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ORIGINAL ARTICLE

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Horizontal and vertical distribution of meiofauna on sandy beaches of the North Sea (The Netherlands, Belgium, France)

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Abstract Sandy intertidal zones were analysed for the presence of meiofauna. The material was collected on six macro-tidal sandy beaches along the North Sea (The Netherlands, France, Belgium), in order to analyse the vertical and horizontal meiofaunal distribution patterns. Eleven higher meiofauna taxa (one represented by larval stage—Copepoda nauplii) were recorded. The maximum total meiofauna abundance was observed on the Dutch beach (4,295 ± 911 ind. 10 cm^{-2}) in the Westerschelde estuary, while the lowest values (361 ± 128 ind. 10 cm^{-2}) were recorded in France at the Audresselles beach. Meiofauna of the different localities consisted mainly of nematodes, harpacticoids and turbellarians. Nematodes numerically dominated all sampled stations, comprising more than 45% of the total meiofauna density. Meiofauna was mainly concentrated at the sand surface with about 70% present in the uppermost 5 cm. Meiofauna occurred across the entire intertidal zone. A clear zonation pattern in the distribution of meiofauna taxa across the beaches was observed. The present work suggests that designation of exposed sandy beaches as physically controlled (McLachlan 1988) does not explain their biological variability.

Keywords Sandy beach · Meiofauna · Vertical and horizontal distribution · North Sea

Introduction

The European coast consists for more than 30% of soft sediments. Sandy shorelines are one of the most extensive intertidal systems worldwide (Short 1999), dominating most of the temperate coastlines, where they represent both excellent recreational assets and buffer zones against the sea (Davies 1972). As an example, the coastline of France (3,830 km) consists for about 40% of sandy sediments (Richard and Dauvin 1997) while Belgium and the Netherlands are characterised by exclusively sandy coastlines. Despite their initial barren and sterile appearance, many sandy beaches support a diverse flora and fauna, and a number of sandy littoral localities might even be considered as highly productive (McLachlan 1983).

Most of the faunal research on sandy beaches has been concentrated on macrofauna (> 1 mm) (McLachlan and Jaramillo 1995, and references therein) and more recently also birds (e.g. Cornelius et al. 2001). In contrast, sandy shoreline meiofauna (all metazoans between 1 mm and 38 μm) have received considerably less attention notwithstanding their high diversity (even on taxon level) and density (up to one million individuals per m^2 (McIntyre 1969).

With the recent increasing interest in faunal zonation patterns of meiobenthos on sandy shorelines, several quantitative studies have been made of European intertidal sandy beaches (Renaud-Debyser 1963; Renaud-Debyser and Salvat 1963; Fenchel et al. 1967; Jansson 1968; Schmidt 1968; Gray and Rieger 1971; Harris 1972; Schmidt 1972; Arlt 1977; Jonczyk and Radziejewska 1984; Armonies and Hellwig-Amonies 1987; Reise 1988; Ólafsson 1991; Armonies and Reise 2000; Gheskiere et al. 2004a, b). Much of the previous meiofauna research on sandy beaches is in essence restricted to general surveys using bulk samples or to the complex of factors influencing the interstitial habitats (Blome et al. 1999) while vertical and horizontal zonation surveys are scarce.

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Meiofauna inhabiting Belgian sandy beaches has been poorly documented. Horizontal distribution of the Plathelminthes and Nematoda (Mariakerke and De Panne region) were described by Martens (1984), Jouk et al. (1988) and Gheskiere et al. (2002, 2004). Meiofauna (on the Nematoda species level) of the Westerschelde was investigated along a salinity transect by Soetaert et al. (1994), however this study excluded the sandy beaches of this estuary.

Given the importance of sandy beaches for the marine ecosystem, baseline data describing the benthic life and ecosystem processes are needed in order to propose sustainable management policies for these sandy areas. Furthermore, sandy beaches have a high socio-economical value, as it is reflected in their importance for coastal fisheries and tourism. Each year high numbers of tourists are visiting the European coastlines. Although beaches are impacted by numerous stress factors, man has always used sandy beaches and will continue to do so, partly through ignorance and inability to learn from experience but also in the belief that it must be possible to shape nature to his own needs and desires (Brown and McLachlan 1990).

In the present study, 'beach' is defined as 'the zone between lowest and highest water mark, the swept prism, undergoing periodical inundation by marine water' (Short 1999). In this study, we focus on dissipative, medium-grained sandy beaches with a macrotidal regime sensu Short.

Since the work of McLachlan (1988), exposed sandy beaches have been considered as physically stressful environments. Thus, one expects that the interstitially living meiofaunal communities are regulated by physical rather than by biological factors. As there is a full array of organisms from bacteria (decomposers), microphytobenthos (producers) and meio- and macrofauna (consumers) to fish and birds (top trophic levels), we consider sandy beaches as open, functional entity—ecosystems. Hence, we aimed to get a two-dimensional view of meiofauna distribution on sandy beaches, that is, both horizontal and vertical distribution patterns.

