

Nematode communities from the North Sea: environmental controls on species diversity and vertical distribution within the sediment

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Nematode assemblages were sampled seasonally at three subtidal stations along the Belgian coast. The stations were characterized by muddy sediments (station 115), fine sand (station 702) and fine to coarse sand (station 790). The forces structuring vertical distribution were investigated by evaluating abundance, species composition, diversity and trophic composition, and relating these to sediment composition, redox state and food sources.

The nematode assemblages at the two finer grained stations (115, 702) were dominated by *Daptonema tenuispiculum* and *Sabatieria punctata*. For both species, the vertical distribution in the sediment seemed not dependent on the redoxchemistry, as former believed for *S. punctata*, but primarily influenced by food availability. This feature could also be recognized for *Ixonema sordidum* and *Viscosia langrunensis*, the most abundant nematodes at the coarse sandy station (790).

In general, nematode diversity was regulated primarily by sediment granulometry. Coarser sediments (station 790) yielded more diverse communities compared to the fine sediments (station 115, 702), however seasonal fluctuations and variations with depth into the sediment were not obvious. At the silty stations, when the sediment column was more oxidized in March, overall diversity was higher and showed a positive relationship to the mud content which varied with depth into the sediment. This positive relation is probably explained by an enhanced deposition of organic matter associated with the accumulation of fine particles near the river-mouths. Furthermore, the higher abundance, the lower diversity and the higher dominance found at the two silty stations of the eastern and the western part of the Belgian coast, pointed to a stressed, organically enriched environment.

The results demonstrate that controls on nematode community structure are complex and that information at both species and community level are required to properly evaluate the effects of natural and anthropogenic impacts.

INTRODUCTION

Meiobenthos often shows an aggregated spatial distribution within the sediment, both horizontally and vertically. The causes of this patchiness are often complex and involve a variety of biological, physical and chemical variables, including granulometry, salinity, oxygen tension, food availability and chemical compounds in the pore water (e.g. Giere, 1993; Jian, 1993; Ndaró, 1995). The processes that generate and maintain the vertical distribution patterns in different localities are particularly poorly understood and form an important challenge for contemporary ecological research. For nematodes, oxygen and hydrogen sulphide are thought to be of prime importance (Platt, 1977; Giere, 1993; Hendelberg & Jensen, 1993; Wetzel, 1995) at least in shallow waters. Moreover, both of these ecofactors indirectly or directly determine all other biogeochemical characteristics of the sediment such as nutrient concentrations. In addition to these natural variables, anthropogenic impacts, including eutrophication, pollution and physical disturbance, may have a substantial influence on meiofauna, particularly in

coastal areas. As the meiobenthos lives in the interstitial spaces of the sediment, and thus in direct contact with the porewater and its pollutants, the impact of pollution also needs attention when considering the structural forces on the vertical distribution of the meiobenthos.

The present investigation is concerned with nematode communities at three localities on the Belgian coast in the southern part of the North Sea. The main aims are to describe patterns of vertical distribution and species diversity and to relate these patterns to: (1) particular natural environmental parameters including redox chemistry, sediment granulometry, bacterial densities, chlorophyll-*a* concentrations; and (2) the broader question of anthropogenic influences. The results demonstrate that controls on nematode community structure are complex and that information at both species and community level are required to properly evaluate the effects of natural and anthropogenic impacts. Previous studies, addressing nematode diversity and distribution patterns along the Belgian coast include those of Heip et al. (1974, 1983, 1984), Willems et al. (1982) and Vincx et al. (1990a,b).

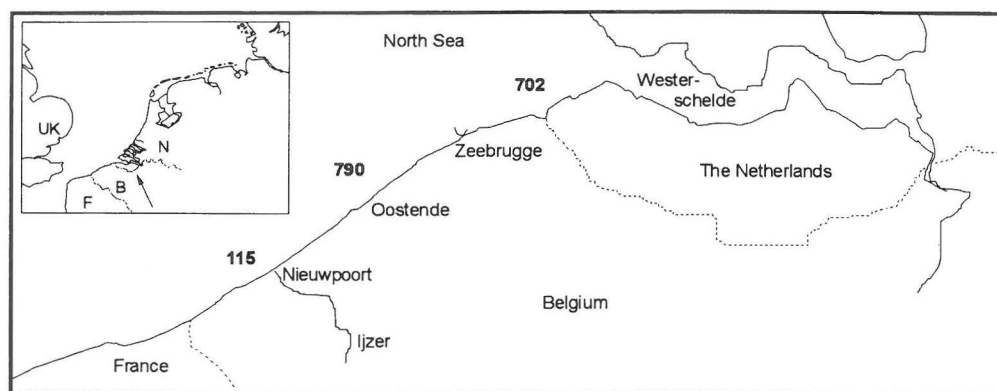


Figure 1. Location of the sampling stations.

THE STUDY AREA

The study sites are located on the Belgian coast in the Southern Bight of the North Sea (Figure 1). This long straight coast, 65 km long, is remarkably free of muddy sediments, except at river mouths. Earlier studies have revealed an extensive development of muddy sedimentation off the eastern Belgian coast, mostly caused by suspended material discharged from the Westerschelde Estuary, as well as by local effluents from the River IJzer. The nematode communities of these silty sediments are much less diverse than those from other areas of the same sediment type in the North Sea and in the rest of Europe, possibly because of higher levels of pollution (Vincx et al., 1989).

The presence of the Westerschelde Estuary seems to induce a gyre off the eastern part of the Belgian coast, where the freshwater from the Westerschelde resides for some time (Nihoul & Ronday, 1975). As a consequence of this current regime, fine polluted material precipitates near the mouth of the Westerschelde (Govaere et al., 1980). During the 1970s and 1980s, nematode communities along the Belgian coast showed a decreasing species diversity towards the Westerschelde mouth (Vincx et al., 1989). The present study describes the nematode community of a station within this impoverished area (Station 702), which has been monitored for almost 20 y (Figure 1, Table 1). At the western end of the Belgian coast, off the Flemish sandbanks, the sediments tended to be more sandy, compared to the eastern zone, during the seventies and eighties. This was reflected in a more diverse nematode association (Vincx et al., 1989). The second station (115) was selected in this western zone, around Nieuwpoort (Figure 1, Table 1). To compare extreme sediment types, a third station (790), which was situated in the central coarse sandy area of the coast, was sampled (Figure 1, Table 1). The present study indicates a major change in nematode diversity trends since the work of Vincx et al. (1989).

Table 1. Sampling sites with the coordinates and the water depth.

