

CHAPTER II

**Horizontal zonation patterns and feeding
structure of marine nematode assemblages on a
macrotidal, ultra-dissipative sandy beach
(De Panne, Belgium)**

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ABSTRACT

Macrobenthic zonation on sandy beaches has been studied widely, whereas meiobenthic/nematofaunal species richness and zonation patterns have received little attention. We investigated community structure, intertidal zonation of nematode species and feeding structure across a macrotidal, ultra-dissipative, sandy beach (De Panne, Belgium). A total of 88 free-living marine nematode species were recorded along transects. Average nematode densities increased from the upper beach (320 ± 45 Ind/10 cm²) towards the low-tidal level (2784 ± 6 Ind/10 cm²), which corresponds well to the better-known macrobenthic patterns on sandy beaches. While macrobenthic species richness usually increases towards the low-tidal level, nematode species richness reached highest values around the mid-tidal level (34 ± 3 sp.). This can be explained by an optimal balance between time of submergence, oxygen supply and sediment stability. Multivariate analyses indicated four different nematode assemblages that reflect the tidal zonation patterns: the upper beach, the strandline, the middle beach association and the lower beach association. The assemblages were significantly different from each other although similarities tended to increase down the beach, indicating a more gradual transition between the mid-tidal and low-tidal assemblages. Non-selective deposit feeders dominated all zones except in the strandline, where epistratum feeders were dominant. Percentage of very fine sand and percentage of shell fragments provided the best granulometric variables in determining these assemblages.

KEYWORDS: nematodes, species diversity, sandy beach, faunal zonation patterns, feeding types, sediment, North Sea

INTRODUCTION

Sandy beaches are among the most extensive intertidal systems worldwide (Short 1999), dominating most temperate coastlines where they represent both important recreational assets and buffer zones against the sea (McLachlan 1983; Davies 1972). In the present study, a sandy beach is defined following Brown and McLachlan (1990). It is considered to be a marine sandy littoral area open to the sea including the zone of wave shoaling across the near-shore zone, wave breaking across the surf zone and wave dissipation in the swash zone. This definition does not include sandflats in estuaries or closed lagoons but refers only to open marine beaches.

In contrast to rocky shores, sandy beaches seem to harbour no life at first sight and appear to be 'marine deserts'. However, some sandy beaches are very productive, harbouring a little-known interstitial life (McLachlan 1983). The beaches along the 67-km-long Belgian coastline act as important foraging grounds for many fish (Beyst *et al.* 2002) and birds (Devos *et al.* 1998). The shallow marine habitats on the Belgian west coast are known for their great ecological value and are designated as an area of international importance for waterfowl, according to the Ramsar Convention (Kuijken 1972), and fulfils all criteria of the EC Bird and Habitat Directives (Anonymous 1979; 1992). Since shallow marine habitats include not only the subtidal, but also the intertidal zone up to the highwater level (Reilly *et al.* 1996), baseline data describing benthic life and ecosystem processes in the intertidal zone are needed in order to propose a sustainable management policy for these areas.

Most of the ecological studies on sandy beaches have been restricted to the macrofauna (McLachlan and Jaramillo 1995 and references therein), while meiofauna has received little attention. The dominant taxa of the sandy beach meiofauna are generally free-living nematodes, harpacticoid copepods and turbellarians, followed by several other groups of diverse importance (Giere 1993). Sandy beach meiofaunal research has been focused mainly at the higher taxon level (Gray and Rieger 1971; Harris 1972; McIntyre and Murison 1973; McLachlan *et al.* 1977; Olafsson 1991; Rodriguez *et al.* 2001; Menn 2002), while research at species level is scarce.

Although nematodes are among the most abundant metazoans in marine (littoral, estuarine, coastal and oceanic) sediments (Nicholas 1975, 2001), only few papers, apart from purely taxonomic ones, have described the nematode species composition of sandy beaches (Platt and Warwick 1980; Blome 1983; Sharma and Webster 1983; Nicholas and Hodda 1999). This is probably due to the time-consuming research and the overall high densities and diversities of nematofaunal assemblages. Theoretically, nematodes are an excellent taxon to use as ecological indicators for benthic environments (Heip *et al.* 1985; Sanduli and De Nicola 1991; Schratzberger *et al.* 2000). They reach very high abundances, so a small sediment sample yields enough animals to make scientifically sound statements.

They have a ubiquitous distribution, a high diversity (with a range from very tolerant to very sensitive species), short generation time and a continuous reproduction. Moreover, they are restricted to the sediments throughout their life. As a consequence of their wide range of adaptations, nematodes have exploited all

littoral habitats, including the biologically hostile sandy beaches. Therefore the state and composition of nematode assemblages may reflect the general health of the benthos (Kennedy and Jacobi 1999). Platt and Warwick (1980) conclude that 'any general assessment of the ecology of intertidal habitats is incomplete if the nematode fauna is not taken into consideration'.

The present study on a Belgian macrotidal, ultra-dissipative sandy beach adds to the rare studies on meio-benthic/nematofaunal zonation patterns, investigating:

- (1) The horizontal nematode zonation patterns (diversity and feeding structure) at species level;
- (2) The relation with granulometric variables;
- (3) The (dis)similarities with macrofaunal sandy beach zonation patterns.

MATERIAL AND METHODS

Study site

The study area is located ($51^{\circ}05'30''\text{N}$, $02^{\circ}34'01''\text{E}$) at the western Belgian coast, nearby the Belgian-French border, in front of the nature reserve 'Westhoek' (Figure 1). The natural beach-dune transition is disturbed by a concrete storm water dyke (fixed at 6.93 cm MLWS), constructed to protect the low-lying hinterland from flooding during extreme storms. However, as a result of the position and the depth of anchorage of the dyke, freshwater bells can easily connect the low-lying hinterland dune slacks and the beach. Its influence on the beach morphology is negligible. (Lebbe 1978, 1981) The width of the intertidal zone is approximately 440 m and the beach has several runnels parallel to the water's edge, retaining seawater on the outgoing tide. The slope of the beach is about 1:90 to 1:100. The mean spring and neap tide ranges are 4.97 m and 3.02 m, respectively (Coastal Waterways Division, Flemish Community).