Methods

Six sandy beaches along the North Sea were surveyed in 2000 (Fig. 1). In the Netherlands two intertidal sites (indicated as Westerschelde 1 and Westerschelde 2) were investigated. Three major European rivers (the Rhine, Meuse and Schelde) enter the North Sea in the so-called Dutch Delta in the south-western part of the Netherlands. Most of the former estuaries in this area have been altered by man. The lower part of the river Schelde is generally known as the Westerschelde estuary. It is the last true estuary of the Delta area in the southwest of the Netherlands with a marked salinity gradient (Soetaert et al. 1994). The input of organic and inorganic pollutants is very high (Hummel et al. 1988). The study sites were in the brackish intertidal zone of the Westerschelde estuary, a turbid, nutrient-rich, heterotrophic system. Most of the tidal flat where samples have been taken is located between −1 m and +1 m relative to mean tidal level and is subjected to tidal amplitudes of about 5 m. The sampling stations (Westerschelde 1 and Westerschelde 2) have a silt percentage of up to 3% (fraction $<63\ \mu$m) and a median grain size of 168 and 230 μm, respectively (Hummel et al. 1988; Soetaert et al. 1994).

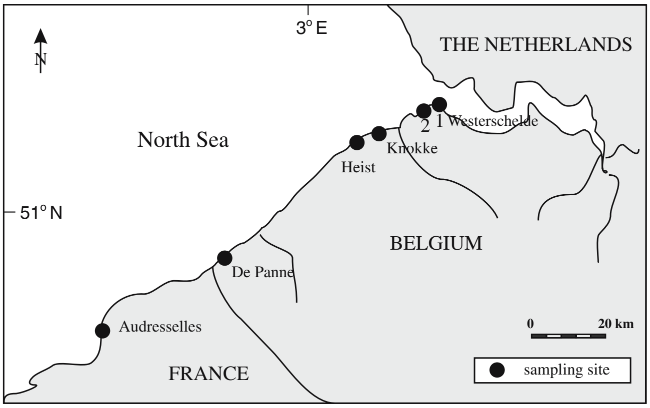

Fig. 1 Location of the investigated sandy beaches

In Belgium three sandy beaches were studied (Heist, Knokke-Heist and De Panne). The beaches sampled in Heist and De Panne are dissipative beaches, characterised by a low beach gradient, a surf zone with the presence of numerous spilling lines of breakers and by fine to medium sandy sediments. The beach in Knokke-Heist can be classified as a 'low tide bar/rip' beach [beach morphodynamical classification after (Masselink and Short 1993), and Short (1999)]. The width of the intertidal zone is up to 450 m with a Relative Tidal Range (RTR) of 8.5–10 m (Degraer et al. 2003). The beaches have several shallow depressions parallel to the waterline, in which water is retained when the tide recedes.

In France (North Brittany), a beach with medium sandy sediments in the Audresselles region was investigated. This beach is characterized by an intertidal zone of about 200 m with a RTR up to 8 m.

At each of the sampling stations triplicate meiofauna samples (0–10 cm) were taken using a 30 cm long perspex meiocore with an inner diameter of 3.6 cm (sampling surface 10 cm^2) and immediately fixed with heated (70°C) 4% buffered formaldehyde water solution (Vincx 1996).

In order to analyse the vertical distribution of the meiofauna, mid-tidal level samples from four sandy beaches (Westerschelde 1 and 2, Knokke-Heist, Audresselles) were subdivided into nine depth horizons (0–0.5, 0.5–1, 1–1.5, 1.5–2, 2–2.5, 2.5–3, 3–4, 4–5, 5–10 cm; Fig. 2a).

In order to analyse the horizontal distribution, two transects across the continuum from the mean high water spring level to the Mean Low Water Spring level

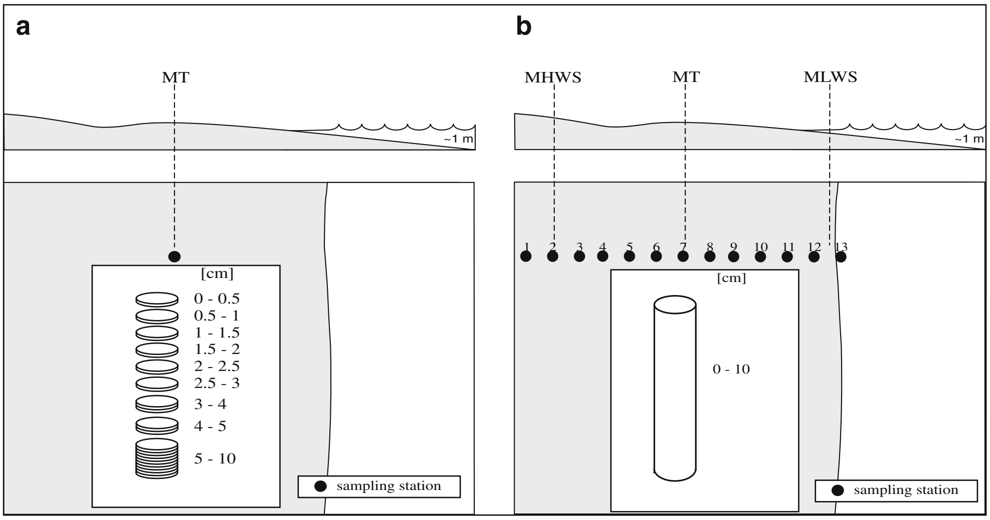

Fig. 2 Sampling stations and sampling strategy applied for **a** Westerschelde, Knokke-Heist, Audresselles sandy beaches and **b** Heist, De Panne sandy beaches; *MHWS* Mean High Water Springs, *MHWN* Mean High Water Neaps, *MT* Middle Tide, *MLWN* Mean Low Water Neaps, *MLWS* Mean Low Water Springs

(MLWS) and perpendicular to the waterline were sampled (Fig. 2b), on the beaches of Heist and De Panne. The distance from the dyke to the shore was divided into 14 (De Panne) and 13 (Heist) separate stations according to the removing water line. Sampling began at high tide, and followed the receding water down to the beach. The highest station (station 1) was immediately in front of the storm-water dyke on the dry beach while the lowest (station 13 or 14) was about 1 m below the MLWS level.

