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Spatial Patterns of Westerschelde Meiobenthos

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The meiobenthic fauna of the Westerschelde, a highly polluted and physically disturbed estuary in the south-west Netherlands, was investigated. Samples were taken in spring from six transects, including the intertidal, subtidal and channel area, and located along the salinity gradient. The samples were subdivided into slices to examine the vertical distribution of meiobenthos. Meiobenthos densities were higher in the intertidal than in most permanently submersed areas; the subtidal sites below 7 salinity were nearly devoid of meiobenthic life. Nematodes were by far the most abundant meiobenthic organisms in the intertidal, but were less dominant in the other areas. Gastrotrichs, turbellarians, copepods and large ciliates were usually more numerous in the subtidal and channels compared to the intertidal, both in relative and absolute terms. Vertical distribution of the meiobenthos was rather heterogeneous. Most intertidal stations exhibited a subsurface density peak, whereas in the subtidal and channel area, both subsurface and surface maxima were found. The nematode fauna was examined in more detail and the distributional characteristics of the most important species, with respect to salinity, grain size, water depth and sediment depth were reported. The majority of species had their centre of distribution in the intertidal, although some extended substantially into the subtidal zone. Only a few species had a predominantly subtidal distribution. Most nematode species penetrated relatively deep into the sediment and only some species were real surface dwellers. The nematode diversity per unit of surface reflected more or less the density differences and was higher in the intertidal than in the subtidal sites within a comparable salinity regime. When expressed per common number of individuals, however, there were no differences in diversity in the different areas. Canonical correspondence analysis showed sediment depth to be as important as water depth, salinity or sedimentary characteristics in the determination of community structure. Intertidal communities exhibited a well-developed community gradient with depth into the sediment, whereas the vertical structure of subtidal and channel stations was different from the intertidal zonation and in some cases showed a distorted pattern. This was probably caused by sediment disturbance due to higher current velocities and

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dredging activities in these regions. It is argued that, although at some subtidal sites a characteristic subtidal nematode population may persist, in many cases the sublittoral of the Westerschelde is either too dynamic an environment or food availability is too low to meet requirements for growth and reproduction of the nematodes. The populations are probably not self-sustaining but persist due to continuous replenishment from less harsh areas by means of the estuarine circulation.

Introduction

The Westerschelde is the only remaining true estuary of the Dutch delta and it is subjected to a large input of, mainly untreated, industrial and domestic wastes. It is also the site of intense dredging and dumping activities (Heip, 1989).

Benthic organisms are especially vulnerable to all kinds of disturbances. Many contaminants typically end up in the sediment where they may persist for a long period of time and can be incorporated into the benthic organisms. Physical disturbances of natural (tides, waves, storms) and of man-made origin (dredging) will have an effect on the benthos. Dredging mainly affects benthic animals in the channels, where sediment is extracted, and in the vicinity of the major dump sites, where they could suffer from increased sedimentation. However, the usefulness of the benthos as indicators of disturbances may be hampered by the great spatial and temporal variability that these organisms usually exhibit (Heip *et al.*, 1985; Coull, 1988) and which in part reflects the variability of the habitat.

Estuaries have strongly pronounced gradients of various characteristic substances and typically show a large temporal variability in these gradients. The most obvious is the salinity gradient, and many abiotic factors (nutrients, suspended matter) change in parallel with this. Several geomorphological benthic structures result from the interplay of the topography and differential action of currents and wind-induced waves: intertidal flats which are semi-diurnally flooded are the sites of a more intense sedimentation; the bottom of the subtidal areas and channels is subjected to a resuspension–sedimentation cycle related to tidal currents. These currents are especially strong in the deeper channels, and along their edges most dredging activities take place in the Westerschelde. However, the most pronounced gradients occur vertically into the sediment and the meiofauna species composition and abundance can be substantially different even over a depth of a few centimetres (Joint *et al.*, 1982; Jensen, 1983).

Despite its evident importance, there are remarkably few studies of estuarine meiobenthos that cover both a wide range of salinity regimes and of benthic morphological units (Gerlach, 1953; Riemann, 1966; Warwick, 1971; Van Damme *et al.*, 1980, 1984; Bouwman, 1983; Smol *et al.*, 1994). Some meiobenthic studies were restricted to only a few estuarine sites along the salinity gradient (Capstick, 1959; Warwick & Gee, 1984; Austen & Warwick, 1989). Few of these studies have considered vertical stratification (Bouwman, 1983; Warwick & Gee, 1984).

Studies of Westerschelde macrofauna have indicated that the density as well as the diversity is higher in the more saline part of the estuary, and that the subtidal areas and channels are nearly defaunated in terms of both species and biomass (Vermeulen & Govaere, 1983; Ysebaert & Meire, 1992). The meiobenthic fauna of the Westerschelde was examined by Van Damme *et al.* (1980) and copepods were studied by Van Damme *et al.* (1984). However, these studies (dating back to the period 1977–78) were mainly restricted to the intertidal zone and samples were vertically integrated. Claassen (1991) examined the meiobenthos in Saaftinge, which is the largest salt marsh of the estuary, situated in the brackish part.

As part of the Joint European Estuaries Programme (JEEP 92) of the EEC, the community structure of the Westerschelde meiobenthos was examined. Samplings were performed along a salinity gradient and included the intertidal, the subtidal and the deep channels. The vertical distribution into the sediment was investigated. Both the general meiobenthic community and more specifically the nematode species assemblages were examined.

Study site

The Westerschelde is a partly mixed estuary in The Netherlands and drains large areas in Belgium and France. Yearly averaged river outflow ranges from 100 to 150 $m^3 s^{-1}$ which is relatively small compared to tidal exchange (Van Eck *et al.*, 1991). Dispersion induced by the tidal currents and geomorphology of the Westerschelde provokes the establishment of salinity and related gradients. The tides and freshwater discharge produce a shift of particulates within the estuary (Postma, 1967), which results in the formation of a zone of maximal turbidity near Antwerp. Here sediment of fluviatile and marine origin is deposited (Van Eck & de Rooij, 1990). The high load or organic matter in this zone induces a high microbial activity which causes a serious depletion of oxygen in the water column in summer (Billen *et al.*, 1988; Heip, 1988). Annual phytoplankton primary production is lowest in the high-turbidity region and increases both upstream and downstream (Kromkamp *et al.*, 1992). The zooplankton shows maximum biomass in a zone downstream from the turbidity maximum in winter and early spring, while in summer highest biomass is observed near the mouth of the estuary (Soetaert & Van Rijswijk, 1993). The macrobenthos in the estuary is well developed on the intertidal flats only (Vermeulen & Govaere, 1983; Meire *et al.*, 1991; Ysebaert & Meire, 1992).

The Westerschelde is a highly polluted estuary due to the injection of large amounts of, mainly untreated, domestic sewage and industrial effluents. Moreover, in order to preserve the shipping lanes of the port of Antwerp, a large amount of sediment (15 million m^3 $year^{-1}$) is removed from the channels and largely dumped back again into the flood channels (Belmans, 1988).

Methods

The meiobenthos was sampled in March 1990 along six transects located at different salinity regimes and comprising three different morphological units: the intertidal, the subtidal area and the channels (Figure 1). Four subtidal samples were taken from the part more upstream.

Samples were taken with a Reineck box-corer (surface 170 cm^2) which was subsequently subsampled with plastic cores of 10-cm^2 surface. Some intertidal stations (of transect numbers 2 and 4) were directly sampled with cores. Some samples were used for chemical and sediment analyses; at least two cores were used for meiobenthic study. They were vertically subdivided into slices, 0–1, 1–2, 2–4 and 4–10 cm deep and fixed with a hot (70 °C) 4% formaldehyde solution. Various abiotic characteristics of the overlying water column at the time of sampling were measured: salinity, oxygen content ($g\ m^{-3}$), temperature and suspended matter content ($g\ m^{-3}$).