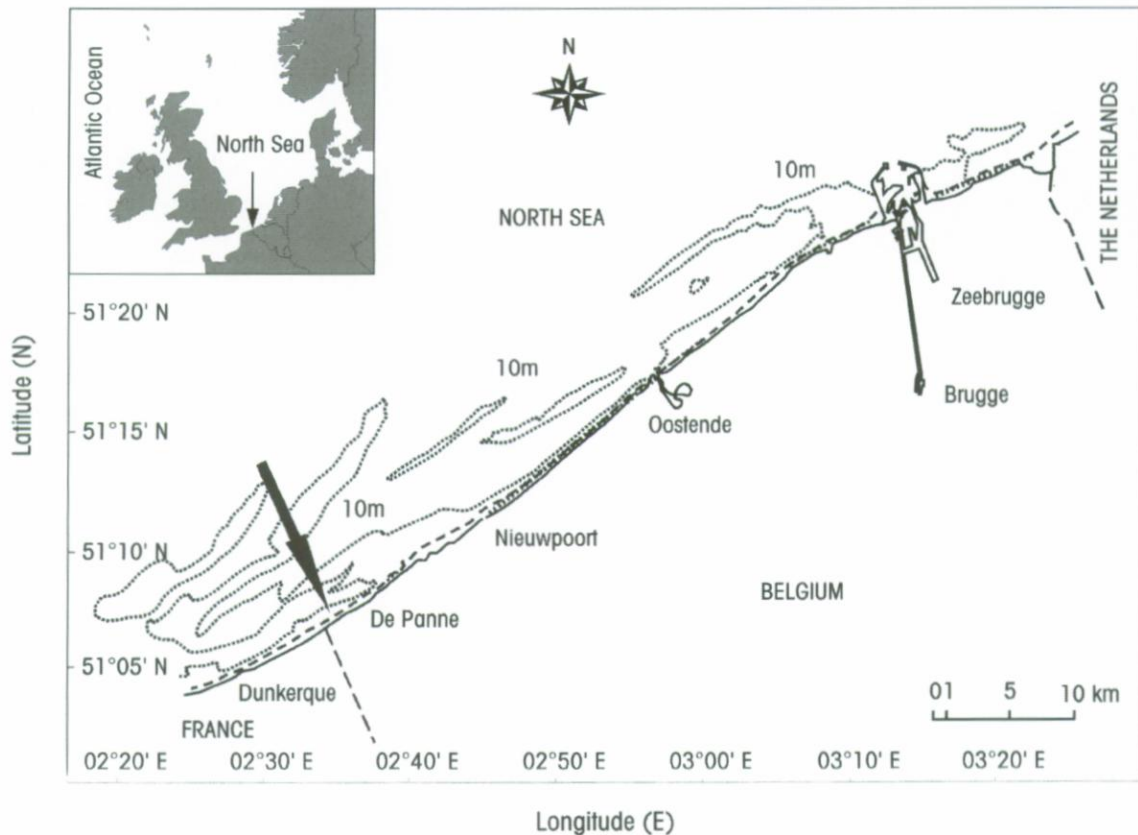


Figure 1: Geographical disposition of the studied beach.

Sampling strategy

Sampling was done in August 2000, when high tide was expected at 02.22 pm (4.43 m relative to Mean Low Water Spring level, MLWS) and low tide at 09.39 pm (-0.79 m relative to MLWS). A 15 m wide, orientated perpendicular to the waterline, section of the beach (four transects spaced 5 meters apart) was sampled. Each transect had nine equally distributed stations across the continuum from the mean high-water spring level (MHWS) to the mean low-water spring level (MLWS) in order to sample different pre-defined zones (upper beach (S1 and S2), middle beach (S4, S5, S6 and S7), lower beach (S8 and S9)). These zones were discerned as each zone is varying in degrees to swash, surf and shoaling wave processes, which is visible in the granulometry, following Short (1999). The strandline (S3) was added (based on visual properties) because we expected this zone to harbour a specific nematode community (a distinct macrofaunal assemblage was already detected by De Backer 2001). The number in sampling points in each zone is not the same because these zones differ in width along the beach profile. The beach of De Panne consists of a series of ridges and runnels, each with different habitat characteristics. As the retention of sea water in the runnels might harbor subtidal fauna, (Dörjes 1976), all the samples were taken on the top of the ridges. Thus, this study excluded the nematodes of the runnels.

As the granulometry and flat slope of this beach results in a faunal concentration fairly close to the surface (Elliott *et al.* 1996), the upper 15 cm is the most ecologically significant (Platt and Warwick 1980). To exclude truly terrestrial nematodes in the freshwater table, only the top 15 cm of sediment (including a few cm of overlying seawater) was sampled using perspex cores (inner diameter 3.6 cm). Additional cores at each elevation were used for sedimentological analyses. Meiofaunal samples were fixed with a heated (70°C) 4% buffered formaldehyde water solution. Sampling began at high tide and followed the receding water down the beach ending at low tidal level. The highest sampling station (S1) was situated on the upper beach (4.90 m MLWS), the lowest (S9) at -0.42 m MLWS (see also Figure 5).

Laboratory treatment

In the laboratory, all meiofaunal samples were rinsed with a gentle jet of freshwater over a 1 mm sieve to exclude macrofauna, decanted over a 38 μm sieve, centrifugated 3 times with Ludox HS40 (specific density 1.18) and stained with Rose Bengal. All animals were counted and classified. From three of the four transects (including the two outermost ones), the first 200 nematodes were picked out using a stereomicroscope, transferred from formalin to glycerol through a series of ethanol-glycerol solutions and mounted in glycerine slides following the procedure described in Heip *et al.* (1985). Working with a fixed number of individuals (*i.e.* 200) has long been common practice in marine nematofaunal research and has proved to give a good representation of the nematode species composition (Vincx 1996 and references therein). However, some researches now think this is debatable. The nematodes were identified at species level and classified according to the phylogenetic system of Lorenzen (1994). The four feeding groups, distinguishing selective (1A) and non-selective (1B) deposit feeders, epistratum feeders (2A) and predators/omnivores (2B), based on buccal morphology (Wieser 1953), were used to investigate the trophic structure of the nematode assemblages as this classification is the most widely used among marine nematologists. Sediment particle-size distribution was determined using Coulter LS 100^o particle-size analysis equipment. The sediment fractions up to 1000 μm (clay, silt, very fine sand, fine sand, medium sand and coarse sand) were expressed as volume percentages, while the gravel fractions (>1000 μm), consisting mainly of shell fragments, were reported as mass percentages. Sediment fractions were defined according to the Wentworth scale (Buchanan 1984).

Data analysis

Using the M2 reduction model, combined with the continuous tidal elevation measurements (obtained from the Waterways and Maritime Affairs Administration, Flemish Community), the absolute elevation (relative to the mean low water spring level, MLWS) of the lowest station of each transect was determined, from which the values of the absolute elevation of all other stations and the beach profile were derived.

The morphodynamic state of the beach is given by means of two dimensionless parameters: Dean's parameter ($\Omega = H_b/W_s T$) and the relative tidal range ($\text{RTR} = \text{MSR}/H_b$), where H_b is the modal breaker height in m, W_s is the sediment fall velocity in m s^{-1} , T is the modal wave period in s and MSR is the mean spring tide range in m (Short 1999). Sediment fall velocity was calculated (Gibbs *et al.* 1971) from the median grain size of the upper beach as recommended by Short (1999). The distribution of granulometric data along transects was analysed using correlation-based principal-component analysis (PCA). Data were converted to approximately normality using a $\log(x+1)$ transformation prior to the analysis as described by Clarke (1993).

Nematode species data ($\text{Ind}/10 \text{ cm}^2$) were used to calculate the diversity as the number of species per sample (S), the Shannon–Wiener diversity index (H' , calculated using naperian logarithms) (Shannon and

Weaver 1949) and Hill's N_m (Hill, 1973). Evenness was calculated using Pielou's J' ($J'=H'/\log S$) (Pielou 1975). Diversity patterns were visualised by k -dominance curves (Lambhead *et al.* 1983). Differences in biotic and abiotic data between sampling stations and between zones were analysed using one-way ANOVA. Bartlett's and Cochran's tests were used to verify for homogeneity of variances prior to the analysis. When significant differences ($p<0.05$) were detected, Tukey's HSD for unequal N was used for a pair-wise comparison of sampling stations. Analyses were performed using the STATISTICA v5.5 software package (StatSoft 1995).

