudonchus	2B	0.6			0.2				
Ptycholaimellus	2A	0.6	0.1						
Rhabdocoma	1A				0.5				

Table 4 (*continued*)

Genus	Trophic group	North Sea				Baltic Sea			
		August	November	February	May	August	November	February	May
Rhynchonema	1B			0.6					
Sabatieria	1B	0.3	0.2	0.5	0.8				
Siphonolaimus	2B	0.6			0.2				
Sigmophoranema	2B	0.1	0.6	0.4	0.7				
Sphareolaimus	2B			0.6					
Spirinia	2A	**3.2**	**2.7**	**2.7**	**6.3**				
Stephanolaimus	1A	0.2	0.4	0.3	0.4				
Thalassolaimus	1A	0.5			0.6				
Theristus	1B	0.5		0.5	0.2	0.2	0.2	0.9	0.2
Tripyloides	1B	0.5	0.5	0.1		**0.6**	**2.8**	**0.1**	**0.5**
Tubolaimoides	1A					0.2	0.1		
Viscosia	2B	**43.3**	**44.8**	**34.8**	**32.2**				

would seem to be well suited for similar experiments in the aquatic environment.

4.2. Trophic structure

The relative proportions of each of the four nematode feeding guilds in a community depend on the nature of the available food, which in turn is reflected by the nature of the sediment (Platt and Warwick, 1980). Although, Wieser's scheme suffers from many shortcomings and restrictions as it confines nematode species to a single trophic status, the absence of experimental evidence on feeding habits of most free-living aquatic nematodes prohibits a better functional
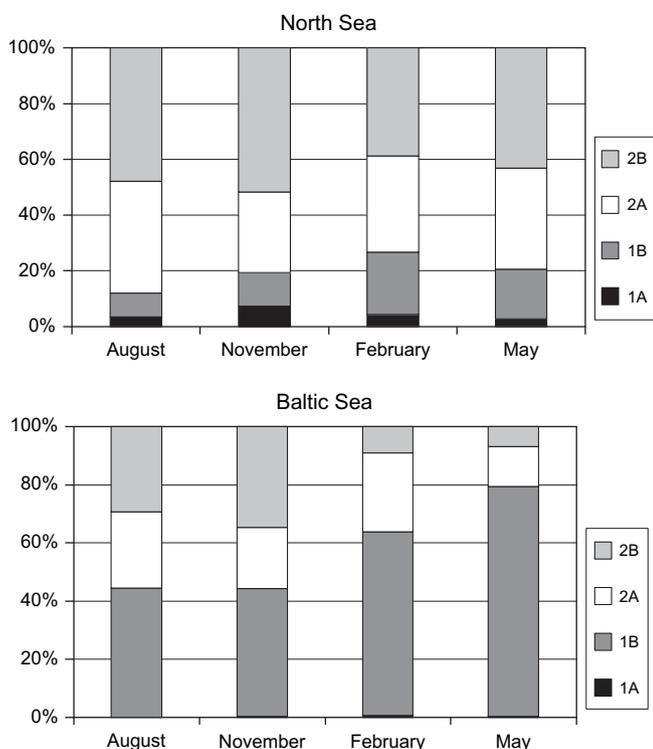

Fig. 5. Contribution of different trophic groups (integrated sediment column, 0–15 cm) at both study sites. 1A – selective deposit feeders, 1B – non-selective deposit feeders, 2A – epistrate feeders, 2B – omnivore/predators.

classification (Moens et al., 2004), thus Wieser's scheme is still accepted as a valuable analytical tool.

The non-selective deposit feeders were the dominant trophic group in Hel, confirming previous findings of Rokicka-Praxmajer and Radziejewska (2002) and Drgas (1993) in the Southern Baltic. Non-selective and selective deposit feeders both have no teeth and exploit the same food source, however non-selective feeders with larger buccal cavities swallow whole organic particles (including diatoms and bacteria), whereas selective feeders having smaller buccal cavities consume smaller particles (detritus and bacteria; Heip et al., 1985). Vanaverbeke et al. (2004) observed in subtidal sediments a substantial increase of the importance of selective deposit feeders as a response to the sedimentation of a phytoplankton bloom. In the study performed by Vanhove et al. (1999), selective deposit feeding was positively correlated with decomposing, older material, whereas non-selective deposit feeding was associated with sites where fresh organic matter was abundant. Thus, selective deposit feeding was dominating in environments, where the nematodes had to distinguish between particles in different stages of decomposition in order to maximize energy yield. These correlations are supported by our study. The relatively low organic carbon, nitrogen and Chl *a* concentrations at the Baltic site indicate that the benthic system is food limited. Fresh organic matter entering the benthic system at the Hel site likely is rapidly utilized preventing the accumulation of detrital material that would provide a food source for selective deposit feeders. Indeed, very low abundances (0.5% of the community at maximum) and diversity of selective deposit feeders may indicate rather small importance of decomposed material and bacteria (reduced bacterial quantity and/or reduced bacteria diversity) as a food source in the Baltic when compared with the North Sea study site.