In the laboratory meiofauna samples were processed using standard procedures as described by Vincx (1996).

To clarify meiofaunal zonation patterns across the studied beaches, polynomial functions were fit to the data according to the distance-weighted least squares smoothing procedure, using the STATISTICA 5.1 software (StatSoft 1996).

Results

Meiofauna taxa composition and their frequency of occurrence

Eleven higher taxa of meiofauna (one represented by larval stage—Copepoda nauplii) were recorded in the sandy beach zones (Table 1). The most common taxa were Nematoda, Harpacticoida, Turbellaria and Oligochaeta which were present at all stations, while Ostracoda, Tardigrada, Gastrotricha and Copepoda nauplii were less frequent (present in five out of six stations). Polychaeta, Bivalvia and Halacaroidea were found on 4, 3 and 3 beaches, respectively. The number of taxa on each beach ranged from 7 to 11. The most diverse fauna, that is, 10 and 11 taxa, was observed in the samples of Westerschelde 1 and the beach of Heist, respectively.

Density of the main taxa of meiofauna

The highest meiofauna densities were observed on the Dutch beaches, that is, 4,295 ± 911 ind. 10 cm^{-2} at Westerschelde 1, and 2,342 ± 1,101 ind. 10 cm^{-2} at Westerschelde 2 (Table 2). In Belgium, at Knokke-Heist, Heist and De Panne the total meiofauna abundance was much lower, that is, 1,267 ± 382 ind. 10 cm^{-2}, 868 ± 420 ind. 10 cm^{-2} and 1,012 ± 311 ind. 10 cm^{-2}, respectively. The lowest values (361 ± 128 ind. 10 cm^{-2}) were noted in France at the Audresselles beach. Nematodes were numerically dominant at all beaches, ranging from 235 ± 116 ind. 10 cm^{-2}

Table 1 Distribution of the meiofauna taxa in the different study sites

Taxon	Study sites					
	Westerschelde 1	Westerschelde 2	Knokke-Heist	Heist	De Panne	Audresselles
Nematoda	+	+	+	+	+	+
Harpacticoida	+	+	+	+	+	+
Turbellaria	+	+	+	+	+	+
Ostracoda	+	+	+	+	+	–
Tardigrada	+	–	+	+	+	+
Gastrotricha	+	+	+	+	+	–
Copepoda nauplii	+	–	+	+	+	+
Oligochaeta	+	+	+	+	+	+
Bivalvia	+	+	–	+	–	–
Polychaeta	+	–	–	+	+	+
Halacaroidea	–	–	+	+	+	–
Number of taxa	10	7	9	11	10	7

in the Audresselles region up to 4,116 ± 805 ind. 10 cm^{-2} on the Westerschelde 2 beach. Turbellaria were subdominant in terms of average density at all beaches except for the Knokke-Heist region, with mean abundances from 16 ± 11 (Westerschelde 2) up to 215 ± 11 ind. 10 cm^{-2} (Heist). On the Knokke-Heist beach harpacticoids were of secondary importance, reaching a mean density of 384 ± 226 ind. 10 cm^{-2}. The lowest density of this taxon was observed in the Westerschelde region with only 3.7 ± 2 ind. 10 cm^{-2}. The taxon Ostracoda was important in meiofauna composition in the Westerschelde 1 region, attaining 130 ± 61 ind. 10 cm^{-2}. Polychaeta and Halacaroidea were important groups in terms of meiofaunal densities, with 63 ± 36 and 59 ± 100 ind. 10 cm^{-2}, respectively, on the beach of Heist.

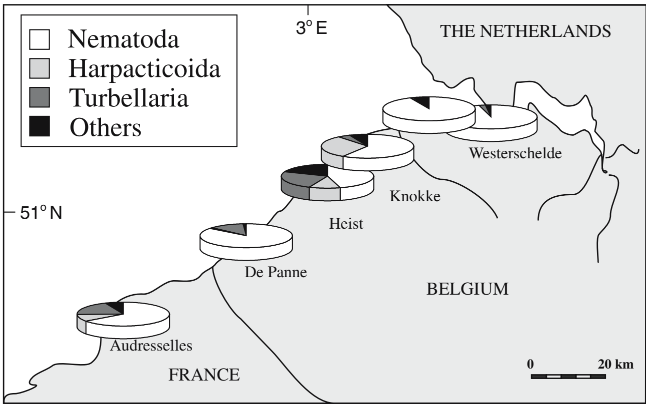

Fig. 3 Relative abundance of major meiofauna taxa at different sampling sites

Relative meiofauna composition

At all stations, Nematoda comprised more than 45% of the total meiofaunal density (Fig. 3). They were particularly dominant (96 and 93%) in the Westerschelde region. The lowest percentage of this taxon (46%) was noted on the Heist beach. Harpacticoida were the second important group in the Knokke-Heist region, comprising 30% of the meiofauna density. On other beaches the percentage of Harpacticoida varied from less than 1% (Westerschelde 1) up to 11% (Heist). The percentage of Turbellaria, as second important taxon in Audresselles and the Heist region, reached 19 and 25% of the total meiofaunal density, respectively. Other meiofaunal taxa occurring in smaller numbers were grouped as ‘Others’.