Station	Coordinates	Depth (m)
115	51°09.1'N 02°36.1'E	15
702	51°23.2'N 03°19.4'E	10
790	51°16.0'N 02°65.0'E	8

MATERIALS AND METHODS

Sample collecting

The three subtidal stations were sampled seasonally—in March, June and August 1993—to cover the periods of high and low organic input into the sediment. Samples were taken with a boxcorer (surface area 804 cm²) which was subsequently subsampled with Perspex cores (diameter 3.6 cm) on board of the RV 'Belgica'. For all abiotic and biotic determinations, the sediment was divided into ten slices, each 1 cm thick.

Chemical analysis

The redox potential of the first 10 cm was recorded simultaneously with a mV-meter.

For the determination of bacterial abundances two subsamples of 1 ml each were removed from one core and fixed in a 2% formaldehyde solution. To release bacteria from the sediment particles, the samples were sonicated ten times for one second. Subsequently, the bacteria were stained with acridine orange and counted by epifluorescence microscopy, according to the method of Hobbie et al. (1977). Three subsamples were removed from one core and frozen immediately for pigment analysis. In the laboratory, the concentration of chlorophyll-*a* was determined by chromatography, with a Gilson high-performance liquid chromatography-chain, using a slightly modified method of Mantoura & Llewellyn (1983). For the analysis of pore water nutrients, three cores of 6 cm diameter were processed and frozen immediately after slicing. In the laboratory, the samples were passed through Whatman GF/C filters. The concentrations of nitrate plus nitrite and ammonia in the interstitial water were measured through an automatic chain (SAN^{plus} segmented flow analyser, SKALAR). The concentration of important oxidized (nitrate and nitrite) and reduced (ammonia) nitrogen compounds, together with redox potential measurements, were used to evaluate the oxidation status of the sediment. Redox potential values are reported in four classes representing strongly oxidized (>100 mV), oxidized (0 mV < x < 100 mV), reduced (0 mV < x < -100 mV) and strongly reduced sediment (< -100 mV). Triplicate samples were processed with a Coulter Counter LS particle size analyser to measure the median grain size and the fraction of mud (<63 µm).

Table 2. Main characteristics for the three stations (mean values over depth): abundance for March, June and August respectively, abundance and Rank 1 Dominance (RID) (mean values), mud fraction and median grain size (lowest highest value).

Station	Abundance (ind 10 cm ⁻²)	No. of species	RID (%)	Mud (% < 63 µm)	Median (µm)
115	1847,2805,1156	56.0	73.3	36.1–83.6	47.2–143.8
702	270,786,2326	45.0	51.4	5.9–53.3	76.5–198.1
790	141,247,622	98.0	24.7	0.0–0.3	402.5–487.1

Faunal analysis

Triplicate cores were processed for metazoan meiofauna. The sediment slices were fixed in hot (70°C) 4% formaldehyde solution. Meiofaunal organisms passing a 1-mm sieve and retained by a 38-µm sieve were extracted from the sediment by centrifugation with Ludox (Heip et al., 1985). All meiofaunal taxa were counted after staining with Rose Bengal. For each sample, 120 nematodes were picked randomly and mounted on Cobb slides for identification to species level. According to the feeding type classification of Wieser (1953), a distinction is made between selective deposit feeders (1A), non-selective deposit feeders (1B), epistratum feeders (2A) and omnivores (2B). The influence of biogeochemistry on the vertical distribution of the nematodes was analysed seasonally in terms of abundance patterns, dominance and species diversity. Dominance is expressed as the relative abundance of the most abundant species (RID), i.e. the first point on a k-dominance curve (Lambshead et al., 1983). The diversity is expressed as the N₁ diversity index (Hill, 1973) which is a normalization of the Shannon–Wiener index H and recommended for meiofaunal assemblages by Heip et al. (1988). It summarizes the structure of the community, taking into account the most common as well as the most rare species. Because diversity indices are dependent on the sample size as well as on the number of analysed species, N₁ values are given as the means of three replicates, rather than being calculated from the sum of three replicates. This allowed comparison with earlier research on the Belgian coastal zone. The distribution patterns of the most abundant species were followed during the field study. Non-parametric Spearman rank correlation coefficients were calculated ($P < 0.05$) to determine a relationship between diversity and environmental variables along a depth gradient.

RESULTS

The main characteristics of the nematode assemblages and the abiotic environments are summarized in Table 2.

The abiotic environment

Station 115 had fine sediments with a higher percentage of mud compared to other stations. Redox potential profiles and nitrogen compounds indicate that the top 5 cm of the sediment in winter or early spring was oxidized (Figure 2). The sediment was nearly anoxic from the top downwards in June and returned back to a somewhat less reduced situation in August. Figure 3 shows the vertical distribution of bacterial densities and chlorophyll-*a* content. The chlorophyll-*a* concentration remained very

low during March compared to June and August, when a gradual decrease within depth is recorded. The bacterial densities were greatest in deeper sediment layers in March, while in June and August, the densities were highest in the surface layer and decreased gradually within depth.

Sediments at station 702 consisted mainly of fine sand with a low mud content. The sediments were fully oxidized in March with nitrate concentrations not lower than 0.035 mmol l⁻¹ and very low ammonia concentrations (<0.078 mmol l⁻¹) (Figure 4). An intermediate situation existed in June with only the upper 3 cm oxidized and lower layers strongly reduced. In August, however, the sediment was completely reduced. Zones of higher redox potential shown in Figure 4 may be related to burrows. No positive redox potential values were measured and the ammonia concentrations were extremely high (up to 4.09 mmol l⁻¹). The chlorophyll-*a* concentrations were rather low in March and June (Figure 3). Concentrations were higher in August, and fluctuated considerably with depth. The bacterial profiles were similar to those of station 115, apart from the higher densities in March compared to those in June and August.

At station 790 the sediment consisted of fine to coarse sand, almost devoid of mud and characterized by large interstitial spaces. Redox potential values were mostly positive (Figure 5) and nitrogen compounds exhibited a fairly stable seasonal depth pattern. Chlorophyll-*a* concentrations were rather low and constant with depth in March. In June, the pigment concentration started to increase within the upper sediment layers, and reached the highest values in August. However, in August, pigment maxima shifted towards deeper sediment layers. Bacterial densities showed the same pattern as at the other two stations. However, the difference in overall density between March on one hand, and June and August on the other hand, were more obvious.

Density and faunal composition

Based on mean total densities, a clear distinction could be made between the three subtidal stations (Figure 6). Highest abundances were recorded in station 115, especially in June. At station 702 lower abundances were found, except for the very high August value. The meiofauna exhibited lowest values in station 790. Here, as well as at station 702, densities increased from March to August.