The high proportion and diversity of epistrate feeders in the North Sea points towards the importance of diatoms and other microalgae as a food source. Microphytobenthic biomass was about four times higher at the North Sea site, primary production was on average three times higher than in the Baltic (Cook and Huettel personal communication), explaining the finding that both the abundances and number of genera
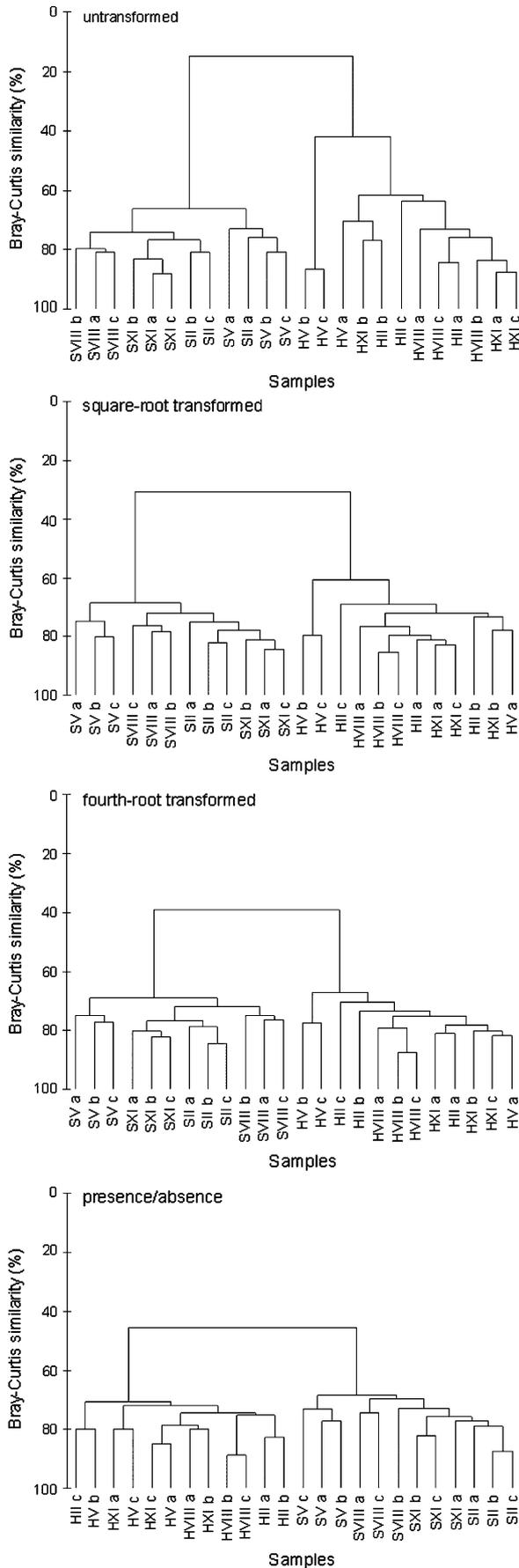
representing epistratum feeders were on average 2-times higher in Sylt than in Hel.

Although predators and omnivores constituted an important trophic group both at Sylt and at Hel, there were substantial differences between these two sites with respect to the feeding habits of the dominant genera. *Viscosia*, which dominated the nematode community in Sylt can be classified as a facultative predator, as scavenging and uptake of dissolved organic material are, next to predation, typical feeding strategies of oncholaimids. There is evidence that oncholaimid nematodes are attracted to decaying plant or animal material, and these nematodes are known to aggregate in organically enriched sites (Jensen, 1987; Lorenzen et al., 1987; Prein, 1988; Moens et al., 1999, 2004). Jensen (1987) called all *Oncholaimidae* "garbage collectors" among nematodes, thus high abundances of *Viscosia* in Sylt may reflect availability and importance of decaying organic material at this site. In contrast, oncholaimids were much less abundant at Hel, where a predator *Enoplolaimus*, which feeds on living prey, dominated the nematode community.

