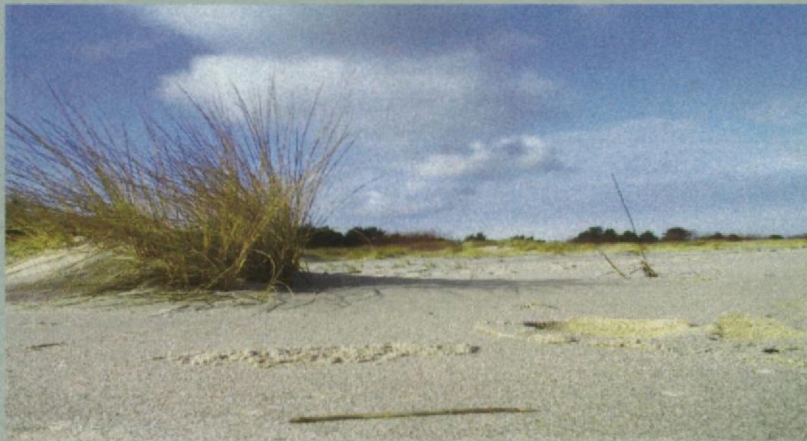# Nematode Assemblages from European Sandy Beaches - Diversity, Zonation Patterns and Tourist Impacts

Nematodengemeenschappen van Europese Zandstranden - Diversiteit, Zonatiepatronen en Impacts van Toerisme

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Academic Year 2004-2005

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A thesis submitted in partial fulfilment of the requirements for the degree of
Doctor in Sciences (Biology)

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There are more Things on the Beach and between the Sand Grains
Than are dreamt of in your Philosophy ...
(modified from *W. Shakespeare*, 1601)

Beach beauns (To Glasktere)

One Belgian he wanted to teach us
what meiofauna do on the Beaches.
Big sieves they survive
under tourists they thrive.
Their secret? They diapause, these creatures!

Olav Giere

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DANKWOORD

Tijdens de kerstvakantie 2000 was ik *uitgebreid* het behalen van mijn IWT-specialisatiebeurs aan het vieren. Nu, kerstvakantie 2004, ben ik de laatste hand aan het leggen aan wat je verwacht wordt te schrijven na het behalen van een dergelijke beurs. Wat vliegt de tijd snel! Het moment is dan ook gekomen om een ganse boel mensen te bedanken die me de voorbije 4 jaar met raad en daad hebben bijgestaan.

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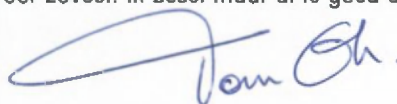
Ma & Pa, zusje Sylvie, skoane broere Gil, kleine Tim en konijn Wannes volgden de afgelopen jaren mijn wormenavontuur op de voet en hoewel ze waarschijnlijk nog altijd denken dat het hier regenwormen betreft werd steeds de nodige steun gegeven waar nodig. Merci!

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30 december 2004,
Ergens tijdens de zoveelste herhaling van het Journaal,

SUMMARY -

SAMENVATTING

SUMMARY

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 (Davies 1972; McLachlan 1983). A unique feature of beaches as a habitat is its narrowness (*e.g.* 500 km of continuous sandy coast, covers only 5 to 10 km^2). Partly due to their barren appearance sandy beaches have not been regarded as vulnerable to human disturbance and, consequently, coastal recreational activities are increasing rapidly in developed countries during the last decades as people enjoy more leisure time and higher standards of living.

Pristine sandy beach sediments offer a considerable range and diversity of biotic habitats: horizontally, the sub-aerial (dunes and upper beach), the intertidal (swash zone/shoreline) and the subtidal area (surfzone and near-shore) while vertically there are pelagic, benthic and interstitial environments. As the beach is the dynamic interface between the terrestrial and marine ecosystem, several biotic and abiotic gradients characterize this narrow interface. Most of the interstitial faunal research on sandy beaches has been mainly concentrated on macrofauna (>1 mm) (McLachlan and Jaramillo 1995 and references therein), while more recently also shore birds has become a well-studied group (*e.g.* Cornelius *et al.* 2001).

In contrast, sandy beach meiofauna (all metazoans between 1 mm and 38 µm) have received considerably less attention notwithstanding their high diversity (even at taxon level) and density (up to 1.10^6 individuals per square metre (McIntyre 1969)) in sandy sediments. Despite their high dominance within the meiofauna, research on sandy beach nematodes is mainly restricted to treating nematodes as a single taxonomic unit although the phylum has been considered as a diverse (Heip *et al.* 1985) and possibly as a hyper-diverse taxon (Lambshead 1993; Lambshead and Boucher 2003) with a global distribution in soils and sediments. Nematodes also have several features favourable for using them as bio-indicators of environmental conditions (Schratzberger *et al.* 2000).

Because of the limited knowledge of the meiofaunal life in European sandy beach ecosystems, a thorough survey of the species biodiversity patterns is one of the general aims of this thesis. Three different European sandy beaches were investigated: one in the North Sea, one in the Baltic Sea and one in the Mediterranean Sea. In the second part of the thesis, the impact(s) of tourism and tourism-related activities on the sandy beach meiofaunal assemblages were evaluated. Comparisons were made between tourist and non-tourist (pristine) beaches in the same geographic area and a short term experiment with emphasis on the immediate effects of beach cleaning was conducted.

Community structure, intertidal zonation and feeding structure of nematode species across a macro-tidal, ultra-dissipative, sandy beach (De Panne, Belgium) were investigated in **Chapter II**. A total of 88 free-living nematode species was recorded along the studied transects. Average nematode densities increased from the upper beach towards the low-tidal level, 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. 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 were found to be the dominant feeding type in 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.

Spatial patterns of nematode community structure and biodiversity patterns from two geographically spaced, intermediate, micro-tidal beaches in the Mediterranean and Baltic area were investigated in Chapter III. Differences in the nematode assemblages were found to be significant and related to the morphodynamic characteristics of the studied zones (upper beach, swash/breakers and subtidal). Highest nematode densities and species diversities were recorded on the coarse-grained, more physically controlled, Mediterranean beach in contrast to the fine-grained more chemically controlled Baltic beach. This is in contrast to the worldwide patterns of macrofaunal communities. As demonstrated by higher taxonomic distinctness measurements, upper beaches were found to harbour species from both the marine and terrestrial ecosystem and are considered to be important ecotones between these adjacent systems. The swash/breaker zones were characterised by the loss of distinctive species caused by the high water percolation in these zones. At the meiofauna level, Por (1964) was the first to report that the phenomenon of 'parallel level-bottom communities' or 'isocommunities' was not only restricted to macrofauna but that the homogeneity and parallelism was even more pronounced for meiofaunal assemblages. He stated that isocommunities are typical for benthic environments and are defined as ecological parallel assemblages: 'the same types of bottoms are everywhere inhabited by species of parallel animal communities in which different species, of the same genera, replace one another as the characterising species'. We showed that this concept was only supported for the upper beaches.

The study in Chapter IV demonstrated, in two different coastal systems (Mediterranean and Baltic), that tourism related activities are particularly affecting the sandy beach meio- and nematofauna in the upper beach zone, the specific ecotone in which many meiofauna species from both the marine and the terrestrial environment co-exist. Tourist upper beaches were characterized by a lower % Total Organic Matter (%TOM), lower densities, lower diversities (absence of Insecta, Harpacticoida, Oligochaeta, terrestrial and marine Ironidae nematodes) and higher community stress compared to nearby pristine, non-tourist locations. The %TOM was found to be the single most important factor for the observed differences in meiofauna assemblage structure at tourist versus non-tourist beaches in both the Mediterranean and the Baltic region. The free-living nematode assemblages from tourist upper zones departed significantly from expectations based on random selections from the regional nematode species pool. Furthermore upper zone assemblages were characterised by a much lower species diversity consisting of taxonomically closely related nematode species with r-strategist features. Faunal differences between tourist and non-tourist beaches were generally decreasing towards the lower beach zones.

In **Chapter V**, a field experiment, following a BACI design (Before-After Control- Impact) was conducted at the strandline of De Panne (Belgium) to investigate the impact of mechanical beach cleaning on the strandline-associated meiofaunal assemblages. Natural strandline assemblages were exposed to a one-off 5 cm deep mechanical beach cleaning (which completely removed the strandline) and observed for 24 hours. The power of the experiment to detect ecologically significant effects of mechanical beach-cleaning was assessed and a 99% chance of detecting a 50% change in total abundance, evenness and taxonomic diversity and a 74% chance in detecting a 50% change in species richness was recorded. This illustrated the sound use of these biological factors in this field disturbance experiment. Differences between cleaned plots and those from the un-cleaned control plots in terms of decreased %TOM, total abundance and changed community structure were visible from immediately after the experimental cleaning onwards and came again to resemble those in the control plots after the following high water. Any impacts due to cleaning on species richness, evenness and taxonomic diversity were showed to be minor in relation to the daily changes. Recolonization of the cleaned sediments was assumed to occur from the underlying sediments as a result of the elevated water table during the rising tide. We suggested that strandline meiofauna are more resistant to mechanical beach cleaning than are macrofauna.

SAMENVATTING

Zandstranden behoren tot de meest verspreide intertidale systemen wereldwijd (Short 1999). Ze zijn het dominante kustype langs de gematigde kusten waar ze zowel een belangrijke beschermende functie tegen de krachten van de zee, als een belangrijke socio-economische functie vervullen (Davies 1972; McLachlan 1983). Een uniek kenmerk van zandstranden is de geringe breedte (*e.g.* 500 km zandstrand beslaat een oppervlakte van slechts 5 tot 10 km²). Als gevolg van het dorre en droge uitzicht werden (worden) zandstranden aanzien als weinig kwetsbare landschappen die niet of nauwelijks invloed ondervinden van antropogene verstoringen. Als gevolg hiervan worden zandstranden wereldwijd recreationeel overgeëxploiteerd. Voornamelijk gedurende de laatste decennia is de recreationele druk op deze zandstranden zeer snel toegenomen als gevolg van de stijgende levenskwaliteit en het algemene welzijn van de mens.

Ongerepte en onverstoorde zandstranden bieden een ruime waaier en diversiteit aan habitats. Enerzijds onderscheiden zich horizontaal, het supra-litoraal (duinen en droog strand), het intergetijdengebied (swash zone en waterlijn) en het subtidaal (surfzone en vooroever) terwijl verticaal, pelagische, benthische en interstitiële habitats kunnen onderscheiden worden. Het strand is tevens de dynamische transitiezone begrensd door zowel het mariene ecosysteem als het terrestrische ecosysteem. Hierdoor wordt deze smalle overgangszone gekenmerkt door verschillende belangrijke biotische en abiotische gradiënten.

Onderzoek naar de interstitiële fauna van zandstranden is hoofdzakelijk geconcentreerd op macrofauna niveau (>1 mm) (McLachlan en Jaramillo 1995 en referenties daarin) terwijl zandstrand meiofauna (alle meercelligen begrepen tussen 1 mm en 38 µm) slechts zelden onderzocht werd, niettegenstaande de doorgaans zeer hoge diversiteit (zelfs op hoger taxon niveau) en densiteit (tot 1.10^8 individuen per vierkante meter, McIntyre 1969) in zandige sedimenten. Recentelijk kreeg ook de avifauna van zandstranden meer aandacht (*e.g.* Cornelius *et al.* 2001).

Nematoden vormen meestal de dominante groep binnen de meiofauna van zandstranden (Brown en McLachlan 1990) maar desondanks is het onderzoek ernaar beperkt gebleven tot het behandelen van nematoden als een taxonomische eenheid (Nematoda sp.) en zijn studies naar de soortendiversiteit op zandstranden schaars. Verscheidene studies klasseerden de nematoden nochtans als een soortenrijke (Heip *et al.* 1985) en mogelijks een uiterst soortenrijke stam binnen het dierenrijk (Lambshead 1993; Lambshead en Boucher 2003) met een algemene wereldwijde verspreiding in bodems en sedimenten. Nematoden bezitten eveneens verschillende kenmerken die het phylum bruikbaar maken als bio-indicator in omgeving- en impactstudies (Schratzberger *et al.* 2000)

Door de beperkte huidige kennis van de meiofauna van Europese zandstranden is een grondige studie van hun soortenrijkdom en gemeenschapspatronen één van de algemene doelstellingen van deze doctoraatsthesis. Hiervoor werden de vrijlevende nematoden, als belangrijkste groep binnen de meiofauna, tot op soortniveau gedetermineerd. De meio- en nematofauna van drie, min of meer ongerepte, Europese zandstranden werd onderzocht; een strand aan de Noordzee, een strand aan de Baltische Zee en een strand

aan de Middellandse Zee. In een tweede deel van deze thesis werden de mogelijke invloeden van toerisme en hieraan gerelateerde activiteiten op deze meiofauna onderzocht. Hiervoor werd in verschillende geografische regio's de samenstelling en structuur van meiofauna gemeenschappen van zowel toeristische als ongerepte zandstranden met elkaar vergeleken. Ook werd een korte termijn experiment opgezet om de directe gevolgen van mechanische strandreiniging op de interstitiële fauna in te schatten.

Hoofdstuk II behandelt gemeenschapsstructuur, intertidale zonering en voedingsstructuur van nematoden op een macrotidaal, ultra-dissipatief zandstrand in De Panne (België). In totaal werden 88 verschillende soorten vrijlevende nematoden aangetroffen op dit fijnzandig strand. Gemiddelde dichtheden namen toe van het hoogstrand naar het laagstrand, wat overeenkomt met de gekende patronen van macrofauna op dergelijke stranden. De soortenrijkdom van de nematoden bereikte de hoogste waarden in de stations gelegen op het middenstrand wat dan weer afwijkt van de macrofauna trend, waar hoogste soortenrijkdom meestal op het laagstrand gevonden wordt. Deze hoge diversiteit van meiofauna op het middenstrand kan verklaard worden door in acht te nemen dat op het middenstrand een optimale balans bestaat tussen overstroming door het getij, zuurstofbalans en stabiliteit van het sediment. Multivariate technieken duidden het bestaan aan van vier gemeenschappen die min of meer overeenkomen met de getijdenzonatie: een hoogstrand-, een vloedmerklijn-, een middenstrand- en een laagstrand-gemeenschap. Deze gemeenschappen waren significant verschillend van elkaar; de verschillen werden echter kleiner naar het laagstrand toe. Dit duidt op een meer graduele overgang tussen deze gemeenschappen. De voedingsstructuur van de nematodengemeenschappen werd gedomineerd door niet-selectieve detrituseters; uitgezonderd in de vloedmerklijn waar epistratumeters domineerden. Percentage fijn zand en hoeveelheid schelpengruis waren de omgevingsvariabelen die het best de afgebakende gemeenschappen verklaarden.

Ruimtelijke patronen en biodiversiteit van nematodengemeenschappen van microtidale zandstranden in de Mediterrane en Baltische regio werden bestudeerd in Hoofdstuk III. Er werden significante verschillen in de compositie van de nematodengemeenschappen op deze stranden waargenomen. De kenmerken van de waargenomen gemeenschappen waren nauw verbonden met de morfodynamiek van de onderzochte zones (hoogstrand, swash- en brekerzone en subtidale zone). Hoogste densiteit en soortenrijkdom werden waargenomen op het grofkorrelige, fysisch gecontroleerde, Mediterrane strand in vergelijking met het fijnzandige, meer chemisch gecontroleerde, Baltische strand. Deze bevinding is in strijd met de wereldwijde trend in zandstrand macrofauna waar het omgekeerde de regel is. Met behulp van taxonomische diversiteitindices werd aangetoond dat het hoogstrand kan beschouwd worden als een belangrijke ecotone gekarakteriseerd door zowel een terrestrische als een mariene nematofauna. Tengevolge van de strenge hydrodynamische condities (hoge waterfiltratie) in de swash-en brekerzone bevolken enkel aangepaste en dikwijls nauwverwante soorten deze zone. Por (1964) was de eerste onderzoeker die concludeerde dat parallelle gemeenschappen of iso-gemeenschappen niet enkel beperkt waren tot macrofauna maar zelfs nog meer uitgesproken waren in meiofauna. Hij postuleerde dat isogemeenschappen typisch waren voor benthische habitats en definieerde het *parallelle gemeenschappenconcept* als: 'gelijkaardige bodems en sedimenten worden gelijk waar bevolkt door soorten van parallelle dierlijke gemeenschappen waarin verschillende soorten, tot het zelfde genus behorend, elkaar vervangen als karakteriserende soort'. Tijdens dit onderzoek werd het bestaan van iso-gemeenschappen aangetoond enkel voor het hoogstrand.

In **Hoofdstuk IV** werd, in twee geografisch verschillende kustsystemen, aangetoond dat toerisme en hieraan gerelateerde activiteiten een negatieve invloed hebben op de meio- en nematofauna van het hoogstrand, de specifieke ecotone waarin verschillende terrestrische en mariene nematode coëxisteren. Hoogstranden van toeristische stranden zijn gekenmerkt door een lager gehalte aan Totaal Organisch Materiaal (%TOM), lagere dichtheden, lagere soortenrijkdom (afwezigheid van Insecta, Harpacticoida, Oligochaeta, terrestrische nematoden en mariene Ironidae nematoden) en hogere gemeenschapsstress in vergelijking met nabije ongerepte, niet-recreationele locaties. Zowel in de Mediterrane als in de Baltische regio bleek het %TOM de belangrijkste factor te zijn die de waargenomen verschillen in de meio-nematofauna gemeenschappen kan verklaren. De nematodengemeenschappen van deze verstoorde hoogstranden vertoonden significante verschillen in taxonomische samenstelling (een verarming) in vergelijking met wat men zou verwachten op basis van willekeurige selecties uit de regionale species pool. Deze verstoorde hoogstrandgemeenschappen vertoonden eveneens een lagere nematoden soortenrijkdom, gekarakteriseerd door taxonomisch nauwverwante soorten met *r*-strateeg kenmerken. Verschillen in samenstelling en kenmerken van de nematodengemeenschappen waren minder duidelijk strandafwaarts.

In **Hoofdstuk V** werd aan de hand van een BACI-design (Before-After Control-Impact) een veldexperiment opgezet om de impact van mechanische strandreiniging op de vloedmerklijn meiofauna in te schatten. De natuurlijke vloedmerklijn van het strand van De Panne werd onderworpen aan een éénmalige, 5 cm diepe, mechanische reiniging (die nagenoeg de complete vloedmerklijn verwijderde) en de interstitiële meiofauna werd gedurende 24 h geobserveerd. De *power* van het experiment om ecologisch significante effecten waar te nemen werd geschat en er werd een 99% kans berekend om een 50% (*i.e.* ecologisch significant) verandering in dichtheden, evenness en taxonomische diversiteit waar te nemen. De kans op het waarnemen van een halvering van het aantal soorten bedroeg 74%. Deze hoge probabiliteiten illustreren het verantwoord gebruik van deze indices in dit experiment. Gereinigde plots verschilden nagenoeg onmiddellijk na de mechanische reiniging significant van de controle plots (lagere %TOM, lagere dichtheden en verschillende gemeenschapsstructuur). Deze verschillen waren grotendeels verdwenen na het volgende hoogwater. Mogelijke effecten van de mechanische strandreiniging op de soortenrijkdom en taxonomische diversiteit waren ondergeschikt aan de temporele patronen. Rekolonisatie van de verstoorde sedimenten werd verondersteld te gebeuren vanuit de onderliggende sedimentlagen tengevolge van de stijgende watertafel bij het opkomend getij. Er werd gesuggereerd dat meiofaunagemeenschappen van vloedmerklijnen minder gevoelig zijn voor mechanische strandreiniging dan macrofaunagemeenschappen.

CHAPTER I

General introduction, state of the art,

aims and thesis outline

INTRODUCTION

Beach systems: definitions, characteristics and classifications

Beaches occur on all sedimentary shorelines exposed to waves and may be composed of grain sizes from sand (63-2000 µm) over cobbles (2000-64000 µm) to boulders (>64000 µm). They are among the most dynamic systems on the Earth's surface, and exist wherever there is sufficient sediment for the waves to deposit above sea level. While beaches are totally dependent on waves and sediment, their presence is independent of most other surface processes. Consequently they occur in all latitudes, in all tidal ranges and on all manner of coasts. (Short 1999)

Beaches can be defined in numerous ways; however, two factors are essential: waves and sediments. Therefore the simplest physical definition of a beach is *a wave-deposited accumulation of sediment lying between modal wave base and the upper swash limit, where wave base is the maximum depth at which waves can transport material shoreward, and the swash limit, the landward limit of wave action and sediment transport* (Short 1999). However, as this definition includes all beaches, it does not take into account additional processes and parameters that can influence the character of a beach. They are influenced and modified by numerous other processes, especially tidal currents, wind and parameters such as size and type of sediment, biota, air and water temperature, and sediment chemistry.

The sediments on beaches mainly originate from erosion of the land and are transported to the sea by rivers and streams but they may also receive biogenic sources from the sea (animal skeletons) and materials from sea cliff erosion. Sand is predominantly silica (SiO_2) together with calcium carbonate ($CaCO_3$), which are derived from rocks and shelled animals, in varying proportions. Beaches in areas where deposition is predominantly from coralline material are dominated by calcium carbonate and tend to be very white. Those found on volcanic islands are dominated by products from rock erosion and generally consist of very dark sand. There is also usually some complex chemical clay material present, and a component of organic matter (Short 1999). For the purposes of this doctoral thesis a beach is considered to be a siliclastic beach, thus excluding high latitude cobble and boulder beaches and tropical coralline beaches.

The main variable in sands is grain size, which in turn affects a number of other features. Water percolation and drainage are the most important of these, being the outcome of gravity working against capillarity, resulting in fine grains being more water-retentive when wetted. Oxygenation is also affected, with well-drained large grain sands being highly oxygenated when compared to fine grained sands. Small-grain fine sand may retain considerable volumes of water for long periods and so readily become anoxic as anaerobic decomposition products build up. Another factor differing between beaches is sorting. Some beaches have a very uniform particle size and are said to be well-sorted, while others are highly variable, having a poor sorting factor. Thus two beaches can have the same mean grain size but very different sorting factors which in turn will affect their drainage and oxygenation. Other factors which may affect sorting include the processes of bioturbation, biodeposition and biosecretion by benthic fauna present within the sediment

(McLachlan and Turner 1994). Sediment size will, in conjunction with waves, control the morphology and dynamics of a beach (Short 1999). Fine sand produces a lower gradient (1-3°) swash zone, wider surf zone and potentially highly mobile sand while coarse sediment beaches have a steeper gradient (5-10°), a narrower surf zone and less mobile sand. Therefore, identical waves arriving at adjacent fine, medium and coarse sand beaches will interact to produce three distinctly different beaches. Sandy beaches dominate most of the temperate and tropical coasts where they represent both important recreational assets and buffer zones against the physical forces of the sea (McLachlan 1983). On a global scale the estimate of sandy beach coast varies from 11% (*i.e.* 53000 km) to 34% (*i.e.* 170000 km) of the total coastline (Hardisty 1994).

Tides (the periodic rise and fall of the ocean surface due to the gravitational force of the moon and the sun, acting on a rotating Earth) are a non-essential beach component (Davies 1964). The contribution can range from none in tide-less seas and lakes to a dominating factor in macrotidal environments. This observation has resulted in a geographical classification of coastal environments based on the absolute tidal range. It is common to divide sandy beaches into three categories: microtidal ranges of less than 2 m, mesotidal ranges between 2 and 4 m, and macrotidal ranges in excess of 4 m (Davies 1964). Distinct coastal morpho-types that are characteristic of each of these tide range classes may be identified. The common assumption is that microtidal coasts are by definition wave-dominated and typified by beaches and barriers, in contrast to macrotidal environments, which are tide-dominated and mesotidal coasts are influenced by both waves and tides. However, while tidal range will always play a secondary role to waves in beach morphodynamics (the mutual interaction of waves with the beach topography), increasing tide range will in combination with wave conditions, contribute substantially to beach morphology and will increasingly spread the impact of shoaling, breaking and swash wave activity.

Masselink (1993) developed an empirical model to simulate the tide-induced migration of hydrodynamic processes across beaches and found that a useful parameter to quantify tidal effects was the Relative Tide Range:

$$RTR = MSR/H_b \qquad \text{(Equation 1.1)}$$

Where H_b is the wave height and MSR is the mean spring tide range. The larger the relative tide range, the more important become the tidal effects relative to the wave effects.

As beaches are a product of waves and sediment and are influenced by a range of additional parameters, measurable characteristics of these have been used to quantify beach types and behaviour. Wave height (H_b), wave period (T) and grain size (as defined by sediment fall velocity, W_s) were first combined by Gourlay (1968), based on his observations on laboratory beaches, into the dimensionless fall velocity or Dean's parameter:

$$\Omega = H_b/W_s T \qquad \text{(Equation 1.2)}$$

Wright and Short (1984) adapted Ω for use on natural beaches and found that when $\Omega<1$ beaches tend to be reflective (steep, coarse sediment, bar-less), when $\Omega>6$ they tend to be dissipative (flat, fine sediment, multi-barred), and when $\Omega=2-5$ they are intermediate with characteristics in between reflective and dissipative states. The most important processes that control the morphology and hydrodynamics of beach environments are associated with the dissipation of the incident wave energy.

Fully dissipative beaches tend to have relatively stable morphologies and exhibit minimal shoreline change (Short and Hesp 1982). They are a product of high waves moving over fine sand, which results in a flat beach face and a wide surf zone. Waves are typically spilling breaker waves dissipating their energy over a nearly flat, multi-barred, sandy subtidal zone at a considerable distance from the shore. Consequently the water pressure at the sediment surface is low when a wave crest passes and there is a low rate of flushing (or low wave pumping) between the small sand particles. This allows a build-up of organic matter and microbial life, which in turn leads to sharp gradients in oxygen, nutrients, RPD-layer and pH.

At the other extreme are fully **reflective beaches** characterised by small waves with longer periods, which surge directly up steep beach faces (as there are no bars) where they collapse, resulting in much of their energy being reflected back into the sea. There is often a characteristic zone where incoming waves and backwash collide and deposit sediment to form a small step. Reflective beaches are almost always characterised by a relatively narrow beach and swash zone, and the absence of a surf zone. As the energy of the waves is not dissipated when reaching the beach, due to the coarse grained, well drained nature of these beaches, there is a high rate of flushing through the sediment and thus sediment organic matter content is low.

Intermediate beaches, whether closer to the dissipative or to the reflective end of the spectrum are the most common beaches worldwide and occur under a wide range of conditions, ranging from moderate to high wave (0.5-2.5 m), fine to medium sands and a range of wave heights. They typically have a few foreshore bars on which a portion of the wave energy is dissipated, and a relatively steep beach face on which the remainder of the wave energy is expended. Intermediate beaches occur under a wide range of conditions. Short and Wright (1983) distinguished four different states of intermediate beaches mainly in response to wave conditions. Generally intermediate beaches can be regarded as a transition from high energy dissipative to low energy reflective beaches. Morphodynamically, they are reflective close to the shore and dissipative further off-shore.