The nematode community structure was analysed by non-metric Multi-Dimensional Scaling using the Bray-Curtis similarity measure (MDS) (Kruskal 1964) and a Detrended Canonical Analysis (DCA) (Ter Braak 1988) both on square-root-transformed nematode species data per station. Using both MDS and DCA allows for checking the validity of the groups discerned. Non-parametric Multi-Response Permutation Procedures (MRPP) were used for testing multivariate differences among pre-defined groups (Mielke *et al.* 1976). All community analyses were done using the PC-ORD software package (McCune and Mefford 1999).

The species contributing to dissimilarities between zones were investigated using a similarity-percentages procedure (SIMPER, Clarke 1993). Formal significance tests for differences in nematode community structure between the zones were performed using the one-way ANOSIM tests (Clarke 1993). The relationship between nematode and granulometric data was analysed using the Spearman rank correlation (σ) and the significance was determined using a permutation procedure (RELATE, Clarke and Warwick 1994). The BIO-ENV procedure (Clarke and Warwick 1994) was used to define suites of sedimentological variables that best determine the nematode assemblage structures. ANOSIM, SIMPER and BIO-ENV analyses were performed using the PRIMER v5.2.9 software package (Clarke and Gorley 2001).

RESULTS

The environmental variables

A clay fraction (0–63 μm) was absent at all sampling stations. Fine sand (125–250 μm) was found to be the most dominant ($p < 0.001$) grain size fraction (Figure 2). A trend of decreasing median grain size (221 μm to 171 μm) with decreasing elevation relative to MLWS was noted, except for station S3 (230 μm). Shell fractions were only recorded at the 3 uppermost stations: 3% at station S1, 5% at station S2 and 16% at station S3.

The ordination of granulometric data by PCA (Figure 3) showed that there was a clear separation between the pre-defined tidal zones. The first two components of the ordination plot accounted for 84% of the total variance of the data. With an average median grain size of 211 μm of the uppermost beach station, H_b of 0.5 m, T of 3 s and MSR of 4.97 m, Dean's parameter (Ω) was estimated at 7.34 and RTR was 9.94. According to the morphodynamical classification scheme of Masselink and Short (Masselink and Short 1993; Short 1996), the beach was classified as an ultra dissipative beach with a semi-diurnal, macrotidal regime.

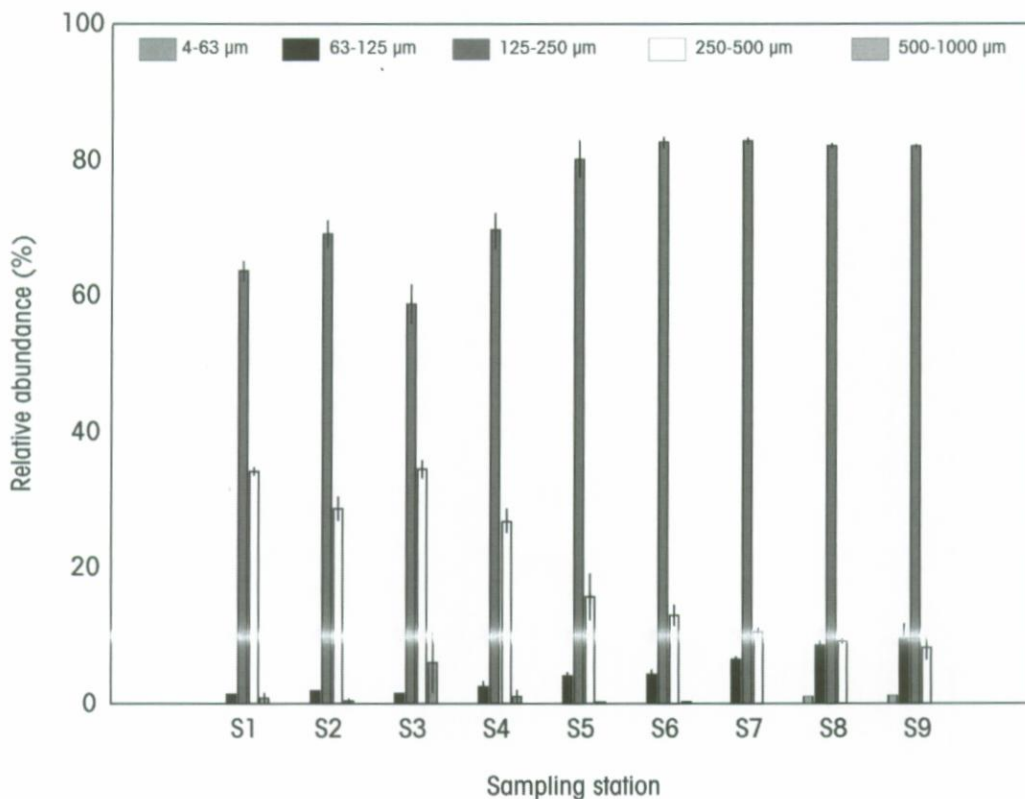


Figure 2: Sediment characteristics \pm SD per station. ($n=2$)

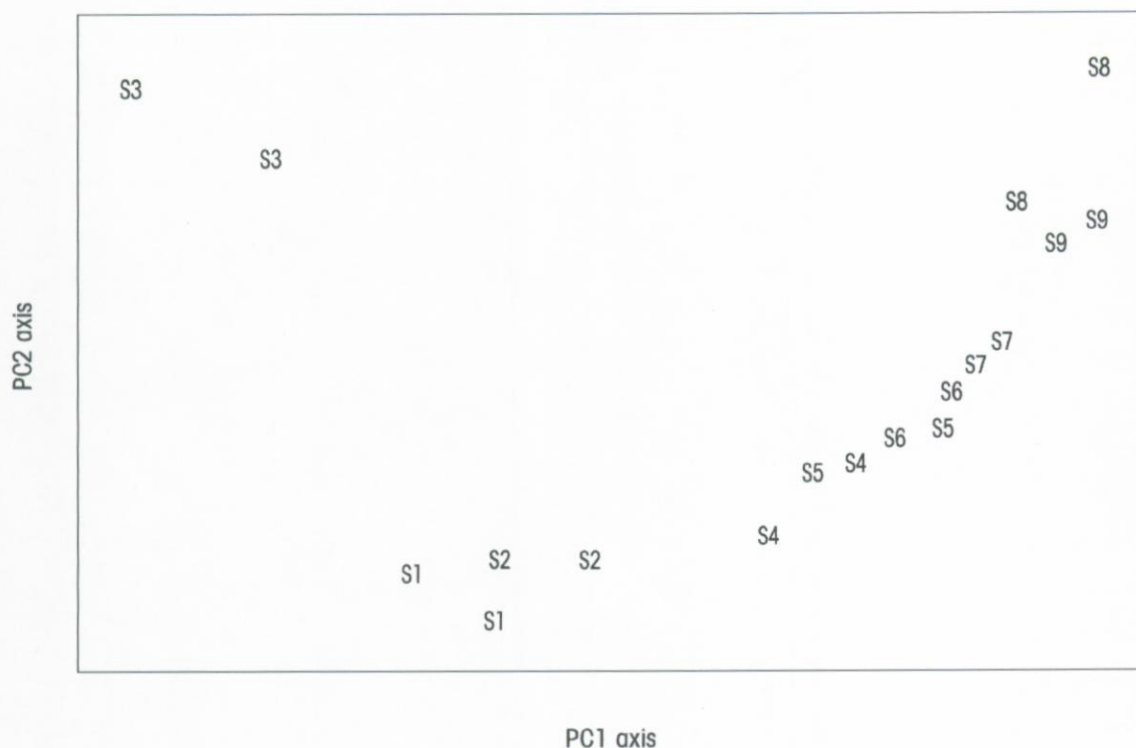


Figure 3: Ordination (first two components) of the granulometric variables by a correlation-based principal-component analysis (PCA). (n=2)

Nematode species composition, density and diversity

About 5400 specimens of nematodes were identified, belonging to 88 species, 65 genera and 26 families. Among the 26 families, Xyalidae were most dominant in densities (30%), number of genera (11) and number of species (20) (Table 1).