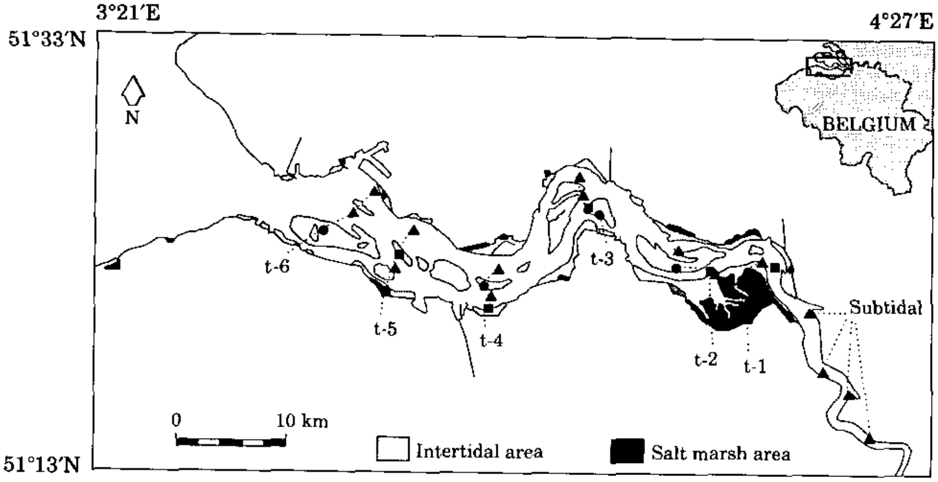

Figure 1. Position of the sampling stations with indication of the transect number (t-1–6) and the four additional subtidal stations. ●, Intertidal; ▲, subtidal; ■, channel.

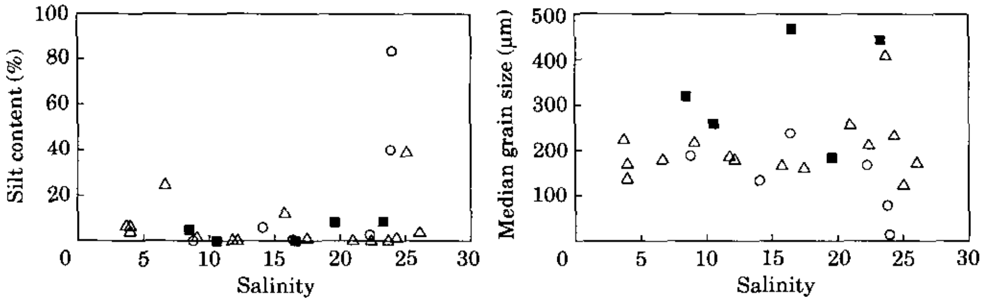

Figure 2. Grain size characteristics of the stations along the salinity gradient. ○, Intertidal; △, subtidal, ■, channel.

A first extraction of the meiobenthos occurred through decantation over a 38 µm sieve. The meiobenthos of fine sedimentary samples was then further extracted using LUDOX TM as described in Heip *et al.* (1985). After colouring with Rose Bengal all meiofaunal taxa were enumerated after which nematodes of one replicate were put onto slides for further identification. The other replicate was processed directly under an inverted microscope LEITZ Diavert.

Sediment particle-size distribution was determined using Coulter LS particle size analysis equipment. Nutrient load (ammonium, nitrate, nitrite, phosphate and dissolved silicate) in the sediment was determined for sediment slices of 0–1, 1–2, 2–4 and 4–6 cm. They were analysed with a Cenco M4 automatic analyser.

At most 100 nematodes per sediment slice (or all if total abundance was less than 100) were determined to species level. The multivariate species-abundance data (ind. 10 cm^{-3}) were explained as a function of the major environmental gradients by a canonical correspondence (CANOCO) analysis (Jongman *et al.*, 1987). Diversity was calculated as Hill's diversity indices of various order as recommended in Heip *et al.*

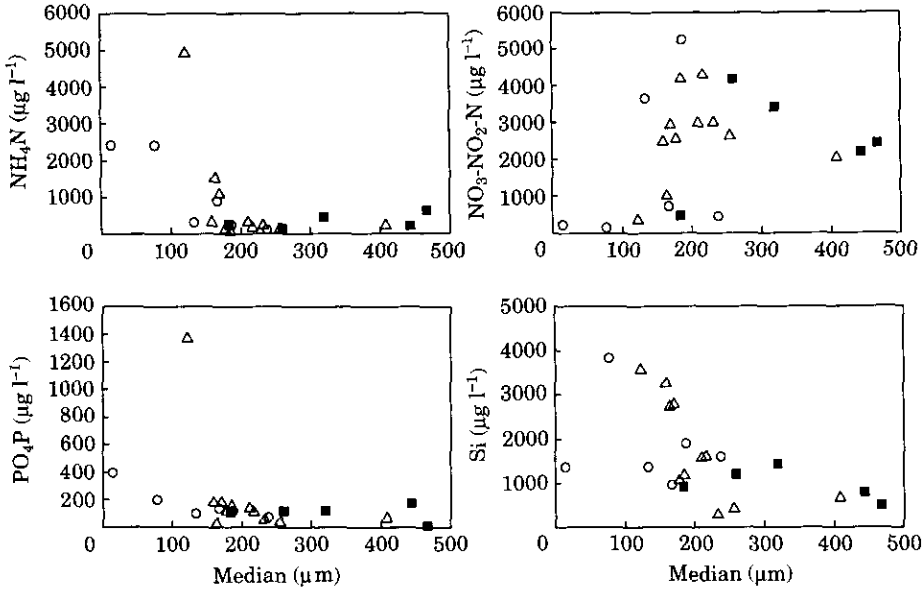

Figure 3. Mean nutrient load of the first 6 cm sediment in relation to median grain size. ○, Intertidal; △, subtidal; ■, channel.

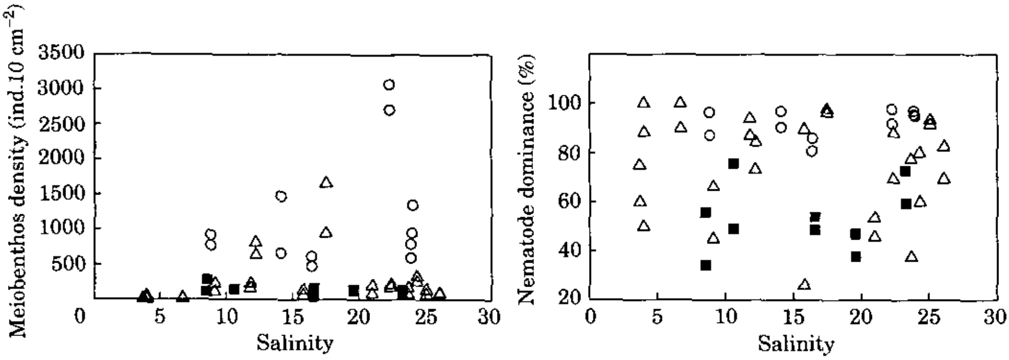

Figure 4. Vertically integrated meiobenthos density and fraction of nematodes along the salinity gradient. ○, Intertidal, △, subtidal; ■, channel.

(1988) and calibrated on a common number of individuals as described in Soetaert and Heip (1990). Areal densities were integrated through the vertical column.