By combining the tidal effects on beaches with Gourlay's dimensionless fall velocity (1968), Masselink and Short (1993) proposed a grouping of natural beaches on the basis of four physical constraints: modal breaking wave height (H_b), modal breaking wave period (T), sediment fall velocity of the upper beach face (W_s) and mean spring tide range (MSR). These variables are simply quantified by two dimensionless parameters, namely the relative tide range RTR (Equation 1.1) and the dimensionless fall velocity Ω (Equation 1.2). The dimensionless fall velocity parameter indicates whether reflective, intermediate or dissipative surf conditions will prevail while the relative tide range parameter indicates the relative importance of swash, surf zone and shoaling wave processes in determining the beach profile morphology. The conceptual beach model is shown in Figure 1 and consists of seven major beach types that fall into three groups. Definitions of different positions on the beach are shown in Figure 2.
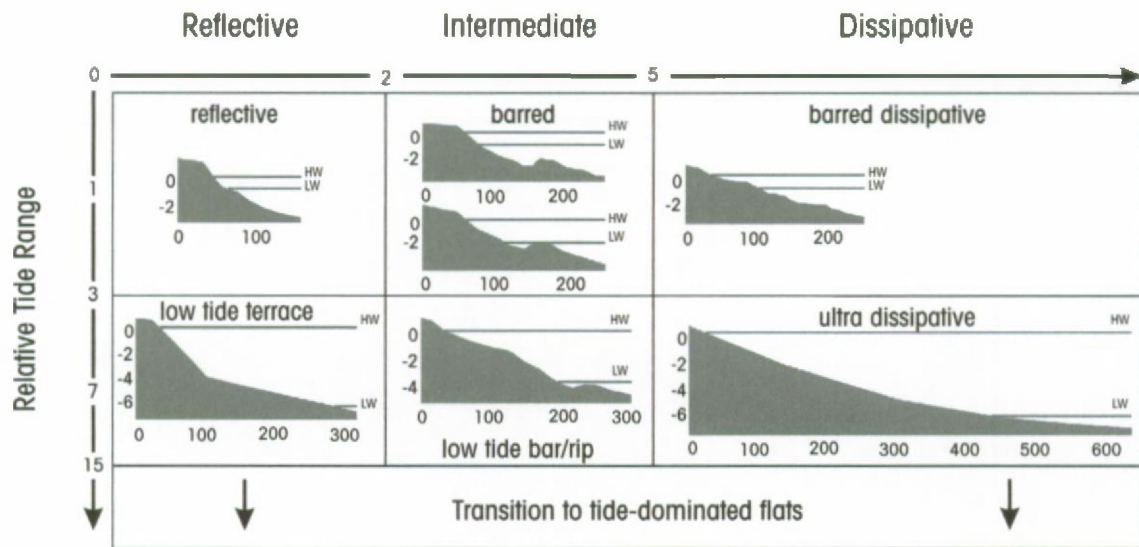
Figure 1: Conceptual beach model. Natural beach state is a function of dimensionless fall velocity and relative tidal range. (Modified from Masselink and Short 1993)
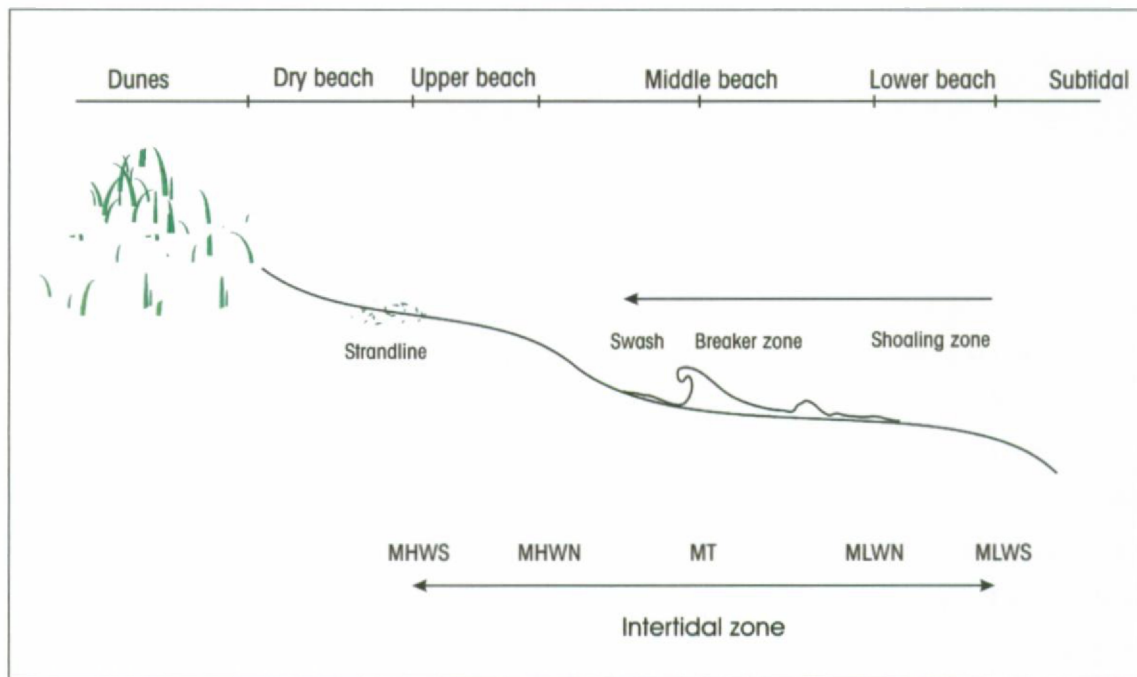

Figure 2: Positions on the beach. MHWS=Mean High Water Spring, MHWN=Mean High Water Neap, MT=Mid-Tidal level, MLWN=Mean Low Water Neap, MLWS=Mean Low Water Spring. (After Short 1999)

Sandy beach biota

Beach systems at first glance have a barren and arid appearance, particularly bare sands, which seem to be akin with desert environments. However, sandy beaches offer a wide range of diverse biotic habitats. Horizontally these include the sub-aerial (upper dry beach and fore dunes), the intertidal (swash zone/shoreline) and the subtidal (surf zone and near shore) while vertically there are pelagic (water column) and benthic (surface and interstitial) environments. Each vertically defined habitat is relatively shallow and consequently receives good penetration of sunlight, which stimulates primary production (Brown and McLachlan 1990). Most are also exposed to constant water movement, which has the potential to circulate nutrients and exchange water and nutrients with the open sea, estuaries and streams. While this may favour a range of organisms there are also disadvantages related to the sandy, unstable nature of the benthic layer. These include the potential for substrate erosion and burial by sediment deposition and the extreme hydrodynamics and turbulences generated in particular places on the beach (*e.g.* surf and swash zones). Consequently fauna is restricted to highly mobile and/or microscopic forms specially adapted to exist within such a physically perturbed environment.

It is common to separate the endofaunal biota of sediments according to size into macrobenthos (>1 mm mainly molluscs, crustaceans and polychaetes), meiobenthos (38 µm-1 mm) and microbenthos (<1 mm mainly bacteria, autotrophic flagellates and diatoms). The pore spaces between the grains can total up to 40% of a beach volume, while the surface area of sand grains increases exponentially with decreasing grain size (McLachlan 1983). The surface of sand grains hosts the microbenthos which, can serve as food initially for meiobenthos (or meiofauna) but also for macrobenthos. Other biotic components of the beach ecosystem include epibenthic predators, such as shrimps, crabs, fish and hyperbenthos (the association of small animals living in the water layer close to the seabed), such as mysids and cumaceans. Birds both land- and sea-based are perhaps the most visible part of the sandy beach ecosystem and may even equal or exceed the macrofauna in biomass. Birds also have a significant impact on the ecosystem due to predation and scavenging (Brown and McLachlan 1990). Birds may be partially or totally migratory on beaches resulting in their densities varying according to the season, overwintering and breeding patterns. Birds which feed intertidally include Laridae (gulls), Scolopacidae (sandpipers), Haematopodidae (oystercatchers) and Charadriidae (plovers). The entire beach ecosystem comprises of complex interactions between all components of the biota, which take place within a dynamic system open to both land and sea influences and biota.

Two food chains generally occur within the beach ecosystem with varying degrees of interaction (Figure 3). These are the macroscopic and the interstitial (or so-called small food web). Both food chains are dependent on wave energy to drive water filtration, which delivers marine inputs. The macroscopic food chain consists of large benthic organisms, including filter feeders, herbivore and carnivorous scavengers/predators, zooplankton, fish and birds. The small food web consists of bacteria, protozoans and meiofauna, with some albeit non-significant predation by macrofauna. Dissolved and particulate organic matter accumulates in the interstices by the filtering of seawater. For a given particle size, the amount of

organic matter retained is greatest where the wave action is the strongest. The organic matter is utilised by bacteria, which in turn are consumed by protozoa and meiofauna. Owing to their high abundances, high species richness and trophic diversity, meiofauna occupies a position of considerable importance in biodegradation-related processes in sediments. These processes are of major importance in the strandline (or high tide mark). The strandline marks the very edge of the sea and provides a very unique although fringe habitat, neither fully marine nor completely terrestrial, which is colonised by invertebrates from both ecosystems. Richest strandline communities, both in density and diversity, are commonly found in the thickest, wettest, rotting flotsam. These rotting materials provide a rich food source for a great variety of both marine and terrestrial invertebrates with large pieces of driftwood providing shelter on the shore for active predators that emerge at night. Once wrack is cast ashore it undergoes physical processes of fragmentation, decomposition and remineralization by bacteria, meiofauna and grazers (Jedrzejczak 2002a, b). Colombini and Chelazzi (2003), in their recent review, have described the macrofaunal beach-wrack assemblages and species succession associated with decaying organic matter, including marine as well as terrestrial representatives. The presence of all these invertebrates provides an important food source for birds, including waders, *e.g.* sanderling, knot, dunlin and ringed plover, as well as crows and seabirds.
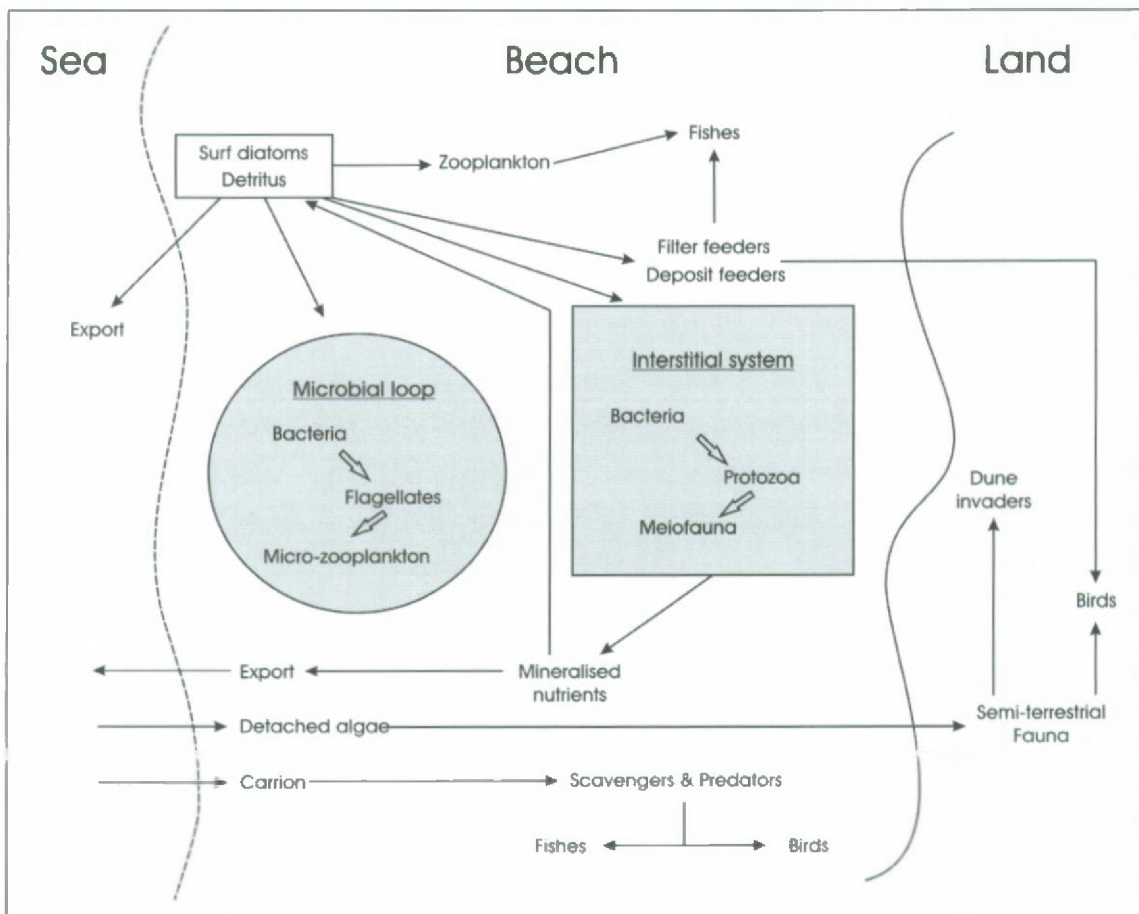

Figure 3: Simplified sandy beach food chains and their relations. (Modified from Brown and McLachlan 2002)

Beach benthic ecology is intimately tied to the physical beach conditions including grain size and wave energy, it is also closely related to beach type. McLachlan and Lewin (1981) primarily found that macrofaunal species diversity and abundance were related to physical parameters including beach slope (as determined by the wave conditions) and particle size. They recorded a substantial increase in both diversity and abundance with decreasing beach slope and particle size. Meiofaunal species diversity has been shown to display an opposite trend with highest species diversity in medium coarse sediments (Brown and McLachlan 1990). In contrast to the wave-swept surface sand inhabited by most of the macrofauna, the interstitial system is truly three-dimensional often having a great vertical extent in the sand. The interstitial environment experiences a continuum of conditions ranging between chemically and physically controlled extremes.

The chemical extreme is represented by fine grained beaches where water drainage through the sand is negligible and organic inputs are high. Here the consumption of oxygen by the interstitial inhabitants exceeds the poor supply, which is limited by poor wave action and low sediment permeability. As a consequence the sediment becomes deoxygenated and steep vertical gradients in interstitial chemistry develop. Oxygenated sand occurs at the surface with reduced layers below. In these conditions (which occur on low energy dissipative beaches) the interstitial fauna will concentrate in the top layers of the sediment. The meiofauna is thought to be primarily adapted to these chemical stresses as physical stresses like high flushing rate, desiccation and sediment disturbance by the waves are benign.

The physical extremes occur on coarse-grained beaches subjected to strong wave action (*i.e.* on reflective beaches). On these beaches, huge amounts of water are flushed through the sediment and drain rapidly due to high sediment permeability. The interstices are always highly oxygenated and drain out during low tide. Whatever the organic inputs, oxygen demand never exceeds supply. Here the interstitial meiofaunal community has a deep vertical distribution and has adapted primarily to the physical environment (*i.e.* high interstitial flushing rates, desiccation during low tide and disturbance of the sediment by wave action). Assuming a similar importance of the two extremes, optimal conditions can be expected to occur on beaches with elements of both chemical and physical gradients shaping the interstitial environment. These conditions generally occur on intermediate beaches.

Higgings and Thiel (1988) demonstrated that interstitial communities are tightly connected to their granulometric environment and that variations within the taxonomic composition could be expected according to sediment type *e.g.* siliceous or cancerous. Depending on local geological and physiological conditions, generalizations on the occurrence of certain sediments are seldom possible. In temperate and boreal regions, siliceous sands prevail, while in warmer, tropical regions, biogenic calcareous sediments dominate. Generally, the shape of the sediment particles, by indirect action via water content and by permeability, is a governing factor in meiofauna colonization of the sediment (Giere 1993). More precisely meiofaunal colonisation is determined by the grain structure, the roughness of the edges and the shape of the grain surfaces. These are also important parameters in the structuring of the microhabitat for bacterial colonies and as a consequence influence the meiofaunal assemblages feeding on them (Meadows and Anderson 1966). Marcotte (1986) demonstrated that sand grains with diameters >300 μm frequently have more plain surfaces than do smaller particles and that they harbour a different bacterial 'Aufwuchs' which

attract a different meiofaunal community. In siliceous sediments Fenchel (1978) distinguished three main meiofaunal assemblages. In well-sorted and coarse sands rich meiofauna communities dominated by interstitial forms have been described by Wieser (1959). Meiofauna communities comprise of nematodes, harpacticoid copepods, ciliates, tardigrades, gastrotrichs, oligochaetes, and rare taxa such as gnathostomulids, although are usually dominated by nematodes and harpacticoid copepods. In fine-grained sediments with considerable amounts of silt and clay, meiofaunal communities are mainly dominated by burrowing forms of nematodes and kinorhynchs, other taxa are usually scarce. However, there is usually a richer fauna inhabiting the upper layers of these sediments. Purely interstitial forms (like gastrotrichs) are excluded from fine sands and mud while exclusively burrowing forms (like kinorhynchs) are excluded from medium to coarse sediments (Coull 1988). Another meiofaunal assemblage is that which inhabits the anoxic sediments below the Redox Potential Discontinuity layer (RPD). Here anaerobic species of ciliates, together with a few species of nematodes (*e.g. Leptonemella* spp.), plathelminthes, oligochaetes are the dominant taxa. As a consequence of their rich heterogeneity and often high content of detritus, biogenic calcareous sands of the tropics are generally thought to have taxonomically more diverse meiofauna than beaches in temperate and boreal regions (Giere 1993); however some studies (*e.g.* Coull and Herman 1970) would disagree.

Usually, free-living nematodes dominate the meiofaunal communities of sandy sediments and therefore, are theoretically an excellent taxon to use as ecological indicator of different kinds of natural and anthropogenic disturbances within benthic marine habitats (Heip *et al.* 1985; Sandulli 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) and density, often short generation time and a continuous reproduction. Moreover, they are restricted to the sediments throughout their life. An important argument against the use of nematodes as ecological indicator is their difficult taxonomy which makes them hard to use for non-specialists. However, Vanaverbeke *et al.* (2003) demonstrated that this problem can be overcome by using their biomass spectra. As a consequence of their wide range of adaptations, nematodes have exploited all littoral habitats, including the biologically hostile sandy beaches.

Human Impacts on sandy beaches

Shorelines are a part of the natural environment that greatly suffers from human impacts. These impacts include fishing, harbour activities, industry, and power generation from wind turbines. As a result, the impacts on the ecosystem are in keeping. Shorelines are also preferred sites for tourism and recreation and therefore are of great socio-economic importance. Beaches are very popular for a number of reasons. These include scenic walks and recreational fishing; the surf-zone provides an area for water recreation and dry beaches an area for sitting and playing with the dunes providing an area for nature studies. As a rule the major stresses on the coastal environment have been linked with overexploitation of natural resources, pollution, industrialisation and erosion (McIntyre 1995; Dronkers and Devries 1999) while tourism and recreational activities have been largely neglected. However, during the last decades, recreational activities have been increasing rapidly in developed countries as people enjoy more leisure time and higher standards of living. Clearly many of these activities are, and will increasingly be, focused on coastal tourism. Gormsen (1997) estimated that 25% of all hotel beds worldwide are located along sandy coastlines. Thus beaches are subject to ever-increasing pressure from recreational activities and the litter left by human visitors has become an escalating problem.

The impact of tourism on the beach environment does not only include human trampling but also so-called beach management operations. In tourist popular regions dune systems are largely destroyed by the construction of vacation facilities (Cori 1999; Nordstrom *et al.* 2000). Resulting changes in sand budgets and dune profiles may only become apparent after some time, sometimes with disastrous consequences (*e.g.* increased erosion). The fore dunes and backshore are extremely sensitive to changes in the sand budget and so generally the most affected (Mann 2000). Roads in tourist resorts are commonly constructed only a few meters above the high tide mark and in front of the fore dunes where they not only prevent many organisms from making excursions to the beach and the intertidal zone but also modify the supply of sand to the dune ecosystems (needed for the formation of embryonic dunes). In places where access to popular beaches is via the sand dunes, the dune vegetation is weakened or destroyed by repeated trampling which often result in major breaks (blowouts) in the dune system. Partly due to their barren appearance sandy beaches and dunes have not been regarded as vulnerable to these human disturbances, while salt marshes are widely recognized as very fragile systems which have even been shown to be sensitive to barefoot human trampling (Andersen 1995; Poulson and McClung 1999). Human trampling has long been recognised as a critical factor for many vulnerable land biotas, however it has only recently been considered to play a key role in marine coastal conservation management having marked effects on some members of beach fauna and flora.

Recently, the increased use of beaches has pressed regional authorities in an attempt to make the beach appear much 'cleaner' and attractive to visitors to remove natural and artificial flotsam. This includes detached macrophytes, driftwood and carrion, together with sanitary refuse and other litter from anthropogenic origin such as glass and plastics (Ryan and Swanepoel 1996). Nowadays upper beach and strandline mechanical beach cleaning (or beach grooming) is seen as a cost-effective way of removing unwanted debris and litter and has become a common (almost daily) practice on bathing beaches without considering the long-term consequences to coastal environments. Unfortunately not only the litter of human origin but also a significant part of the organic beach-cast material is removed by the use of these machines (Llewellyn and Shackley 1996). Both the removal of strandline debris by cleaning machines (that scour to a depth of at least 5 cm) as well the compression of the sand by the equipment (most cleaning machines are pulled by heavy tractors) may have adverse effects on the invertebrate beach and bird assemblages, the sediment transport and the fore dune stabilisation. These mechanical beach-cleaning activities are also thought to seriously destroy or completely remove the beach habitat. Further effects on faunal assemblages include the deprivation of shelter and/or food and also serious injury and/or death of animals (Colombini and Chelazzi 2003). Compaction of the sand can reduce the air spaces between the sand grains; these spaces provide air for burrowing habitants and organisms in deeper layers. Strandlines are particularly important as they act as precursors to sand dunes. The strandline stabilises the foreshore by enhancing organic and moisture content; pioneer plants can then become established and sand dune formation is initiated. If the strandline is removed frequently, sand dune formation and stabilization is severely limited.

STATE OF THE ART AND AIMS OF THE THESIS

Because of the limited biological knowledge of the benthic life in European sandy beach ecosystems, a thorough survey of the spatial and temporal patterns of the target organisms (free-living nematodes) is required first. In this work three different European sandy beaches will be investigated: one in the Baltic Sea, one in the North Sea and one in the Mediterranean Sea. The biodiversity and nematofaunal zonation patterns from the three localities, which have different morphodynamic states, will be examined. In the second part of the thesis, the impact(s) of tourism and tourism-related activities on the sandy beach meiofaunal assemblages will be evaluated. Comparisons are made between tourist and non-tourist beaches in the same geographic area and a short term experiment based on the effects of beach cleaning.

Most of the biodiversity research on sandy beaches has mainly concentrated on macrofauna (>1 mm) (McLachlan and Jaramillo 1995) and more recently also on birds (e.g. Cornelius et al. 2001). In contrast, sandy beach meiofauna have received considerably less attention despite their high structural and functional diversity and density (McIntyre 1969). Much of the previous meiofauna research on sandy beaches is in essence restricted to general surveys at higher taxon levels (e.g. Gray and Rieger 1971; Harris 1972; McIntyre and Murison 1973; McLachlan et al. 1977; Olafsson 1991; Rodriguez et al. 2001, 2003). Other studies have concentrated on the complex factors influencing the interstitial habitats (e.g. Blome et al. 1999) while information about species diversity is scarce. Nematodes are usually the dominant group accounting for more than 80% of the total meiofauna (Giere 1993). Despite this high dominance within the meiofauna, research on sandy beach nematodes is mainly restricted to treating nematodes as a single taxonomic unit. Despite of the fact that the phylum has been flagged as a diverse (Heip et al. 1985) and possibly as a hyper-diverse taxon in deep sea environments (Lambshead 1993; Lambshead and Boucher 2003) with a global distribution in sandy sediments. Apart from purely taxonomic ones, only a few publications have described the nematode species diversity of sandy beaches in a quantitative way (Gerlach 1953, 1954; Platt and Warwick 1980; Blome 1983; Sharma and Webster 1983; Nicholas and Hodda 1999). This lack of nematode species research on beaches is probably due to the time-consuming research, difficult taxonomy and the overall high densities and diversities of the nematofaunal assemblages. As beaches act as the interface between marine and the terrestrial ecosystem, both marine and terrestrial free-living nematodes can be found. The presence of both terrestrial and marine nematodes makes it difficult to identify to species level because of the taxonomic difficulties. It is also known from experiments that nematodes are ecologically very heterogeneous and occupy different positions in benthic food webs (Schmid-Araya and Schmid 2000; Aarnio 2001). These differences may be as large between nematode species as they are between orders in macrofauna groups (Heip et al. 1982). Consequently, a thorough inventory describing species diversity and community structure is of primary importance to further investigate the importance of nematodes in the sandy beach ecosystem. This descriptive work forms the basic information of the thesis.

Therefore, in the first part of the thesis, undisturbed (*i.e.* non-tourist) sandy beaches were studied from the upper beach towards the low water limit to formally address questions about nematode species diversity and faunal zonation patterns. These aims are extended by studying the existence of isocommunities on geographically spaced beaches. Isocommunities are typical for benthic environments and are defined as ecological parallel assemblages: '*the same types of bottoms are everywhere inhabited by species of parallel animal communities in which different species, of the same genera, replace one another as the 'characterising species*'' (Thorson 1957). The studied beaches differ in tidal regime (macrotidal, microtidal), beach topography (ultra-dissipative, intermediate/dissipative, and intermediate/reflective) and geography (Atlantic, Mediterranean and Baltic)

In the second part of the thesis, the possible impacts of human use of beaches on meiofaunal assemblages are evaluated. As a rule, the major stresses on the coastal environment have been mainly linked with overexploitation of natural resources, pollution, industrialisation and erosion (McIntyre 1995; Dronkers and Devries, 1999) while tourism and recreational activities have been largely neglected. Meiofauna and especially free-living nematodes are known to be sensitive indicators of environmental perturbations (Coull and Palmer 1984, Schratzberger *et al.* 2000). However, many disturbance and perturbation studies prefer not to include nematode species data because of the previously described difficulties. As a result many disturbance studies have worked with ratios (such as Raffaelli and Manson's (1981) Nematode/Copepod ratio) which eliminate the need for detailed, time-consuming species identifications. Despite their wide utilisation, such ratios have not been proven to be accurate predictors of environmental impacts and have generated considerable controversies (*e.g.* Lambshead 1984). In contrast, this research has used nematode species data (*i.e.* the highest possible taxonomical resolution) to compare faunal assemblages (in terms of diversity, density and taxonomic composition) from beaches impacted and un-impacted by tourism on a geographical scale (Mediterranean and Baltic). A comparison between impacted and un-impacted beaches on the Belgian coast was not done as all Belgian beaches receive very similar pressure from tourism. Therefore, a true pristine beach ecosystem in my opinion does not exist along the Belgian coast. The beach of De Panne in front of the Westhoek Nature Reserve is perhaps the most un-impacted beach (with a natural beach-dune connection which was restored recently) along the Belgian coastline. However the intertidal zone is increasingly being used for land yachting events due to the absence of groins and breakwaters. As this beach is infrequently cleaned, a strandline beach-cleaning experiment was performed, rather than a comparison between impacted and un-impacted sites. The increasing use of sandy beaches as recreational resources has forced regional authorities of many tourist resorts to remove all natural wrack and litter of man-made origin (Ryan and Swanepoel 1996). Consequently during the last two decades, a variety of cleaning techniques have been developed and employed in attractive coastal areas all over the world (Taylor *et al.* 1994). Resulting in beach-cleaning becoming one of the major tools employed during beach management operations. The most cost effective method of removing the unwanted strandline has been the use of large tractor-pulled cleaning machines which has become an almost daily phenomenon in many sandy beach resorts.