Nematode density increased from the upper (320 ± 45 Ind/10 cm², S1) towards the lower beach (2784 ± 6 Ind/10 cm², S8) (Figure 4). Nematodes were dominant at all stations and contributed 93% of the total meiofauna across the beach. With regard to the distribution of the species richness between tide marks (Figure 5), the number of species (S) increased significantly ($p < 0.001$) from the upper beach (8 ± 2 sp. in S1) towards the mid-tidal zone (34 ± 3 sp. in S4) from where it remained more or less constant (notwithstanding the much higher densities at the lower beach) (Table 2; Figure 5).

Family	% of total	Number of genera	Number of species
Xyalidae	29.72	11	20
Oncholaimidae	10.28	4	4
Chromadoridae	8.70	5	8
Cyatholaimidae	8.40	4	6
Axonolaimidae	8.36	3	6
Thoracostomopsidae	5.77	2	4
Desmodoridae	5.25	5	5
Aegiolaimidae	4.70	2	2
Monoposthiidae	3.60	1	2
Rhabditidae	3.29	1	1
Microlaimidae	2.38	2	4
Linhomoeidae	2.37	5	4
Selachinematidae	1.61	4	4
Leptolaimidae	1.55	2	3
Anoplostomatidae	0.96	1	1
Tripyloididae	0.81	1	1
Tarvalidae	0.54	1	1
Comesomatidae	0.51	2	3
Ironidae	0.38	1	1
Diplopeltidae	0.34	1	1
Sipholaimidae	0.18	1	1
Trefusiidae	0.17	2	2
Neotonchidae	0.06	1	1
Phanodermatidae	0.03	1	1
Rhabdodemanidae	0.03	1	1
Coninckidae	0.02	1	1
TOTAL	100	65	88

Table 1: Overall relative abundance of the nematode families collected at De Panne beach, listed in descending order of dominance, with indication of the number genera and species found.

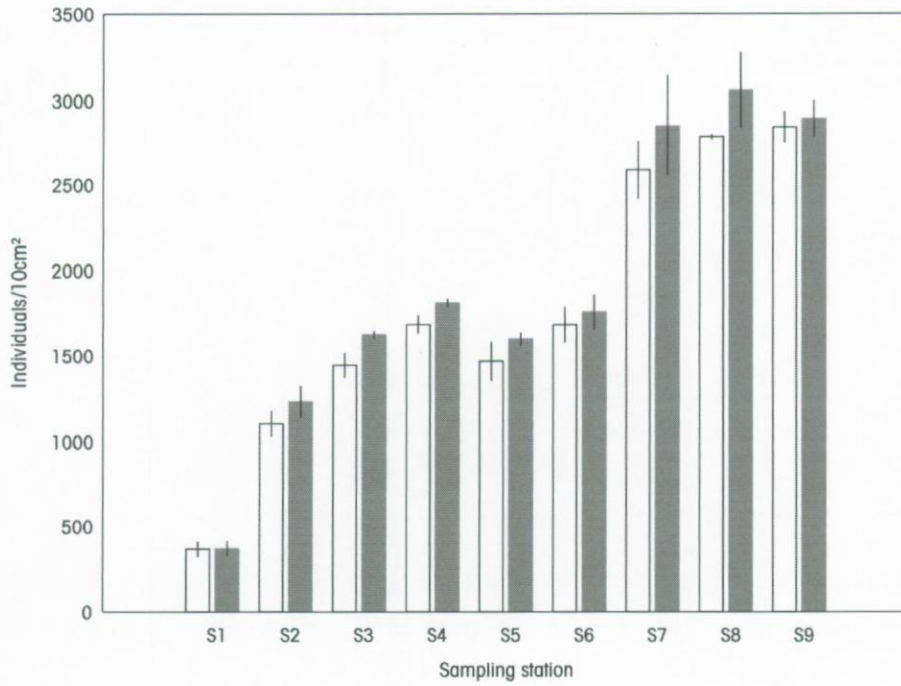


Figure 4: Mean densities and standard errors (calculated by pooled variance of four replicates) per sampling station for nematode densities (white bars) and total meiobenthic densities (gray bars).

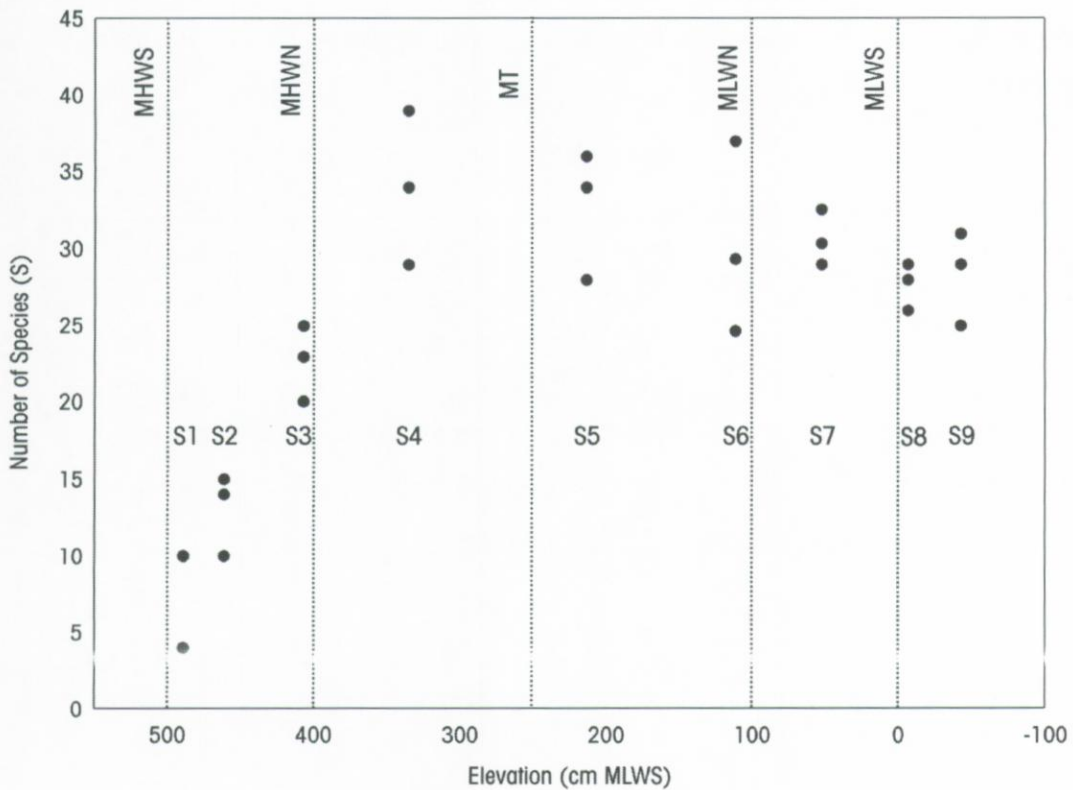


Figure 5: Intertidal distribution (cm relative to MLWS) of the nematode species richness (S) per sampling stations (S1 to S9). (n=3)