Analyses of the seasonal patterns in trophic structure of the communities show that good food conditions all over the year at Sylt are resulted in relatively stable trophic structure of the community what is in contrast to the results from the food-limited environment at Hel and from deeper sandy subtidal of the North Sea (20 m water depth) (Vanaverbeke et al., 2004), where significant temporal changes in the relative contribution of feeding types were observed.

4.3. Vertical pattern

At both study sites, nematode diversity within the sediment column changed over depth and showed different distribution patterns. The observed patterns are very similar to those reported by Steyaert et al. (2003). The decrease of diversity over sediment depth found at Sylt is very similar to the typical diversity pattern in muddy sediments, whereas the vertical pattern at Hel, with a maximum diversity in 3 to 5 cm sediment depth is similar to that observed in sandy sediment by Steyaert et al. (2003). These authors related the relatively low diversities in the uppermost layers to the strong hydrodynamic regime and tidal disturbance, which influenced sediment granulometry. This is in contrast to our results. The vertical patterns of sediment grain size are not explaining the diversity patterns of nematodes. Furthermore, despite the fact that due to tidal currents the surface sediment transport at Sylt was more intensive than at Hel (Janssen, pers. comm.) the diversity in the uppermost layers was high at Sylt and low at Hel. Surprisingly, pore-water flow velocity measurements performed by Janssen (pers. comm.) showed that despite much higher flow velocities at Sylt, water flushing was more intensive at

Fig. 6. Dendrograms (group-average clustering, Bray-Curtis similarities) on untransformed and transformed nematode genera abundances in integrated sediment column. H-Hel, S-Sylt; VIII – August, XI – November, II – February, V– May; a, b, c – replicates.
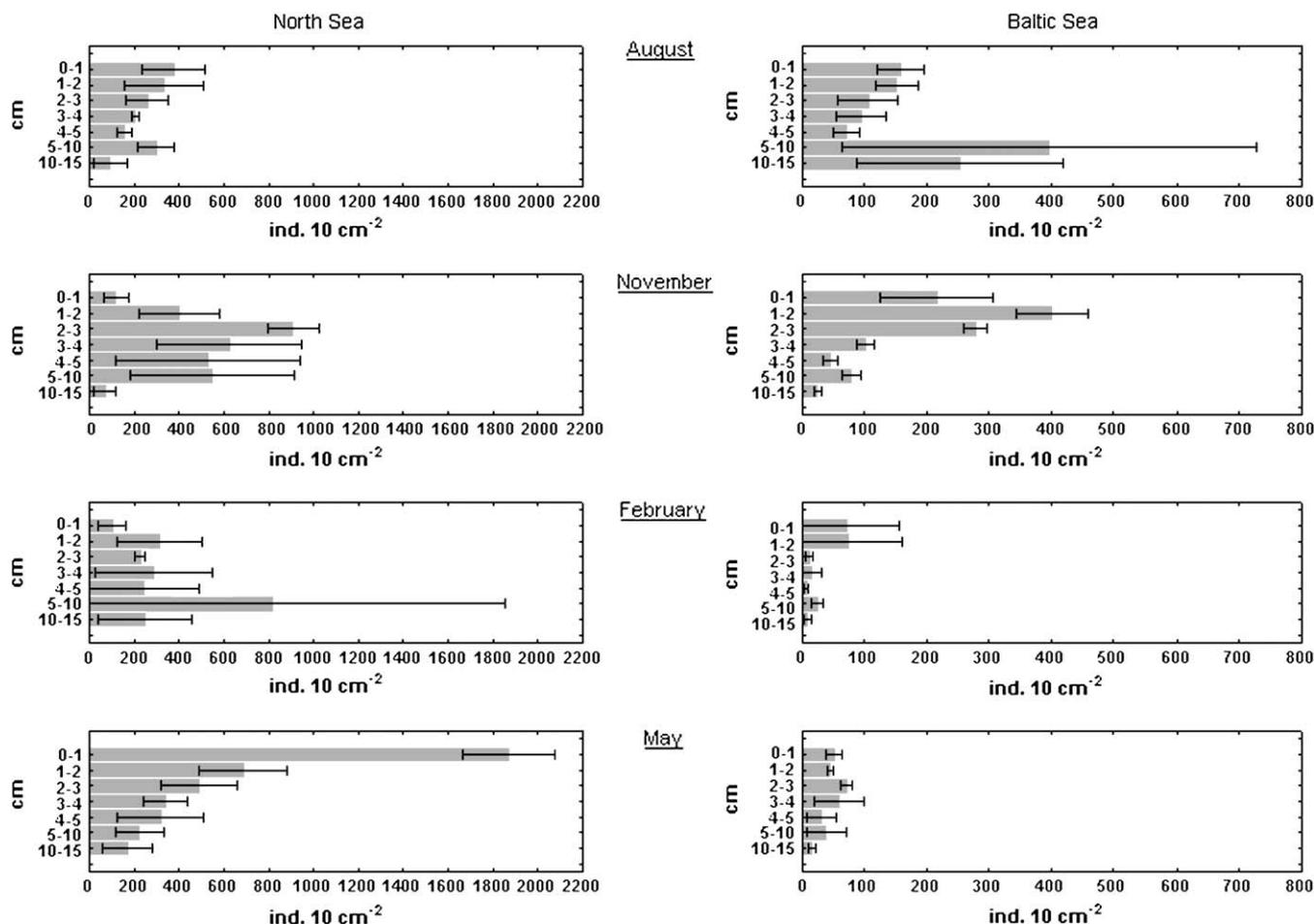
Fig. 7. Nematode densities (means and standard deviations) in vertical sediment profile at both study sites (different scales on X axes).