The purpose of the last part of this PhD project was therefore to set up a beach-cleaning experiment on a relatively un-impacted, almost never cleaned, sandy beach. The aim of the experiment was to answer questions about impact and recovery of interstitial strandline communities following a once-only experimental cleaning operation.

In summary, the present PhD thesis compares the interstitial biodiversity of sandy beach ecosystems with contrasting morphodynamical conditions and sets out to evaluate the effects of tourism and tourism-related interferences on the beach ecosystem, offering the first ideas on the ecological consequences of increasing human use of the sandy beach habitats.

THESIS OUTLINE

The thesis is divided in two main parts, each with two chapters. In the first part, the biodiversity and nematofaunal zonation patterns of geographically spaced beaches with different morphodynamic states (Chapter II and III) are described while in the second part, the Impacts of tourist activities on the sandy beach meiofaunal assemblages based on field observations (Chapter IV) as well as on experimental observations (Chapter V) are evaluated. The general discussion, conclusions and recommendations are presented in Chapter VI.

Several parts of this thesis have already been published in the international literature and the remaining data are submitted for publication. For that reason the outline and output of the chapters is almost exactly like the published papers. Each chapter is also intended to be an autonomous part, which can be read separately from other chapters. Inevitably, there may be some overlap between the introductions, the sections on study sites and material and methods of the different chapters or manuscripts. CITED LITERATURE is generalised and listed at the end of the thesis. The recorded nematode species and their taxonomic position are listed in APPENDIX I. The author's publication list is given in APPENDIX II.

Chapter II ('Horizontal zonation patterns and feeding structure of marine nematode assemblages on a macrotidal, ultra-dissipative sandy beach (De Panne, Belgium)') is concerned with the biodiversity of nematode assemblages along the slope of a broad, relatively undisturbed, fine-grained sandy beach. The main aims are to describe (1) the horizontal nematode zonation patterns (diversity and feeding structure) at species level; (2) the relationship with granulometric variables and (3) the (dis)similarities with macrofaunal sandy beach zonation patterns. This chapter has been published as GHESKIERE T, HOSTE E, VANAVERBEKE J, VINCX M, DEGRAER S (2004) Horizontal zonation patterns and feeding structure of marine nematode assemblages on a macrotidal, ultra dissipative sandy beach (De Panne, Belgium). *Journal of Sea Research* 52:211-226

Free-living nematode zonation patterns on microtidal (wave-dominated) sandy beaches were investigated in **Chapter III** ('Nematodes from wave-dominated sandy beaches: diversity, zonation patterns and testing of the isocommunities concept'). This research aimed to investigate and describe the biodiversity (nematode species level) and zonation patterns in relation to several abiotic variables on two undisturbed wave-dominated European sandy beaches (Mediterranean and Baltic Sea), and secondly to examine if community convergence (isocommunities) exists between geographically spaced beaches with more or less the same morphodynamic state. This chapter has been published as GHESKIERE T, VINCX M, URBAN-MALINGA B, ROSSANO C, SCAPINI F, DEGRAER S (2005) Nematodes from wave-dominated sandy beaches: diversity, zonation patterns and testing of the isocommunities concept. *Estuarine, Coastal and Shelf Science* 62:365-375

In **Chapter IV** ('Meiofauna as descriptor of tourism-induced changes at sandy beaches') we examined the differences in meiofaunal assemblages between tourist and non-tourist beach zones in both the Mediterranean and the Baltic region, as well as the changes in taxonomic structure of the nematode communities. The aims of this study were to: (1) compare the meiobenthic composition at higher taxon levels between tourist and non-tourist beaches in both the Baltic Sea and the Mediterranean Sea, (2) assess possible changes in the taxonomic composition of the nematofauna and (3) determine the environmental variables that are primarily responsible for potential differences at tourist versus non-tourist beaches. This chapter has been published as GHESKIERE T, VINCX M, WESLAWSKI JM, SCAPINI F, DEGRAER S (2005) Meiofauna as descriptor of tourism-induced changes at sandy beaches. *Marine Environmental Research* 60:245-265

Chapter V ('Are strandline meiofaunal assemblages affected by mechanical beach cleaning? Experimental findings') describes the impact of mechanical beach cleaning. Therefore a beach-cleaning experiment on an undisturbed, infrequently cleaned, macrotidal sandy beach was set up through time to address the following aims: (1) to describe the meio- and nematofauna of a freshly deposited strandline, (2) to asses the possible impact of a mechanical beach-cleaner on the assemblages and (3) to asses the recovery rates and the resilience of the assemblages after cleaning. This chapter is submitted to *Marine Ecology Progress Series* as GHESKIERE T, VINCX M, VAN DE VELDE B, PISON G, DEGRAER S Are strandline meiofaunal assemblages affected by mechanical beach cleaning? Experimental findings

In the general discussion and conclusions (**Chapter VI**), key issues and considerations are deduced from the main results of the different chapters.

CHAPTER II

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

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 cm^2) towards the low-tidal level (2784 ± 6 Ind/10 cm^2), 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°05'30"N, 02°34'01"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).
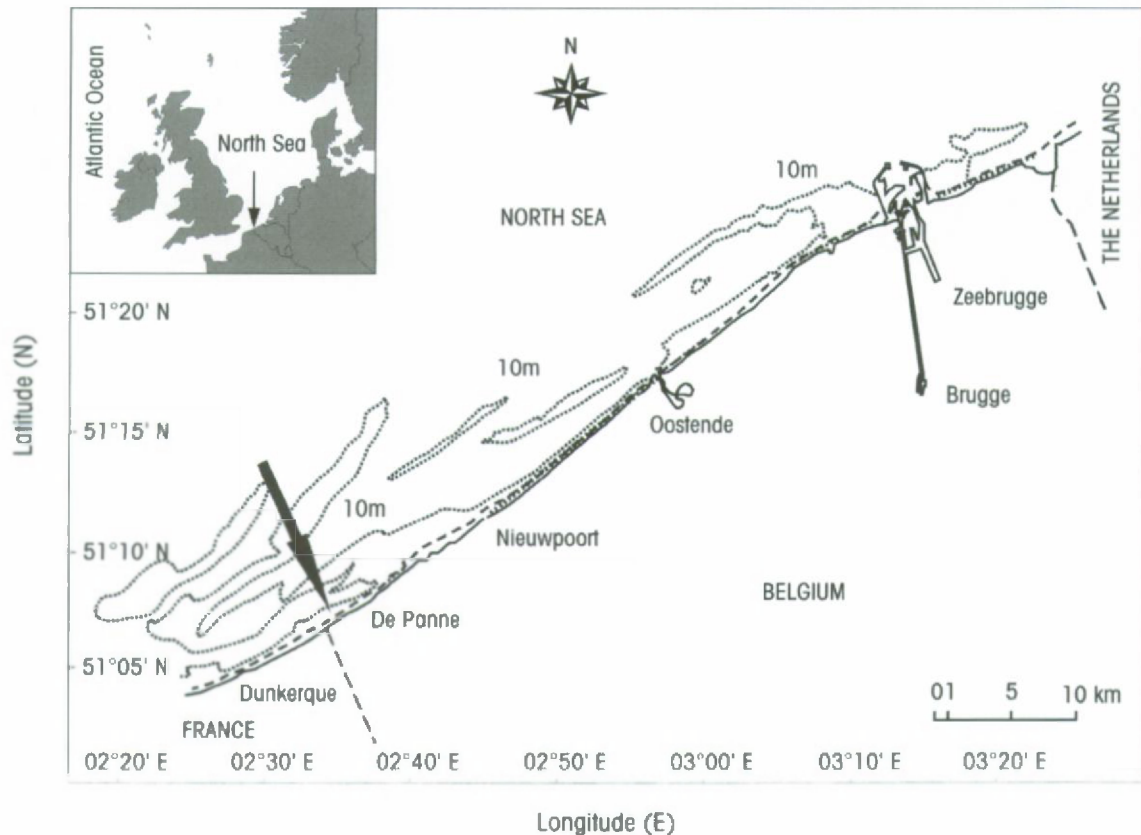
Figure 1: Geographical disposition of the studied beach.

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® 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 ($\Omega=H_b/W_sT$) and the relative tidal range (RTR=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 (Ind/10 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_{inf} (Hill, 1973). Evenness was calculated using Pielou's J' (J'=H'/log S) (Pielou 1975). Diversity patterns were visualised by *k*-dominance curves (Lambshead *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 permuation 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 (Masselinck and Short 1993; Short 1996), the beach was classified as an ultra dissipative beach with a semi-diurnal, macrotidal regime.
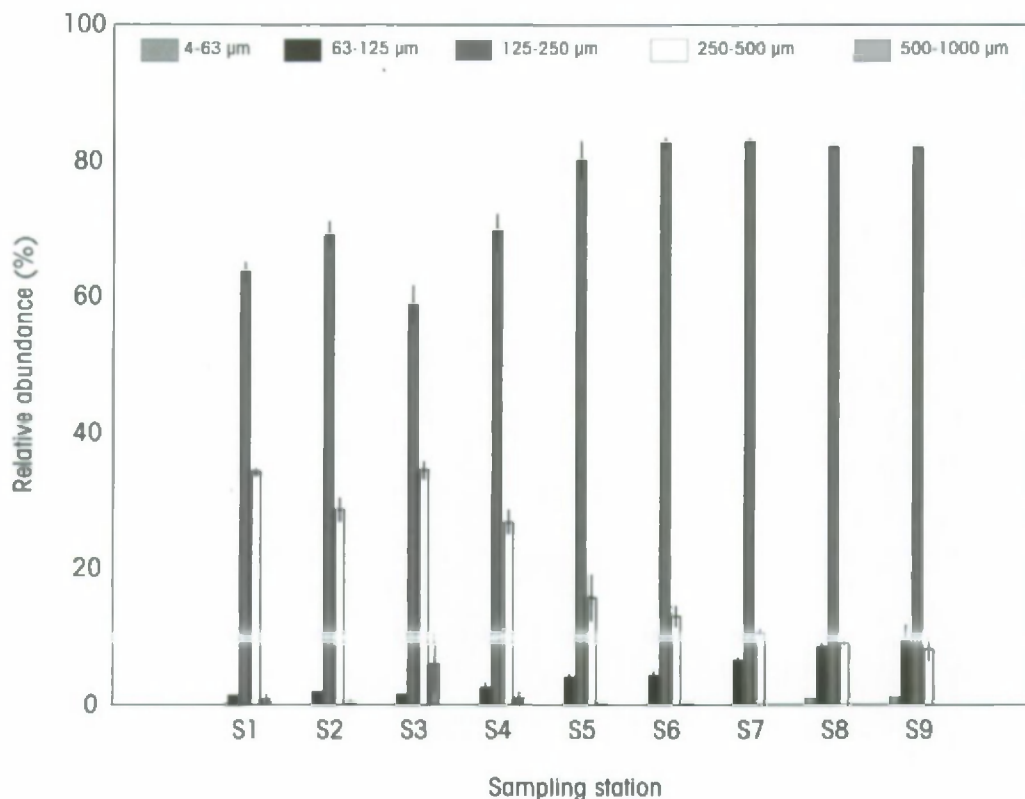
Figure 2: Sediment characteristics ± SD per station. (n=2)
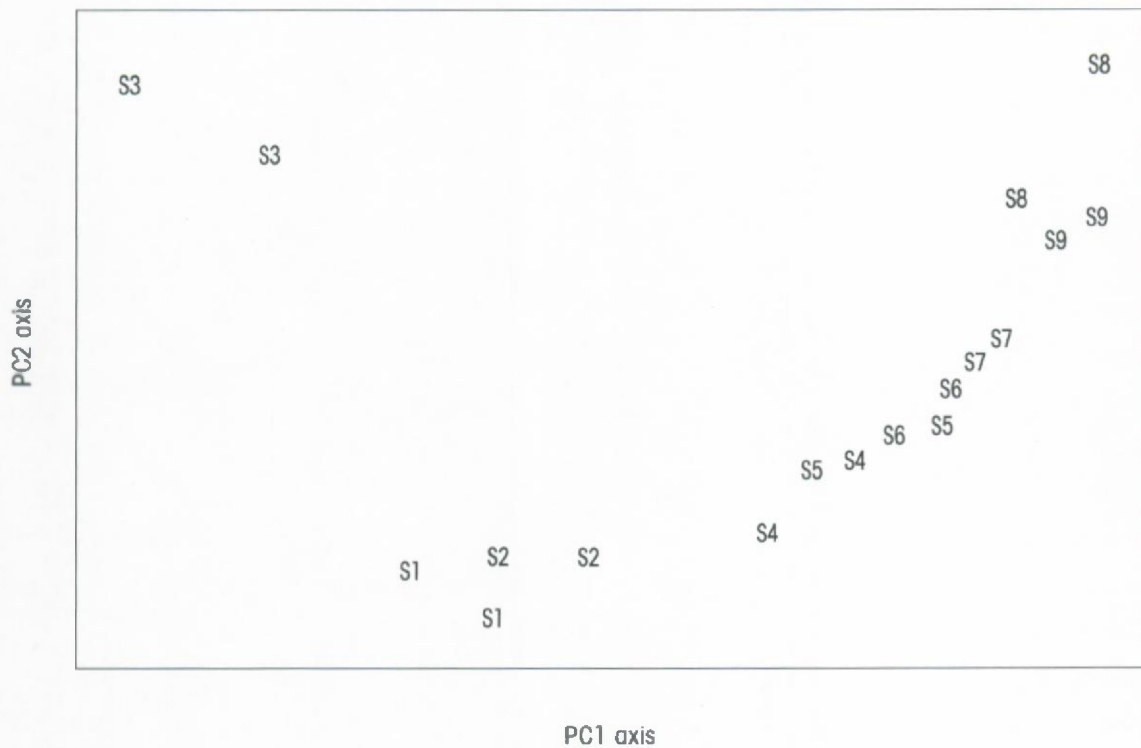
Figure 3: Ordination (first two components) of the granulometric variables by a correlation-based principal-component analysis (PCA). (n=2)

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 cm^2, S1) towards the lower beach (2784 ± 6 Ind/10 cm^2, 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
Aegialolaimidae	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
Tarvaiidae	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
Rhabdodemaniidae	0.03	1	1
Coninckiidae	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).

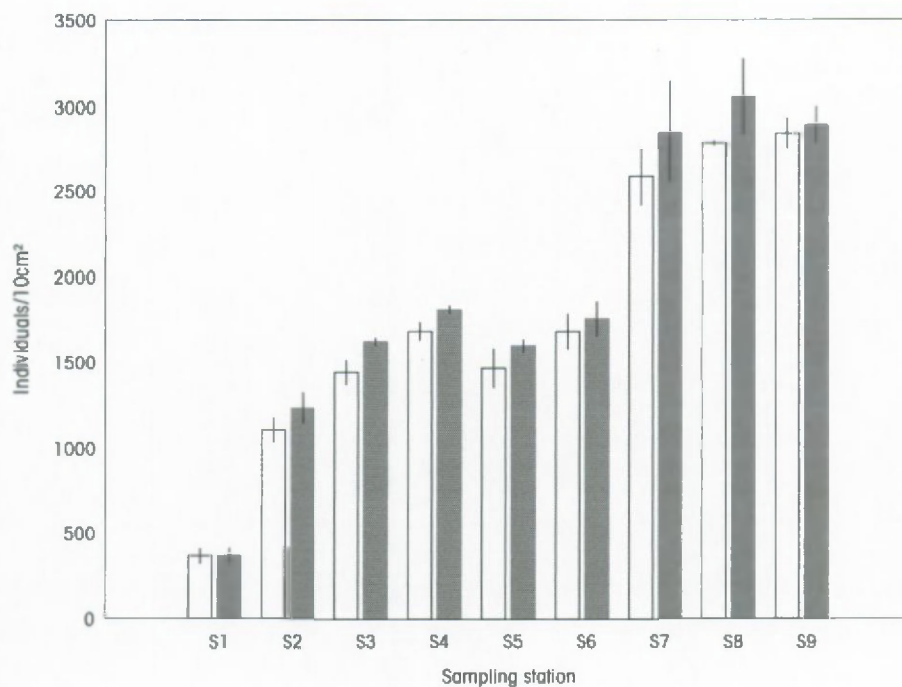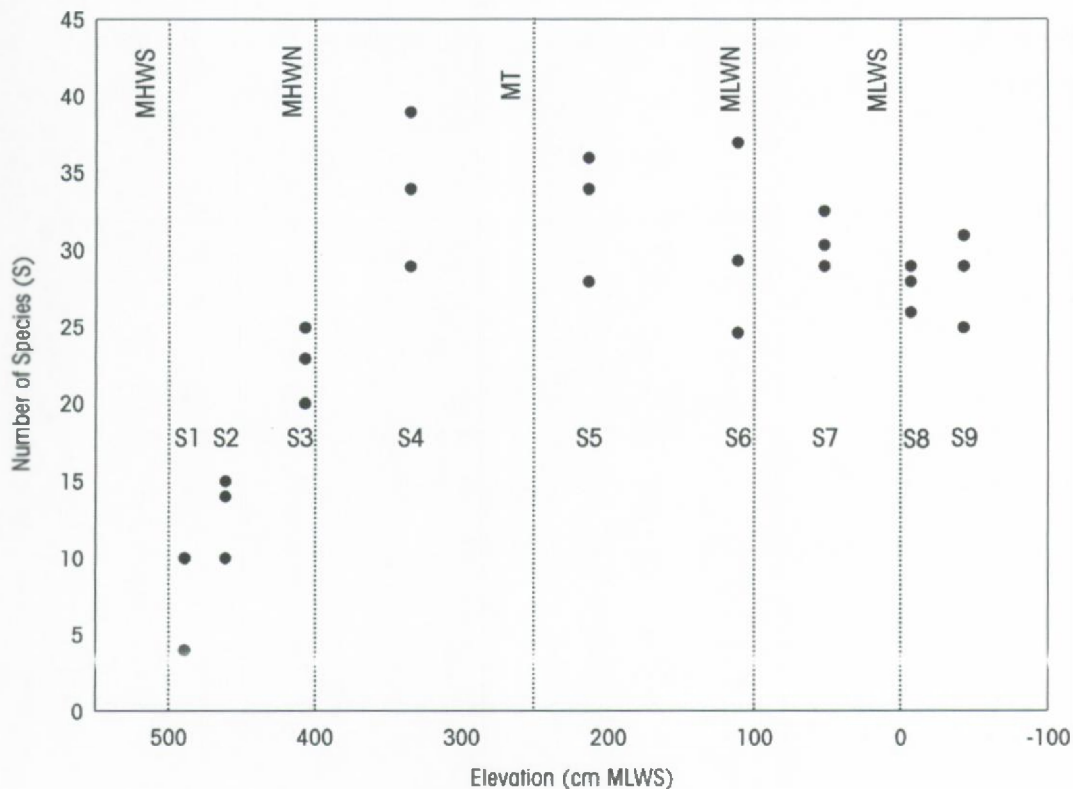**Figure 5**: Intertidal distribution (cm relative to MLWS) of the nematode species richness (S) per sampling stations (S1 to S9). (n=3)

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), Eveness (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

$df_{effect} = 8$ $df_{error} = 18$

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.

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[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.
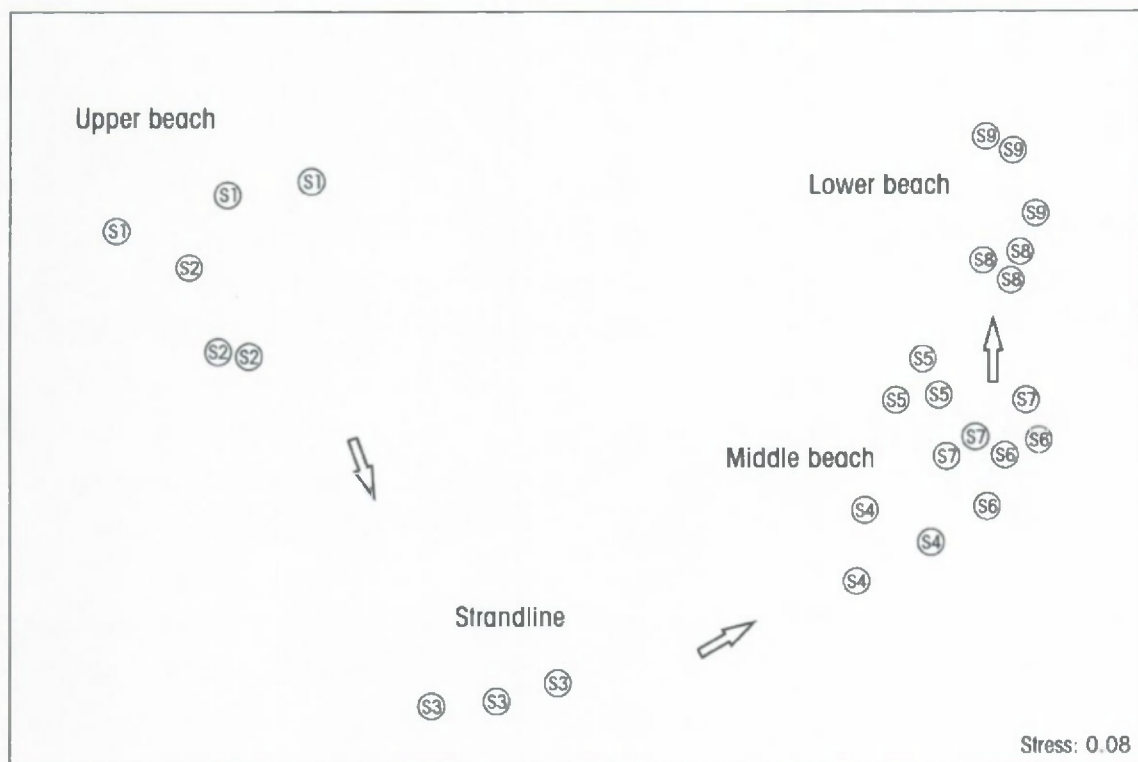

Figure 6: Nematode assemblages: Output of non-metric Multi-Dimensional Scaling (MDS) on square-root-transformed species abundance data with indication of the four intertidal zones. (Stress: 0.08) (n=3)

	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 (*Paracanthonchus thaumasius* (SCHULTZ, 1932); *Monoposthia mirabilis* (SCHULTZ, 1932) and *Daptonema normandicum* (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 | | | Species association 3 | | |
Upper beach			Middle beach		
Pellioditis marina	41%	1B	*Oncholaimellus calvadosicus*	12%	2B
Daptonema sp. 1	21%	1B	*Paracanthonchus thaumasius*	9%	2A
Axonolaimus helgolandicus	14%	1B	*Daptonema normandicum*	7%	1B
Chromadorita nana	4%	2A	*Odontophora phalarata*	7%	1B
Calyptronema maxweberi	4%	1B	*Monoposthia mirabilis*	5%	2A

| Species association 2 | | | Species association 4 | | |
Strandline			Lower beach		
Theristus otoplanobius	16%	2A	*Daptonema normandicum*	10%	1B
Daptonema sp. 1	14%	1B	*Odontophora rectangula*	7%	1B
Spilophorella candida	11%	2A	*Paracanthonchus thaumasius*	7%	2A
Onyx sagittarius	11%	2B	*Cyartonema elegans*	7%	1A
Enoplolaimus litoralis	10%	2B	*Monoposthia mirabilis*	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.
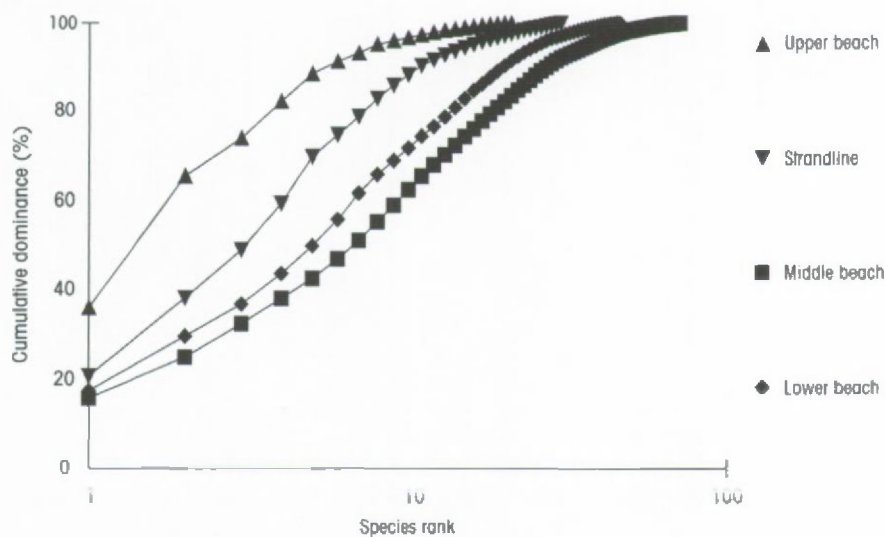
Figure 7: k-dominance curves for nematode species data. (Sum of stations, each three replicates per species association)

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[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

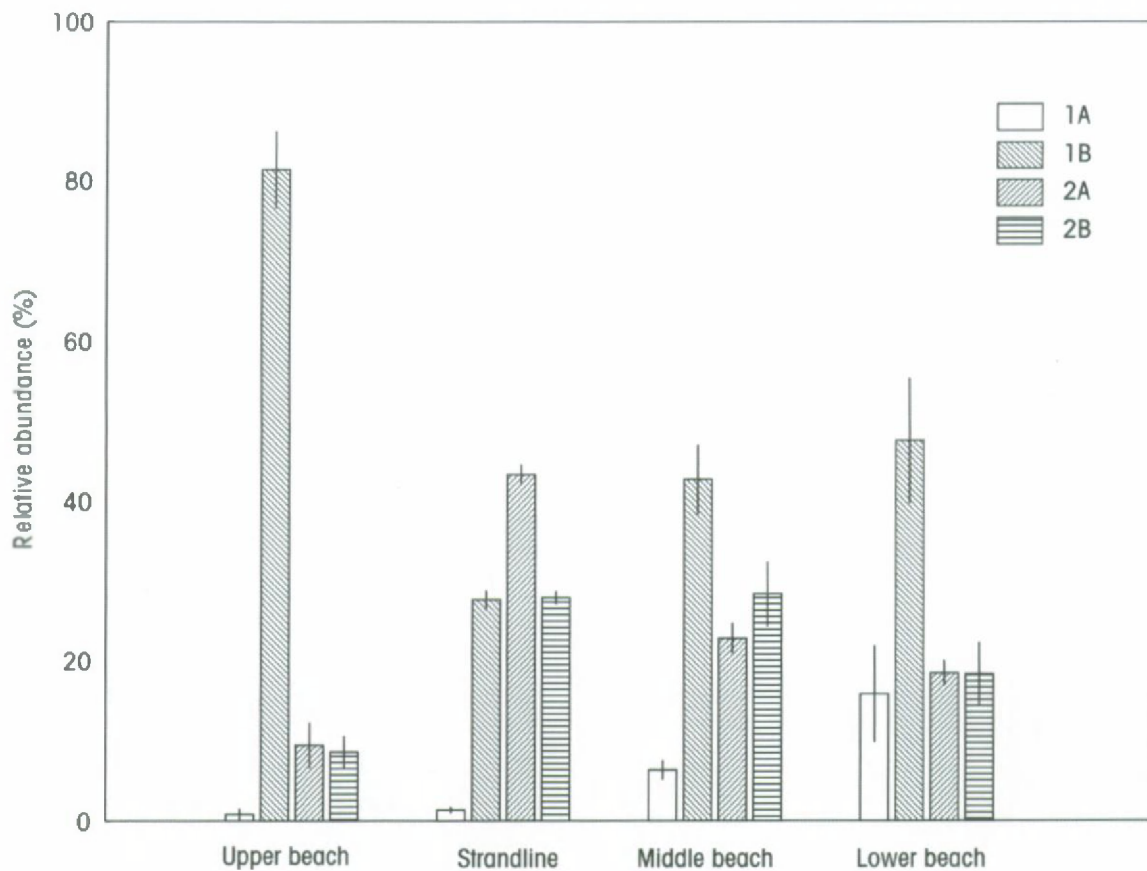All free-living marine nematodes are considered to be members of the meiobenthos, small organisms separated from the larger macrobenthos on a methodological basis (*i.e.* animals passing a 1 mm sieve). Worldwide dominance of nematodes as taxonomic unit within the meiofauna of fine-grained marine sandy 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 *Paracanthonchus* 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 *Scolelepis 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.