Station	Number of species (S)	Evenness (J')	Shannon diversity (H')	N _{inf}	Trophic Index (T)
S1	8 ± 2	0.52 ± 0.13	1.10 ± 0.37	1.60 ± 0.33	0.78 ± 0.13
S2	13 ± 2	0.66 ± 0.03	1.69 ± 0.15	2.10 ± 0.18	0.62 ± 0.08
S3	23 ± 2	0.77 ± 0.03	2.40 ± 0.09	4.85 ± 0.40	0.34 ± 0.01
S4	34 ± 3	0.78 ± 0.01	2.76 ± 0.04	3.07 ± 0.09	0.35 ± 0.01
S5	33 ± 2	0.86 ± 0.01	2.89 ± 0.05	6.80 ± 0.80	0.35 ± 0.04
S6	33 ± 2	0.81 ± 0.01	2.73 ± 0.04	6.43 ± 0.24	0.42 ± 0.00
S7	30 ± 1	0.86 ± 0.01	2.90 ± 0.04	7.27 ± 1.16	0.33 ± 0.01
S8	28 ± 1	0.82 ± 0.02	2.73 ± 0.07	5.69 ± 0.70	0.36 ± 0.05
S9	28 ± 2	0.75 ± 0.02	2.52 ± 0.10	3.45 ± 0.58	0.39 ± 0.08

Table 2: Comparison of the nematode species richness (S), Evenness (J'), Shannon diversity (H'), Hill's N_{inf} and Heip's trophic index (T)¹ between the nine intertidal sampling stations. Data are represented as means and standard errors. (Calculated by pooled variance of three replicates)

Results of one-way ANOVA showed that dominance, expressed as Shannon Wiener index (H') and N_{inf}, was significantly different between stations (Table 3). Tukey's HSD analysis for unequal N showed that these differences were mainly caused by the upper beach stations (S1 and S2) and the strandline (S3). Dominance (except N_{inf}) and species richness were not significantly different between mid-tidal and lower beach stations.

	F-value	p-value	Comparison
Number of species (S)	25.10	0.00001	1,2<3<4-9
Evenness (J')	5.61	0.00117	1>2<3-9
Shannon diversity (H')	17.77	0.00007	1,2<3-9
N _{inf}	13.30	0.00001	1,2<3,4<5-8>9
Trophic Index (T)	6.64	0.00056	1,2>3-9

df_{treat} = 8 df_{error} = 18

Table 3: Results of one-way ANOVA for mean univariate indices. Degrees of freedom (df), F-values and p-values are reported. Significant differences between sampling stations evaluated with Tukey's unequal HSD multi-comparison test.

¹ Heip's trophic diversity index (T) was calculated to describe the diversity in feeding types as $T = \sum \theta^2$, with θ the relative proportion of each Wieser feeding type in the assemblage (Heip *et al.* 1984). Trophic diversity is highest when all four feeding types are equally present (*e.g.* T=0.25) and lowest when only one trophic type is present (*e.g.* T=1).

Nematode communities

MDS-analysis (Figure 6) and Detrended Canonical Analysis (DCA) divided the total nematode community of the beach into four different species associations, reflecting their intertidal distribution: the upper beach (S1 and S2), the strandline (S3), the middle beach (S4, S5, S6, and S7) and the lower beach association (S8 and S9). The MDS-ordination for nematode species showed a considerable degree of similarity and a low stress value (0.08), indicating a good and useful 2D-representation of the groups in a subset of habitats (runnels were excluded) occurring across the beach. MRPP showed these groups to be significantly different at $p < 0.0001$. The ANOSIM results (Table 4) indicate that the four nematode species associations were significantly different.

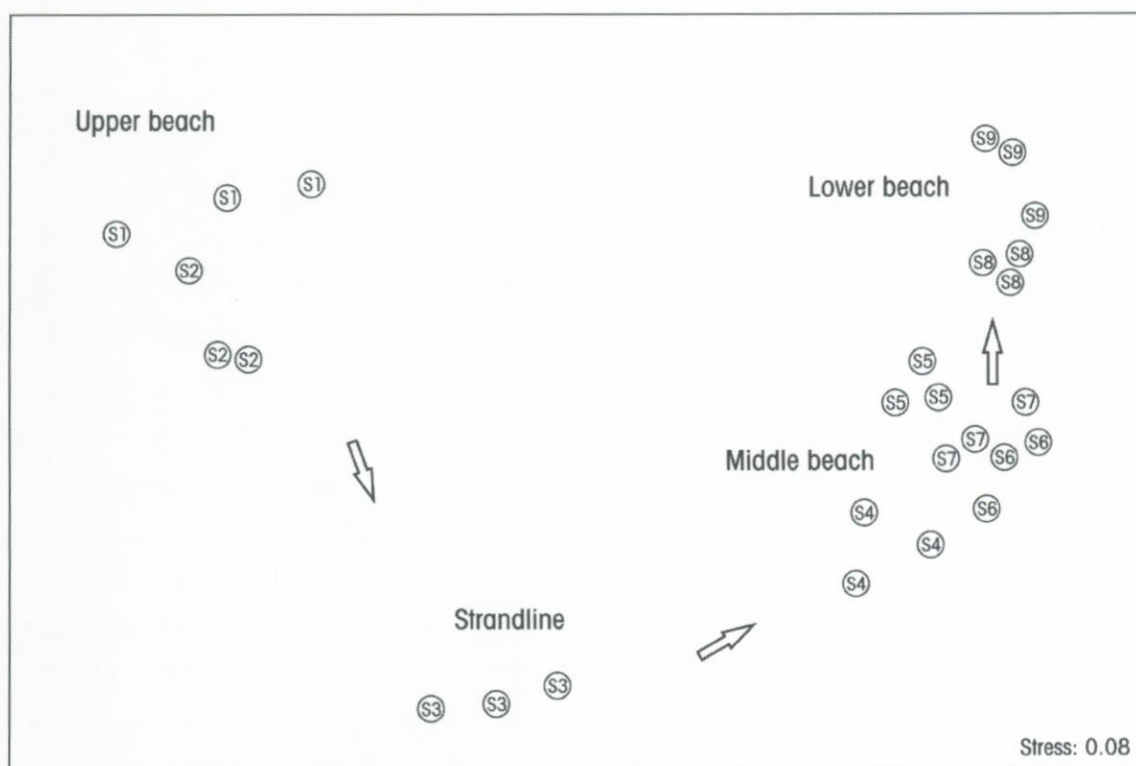


Figure 6: Nematode assemblages: Output of non-metric Multi-Dimensional Scaling (MDS) on square-root-transformed species abundance data with indication of the four intertidal zones. (Stress: 0.08) (n=3)