Hel, what was mainly attributed to different sediment topography at both study sites (flat ripple surfaces at Sylt and more pronounced ripples at Hel). It must be emphasized that 3—5 cm where maximum nematode diversity at Hel was recorded, refers to the depth affected by ripple migration (Cook, pers. comm.) what coincides with the oxygenation of the sediment.

Oxygen penetration into the sediment was measured on several occasions during this project and revealed that at the Baltic site oxygen penetrated at maximum to the depth of 32—43 mm (April 2004 and August 2003, respectively) whereas at the North Sea site penetration to 13 mm (July 2004) was measured (Wenzhöfer et al., in prep.). It was shown by the BIO-ENV analysis performed on the data from the North Sea that food quality/quantity and ammonium concentration were the factors explaining best the vertical community structure. The upper-most sediment centimetre at Sylt, well oxygenated and rich in food, supported the most diverse nematode community. An increase of diversity with sediment depth observed in warmer months can be related to intensive microbial and biochemical processes in deeper sediment layers. Furthermore, bioturbation by macrofauna consisting in Sylt mainly of polychaetes (Weslawski et al., in prep.) may be responsible for sediment oxygenation and stimulating microbial activity in deeper sediment layers.

In contrast, in Hel, despite good oxygen conditions at the sediment surface, the diversity of the nematode fauna was low in the uppermost layers, probably due to poor food conditions and sediment disturbance caused by ripple migration. Increased microbial abundances at the boundary between oxic and anoxic sediment layers may have resulted in diversity peaks at 3 to 5 cm depth. The fact that selective deposit feeders found occasionally at the Hel site occurred in that depth interval supports our hypothesis. The peak of nematode diversity observed in the Baltic at the border between oxic and anoxic conditions underlines that this biogeochemically