Acknowledgements

Chapter II: Nematode zonation patterns on a macrotidal, ultra-dissipative beach

CHAPTER III

Nematodes from wave-dominated sandy beaches: diversity, zonation patterns and testing of the isocommunities concept

ABSTRACT

Spatial patterns of nematode community structure from two geographically spaced intermediate, microtidal beaches (*i.e.* Mediterranean and Baltic) were investigated. Differences in the nematode assemblages were found to be significantly different and related to the morphodynamic characteristics of the studied zones (upper beach, swash/breaker and subtidal). Highest nematode densities and species diversities were recorded on the coarse-grained, more physically controlled, Italian beach in contrast to the more chemically controlled Polish beach. This is in contrast to the worldwide patterns of macrofaunal communities. As demonstrated by higher taxonomic distinctness measurements, upper beaches were found to harbour species from both the marine and terrestrial ecosystem and are considered to be important ecotones between these adjacent systems. The swash/breaker zones are characterised by the loss of distinctive species caused by the high water percolation in these zones. The concept of parallel ecological communities 'isocommunities' is only supported for the upper beach zones.

KEYWORDS: free-living nematodes, diversity, taxonomic relatedness, isocommunities, sandy beach morphodynamics, Mediterranean, Baltic

INTRODUCTION

Sandy beaches are examples of simple ecosystems, driven principally by the interacting physical forces of waves, tides and sediment movements. Wave dominance varies from total on sandy, tide-less shores, decreasing as other processes, especially tides, increase their influence on the shore face topography. Microtidal (wave-dominated) sandy beaches represent widely fluctuating environments which have been classified into three distinctive types (reflective, intermediate and dissipative) according to the modal breaker height, modal wave period and sediment fall velocity, which are all combined in the dimensionless fall velocity or Dean's parameter (Ω) (Short 1999).

These sandy sediments offer a considerable range and diversity of biotic habitats: horizontally, the sub-aerial (dunes and upper beach), the intertidal (swash zone/shoreline) and the subtidal (surfzone and near-shore) while vertically there are pelagic, benthic and interstitial environments. As the beach is the dynamic interface between the terrestrial and marine ecosystem several biotic and abiotic gradients characterize this interface. Due to these steep gradients (*e.g.* in oxygen, temperature, organic material, etc.) and the sediment heterogeneity, zones with specific physico-chemical properties can develop, harbouring, as a consequence, a different benthic fauna (Wieser *et al.* 1974). Most of the faunal research on sandy beaches has been concentrated mainly 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 beach meiofauna (all metazoans between 1 mm and 38 µm) have received considerably less attention notwithstanding their high diversity (even at taxon level) and density (up to one million individuals per square metre (McIntyre 1969)). Much of the previous meiofauna research on sandy beaches is in essence restricted to general surveys (at higher taxon level) or to the complex of factors influencing the interstitial habitats (Blome *et al.* 1999) while ecological research at species level is scarce. Despite their high dominance within the meiofauna, research on sandy beach nematodes is mainly restricted to treating nematodes as a single taxonomic unit although the phylum has been considered as a diverse (Heip *et al.* 1985) and possibly as a hyper-diverse taxon (Lambshead 1993; Lambshead and Boucher 2003) with a global distribution in soils and sediments. Nematodes also have several features favourable for using them as bio-indicators of environmental conditions (Schratzberger *et al.* 2000) and it is known from experiments that they are ecologically very heterogeneous and occupy different positions in benthic food webs (Aarnio 2001; Schmid-Araya and Schmid 2000). These differences may be as large between nematode species as they are between orders in macrofauna groups (Heip *et al.* 1982). However, quantitative data at the nematode species level from sandy beaches are scarce and each new research yields several species new to science (Gheskiere *et al.* 2004). Therefore, more baseline data describing species diversity and community structure are needed to further investigate the importance of nematodes to the sandy beach ecosystem. Sampling one selected ecosystem (microtidal beaches) in different localities makes it possible to compare patterns of nematode diversity and density over a larger scale.

This research aims to investigate and describe the biodiversity (nematode species level) and zonation patterns (H_0: no differences between beaches) in relation to several abiotic variables on two undisturbed wave-dominated European sandy beaches (Mediterranean and Baltic Sea) and secondly examine if community convergence (isocommunities) exists between geographically spaced beaches with more or less the same morphodynamics.

MATERIAL AND METHODS

Study sites

Two microtidal beaches in two different climatic areas and with different salinities were investigated. (1) Hel (54° 37' N, 18°49' E, Poland) is located on the northern coast of Poland (Gulf of Gdansk, Baltic Sea), at the end of the Hel Peninsula (Figure 1). The beach was closed to public access for more than 50 years due to its role as a strategic military area. Since only limited access is now available, human impact can be considered as relatively low. Hel is an almost non-tidal (tidal elevation 10 cm at maximum) intermediate broad sandy beach (60-85 m in width), slightly tending to the dissipative beach state and is exposed to moderate to heavy wave action from the open Baltic Sea. For most of its length, the beach is backed by a well-developed dune system forming the upper limit of storm accumulation. Littoral water temperature annually ranges from -1°C to 22°C, salinity between 4 and 7 PSU.

(2) The beach at San Rossore, (43°42' N 10°16' E, Italy) is situated in the San Rossore Massaciuccoli Natural Park (Figure 1). This park occupies 30 km of flat coastal strip in Tuscany (Ligurian Sea), between the provinces of Pisa and Lucca. San Rossore is a microtidal (tidal elevation 50 cm at maximum) intermediate beach (45-60 m in width) covered by detritus both from terrestrial and marine origin. This beach is classified at the reflective end of the intermediate beach spectrum. Like the beach in Hel, it is backed by a dune system and forests of *Pinus pinaster*. Littoral water temperature annually ranges from 5°C to 30°C and salinity between 32 and 36 PSU. There is free public access to the Massaciuccoli Natural Park but since access to the littoral area is restricted, this beach can also be classified as relatively undisturbed. Table 1 shows some general characteristics of the sampled beaches.
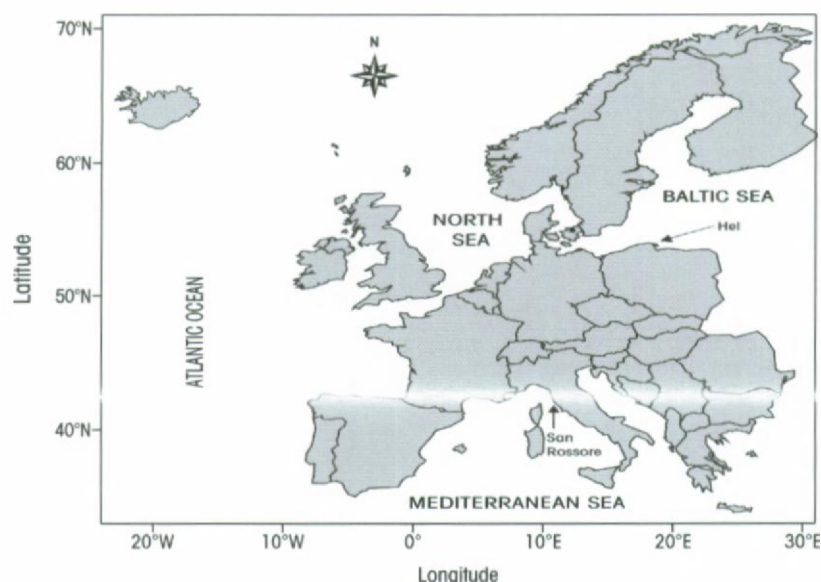
Figure 1: Geographical location of the studied beaches.

Beach Characteristics	San Rossore Beach	Hel Beach
Breaker type	plunging-surging	plunging-spilling
Median grain size (μm)	509 ± 19	385 ± 14
Sediment textural group	coarse sand	medium sand
Sediment sorting (Φ)	0.322 ± 0.004 well sorted	0.309 ± 0.01 well-sorted
Beach exposure	very exposed	very exposed
Dean's parameter (Ω)	2.39	5.29
Relative Tidal Range (RTR)	0.5	0.1
Beach type	intermediate/reflective	intermediate/dissipative

Table 1: Environmental characteristics of the beaches studied.

Sampling strategy

Sampling was done in September (Poland) and October (Italy) 2000. Three transects, spaced 25 m apart over the beach, orientated perpendicular to the waterline were sampled for meiofauna. Each transect was extended from the upper beach to beyond the lower limit of the swash zone in order to sample the meiofauna at different elevations on the beach. Six sampling stations per transect were established over the beach, which were divided into three more or less pre-defined zones (upper beach (S1 at 2 m MLWS and S2 at 1 m MLWS), swash and breaker (S3 at 0.5 m MLWS and S4 at -1 m MLWS), subtidal (S5 at -2 m MLWS and S6 at -3 m MLWS)). Nematodes were sampled using transparent plexi cores (sampling surface area 10 cm²) to a depth of 15 cm. Additional samples at each sampling stations were collected with the same cores to the same depth for granulometric and Total Organic Matter (%TOM) analyses. Salinities of interstitial water and sediment temperature were also recorded at each sampling point. Meiofauna samples were immediately fixed with heated (70°C) 4% buffered formaldehyde water solution (Heip *et al.* 1985; Vincx 1996).

Laboratory treatment

In the laboratory, meiofauna samples were rinsed with a gentle jet of freshwater over a 1 mm sieve to exclude macrofauna, decanted over a 38 μm sieve, centrifuged three times with Ludox° HS40 (specific density 1.18) and stained with Rose Bengal. Nematodes were counted, 200 individuals were picked out randomly using a stereomicroscope, transferred from formalin to glycerol through a series of ethanol-glycerol solutions and mounted in glycerine slides (Vincx 1996), identified to the species level and classified according to the phylogenetic system, based on SSU rDNA data, of De Ley and Blaxter (2002, 2003). Sediment samples were oven-dried at 105°C for 12 h and ashed at 500 ± 50°C for 2 h to determine the

%TOM by loss of mass. Sediment particle-size distribution was determined using Coulter LS100$^©$ particle size analysis equipment. The sediment fractions were defined according to the Wentworth scale (Buchanan 1984). Sediment sorting coefficient (Quartile Deviation) and skewness were calculated as described by Dyer (1986).

Data analysis

Wave-dominated, microtidal beaches can be classified using three parameters: the modal breaker height in meters (H_b), modal wave period in s (T) and sediment fall velocity (W_s) in ms^{-1}. W_s is calculated from the median grain size following Gibbs *et al.* (1971). These three parameters were first combined by Gourlay (1968) into the dimensionless fall velocity $\Omega = H_b/W_sT$ (or Dean's parameter). When $\Omega < 1$ beaches tend to be *reflective*, when $\Omega > 6$ they tend to be *dissipative* and in between ($1 < \Omega < 6$) are the so called *intermediate beaches* (Masselink and Short 1993). Values for tide range, breaker height and period for San Rossore and Hel were obtained from Pranzini (pers. comm.) and Urban-Malinga (pers. comm.) respectively.

The distribution of environmental variables along transects was analysed using correlation-based principal-component analysis (PCA) on normalised log(x+1) transformed values as described by Clarke (1993).

The square-root transformed nematode data were ordinated by non-metric Multi-Dimensional Scaling (MDS) (Kruskal 1964) and by a Detrended Canonical Analysis (DCA) (Ter Braak 1988). A measurement of goodness-of-fit test of the MDS ordination was given by the stress value. A low stress value (<0.2) indicated a good ordination with no real prospect of a misleading interpretation (Clarke 1993). Two-way crossed Analysis of similarities (ANOSIM, Clark 1993) was used to test for significant differences between beaches (across zones). One-way ANOSIM was subsequently applied to asses the significance of differences between groups of multivariate samples from different zones at the individual beaches. The similarity percentages programme (SIMPER, Clarke 1993) was applied to identify the species primarily providing the discrimination between the zones on the beaches. The relationships between multivariate assemblage structure and combinations of environmental variables were analysed using the BIO-ENV procedure (Clarke and Ainsworth 1993) to define suites of variables that best explain the nematode assemblage structure. Scatter plots of all pair wise combinations of environmental variables indicated that conversion to approximate normality using log(x+1) transformation was appropriate before multivariate analysis.

Nematode species abundance data (Ind/10 cm^2) were used to calculate the number of species per sample (S), Pielou's evenness (J') (Pielou 1975), Hill's N_{∞} (Hill 1973), average taxonomic diversity (Δ) and average taxonomic distinctness (Δ^*) (Warwick and Clarke 1995). Equal step-lengths between each taxonomic level were assumed, setting the path length ω to 100 for two species connected at the highest (taxonomically coarsest) possible level as stated by Clarke and Warwick (1999). Eight taxonomic levels were used (species, genus, family, superfamily, suborder, order, subclass and class) and consequently weights are $\omega=12.5$ (species in the same genus), 25 (same family but different genus), 37.5 (same

superfamily but different family), 50 (same suborder but different superfamily), 62.5 (same order but different suborder), 75 (same subclass but different order), 87.5 (same class but different subclass) and 100 (different class), respectively.

Calculation of average taxonomic distinctness and variation in taxonomic distinctness from simulated sub-samples of different numbers of species from the master nematode list (Δ^* and Λ^*, respectively) were used to produce probability funnels against which distinctness and variation of distinctness values for all zones were checked and formally address the question whether these zones have a 'lower than expected' taxonomic spread (Clarke and Warwick 1998). Taxonomic diversity measurements and community analyses were performed using the PRIMER v5.2.9 software package (Clarke and Gorley 2001).

Differences in density, richness measures and abiotic data were analysed using two-way ANOVA for differences between beaches and one-way ANOVA for differences per beach. Bartlett's and Cochran's tests were used to verify for homogeneity of variances prior to the analysis. To further explore statistically significant differences, the Tukey HSD multi-comparison test for equal n was used in a pairwise comparison (Zar 1996). Statistical analyses were performed using the STATISTICA v6.0 software package (StatSoft 2001).

RESULTS

The environmental variables

A silt (4-63 μm) and very fine sand fraction (63-125 μm) were not recorded on the beaches. Ordination by PCA of environmental data revealed that, on each beach, the sampling stations were more or less aggregated into the three zones (Figure 2). The first two components (eigenvalues 6.9 and 1.41) accounted for 83% of the total variance of the original 10 variables (as listed in Table 2), suggesting that the two-dimensional ordination gave an appropriate representation of the similarity between the sampling stations. The PC1 axis (70%) represents mainly decreasing values of salinity while PC2 axis (13%) represents decreasing values of >1000 μm and median grain size. (Eigenvectors are not shown). Several environmental variables changed significantly across transects from upper beach to the subtidal (Table 2). Median grain size and >1000 μm were significantly higher in the swash/breaker zone both beaches, a known feature caused by the wave-dominated character of these microtidal beaches (Short 1999). %TOM was found to be significantly higher on both upper beaches (2.25 ± 0.01 for San Rossore and 2.11 ± 0.04 for Hel respectively). The zones across the Polish beach all belong to the medium sand (250-500 μm) granulometric group, whereas on the Italian beach two zones (swash/breaker and subtidal) were in the coarse sand (500-1000 μm) granulometric group. Salinity differed significantly between study sites and increased along transects on both beaches, being significantly lower on both upper beach. Temperature values of the interstitial water showed a similar pattern on both beaches, with significantly higher values on the upper beach (Poland 13.5°C, Italy 25.3°C) followed by a very slight decrease towards the swash/breaker zones and an increase in the subtidal zones.
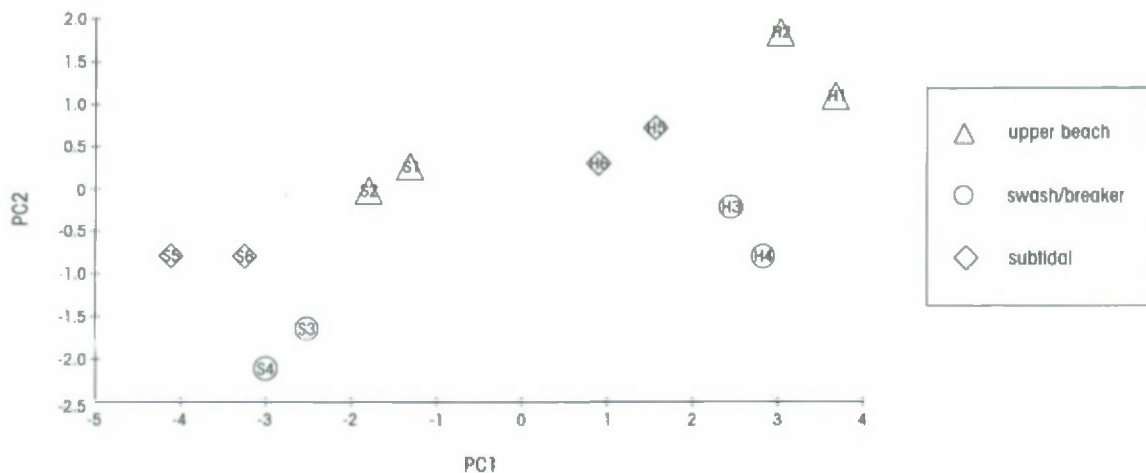
Figure 2: 2-Dimensional correlation-based principal-component analysis (PCA) of log(x+1)-transformed abiotic data from sampling stations across the two beaches studied. (San Rossore beach=S; Hel beach=H) (n=3 per station)

	San Rossore				
	Upper beach (I)	Swash & breaker (II)	Subtidal (III)	p-value	Comparison
Median grain size (µm)	433 ± 10	564 ± 20	522 ± 8	<0.001	I<II>III
125-250 µm (%)	1.6 ± 0.1	0.9 ± 0.3	0.4 ± 0.1	0.002	I>II,III
250-500 µm (%)	57.9 ± 2.7	26.8 ± 3.0	17.6 ± 0.6	<0.001	I>II>III
500-1000 µm (%)	40.7 ± 2.7	65.3 ± 2.5	67 ± 2.4	<0.001	I<II,III
>1000 µm (%)	0.9 ± 0.0	14.8 ± 1.8	6.9 ± 0.8	<0.001	I<II>III
Sorting (QD)	0.31 ± 0.01	0.34 ± 0.01	0.32 ± 0.00	0.054	-
Temperature (°C)	25.3 ± 0.1	22.7 ± 0.9	24.4 ± 0.2	0.027	I>II
Salinity (PSU)	27.8 ± 0.22	35.9 ± 0.7	37.1 ± 0.1	0.001	I<II,III
%TOM	2.25 ± 0.01	1.0 ± 0.09	0.8 ± 0.04	<0.001	I>II>III
Skewness	-0.35 ± 0.17	-1.27 ± 0.8	-3.73 ± 1.15	0.975	-

	Hel				
	Upper beach (I)	Swash & breaker (II)	Subtidal (III)	p-value	Comparison
Median grain size (µm)	348 ± 7	426 ± 21	379 ± 16	0.013	I<II>III
125-250 µm (%)	11.7 ± 1.8	6.3 ± 0.8	11.3 ± 1.9	0.051	-
250-500 µm (%)	80.6 ± 1.1	62.9 ± 5.3	64.9 ± 2.5	0.008	I>II,III
500-1000 µm (%)	7.2 ± 0.4	27.7 ± 4.7	22.1 ± 3.7	<0.001	I<II,III
>1000 µm (%)	0.7 ± 0.3	3.1 ± 0.4	1.8 ± 0.8	0.041	I<II>III
Sorting (QD)	0.26 ± 0.01	0.34 ± 0.02	0.32 ± 0.01	0.001	I<II,III
Temperature (°C)	15.3 ± 0.2	12.2 ± 0.9	13 ± 0.2	0.192	I>II
Salinity (PSU)	5.2 ± 0.5	7.3 ± 0.02	7.4 ± 0.01	<0.001	I<II,III
%TOM	2.11 ± 0.04	1.4 ± 0.09	0.95 ± 0.02	<0.001	I>II>III
Skewness	-0.11 ± 0.02	-0.21 ± 0.02	-0.03 ± 0.03	<0.001	I>II, II<III

Table 2: Mean values (± SD) of environmental variables and significance levels from one-way ANOVA tests for differences between the different zones across the beaches. Analyses performed on log(x+1) transformed data. Significant differences evaluated with Tukey's HSD multi-comparison test for equal n.

Nematode assemblages

A total of 108 nematode species was recorded on the two beaches, only 14 species were shared. The beach of San Rossore harboured 66 species and Hel beach 56 species. Differences in species lists (presence/absence data) exist among beaches with an average Bray-Curtis dissimilarity of 96%. (2-way ANOSIM across zones, R=0.907, p<0.001).

The null hypothesis (H_0) that nematode assemblage structure was similar at the beaches was rejected as MDS (Figure 3) and DCA (not shown) for square root-transformed nematode abundance data (all stations combined) both indicated a clear separation of the two beaches tested. This was confirmed by 2-way ANOSIM across zones (R=0.680, p<0.001). Sampling stations per beach were clustered into the three putative zones, indicating different nematode assemblages across the beach slope. The stress factor (0.12) indicates a good MDS ordination. 1-way ANOSIM results confirmed that the composition of the nematode assemblages differed significantly between zones per beach (Table 3). At San Rossore, the Bray-Curtis dissimilarity decreased (77% to 57%) from upper beach to the subtidal, reflecting more similarities between the swash/breaker and subtidal zones than between the upper beach and swash/breaker zones. This decrease is less clear on the Polish beach (82% to 78%). Generally, dissimilarities were highest when comparing the upper beaches and the subtidal zones, 84% and 86% for Italy and Poland respectively. The five main discriminating nematode species for each zone and beach, their relative abundance and their corresponding Wieser feeding type (1953) are listed in Table 4. Only nematodes belonging to the terrestrial free-living nematode order Dorylaimida (*Aporcelaimus* spp. and *Aporcelaimellus* spp.) are common between the two beaches. Upper beaches were also sharing some other Dorylaimida (*Nygolaimus* sp. and *Mesodorylaimus* spp.) and some Rhabditida (*Acrobeles* spp.) however these species occurred in very low abundances (>0.5%) at both sites. The slightly higher similarity between swash/breaker and subtidal zone is suggested by the commonality of the nematode species *Epsilonema pustulatum* and *Theristus heterospiculum* in Italy and *Trissonchulus benepapilosus* in Poland. *Epacanthion enoploidiforme* seems to be an important predator in all zones across the Italian beach.
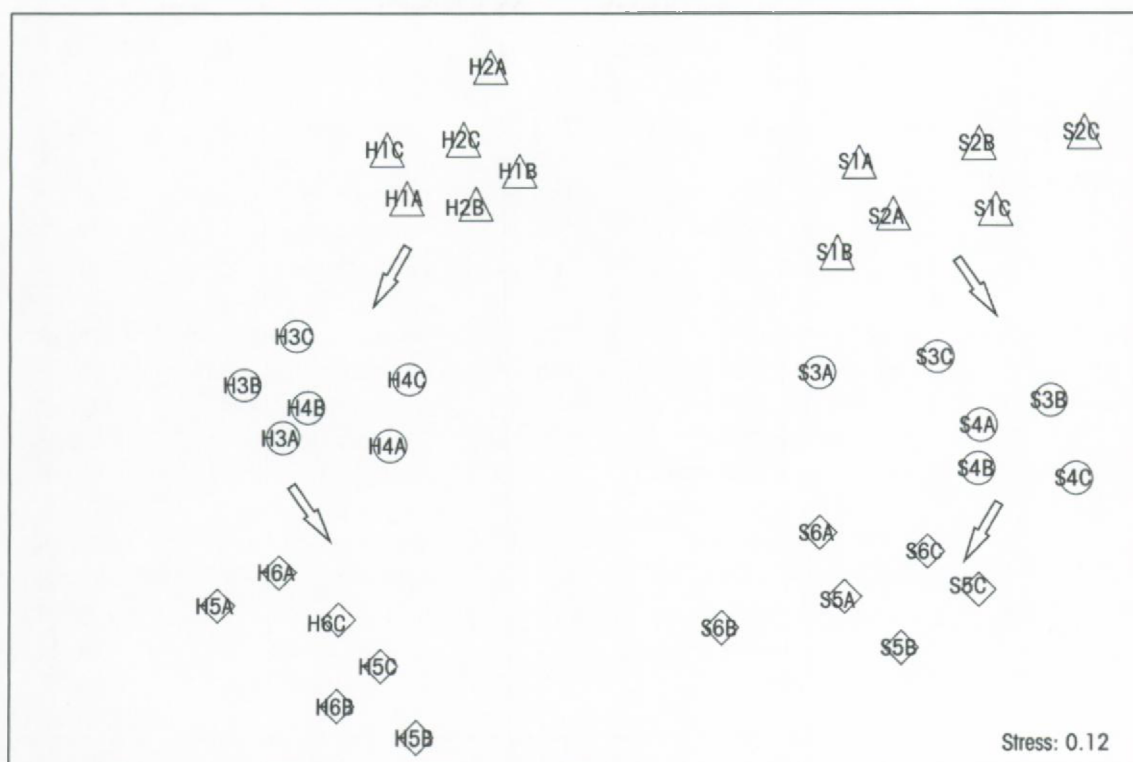
Figure 3: Nematode assemblages: Output of non-metric Multi-Dimensional Scaling (MDS) on square-root-transformed species abundance data (three replicates per sampling station) with indication of the different zones across the beaches. (Symbols as in Figure 2) (Stress: 0.12)

Zones compared	San Rossore			Hel		
	Dissimilarity (%)	R-value	p-value	Dissimilarity (%)	R-value	p-value
I-II	77	0.656	0.029	82	0.665	0.02
I-III	84	0.510	0.029	86	0.839	0.02
II-III	57	0.354	0.029	78	0.470	0.04
	Global test	0.444	0.00001	Global test	0.670	0.001

Table 3: Results of the 1-way ANOSIM and pair-wise tests for difference on the nematode assemblage structure between the zones of the two beaches studied (R-values and p-values are reported). Percentage of Bray-Curtis dissimilarity as calculated from the SIMPER analyses. (All analyses performed on square-root transformed data)