Nematode community structure			
	Dissimilarity	R-value	p-value
Global test	77 %	0.878	0.001
Zones compared			
I-II	75%	0.926	0.012
I-III	87%	0.998	0.001
I-IV	92%	0.992	0.002
II-III	74%	0.986	0.002
II-IV	79%	0.987	0.012
III-IV	56%	0.614	0.001

Table 4: Results of the ANOSIM and pair-wise tests (R-values and p-values are reported) for difference on nematode community structure between zones of De Panne Beach (I= upper beach; II= strandline; III= middle beach; IV= lower beach). Dissimilarities as calculated by SIMPER-analyses. (Analyses performed on square-root transformed data)

The SIMPER-analysis indicated a strong dissimilarity between the upper beach species assemblage and the other assemblages: 75% with the strandline, 87% with the middle beach, and 92% with the lower beach assemblage. These significant differences were largely the result of high abundances of the brackish water nematode *Pellioditis marina* (BASTIAN, 1865) in the upper beach assemblage, while this species was absent in the other assemblages. The average dissimilarity between all nematode assemblages was 77%. Pair-wise dissimilarities between species associations decreased down the beach; the middle and low beach differed by about 56%. (Table 4) This is also clear from the SIMPER-lists, showing the contribution percentages of the top five discriminating species for each species association. The middle beach and the lower beach share more top five species in more or less the same relative abundances (*Paracanthochus thaumasius* (SCHULTZ, 1932); *Monoposthia mirabilis* (SCHULTZ, 1932) and *Daptonema normadicum* (DE MAN, 1890)), while this is not the case between the other associations (with the exception of *Daptonema* sp.1 in the upper beach and strandline). (Table 5)

Species association 1 Upper beach			Species association 3 Middle beach		
<i>Pellioditis marina</i>	41%	1B	<i>Oncholaimellus calvadosicus</i>	12%	2B
<i>Daptonema</i> sp. 1	21%	1B	<i>Paracanthochus thaumasius</i>	9%	2A
<i>Axonolaimus helgolandicus</i>	14%	1B	<i>Daptonema normandicum</i>	7%	1B
<i>Chromadorita nana</i>	4%	2A	<i>Odontophora phalarata</i>	7%	1B
<i>Calyptronema maxweberi</i>	4%	1B	<i>Monoposthia mirabilis</i>	5%	2A

Species association 2 Strandline			Species association 4 Lower beach		
<i>Theristus otoplanobius</i>	16%	2A	<i>Daptonema normandicum</i>	10%	1B
<i>Daptonema</i> sp. 1	14%	1B	<i>Odontophora rectangula</i>	7%	1B
<i>Spilophorella candida</i>	11%	2A	<i>Paracanthochus thaumasius</i>	7%	2A
<i>Onyx sagittarius</i>	11%	2B	<i>Cyartonema elegans</i>	7%	1A
<i>Enoplolaimus littoralis</i>	10%	2B	<i>Monoposthia mirabilis</i>	6%	2A

Table 5: SIMPER-lists, showing the contribution percentages of the top five discriminating species for each species association and their feeding strategy. (See text for details)

The k -dominance curves ² (Figure 7) clearly indicate the middle beach species association as the most diverse one on the beach.

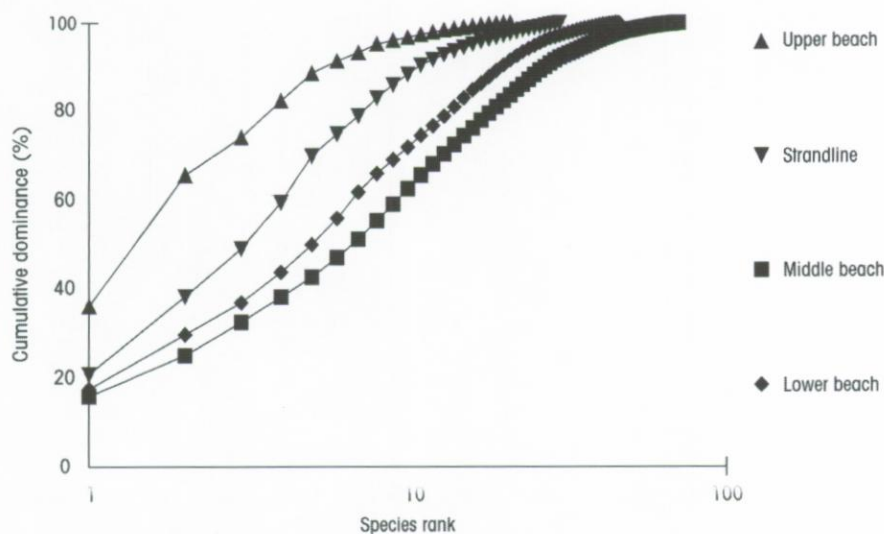


Figure 7: k -dominance curves for nematode species data. (Sum of stations, each three replicates per species association)

² As these k -dominance curves are based on an unequal number of stations per species association, this can lead to a real prospect of a misleading interpretation. However, calculation of individual k -dominance curves per station indicated nearly the same patterns. (i.e. upper beach stations: lowest diversity, highest dominance; middle beach stations: lowest dominance, highest diversity)

Analysis of the feeding types according to Wieser (1953) showed a significant dominance ($p < 0.001$) of non-selective deposit feeders (1B) in each assemblage, except in the strandline where epistratum feeders (2A) dominated. Nematodes with an armed (stilet, teeth, denticles) buccal cavity (2A + 2B) dominated the strandline, while in all other zones deposit feeders (1A + 1B) dominated. The selective deposit feeders (1A) became more important towards the lower beach (Figure 8).

Results from the RELATE-analyses reveal that Spearman rank correlations between Euclidean distance matrix from granulometric data and similarity matrices from the nematode data were all significant ($p < 0.05$). In a Pearson product-moment correlation analysis, none of the granulometric variables were highly correlated (> 0.95), and thus all variables were used in the BIO-ENV analyses. Along the beach, a combination of very fine sand (63-125 μm) and percentage of shells best explained ($\sigma = 0.532$) the nematode assemblages structure.

