The sandy beach meiofauna and free-living nematodes from De Panne (Belgium)

T. GHESKIÈRE, E. HOSTE, L. KOTWICKI, S. DEGRAER, J. VANAVERBEKE & M. VINCX

Summary

Despite their rather barren and arid appearance, European sandy beaches harbour a highly diverse fauna and flora and some of them are even highly productive. In contrast to tropical sandy beaches little is known about the structural and functional diversity of the different benthic components. This study aims to investigate the structural diversity of the meiobenthos, emphasizing on free-living marine nematodes on a Belgian sandy beach.

The samples were collected on the sandy beach of De Panne in the swept prism, *i.e.* the zone between highest and lowest watermark, subjected to tidal inundation. The beach, situated before the nature reserve "Westhoek Reservaat", is a macrotidal, dissipative, little exposed beach with fine-grained sediment. Within the meiobenthos, 11 taxa were recognized. Free-living Nematoda were the dominant (75.8 %-97.1 %) metazoans in all the stations, mostly followed by Turbellaria. The meiobenthic densities increased towards the low water mark as a consequence of macroscaled physical gradients. A patchy distribution of meiobenthos is primarily caused by gradients on microscale. Within the nematodes a total of 87 species, belonging to 67 genera, were recognized. Multivariate and statistical techniques in combinations with indicator species analysis revealed nematode communities associated with dry sand (*Rhabditis* sp.1 and *Axonolaimus helgolandicus*), upper (*Trissonchulus* sp.1 and *Dichromadora hyalocheile*) and lower littoral (*Odonthophora phalarata*, *Odonthophora rectangular*, *Chaetonema riemanni* and *Cyartonema elegans*).

Keywords: meiofauna, sandy beach, free-living marine nematodes.

Samenvatting

Niettegenstaande Europese zandstranden soms verdroogd en verdord lijken herbergen deze toch een zeer diverse fauna en flora. Sommige zandstranden zijn zelfs zeer productief. In tegenstelling tot tropische zandstranden is er bijna geen informatie beschikbaar over de structurele diversiteit van de verschillende benthische componenten. Deze studie heeft tot doel een beeld te schetsen van de structurele diversiteit van het meiobenthos met speciale aandacht voor de vrijlevende mariene nematoden op een Belgisch zandstrand. Hiervoor werden stalen genomen in het intergetijdengebied van het strand van De Panne. Dit fijnzandig strand, gesitueerd voor het "Westhoek Reservaat", is een macrotidaal, dissipatief en weinig geëxposeerd zandstrand. Binnen de meiobenthische component werden 11 verschillende taxa herkend. Vrijlevende mariene Nematoda waren de dominante meercelligen (75.8 %-97.1 %) in alle bemonsterde stations, meestal gevolgd door Turbellaria. De meiobenthische densiteiten stegen naar de laagwaterlijn toe als gevolg van fysische gradiënten op macro-schaal en vertoonde eveneens een gevlekt distributiepatroon als gevolg van gradiënten op micro-schaal. In totaal werden 87 nematodensoorten geïdentificeerd behorende tot 67 genera. Multivariate technieken werden gebruikt om zonatiepatronen te herkennen en samen met indicatorsoorten analyse resulteerde dit in nematodengemeenschappen geassocieerd met droog strand (*Rhabditis* sp.1 en *Axonolaimus helgolandicus*), hoogstrand (*Trissonchulus* sp.1 en *Dichromadora hyalocheile*) en laagstrand (*Odonthophora phalarata*, *Odonthophora rectangular*, *Chaetonema riemanni* and *Cyartonema elegans*).

Trefwoorden: meiofauna, zandstrand, vrijlevende mariene nematoden.

Introduction

With the recent concern about enhanced rates of species extinction caused by human activity, the need for a reliable estimate on the global number of species has become important (MAY 1988). Sandy shorelines provide an environment of high physical stress to the marine fauna and as a result relatively few species inhabit this specific transitional ecosystem between the terrestrial and the marine environment. In contrast to rocky shorelines, sandy beaches seem to harbour no life at first sight and appear as "biological deserts". However, these sandy beaches act as important fouraging grounds for many birds such as sanderlings (*Calidris alba*) and oystercatchers (*Haematopus ostralegus*) (ENGLEDOW *et al.* 2001). Despite the fact that 30 % of the European coastline consists of sandy shores, their ecological importance and their close interaction with human life, there is only limited information, apart from taxonomic papers, available about the meiobenthos (a.o. COVAZZI *et al.* 2000, HARRIS 1972, RENAUD-DEBYSER & SALVAT 1963, JOUK *et al.* 1988, MARTENS 1984, MARTENS *et al.* 1985). This is in sharp contrast with the tropical sandy beaches, which are well documented (a.o. ANSARI *et al.* 1990, ANSARI & INGOLE 1983, INGOLE & PARULEKAR 1998, ANSARI *et al.* 1984, GOURBAULT *et al.* 1998).