Results

Sediments in the Westerschelde varied from muddy in the marine intertidal and some subtidal stations to very coarse (median grain diameter larger than 400 µm) in the channels. On average the sediments in the intertidal stations (average median grain diameter 136 µm, 22% silt) were finer than in the subtidal stations (average 200 µm, 7% silt) which in turn had finer sediments than most stations situated in the channels (334 µm, 4% silt) (Figure 2). Somewhat related to the grain characteristics was the

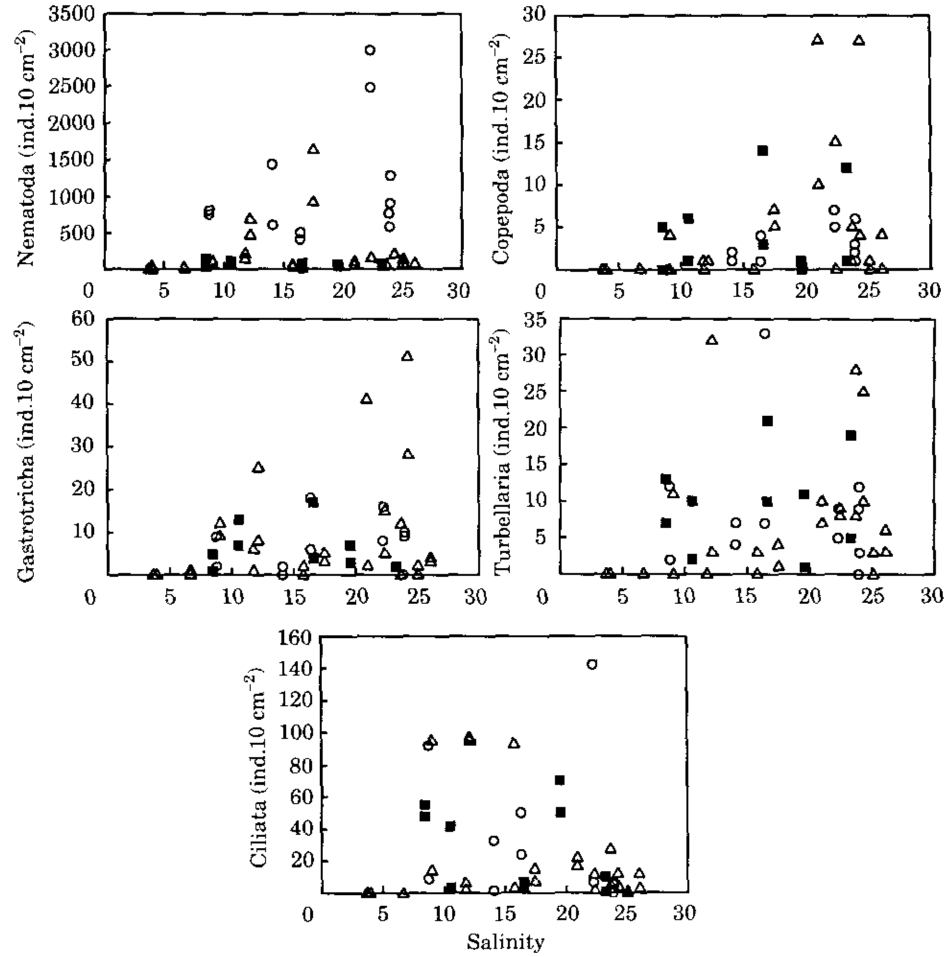

Figure 5. Vertically integrated density of various meiobenthic taxa along the salinity gradient. ○, Intertidal; △, subtidal; ■, channel.

nutrient load of the sediment: relatively high concentrations of ammonium and silicate were observed in sediment with a median grain size less than about 150–200 μm. Nitrate content was low in the most silty sediments and highest in those with intermediate grain sizes (Figure 3). Phosphate concentrations were rather constant.

Meiobenthos densities (Figure 4) were higher in the intertidal zone (482–3076, mean 1204 ind. 10 cm^{-2}) than in most permanently submersed stations. When excluding the channel and the subtidal sites most upstream, sublittoral densities varied from 67 to 1666 (mean 235 ind. 10 cm^{-2}). The channel stations always had very low meiobenthos densities (43–282, mean 137 ind. 10 cm^{-2}). The most upstream subtidal stations were nearly devoid of meiobenthic life (2–46, mean 16 ind. 10 cm^{-2}). There was no significant trend of meiobenthic density with either the sedimentary or salinity gradient, but densities tended to have a broader range with increasing salinity. Nematodes were in most instances the most important member of the meiobenthos, and this dominance was especially well pronounced in the intertidal zone (81–98%, Figure 4). Many subtidal and

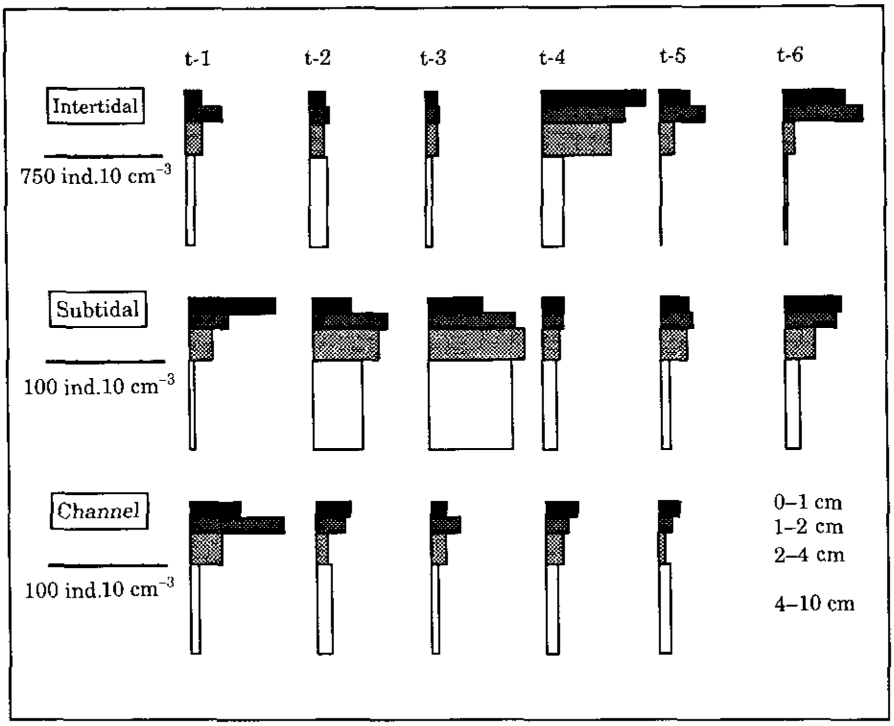

Figure 6. Vertical distribution (0–1, 1–2, 2–4 and 4–10 cm) of total meiobenthic density for intertidal, subtidal and channel stations (six transects).

channel stations on the other hand were characterized by a much higher contribution of other groups: Copepoda, Gastrotricha and, less so, Turbellaria and Ciliata were often both in absolute and relative terms more abundant in the permanently submersed areas (Figure 5). The nematode contribution to total meiofauna density in these areas was in many instances lower than 60% and in some places dropped to less than 30% (Figure 4).

The vertical distribution of total meiobenthos was such that the second centimetre was usually most densely populated in the intertidal area, whereas subtidal and channel stations had a more variable vertical distribution, with densities peaking either in the surface layer or deeper down (Figure 6).

A total of 148 nematode species, belonging to 79 genera, and 37 families were found in this study (see Appendix for a species list).