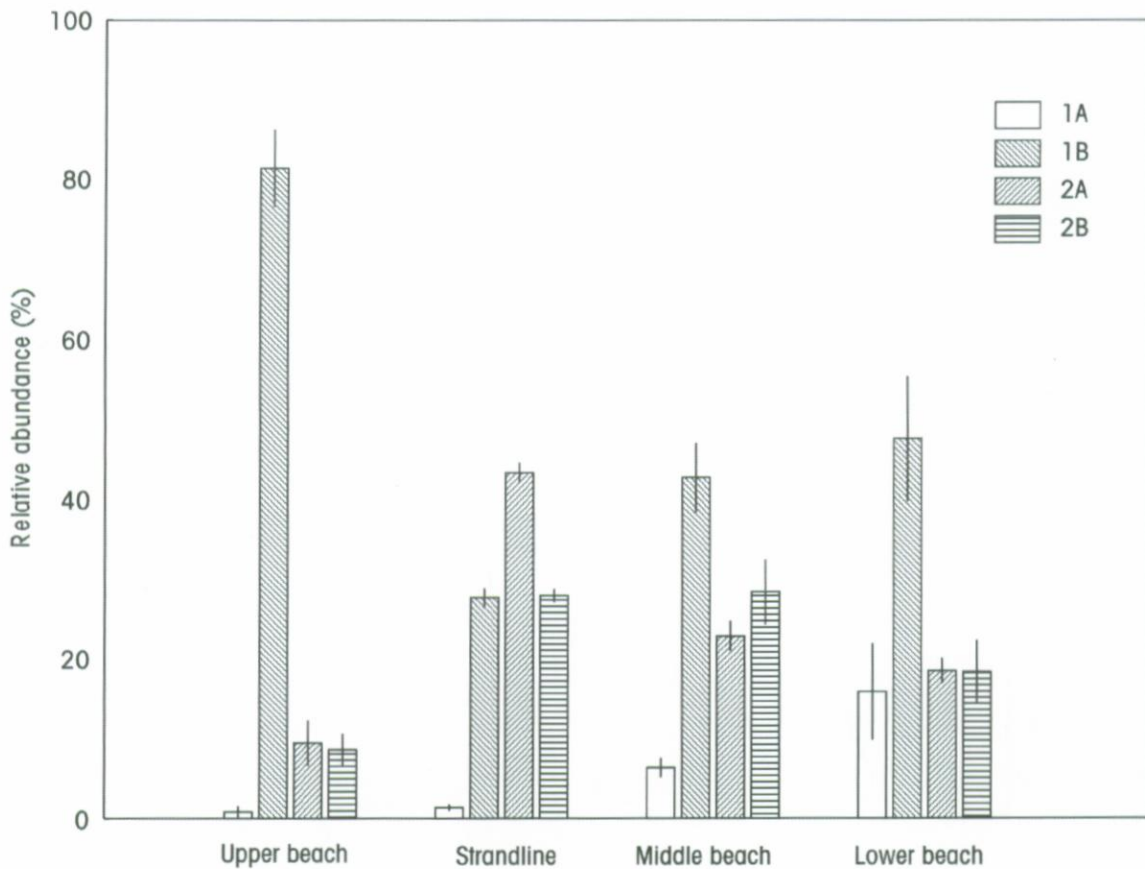


Figure 8: Means and standard errors for Wieser feeding types (described in text) within the four zones of De Panne beach. (Calculated by pooled variance) ($n=3$)

DISCUSSION

Nematode species composition and abundance

All free-living marine nematodes are considered to be members of the meiobenthos, small organisms separated from the larger macrobenthos on a methodological basis (*i.e.* animals passing a 1 mm sieve). Worldwide dominance of nematodes as taxonomic unit within the meiofauna of fine-grained marine sandy beach sediments (Brown and McLachlan 1990) is also obvious for the beach of De Panne. Total nematode densities are fairly similar to those reported from studies at higher meiofaunal taxon levels on European sandy beaches (Gray and Rieger 1971; Harris 1972; Olafsson 1991) and elsewhere (McIntyre and Murison 1973; McLachlan 1980; Dye and Furstenberg 1978; Rodriguez *et al.* 2001). However, some caution is warranted because different sampling strategies have been used together with different collection and extraction techniques (*e.g.* Karaman/Chappuis versus core sampling (Gourbault and Warwick 1994)). The general increase in nematode densities towards the low water mark is noted in most of these studies although some exceptions with highest densities in the upper beach zone exist (Rodriguez *et al.* 2001). An important feature of nematode populations, perhaps the most significant in understanding their ecological success, is the large number of species present in one habitat. The dominance of Xyalidae in our study site is confirmed by Nicholas and Hodda (1999), who studied the intertidal zone of a high-energy Australian sandy beach. Nematode species number generally falls between 70 (Platt 1977a, b) and 145 (Wieser 1959; Ott 1972; McIntyre and Murison 1973). Blome (1974, 1982, 1983) recorded 179 species on the sandy beach of Sylt but this research covered several intensive campaigns during several years. With a total of 88 species, the beach of De Panne falls within these ranges but the validity of comparing species numbers may be questioned since beach type (reflective versus dissipative), tidal regime (macrotidal versus microtidal), sampling effort and strategy are not always mentioned in the above studies. Especially water percolation (related to the beach morphodynamics) seems to play an important role in understanding meiobenthic life on sandy beaches. Dissipative beaches consist of finer sands with lower permeabilities and therefore filter smaller volumes of water and nutrients at lower rates, resulting in the fauna being concentrated mainly at the surface centimetres (McLachlan and Turner 1994). Nematodes can be found much deeper in the sediment on well-oxygenated, high-energy, coarse-grained reflective beaches (McLachlan *et al.* 1977). Munro *et al.* (1978) recorded nematodes down to 105 cm at such well-oxygenated beaches. Thus, most of the nematode data from these beaches are likely to be underestimated due to inadequate depths of core sampling. However, it remains uncertain whether such deep-dwelling nematodes belong to marine species, or are terrestrial/fresh-water ones living in association with the freshwater table.

The increase in meiobenthic species diversity towards the mid-tidal level is also known from Sylt (Armonies and Reise 2000), one of the most intensively studied sandy beaches in Europe. According to Armonies and Reise (2000) interstitial species on sandy beaches are faced with two gradients, a physical-horizontal (time

of submergence and sediment stability) and a chemical-vertical (oxygen concentration) gradient. The combination of those horizontal and vertical gradients may generate a complex spatial matrix of living conditions (Fenchel *et al.* 1967). Assuming a similar importance of the two gradients, optimal conditions can be expected to occur somewhere in the middle of the beach. On most dissipative beaches, this is the place where the water table comes closest to the surface, the so called exit point (Short 1999) where an optimal balance may exist between organic matter supply and oxygen and water retention (McIntyre 1969; Ott 1972). Highest diversity near the mid-tidal zone also fits well with Huston's dynamic equilibrium hypothesis (Huston 1979). Along dissipative beaches, highest sediment stability and longest submergence (*i.e.* less oxygen and consequently an RPD-layer closer to the surface, less desiccation and temperature variability) are found on the lower beach, while lowest sediment stability and shorter submergence (and thus better oxygenation, more desiccation and temperature variability) are found on the upper beach (Short 1999). According to Huston (1979), optimal conditions (in terms of sediment stability and submergence) will probably be found somewhere around the mid-tidal level. Further, the mid-tidal level at an ultra-dissipative beach is dominated by a mixture of swash processes (which are dominating on the upper beach) and surf zone processes (which are dominating the lower beach). The observed maximum in species richness near the mid-tidal is, however, not in line with sandy beach macrofauna which normally tends to increase gradually from the upper beach towards the low water mark (McLachlan and Jaramillo 1995). This higher macrobenthic diversity near the lower beach may be explained by a direct dependence of feeding activity in most macrofaunal species on submergence time (Armonies and Reise, 2000). Also a continuous influx of mobile animals from the subtidal seems plausible. The nematode species richness found on this beach (88 species) is higher than the 39 macrofauna species recorded by Degraer *et al.* (1999) on the same transects along the beach. Since nematodes constitute only a fraction of the meiofauna, it is most likely that meiobenthic diversity on beaches is usually an order of magnitude higher than macrobenthic diversity. This high nematode diversity on beaches (compared with macrofauna) can be explained by its ability to partition the environment extensively in various ways and of which food partitioning (Platt and Warwick 1980; Heip *et al.* 1985) seems to be the most crucial one. The relative proportion of each of the four Wieser feeding types in a community depends on the nature of the available food (*e.g.* organic enrichment in the strandline), which in turn is reflected by the nature of the sediment (Platt and Warwick 1980). According to Armonies and Reise (2000), it is the long history of a structurally complex beach habitat (which has persisted essentially unchanged since the beginning of metazoan life) together with founder effects and genetic drift in small meiobenthic populations (caused by the absence of rapid dispersal) that generates high meiobenthic species richness.