Vertical distribution of meiofauna taxa in a sandy beach zone

Depth distribution patterns of Nematoda, Harpacticoida and Turbellaria were analysed at four midtidal sampling stations (Fig. 4). The meiofauna was mainly concentrated at the sand surface, with about 70% present in the upper first 5 cm. Nematoda were found at all depth intervals. The vertical distribution of the nematodes was rather uniform at three stations (Audresselles, Westerschelde 1 and 2), with about 90% present in the top 5 cm, and more than 56% in the first 2 cm. A different situation was observed at the Knokke-Heist beach where nematodes occurred deeper within the sediments, although they were still most abundant in the top layers. Harpacticoida were largely confined to the surface layer, above 80% within the first 2 cm at all stations. Harpacticoida were found in high numbers only at the station in Knokke-Heist, where they showed the general vertical distribution pattern. Turbellaria were found at all depth intervals examined, yet highest densities were found in the 1–2 cm layer of the sediment.

Nematodes were dominant in all layers from the Westerschelde samples, comprising more than 84% of the total meiofauna density (Fig. 5). Nematoda also dominated on the beach of Knokke-Heist in the deeper

Table 2 Density of the meiofauna taxa at the different sampling sites in the 1–10 cm layers of sediment mean abundance

Taxon	Westerschelde				Knokke-Heist		Heist		De Panne		Audresselles	
	W 1		W 2		M	SD	M	SD	M	SD	M	SD
	M	SD	M	SD								
Nematoda	4116.3	805	2187.0	1,050	747.7	133	395.8	314	866.3	285	235.0	116
Harpacticoida	3.7	2	6.7	2	384.0	226	92.8	19	9.7	5	33.7	18
Turbellaria	94.0	50	15.7	11	55.7	28	214.7	11	125.7	47	69.0	41
Ostracoda	61.3	40	129.7	61	0.3	1	28.3	42	–	–	–	–
Tardigrada	0.3	1	–	–	39.0	21	0.2	0	2.7	3	4.3	8
Gastrotricha	12.7	9	1.3	2	9.0	3	1.8	1	2.7	1	–	–
Copepoda nauplii	1.0	1	–	–	23.3	5	11.8	10	0.7	1	1.0	2
Oligochaeta	5.0	3	2.0	2	8.3	5	0.7	0	4.3	3	2.0	3
Bivalvia	0.3	1	0.3	1	–	–	–	–	–	–	–	–
Polychaeta	0.7	1	–	–	–	–	63.0	36	–	–	16.0	16
Halacaroidea	–	–	–	–	0.3	1	59.2	100	–	–	–	–
Total	4295.3		2342.7		1267.7		868.3		1012.0		361.0	

M Individuals per 10 cm^2 ± standard deviation (SD)

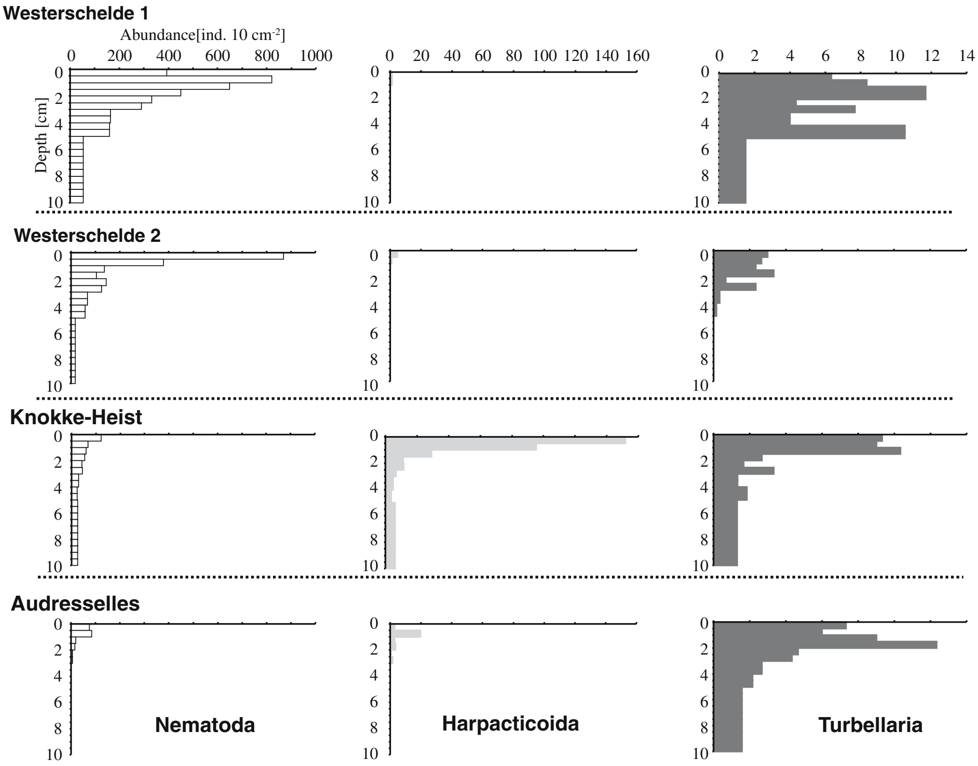

Fig. 4 Vertical distribution of Nematoda, Harpacticoida and Turbellaria at the sampling stations Westerschelde 1 and 2, Knokke-Heist and Audresselles