Average relative abundances of species constituting >1% of the fauna at the three stations are shown in Table 3. *Sabatieria punctata* was most abundant at the fine sandy, subtidal stations (115 and 702), followed by *Daptonema tenuispiculum*. In the coarse sandy station (790), *Ixonema sordidum* was the most important species, followed

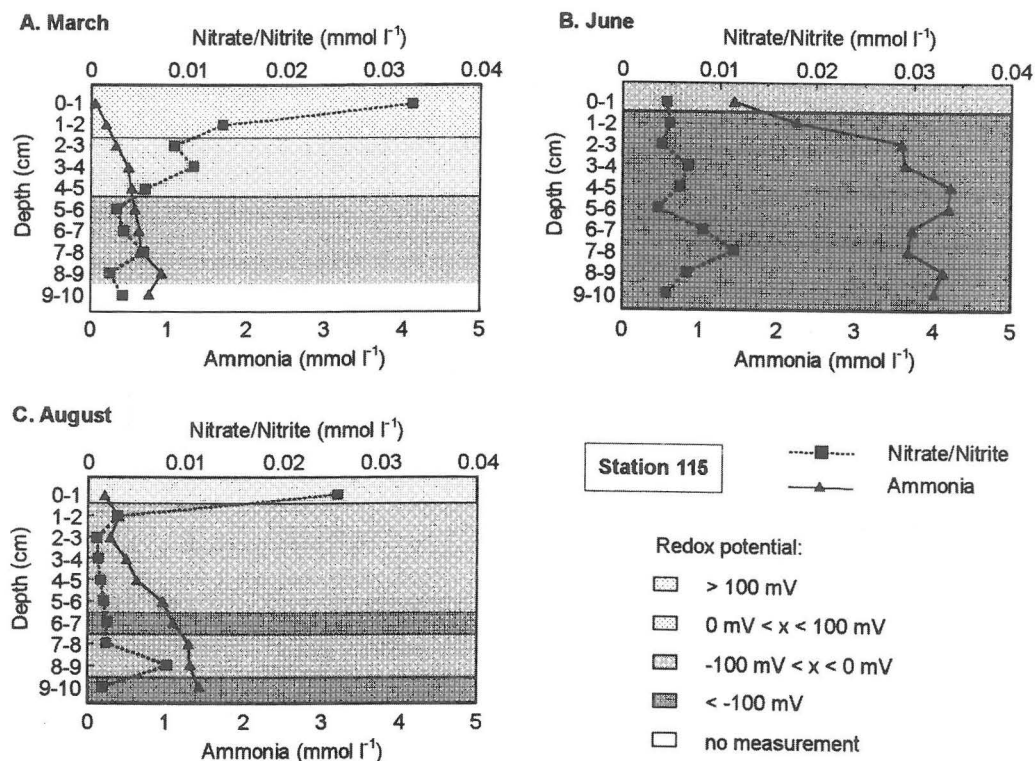


Figure 2. Redox potentials and nitrogen compounds at station 115.

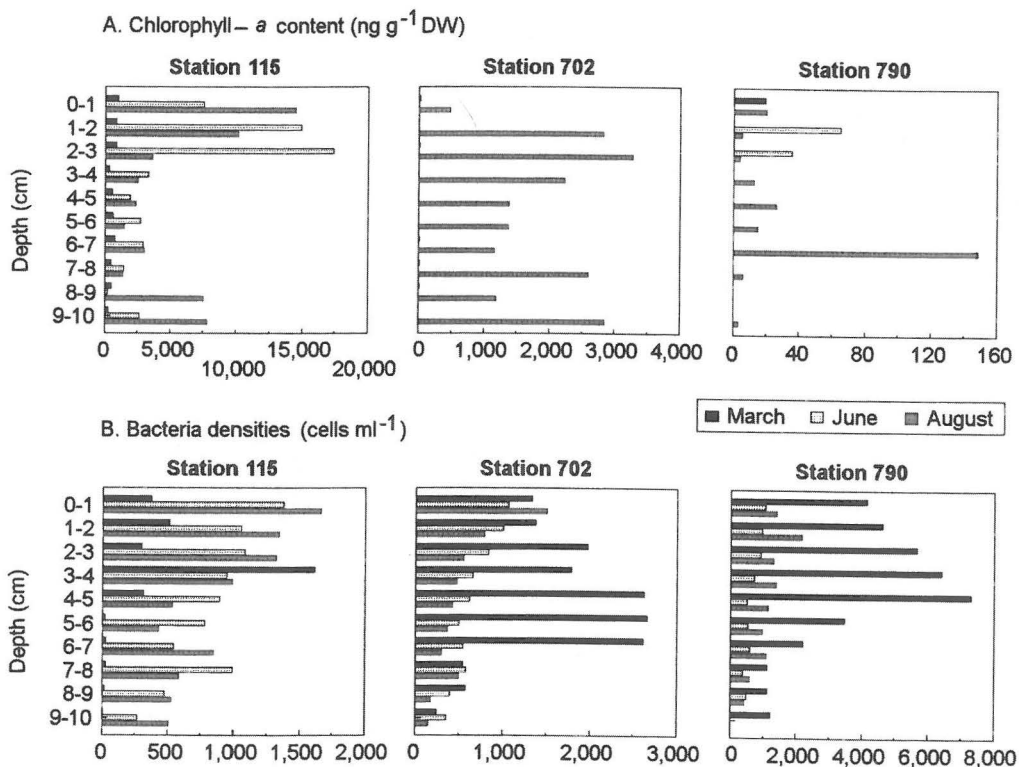


Figure 3. Chlorophyll-*a* concentrations and bacterial density.

by *Rhynchonema quemer* (Boucher, 1974), *Viscosia langrunensis* and *Neochromadora hyalocheile*. Except for *V. langrunensis*, which has also been recorded in station 702, these species were found only at Station 790.

Stations 115 and 702 were dominated (>80%) by non-selective deposit feeders (1B), whereas at Station 790 the epistratum feeders (2A) formed the most important trophic group (>40%; Table 3).

Diversity and dominance

In total, 56 species were found at station 115, 45 species at station 702 and 98 species at station 790. Rank 1 dominance (RID) values were higher at stations 115 (73.3%) and 702 (51.4%) than at station 790 (24.7%). The overall species diversity (N_1) was similar at both muddy to fine sandy stations (115 and 702), but lower than June and