Nematode zonation

The sampling design used means that the following discussion on the nematofaunal zonation is limited to a small section (15 m) of the beach. However, as the multivariate analyses based on individual transects (not shown) are showing the same trends as the pooled analyses we assume that they might be more widely relevant. Apart from the extensive study on an open-sea dissipative beach in Sylt by Blome (1974, 1982, 1983) zonation studies based on nematode species on European sandy beaches are lacking. According to McLachlan and Turner (1994) and McLachlan and Jaramillo (1995), zonation on sandy beaches should mainly be explained physically by desiccation of the sediment during low tide (osmotic stress) and by dissolved oxygen concentrations in the interstitial water, while predation and competition for food are important biological factors. At De Panne, four nematode species associations reflecting the tidal zonation were discerned by multivariate analysis. Species association 1, associated with the upper beach, is a community experiencing momentary flooding by the seawater. Additionally, the temperature rises during low-tide exposure, reaching maximal values at the sediment surface. These temperatures may exceed optima and perhaps even upper tolerance limits of many free-living marine nematode species.

Between optimal and upper lethal temperatures, even slight temperature changes can impact reproductive and metabolic activity (Moens and Vincx 2000). Species in this community have to deal with very high osmotic stress, and consequently only a few species can survive in this harsh environment. This part of the beach is also where recreation activities are most intense (pers. obs.). As noted by Chandrasekara and Frid (1996), a decrease in diversity of the infauna caused by human trampling is to be expected. The high values for dominance and the unequally distributed feeding types (as noticed in a higher trophic index) are indicative of the stress in this community. High dominance is caused by *Pellioditis marina* (Bastian 1865) Andrassy 1983, a bacterivorous brackish-water nematode. *P. marina* populations have a high colonisation capability and short generation times and can thus rapidly exploit short-lived habitats. They are typical enrichment opportunists (Bongers *et al.* 1991) living in association with high microbial activity around decaying seaweed, uplifted from the nearby strandline. Normally, one would expect *P. marina* to be associated with the decaying organic matter in the strandline, but the increase towards truly marine salinities (34 PSU) from the upper beach to the strandline probably excludes this species from the strandline as its scope for food decreases with salinities above 30 PSU (Moens and Vincx 2000). The detection of *P. marina* on the upper beach is in concordance with the survey of Blome (1983) on the beach of Sylt. The second species association comprises only sampling station S3 and is associated with the strandline on the beach of De Panne. This line demarcates a sharp boundary between species association 1, which has some affinities with the terrestrial ecosystem, and the truly marine species associations. In this area various deposits (mostly algae) are left behind by the receding water, causing organic enrichment of the sediment. This zone is dominated by epistratum feeders (2A) and predators/omnivores (2B). An explanation could be the presence of a high proportion of shell fragments and coarse sand, in combination with the organic enrichment, from which these epistratum feeders are scraping off bacteria and unicellular eukaryotes. Further, because of the coarser sediment, the upper sediment layers dry out faster and are therefore

disadvantageous to a deposit-feeding feeding strategy. The predators/omnivores feed on organisms (other meiofauna or small macrofauna) that are taking advantage of the organic enrichment (Jensen 1987) associated with the strandline. Warwick (1976) recorded a predominance of predators/omnivores in sediments around several weed types in the intertidal. As De Backer (2001) found a strandline-specific macrobenthic life in De Panne, it seems likely that this is also true for nematodes. The third species association, associated with the mid-tidal beach, is exposed to longer tidal immersion and is found in sediments with a smaller grain size. As a consequence, different stress factors (osmotic stress, temperature, salinity) important in structuring nematode communities (Schratzberger and Warwick 1998, 1999) are more buffered. In this zone optimal conditions (see above) are encountered, resulting in higher nematode diversities. As a consequence of the longer tidal immersion and the fine median grain size, deposit-feeding (1A + 1B) nematodes are dominant. The fourth community groups the lower beach stations, which become dry only a few hours a day and are characterised by finer sediments than the other stations. Consequently, temperature and salinity are relatively constant and interstitial spaces are almost always filled with water. This favours a deposit-feeding life strategy. However, nematode diversity is less than on the middle beach, because at the lower tidal level sediment cores showed black sediments at a few cm depth (pers. obs.), indicating reduced oxygen levels. Lower nematode diversity in shoreline fine-grained sediments, associated with low oxygen content or oxygen depletion, has been documented before by Steyaert *et al.* (1999). The presence of *Monoposthia mirabilis* (Schultz 1932), several *Odontophora* and *Paracanthochus* species in the mid- and low-tidal zone is confirmed by the study of Blome (1983), probably indicating that, just like macrofauna, the different intertidal zones of sandy beaches harbour more or less the same or related (at genus level) species. The multivariate analyses, average dissimilarities and *k*-dominance curves indicate that the differences between the middle and lower beach communities are not well defined and tend to overlap. This corresponds with the conclusion of McLachlan and Jaramillo (1995) that the zonation on sandy beaches is dynamic and variable, usually being most distinct in the upper part and becoming less clear down the beach. The zonation patterns described above also have some affinities with the general zonation scheme of Davenport (1903) and Dahl (1952), who (based on macrofauna species) discerned: (1) a subterrestrial fringe, (2) a midlittoral and (3) a sublittoral species association in the intertidal zone. Degraer *et al.* (1999) described two macrofaunal species associations on the same beach: a species-poor high-intertidal species association dominated by *Scolecopsis squamata* and a relatively species-rich, low-intertidal species association characterised by *Nephtys cirrosa*. Degraer *et al.* (1999) suggested that the low-intertidal species association is in fact an intertidal extension of subtidal species associations. As 82% of the recorded nematode species in the mid- and lower-beach assemblages are also known from the crests of the well-studied Belgian subtidal sandbanks and offshore stations (Vincx 1986; Vanaverbeke *et al.* 2002) this possibly also holds true for nematode species.

CONCLUSIONS

We conclude that, as for macrobenthos, overall meiobenthic/nematode densities increase towards the low-tidal level. In contrast to the well-known increase in macrobenthic diversity towards the low-tidal level, nematode diversity is highest in the mid-tidal zone. In general, meiobenthic diversity on the beach is higher than macrobenthic diversity even when only the nematode fraction is analysed. Nematode communities are indeed zoned along the beach gradient within four assemblages associated with the tidal zonation: upper-beach, strandline, mid- and low-tidal level. A combination of very fine sand and percentage of shell fragments provided the best suite of variables to determine the different nematode assemblages. The assemblages tended to show more similarities down the beach, indicating a more gradual transition between the lowest communities.

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