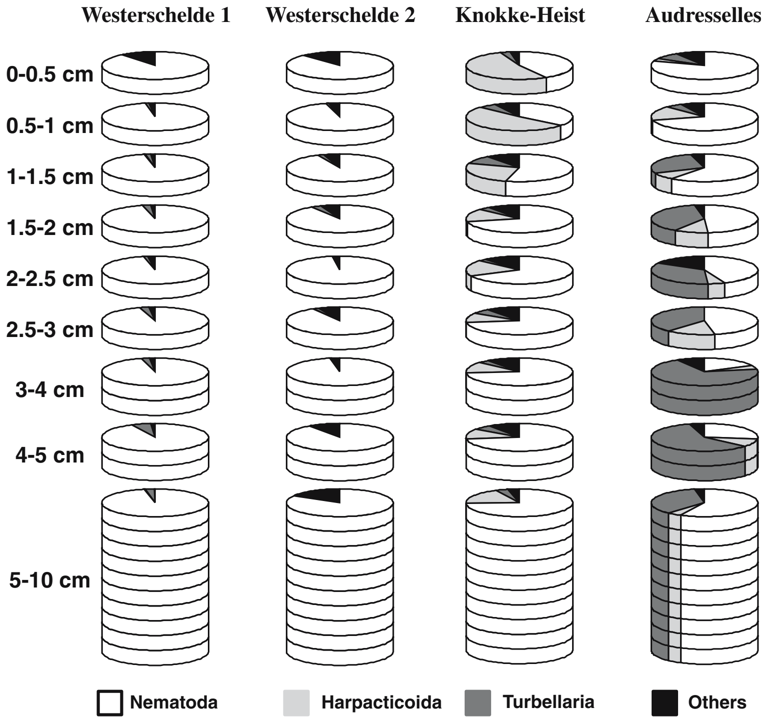

Fig. 5 Vertical distribution of meiofauna: relative abundance of major meiofauna taxa in different depth layers

layers from 54% (1–1.5 cm) to 75% (5–10 cm). In the top layers (0–0.5 cm and 0.5–1 cm), however, harpacticoids were dominant with 52 and 51% of the total meiofauna abundance, respectively. The percentage of Harpacticoida decreased towards deeper layers and the percentage of Nematoda increased with depth. In the Audresselles samples Nematoda and Turbellaria were dominant in total meiofaunal abundance. The percentage of nematodes decreased towards deeper layers from about 75% on the surface to 15% in the 4–5 cm layer. In the deepest 5–10 cm layer of the sediment nematodes were dominant comprising about 60% of the meiofauna abundance.

The maximum percentage of turbellarians in meiofauna abundance was found in the 3–4 and 4–5 cm layers, with 70 and 59%, respectively. Their percentage decreased towards the sediment surface and was lower in the deepest layer (5–10 cm).

Horizontal distribution of the meiofauna at the sandy beaches of Heist and De Panne

Polynomial functions, showing the general intertidal zonation trends of the meiofauna abundance on two sandy beaches (Heist and De Panne), were developed using a distance-weighted, least squares smoothing procedure in the Statistica v 6.1 software package (Fig. 6). The trend lines do not show min and max values in Fig. 6, the data of meiofauna abundance are presented in Table 3. Different zonation patterns of the meiofauna were observed for the two investigated beaches. Meiofauna was generally recorded through the whole intertidal zone.

At Heist beach, average density of meiofauna per station ranged from 52 (station 1) to 1,169 ind. 10 cm^{-2} (station 8). From the mid-tidal zone towards the MLWS a general decrease in meiofauna density was observed.

At De Panne beach, average meiofaunal density per station varied from 83 ind. 10 cm^{-2} (station 1) to almost 3,400 ind. 10 cm^{-2} (station 12). In contrast to Heist, abundance of meiofauna decreased from station 2 (MHWS) towards the mid-intertidal zone (min. values—780 ind. 10 cm^{-2} at station 7) and then increased generally to the Mean Low Water Neap level (MLWN), reaching highest values (3,385 ind. 10 cm^{-2}) at station 12.