The distribution characteristics of the 33 most abundant species (defined as making up at least 10% of the total community in at least one station and observed in more than three stations) were calculated in relation to salinity, sediment grain, water depth and sediment depth preferences (Figures 7 and 8). Many species showed a preference for some of these factors, the degree of which can be appreciated by comparing with the distribution of total nematode density.

The majority of the species had a predominantly intertidal distribution, but some penetrated fairly extensively into deeper water (Figure 7): *Theristus blandicor, Ascolaimus elongatus, Viscosia viscosa, Theristus pertenuis, Enoplolaimus propinquus* and *Daptonema setosum*. Few were most commonly observed in the permanently submersed area:

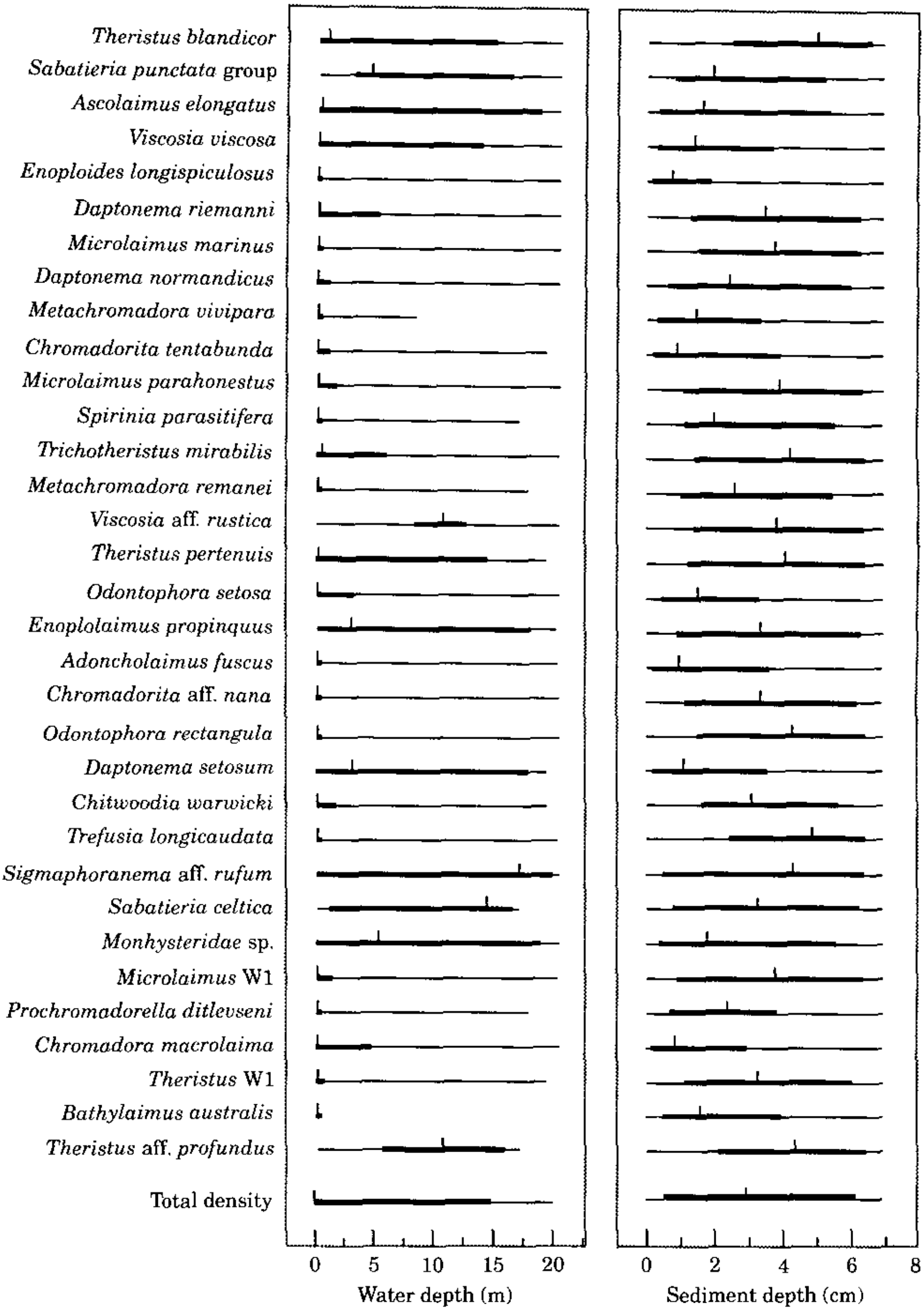

Figure 7. Distribution characteristics of the most abundant nematode species with respect to water depth and sediment depth. Indicated are the total range (horizontal line), the median occurrence (vertical dash) and the 10–90% occurrence (horizontal bar). Species are arranged according to decreasing abundance.