As a result of their high abundance, a spectrum from tolerance to non-tolerance for several kinds of pollution and disturbances, ubiquitous distribution, rapid generation and fast metabolic rates, free-living marine nematodes have an important role in the ecosystem functioning. Therefore the state and composition of meiofauna assemblages may reflect the general health of the marine benthos (KENNEDY & JACOBI 1999). Moreover, by the virtue of their universal dominance and robust bodies, nematodes are good indicators for studying the impacts of different kinds of natural and anthropogenic disturbances on the marine environment (SANDULI & NICOLA 1991). The theoretical and practical advantages and disadvantages of using meiofauna and nematodes as bio-indicator are summarized in SCHRATZBERGER *et al.* (2000).

Meiofauna (all Metazoans between 1 mm and 38 μm) is thought not to be incorporated in foodchains leading to higher trophic levels; the assemblages are mainly controlled by internal predation (MCINTYRE 1971, MCINTYRE & MURISON 1973). However, several studies (COULL *et al.* 1989, COULL *et al.* 1995, AARNIO 2000) have shown that meiofauna is an optimally sized prey for many small and juvenile fish. Also deposit-feeding macrofauna have been shown to consume meiofaunal organisms (GERLACH 1978).

In this paper we report preliminary results of a study of meiofaunal abundance with emphasis on the composition of the free-living nematode assemblages at species level from a dissipative, macrotidal Belgian sandy beach in De Panne.

Study site

The study area is located (51°05'30''N, 02°34'01''E) at the Belgian West Coast in front of the nature reserve ''Westhoek reservaat'', nearby the French border (fig. 1). The landward margin of the intertidal zone is interrupted by a concrete stormwater dyke, constructed to protect the low-lying ''Westhoek'' dune reserve from seawater erosion. According to the morphodynamical classification scheme of MASSELINK and SHORT (MASSELINK & SHORT 1993, SHORT 1996) this beach is classified as a dissipative beach (low beach gradient, fine to very fine sediment and a surf zone with the presence of numerous spilling lines of breakers) with a semi-diurnal, macrotidal regime. The width of the intertidal zone is approximately 430 m and the beach has some runnels parallel to the water's edge in which seawater is retained on the outgoing tide.

Materials and methods

Sampling was done in August 2000 when high tide was expected at 02.22 pm (443 cm above Mean Low Low Water Spring, M.L.L.W.S.) and low tide at 09.39 pm (−79.8 cm above M.L.L.W.S.). Sampling began at the high tide and followed the receding water down the