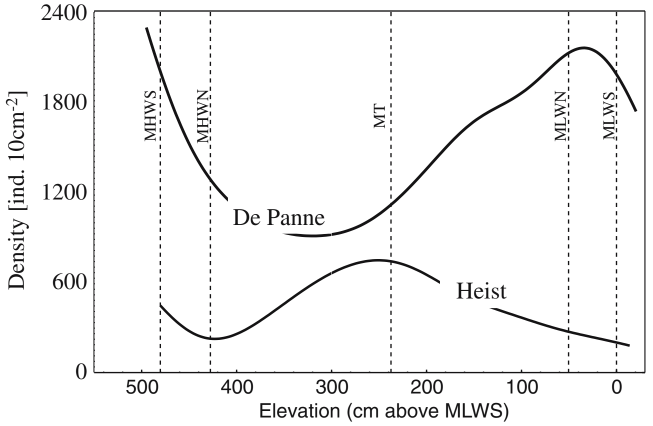

Fig. 6 The general intertidal zonation trends (polynomial function) of distribution of meiofauna at the beaches of Heist and De Panne

The general intertidal zonation trends of major meiofauna taxa showed also a different pattern on the beaches of Heist and De Panne (Fig. 7). A similar, although different in numbers, density peak of nematodes was found at the MHWS at both beaches. A second

Table 3 Average abundance of meiofauna (individuals per 10 cm^2) across the beaches of Heist (a) and De Panne (b)

Taxon	Station													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Heist														
Nematoda	38	506	361	83	41	277	158	753	690	331	209	175	163	
Harpacticoida	2	253	15	4	28	99	108	72	42	36	367	106	138	
Turbellaria	9	8	14	8	113	222	220	203	216	81	84	125	89	
Ostracoda	–	–	1	–	–	5	4	77	20	15	5	5	1	
Tardigrada	–	1	–	–	–	–	–	1	–	–	–	–	–	
Gastrotricha	1	–	1	–	–	1	4	1	1	11	–	1	–	
Nauplii Copepoda	1	42	12	9	5	3	22	11	17	–	1	1	9	
Oligochaeta	1	3	1	–	1	1	–	1	–	3	3	1	–	
Bivalvia	–	–	–	1	–	–	–	–	–	–	–	–	–	
Polychaeta	–	4	2	4	9	34	103	52	16	5	13	10	–	
Halacaroidea	2	19	84	16	95	3	175	–	–	–	–	–	–	
Total	52	834	490	123	290	644	793	1,169	1,000	480	681	421	399	
De Panne														
Nematoda	81	2,536	804	1,298	521	850	590	1,159	1,101	1,837	1,105	2,663	1,920	1,359
Harpacticoida	–	2	20	41	35	12	13	4	2	4	3	1	5	6
Turbellaria	–	68	80	135	168	170	130	77	74	658	85	721	263	10
Ostracoda	–	–	–	–	–	–	–	–	–	–	1	–	2	–
Tardigrada	–	38	11	12	9	–	6	2	1	–	–	–	4	6
Gastrotricha	–	–	–	–	–	3	3	2	6	8	6	–	–	–
Nauplii Copepoda	–	–	–	4	2	–	2	–	1	–	–	–	1	–
Oligochaeta	2	9	3	–	–	2	4	7	6	5	3	–	3	1
Bivalvia	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Polychaeta	–	–	1	3	2	–	–	–	–	–	–	–	–	–
Halacaroidea	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Total	83	2,653	919	1,493	737	1,037	748	1,251	1,191	2,512	1,209	3,385	2,198	1,382

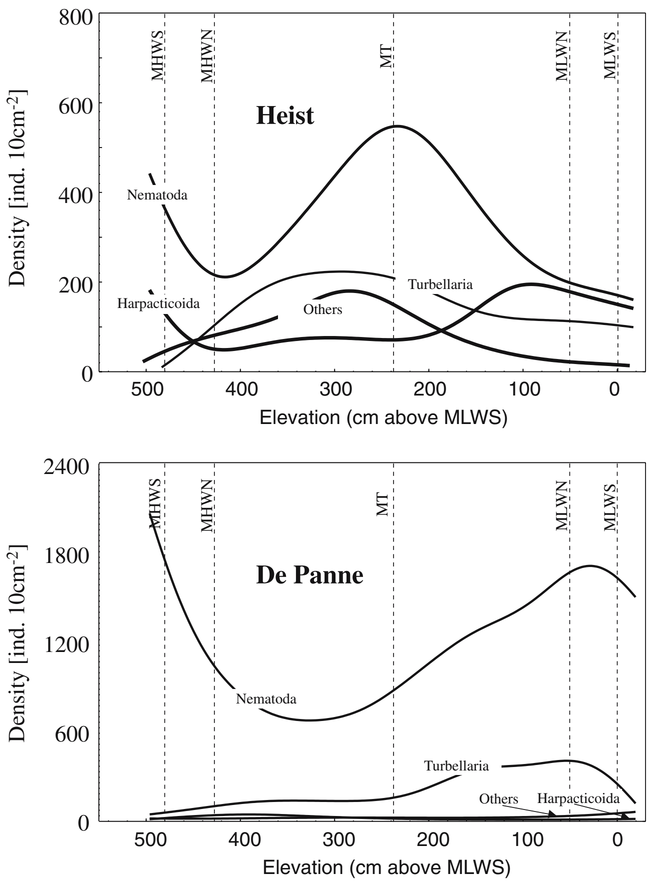

Fig. 7 The general intertidal zonation trends (polynomial function) of distribution of major meiofauna taxa at the beaches of Heist and De Panne

density peak of nematodes was observed in the Middle Tide (MT) at Heist beach, while at De Panne it was observed just below the MLWN. Also the distribution of Turbellaria showed different patterns on the two beaches. In the Heist region an increase towards the MT and a slight decrease towards the subtidal was observed. At De Panne beach, a smooth increase of turbellarian density from MHWS towards MLWN followed by a decrease to the subtidal was recorded. Only the distribution of Harpacticoida showed similar patterns at both beaches, that is, increasing density from MHWS towards MLWS.