active transition zone is attractive for many groups of nematodes under conditions of limited food resources. At the North Sea site, where many specialized species successfully exploit the abundant food in the uppermost sediment layers, the redox discontinuity layer looses relative importance as feeding site and supports a less diverse nematode community. These results demonstrate that generalizations, presented quite often in the literature, stressing the key importance of single factors e.g. sediment grain size, in structuring nematode diversity patterns, should be treated with caution. These patterns are resultant of
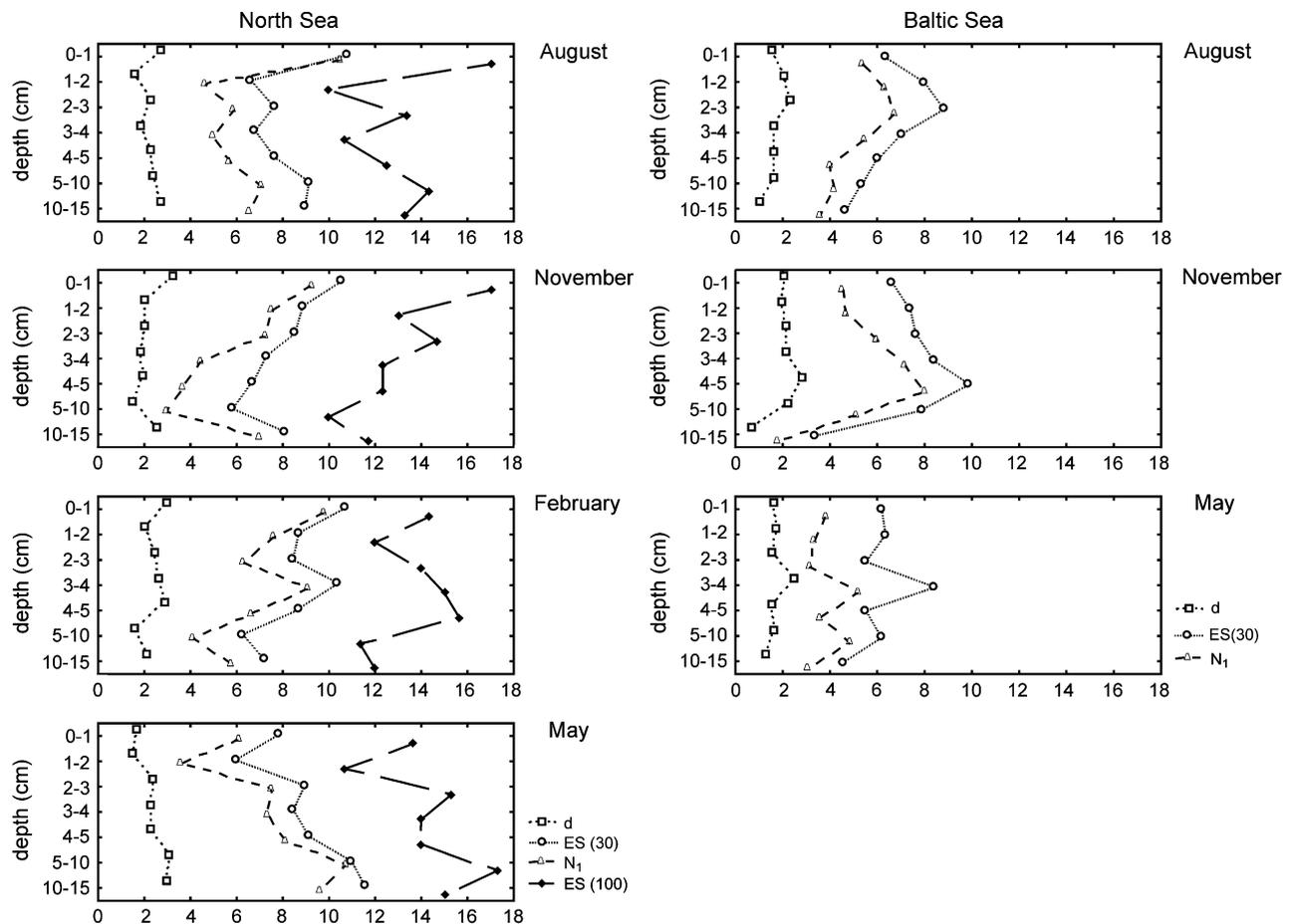
Fig. 8. Vertical patterns of nematode diversity indices (d-Margalef's index; ES(30), ES(100)-expected number of species; N$_1$-Hill's diversity index) at both study sites.

Table 5
Summary of BIOENV results. Environmental variables (x) contributing to subset providing the five best matches (ρ = Spearman's rank correlation) with nematode abundances in different sediment layers in the North Sea

ρ	C	C/N	Ammonium	Mean particle size
August				
0.871	×		×	
0.871	×	×	×	
0.864	×			
0.864	×	×		
0.821	×		×	×
November				
0.769	×		×	
0.768			×	
0.748		×	×	
0.74			×	×
0.738		×	×	×
February				
0.926		×	×	
0.904	×	×	×	×
0.903	×	×	×	
0.888	×		×	×
0.883	×		×	
May				
0.86	×		×	
0.858	×	×		
0.858	×	×	×	
0.851	×			
0.851		×	×	

a complex of both external factors and flexibility and potential of the local community to exploit the environment.

References

Billerbeck, M., Werner, U., Bosselmann, K., Walpersdorf, E., Huettel, M., 2006. Nutrient release from an exposed intertidal sand flat. Marine Ecology Progress Series 316, 35–51.

Blome, D., 1974. Zur Systematik von Nematoden aus dem Sandstrand der Nordseeinsel Sylt. Microfauna des Meeresbodens 33, 77−99.

Blome, D., 1982. Systematike der Nematoda eines Sandstrandes der Nordseeinsel Sylt. Microfauna des Meeresbodens 86. Akademie der Wissenschaften und der Literatur Mainz, Franz Steiner Verlag GMBH, Wiesbaden, 194 pp.