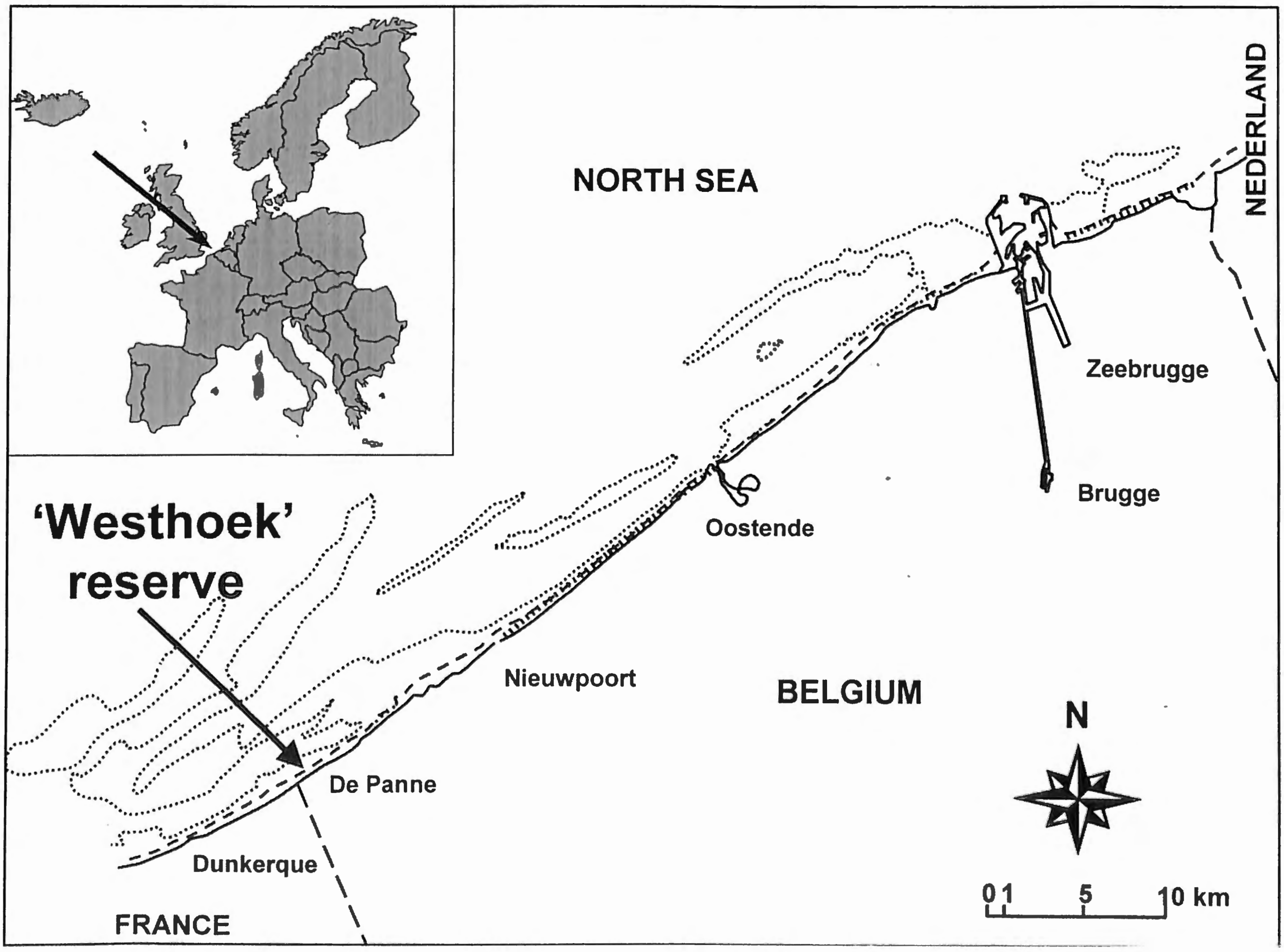

Fig. 1 — Map of the Belgian coastline, with indication of the study site.

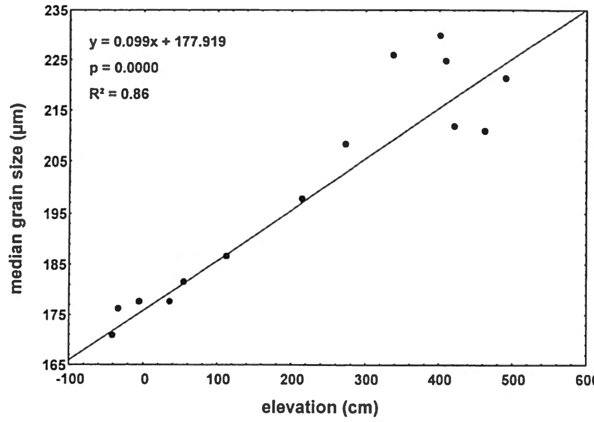

Fig. 2 — Correlation between median grain size and elevation above M.L.L.W.S.

beach. The highest sampling station (station 1) was situated immediately in front of the dyke (558 cm above M.L.L.W.S). Four meio perspex cores, each with a surface of 10 cm^2 and a depth of 10 cm^2, were taken at each of the fourteen sampling stations for the meiofauna while two additional cores were used for sediment analyses. The samples (except those for sedimentological analyses) were fixed with a (70°C) hot formaldehyde solution to a final concentration of 4 %. Hot formaldehyde prevents curling of the nematodes (HEIP *et al.* 1985, VINCX 1996). The meiofauna samples were treated in the laboratorium by passing through a 1 mm sieve and retaining on a 38 μm sieve. A density-gradient was used to extract the meiofauna from the fine-grained sediments (HEIP *et al.* 1985, VINCX 1996). Meiofauna was stained with Bengal Rose, counted and identified to the taxon level (Phylum, Classis, Subclassis or Ordo) under a stereomicroscope. From two of the four replicates of stations 1, 2, 4, 6, 8, 9, 10, 12 and 14, 200 nematodes were randomly picked, mounted into glycerine slides according to VINCX (1996) and identified to species level. Sediment particle-size distribution was determined using Coulter LS 100 particle size analysis equipment and the sediment fractions were defined according to the Wentworth scale (BUCHANAN 1984). In order to compare the meiobenthic and nematode densities and communities, uni- and multivariate techniques were performed. Nematode diversity was calculated as Hill's diversity indices (HILL 1973) of various order as recommended by HEIP *et al.* (1988). Indicator species were found using the method of DUFRENE & LEGENDRE (1997).

Results

Abiotic variables

The median grain size is highest on the upper parts of the intertidal zone and is decreasing towards the lower watermark. Fine sand (125μm-250μm) is the main sediment fraction in all stations and the percentage of this fraction is increasing towards the lower beach while the percentage of medium sand (the second most important sediment fraction) is decreasing. The median grain size was significantly correlated with elevation above M.L.L.W.S. (Spearman-rank $p<0.001$) (fig. 2).

Composition of the meiofauna

Eleven meiofaunal taxa (Nematoda, Turbellaria, Polychaeta, Oligochaeta, Gastrotricha, Tardigrada, Ostracoda, Harpacticoida, Bivalvia, Calanoida, Amphipoda) and naupliar larvae were found on the investigated sandy beach (ranging from two taxa at station 1 to eight taxa at station 13). Total meiobenthic densities ranged from 56 ± 13 ind/10 cm^2 at station 1 to 3518 ± 540 ind/10 cm^2 at station 12 (table 1). Nematodes were the only taxon occurring in all stations and represented between 75.8 % (station 5) and 97.1 % (station 14) of the total meiobenthic composition. The sampling stations were significantly different when considering nematode and total meiobenthic densities (Kruskal-Wallis $p<0.001$). Nematodes were the dominant metazoan organisms at the entire sampling transect, mostly followed by Turbellaria except in the first three stations where respectively Oligochaeta, Tardigrada and Tardigrada were subdominant. Generally, the total meiobenthic densities increased towards the low watermark.