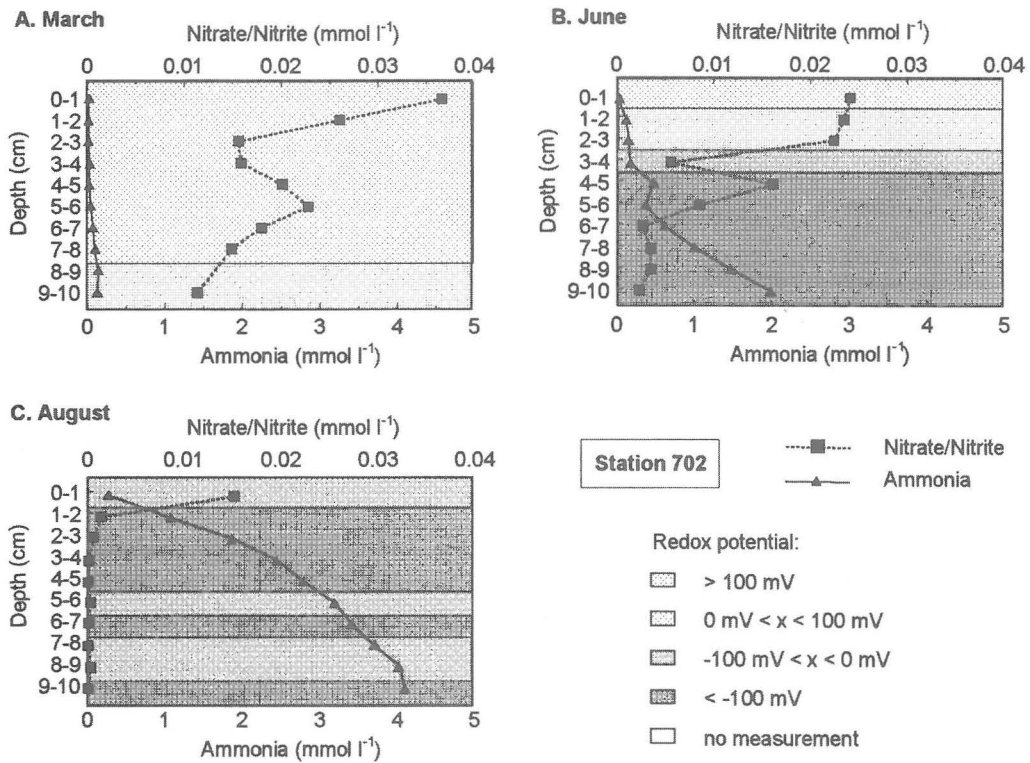


Figure 4. Redox potentials and nitrogen compounds at station 702.

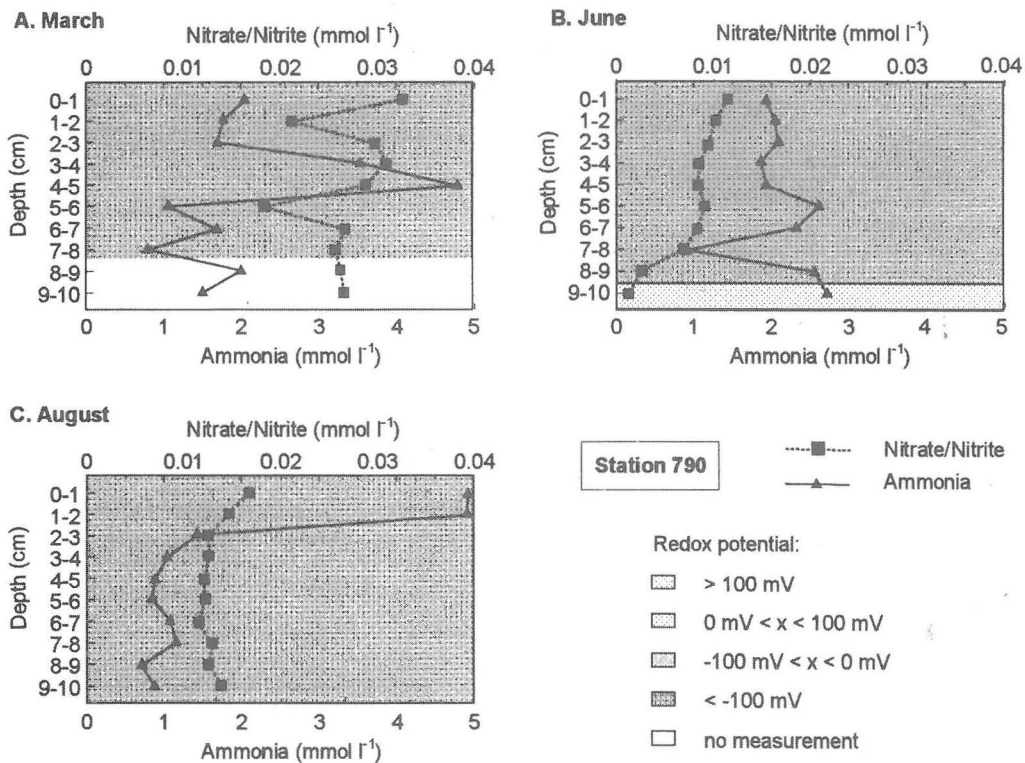


Figure 5. Redox potentials and nitrogen compounds at station 790.

August values at station 790, where the sediment consisted of coarse sand (Figure 7). At the former two stations, the highest species diversity was recorded in March and the lowest in August. This contrasts with station 790, where diversity levels increased from March to August.

Vertical trends within the sediment

Abundance trends

The vertical distribution of nematodes within the sediment varies between stations and seasons. At Station 115, nematodes were most abundant at 3–4 cm depth

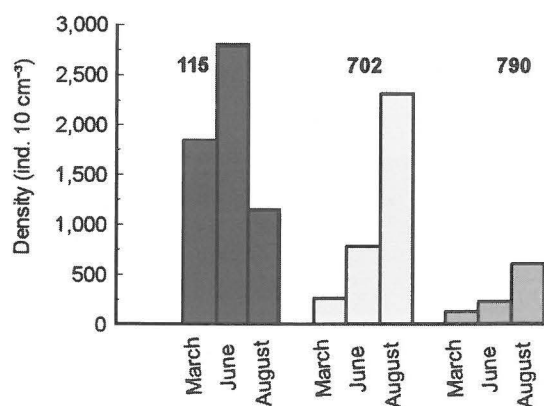


Figure 6. Mean total densities.

during the three sampling periods. Except in June, when the sediment column was most strongly reduced, a second peak was developed at the surface. At Station 702, densities were rather low and nearly constant with depth in March, but higher during June and August, reaching maximum values in subsurface sediment layers (1–2 cm) and thereafter decreasing gradually with depth. At station 790, nematode abundance was low and constant with depth in March whereas in June, there was a clear decrease with depth. In August, there was no distinct trend.

Table 3. Composition of nematode assemblages at subtidal stations (115, 702 and 790).