Blome, D., 1983. Ökologie der Nematoda eines Sandstrandes der Nordseeinsel Sylt. Microfauna des Meeresbodens 88, 517−590.

Boggs Jr., S., 1987. Principles of Sedimentology and Stratigraphy. Prentice Hall, New Jersey, 726 pp.

Buchanan, J.B., 1984. Sediment analysis. In: Holme, N.A., McIntyre, A.D. (Eds.), Methods for the Study of Marine Benthos. Blackwell Scientific Publication, Oxford, pp. 41−65.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18, 117−143.

Clarke, K.R., Warwick, R.M., 1994. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Plymouth Marine Laboratory, Plymouth, UK, 144 pp.

Coull, B., 1988. Ecology of the marine meiofauna. In: Higgins, R.P., Thiel, H. (Eds.), Introduction to the Study of Meiofauna. Smithsonian Institution Press, Washington D.C., London, pp. 18−38.

Drgas, A., 1993. Seasonal fluctuation in abundance and taxonomic composition of meiofauna of the Gdansk Basin (Southern Baltic). Bulletin of the Sea Fisheries Institute 128, 17−22.

Emery, K.O., 1968. Relict sediments on continental shelves of world. American Association Petrolium Geologists 52, 445−464.

Elmgren, R., 1978. Structure and dynamics of Baltic benthos communities, with particular reference to the relationship between macro- and meiofauna. Kieler Meeresforschungen 4, 1−22.

Elmgren, R., Hill, C., 1997. Ecosystem function at low biodiversity − the Baltic example. In: Ormond, R.P., Gage, J.D., Angel, M.V. (Eds.), Marine Biodiversity Patterns and Processes. Cambridge University Press, pp. 319−336.

Franke, U., Polerecky, L., Precht, E., Huettel, M., 2006. Wave tank study of particulate organic matter degradation in permeable sediments. Limnology and Oceanography 51, 1084−1096.

Gätje, Ch., Reise, K. (Eds.), 1998. Ökosystem Wattenmeer: Ausstausch-, Transport- und Stoffumwandlungsprozesse. Springer Verlag, Berlin, p. 571.

Gessner, M.O., Inchausti, P., Persson, L., Raffaelli, D.G., Giller, P.S., 2004. Biodiversity effects on ecosystem functioning: insights from aquatic systems. Oikos 104, 419−422.

Gheskiere, T., Hoste, E., Vanaverbeke, J., Vincx, M., Degraer, S., 2004. Horizontal zonation patterns and feeding structure of marine nematode assemblages on a macrotidal, ultra-dissipative sandy beach (De Panne, Belgium). Journal of Sea Research 52, 211−226.

Gheskiere, T., Vincx, M., Urban-Malinga, B., Rossano, C., Scapini, F., Degraer, S., 2005. Nematodes from wave-dominated sandy beaches: diversity, zonation patterns and testing of the isocommunities concept. Estuarine, Coastal and Shelf Science 62, 365−375.

Giere, O., 1993. Meiobenthology, the Microscopic Fauna in Aquatic Sediments. Springer Verlag, Berlin, 273 pp.

Haque, A.M., Szymelfenig, M., Weslawski, J.M., 1997. Small-scale vertical distribution of zoobenthos in the sandy littoral of the Gulf of Gdansk. Oceanologia 39, 433−446.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, E., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Hogberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Korner, C., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Pereira, P.S., Prinz, A., Read, D.J., Scherer-Lorenzen, M., Schulze, E.D., Siamantziouras, A.S.D., Spehn, E.M., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S., Lawton, J.H., 1999. Plant diversity and productivity experiments in European grasslands. Science 286, 1123−1127.

Heip, C., Decraemer, W., 1974. The diversity of nematode communities in the southern North Sea. Journal of Marine Biological Association of United Kingdom 54, 251−255.

Heip, C., Vincx, M., Smol, N., Vranken, G., 1982. The systematics and ecology of free-living marine nematodes. Helminthological Abstracts Series B 51, 1−31.

Heip, C., Vincx, M., Vranken, G., 1985. The ecology of marine nematodes. Oceanography and Marine Biology an Annual Review 23, 399−489.

Heip, C., Herman, M.J., Soetaert, K., 1988. Data processing, evaluation and analysis. In: Higgins, R.P., Thiel, H. (Eds.), Introduction to the Study on Meiofauna. Smithsonian Institution Press, Washington D.C., London, pp. 197−231.