The nematodes: diversity and community analysis

During this first survey of the Belgian sandy beach nematodes, a total of 2988 identifications have been done, resulting in 87 nematode species belonging to 67 genera and 28 families. The species list (table 2) possibly in-

Table 1 — Average densities of meiofaunal taxa at the sandy beach of De Panne Westhoek.

Taxa \ Station	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Nematoda	54 ± 12	1602 ± 473	890 ± 165	1430 ± 149	598 ± 88	1310 ± 280	498 ± 35	1801 ± 257	1013 ± 94	1854 ± 574	913 ± 291	3280 ± 601	3066 ± 694	1428 ± 297
Harpacticoida	–	1 ± 1	19 ± 3	40 ± 6	29 ± 4	38 ± 9	11 ± 1	5 ± 3	1 ± 0	3 ± 1	3 ± 1	1 ± 0	4 ± 1	7 ± 2
Turbellaria	–	46 ± 8	43 ± 21	91 ± 31	147 ± 36	123 ± 52	90 ± 27	119 ± 51	67 ± 32	271 ± 143	67 ± 12	235 ± 164	23 ± 47	21 ± 7
Ostracoda	–	–	–	–	–	–	–	–	5 ± 4	–	–	1+1	2+1	2+1
Tardigrada	–	63 ± 11	48 ± 13	30 ± 19	7 ± 2	–	3 ± 1	7 ± 3	2 ± 1	1 ± 0	3 ± 2	–	18 ± 8	11 ± 5
Gastrotricha	–	–	–	6 ± 4	1 ± 1	11 ± 10	11 ± 8	6 ± 4	77 ± 7	5 ± 3	14 ± 14	–	1 ± 1	–
Napliar larvae	–	–	2 ± 2	9 ± 7	3 ± 1	3 ± 2	4 ± 2	1 ± 1	1 ± 0	–	6 ± 5	–	2 ± 1	1 ± 0
Oligochaeta	2 ± 1	18 ± 10	5 ± 3	3 ± 2	1 ± 0	5 ± 2	2 ± 1	3 ± 1	2 ± 1	2 ± 1	1 ± 1	1 ± 1	1 ± 1	–
Polychaeta	–	–	1 ± 0	4 ± 1	2 ± 1	4 ± 2	–	–	–	–	1 ± 0	–	1 ± 0	–
Calanoida	–	–	–	1 ± 1	–	–	–	–	–	–	5 ± 5	–	1 ± 1	–
Amphipoda	–	–	–	–	1 ± 1	1 ± 1	1 ± 1	2 ± 1	–	–	–	1 ± 1	–	–
Total	56 ± 13	1731 ± 472	1007 ± 169	1614 ± 130	789 ± 118	1495 ± 255	620 ± 47	1943 ± 264	1084 ± 78	2136 ± 562	1012 ± 314	3518 ± 540	3324 ± 676	1470 ± 303

Table 2 — Preliminary species list of free-living marine nematodes from De Panne Wetshoek

Adoncholaimus sp.1	*Monhystera* sp.1
Aegialoalaimus sp.1	*Monoposthia costata* Bastian, 1865
Ammotheristus sp.1	*Monoposthia mirabilis* Schultz, 1932
Ascolaimus elongatus Bütschli, 1974	*Nannolaimus* sp.1
Axonolaimus helgolandicus Lorenzen, 1972	*Neotonchus* sp.1
Axonolaimus orcombensis Warwick, 1970	*Odonthophora phalarata* Lorenzen, 1972
Bathylaimus paralongisetosus Stekhoven & De Coninck, 1933	*Odontophora ornata* Lorenzen, 1971
Calomicrolaimus monstrosus Gerlach, 1953	*Odontophora rectangula* Lorenzen, 1972
Calyptronema maxweberi De Man, 1920	*Oncholaimellus calvadosicus* De Man, 1890
Chaetonema riemanni Platt, 1973	*Onyx perfectus* Cobb, 1891
Choniolaimus sp.1	*Paracanthonchus thaumasius* Schultz, 1932
Chromadorita nana Lorenzen, 1971	*Parachromadorita* sp.1
Chromadorita sp. 1	*Paracyatholaimus pentodon* Riemann, 1966
Chromaspirina parapontica Luc & De Coninck, 1959	*Paralinhomoeus* sp.1
Comesoma sp.1	*Paramonhystera* sp.1
Coninckia sp.1	*Phanodermopsis* sp.1
Cyartonema elegans Jayasree & Warwick, 1970	*Pomponema elegans* Lorenzen, 1972
Daptonema hirsutum Vitiello, 1967	*Pomponema multipapilatum* Filipjev, 1922
Daptonema normandicum De Man, 1890	*Pomponema* sp.1
Daptonema sp.1	*Prochromadorella ditlevensi* De Man, 1922
Daptonema sp.2	*Promonhystera faber* Wieser, 1956
Daptonema sp.3	*Pseudonchus deconincki* Warwick, 1969
Daptonema sp.4	*Rhabdidtis* sp.1
Daptonema stylosum Lorenzen, 1973	*Rhabdocoma* sp.1
Daptonema tenuispiculum Ditlevsen, 1918	*Rhabdodemania* sp.1
Dichromadora abnormis Gerlach, 1953	*Rhynchonema* sp.1
Dichromadora hyalocheile De coninck & stekhoven, 1933	*Sabatieria celtica* Southern, 1914
Dichromadora sp.1	*Sabatieria longispinosa* Lorenzen, 1972
Enoplolaimus litoralis Schultz, 1936	*Siphonolaimus* sp.1
Enoplolaimus longicaudatus Southern, 1914	*Southerniella* sp.1
Enoplolaimus propinquus De man, 1922	*Spilophorella candida* Gerlach, 1951
Eumorpholaimus sabulicolus Schultz, 1932	*Spirinia laevis* Bastian, 1865
Gammanema conicauda Gerlach, 1953	*Stephanolaimus elegans* Diltevsen, 1918
Halichoanolaimus sp.1	*Stephanolaimus* sp.1
Leptolaimus ampullaceus Warwick, 1970	*Synonchiella riemanni* Warwick, 1970
Leptonemella aphanothecae Gerlach, 1950	*Tarvaia* sp.1
Mesacanthion hirsutum Gerlach, 1953	*Terschellingia* sp.1
Metadesmolaimus gelana Lorenzen, 1977	*Therisus interstitialis* Warwick, 1970
Metadesmolaimus pandus Lorenzen, 1972	*Trefusia* sp.1
Metalinhomoeus sp.1	*Trichoteristus* sp.1
Metoncholaimus sp.1	*Trissonchulus* sp.1
Microlaimus conspicuus Lorenzen, 1973	*Xenolaimus* sp.1
Microlaimus ostracion Stekhoven, 1935	*Xyala striata* Cobb, 1920
Microlaimus sp.1	