	San Rossore		Hel	
UPPER BEACH	*Aporcelaimus* sp1	23% 2B	*Aporcelaimus* sp2	20% 2B
	Theristus aculeatus	20% 1A	*Tripyloides acherusius*	17% 2B
	Epacanthion enoploidiforme	10% 2B	*Chromadorita* sp1	13% 2A
	Trileptium subterraneum	10% 2B	*Aporcelaimellus* sp3	12% 2B
	Aporcelaimellus sp2	6% 2B	*Leptolaimus* sp.1	6% 1A
SWASH/BREAKER	*Epsilonema pustulatum*	37% 1B	*Trissonchulus benepapillosus*	40% 2B
	Theristus heterospiculum	24% 1A	*Bathylaimus stenolaimus*	31% 1B
	Dracognomus simplex	15% 1B	*Tripyloides acherusius*	10% 2B
	Axonolaimus tirrenicus	10% 1B	*Chromadorita* sp1	6% 2A
	Epacanthion enoploidiforme	7% 2B	*Anoplostoma exceptum*	4% 1B
SUBTIDAL	*Theristus heterospiculum*	12% 1A	*Ascolaimus elongatus*	26% 1B
	Epsilonema pustulatum	10% 1B	*Metadesmolaimus* sp1	22% 1B
	Epacanthion enoploidiforme	9% 2B	*Trissonchulus benepapillosus*	11% 2B
	Platycoma sudafricana	7% 1A	*Enoplolaimus balgensis*	10% 2B
	Theristus inermis	7% 1B	*Metachromadora remanei*	8% 2B

Table 4: The top five discriminating species for each association per zone and per beach (relative abundance) and their associated Wieser (1953) feeding strategy. (1A: selective deposit feeders; 1B: non-selective deposit feeders; 2A: epistratum feeders and 2B: omnivores and predators)

2-way ANOVA indicated significant differences ($p < 0.01$) for all investigated indices between beaches, zones and beach x zone interaction (table not shown). Nematode density and total species richness per zone are illustrated in Figure 4. The density of Italian nematodes ranged from 130 ± 3 Ind/10 cm^2 up to 2001 ± 36 Ind/10 cm^2, being statistically higher (ANOVA, $p < 0.05$) in the swash/breaker zone. Across the Polish beach mean nematode densities did not change much. Highest densities were noted on the upper beach (120 ± 14 Ind/10 cm^2) and lowest in the swash and breaker zone (102 ± 6 Ind/10 cm^2). The highest species diversity at the Italian beach was found in the subtidal zone (45 ± 1), which was statistically higher (ANOVA, $p < 0.02$) than both the upper beach (33 ± 2) and swash/breaker zone (31 ± 1). At the Polish beach, species richness was found to be significantly higher (ANOVA, $p < 0.05$) on the upper beach (35 ± 1) in comparison with the swash/breaker zone (28 ± 1) and the subtidal zone (29 ± 2).
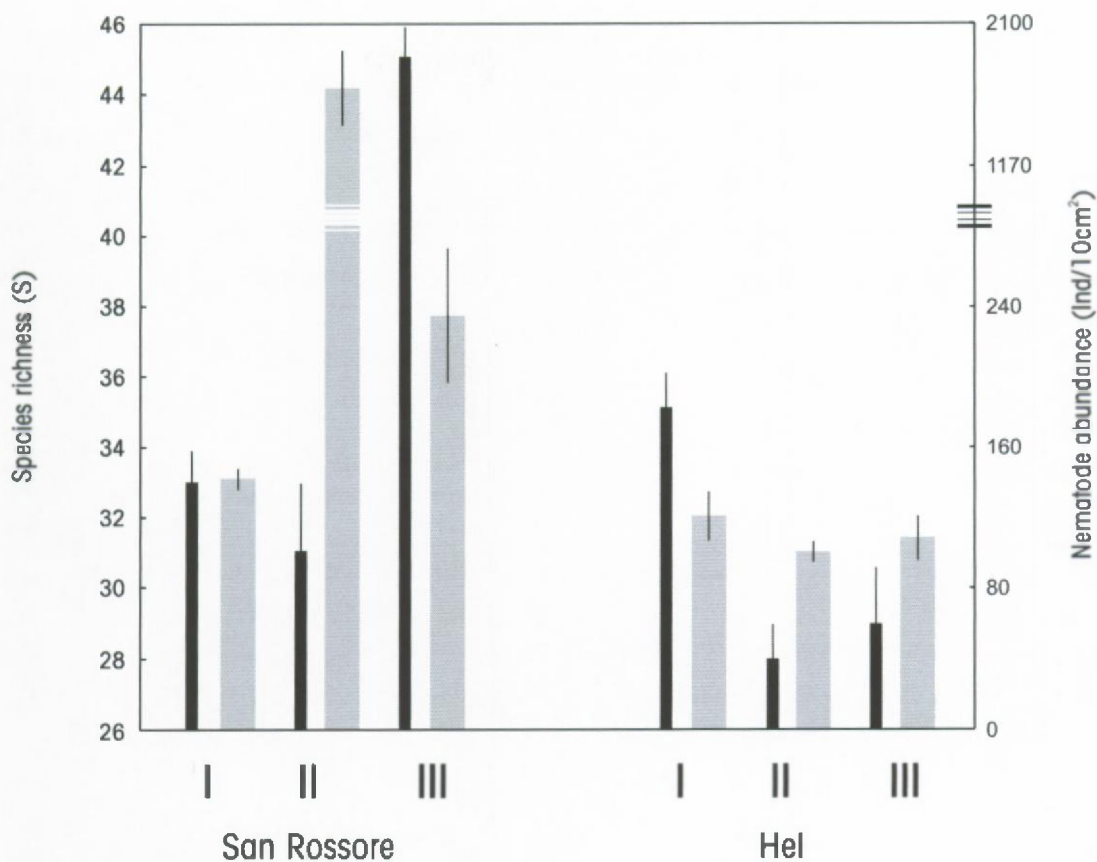
Figure 4: Mean nematode species richness (black bars ± standard errors, left ordinate) and total nematode densities (grey bars ± standard errors, right ordinate). All calculated by pooled variance of replicates per zone and per beach. (I= upper beach, II=swash/breaker zone and III=subtidal zone)

At both beaches average taxonomic distinctness (Δ^*) showed more or less similar patterns: a steep decrease from the upper beach towards the swash/breaker zone followed by an increase towards the subtidal zone, indicating the loss of taxonomic distinctive species in the swash/breaker zones (Figure 5A). A noticeable lower value of average taxonomic diversity (Δ) was noted in the swash/breaker zone at the Italian beach. In general, higher taxonomic diversity values were noted across the Polish beach (Figure 5A). Changes in evenness (J') and N_{inf} (Figure 5B) generally mirrored the changes in taxonomic diversity measures along the beaches. Evenness differed significantly (ANOVA, $p<0.05$) between zones at both beaches, being lower in the swash/breaker zone, suggesting, together with Hill's N_{inf} a higher dominance of some species (*Epsilonema pustulatum* and *Theristus heterospiculum* in Italy; *Trissonchulus benepapilosus* and *Bathylaimus stenolaimus* in Poland). Figure 6A displays the 95% funnel for the simulated distribution of average taxonomic distinctness (Δ^+) for random subsets of fixed size m from the master nematode list (108 species). Superimposed on this plot are the true values of Δ^+ generated from species lists for each of the zones across the beaches. From this figure the lower distinctness Δ^+ in the Italian swash/breaker zone assemblage is obvious. Figure 6B similarly shows the values of variation of taxonomic distinctness (Λ^+) for the same datasets. It is clear that the average taxonomic distinctness and variation in taxonomic distinctness

is different between the zones on the beaches. The swash/breaker zone of the Italian beach is seen to have a reduced Δ^* (taxonomically closely related species) and a significantly ($p<0.05$) increased Λ^*. The values of other zones fall within the 95% confidence limit of simulated values from the master list of 108 nematode species.

Table 5 reports the Bray-Curtis similarities between corresponding zones on the two beaches for three taxonomical resolutions (species, genus and family). Most species and genera were similar between the upper beaches, 17% and 27% respectively.
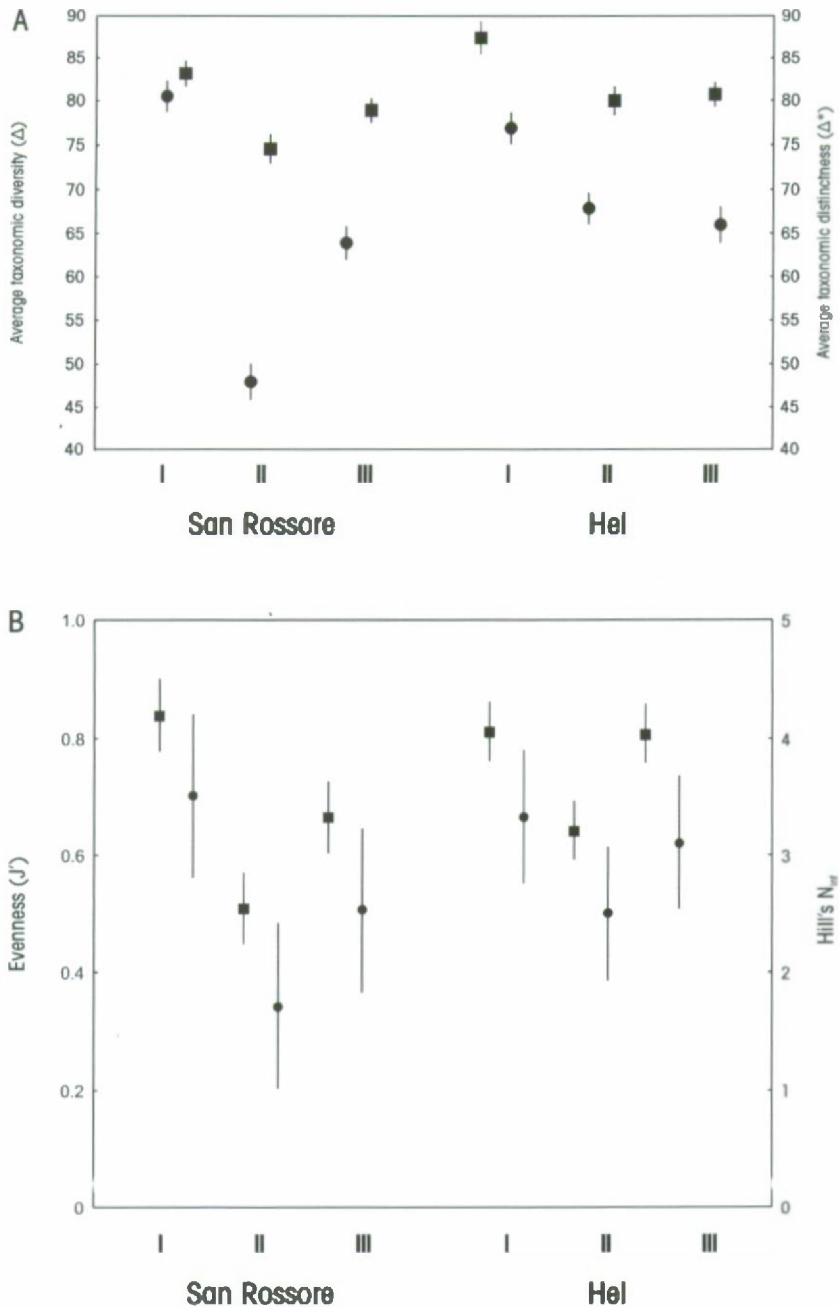
Figure 5: Various diversity indices across the beaches (zones as in Fig. 4). (A) Average taxonomic diversity (Δ) ($\bullet$) and Average taxonomic distinctness (Δ^*) ($\blacksquare$). (B) Evenness (J') ($\blacksquare$) and Hill's N_{inf} ($\bullet$). (All calculated by pooled variance of replicates $\pm$ SE)
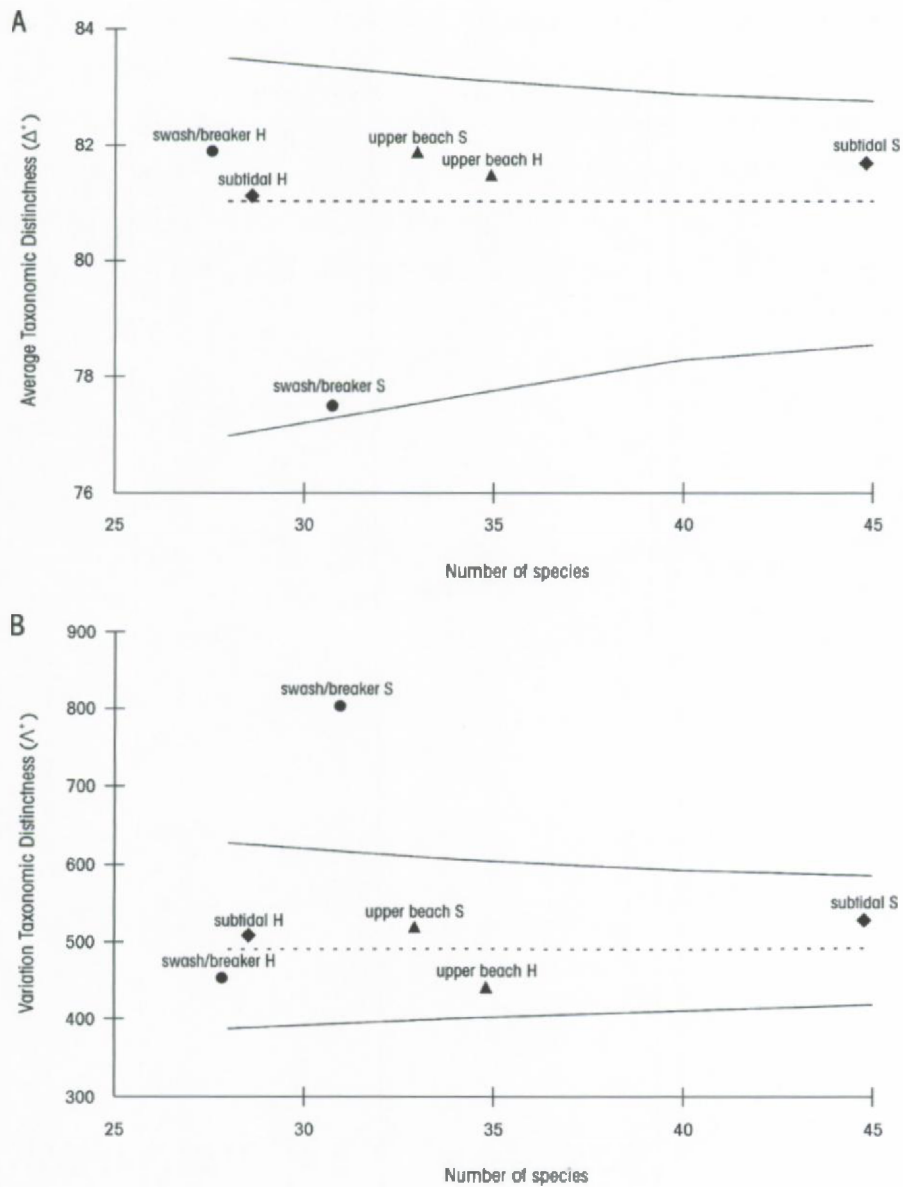
Figure 6: The 95% probability funnels for Average Taxonomic Distinctness (Δ⁺) and Variation in Taxonomic distinctness (Λ⁺) plotted against the number of species for the different nematode assemblages on the two beaches studied. Dashed lines indicate the simulated mean Δ⁺ and Λ⁺ from 15000 random selections from the master list of 108 nematode species from this study for each sublist size.

	Species	Genus	Family
upper beach	17%	27%	37%
swash/breaker	2%	16%	27%
subtidal	5%	19%	40%

Table 5: Bray-Curtis similarities as calculated from the SIMPER analyses at different taxonomical resolutions between corresponding zones on the two beaches studied.

Relationship between nematode assemblage structure and environmental variables

In a Pearson product-moment correlation analysis, none of the environmental variables were highly correlated (>0.95) and consequently all 10 abiotic variables were incorporated in the BIO-ENV analysis. The highest resulting correlation achieved for Italy ($\sigma=0.744$) was with a combination of the sediment fraction >1000 µm and sediment sorting coefficient. On the Polish beach, highest correlation ($\sigma=0.523$) was found with %TOM.

DISCUSSION

McLachlan and Turner (1994) envisaged the interstitial environment of sandy beaches as a continuum with at one extreme the coarse-grained, reflective beach state characterised by high water percolation and, consequently, high oxygenation while at the other extreme there are dissipative beaches with finer sands and lower permeabilities which tend to harbour higher organic inputs and anaerobic conditions. The two microtidal beaches studied in this paper are so-called intermediate beaches. Intermediate refers to the state between the dissipative and reflective beaches (Wright and Short 1984; Short 1999). Intermediate beaches occur under a wide range of environmental conditions, ranging from moderate to high waves (0.2 to 2.5 m), fine to coarse sands and long wave periods. In these systems spatial wave transformation gradients are large, near shore slopes are steep and incident waves tend to break through plunging, especially when the beach has a relatively low steepness. In our study, the Italian beach is more tending to the reflective (high energetic interstitial water movement) end of the intermediate state. On intermediate-reflective beaches the waves surge directly up the steep beach face and much of their energy is reflected to the sea. As the waves swash over the sloping, coarse-grained, beach, large volumes of water sink into the sand and are filtered as they percolate back to lower levels. This has the effect of transferring large amounts of particulate and dissolved organic matter and oxygen to the interstitial community. Therefore this type of beaches is so-called physically-controlled. On the other hand the Polish beach is more at the dissipative (low energetic interstitial water movement) end of the intermediate state, characterized by waves dissipating most their energy at a considerable distance from the shore. The low rate of flushing between the fine particles allows a build-up of microbial communities which in turn leads to sharp gradients in oxygen, nutrients, redox potential, sulphides and pH. Accordingly, these beaches are called chemically-controlled.

McLachlan and Turner (1994) predicted that optimum conditions for the development of a rich and abundant meiofauna were likely to occur on these intermediate beaches (unimodal trend) because an optimal equilibrium exist between organic input and aeration. Higher meiofauna densities and diversities (at the taxon level) in coarser and therefore more oxygenated sands, in contrast to finer more sulphidic sands have been reported frequently (Gray and Rieger 1971; McLachlan 1977a, b; Giere 1993; Rodríguez *et al.* 2003). Grain size is probably the cardinal factor upon which virtually all other interstitial (a)biotic factors are dependent in varying degrees (Fricke and Flemming 1983). Organic material and aerobic conditions, together with temperature and salinity, are among the most important abiotic factors for meiofauna settlement (Giere 1993). This is also obvious from our BIO-ENV analyses as percentage of very coarse sand (>1000 μm) which is linked with better water percolation and therefore more oxygenation for Italy and %TOM for Poland were the environmental variables best correlated with the nematode assemblages. Lower nematode species richness associated with finer, more chemically controlled sandy sediments has been recorded several times in subtidal areas (amongst others Steyaert *et al.* 1999 and references therein) and is supported by the results of this study. The coarse-grained Italian beach is higher in densities and species richness than the finer grained Polish beach. This is in contrast with the worldwide trend within the

macrofauna which tend to have highest diversities on fine-grained (dissipative) beaches (McLachlan and Jaramillo 1995). Such beaches have a relatively stable morphology and exhibit minimal shoreline change (Short and Hesp 1982) as (1) the fine low gradient profile is less susceptible to changes compared to steeper, coarse profiles, (2) the beach accommodates higher waves by breaking them further seaward and thereby dissipating their energy over a wider zone and (3) the greater dissipation in turn increases the wave set-up which accommodates the greater inshore volume of water (*i.e.* the atmosphere is eroded rather than the beach). It appears that meiofauna maybe somewhat buffered against the physical forces of the seashore as they tend to live below the sediment surface during their entire life (Armonies and Reise 2000) while most macrofauna species tend to occur at or very close to the sand surface, depending on the latter for respiration or feeding. The coarse sand and steep beach face may also limit the macrofauna as the high permeability may lead to desiccation and hinder burrowing (Croker 1977; Alexander *et al.* 1993).

The severe climatologically conditions (*e.g.* larger temperature range) and the lower salinities in the Baltic region are certainly co-responsible for the lower nematode density and number of species. Temperature has a profound effect on the minimum generation time in all nematodes studied so far and development is more temperature dependent in the lower temperature range than near their optimum. Concerning the low salinities, benthic communities in brackish water have fewer nematode species than either pure marine or pure freshwater communities (Heip *et al.* 1985). Some of the nematodes (*e.g. Viscosia viscosa, Tripyloides acherusius, Bathylaimus stenolaimus, Trichotheristus mirabilis, Trissonchulus benepapilosus*) found on the Hel beach are typical brackish-water nematodes which have been recorded frequently in European estuaries (Remane 1933; Gerlach 1954; Bouwman unpublished data). Heip *et al.* (1985) noted that the lower salinity values for first four species were 0.9, 0.5, 5.3 and 2.1 respectively, which is in concordance with our recordings.

Both MDS and DCA revealed three separated nematode assemblages on both beaches. Comparison with nematofaunal assemblages of other microtidal beaches is not possible as to our knowledge this is the first quantitative survey of the nematodes on such beaches. Thorson (1957) for macrofauna and Por (1964) for meiofauna both stated that 'parallel level-bottom communities' or 'isocommunities' are typical for benthic environments and are defined as ecological parallel assemblages: 'the same types of bottoms are everywhere inhabited by species of parallel animal communities in which different species, of the same genera, replace one another as the 'characterising species'. From the five main discriminating species lists (Table 4) and the similarities between corresponding zones at different taxonomic resolutions (Table 5) it is clear that the existence of isocommunities between the beaches is only fully supported for the upper beaches (27% of genus similarity, and a different characterising species- *Aporcelaimus* sp1 and *Aporcelaimus* sp2 within the same genus). This supports the idea of community convergence in similar but widely separated habitats. Several twin-species (*i.e.* pairs of species that show slight morphological differences but have widely separated areas of distribution and are ecological counterparts) were detected between both beaches. *Trissonchulus oceanus, Axonolaimus tirrenicus, Enoplolaimus subterraneus, E. attenuatus, E villosus, Viscosia cobbi, Leptolaimus setiger* on the Italian beach were found to have *T. benepapilosus, A. spinosus, E. balgensis, E. propinquus, V. viscosa* and *Leptolaimus* sp2 as ecological counterpart on the Polish beach.

A reduction in species richness is expected on the upper shore as environmental conditions were more extreme and the abundance and distribution of organisms are controlled by physical factors such as extremes of temperature and desiccation (Knox 2001). This is in contrast with our results. The upper beach possesses a set of characters defined by the interactions between the physical contrasts of the adjacent ecological systems (sea/land) and consequently a unique microhabitat is created. Therefore the upper beach can be seen as the transition zone (an ecotone) where nematode species from both pure terrestrial and pure marine ecosystem co-exist. Consequently, the occurrence of the several terrestrial Dorylaimida and Rhabditida on the upper beach is not unexpected. This was confirmed by the study of Wall *et al.* (2002) who recorded high numbers of Dorylaimida in the front of dunes and on the upper beach. These terrestrial nematodes (different subclasses within the Phylum Nematoda) are responsible for the higher average taxonomic diversity and distinctness on both upper beaches. The continuous influx of fresh water from the hinterland dunes may promote terrestrial nematodes to invade the upper beaches as well (Gheskiere *et al.* 2004).

In the swash/breaker zones, nematofauna is subjected to greater physical stress in contrast to other zones. As the Italian beach is at the reflective, physically controlled end of the intermediate beach state, this swash/breaker zone is characterised by continuous and high energetic water flushing through the coarse sediment. This is reflected in the nematode assemblage structure. From results from the taxonomic distinctness analyses it is clear that the swash/breaker nematode assemblage is not behaving like a random selection from the regional species pool, which is a feature of stress within this assemblage (Warwick and Clarke 2001). Consequently, only tiny, well-adapted species can inhabit these very hydrodynamic zones (Brown and McLachlan 1990). Epsilonematid and Draconematid nematodes, which are small, selective deposit feeders (1A), typically have rows of stout setae and spines, used to adhere to large sand particles and make these groups particularly adapted for high energy niches. *Epsilonema pustulatum* has been reported several times in the coarse, strongly hydrodynamic sediments of a sand extraction site at the Kwintebank (Belgian Continental Shelf, Vanaverbeke *et al.* 2000), a habitat which is in some sense comparable with the surging waves and coarse sand of the swash/breaker zone on the Italian steep reflective, microtidal beach. The occurrence of *Trissonchulus benepapilosus* as a characterising species in the Polish swash/breaker zone is somewhat unusual as these nematodes are quite long (3-4 mm), are predators (2B), and have a bare cuticle with no possibilities to attach themselves to the sand grains. However, as this beach is at the dissipative, more chemically controlled end of the intermediate spectrum, water percolation in the swash/breaker zone is expected to be much lower than on the Italian beach.

CONCLUSIONS

It is concluded that across intermediate, microtidal sandy beaches different nematode assemblages exist. These assemblages are associated with the upper beach, swash/breaker and subtidal zones. The isocommunities concept is only supported for the upper beach assemblages and several twin-species were noted between the geographically spaced intermediate beaches. Changes in nematode diversity measurements mirrored the physical and chemical characteristics of the different zones. Highest average taxonomic diversity and distinctness was noted on both upper beaches. The latter are considered to be important ecotones between the terrestrial and marine environment with nematode species from both adjacent ecosystems.

ACKNOWLEDGEMENTS

CHAPTER IV

Meiofauna as descriptor of

tourism-induced changes at sandy beaches

ABSTRACT

Tourism has long been considered as a 'clean industry' with almost no negative effects on the environment. This study demonstrated, in two different coastal systems (Mediterranean and Baltic), that tourism related activities are particularly affecting the sandy beach meio- and nematofauna in the upper beach zone, the specific ecotone in which many meiofauna species from both the marine and the terrestrial environment congregate. Tourist upper beaches are characterized by a lower % Total Organic Matter, lower densities, lower diversities (absence of Insecta, Harpacticoida, Oligochaeta, terrestrial and marine Ironidae nematodes) and higher community stress compared to nearby non-tourist locations. The %TOM was found to be the single most important factor for the observed differences in meiofauna assemblage structure at tourist versus non-tourist beaches in both the Mediterranean and the Baltic region. The free-living nematode assemblages from tourist upper zones depart significantly from expectations based on random selections from the regional nematode species pool. Furthermore upper zone assemblages are characterised by a low species diversity consisting of taxonomically closely related nematode species with *r*-strategist features.

Generally, faunal differences between tourist and non-tourist beaches are decreasing towards the lower beach zones.

KEYWORDS: meiofauna, free-living nematodes, sandy beach, taxonomic diversity, tourist impacts, Mediterranean, Baltic

INTRODUCTION

Sandy beaches are examples of simple ecosystems, principally driven by the physical forces of waves, tides and sediment movements (Short 1999). The simplicity is mainly related to the biodiversity of the system rather than to the adaptation of the organisms which may be very specialized and therefore, because of the highly dynamic environment, very fragile (Brown and McLachlan 1990). Notwithstanding their barren appearance sandy beaches, they support diverse populations of benthic invertebrates, bacteria, diatoms and algae. While the variety of animal life inhabiting sandy beaches is strikingly less than that on the rocky intertidal or shallow tidal flats, the individual species are often highly abundant (Hedgpeth 1957). These species play important roles in the ecological functioning of the beach, as primary producers (diatoms and algae), as decomposers (bacteria), as first line (heterotrophic bacteria and meiobenthos) or as second line consumers (macrobenthos) (Knox 2001). The latter are consumed by juvenile flatfish and wading birds, which can be considered as the top predators in the sandy littoral. Since the beach is considered to be the dynamic natural transition zone between land and sea representatives from both terrestrial and marine origin can be found.