Species	Trophic group (Wieser, 1953)	Relative abundance of most important species (>1%)		
		Station 115	Station 702	Station 709
<i>Ascolaimus elongatus</i>	1B	2.1	7.7	
<i>Chromadorina demani</i>	2A			2.4
<i>Cyartonema elegans</i>	1A			3.0
<i>Daptonema</i> sp.	1B	5.3		1.1
<i>Daptonema normandicum</i>	1B	2.3		
<i>Daptonema tenuispiculum</i>	1B	6.5	11.2	
<i>Daptonema trichinius</i>	1B		1.6	
<i>Desmodora</i> sp.	2A			1.3
<i>Desmolaimus zeelandicus</i>	1B		1.1	
<i>Enoploides</i> sp.	2B			2.9
<i>Ixonema sordidum</i>	2A			24.7
<i>Metalinhomoeus</i> sp.	1B	2.3		
<i>Microlaimus</i> sp.	2A			1.5
<i>Microlaimus conothesis</i>	2A			2.2
<i>Neochromadora hyalocheile</i>	2A			7.1
<i>Odontophora phalarata</i>	1B		2.2	
<i>Onyx perfectus</i>	2B			1.6
<i>Paracanthochus</i> sp.	2A		1.0	1.8
<i>Rhynchonema quemer</i>	1B			8.1
<i>Richtersia</i> sp.	1B		1.5	
<i>Richtersia inaequalis</i>	1B		7.2	
<i>Sabatieria punctata</i>	1B	73.3	51.4	2.4
<i>Sigmophoranema rufum</i>	2B		1.6	1.7
<i>Spirinia parasitifera</i>	2A	1.3		
<i>Syringolaimus</i> sp.	2B		1.8	1.5
<i>Syringolaimus caspedum</i>	2B			2.8
<i>Tubolaimoides</i> sp.	1A			4.1
<i>Viscosia langrunensis</i>	2B		4.4	7.9
<i>Xyala imparis</i>	1B			1.9
Total		93.1	92.6	80.1

Diversity trends

At station 115 in March, N_1 diversity decreased down to 8 cm depth below which an abrupt increase occurred to a level even higher than in the top centimetre (Figure 7). These higher N_1 values were attributed to five species, *Daptonema normandicum* (de Man, 1890), *Leptolaimus* sp. (de Man, 1876), *Metalinhomoeus* sp. (de Man, 1907), *Microlaimus conothesis* (Lorenzen, 1973) and *Molgolaimus cuanensis* (Platt, 1973), which became more important in these deep sediment layers. A positive correlation between N_1 species diversity and the mud content (<62 μ m fraction) of different layers could be demonstrated using a Spearman rank test (Figure 8, Table 4). There was a similar trend between the diversity of non-selective deposit feeders and the amount of mud in the sediment (Table 5). In June and August, diversity decreased with depth at this station, showing a sharp contrast between the first centimetre and the remainder of the sediment column, where the diversity was much lower.

Sediment samples obtained from station 702 in March exhibited a high degree of oxidation and a very gradual decrease in N_1 species diversity with depth (Figure 7). Here, too, a positive correlation could be found between N_1 values and mud fraction (Table 4). In June, the overall diversity pattern with depth at this station resembled that of station 115 in June and August. Only species diversity of non-selective deposit feeders, the dominant trophic

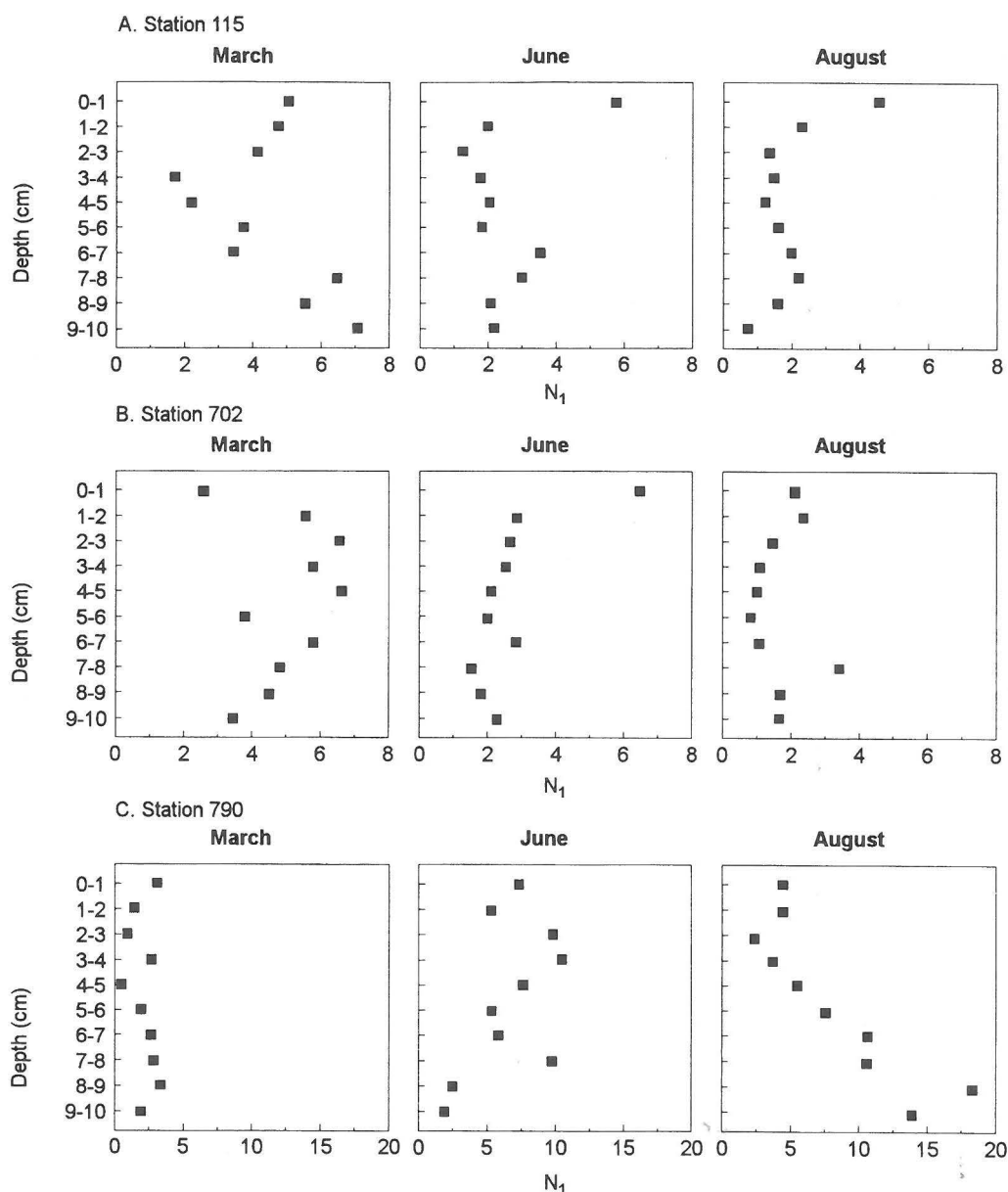


Figure 7. Variability of N_1 species diversity in each station (average of three replicates).

group of station 702, was positively correlated with the redox potential (Table 5). In August, when the sediments at station 702 were most strongly reduced, a nearly constant, low species diversity prevailed throughout the sediment, except at 7–8 cm depth, where a peak of higher diversity could be noticed. Although this higher diversity coincided with a higher redox potential, no correlation with any measured abiotic factor could be established.