cludes some new marine nematode species but this has to be verified in future research. Looking at the N_0 diversity index (the number of species) it is clear that the diversity increased (from 12 to 45 spp./10 cm^2) from the upper beach downwards to reach a maximum at about the mid tidal level. Out of the other indices, which are mainly dominance indices, one could conclude that the upper beach parts are characterized by a higher dominance of a few species (fig. 3).

The Canonical Correspondance Analysis (CCA) (eigenvalues: first axis 0.8042, second axis 0.2522) divided the total nematode community into three major groups: the dry beach stations (1, 2 and 4), the upper littoral stations (6, 8 and 9) and the lower littoral stations (10, 12 and 14) (fig. 4). Indicator species analysis found indicator species for each community (dry sand: *Rhabditis* sp. 1 and *Axonolaimus helgolandicus*; upper littoral: *Trissonchulus* sp. 1 and *Dichromadora hyalocheile*; lower littoral: *Odonthophora phalarata*, *O. rectangular*, *Chaetonema riemanni* and *Cyartonema elegans*). All the indicator species have an indicator value between 83 and 99 % at p-levels < 0.005.

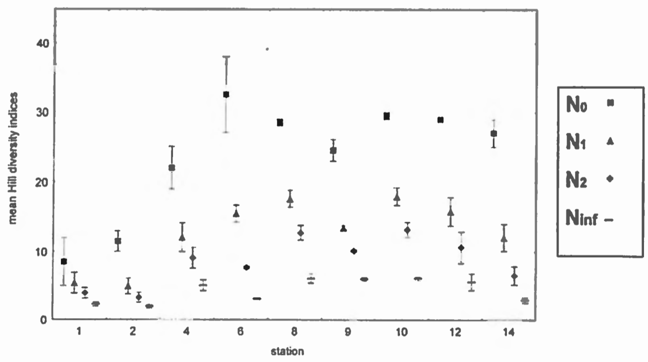

Fig. 3 — Hill diversity indices.

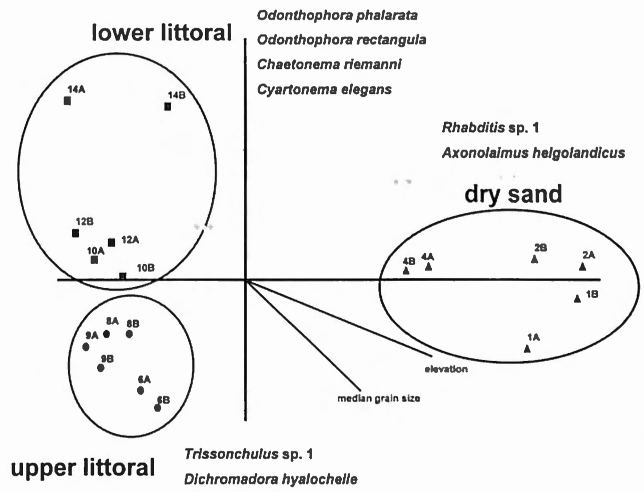

Fig. 4 — Output of ordination (CCA environmental biplots with indication of the communities. Maximum variance was 80 % (first axis).