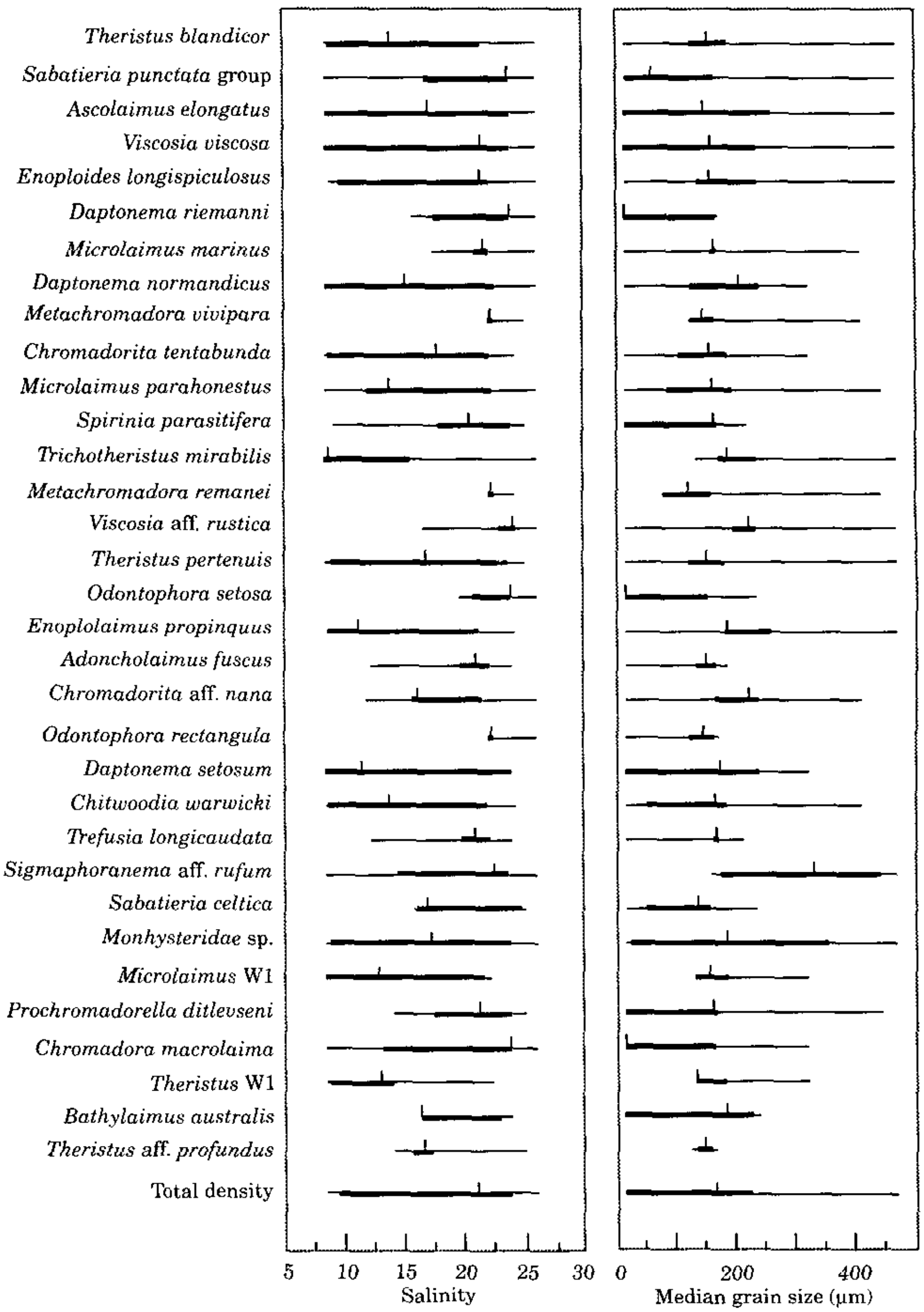

Figure 8. Distribution characteristics of the most abundant nematode species with respect to salinity and median grain size. For further explanation, see Figure 7.

Sabatieria punctata (group) (comprising *S. breviseta* and *S. pulchra*), *Viscosia* aff. *rustica*, *Sigmaphoranema* aff. *rufum*, *Sabatieria celtica*, *Monhysteridae* sp. and *Theristus* aff. *profundus*. For the calculation of sediment depth preferences, it was assumed that

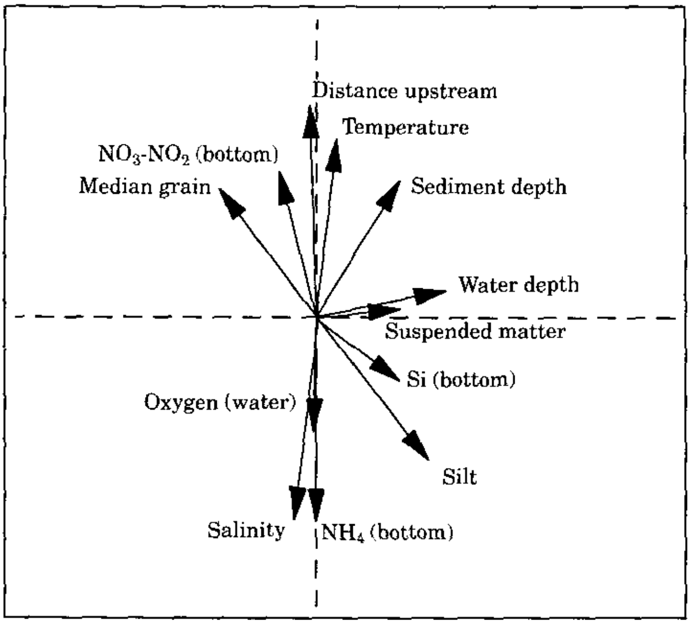

Figure 9. CANOCO plot of environmental variables along the two main ordination axes.

nematodes were evenly distributed in the sediment slices and that nematodes did not penetrate deeper than 7 cm. The median, 10% and 90% occurrence were then calculated as in Sokal and Rohlf (1981). It appeared that the bulk of species extended relatively deep into the sediment and some were real deep-dwelling species, having more than half of the population deeper than 3 cm: *Daptonema riemanni, Microlaimus marinus, Odontophora rectangula* and *Trefusia longicaudata* in the marine part; *Theristus blandicor, Microlaimus parahonestus, Trichotheristus mirabilis, Enoplolaimus propinquus, Chromadorita* aff. *nana, Chitwoodia warwicki* and *Microlaimus* W1 in the brackish part of the estuary (Figures 7 and 8). *Theristus pertenuis* was observed in the deeper sediment layers of both the marine and brackish stations. *Viscosia* aff. *rustica, Sigmaphoranema* aff. *rufum* were observed in the deeper layers of the marine subtidal; *Theristus* aff. *profundus* and *Sabatieria celtica* were brackish subtidal deep-dwelling species. Only few species occurred predominantly in the first centimetre and could be considered as real surface dwellers. They were *Adoncholaimus fuscus* and *Chromadora macrolaima* (marine part), *Daptonema setosum* (brackish area), *Enoploides longispiculosus* and *Chromadorita tentabunda* (all salinity regimes).

A canonical correspondence analysis on nematode species composition revealed upstream distance (with correlated salinity, oxygen and temperature), grain characteristics (median grain, silt content), water depth and sediment depth to be important parameters in the determination of community structure (Figure 9). In Figure 10, the position of samples in two-dimensional CANOCO space is represented with indication of the vertical distribution (arrow). Although the sediment slices of all samples were combined into one analysis, the samples belonging to different transects and morphological units are plotted separately for convenience. There is a pronounced vertical gradient in the intertidal samples: subsequently deeper sediment slices follow a