At station 790, species diversity levels remained relatively low and nearly constant with depth in March and were not correlated with any abiotic factor. However, diversity of epistratum feeders was positively correlated with chlorophyll-*a*, suggesting a relation with food resources. The fluctuating pattern in species diversity which was found in June, could not be linked to any measured abiotic factor. In August, an extraordinary increase in species diversity with depth occurred. This trend was also reflected in the species diversity of different trophic groups. Thus, negative correlations with bacteria densities were found between N_1 species diversity of the total community, N_1 diversity of epistratum

feeders and, somewhat surprisingly, N_1 diversity of non-selective deposit feeders (Tables 4 & 5).

Species distribution

The depth distribution of the most important species, *S. punctata*, *D. tenuispiculum*, *I. sordidum* and *V. langrunensis* are summarized in Figure 8. *Viscosia langrunensis* is included in this list of species because it is particularly abundant in one sampling period.

The highest overall abundances (total sediment column) of *D. tenuispiculum* and *S. punctata* were recorded in June at station 115 and August in station 702, when sediments at these stations were most reduced (Figures 2, 4, 8). Extremely low abundances were recorded for both species at station 702 in March, when sediments were highly oxidized. Despite their fluctuating abundance, the two species exhibited similar distribution patterns with depth at both stations and during different seasons, apart from the aberrant March sample from station 702

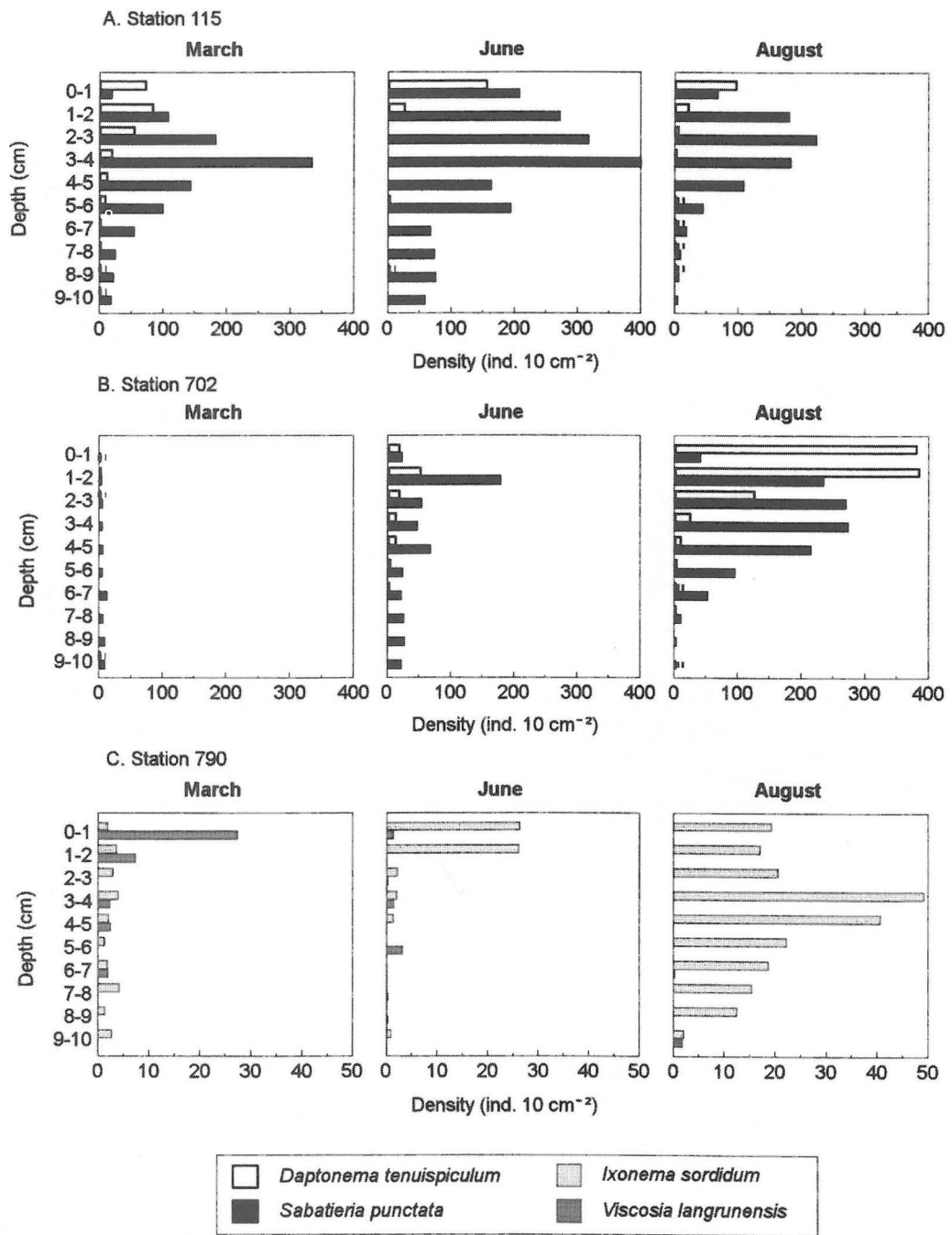


Figure 8. Depth distribution of *Daptonema tenuispiculum*, *Ixonema sordidum*, *Sabatiera punctata* and *Viscosia langrunensis*.

Table 4. Spearman rank order correlations. Only significant correlations of the different sediment layers between species diversity (N_1) of total nematode community and particular environmental factors are shown.

Station	Month		Spearman (r)	P-level
702	March	% mud	0.661	0.04
	June	% mud	0.744	0.01
		Ammonia	-0.709	0.02
115	March	% mud	0.915	0.0002
790	August	Bacteria	-0.855	0.002

when abundance were too low to determine patterns reliably. The maximum densities for *D. tenuispiculum* always occurred in the surface layers. From 3 to 4 cm downwards, densities were halved or even reached zero. Only in two cases, March at station 115 and August at station 702, were significant correlations found with redox compounds. Concerning other variables, the only other correlation was a positive one with bacteria densities for August at station 702. *Sabatiera punctata* appears to penetrate deeper into the sediment; highest densities were found from 3 to 4 cm depth. The only significant correlation was found with the sediment mud content for August at station 702.

Table 5. Spearman rank order correlations. Only significant correlations of the different sediment layers between species diversity (N_1) within trophic groups and particular environmental factors are shown.

Station	Month	Feeding type		Spearman (r)	P-level
702	June	1B	Redox potential	0.786	0.04
			Nitrate/nitrite	0.644	0.04
			Ammonia	-0.673	0.03
115	March	1A	% mud	0.720	0.03
790	March	2A	Chlorophyll- <i>a</i>	0.937	0.00006
	August	1B	Bacteria	-0.879	0.0008
		2A	Bacteria	-0.891	0.0005

Table 6. Diversity of the eastern and the western Belgian coast.