Discussion

Dissipative beaches are considered the richest beaches both in terms of density and diversity. This is caused by the abundance of diatom mats which are responsible for the main part of the primary production on these beaches, providing food for the meiobenthos (ANONYMOUS 2000, PINCKNEY & SANDULLI 1990).

Macrotidal, dissipative beaches are very flat and fine-grained beaches with a high and constant wave energy (MCLACHLAN & TURNER 1993) and as a consequence, the sediment is very well sorted. Sorting of the sand, median grain size and shape of the sand grains have a great influence on the interstitial spaces between sand grains. According to COULL (1988), HEIP *et al.* (1985) and VANAVERBEKE *et al.* (2000), the density and diversity of the meiofauna is primary influenced by the median grain size of the sediment.

As this study was a first survey of meiofauna on Belgian sandy beaches based on a single sampling date along one transect, the generalization of the results to all Belgian beaches is difficult, but nevertheless some comparisons with other European Atlantic sandy beaches could be made. The meiobenthic composition (11 taxa) and mean total density recorded during this survey of a Belgian sandy beach were similar in comparison with the studies along the French (RENAUD-DEBYSER & SALVAT 1963) and Yorkshire sandy coastlines (GRAY & RIEGER 1971). These authors also noticed a high dominance (>70 %) of free-living marine nematodes but harpacticoids were the second most important taxon here. Significantly lower mean densities of nematodes (France 268 ind/10 cm^2, Yorkshire 827 ind/10 cm^2) were noticed in comparison with this study. But on the other hand the general increase of meiobenthic densities with decreasing grain size was found on these sandy beaches as well. The significant differences between sampling stations for nematode and total meiofaunal densities found during this study are probably caused by macroscaled physical gradients (tidal exposure). Patchy distributions within sampling stations were probably caused by gradients on microscale (availability of organic matter, oxygen concentration, microtopography, biological interactions; BLOME *et al.* 1999, COULL & GIERE 1988).

Nematodes are very slender and are very well adapted to live in small, water-filled interstitial spaces (FORSTER 1998). According to MCLACHLAN *et al.* (1977) fine grain sized sandy beaches are very suitable environments for nematodes and this could explain the high nematode densities found in De Panne in comparison with the two beaches mentioned above which were mainly characterized by medium (250-500 μm) to coarse (500-1000 μm) sand. These differences in sediment characteristics could also explain the absence of harpacticoids as subdominant meiofaunal taxon in De Panne since they are more common in exposed, coarse sandy substrates (HEIP *et al.* 1982).

Following MCLACHLAN (1980) and MCLACHLAN & JARAMILLO (1995), meiobenthic zonation on sandy beaches can mainly be explained by oxygen content and dehydration (osmotic stress) of the sediment. At De Panne, three nematode communities were discerned on the basis of species distribution and abundance represented by CCA. The first community, associated with the dry beach, is a community which is merely momentary flood by the seawater and is most of the day relatively dry. Species in this community are dealing with very high osmotic stress, so only a few species can inhabit this stressful environment. Looking at the diversity indices N_1, N_2 and N_∞ it is clear that this community is characterized by low species diversity (N_0) and strong dominance of some species. This strong dominance is caused by an unidentified species of *Rhabditis*, a genus more common in terrestrial ecosystems. Since the dry beach is more or less the transition zone between the terrestrial and the marine ecosystem, the presence of this *Rhabditis* species could be expected. However, one should take in consideration that this community is probably atypical because of the presence of a dyke. This dyke forms an abrupt obstacle between the dry beach and the low-lying dune area of the Westhoek reserve and hence a natural transition between the terrestrial and the marine ecosystem is severely disturbed. Only freshwater belts connect both ecosystems. The second community has *Trissonchulus* sp.1 and *Dichromadora hyalocheile* as indicator species. This community is characterized by longer tidal immersion and finer sand grains so different stress factors (osmotic stress, temperature, salinity) important in structuring nematode communities (SCHRATZBERGER & WARWICK 1999) are less important, resulting in higher nematode densities and diversities. The third community groups the lower littoral stations, which become dry only a few hours a day and are characterized by finer sand in comparison with the other communities. Interstitial spaces here are almost always filled with water so osmotic stress is virtually absent and temperature and salinity are constant. This community has also more affinity with the subtidal sandbanks on the Belgian Continental Shelf (BCS) since some of the indicator species are similar (GHESKIERE 2000).

Conclusion

Although at first sight sandy beaches look like biological deserts, a detailed investigation of the meio- and nematofauna demonstrated the presence of a rich benthic life and a quite unknown nematofauna with probably some marine species new to science. This rich benthic life, although not demonstrated so far for Belgian sandy beaches, will certainly play an important role in the benthic food web.

Acknowledgements

The first author acknowledges a grant (n°1161) from the Institute for the Promotion of Innovation by Science and Technology in Flanders (IWT, Flemish Government). Several persons assisted in the field and in the laboratory; our well meaning thanks to Wies GYSELINCK (nematode slides), Bernard TIMMERMAN (meiofauna extraction), Daniëlle SCHRAM (granulometry).

This study is part of LITUS, an international research project to investigate the influence of industrial and recreational activities on the functioning of the sandy littoral (shallow water and beach).