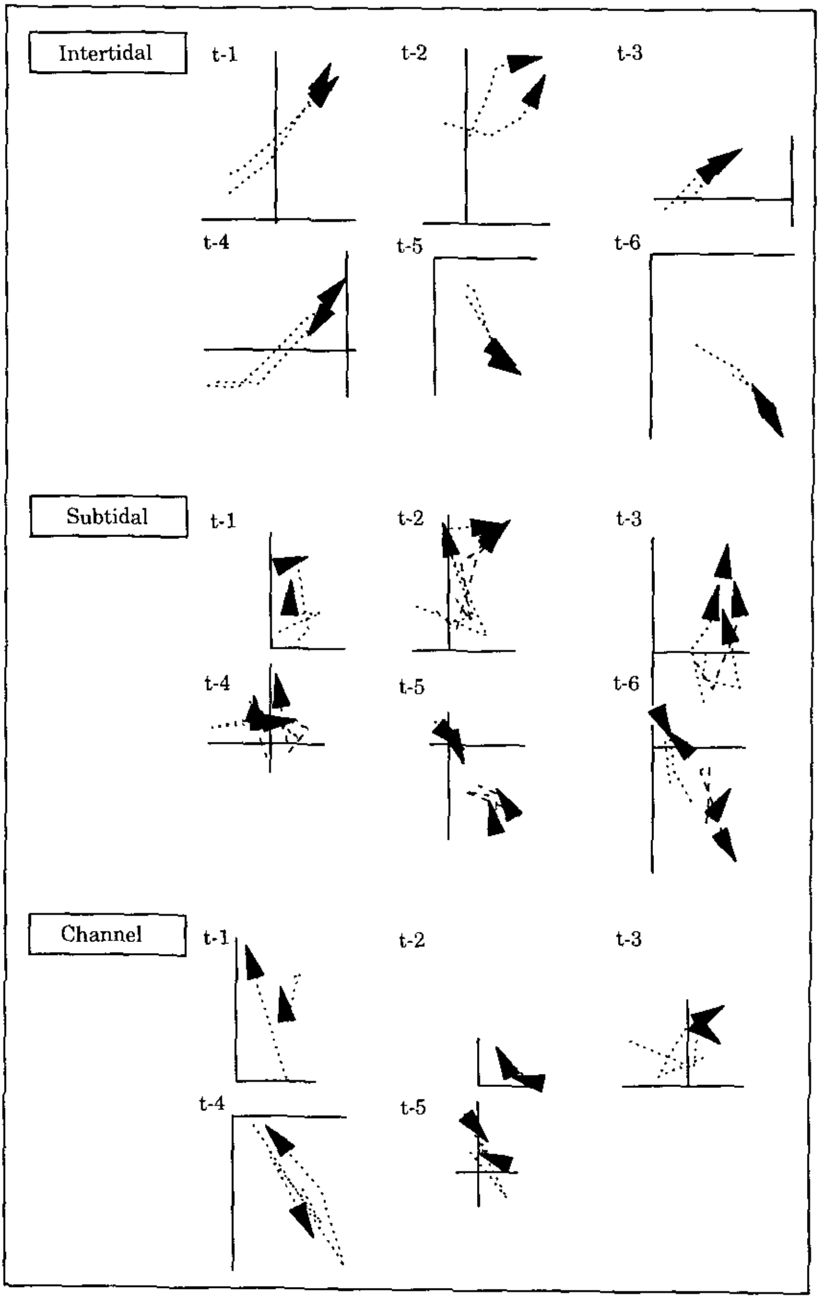

Figure 10. CANOCO plot of the various sediment slices along the same ordination axes as in Figure 9. For clearness' sake, the samples (consisting of four sediment slices and two replicates) of different morphological types and transect numbers (t-1 to t-6) are plotted separately. For each replicate, the arrow represents the vertical gradient. It connects the position of the 0–1-cm slice in CANOCO space with the 1–2-cm slice, the 2–4-cm slice and ends with the position of the 4–10-cm slice.

TABLE 1. Relative abundance (%) of the most dominant nematode species (>10% of total abundance in at least one sediment layer) in the sediment layers of the intertidal samples of transects 5 and 6

	Sediment layer (cm)			
Species	0–1	1–2	2–4	4–10
Transect 5				
Viscosia viscosa	10	7	1	1
Daptonema riemanni	2	6	12	4
Sabatieria punctata group	27	62	70	82
Transect 6				
Ascolaimus elongatus	25	15	3	2
Viscosia viscosa	24	15	2	2
Daptonema riemanni	2	13	57	68
Sabatieria punctata group	2	10	2	2
Metalinhomoeus aff. *biformis*	0	1	2	10
Odontophora setosa	9	15	4	0

more-or-less straight path and there is a strong resemblance of subsamples. Subtidal and channel stations showed a much more distorted pattern and less resemblance among replicates. The same analysis was done excluding the intertidal stations, and now some of the subtidal stations showed a more straight course in two-dimensional CANOCO space, but most were still heavily erratic (not depicted).

Whereas the arrows representing the vertical structure in the intertidal of the transects 1–4 (Figure 10), are parallel to the environmental axis of sediment depth (Figure 9), this is not the case for the intertidal stations of transects 5 and 6. These stations had silty sediments and subsequently deeper sediment layers are stretched along the axis indicating increasing silt content. Yet all these sediment layers have the same granulometric characteristics. This phenomenon can be explained by the fact that nematodes of the superficial layers occur in more sediment types whereas the distribution of nematode species observed in the deeper layers is more restricted to silt. In Table 1 the relative abundance of the most dominant species in the different sediment layers is represented. In the uppermost sediment layers of the intertidal station of transect 6, *Ascolaimus elongatus* and *Viscosia viscosa* were most dominant. Both species attain greatest abundance in more sandy sediments (see Figure 8). With increasing depth, species like *Daptonema riemanni* and *Metalinhomoeus* aff. *biformis* became more important. The first species was also observed in sandy sediments, but was most prominent in silts (Figure 8), the latter species was exclusively found in silts (not depicted). *Odontophora setosa* and *Sabatieria punctata* (group), also silt-colonizing species (Figure 8), were most prominent in the second layer of sediment. In the intertidal station of transect 5, *Viscosia viscosa* (most common in sand) was most prominent in the upper sediment layers, while *Sabatieria punctata* (group) became more dominant with increasing depth into the sediment. Here too *Daptonema riemanni* (silt-colonizing species) was prominent in the deeper layers.

Nematode diversity of whole samples was somewhat higher in the intertidal compared to many permanently submersed areas for a comparable salinity regime [Figure 11(a,b)]. However, as diversity indices are sensitive to the number of individuals on which they were calculated (Soetaert & Heip, 1990), this trend in whole sample diversity partly

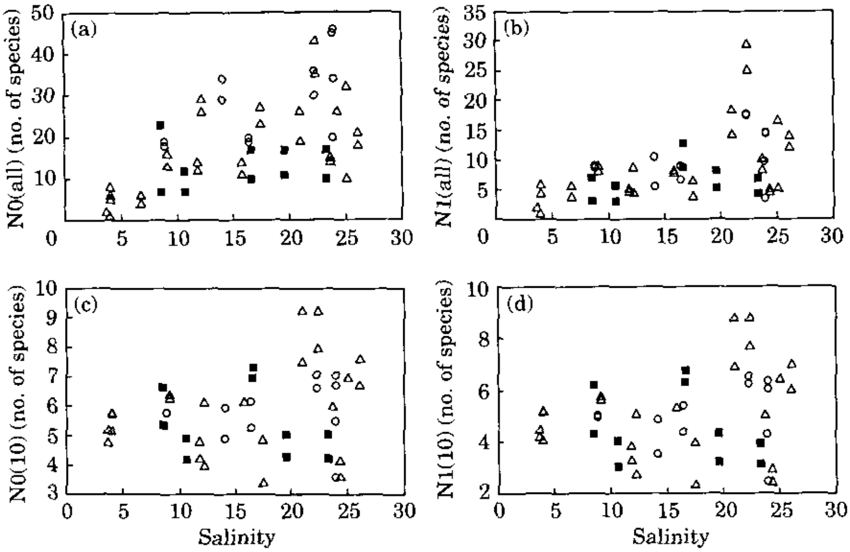

Figure 11. Nematode diversity indices (Hills number of order 0 and 1), based on total abundance (a,b) and on 10 randomly drawn individuals (c,d) along the salinity gradient. N0 is equivalent to the number of species, N1 equals exp (H') where H' is the Shannon–Wiener diversity index. ○, Intertidal; △, subtidal; ■, channel.

reflects density differences. Using this method, one is likely to find more species in an intertidal sample, with about 1000 nematodes, compared to a subtidal site where only 20 nematodes are present. To correct for the density dependence of diversity indices, the diversity of a common number of individuals (i.e. 10) was also calculated [Figure 11(c,d)]. There was no real trend with salinity nor other abiotic parameters, nor could a difference between the gross morphological units be detected. Due to the low nematode densities in many submersed sites and the relatively high diversity there, the mean density per species is very low. When taking into account only stations with a total density of less than 100 ind. 10 cm^{-2} it appears that 50% of the species had an abundance of less than 1 ind. 10 cm^{-2} and 90% of all species had densities of less than 6 ind. 10 cm^{-2}.

Discussion

An estuary such as the Westerschelde is a very dynamic environment. With the incoming tide, sediment is resuspended, carried inward and settles when the current velocities are low. With the outgoing tide the process is repeated, now shifting sediment downstream but typically the current velocities are lower and hence resuspension of the sediment is not so pronounced (Postma, 1967). This results in a net transport of particles towards the tidal flats and upstream (Peters & Sterling, 1976; de Jonge, 1985). In the intertidal zone, currents will rework and sort the sediments during submersion, a process which is amplified by wind-induced waves and storms. The eroded matter is partly redistributed onto the intertidal flat, but some of it is transported to the deeper parts, where it is incorporated in the global estuarine circulation.