Statistical analyses

Based on the results of cluster analysis using Bray-Curtis similarity index comparing the physical parameters of the studied beaches, two groups of beaches were distinguished: De Panne, Heist and Knokke-Heist on the one hand, and Westerschelde 1, 2 with Audresselles on the other (Fig. 8a). A different pattern of grouping was discerned when using meiofauna assemblage data (Fig. 8b).

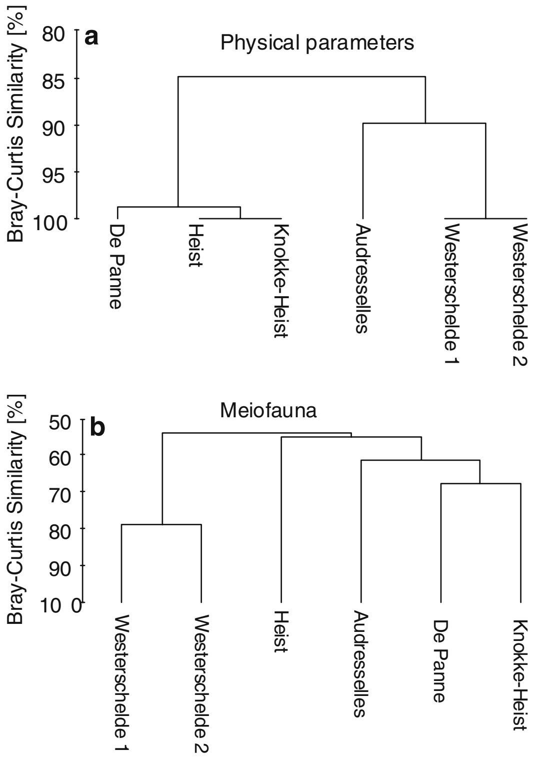

Fig. 8 Similarity of the investigated beaches based on **a** physical parameters, **b** meiofaunal assemblages

Discussion

Although this study is limited to six sites along the North Sea coast, several trends were observed. The average meiofauna densities recorded in the present study (0.23 – 4.29×10^4 ind. 10 cm^2) are in general of the same order of magnitude as the meiofauna densities in sandy beaches reported in the literature (for overview, see Table 4). The highest abundance of meiofauna was observed in the Schelde estuary. In general, higher meiofauna densities can be found in intertidal estuarine habitats (Coull 1988). In sediments such as organic rich sand, meiofauna densities of 10^4 ind. 10 cm^{-2} and more are common (Ellison 1984). The highest values are known from intermediate beaches, where an optimal balance exists between organic input and oxygenation. These abundances, of course, vary according to temperature, tidal exposure, wave action, grain size, oxygen availability, substratum porosity, water percolation, organic input etc. (Gheskiere et al. 2005a). In addition, sediment grain size is a cardinal factor for the abundance and composition of meiofaunal organisms (Wieser 1959; Boaden 1962; Jansson 1967; Gray 1981; Coull 1988). In general, nematodes dominate benthic meiofauna communities comprising more than half of the total meiofauna abundance (Harris 1972; Dye 1983; McLachlan 1983). This was indeed the case for all sites sampled during this study. Harpacticoids are usually sub-

Table 4 Overview of meiofauna densities (individuals per 10 cm^2) reported from different sandy littoral sites

Location	Nematoda	Copepoda	Meiofauna	Author
Asko, Baltic Sea	38–169	29–830	391–152	Jansson (1968)
Tafta, Baltic Sea	8–14	0	225–104	Jansson (1968)
Simrishamn, Baltic Sea	1	2–43	49–318	Jansson (1968)
Tylosand, Baltic Sea	6–106	1–52	11–845	Jansson (1968)
Oresund, North Sea	115–497	1–10	249–764	Fenchel et al. (1967)
Wadden Sea, Denmark	10–1,050	1–840	13–191	Smidt (1951)
Blyth estuary, UK	330–1,320	–	–	Capstick (1959)
Filey, Yorkshire UK	827	20	942	Gray and Rieger (1971)
Whitsand, UK	109–1,062	65–588	220–1,896	Harris (1972)
France, Big Channel	2–268	2–192	19–389	Renaud-Debyser and Salvat (1963)
France, Atlantic	61–204	5–331	83–591	Renaud-Debyser and Salvat (1963)
White Sea, Russia	7–239	20–261	319–427	Galtsova (1971)
Germany	322–1,559	34–93	636–1,837	Arlt (1977)
Delaware, USA	57–538	2–8	125–896	Hummon et al. (1976)
New York, USA	1–2,262	0–34	4–2,293	Martinez (1975)
South Africa	35–1,328	10–502	60–2,250	McLachlan (1977)
South Africa	47–450	2–211	55–584	McLachlan et al. (1977)
India	158–524	0–224	215–1,337	Munro et al. (1978)
Scotland	168–2,100	2–1,125	203–4,262	Munro et al. (1978)
Isle of Man, UK	180–2,771	20–353	802–2,939	Moore (1979)
Alaska, USA	300–2,900	86–1,249	420–4,790	Feder and Paul (1980)
India	584–4,597	102–888	2,270–6,116	Ansari and Ingole (1983)
Baltic beach, Poland	–	–	325–2,250	Jonczyk and Radziejewska (1984)
Kali estuary, India	–	–	129–4,731	Bhat and Neelakantan (1991)
Sylt island, Niemcy	–	–	4,812–6,960	Armonies and Hellwig-Armonies (1987)
York, Australia	–	–	66–302 (winter)	Alongi (1987)
York, Australia	–	–	217–1,672 (summer)	Alongi (1987)
Gopalpur, India	–	–	52–5,249	Pattnaik and Lakshmana Rao (1990)