References

AARNIO, K., 2000. Experimental evidence of predation by juvenile flounder, *Platichthys flesus*, on a shallow water meiobenthic community. *Journal of Experimental Marine Biology and Ecology*, 246: 125-138.

ANONYMOUS, 2000. Interactions of biodiversity, productivity and tourism on European sandy beaches. Proposal LITUS project.

ANSARI, Z.A. & INGOLE, B.S., 1983. Meiofauna of some sandy beaches of Andaman Islands. *Indian Journal of Marine Sciences*, 12: 245-246.

ANSARI, Z.A., INGOLE, B.S. & PARULEKAR, A.H., 1984. Macrofauna & Meiofauna of two sandy beaches at Mombasa, Kenya. *Indian Journal of Marine Sciences*, 13: 187-189.

ANSARI, Z.A., RAMANI, P., RIVONKER, C.U. & PARULEKAR, A.H., 1990. Macro- and meiofaunal abundance in six sandy beaches of Lakshadweep Islands. *Indian Journal of Marine Sciences*, 19: 159-164.

BLOME, D., SCHLEIER, U. & VON BERNEM, K.H., 1999. Analysis of the small-scale spatial patterns of free-living marine nematodes from tidal flats in the East Frisian Wadden Sea. *Marine Biology*, 133: 717-726.

BUCHANAN, J.B., 1984. Sediment analysis. *In*: HOLME, N.A. & MCINTYRE, A.D. (eds), Methods for the study of marine benthos. Oxford and Edinburg Blackwell Scientific Publications: 41-65.

COULL, B.S., 1988. Ecology of the marine meiofauna. *In*: HIGGINGS, R.P. & THIEL, H. (eds), Introduction to the study of meiofauna Washington DC, USA: Smithsonian Institute Press: 297-330.

COULL, B.S. & GIERE, O., 1988. The history of meiofaunal research. *In*: HIGGINGS, R.P. & THIEL, H. (eds), Introduction to the study of meiofauna Washington DC, Smithsonian Institute Press: 14-17.

COULL, B.S., GREENWOOD, J.G., FIELDER, D.R. & COULL, B.A., 1995. Subtropical Australian juvenile fish eat meiofauna: experiments with winter whiting *Sillago maculata* and observations on other species. *Marine Ecology Progress Series*, 125: 13-19.

COULL, B.S., PALMER, M.A. & MEYERS, P.E., 1989. Controls on the vertical distribution of meiobenthos in mud, field and flume studies with juvenile fish. *Marine Ecology Progress Series*, 55: 133-139.

COVAZZI, A., PUSCEDDU, A., DELLA CROCE, N. & DANOVARO, R., 2000. Spatial and temporal changes in beach communities of the Ligurian Sea (NW Mediterranean). *Revista de Biologia Marina y Oceanografia*, 35 (1): 57-64.

DUFRÊNE, M. & LEGENDRE, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, 67: 356-366.

ENGLEDOW, H., SPANOGHE, G., VOLCKAERT, A., COPPEJANS, E., DEGRAER, S., VINCX, M. & HOFFMANN, M., 2001. Onderzoek naar de fysische karakterisatie en de biodiversiteit van strandhoofden en andere harde constructies langs de Belgische kust. Eindrapport van de onderhandse overeenkomst dd. 17.02.2000 i.o.v. de Afdeling Waterwegen Kust van het ministerie van de Vlaamse Gemeenschap, IN.D.2001.20.

FORSTER, S.J., 1998. Osmotic stress tolerance and osmoregulation of intertidal and subtidal nematodes. *Journal of experimental Marine Biology and Ecology*, 224: 109-125.

GERLACH, S.A., 1971. On the importance of marine meiofauna for benthos communities. *Oecologia*, 6: 176-190.

GHESKIÈRE, T., 2000. Structurele diversiteit van nematodengemeenschappen van de Bligh Bank (Zuidelijke bocht van de Noordzee). Licenciaatsverhandeling RUG: 92 pp.

GOURBAULT, N., WARWICK, R.M. & HELLÉOUET, M.-N., 1998. Spatial and temporal variability in the composition and structure of meiobenthic assemblages (especially nematodes) in tropical beaches (Guadeloupe, FWI). *Cahiers de Biologie Marine*, 39: 29-39.

GRAY, J.S. & RIEGER, R., 1971. A quantitative study of the meiofauna of an exposed sandy beach, at Robin Hoods Bay, Yorkshire. *Journal of the Marine Biology Association of the United Kingdom*, 51: 1-19.

HARRIS, R.P., 1972. The distribution and ecology of the interstitial meiofauna of a sandy beach at Whitsand Bay, East Cornwall. *Journal of the Marine Biology Association of the United Kingdom*, 52: 1-18.

HEIP, C., HERMAN, P.M.J. & SOETAERT, K., 1988. Data processing, Evaluation and Analysis. *In*: HIGGINGS, R.P. & THIEL, H. (eds), Introduction to the study of meiofauna, Washington DC, *Smithsonian Institute Press*: 197-231.