	Eastern		Western	
	June 1977	June 1993 This study	June 1977	June 1993 This study
N_1 diversity	1.79	3.89	8.61	3.44
Number of species (per 10 cm ⁻²)	4	23	19	26
Number of individuals (per 10 cm ⁻²)	45	740	98	2573

The two most abundant species at the coarse sand station (790), *I. sordidum* and *V. langrunensis*, constitute a lower proportion of the total fauna at that station, than do *D. tenuispiculum* and *S. punctata* at the fine sand stations (Figure 8). The density of *I. sordidum* was mostly low, particularly in March. However, in June samples, the density of this species was six times higher in the upper 2 cm than in deeper layers, while in August samples it exhibited a peak at a depth of 4–5 cm. For *V. langrunensis*, on the other hand, abundance was high in the upper layers of samples obtained in March, but a constant low abundance prevailed otherwise. Though the oxidation state of the sediment at station 790 did not show any obvious seasonal fluctuations, an apparent periodicity existed in the depth distribution of both species. This could not be attributed to any single abiotic factor measured in this study.

DISCUSSION

Limitation of the data set

At a particular station, characterization of the nematode fauna during each month (May, June, August) was made on three subcores. However, the sets of subcores were not strictly replicates since they were each taken from a simple boxcore. Hurlbert (1984), discussing pseudoreplication vs the design of ecological field experiments, stated that replication reduces the effects of 'noise' or random variation or error, thereby increasing the precision of an estimate, e.g. the mean of a treatment or the difference between two treatments. On the other hand pseudoreplication was defined as the use of inferential statistics to test for treatment effects with data from experiments where either treatments are not replicated (though samples may be) or replicates are not statistically independent. In the case of this study, pseudoreplicates

are justified because the mathematical analysis adopted did not demand statistical independent samples.

The aim of this study was to establish microscale vertical distribution patterns in relation to different biogeochemical variables. To do this, replicates of the same sediment type, from the same micro environment were needed. Although the Belgian coastal zone is, in general, rather fine grained, compared to the offshore North Sea, the sediment granulometry within this narrow zone is heterogeneous and variable, especially in highly dynamic regions such as the Westerschelde mouth. Only sampling on a detailed horizontal scale, i.e. within one boxcore, ensured uniformity of sediment type at each station. This is the most important reason why the boxcore, as a treatment, could not be replicated. It should also be noted that a total 10,800 nematodes (3 stations \times 3 subsamples \times 10 slices \times 120 nematodes) were separated and identified, which obviously indicates the enormous cost of analysing vertical distribution patterns of nematodes at species level.

Controls on species vertical distribution profiles

Literature data on the autoecology of *Daptonema tenuispiculum*, *Ixonema sordidum*, *Sabatieria punctata*, *Viscosia langrunensis*, and indeed of most free-living nematode species, are very scarce. However, *D. tenuispiculum* and *S. punctata*, both non-selective deposit feeders, are known to be typical of silty sediments. They are eurytopic species, which can tolerate unstable, highly polluted environments (Vincx, 1989; Heip et al., 1990; Vanreusel, 1991). This study suggests *D. tenuispiculum* to be a typical surface dweller which is not affected by the redox state. *Sabatieria pulchra* (Schneider, 1906), a brackish water species related to *S. punctata* (Vincx, 1986; Jensen, 1981), is also very abundant in disturbed environments, independent of the sediment composition. Several authors have suggested

that *S. pulchra* is physiologically well-adapted to stressed conditions (Heip & Decraemer, 1974; Tietjen, 1980; Heip et al., 1984; Jensen, 1984). It can even survive as a facultative anaerobic species in deoxygenated sediments (Jensen, 1984). However, it is incorrect to state that *Sabatieria* spp. in general exhibit tolerance to long periods of anoxia (Hendelberg & Jensen, 1993). Based on morphological characteristics and microhabitat preferences, a distinction can be made between a *S. pulchra* group and a *S. ornata* (Ditlevsen, 1918) group. The *S. pulchra* group consists of *S. pulchra*, *S. punctata*, *S. granulosa* (Vitiello & Boucher, 1971) and *S. claviculata* and lives in reduced sediments, while the *S. ornata* group consists of *S. ornata*, *S. proabyssalis* (Vitiello & Boucher, 1977) and *S. abyssalis* (Filipjev, 1918) and is limited to oxidized sediments. Furthermore, some authors found that *S. pulchra* and closely related *Sabatieria* species living in muddy sediments had their population maximum at the RPD-layer (Jensen, 1981; Bouwman et al., 1984; Platt & Lamshead, 1985; Jensen et al., 1992). The present study shows that *S. punctata* is able to penetrate deep into the sediment, having its highest density at a depth of 3–4 cm in both reduced and oxidized sediments. The vertical distribution of this species into the sediment seems to be dependent on food availability, rather than on oxygen concentrations. Clearly, *Sabatieria* spp. display a range of ecological preferences, making identification at the species level essential.

The distribution profiles of *I. sordidum* and *V. langrunensis* could not be linked to any measured geochemical characteristic. On the other hand, similar seasonal fluctuations in *I. sordidum* densities and the chlorophyll-*a* content of the sediment suggest a close relationship between the species distribution and the availability of food sources. Before the spring bloom, both were rather uncommon. In June, as algal concentrations in the sediment started to increase, *I. sordidum* became more abundant and reached highest densities in late summer (August), when algae were most abundant. However, it is interesting to note that the maximum abundances of chlorophyll-*a* and *I. sordidum* within the sediment profile do not coincide in August. This may be because these nematodes avoid competition for food and space in densely populated sediment layers rich in algae. *Ixonema sordidum* is a rather small nematode, which can move easily within the interstitial spaces. Furthermore, its cuticle is always covered with agglutinated grains and presumably also food particles such as algae. This suggests that it is able to 'carry' its own food reserve to sediment layers where competition from other meiofaunal organisms is less intense.

Controls on diversity

Stations 115 and 702 had similar sedimentological characteristics. As eutrophication will be indirectly reflected through the redoxstate of the sediment, the seasonal samples collected at these stations can be arranged in the following order ranging from low to high eutrophication impact: March, August, June (Station 115), March, June, August (Station 702). In general, station 115 was less reduced than station 702 and the situation in June at station 115 was comparable to the situation in August at station 702.

With these characteristics in mind, three models relating diversity to the redox state of silty sediments, can be put forward.