Hendelberg, M., Jensen, J., 1993. Vertical distribution of the nematode fauna in a coastal sediment influenced by seasonal hypoxia in the bottom water. Ophelia 37, 83−94.

Hill, M.O., 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54, 427−432.

Huettel, M., Rusch, A., 2000. Transport and degradation of phytoplankton in permeable sediments. Limnology and Oceanography 45, 534−549.

Huettel, M., Webster, I.T., 2000. Porewater flow in permeable sediment. In: Boudreau, B.P., Jørgensen, B.B. (Eds.), The Benthic Boundary Layer: Transport Processes and Biogeochemistry. Oxford University Press, pp. 144−179.

Huettel, M., Ziebis, W., Forster, S., 1996. Flow-induced uptake of particulate matter in permeable sediments. Limnology and Oceanography 41, 309−322.

Huettel, M., Røy, H., Precht, E., Ehrenhauss, S., 2003. Hydrodynamical impact on biogeochemical processes in aquatic sediments. Hydrobiologia 494, 231−236.

Hurlbert, S.H., 1971. The non-concept of species diversity: a critique and alternative parameters. Ecology 52, 577−586.

Jensen, P., 1984. Ecology of benthic and epiphytic nematodes in brackish waters. Hydrobiologia 108, 201−217.

Jensen, P., 1987. Feeding ecology of free-living aquatic nematodes. Marine Ecology Progress Series 35, 187−196.

Juario, J.V., 1975. Nematode species composition and seasonal fluctuations of a sublittoral meiofauna community in the German Bight. Veröffentlichungen des Instituts fürMeeresforschung in Bremerhaven. Kommissionsverlag Franz Leuwer. Bremen 15, 283−337.

Kinzig, A.P., Pacala, S.W., Tilman, D., 2001. The Functional Consequences of Biodiversity. Princeton Univ. Press, 392 pp.

Li, J., Vincx, M., Herman, P.M.J., Heip, C., 1997. Monitoring meiobenthos using cm-, m- and km-scales in the Southern Bight of the North Sea. Marine Environmental Research 43, 265−278.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294, 804−808.

Lorenzen, C.J., 1967. Determination of chlorophyll and phaeo-pigments: spectrophotometric equations. Limnology and Oceanography 12, 343−346.

Lorenzen, S., Prein, M., Valentin, C., 1987. Mass aggregations of the free-living marine nematode Pontonema vulgare (Oncholaimidae) in organically polluted fjords. Marine Ecology Progress Series 37, 27−34.

Moens, T., Verbeeck, L., Vincx, M., 1999. Feeding biology of a predatory and a facultatively predatory nematode (*Enoploides longispiculosus* and *Adoncholaimus fuscus*). Marine Biology 134, 585−593.

Moens, T., Yeates, G.W., De Ley, P., 2004. Use of carbon and energy sources by nematodes. Nematology Monographs and Perspectives 2, 529−545.

Pallo, P., Widbom, B., Olafsson, E., 1998. A quantitative survey of the benthic meiofauna in the Gulf of Riga (Eastern Baltic Sea), with special reference to the structure of nematode assemblages. Ophelia 49, 117−139.

Platt, H.M., Warwick, R.M., 1980. The significance of free living nematodes to the littoral ecosystem. In: Price, J.H., Irvine, D.E.G., Farnham, W.F. (Eds.), The Shore Environment, vol. 2, Ecosystems. Academic Press, London and New York, pp. 729−759.

Platt, H.M., Warwick, R.M., 1983. Free living marine nematodes. Part I. British Enoplids. In: Kermack, D.M., Barnes, R.S.K. (Eds.), Synopses of the British Fauna (New Series), No. 28. Cambridge University Press, Cambridge, London, New York, New Rochelle, Melbourne, Sydney, 307 pp.

Platt, H.M., Warwick, R.M., 1988. Free living marine nematodes. Part II. British Chromadorids. In: Kermack, D.M., Barnes, R.S.K. (Eds.), Synopses of the British Fauna (New Series), No. 38. E.J. Brill/Dr. W. Backhuys, Leiden, New York, København, Köln, 501 pp.

Precht, E., Huettel, M., 2003. Advective pore-water exchange driven by surface gravity waves and its ecological implications. Limnology and Oceanography 48, 1674—1684.