HEIP, C., VINCX, M., SMOL, N. & VRANKEN, G., 1982. The systematics and ecology of marine nematodes. *Helminthological Abstracts*, 51 (1): 1-31.

HEIP, C., VINCX, M. & VRANKEN, G., 1985. The ecology of marine nematodes. *Oceanographic and Marine Biology Annual Review*, 23: 399-489.

HILL, M.O., 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology*, 54 (2): 427-432.

INGOLE, B.S. & PARULEKAR, A.H., 1998. Role of salinity in structuring the intertidal meiofauna of a tropical estuarine beach: field evidence. *Indian Journal of Marine Sciences*, 27: 356-361.

JOUK, P.E.H., MARTENS, P.M. & SCHOCKAERT, E., 1988. Horizontal distribution of the Plathelminthes in a sandy beach of the Belgian coast. *Fortschritte der Zoologie - Progress in Zoology*, 36: 481-487.

KENNEDY, A.D. & JACOBI, C.A., 1999. Biological indicators of marine environmental health: meiofauna a neglected benthic component? *Environmental Monitoring and Assessment*, 54: 47-68.

MARTENS, P.M., 1984. Comparison of three different extraction methods for Turbellaria. *Marine Ecology Progress Series*, 4: 229-334.

MARTENS, P.M., JOUK, P.E.H., HUYS, R. & HERMAN, R., 1985. Short note on the relative abundance of the Turbellaria in the meiofauna of sandy habitats in the Southern Bight of the North Sea and on Belgian sandy beaches. Proceedings "Progress in Belgian Oceanographic Research": 341-342.

MASSELINCK, G. & SHORT, A.D., 1993. The effect of tide range on beach morphodynamics: a conceptual beach model. *Journal of Coastal Research*, 9: 785-800.

MAY, R.M., 1988. How many species are there on earth? *Science*, 241: 1441-1449.

MCINTYRE, A.D., 1971. Control factors on meiofauna populations. *Thalassia Jugoslavica*, 7: 209-215.

MCINTYRE, A.D. & MURISON, D.J., 1973. The meiofauna of a flatfish nursery ground. *Journal of the Marine Biology Association of the United Kingdom*, 53: 93-118.

MCLACHLAN, A., 1980. Intertidal zonation of macrofauna and stratification of meiofauna on high energy sandy beaches in the Eastern Cape, South Africa. *Transactions of the Royal Society of South Africa*, 44, part 2: 213-223.

MCLACHLAN, A., ERASMUS, T. & FURSTENBERG, J.P., 1977. Migrations of sandy beach meiofauna. *Zoologica Africana*, 12 (2): 257-277.

MCLACHLAN, A. & JARAMILLO, E., 1995. Zonation on sandy beaches. *Oceanography and Marine Biology*, 33: 305-335.

MCLACHLAN, A. & TURNER, I., 1994. The interstitial environment of sandy beaches. *Marine Ecology*, 15: 177-211.

PINCKNEY, J. & SANDULLI, R., 1990. Spatial autocorrelation of meiofaunal and microalgal populations on an intertidal sandflat: scale linkage between consumers and resources. *Estuarine, Coastal and Sheif Science*, 30: 341-353.

RENAUD-DEBYSER, J. & SALVAT, B., 1963. Eléments de prosperité des biotopes des sédiments meubles intertidaux et écologie de leurs population en microfaune et macrofauna. *Vie Milieu*, 14: 463-550.

SANDULI, R. & DE NICOLA, M., 1991. Responses of meiobenthic communities along a gradient of sewage pollution. *Marine Pollution Bulletin*, 22: 463-467.

SCHRATZBERGER, M., GEE, J.M., REES, H.L., BOYD, S.E. & WALL, C.M., 2000. The structure and taxonomic composition of sublittoral meiofauna assemblages as an indicator of the status of marine environments. *Journal of the Marine Biology Association of the United Kingdom*, 80: 969-980.

SCHRATZBERGER, M. & WARWICK, R.M., 1999. Differential effects of various types of disturbances on the structure of nematode assemblages: an experimental approach. *Marine Ecology Progress Series*, 181: 227-236.

SHORT, A.D., 1996. Beach Classifications and Morphodynamics. *Revista Chilena de Historia Natural*, 69: 589-604.

VANAVERBEKE, J., GHESKIÈRE, T. & VINCX, M., 2000. The meiobenthos of Subtidal Sandbanks on the Belgian Continental Shelf (Southern Bight of the North Sea). *Estuarine, Coastal and Shelf Science*, 51: 637-649.

VINCX, M., 1996. Meiofauna in marine and freshwater sediments. *In*: HALL, G.S. (ed.), Methods for the examination of organismal diversity in soils and sediments: 187-195.

Tom GHESKIÈRE
Eveline HOSTE
Steven DEGRAER
Jan VANAVERBEKE
Magda VINCX
Marine Biology Section
Ghent University
Krijgslaan 281, S8
B-9000 Gent

Lech KOTWICKI
Department of Marine Ecology
Polish Academy of Sciences
Institute of Oceanology
PO Box 197
Powstancow Warszawy 55
PL-81-712 Sopot
Poland