Several authors have noted that perturbed benthic environments are generally kept in an early stage of the successional series (low species diversity and often consisting of taxonomically closely related species), while unperturbed benthic communities, in a late(r) successional stage, often consist of a wider range of taxonomically more distinct species (Warwick and Clarke 1995). Therefore, following Tilman (1996), the taxonomic range of an assemblage may be indicative in maintaining ecosystem stability during natural as well as anthropogenic disturbances. Disturbance is known to represent an important causative factor for spatial heterogeneity, and consequently for the structure and dynamics of natural assemblages (Sousa 1984). As a rule the major stresses on the coastal environment have been linked with overexploitation of natural resources, pollution, industrialisation and erosion (McIntyre 1995; Dronkers and Devries 1999) while tourism and recreational activities have been largely neglected. Gormsen (1997) estimated that 25% of all hotel beds worldwide are located along sandy coastlines. During the last decades, recreational activities have been increasing rapidly in developed countries as people enjoy more leisure time and higher standards of living. Clearly many of these activities are, and will increasingly be, focused on coastal tourism. Partly due to their barren appearance sandy beaches have not been regarded as vulnerable to human disturbance, while sand dunes are widely recognized as very fragile systems, even sensitive to barefoot human traffic (Andersen 1995; Poulson and McClung 1999). Human trampling has long been recognised as a critical factor for many vulnerable land biotas whereas it is only recently considered to play a key role in marine coastal conservation management. Presence of people on the beach and swimming in the surf zone has a marked effect on the activities of macrofauna and the semi-terrestrial crustaceans, inhibiting the intertidal feeding grounds of shorebirds (Andersen 1995). The impact of tourism does not only include the human trampling on the beach itself but also the whole of activities to organise and maintain it (beach management operations). In tourist popular regions dune systems are destroyed by the construction of vacation facilities (Cori 1999; Nordstrom *et al.* 2000) and the upper beaches are cleaned frequently with mechanical beach cleaners. Along with the removal of algae and wrack, almost all macroscopic items are removed from the beach as the upper sand layer is shovelled

up and replaced after sifting. Therefore the % Total Organic Matter (%TOM) can possibly serve as a biological proxy for mechanical beach cleaning. The cleaning may also affect the sand transport, sediment chemistry and fore-dune stabilisation. Physical disturbance by cleaning activities is already known to cause a decrease or disappearance of macrofauna (*e.g.* sandhoppers) as well as the wading birds feeding on them (Brown and McLachlan 1990; Llewellyn and Shackley 1996; Mann 2000). To date, the effects on the interstitial meiofauna (all metazoans between 38 µm and 1mm) are unclear. Owing to the high abundances, high species richness and trophic diversity, meiofauna occupies a significant position in the so-called "small food web" (bacteria, protists, meiofauna) (Kuipers *et al.* 1981) and have many inter-relations with macrofauna (Reise 1979). Nematodes were chosen in this study as a representative group within the sandy beach meiofauna as this group is well suited (overall high abundances, wide spectrum from highly tolerant to non-tolerant species to several kinds of pollution and disturbances, no pelagic life stages, ubiquitous distribution, rapid generation and fast metabolic rates, relatively short life spans) for studying the impacts of different kinds of natural and anthropogenic disturbances in the marine environment (Heip *et al.* 1985; Schratzberger *et al.* 2000).

The aims of this study were to:

(1) Compare the meiobenthic composition at higher taxon levels between tourist and non-tourist beaches in both the Baltic Sea and the Mediterranean Sea, (H_{o1}: no differences in meiofaunal assemblages between tourist and non-tourist beach zones),

(2) Assess possible changes in the taxonomic composition of the nematofauna, (H_{o2}: no differences in taxonomic composition between tourist and non-tourist beach zones) and

(3) Determine the environmental variables that are primarily responsible for potential differences at tourist versus non-tourist beaches.

MATERIAL AND METHODS

Study sites

Two micro-tidal beach systems in two different climatic areas were investigated (Figure 1). At each location a tourist beach and a pristine beach were selected. Both tourist sites are characterized by high tourist pressure and are cleaned frequently by means of mechanical beach cleaners. Detailed information on these beaches and their morphodynamics are described in Table 1 and elsewhere (Gheskiere *et al.* 2005a), but generally all beaches belong to the micro-tidal intermediate group *sensu* Short (Short 1999).

(1) The study sites of Hel and Jurata are located on the northern coast of Poland, at the end of the Hel Peninsula. The beach of Hel has been closed to the public entrance for more than 50 years because it was a strategic military area. Since only limited access is available now, human impact can be considered as relatively low. This beach is backed by a well-developed dune system forming the upper limit of storm accumulation. The study site of Jurata is located in front of a hotel complex, constructed in the dunes. As a consequence of the leisure infrastructure a natural dune system is absent in Jurata.

(2) The Mediterranean study sites are located in the Tuscan region. The beach of San Rossore is situated in the San Rossore Massaciuccoli Natural Park (24.000 ha). This park stretches along 30 km of flat coastal strip in Tuscany (Ligurian Sea), bounded by Viareggio in the North and Livorno in the South. The San Rossore beach is, like the beach in Hel, backed by a natural dune system and forests of pine-trees. There is free public access to the Massaciuccoli Natural Park but since access to the littoral area is restricted, this beach is classified as undisturbed. The study site of Viareggio is located just outside the San Rossore Massaciuccoli Natural Park. Viareggio is a primary place of national and international tourism since the 19th century and has over 400 bathing facilities constructed in or nearby the dunes.
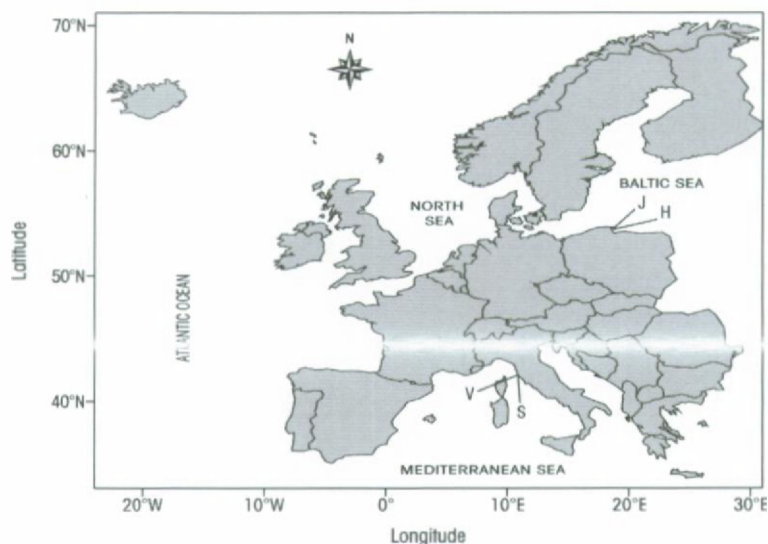
Figure 1: Map showing the tourist and non-tourist beaches studied in each geographic area: Viareggio (V) and San Rossore (S) in Italy and Jurata (J) and Hel (H) in Poland, respectively.

Beach Characteristics Mediterranean	San Rossore	Viareggio
Longitude	10°16'40" E	10°14'39" E
Latitude	43°42'53" N	43°50'56" N
Beach width (m)	45-60	50-60
Breaker type	Spilling-surging	Spilling-surging
Median grain size (μm)	509 ± 19	500 ± 21
Sediment textural group	coarse sand	coarse sand
Sediment sorting (Φ)	0.322 ± 0.004 well sorted	0.342 ± 0.006 well sorted
Beach exposure	very exposed	very exposed
Dean's parameter (Ω)	2.39	2.34
Relative Tidal Range (RTR)	0.5	0.5
Beach type	Intermediate/reflective	Intermediate/reflective

Beach Characteristics Baltic	Hel	Jurata
Longitude	18°45'37" E	18°43'06" E
Latitude	54°37'04" N	54°41'08" N
Beach width (m)	60-85	60-75
Breaker type	Spilling-plunging	Spilling-plunging
Median grain size (μm)	385 ± 14	375 ± 22
Sediment textural group	medium sand	medium sand
Sediment sorting (Φ)	0.309 ± 0.01 well-sorted	0.315 ± 0.02 well-sorted
Beach exposure	very exposed	very exposed
Dean's parameter (Ω)	5.29	5.20
Relative Tidal Range (RTR)	0.1	0.1
Beach type	Intermediate/dissipative	Intermediate/dissipative

Table 1: Detailed information on the beaches studied.

Sampling strategy and sample collection

Sampling was performed in September (Poland) and October (Italy) 2000, just after the end of the tourist summer season. On each of the four beaches, three zones across the beach slope (upper, middle and lower) each with eight randomly positioned replicates were sampled for meiofauna. The tourist and non-tourist beaches in each geographic area are only some kilometres from each other, along the same coastline. Tourism-induces changes were most likely to occur in the surface layers of the sediment and thus only the top 10 cm of sediment were sampled using transparent plexi-cores (sampling surface area 10 cm²). Six additional samples per zone were randomly collected for granulometric, %TOM and interstitial salinity analyses. Meiofauna samples were immediately fixed with a heated (70°C) 4% buffered formaldehyde water solution (Heip *et al.* 1985; Vincx 1996).

Laboratory treatment

In the laboratory, meiofauna samples were rinsed with a gentle jet of freshwater over a 1 mm sieve to exclude macrofauna, decanted over a 38 µm sieve, centrifuged three times with Ludox® HS40 (specific density 1.18) and stained with Rose Bengal. Meiofauna was counted and identified at the higher taxon level using a stereomicroscope. Per replicate, the extract was than placed into a beaker, made up to a standard volume with filtered tap-water and homogenized into suspension before a constant proportion (25%) of the sample was taken with a semi-automatic pipette. Per sub-sample all nematodes were picked out, transferred from formalin to glycerol through a series of ethanol-glycerol solutions, mounted in glycerine slides (Vincx 1996) and then identified to the species level and classified according to the phylogenetic system of De Ley and Blaxter (2002, 2003).

Sediment samples were oven-dried at 105°C for 12 h and ashed at 500 ± 50°C for 2 h to determine the %TOM by loss of mass. Sediment particle-size distribution was determined using Coulter LS100© particle size analysis equipment. The sediment fractions were defined according to the Wentworth scale (Buchanan 1984); sediment sorting coefficient and other granulometric characteristics were calculated as described by Dyer (1986).

Data processing

The meiofauna data were analysed by non-metric Multi-Dimensional Scaling (MDS) (Kruskal 1964) and by a Detrended Canonical Analysis (DCA) (Ter Braak 1988). A measurement of the degree to which the MDS-plots correspond to the dissimilarity values is given by the stress or loss function value. Analysis of similarities (ANOSIM, Clarke 1993) was used to test for significant differences between multivariate groups of samples from different zones and from different beaches. The similarity percentages programme (SIMPER, Clarke 1993) was applied to determine the contribution of higher meiofauna taxa and individual nematode species towards the discrimination between the equivalent beach zones. The Index of Multivariate Dispersion (IMD, Warwick and Clarke 1993) has been applied here as measure of community stress. The IMD is a measure of the increase in variability among replicate samples from perturbed versus pristine situations, *i.e.* a Multivariate Stability Index (MSI) *sensu* Warwick *et al.* (2002). All multivariate analyses were performed using square-root-transformed data in order to indicate the responses of highly dominant species but also put some weight on the rare ones (Clarke 1993).

Nematode species abundance data (Ind/10 cm²) were used to calculate the diversity as the expected number of species per sample based on 100 individuals ES(100) (Sanders 1968; Hurlbert 1971), Simpson Index ($1-\lambda'$) and average taxonomic distinctness based on quantitative (Δ^*) and presence/absence data (Δ') (Warwick and Clarke 1995). For the calculation of the taxonomic indices equal step-lengths between each taxonomic level were assumed, setting the path length ω to 100 for two species connected at the highest (taxonomically coarsest) possible level (Clarke and Warwick 1999). Eight taxonomic levels were used (species, genus, family, super-family, sub-order, order, sub-class and class) and consequently weights are: $\omega=12.5$ (species in the same genus), $\omega=25$ (same family but different genus), $\omega=37.5$ (same super-family but different family), $\omega=50$ (same sub-order but different super-family), $\omega=62.5$ (same order but different sub-order), $\omega=75$ (same sub-class but different order),

ω=87.5 (same class but different sub-class) and ω=100 (different class), respectively. Calculation of average taxonomic distinctness from simulated sub-samples of different numbers of species m from the master list (Δ_m^+) were used to produce probability funnels against which distinctness values for all zones were checked. This formally address the question whether these zones have a 'lower than expected' taxonomic spread, assuming a null hypothesis that each sample is a random selection from the regional species pool (Clarke and Warwick 1998). The same procedure was used to produce joint plots of average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+). Taxonomic diversity measures have the distinct advantage of being unbiased by sampling size and have potential for environmental impact assessment studies (Warwick and Clarke 2001). The relationships between multivariate biotic patterns and environmental variables were assessed using the BIO-ENV procedure (Clarke and Ainsworth 1993). Diversity measurements, community analyses and BIO-ENV calculations were performed using the PRIMER v5.2.9 software package (Clarke and Gorley 2001). Differences in univariate community attributes were analysed using a multi-factorial ANOVA with model terms including 'GEOGRAPHIC AREA' (Mediterranean, Baltic), 'TOURIST' (tourist, non-tourist) and 'ZONE' (upper, middle, lower). Residuals from the fitted models were visually assessed for evidence of outliers or of non-normality. Bartlett's and Cochran's tests were used to verify for homoscedasticity of variances prior to the analysis. Tukey multiple comparison tests were performed to investigate any differences between tourist and non-tourist beach zones (Zar 1996). Statistical analyses were performed using the STATISTICA v6.0 software package (StatSoft 2001). A significance level of p<0.05 was used in all tests.

RESULTS

The abiotic environment

At both non-tourist sites the %TOM showed a similar decreasing pattern, being noticeably higher at the upper beach zone (2.28 ± 0.10 and 1.17 ± 0.04 for San Rossore and Hel respectively) coinciding with a visible cover of marine and terrestrial detritus at these zones. The upper beaches from the tourist sites both showed a significantly lower %TOM in contrast to their non-tourist counterparts, confirming the use of this parameter as biological proxy for upper beach cleaning activities (Viareggio: 0.25 ± 0.12 and Jurata: 0.34 ± 0.07). Values at the middle and lower tourist zones were comparable with the same zones on the non-tourist sites (Figure 2A).

Generally no significant granulometric differences (grain size, sorting, skewness, granulometric size class distribution) were noted between tourist and non-tourist equivalent beach zones in both regions. Figure 2B shows only median grain size. Median grain size was highest at the middle zone (the swash/breaker zone) of all beaches studied, a known feature caused by the wave-dominated character of this kind of micro-tidal beaches (Short 1999).
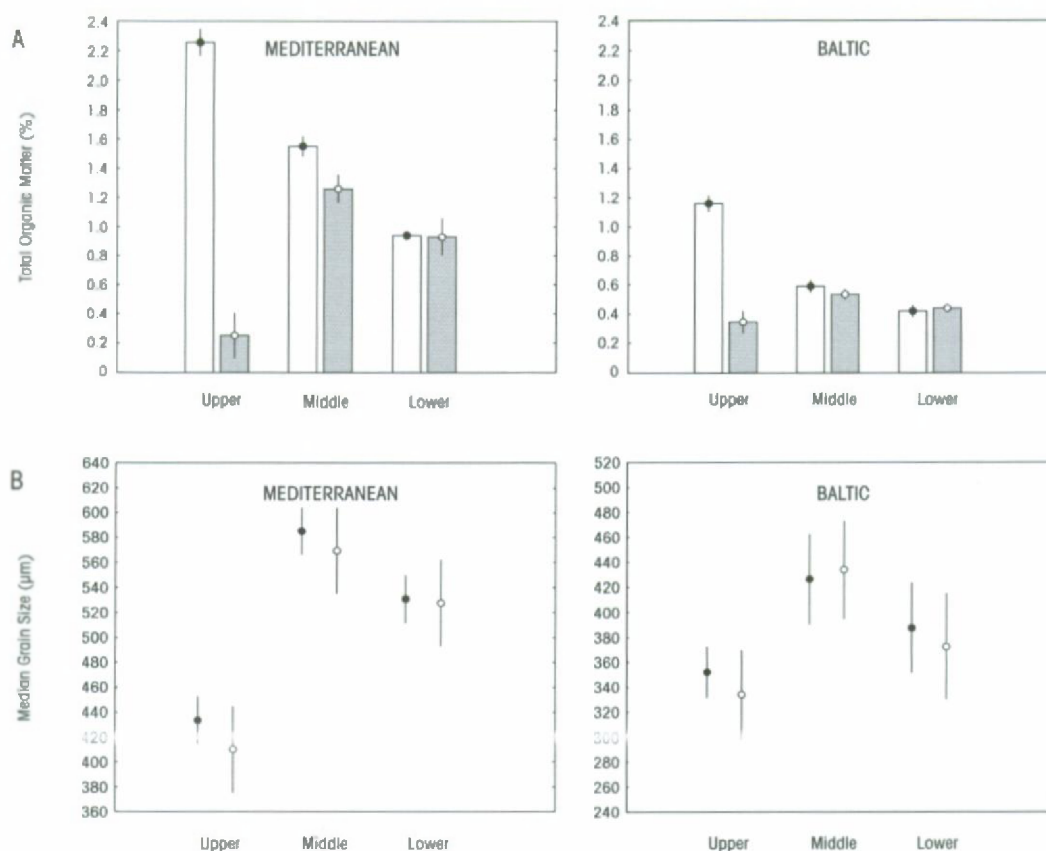
Figure 2: A: Mean % Total Organic Matter (± SD) and B: Mean median grain size (± SD). (All calculated by pooled variance of six replicates per zone and per beach for the Mediterranean and the Baltic area) (Closed symbols=non-tourist, open symbols=tourist)

Assemblage structure

The two geographic areas differed significantly in higher meiofauna assemblage structure (ANOSIM, R=0.319, p<0.01). Following the SIMPER-analyses this is in essence caused by higher numbers of turbellarians in the Mediterranean and high numbers of oligochaetes in the Baltic. MDS-plots and DCA-ordinations (not shown) for total meiofauna (including nematode species data) denoted in each area a clear separation between tourist and non-tourist sites and between the different zones sampled (Figure 3). On the Mediterranean beaches, as well as on the Baltic ones the meiofauna of the upper zones is more dissimilar in assemblage composition than middle and lower zones. Results of the ANOSIM tests (Table 2) confirmed this trend on the total meiofauna as well as on the nematode species level. Similarity of percentage analyses (SIMPER) attributed this discrimination in the Mediterranean region mainly to a complete loss of Insecta, Harpacticoida, Oligochaeta, terrestrial Dorylaimida (*Aporcelaimus* sp.1, *Aporcelaimellus* sp.1, *Aporcelaimellus* sp.2, *Mesodorylaimus* sp.1 and *Nygolaimus* sp.1), Haliplectidae (*Haliplectus* sp.) and marine Ironidae (*Trissonchulus oceanus*) on the tourist upper beach. *Epsilonema pustulatum* and *Theristus heterospiculum* both occurred in very high densities on the non-tourist Mediterranean middle beach zone while these species were nearly or complete absent, respectively on the tourist middle beach zone. *T. heterospiculum* seemed to be entirely replaced by *Theristus heterospiculoides* on the tourist beach. In the Baltic region the tourist upper beach was in essence characterised by the absence of Oligochaeta, Tardigrada, Insecta and also terrestrial nematode species (several *Aporcelaimus* and *Aporcelaimellus* species, *Plectus* sp. and *Acrobeles ciliatus*) and the marine Ironidae *(Trissonchulus benepapilosus)*.

Figure 3: Meiofaunal assemblages (higher taxa and nematode species data combined): Output of non-metric Multi-Dimensional Scaling (MDS) on square-root-transformed abundance data (Six replicates per beach zone). (A: Mediterranean, S= San Rossore, V=Viareggio. B: Baltic, H=Hel, J=Jurata)
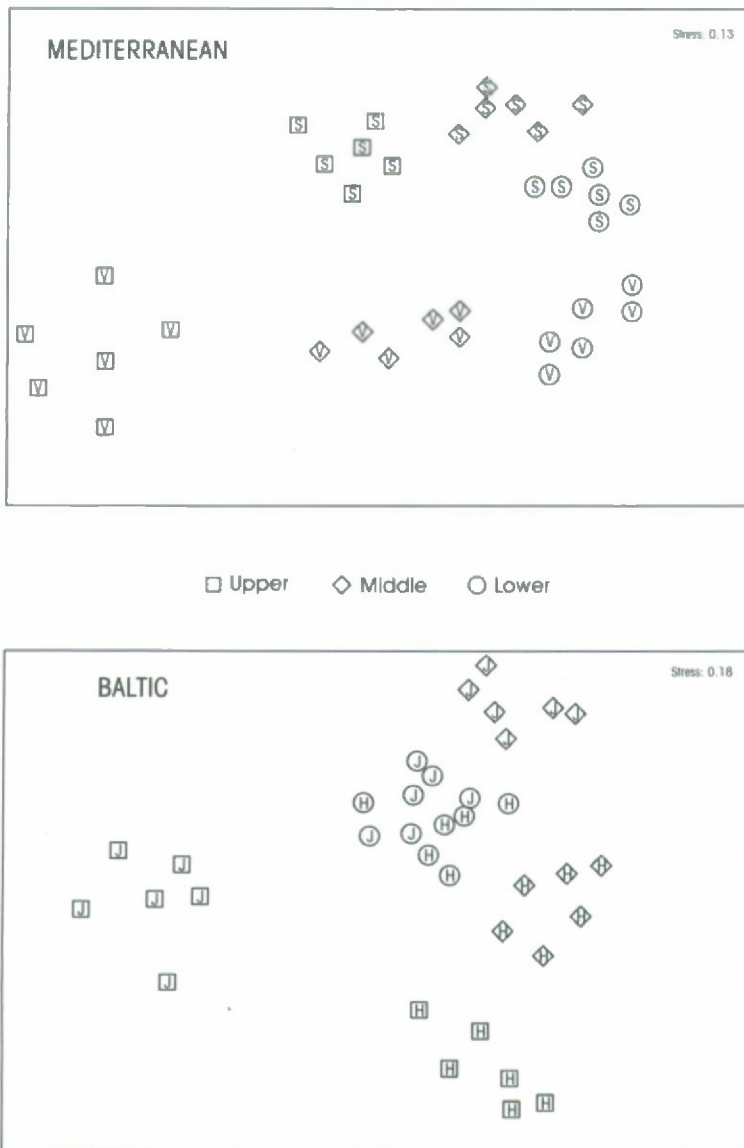
	MEDITERRANEAN				BALTIC			
	Meiofauna		Nematodes		Meiofauna		Nematodes	
	R	p	R	p	R	p	R	p
Global test	0.822	<0.001	0.802	<0.001	0.606	0.001	0.530	<0.001
Zones compared								
UPPER	0.998	0.029	0.997	0.029	0.737	0.020	0.863	0.020
MIDDLE	0.760	0.029	0.875	0.029	0.694	0.020	0.330	0.011
LOWER	0.533	0.049	0.646	0.039	0.206	0.078	0.152	0.087

Table 2: Results of the ANOSIM and pair-wise tests for difference between non-tourist and tourist equivalent beach zones for both areas on the meiofauna and nematode assemblage structure (R-values and p-values are reported). Analyses performed on square-root transformed data.

The MDS-plots also indicated a higher inter-variability among replicate samples from disturbed upper beaches as the replicates are more scattered in the plots. The latter is reflected in the calculations of the indices of multivariate dispersion (IMD). In equivalent zones, the inter-variability among replicate samples from tourist beaches is higher than for non-tourist beaches. Consequently, when making pair-wise comparisons between equivalent zones the multivariate stability indices (MSI) indicated negative values for total meiofauna and for nematodes separately. (Table 3)

AREA	Zones	Non-tourist		Tourist		MSI	
MEDITERRANEAN	All	0.91	(0.90)	1.30	(1.20)	-0.39	(-0.29)
	Upper	1.06	(0.77)	1.44	(0.99)	-0.38	(-0.23)
	Middle	1.17	(1.22)	1.40	(1.42)	-0.23	(-0.21)
	Lower	0.79	(0.76)	0.94	(0.91)	-0.14	(-0.15)
BALTIC	All	0.98	(0.97)	1.13	(1.10)	-0.15	(-0.13)
	Upper	1.19	(0.88)	1.39	(1.10)	-0.20	(-0.22)
	Middle	1.13	(0.99)	1.28	(1.07)	-0.15	(-0.09)
	Lower	0.81	(0.70)	0.90	(0.78)	-0.09	(-0.08)

Table 3: Values of multivariate dispersion from both non-tourist and tourist beaches, separately for both study sites and zones on the beach, based on square-root-transformed total meiofauna abundance data and Bray-Curtis similarities, and the resulting Multivariate Stability Index (MSI). Values for nematodes separately are given in brackets.

Univariate community indices and taxonomic measurements

The results from the three-way ANOVA are presented in Table 4. Figures 4-6 show the graphical summary of means and standard errors of univariate indices for higher meiofauna and nematode assemblages from both tourist and non-tourist beach zones along with the results of Tukey multiple comparison tests. Most indices (except ES(100), p<0.10 and Δ^*, p<0.22) differed significantly between geographic areas. Total meiofauna density and number of taxa were the only indices not showing a significant difference between tourist and non-tourist samples (p<0.48 and p<0.35). For all indices (except Simpson dominance) a significant TOURIST x ZONE interaction was noted. Apart from the number of taxa, a significant GEOGRAPHIC AREA x TOURIST interaction was absent for all indices.

Fourteen higher meiofauna groups were recorded during this study, in overall decreasing order of density: Nematoda, Turbellaria, Oligochaeta, Harpacticoida, Gastrotricha, naupliar larvae, Halacaroidea, Insecta, Amphipoda, Polychaeta, Tardigrada, Kinorhyncha, Gnathostomulida and Acari. Thirteen meiofauna groups were recorded in the Mediterranean region and 12 in the Baltic. Generally, higher average total meiofauna densities were noted in the Mediterranean region: (638 ± 208 Ind/10 cm²) versus (161 ± 23 Ind/10 cm²) in the Baltic. Nematodes numerically dominated all beaches studied (accounting for more than 75% of the total meiofauna). Naupliar larvae and Turbellaria, and Oligochaeta and Turbellaria, were subdominant in Mediterranean and Baltic samples respectively. Significantly higher total meiofauna densities were recorded on the non-tourist middle beach zone (1990 ± 45 Ind/10 cm²) and on the tourist lower beach zone (950 ± 198 Ind/10 cm²) in the Mediterranean. The higher density on the non-tourist middle beach zone is caused by higher numbers of *Epsilonema pustulatum* while naupliar larvae were responsible for the higher density in the tourist lower zone. The nematode abundance is remarkably uniform across both Baltic beaches.

A total of 73 and 68 free-living nematodes species were recorded on the Mediterranean and Baltic beaches respectively. 66 species were recorded in San Rossore, 34 species in Viareggio, 56 species in Hel and 41 species in Jurata. From Figure 5 shows that the most significant differences in univariate measurements (with exception of density) can be found on the upper beach zones. Tourist upper beach zones showed a significant lower expected species diversity (3 ± 2 for Viareggio and 4 ± 1 for Jurata) and significant higher dominance compared to the non-tourist upper zones.