Prein, M., 1988. Evidence for a scavenging lifestyle in the free-living Nematode Pontonema vulgare (Enoplida, Oncholaimidae). Kieler Meeresforschungen. Sonderheft 6, 389—394.

Rokicka-Praxmajer, J., Radziejewska, T., 2002. Free-living nematodes of the Pomeranian Bay (Southern Baltic). Part 1. A preliminary analysis of nematode variability in an area affected by direct river runoff. Acta Scientiarum Polonorum Piscaria 1, 85—104.

Sanders, H.L., 1968. Marine benthic diversity: a comparative study. American Naturalist 102, 243—282.

Shum, K.T., Sundby, B., 1996. Organic matter processing in continental shelf sediments — the subtidal pump revisited. Marine Chemistry 53, 81—87.

Soetaert, K., Heip, C., 1990. Sample-size dependence of diversity indices and the determination of sufficient sample size in a high-diversity deep-sea environment. Marine Ecology Progress Series 59, 305—307.

Soetaert, K., Vincx, M., Wittoeck, J., Tulkens, M., van Gansbeke, D., 1994. Spatial patterns of Westerschelde meiobenthos. Estuarine, Coastal and Shelf Science 39, 367—388.

Soetaert, K., Vincx, M., Wittoeck, J., Tulkens, M., 1995. Meiobenthic distribution and nematode community structure in five European estuaries. Hydrobiologia 311, 185—206.

Somerfield, P.J., Fonseca-Genevois, V.G., Rodrigues, A.C.L., Castro, F.J.V., Santos, G.A.P., 2003. Factors affecting meiofaunal community structure in the Pina Basin, an urbanized embayment on the coast of Pernambuco, Brazil. Journal of the Marine Biological Association of the United Kingdom 83, 1209—1213.

Steyaert, M., Garner, N., van Gansbeke, D., Vincx, M., 1999. Nematode communities from the North Sea: environmental controls on species diversity and vertical distribution within the sediment. Journal of the Marine Biological Association of the United Kingdom 79, 253—264.

Steyaert, M., Vanaverbeke, J., Vanreusel, A., Barranguet, C., Lucas, C., Vincx, M., 2003. The importance of fine-scale, vertical profiles in characterising nematode community structure. Estuarine, Coastal and Shelf Science 58, 353—366.

Thorson, G., 1957. Bottom communities sublittoral of shallow shelf. In: Hedgpeth, J.W. (Ed.), Treatise on Marine Ecology and Paleoecology. vol. I, Ecology. Geological Society of America — Memoir 67, pp. 461—534.

Tita, G., Desrosiers, G., Vincx, M., Clement, M., 2002. Intertidal meiofauna of the St Lawrence estuary (Quebeck, Canada): diversity, biomass and feeding structure of nematode assemblages. Journal of the Marine Biological Association of the United Kingdom 82, 779—791.

Vanaverbeke, J., Gheskiere, T., Vincx, M., 2000. The meiobenthos of subtidal sandbanks on the Belgian continental Shelf (Southern Bight of the North Sea). Estuarine, Coastal and Shelf Science 51, 637—649.

Vanaverbeke, J., Steyaert, M., Soetaert, K., Rousseau, V., Van Gansbeke, D., Parent, J.Y., Vincx, M., 2004. Changes in structural and functional diversity of nematode communities during a spring phytoplankton bloom in the southern North Sea. Journal of Sea Research 52, 281—292.

Vanhove, S., Arntz, W., Vincx, M., 1999. Comparative study of the nematode communities on the southeastern Weddell Sea shelf and slope (Antarctica). Marine Ecology Progress Series 181, 237—256.

Vincx, M., 1996. Meiofauna in marine and freshwater sediments. In: Hall, G.S. (Ed.), Methods for the Examination of Organismal Diversity in Soils and Sediments. CAB International, Wallingford, UK, pp. 187—195.

Vincx, M., Meire, P., Heip, C., 1990. The distribution of nematodes communities in the Southern Bight of the North Sea. Cahiers de Biologie Marine 31, 107—129.

Warwick, R.M., Platt, H.M., Somerfield, P.J., 1998. Free-living marine nematodes. Part III. Monhysterids. In: Barnes, R.S.K., Crothers, J.H., (Eds.), Synopses of the British Fauna (New Series), No. 53. Field Studies Council, Shrewsbury, 296 pp.

Wieser, W., 1953. Beziehungen zwischen Mundhöhlengestalt, Ernährungsweise und Vorkommen bei freilebenden marinen Nematoden. Arkiv für Zoologi 4, 439—484.