dominant in terms of density (McIntyre 1969). A different situation was observed in the Westerschelde region where Harpacticoida were found in very low densities. Apart from a few exceptions (Vopel et al. 1996), copepods are generally more sensitive to oxygen depletion or anoxia than nematodes (Elmgren 1975; Murrell and Fleeger 1989; Moodley et al. 2000; Modig and Ólafsson 1998) which may possibly explain this pattern. The input of organic and inorganic pollutants is very high in the Schelde estuary (Hummel et al. 1988). It is also interesting to note the remarkably low percentage (1% of total meiofauna density) of copepods in De Panne beach. Other taxa (Turbellaria, Ostracoda, Oligochaeta, Gastrotricha) were found on most beaches but the numerical relationship between them varies. A similar pattern was observed on other European sandy beaches (Jansson 1968; Feder and Paul 1980; Jończyk and Radziejewska 1984).

Vertical zonation is generally controlled by the position of the Redox Potential Discontinuity (RPD) layer (Coull 1988; Steyaert and Vincx 1996). The meiofauna was mainly concentrated on the sand surface, with about 70% present in the top 5 cm. Nematodes were found at all depth intervals. Harpacticoid copepods are the most sensitive taxon to decreased oxygen (Moodley et al. 2000). This taxon was almost confined to the surface layer, above 80% in the first 2 cm at all stations. Turbellaria were found at every depth interval examined but they were generally more abundant in the 1–2 cm layer of the sediment. This pattern, that is, meiofauna abundance maxima in the upper 2 cm of sediment, was recorded by almost all meiobenthic studies. Occasionally, sandy beach meiofauna can be distributed to the depth of 50 cm or deeper on well-oxygenated beaches (Brown and McLachlan 1990). Munro et al. (1978) recorded nematodes down to 105 cm at such beaches. McLachlan (1977) suggested that meiofauna remains mainly in conditions where oxygen is plentiful, but also escape from desiccation and feeding activity may affect vertical distribution. The latter was confirmed by studying fine-scaled vertical distribution patterns of marine nematodes (Steyaert et al. 2001, 2003). Moodley et al. (2000) and Widbom and Elmgren (1988) turned attention onto microfaunal (ciliate and protozoan) activity in the sandy beach sediments as an important factor governing the subsurface activity of meiofauna. In addition, anthropogenic factors (e.g. pollution, physical disturbance) may influence distribution of meiofauna in the sediment as well (Schratzberger and Warwick 1998; Gheskiere et al. 2005b).

Community patterns and abundance in exposed sandy beaches have been assumed to be primarily controlled by specific responses to water percolation processes and sediment characteristics (McLachlan 1977; McLachlan et al. 1993). Exposed sandy beaches have been considered physically stressful environments, their faunal assemblages being best understood by observing responses to abiotic factors (Jaramillo and McLachlan 1993). The ‘biotic factors in stable environment’ theory of Hulings and Gray (1976) stated that biological

Table 5 Sedimentological and morphodynamic characteristic of the Heist and De Panne beaches (after Degraer et al. 2003)

	Slope (°)	Grain size (μm)		Ω	RTR	BSI
		Min–max	Mean			
Heist	0.7	227–275	255	6.8	10.0	4.2
De Panne	0.7	177–235	199	6.2	8.7	3.4

Ω (dimensionless) Dean's parameter of dimensionless fall velocity, *RTR* (dimensionless) Relative Tidal Range, *BSI* (dimensionless) Beach State Index

interactions control meiofauna abundances on atidal beaches, while on tidal beaches sediment characteristics are the major controlling factors.

Biological factors are known to play a key role in the establishment and maintenance of macrofauna zonation on rocky shores, with recruitment, predation and competition all playing main roles (Menge and Sutherlands 1976; Underwood and Denley 1984). Thus, predation and competition for food might be important for the zonation of meiofauna on sandy beaches as well, although factors controlling these communities are not necessarily the same as on rocky shores. Zonation on sandy beaches is not nearly as visible as on rocky shores and is in fact three-dimensional. This is a consequence of the dynamic environment of the beach and the shifting of populations that occupy it (McLachlan and Jaramillo 1995). The present study aimed to incorporate at least two dimensions that is, vertical and horizontal distribution.

Although the present paper mainly relates physical factors to meiofauna distribution, some clear trends of niche segregation could be found. Even at the studied higher taxon level, meiofauna organisms showed preferences both in vertical and horizontal ranges. This suggests a taxon-specific distribution which is closely linked to a taxon-specific sensitivity to major abiotic factors. These abiotic factors seem to be very variable among the different beaches studied and this is reflected in different vertical distribution patterns of meiofauna at the sampling sites. In addition, the horizontal distribution of meiofauna along two nearby macro-tidal beaches (Table 5) showed strong differences suggesting that tidal range alone cannot explain most of the variation. In this way, meiofauna is a good predictor for the overall condition of a beach and might be very useful in further monitoring studies.

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