Although middle and lower beach zones from both geographic areas showed similar values, tourist upper beach zones had lower average taxonomic diversity values (Δ^*=60, Δ^*=68) compared to their non-tourist equivalents (Δ^*=78, Δ^*=81) (Figure 6).

	Effect	df	F-value	p-value
N(meio)	GEOGRAPHIC AREA	1	16.50	<0.01*
	TOURISM	1	0.51	0.48
	ZONE	2	9.03	<0.01*
	GEOGRAPHIC AREA x TOURISM	1	0.86	0.36
	GEOGRAPHIC AREA x ZONE	2	7.61	<0.01*
	TOURISM x ZONE	2	4.88	0.01*
	GEOGRAPHIC AREA x TOURISM x ZONE	2	5.76	0.01*
Number of Taxa	GEOGRAPHIC AREA	1	37.14	<0.01*
	TOURISM	1	0.88	0.35
	ZONE	2	59.56	<0.01*
	GEOGRAPHIC AREA x TOURISM	1	31.65	<0.01*
	GEOGRAPHIC AREA x ZONE	2	2.69	0.08
	TOURISM x ZONE	2	9.45	<0.01*
	GEOGRAPHIC AREA x TOURISM x ZONE	2	6.10	<0.01*
N(nema)	GEOGRAPHIC AREA	1	44.94	<0.01*
	TOURISM	1	8.67	0.01*
	ZONE	2	14.20	<0.01*
	GEOGRAPHIC AREA x TOURISM	1	0.03	0.86
	GEOGRAPHIC AREA x ZONE	2	16.99	<0.01*
	TOURISM x ZONE	2	7.06	<0.01*
	GEOGRAPHIC AREA x TOURISM x ZONE	2	4.16	0.02*
ES(100)	GEOGRAPHIC AREA	1	2.72	0.10
	TOURISM	1	34.82	<0.01*
	ZONE	2	14.35	<0.01*
	GEOGRAPHIC AREA x TOURISM	1	0.52	0.47
	GEOGRAPHIC AREA x ZONE	2	7.76	<0.01*
	TOURISM x ZONE	2	1.44	0.05*
	GEOGRAPHIC AREA x TOURISM x ZONE	2	1.27	0.29
$1-\lambda'$	GEOGRAPHIC AREA	1	6.52	0.01*
	TOURISM	1	4.32	0.04*
	ZONE	2	7.29	<0.01*
	GEOGRAPHIC AREA x TOURISM	1	3.17	0.08
	GEOGRAPHIC AREA x ZONE	2	0.47	0.63
	TOURISM x ZONE	2	1.55	0.22
	GEOGRAPHIC AREA x TOURISM x ZONE	2	0.52	0.60
Δ^*	GEOGRAPHIC AREA	1	1.56	0.22
	TOURISM	1	16.15	<0.01*
	ZONE	2	3.67	0.03*
	GEOGRAPHIC AREA x TOURISM	1	0.29	0.59
	GEOGRAPHIC AREA x ZONE	2	1.67	0.20
	TOURISM x ZONE	2	9.93	<0.01*
	GEOGRAPHIC AREA x TOURISM x ZONE	2	0.63	0.54

Table 4: Results from three-way ANOVA for univariate community indices.
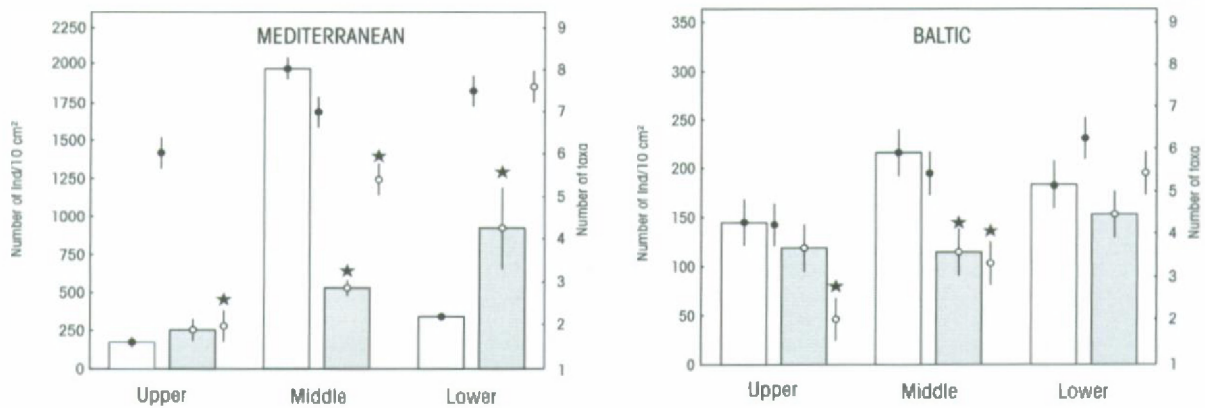
Figure 4: Total meiofauna densities (Ind/10 cm²) (bars ± SE, left ordinate) and mean higher taxon richness (circles ± SE, right ordinate) (All calculated by pooled variance of eight replicates per zone and per beach for the Mediterranean and the Baltic area) (Closed circles=non-tourist, open circles=tourist) ★ Indicates significant differences (p<0.05) from non-tourist samples (Tukey multiple comparison test for equal n).
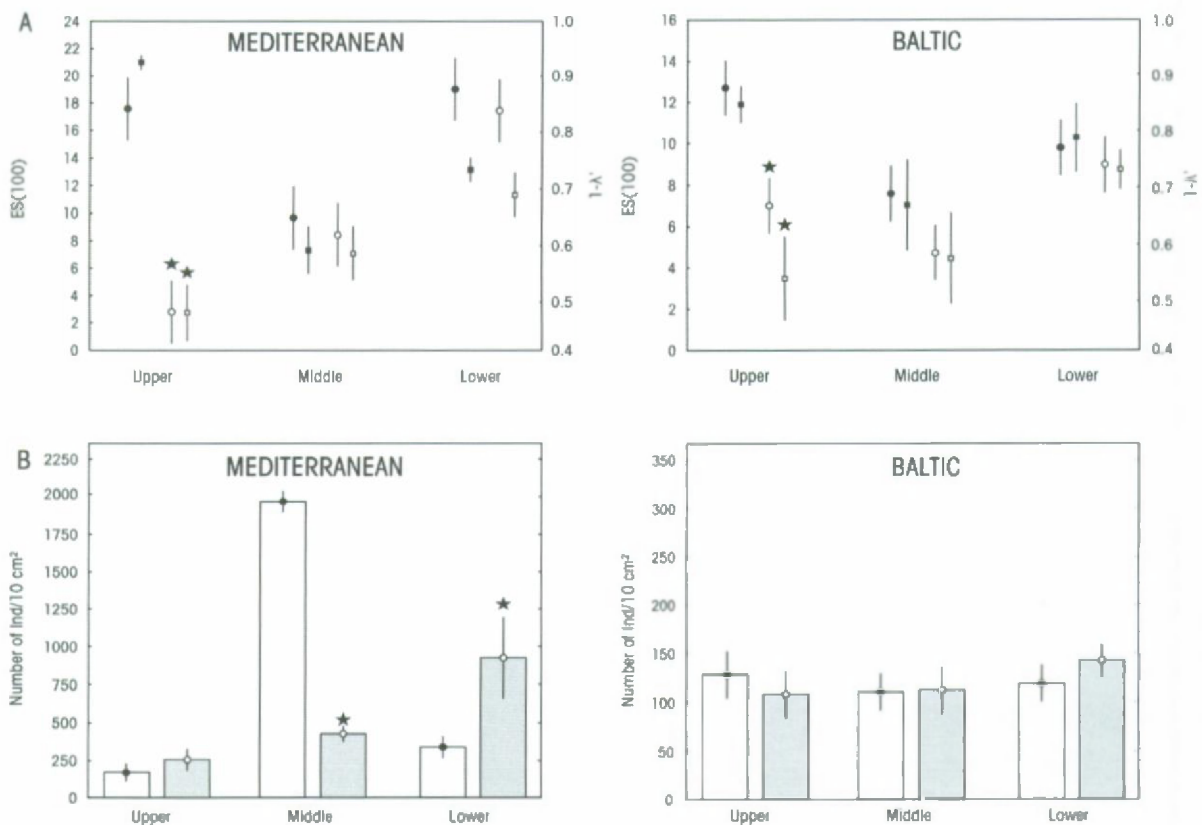
Figure 5: A: Expected number of species ES(100) (circles ± SE, left ordinate) and Simpson Index (1-λ') (squares ± SE, right ordinate). B: Total nematode densities (Ind/10cm²) (bars ± SE). (All calculated by pooled variance of six replicates per zone and per beach for the Mediterranean and the Baltic area) (Closed symbols=non-tourist, open symbols=tourist) ★ Indicates significant differences (p<0.05) from non-tourist samples (Tukey multiple comparison test for equal n)
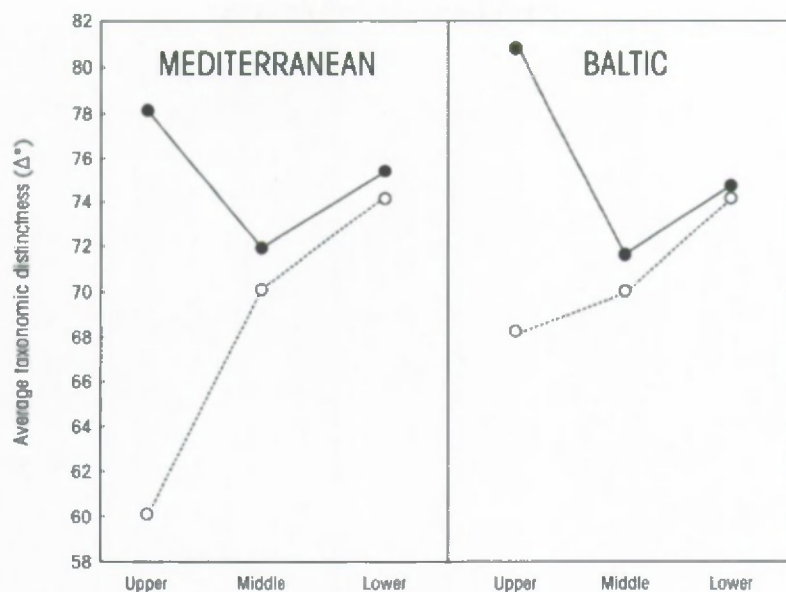
Figure 6: Average taxonomic distinctness values (Δ*) based on quantitative nematode species data for each beach zone in the Mediterranean and the Baltic area. (Closed symbols=non-tourist, open symbols=tourist)

Figure 7A displays the 95% funnel for the simulated distribution of average taxonomic distinctness (Δ*) for 15000 random subsets of fixed size m from the master nematode list for each area (73 species for Italy and 68 species for Poland). Superimposed on this plot are the true values of Δ* generated from species lists for each of the zones across the beaches. Upper beach zones from tourist Mediterranean and Baltic beaches and, to a lesser extent, Mediterranean middle beach zones all have reduced average taxonomic distinctness values, whereas all other zones have Δ* values close to that of their master list suggesting no evidence of reduced taxonomic distinctness for these zones. However, only the decrease in average taxonomic distinctness from both tourist upper beaches is significant ($p < 0.05$). Figure 7B shows a bivariate equivalent of the univariate funnels in which Δ* is considered jointly with the variation in taxonomic distinctness (Λ*) to produce probability regions within which 95% of the simulated values fall for a list of sub-listed sizes from random selections from the master nematode list for the upper beach zones from Mediterranean (m=10, 30) and Baltic (m=15, 40) tourist and non-tourist zones. The observed (Δ*, Λ*) values for these two upper beach zones are superimposed on their appropriate plot. As can be seen, both tourist upper beaches depart significantly ($p < 0.05$) from expectation as they fall outside the 95% ellipse. All other equivalent tourist and non-tourist beaches zones did not show a departure from the expected probability ellipses (plots are not shown).
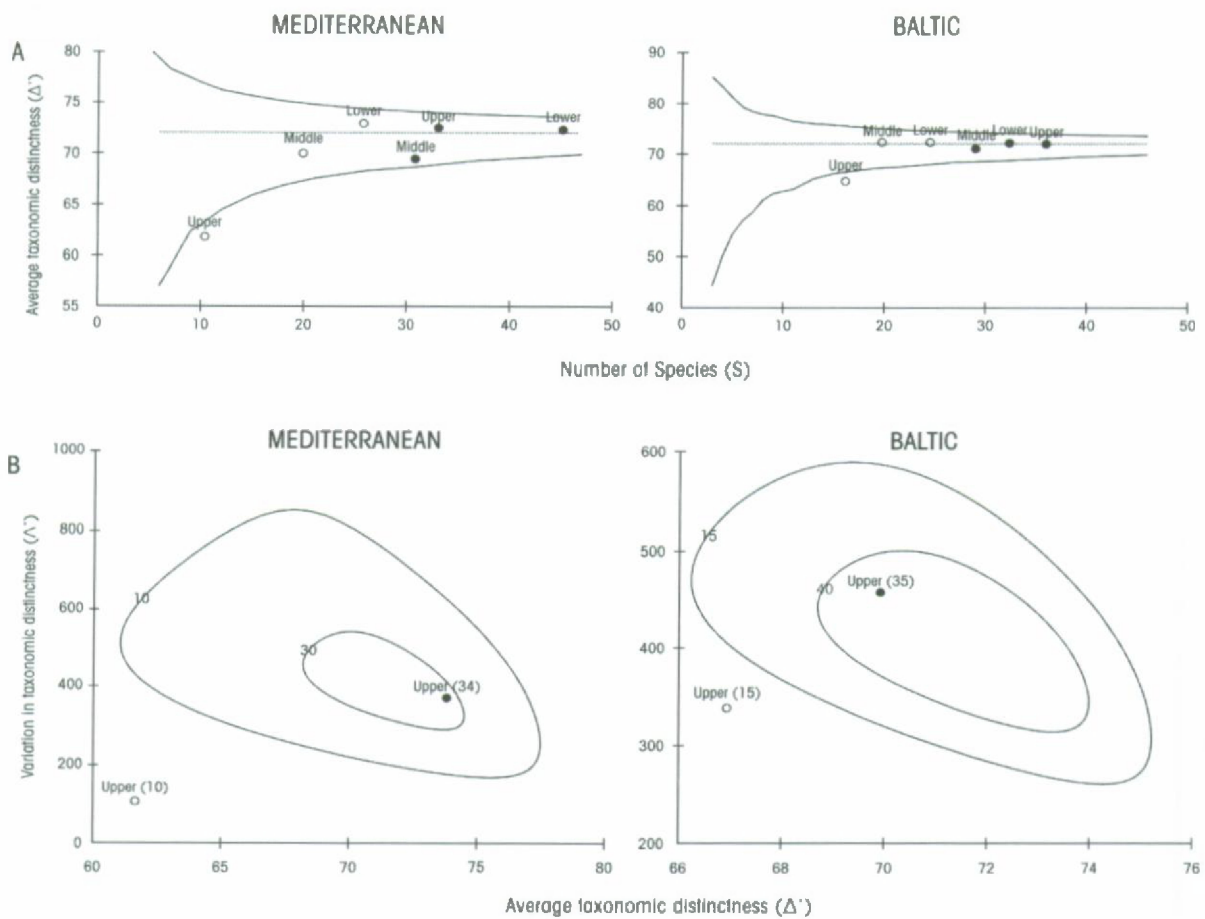
Figure 7 A: The 95% probability funnels for Average Taxonomic Distinctness (Δ⁺) plotted against the number of species for the different nematode assemblages from the non-tourist (closed circles) and tourist (open circles) beach zones in Italy and Poland studied for each sub-listed size. Dashed lines indicates the simulated mean Δ⁺ and Λ⁺ from 15000 ad random selections from the master list of 73 nematode species (Italy) and 68 nematode species (Poland). **B**: `Ellipse` plots of 95% probability areas for (Δ⁺, Λ⁺) pairs from tourist and non-tourist upper beach zones for a range of sub-list sizes in Italy (m=10, 30) and Poland (m=15, 40). The observed (Δ⁺, Λ⁺) values for each upper beach zone are superimposed on the appropriate plot for their particular species list size (given in brackets).

Relationship with environmental variables

The results of the Spearman rank correlation analyses between total meiofaunal assemblage structure and environmental variables for each geographic area are shown in Table 5. The BIO-ENV analyses indicated that both %TOM and salinity were important environmental factors in determining meiofaunal assemblage structure, $\sigma=0.597$, $\sigma=0.444$ for the Mediterranean area and $\sigma=0.444$, $\sigma=0.396$ for the Baltic area, respectively.

	Mediterranean	Baltic
Median grain size	0.499	0.104
Sorting	0.230	0.395
%TOM	0.597	0.444
Salinity	0.533	0.396

Table 5: Spearman rank correlations (σ) between total assemblage structure and environmental variables per geographic area.

DISCUSSION

Tourism has long been considered as a 'clean industry' with almost no negative effects on the environment worthwhile considering. Man has continued to impose changes upon the sandy environment, partly through ignorance and inability to learn from experience but also in belief that it must be possible to shape nature to his own needs and desires (Brown and McLachlan 1990). Yet, this stand is now outmoded as most parties are aware of the possible negative impacts on the coastal biodiversity and see the need for actions (UNEP 2000). However, on the other hand human populations are still increasingly concentrating in the coastal zone, and dunes and beaches are subjected to ever-expanding pressures from recreational activities.

To date, most tourism-impact studies have been mainly focused on changes in abundance and diversity of large macrofauna (Chandrasekara and Frid 1996), loss of individual species (*e.g. Talitrus saltator,* Weslawski *et al.* 2000) or decreasing populations of shore birds (*e.g.* Cornelius *et al.* 2001), whereas smaller animals were largely neglected. However, Kennedy and Jacoby (1999) indicated the meiofauna (a total of 23 phyla are represented) as phyletically more diverse than any other marine benthic component and moreover as an excellent indicator of marine environmental quality. Tourist and non-tourist zones were expected to be similar as they were located close to each other (only a few km), had similar exposure and showed negligible differences in granulometry, these (mean grain size, sorting, skewness, different fractions) being basic factors in meiofauna distribution (McIntyre 1969; Fricke and Flemming 1983).

The overall higher meiofauna densities in the Mediterranean are explained by the coarser and therefore more oxygenated sands, in contrast to finer and therefore more sulphidic Baltic sands (Gheskiere *et al.* 2005a). Higher meiofauna density in coarser sediments has been reported frequently (Gray and Rieger 1971; McLachlan 1977a, b; Giere 1993; Rodríguez *et al.* 2003). Lower salinity in the Baltic region (7 PSU) has most likely contributed to the comparatively lower density at those beaches. Benthic communities in brackish water have lower densities and fewer species than either pure marine or pure freshwater communities (Remane 1933; Gerlach 1954; Bouwman 1983). Major biological differences in assemblage structure (univariate, multivariate and taxonomically) between tourist and non-tourist beaches were found at the upper beach zones. In general these differences were more pronounced on the Mediterranean beaches. This is most likely caused by the length and intensity of the tourist period which is almost all year round in the Mediterranean while only in the summer months (Weslawski *et al.* 2000) in the Baltic region. BIO-ENV analyses clearly indicated the %TOM as the single most important factor responsible for the observed differences in assemblage structure at tourist versus non-tourist beaches in both areas. On pristine beaches, the amount of %TOM generally increases towards the upper beach and dune system (Wall *et al.* 2002) which corresponds with our findings. As a result of the intensive use, almost daily (mechanically) cleaning of the tourist upper beaches and destruction of the natural connections to the dune areas by numerous bathing facilities, considerable less marine and terrestrial debris was found. Consequently a significant decrease of interstitial %TOM was noted on the tourist upper beaches. Mechanical beach cleaning not only removes organic matter and anthropogenic waste from the beach but also physically disturbs the sediment, its micro-topography and its inhabitants, therefore creating a uniform habitat with a short durational stability (Van de Velde 2003; Gheskiere

et al. SUBMITTED). Low levels of organic matter and lack of suitable niches to support rich nematode assemblages are indicative of a stressed or resource-limited environment (Wall *et al.* 2002). Also the human trampling, primarily taking place at the upper beach, possibly influences the meiobenthic environment. Weslawski *et al.* (2000) calculated that one square meter of a Baltic tourist beach receives more than 100 human steps daily during the peak summer season. This causes reduction in soil macro porosity, air/water permeability, changes in sediment topography and perturbs the sand almost continuously. Wynberg and Branch (1994) demonstrated a reduction of oxygen content through compaction of the sediment. Multivariate analyses (ANOSIM) showed a clear significant discrimination of meio- and nematofauna between equivalent zones from tourist and non-tourist beaches at both study sites and therefore H_{01} (no differences in meiofaunal assemblages between tourist and non-tourist beach zones) has to be rejected. As noted above these differences were more defined at the upper beaches and decreased downwards the beach. SIMPER-analyses attributed this discrimination in the Mediterranean region mainly to a complete loss of Insecta, Harpacticoida, Oligochaeta, terrestrial nematodes and marine Ironidae nematode species on the tourist upper beach. In the Baltic region the tourist upper beach was in essence characterised by the absence of Oligochaeta, Tardigrada and Insecta and terrestrial nematode species. The absence of terrestrial nematodes on tourist beaches is most likely due to the destruction of the dunes and probably also a disruption of subterranean freshwater connections from the hinterland which terrestrial nematodes use to invade on the beach (Gheskiere *et al.* 2004). Absence of insects (mainly Coleoptera, Diptera larvae) and perhaps also oligochaetes (Inglis 1989) is linked with the absence of marine/terrestrial organic matter. As tourist beaches are cleaned frequently, the amount and presence of terrestrial and marine debris on the upper shore is reduced significantly. This debris is considered to be the primary food source for many upper shore macrofauna (Stenton-Dozey and Griffiths 1983), serves as a refugium (Colombini *et al.* 2000) and attracts terrestrial insects to invade on the beach (Remmert 1960). Many insects use the wind to travel (anemochory) from the dunes to the beach (Remmert 1960; Desender 1996). At tourist sites the fetch (open distance) of winds coming from the dunes is disturbed by buildings and bathing facilities and this might also contribute to the absence of insects. The colonization and breakdown of stranded wrack and debris by different faunal groups are described in detail by Jedrzejczak (1999). However it is still not clear whether the meiofauna use the dissolved organic matter in the interstitial water below the debris as a direct food source or whether the initial utilisation of the interstitial organic matter is by bacteria and that these in turn constitute the food source of the meiofauna (Jedrzejczak 2002a, b). Malm *et al.* (2004) have noted a significant reduction of %TOM and bacterial production and fewer ciliates on mechanically cleaned beaches in contrast to un-cleaned ones.

Caswell and Cohen (1991) first hypothesised that disturbance might induce higher spatial variability in assemblages (community stress). Warwick and Clarke (1993) and more recently Fraschetti *et al.* (2001) have also consistently recorded increased variability among replicates from several benthic communities (meio- as well as macrofauna) exposed to increasing disturbance levels. Our calculations of the multivariate dispersion indices indeed positively demonstrated an increase in variability on the impact beaches and support this contention. Multivariate stability indices comparing tourist and non-tourist sites generally increased down the studied beaches indicating higher community stress on the upper zones.

Generally, clear changes in the nematode assemblage structure between tourist and non-tourist beaches were found. Multivariate analyses revealed that changes in assemblage structure were less well defined on middle and

lower beaches than on upper beaches. Average taxonomic distinctness (Δ^+) is a measure of the degree to which species in an assemblage are related taxonomically to each other while the degree to which species from the regional species pool are over- or under-represented is reflected in the variation in taxonomic distinctness (Λ^+). The latter can be seen as the 'evenness' of the distribution of taxa across the nematode taxonomical tree. We have found clear differences in the taxonomic diversity range of nematode assemblages between tourist and non-tourist upper beaches while middle and lower beach zones were more similar. Therefore H_{o2} (no differences in taxonomic composition between tourist and non-tourist beach zones) can only be rejected partially. The changes in taxonomic range closely mirror the similar patterns in dominance ($1-\lambda'$) and species diversity. Most of the species absent on tourist upper beaches belong to orders of Nematoda (O. Dorylaimida, O. Ironidae and O. Rhabditida) which are relatively species-poor represented in our samples but which cause the high distinctness (*cfr.* Dorylaimida are in the different subclassis Dorylaimia), within the upper beach assemblages. On the other hand orders like Monhysterida and Enoplida, containing species-rich, well-represented genera such as *Enoplolaimus* (with *E. attenuatus, E. littoralis, E. villosus, E. balgenis*) and *Theristus* (with *T. heterospiculum, T. heterospiculoides, T. inermis, T. aculeatus, T. pictus*) are recorded at both tourist and non-tourist upper beaches. As Dorylaimida are generally thought to have long life-cycles, low colonization abilities and are sensitive to several types of disturbance (Johnson *et al.* 1974; Zullini 1976), their absence on the disturbed upper beaches is not unexpected. Dorylaimid nematodes and especially the Aporcelaimidae are generally known as true K-strategists or extreme persisters while Monhysterid and Enoplid nematodes are known as colonizers or r-strategists (Bongers *et al.* 1991). These findings correspond well with the suggestion of Clarke and Warwick (2001) that benthic communities which have been perturbed switch to an early successional stage community (colonizers) with low species diversity, and are characterized by the loss of distinctive taxa (reduced Δ^+) which are species-poor (reduced Λ^+), consequently leaving an assemblage of opportunist species with close taxonomic affinities. Changes in sandy sediment nematode assemblages subjected to continuous and spasmodic perturbations in contrast to unperturbed situations were also detected by Schratzberger and Warwick (1999) during microcosm experiments.

CONCLUSIONS

This study demonstrated, in two different coastal systems (Mediterranean and Baltic), there is evidence that tourism related activities are: (1) particularly affecting the sandy beach meio-nematofauna, especially in the upper sandy beach zone, the specific ecotone in which many meiofauna species from both the marine and the terrestrial environment congregate and (2) contribute to higher community stress, lower taxonomic range and species diversity of the nematode assemblages compared to nearby pristine locations. The %TOM was found to be an important factor for the observed differences in meiofauna assemblage structure at tourist versus non-tourist beaches in both the Mediterranean and the Baltic region. The tourist upper beach zones are characterized by lower meiofauna diversities and low mature nematode assemblages consisting of taxonomically closely related species with ɼ-strategist features.

ACKNOWLEDGEMENTS

CHAPTER V

Are strandline meiofaunal assemblages affected by mechanical beach cleaning?
Experimental findings

ABSTRACT

The increasing usage of sandy beaches as recreational resources has forced regional authorities of many tourist countries to remove all litter of fabricated origin and natural wrack from the beach. Consequently, a variety of heavy equipment has been developed during the last decades and is now used almost daily in many tourist resources. A field experiment, following a BACI-design, was conducted at the strandline of De Panne (Belgium) to investigate the impacts of mechanical beach cleaning on the strandline-associated meiofaunal assemblages, focussing on the free-living nematodes. Natural strandline assemblages were exposed to a one-off 5 cm deep mechanical beach cleaning and observed for 24 hours. We assessed the power of the experiment to detect the effects of mechanical beach cleaning and recorded a 99% chance of detecting a 50% change in total abundance, evenness and taxonomic diversity and a 74% chance in detecting a 50% change in species richness. Differences between cleaned plots and those from the un-cleaned control plots in terms of decreased percentage of organic matter, total abundance and changed community structure were noticed from immediately after the experimental cleaning onwards and came again to initial values after the following high water. Any impacts due to cleaning on species richness, evenness and taxonomic diversity were showed to be minor in relation to the daily changes. Recolonization in the cleaned sediments is assumed to occur from the underlying sediments initiated by the elevated water table during the rising tide. We suggested that strandline meiofauna are more resistant to mechanical beach cleaning than are macrofauna.