Within the estuary, muds will be deposited predominantly in the more sheltered areas, while the high current velocities in the deep channels prevent small particles from settling there (Oenema *et al.*, 1988). Along with the finer sedimentary material, organic matter is deposited and subsequently degraded, a process which ultimately produces reduced conditions and ammonium. Thus, in the current study one can distinguish between sandy sediments with a low ammonium and silicate load but a higher nitrate content and more fine-grained sediments where the nutrient balance is reversed. The transition between both sedimentary types seemed to lie at 150–200 μm median grain size. The coarse type of sediment was typical for channels and also occurred in some subtidal and intertidal samples; the fine type was observed only in the intertidal and subtidal.

Apart from the larger amount of sedimented organic matter in some intertidal sites, phytobenthos primary production is mainly restricted to these regions and many meiobenthic animals are known to feed on the unicellular algae (Admiraal *et al.*, 1983; Bouwman, 1983; Heip *et al.*, 1985). This at least partly explains the higher meiobenthic densities observed in the intertidal (Bouwman, 1983; Smol *et al.*, 1994; this study). In the Westerschelde, algal feeders comprised about 20% of the total nematode population in the intertidal, while they accounted for less than 10% in the permanently submersed sites.

The greater stability of the sediment environment in the intertidal could provide an additional explanation for the higher densities of nematodes there. Although intertidal sediments are also subjected to a resuspension–sedimentation cycle when flooded, current velocities are somewhat smaller here than in the channels and much of the sediment is redistributed on the tidal flat. Sediments in the sublittoral and especially in the channels experience higher current velocities and are transported over larger (net upstream) distances. Moreover, dredging and (less so) dumping activity mainly affects sublittoral communities. As opposed to nematodes, harpacticoids, gastrotrichs and, less so, turbellarians and large ciliates had higher densities in the permanently submersed areas. This was also the case in the Eastern Scheldt (Smol *et al.*, 1994) and it could indicate that these latter groups are better adapted to sediment disturbances. The predominantly interstitial life-style of, for example, Gastrotricha could further explain why they are so scarce in the more fine-grained intertidal.

Compared to the other meiobenthic groups, nematodes need an intimate contact with the sediments, both for moving (undulatory propulsion) and feeding, and sediments which are in constant turmoil may thus interfere with their basic requirements. This could be the case in many subtidal stations. Moreover, the densities of most nematode species are extremely low at many of these sublittoral sites and this may prohibit their sexual reproduction (for which a minimal specific density is required). It is, thus, very likely that these communities are not self-sustaining but are constantly replenished from less marginal sites. The ability of nematodes to survive in hostile conditions could then allow them to persist at least for a period of time after which they will die. Indicative in this respect was the presence of many badly fixed nematodes in the low-density sublittoral sites, which suggested that many were dead before fixation took place.

The most obvious way of large-scale transport of nematodes is by means of the currents and it has been shown that individual nematodes become suspended in the water column (Palmer & Gust, 1985; Palmer, 1988). Nematodes were also shown to be present in the Westerschelde plankton and were especially abundant near to the turbidity maximum. Here their density (some 10 ind. l^{-1}, i.e. about 100 ind. 10 cm^{-2} in spring 1990), even exceeded the, albeit low, densities in the subtidal bottom beneath (data from

Soetaert & Van Rijswijk, 1993). This involuntary entering of nematodes into the water phase, and their displacement to other sites may be responsible for the continuous repopulation of the subtidal areas.

If the meiobenthic density in many submersed areas was rather low, the four subtidal sites in the most upstream part (salinity <7) were nearly devoid of meiobenthic life: in two stations densities of less than 10 ind. 10 cm^{-2} were found and the maximum density was 46 ind. 10 cm^{-2}. This area is near to the turbidity maximum and it is the site of deposition of polluted sediments (Van Eck & de Rooij, 1990) and consequently lots of dredging takes place (Belmans, 1988). Moreover, the organic and inorganic pollution is very high here. Microbial degradation of these organics results in low oxygen concentrations in the water and near-anoxia is observed during summer months. Finally, pelagic primary productivity is lowest in this region (Kromkamp *et al.*, 1992) which could result in less high-quality food for the benthos. Probably a combination of some of these factors is responsible for the aberrantly low meiobenthic densities here.

Intertidal areas are subjected to cyclic flooding and drying, which will impose stress to the benthos there. This stress is partly due to the sinking groundwater in the sand- and mudflats, but the water table typically does not sink more than 0–2 cm below the surface at low tide (Oenema *et al.*, 1988). Apart from desiccation stress, the absence of the buffering capacities of the overlying water will induce more extreme fluctuations of, for example, temperature and salinity in the upper sediment layers, and this too will affect the benthos. Resuspension and sedimentation processes also act predominantly on the upper layers of the sediment. Hence one observes that the intertidal meiobenthic community in general, and the majority of nematode species in particular, penetrate relatively deep into the sediment, and only few species are real surface dwellers. This is in contrast with the vertical distribution in many subtidal sediments where a high degree of surface accumulation is usually observed (Coull, 1988). In the subtidal area of the Westerschelde, vertical density distributions exhibit either a surface or a subsurface maximum and the nematode community gradients are at least different from gradients in the intertidal areas and in many instances they show a distorted pattern. These atypical vertical distributions are a further indication of the deteriorating effects of human and natural physical disturbances on the subtidal and channel communities.

The distribution of nematode species in the estuary, and consequently the composition of assemblages, is greatly influenced by the sedimentary and geomorphological heterogeneity. Together with salinity and related gradients, these environmental factors explain many of the differences observed in nematode communities. However, apart from this obvious large-scale horizontal heterogeneity, the sharpest gradients in environmental variables such as light, oxygen, temperature, food etc., occur vertically into the sediment and environmental fluctuations are dampened with increasing depth into the sediment. Being small, meiobenthic organisms, and nematodes in particular, strongly experience these small-scale gradients and their distributions are likely to reflect their environmental tolerances. Although on average nematode species had a relatively broad vertical range, a variety of vertical distributions were observed in this study. Moreover, although acting on the scale of centimetres, the effect of sediment depth on community structure proved to be as important as the other abiotic variables which act on the scale of hundreds of metres. Similarly, Joint *et al.* (1982) showed that nematodes and copepods in the intertidal had a typical vertical distribution even on a much finer scale than reported here, though with a broad overlap of species.

Whereas information on the vertical structure is interesting, it is not a prerequisite to include vertical heterogeneity in many studies. Core samples are by definition integrated in the vertical sense and it is much more difficult to deal with horizontal patchiness adequately. However, our ecological understanding can sometimes greatly profit from knowledge on the vertical structure. It has, for instance, been argued that the vertical separation of species will reduce the number of (competitive or predative) interactions, and this could explain the often very high number of species that coexist in a certain small patch (Joint *et al.*, 1982). Species that occur in the surface layers will be more susceptible to epibenthic predation and the vertical distribution will also result in a differential resuspension and transport of nematodes with the sediment. Thus, Warwick and Gee (1984) showed that an abundant surface-dwelling nematode in the Tamar Estuary migrated quickly along with the changing sediment movement, whereas deeper dwelling species did not. Something similar was observed in the intertidal silty sediments of transects 5 and 6: nematode species that were present in the upper layers of these sediments had a more general distribution compared to deeper dwelling species of the same stations. This could be explained by the fact that surface dwellers are more amenable to resuspension and are more easily transported to other areas. It could be interesting to see whether these species also show a more rapid response in time as was the case in the Tamar Estuary (Warwick & Gee, 1984).