- (1) In strongly oxidized sediments (March at stations 115 and 702), an obvious positive correlation existed between mud content of the sediment and N_1 diversity of nematodes. This positive correlation could also be recognized for N_1 species diversity within non-selective deposit feeders (Station 115)
- (2) In oxidized sediments, with the redox potential discontinuity layer (RPD layer) situated somewhat higher in the sediment column (June at station 702), N_1 diversity was coupled both onto mud content and ammonia concentrations. Furthermore, there is a relation between N_1 values of non-selective deposit feeders and the redox state of the sediment
- (3) In reduced sediments with an oxidized layer of only about 1 cm (June and August at station 115 and August at station 702), N_1 values were always low and were not influenced by sediment grain size or by redox values.

Although a relationship between species diversity and sediment grain size has been suggested many times in the literature, some controversy about this issue still exists. Heip & Decraemer (1974) found that nematode species diversity was positively correlated with median grain size and negatively correlated with the silt-clay content of the sediment. They ascribed this to the wider range of microhabitats available for meiofauna in sandy sediments compared to muddy sediments. These findings were confirmed by several other authors (see Giere (1993) for an overview), and are consistent with the observation that overall species diversity is higher at the coarse sand station (790) than at the finer grain stations (115, 702). However, the present study suggests that the opposite trend between species diversity and mud content of the sediment may occur within individual cores, especially in oxidized sediments, since N_1 values were positively correlated with the mud content at both silty stations in March and at Station 702 in June. The contrast between this result and the conclusions of the previous authors may arise from differences of scale. Earlier studies considered diversity differences between localities, while this study addresses variations within the sediment.

When interpreting a correlation between two variables, for example, the diversity of non-selective deposit feeders and the mud content of the sediment, one has to be aware that a significant mathematical relation between both does exist. However, in themselves, correlations do not prove the existence of any causal connection between two variables. The accumulation of mud could be associated with a variety of unknown environmental factors which create a highly favourable habitat for the non-selective deposit feeders. The sediment may have become finer grained because of the enhanced deposition of organic matter which, in turn, could explain the diversification of non-selective deposit feeders. In this sense mud would have an indirect effect on the non-selective deposit feeders.

Diversity in the strongly reduced silty sediments was low and not related to any of the redox components of the

pore water. A plausible explanation is that only a few species can tolerate these conditions. Alternatively, the biochemical composition of the pore water may change over relatively short periods leaving the meiofauna out of phase with the changes.

The coarse sandy sediment of station 790 had a minute fraction of mud which implied the existence of large interstitial spaces, deep oxygen penetration, and a relative stable redox chemistry spatially (with depth) as well as seasonally. Consequently, the nematode fauna at this site was highly diverse and the vertical distribution of species was not affected by redox processes.

Anthropogenic effects and spring bloom food inputs

Hitherto, the nematode fauna of the eastern Belgian coast (Westerschelde Estuary) has been considered poorer (less diverse) than the fauna of the western part of the Belgian coast Vincx et al. (1989). The present study, however, suggests that a shift to an enriched nematode assemblage near the Westerschelde Estuary has occurred over a period of almost 20 y, as indicated by enhanced species diversity values (Table 6). On the other hand, the nematode fauna of the western part of the Belgian coast (Station 115) clearly shows a decreasing trend in N_1 diversity, presumably related to the presence of finer sediments. The changes in sediment types along the Belgian coastal zone is probably the result of the transport of sediments by current activity (Anon., study IHE-BMM, 1993). In addition, the sediment in this region became finer-grained during a period of 1979–1993, probably as a result of dredging activities (Vyncke, 1994).

The nematode association is more diverse at station 790 than at stations 115 and 702. This is certainly the result of differences in sediment granulometry (see above). However, features such as higher abundance, fewer species, higher dominance (RID) and lower N_1 diversity at stations 115 and 702 (Table 2) suggest a close association with stressed, organic enriched environments. As both silty stations are located close to the mouths of highly polluted rivers (Westerschelde, IJzer), the influence of eutrophication on the vertical structure of nematode communities is important at both the eastern and western ends of the Belgian coast. Assuming a seasonally constant input of anthropogenic organic pollutants, the nematode fauna will be most affected in early spring, before the onset of the spring bloom. In this strongly oxidized situation, diversity of the nematode community seems not to be dependent on the redox chemistry of the sediment. However in early summer, after an increased sedimentation of nutrients, originating both from anthropogenic and natural sources, the reduced sediment layer slightly shifts towards the surface, influencing the distribution of nematodes and causing a decrease in species diversity. A tight coupling of the vertical distribution of a nematode assemblage to seasonal hypoxic bottom water was also observed by Hendelberg & Jensen (1993) in sediments from a muddy, sheltered bay at the Swedish west coast. As a consequence of oxygen deficiency and sulphide poisoning induced by hypoxic bottom waters during late summer, a mortality of the surface fauna and an upward migration by the subsurface fauna were observed.

CONCLUSIONS

This study of nematode communities at three different sites on the Belgium coast leads to the following conclusions.

- (1) Caution must be exercised when lumping *Sabatieria* spp. into groups according to their morphological characteristics and their affinity for a certain redox state. *Sabatieria punctata*, a species classified previously within the *S. pulchra* group which is considered to be associated with reduced sediment layers, was abundant in oxidized as well as in reduced sediment layers. The vertical distribution patterns of *Daptonema tenuispiculum*, *Ixonema sordidum* and *Viscosia langrunensis* also show no relation to redox chemistry. It is suggested that food sources have a more important impact on the vertical distribution of *S. punctata* and *I. sordidum*.
- (2) A comparison of the three stations confirms the important influence of sediment granulometry on the diversity of nematode communities. Coarser sediments give rise to a more diverse nematode community, while finer grained sediments are associated with reduced diversity. However, diversity profiles within individual cores indicate that this relationship is not necessarily valid at small spatial scales. These profiles showed the inverse relationship, i.e. the finer the sediment becomes, the more diverse the nematode community, especially the non-selective deposit feeders. This may be explained by an enhanced deposition of organic matter associated with fine grained sediments. In the case of coarse sediments with large, well aerated interstitial spaces, the diversity is high and rather constant with depth and not affected by the redox state of the sediment.
- (3) There have clearly been major shifts in the diversity of nematode communities since the work of Vincx et al. (1989). These changes are attributed to a fining of the sediment due to sediment transport, pollution effects and dredging activities.
- (4) Anthropogenic impact on the whole community along the Belgium coast is reflected in the species diversity of nematode communities. In early spring, before the algal bloom, the sediment pore waters were strongly oxidized, allowing the development of high species diversity deep into the sediment. In these situations, diversity was higher in deeper, muddy sediment layers because of the diversification of non-selective deposit feeders. In early summer, as the sediment became more reduced, diversity values decreased with depth. This could be attributed to more favourable redox conditions in the superficial layers, enabling more species to coexist. For the purpose of assessing anthropogenic impacts, the distribution profiles of single nematode species were much less informative than information on diversity profiles of the whole nematode community. The use of nematodes as ecological indicator still remains highly problematic.

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