The density values found in the intertidal of the Westerschelde in this study are comparable with values from Van Damme *et al.* (1980) from a previous study of the same area, but they are lower than what has been found in an estuary nearby, the Oosterschelde (Smol *et al.*, 1994). Soetaert *et al.* (in press) compared the intertidal densities in the Westerschelde with other estuaries, and concluded that although the abundances in the marine part of the estuary were somewhat lower than in many other estuaries, Westerschelde densities were not aberrant. In the sheltered salt marsh of Saaftinghe, peak densities of 50 000 ind. $10\,\mathrm{cm}^{-2}$ were reported by Claassen (1991). Thus, although Saaftinghe is located at a short distance from transects 1 and 2 (this study), it has densities that are almost two orders of magnitude higher than the nearby intertidal sites. Van Damme *et al.* (1980) also observed higher densities and biomasses here and attributed it to the larger amount of organics present and the more sheltered position with respect to extreme environmental conditions and direct pollution.

The intertidal area of the Westerschelde differed from five other estuaries mainly by the near-absence of harpacticoid copepods (Soetaert *et al.*, in press). This feature was also observed by Van Damme *et al.* (1984) who attributed it to chemical pollution effects. In the current study, slightly higher copepod densities were observed in the subtidal of the Westerschelde but these were still much lower than what was observed in the subtidal zone of the Eastern Scheldt (Smol *et al.*, 1994) and in some stations in the Tagus (unpubl. data). Thus, it appears that the trend of low harpacticoid abundance in the Westerschelde is consistent both in the intertidal and in the subtidal zone.

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Appendix

Species list, indicating the maximum density ($10\,cm^{-2}$) of each species in the Westerschelde. *0–4, **4–16, ***16–64, ****64–256, *****256–1024 individuals.

Enoplida	
Enoplidae	
Enoplus sp.	*
Thoracostomopsidae	
Enoploides longispiculosus	*****
Enoplolaimus propinquus	****
Anoplostomatidae	
Anoplostoma W2	*
Anoplostoma viviparum	**
Ironidae	
Syringolaimus sp.	*
Oxystominidae	
Halalaimus gracilis	***
Thalassoalaimus septentrionalis	*

(*Continued*)

Oncholaimidae	
Adoncholaimus fuscus	****
Oncholaimellus calvadosicus	*
Oncholaimellus mediterraneus	**
Oncholaimus oxyuris	*
Viscosia aff. *rustica*	****
Viscosia viscosa	****
Enchelidiidae	
Calyptronema maxweberi	**
Tripyloididae	
Bathylaimus australis	***
Bathylaimus stenolaimus	**
Bathylaimus tenuicaudatus	**
Tripyloides gracilis	**
Trefusiida	
Trefusiidae	
Trefusia W2	*
Trefusia W3	*
Trefusia longicaudata	****
Chromadorida	
Achromadoridae	
Achromadora sp.	*
Chromadoridae	
Atrochromadora microlaima	*
Chromadora axi	*
Chromadora macrolaima	***
Chromadorita aff. *nana*	****
Chromadorita sp.	*
Chromadorita tentabunda	****
Dichromadora cephalata	**
Dichromadora cucullata	*
Dichromadora geophila	***
Euchromadora sp.	*
Hypodontolaimus W1	**
Hypodontolaimus shuurmansstekhoveni	*
Prochromadorella ditlevseni	***
Ptycholaimellus ponticus	**
Spilophorella candida	*
Spilophorella paradoxa	**
Comesomatidae	
Sabatieria celtica	****
Sabatieria punctata (group)	*****
Setosabatieria hilarula	*
Ethmolaimidae	
Neotonchus aff. *cupulatus*	*
Cyatholaimidae	
Cyatholaimidae sp.	*
Paracanthonchus heterodontus	*
Paracanthonchus thaumasius	***
Paracyatholaimoides W1	**
Paracyatholaimus W1	**
Paracyatholaimus pentodon	*
Pomponema sp.	*
Praeacanthonchus punctatus	**

(*Continued*)

Selachinematidae	
Richtersia inaequalis	*
Desmodoridae	
Metachromadora aff. *suecica*	***
Metachromadora remanei	****
Metachromadora vivipara	*****
Molgolaimus cuanensis	*
Molgolaimus turgofrons	**
Onyx sagittarius	*
Sigmaphoranema aff. *rufum*	***
Sprinia parasitifera	****
Southernia zosterae	**
Microlaimidae	
Microlaimus W1	***
Microlaimus W3	*
Microlaimus W4	*
Microlaimus arenicola	**
Microlaimus globiceps	**
Microlaimus marinus	*****
Microlaimus parahonestus	****
Microlaimus robustidens	**
Monoposthiidae	
Monoposthia mirabilis	**
Leptolaimidae	
Camacolaimus tardus	**
Dagda bipapillata	*
Deontolaimus papillatus	*
Leptolaimus acicula	*
Leptolaimus aff. *membranatus*	*
Leptolaimus aff. *minutus*	**
Leptolaimus ampullaceus	**
Leptolaimus elegans	**
Leptolaimus papilliger	*
Leptolaimus sp.	*
Stephanolaimus elegans	*
Haliplectidae	
Haliplectus dorsalis	*
Aegialoalaimidae	
Cyarthonema W1	*
Southernia zosterae	**
Tubolaimoididae	
Chitwoodia warwicki	***
Ceramonematidae	
Dasynemoides albaensis	*
Monhysterida	
Monhysteridae	
Monhysteridae sp.	**
Xyalidae	
Daptonema cfr Bouwman	**
Daptonema W1	**
Daptonema normandicus	****
Daptonema riemanni	****
Daptonema setosum	***
Daptonema sp.	**
Daptonema tenuispiculum	**

(Continued)

Metadesmolaimus 2	*
Metadesmolaimus gaelicus	**
Paramonohystera aff. *albigensis*	**
Paramonohystera sp.	*
Theristus W1	***
Theristus (Penzancia) W1	*
Theristus W5	**
Theristus aff. *profundus*	***
Theristus blandicor	*****
Theristus cfr *subcurvatus*	**
Theristus ensifer	**
Therisuts interstitialis	**
Theristus longus	**
Theristus pertenuis	***
Theristus sp.	*
Trichoteristus W3	*
Trichotheristus mirabilis	****
Xyala striata	*
Sphaerolaimidae	
Sphaerolaimus sp.	**
Siphonolaimidae	
Siphonolaimus sp.	*
Linhomoeidae	
Eleutherolaimus iniquisetosus	*
Eleutherolaimus stenosoma	***
Eumorpholaimus sp.	*
Linhomoeidae W1	*
Linhomoeidae W2	**
Linhomoeidae W4	*
Linhomoeidae W5	**
Linhomoeidae sp	**
Megadesmolaimus W1	***
Metalinhomoeus aff. *biformis*	***
Metalinhomoeus biformis	***
Terschellingia communis	*
Axonolaimidae	
Ascolaimus elongatus	****
Axonolaimus paraspinosus	**
Odontophora W4	***
Odontophora aff. *paravilloti*	*
Odontophora rectangula	****
Odontophora setosa	****
Diplopeltidae	
Diplopeltula W1	*
Diplopeltula asetosa	*
Diplopeltula belgica	*
Pararaeolaimus nudus	**
Rhabditida	
Cephalobidae	
Cephalobus sp.	**
Diploscapteridae	
Diploscapter sp.	*
Odontopharyngidae	
Odontopharynx sp.	**

(*Continued*)

Tylenchida	
Aphelenchoididae	
Aphelenchoididae sp.	*
Tylenchida	
Tylenchida W1	*
Dorylaimida	
Dorylaimida	
Dorylaimida W1	*
Dorylaimida W2	*
Dorylaimida W3	*
Indeterminata	
Indeterminata	
Indeterminata sp.	***