KEYWORDS: meiofauna, free-living nematodes, sandy beach, mechanical beach cleaning, disturbance, recovery

INTRODUCTION

The strandline is an ephemeral or permanent accumulation area of debris on of the beach where the high tide deposits material from the sea. It provides a very unique although fringe habitat, exclusive neither marine nor terrestrial, and is colonised by invertebrates from both ecosystems (Gheskiere *et al.* 2005a). Strandlines are of great ecological importance, especially on shores where they can act as precursors to sand dunes, enabling the formation of embryonic dunes and subsequently fore dunes (Davidson *et al.* 1991).

Strandline deposited material includes both wrack and inorganic beach-cast material. Wrack beach-cast material or natural flotsam refers to any organic debris of marine and terrestrial origin (Lord and Burger 1984). Once wrack is cast ashore it decomposes very quickly as it undergoes physical processes of fragmentation and biological processes of decomposition and remineralization. On a South African beach, Koop and Griffiths (1982) found that within eight days the weight of algal debris decreased by 73 to 77%. A small amount of the organic matter was consumed by the macrofauna but more than 90% was mineralized by micro-and meiofauna. In their recent review, Colombini and Chelazzi (2003) have described the macrofaunal beach-wrack assemblages and species succession associated with decaying organic matter, including marine as well as terrestrial representatives. This fauna is generally diverse to location, beach morphology, season, climate and vegetation cover. Common terrestrial groups feeding on rotting seaweed are Helcomyzidae (sub-Antarctic kelp flies), Coelopidae (kelp flies), Sphaeroceridae (lesser dung flies), Canacidae (beach flies), Ephydridae (shore or brine flies), darkling beetles (Tenebrionidae) and rove beetles (Staphylinidae), all feed on rotting material. There are also several species of terrestrial spiders, which use the upper strandline for shelter and hunting (Speybroeck *et al.* 2004). Of the marine macrobenthic invertebrates, besides Polychaeta and Bivalvia, especially the Amphipoda (Sandhoppers) are dominant in strandlines all over the world (Llewellyn and Shackley 1996). These macrofaunal organisms are important prey resources, being commonly exploited by large numbers of shorebirds and even passerines (Cramp and Simmons 1983; Davidson *et al.* 1991).

The deposit of manufactured debris has become a growing concern in many countries. Origins of this litter are both oceanic, *e.g.* from ships dumping at sea, and shore based, *e.g.* from rivers, sewage, or careless visitors. Stranded beach litter is more than a visible care, causing a significant threat to many animal life forms (*e.g.* birds) through entanglement or ingestion (Laist 1987) and, occasionally, the debris may become harmful to human health (Philipp *et al.* 1997). The increasing usage of sandy beaches as recreational places has forced regional authorities of many tourist countries to remove all natural wrack and litter of fabricated origin (Ryan and Swanepoel 1996). Consequently, a variety of cleaning techniques (front-end loaders, suction devices ...) has been developed in tourist coastal regions all over the world (Taylor *et al.* 1994; Engelhard and Withers 1997). Especially cleaning with large tractor-pulled sieving machines has been seen as a cost-effective way of removing the "unwanted" strandline and has become an almost daily phenomenon on tourist sandy beaches (Gheskiere *et al.* 2005b). Along with the removal of

wrack and litter almost every macroscopic item is removed from the sand as the beach cleaner shovels up the upper sediment layer with a fast-turning mixer or brush, replaces the sand after sifting and finally compresses the sediment with a dragged weight (personal observation). There is however, a growing concern about the use of these machines and the damaging impact of these cleaning activities on the overall strandline-related species diversity and abundance (Belpaeme *et al.* 2004). On the invertebrate level this has already been documented extensively (*e.g.* Davidson *et al.* 1991; Kirby 1992; Llewellyn and Shackley; 1996, Weslawski *et al.* 2000; Dugan *et al.* 2003). However, these studies have focused on the larger macrofauna and habitat forming species, primarily because reductions in their abundance and species diversity are an important conservation issue. Studies dealing with the possible impacts on the meiofauna (all Metazoa <38 μm) of strandlines are lacking. Usually, free-living nematodes dominate the meiofauna of sandy beach sediments (Brown and McLachlan 1990). Nematodes are generally considered as an excellent taxon to use as ecological indicators for benthic habitats and for studying the impacts of different kinds of natural and anthropogenic disturbances in the marine environment (Heip *et al.* 1985; Schratzberger *et al.* 2000; Gheskiere *et al.* 2005b). 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.

This paper has three major aims:

(1) to describe the meiofaunal diversity of a freshly deposited strandline,

(2) to asses the possible influence of a mechanical beach cleaner on the meio-nematofaunal diversity, community structure and

(3) to asses the recovery of the assemblages after cleaning.

In the context of the present study, we define recovery of an impacted area as having occurred when the cleaned sediments have attained a state that is no longer significantly different to the composition of the control plots.

MATERIAL AND METHODS

Study site

This study was performed at the beach of De Panne (51°05'30"N, 02°34'01"E) at the western Belgian coast, nearby the Belgian-French border, in front of the 'Westhoek' nature reserve. This beach is an, relatively, undisturbed ultra-dissipative, macrotidal, fine-grained sandy beach with a natural strandline. More details about the granulometry and morphodynamics of this beach are described in Gheskiere et al. (2004). During the experiment air temperature varied between 17.6°C and 18.4°C (Oceanographic Meteorological Service Zeebrugge) while interstitial temperature varied between 19.6°C and 19.8°C. Salinity was constant (34 PSU) during the experiment. Gheskiere et al. (2002, 2004) give detailed information about the nematode and meiofaunal species composition of this beach.

Sampling strategy and techniques

The experiment was started on 26 August 2002 when high water was scheduled at 03.52am. To account for any environmental gradient along the strandline, the strandline was divided into five 'blocks' as recommended by Dutilleul (1993). Just after the start of the outgoing tide, the five blocks, each with two plots (Cleaned (C) and Un-cleaned control (U) each 10m x 4m) were delineated and marked with little floats in the freshly formed high water mark (Figure 1). Generally, the strandline was only sparsely loaded with flotsam. If there was any unanticipated spatial variability across the strandline, blocking of the cleaning experiment was expected to be an efficient way to estimate the effects of this variability against the cleaning effect (Underwood 1997). Meiofauna and percentage Total Organic matter (%TOM) were sampled randomly at control and cleaned plots in each block, once before and on several occasions after the experimental cleaning. The design used was, therefore, a "Before-After, Control-Impact" (BACI) design in which the evidence for an impact appears as significant Time (before versus after) by Treatment (cleaned versus control) interaction (Green 1979). Samples were taken using transparent perspex cores (10 cm²) to a depth of 5 cm. After the initial sampling, one plot in each block was cleaned with a 100 horse power, 2.5 m wide mechanical beach cleaner (Hurricane-Eco type°, see Photo 1) and repeated meiofauna sampling was completed in control and cleaned plots in each block. (Figure 2).

Along with the removal of algae and wrack, the beach cleaner scrapes up the upper sand layer (5 cm) with a fast-turning wheel equipped with little shovels (540 tr./min) and replaces the sand after sifting. The machine was fitted with a 30 mm mesh sieve allowing sand to pass and falling down on the beach again. Working speed was adjusted at 5 km/h. Settings of the beach cleaner were the default settings used for the daily cleaning on the Belgian tourist beaches. After experimental cleaning the machine's container contained parts of four different species of brown algae (*Fucus vesiculosus, Ascophylum nodosum, Sargassum*

muticum and *Himanthalia elongata*), parts of *Rhizostoma* sp., several carapaces of *Carcinus maenas*, a dead *Pleuronectes platessa* and considerable amounts of razor shells (*Ensis* sp.).
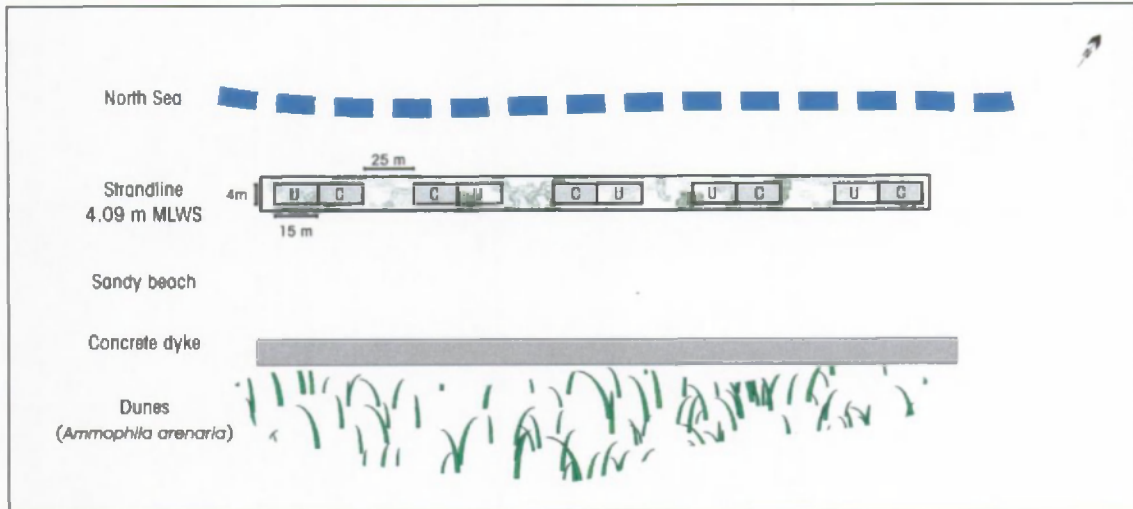
Figure 1: Experimental design on the beach of De Panne Westhoek (Belgium). (C=Cleaned plots, U=Un-cleaned control plots)
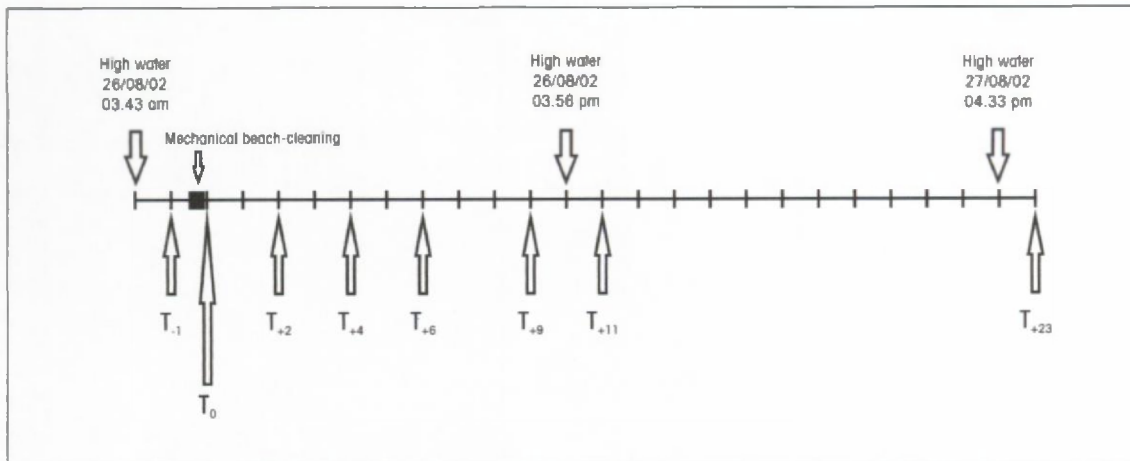
Figure 2: Time schedule of the experimental cleaning. Arrows indicate sampling occasions relative to tides and experimental beach cleaning. Numbers associated with the sampling occasion indicate the time (hours) relative to the experimental beach cleaning.

Photo 1: One of the most used types of mechanical beach-cleaners; the Hurricane-Eco type©.

Laboratory treatment

In the laboratory, meiofauna samples were rinsed with a gentle jet of freshwater over a 1 mm sieve to exclude macrofauna and washed onto a 38-µm sieve. The residue from the 38-µm sieve was separated into heavy and light fractions using repeated decantation (10 times). The light fraction (containing the meiofauna) was centrifuged three times with Ludox© HS40 (specific density is 1.18) and stained with Eosin (Heip *et al*. 1985). The extract was then placed into a beaker, made up to a standard volume with filtered tap water and homogenized into suspension before a constant proportion (30%) of the sample was taken with a semi-automatic pipette. Per sub-sample all meiofauna was counted and identified at the taxon level. All nematodes per sub-sample were picked out, transferred from formalin to glycerol through a series of ethanol-glycerol solutions and mounted on Cobb slides. Afterwards, nematodes were identified to the species level and classified, in order to use the taxonomic diversity index, according to the phylogenetic system of De Ley and Blaxter (2003). Sediment samples were oven-dried at 105°C for 12 h and ashed at 500 ± 50°C for 2 h to determine the %TOM by loss of mass. The sediment fractions were defined according to the Wentworth scale (Buchanan 1984); sediment-sorting coefficient and other granulometric characteristics were calculated as described by Dyer (1986).

Data processing

Meiofauna species abundance data (N) (Ind/10 cm²) were used to calculate the diversity as the expected number of species per sample based on 100 individuals ES(100) (Sanders 1968; Hurlbert 1971) and Pielou's evenness (J'), the last index using $\log_e$ in the formulation. Average taxonomic diversity (Δ) (Warwick and Clarke 1995) was calculated using only the nematode species data. Equal step-lengths between each taxonomic level were assumed for the calculation of the taxonomic indices, setting the path length ω to 100 for two species connected at the highest (taxonomically coarsest) possible level as stated by Clarke and Warwick (1999). Eight taxonomic levels were used (species, genus, family, superfamily, suborder, order, subclass and classis). Consequently, weights are ω=12.5 (species in the same genus), 25 (same family but different genus), 37.5 (same superfamily but different family), 50 (same suborder but different superfamily), 62.5 (same order but different suborder), 75 (same subclass but different order), 87.5 (same classis but different subclass) and 100 (different classes), respectively.

The power of the experimental design (the probability of obtaining a statistically significant response for an assumed size of experimental effect) was computed and evaluated using the observed estimates of the residual variances (Cohen 1977, Lipsey 1990) for each biological response (*i.e.* abundance, ES(100), evenness and average taxonomic diversity).

Differences in density, richness measures, most dominant species and %TOM were analysed using a repeated measure ANOVA design (Hall and Harding 1997) with model terms added: Time (hours before and after the cleaning), Treatment (control or cleaned plots) and Block (five blocks across the strandline). As the same plots were sampled throughout the experiment, there was a probability of non-independence among sampling times consequently leading to an increased or decreased probability of Type I error in assessing differences among times (Underwood 1997). Therefore, to test the effect of Time and Treatment on the biological responses, repeated measure ANOVA tests were conducted in which Treatment and Time were fixed factors and Block was considered a random factor (Green 1993). Bartlett's and Cochran's tests were used to verify for homogeneity of variances prior to the analysis. A multivariate analysis of variance (MANOVA) using the Pillai Trace test statistic (Chatfield and Collins 1980) was performed based on the abundances of the seven most abundant species (accounting for >50% of the total number of individuals) in order to test if the species composition changed as a function of Time, Treatment and Time x Treatment. The abundances were square root transformed to reduce heterogeneity of variance. All power and statistical analyses were performed utilizing the S-PLUS 6.1 software package (Insightful Corp. 2002).

The meiofaunal data were used to produce Detrended Canonical Analysis (DCA) ordination plots (Ter Braak 1988) and non-metric Multi-Dimensional Scaling (MDS) plots (Kruskal 1964). Two-way crossed analysis of similarities (ANOSIM, Clarke 1993) was carried out to test for a Block effect. Where none was found, two-way crossed ANOSIM was repeated with factors Time and Treatment and one-way ANOSIM was carried out to test the significance in meiofaunal assemblages on different sampling occasions. The similarity of percentages programme (SIMPER, Clarke 1993) was applied to determine the contribution of individual species and higher taxa towards the discrimination between samples. The Index of Multivariate Dispersion

(IMD, Warwick and Clarke 1993) has been applied here as a measure of community stress. The IMD is a measure of the increase in variability among replicate samples from cleaned versus control plots. The index contrasts the average rank of the dissimilarities among one set of samples (control) with the average rank among the other set (cleaned), re-ranking the full triangular matrix ignoring all between-group dissimilarities. The IMD is standardised to have a maximum value of +1 when all the dissimilarities among the control samples are higher than any dissimilarities among the cleaned samples and -1 when the reverse is true. All the above-described analyses involved constructing lower triangular similarity matrices from the square-root transformed abundance date using the Bray-Curtis similarity coefficient (Bray and Curtis 1957). Transformation was chosen in order to limit the contributions of the most dominant species, and therefore allow the rarer species to influence the analyses (Elliot 1971). Community analyses were performed using PRIMER version 5.2.9 (Clarke and Gorley 2001). A significance level of $p < 0.05$ was used in all tests.

In the context of the present study, we define recovery of an area as having occurred when the impacted community has attained a state that is no longer significantly different to the composition of the control plots.

RESULTS

Power analysis

Sandy sediment assemblages are known to be highly variable and detection of subtle changes in faunal communities is heavily dependent on the statistical power of the experimental design. Therefore, a power analysis was performed on the data for abundance, species diversity, taxonomic diversity and evenness. This gives the probability of obtaining a statistically significant result for a given effect size based on our sampling design and sample variance from data collected from the control plots immediately after the experimental cleaning, and is simply based on the assumption that sample variability does not change over time (Cohen 1988). Relative to the control plots, a biological response is assumed to decrease by p% immediately after the mechanical beach cleaning and to have recovered by the next or second next high water after the cleaning (Figure 3). This assumption is based on the sediment disturbance experiment of Sherman and Coull (1980) which recorded recovery within two tidal cycles after disturbance.

Generally, changes of <50% of the control mean are not considered ecologically meaningful in a dynamic and highly variable environment like shallow sandy sediments (Southwood 1978, Shaw *et al.* 1994, Schratzberger *et al.* 2002), so we adapted that standard.
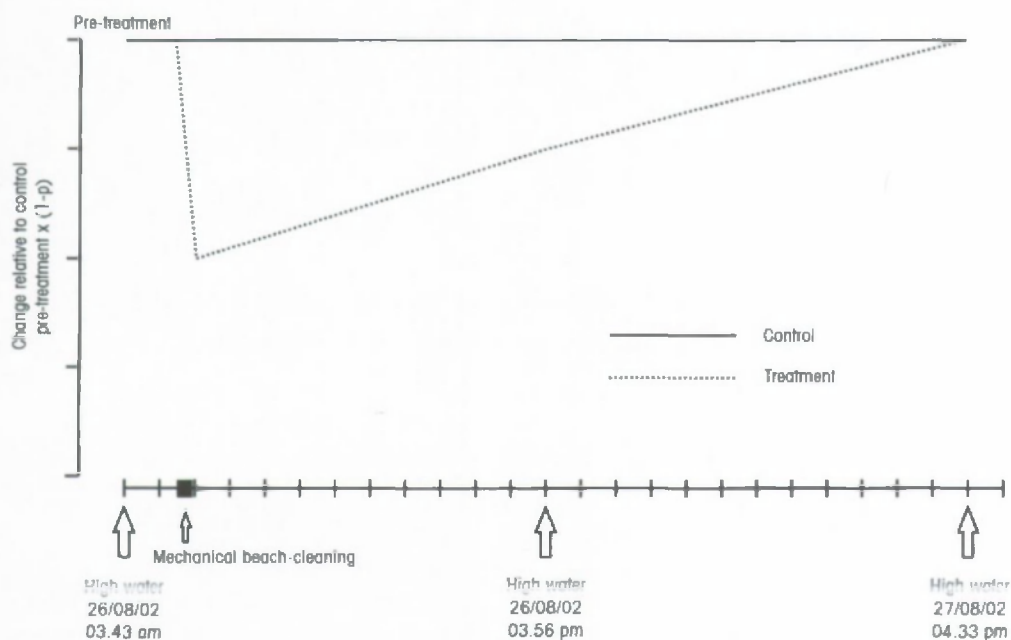
Figure 3: The probability of obtaining a statistically significant result given an assumed size of experimental treatment effect.

Figure 4 reports for each biological response the *a priori* power of the experimental setup corresponding to a hypothetical impact of p% on the sampling immediately after the strandline cleaning. The 5% significance level (corresponding to an impact of 0%) is shown for reference. Abundance (N), Evenness (J'), ES(100), abundance (N), average taxonomic diversity (Δ) are all seen to be extremely sensitive biological responses as the power to detect an ecologically significant change is >99%. The power to detect a 50% change in ES(100) is 74%.
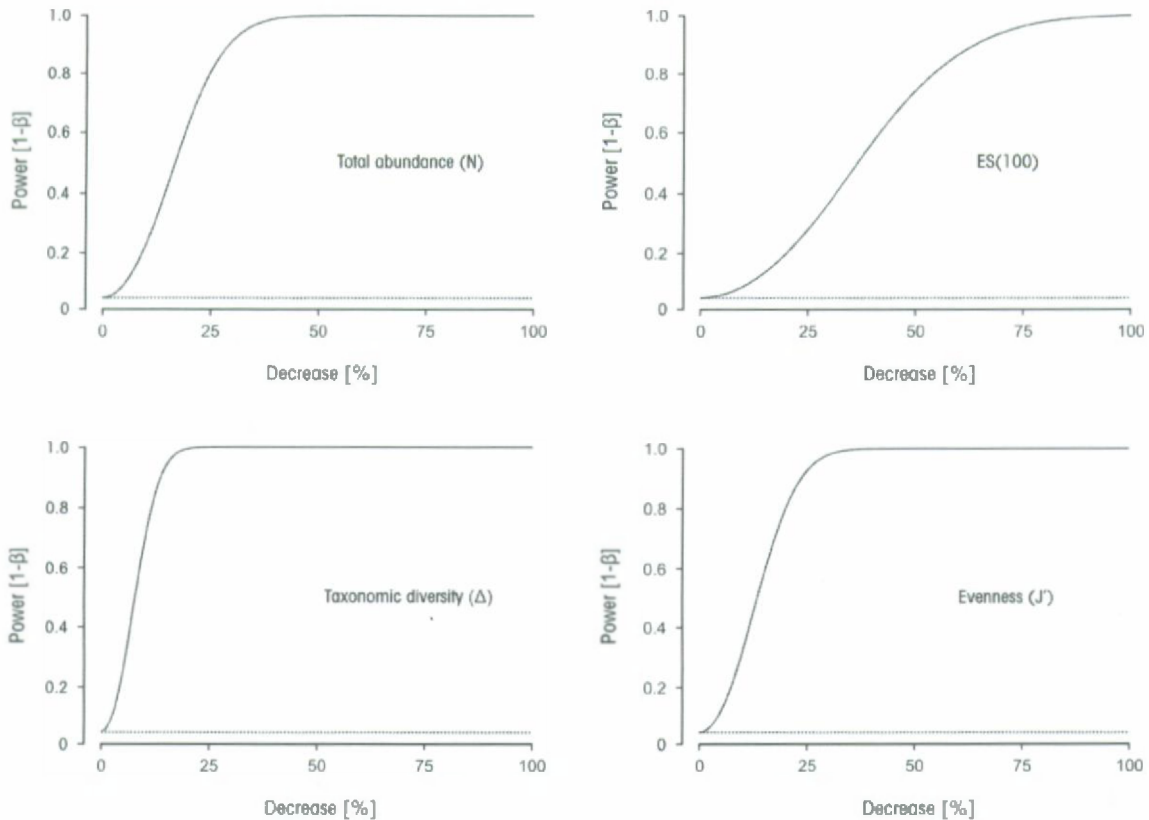
Figure 4: Power of the experimental design corresponding to a hypothetical impact of p% on the first sampling occasion immediately after the experimental cleaning for each biological response. The dotted line indicates the 5% significance level.

The abiotic environment

Generally, no significant granulometric differences (grain size, sorting, skewness, size class distribution) were noted between cleaned and control plots (data not shown). The sediments fell within the category of fine to medium sands, consisting on average of 7% shell fragments, 7% very coarse sand, 10% coarse sand, 33% medium sand, 56% fine sand and 1% very fine sand. Figure 5 reveals the changes of percentage Total Organic Matter (%TOM) at control and cleaned plots during the investigated period. Immediately following the experimental cleaning, the %TOM decreased to a level considerably lower at the

cleaned plots than at the control plots. After the next high water (T_{+11}) the %TOM raised again to more or less the same values compared to the control plots. Variation of %TOM at the control plots was negligible throughout the experiment. No block effects were recorded. Repeated measures analysis of variance indicated a significant effect of Time (p<0.02), Treatment (p<0.01) and Time x Treatment (p<0.001).
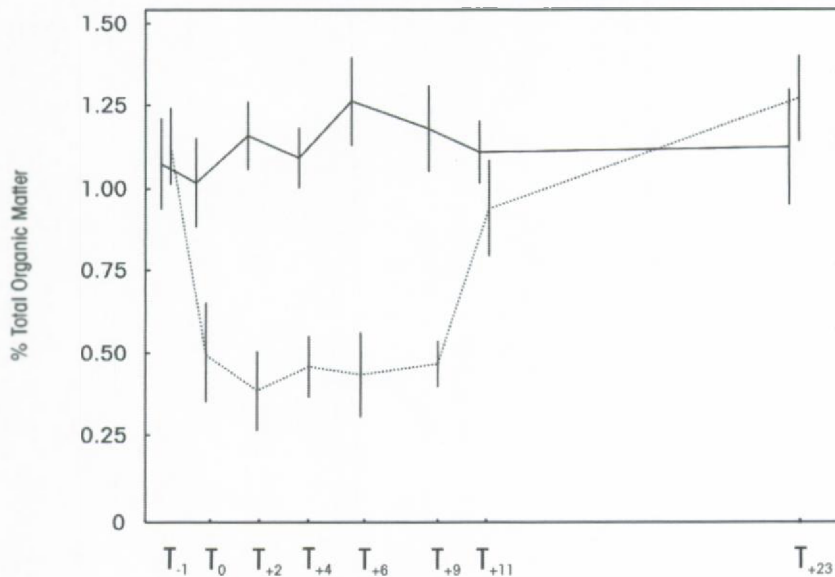
Figure 5: Means of % Total Organic Matter (%TOM) plotted against hours after the experimental cleaning. Solid line: control plots, dotted line: cleaned plots. Vertical lines correspond to 95% confidence limits. (n=5)

Abundance and richness measurements

In total 13 higher meiofauna taxa were recorded in the freshly deposited strandline dominated by nematodes (69% including 55 species), Harpacticoida + nauplii (14%), Oligochaeta (10%) and Turbellaria (4%). Other groups (3%) were present in low numbers or were found only sporadic; these included Polychaeta, Tardigrada, Diptera, Hydrozoa, Ostracoda, Cladocera, Gastrotricha, Aranea and Rotifera. The effect of the cleaning was manifested as a decrease in the total abundances in comparison to the control plots. Immediately after the experimental cleaning (T_0) the total abundance of the cleaned plots, 338 ± 41 Ind/10 cm², is seen to decrease significantly to 191 ± 65 Ind/10 cm² from where it more or less stabilised until it raises again to 261 ± 48 Ind/10 cm². After the second high water, recovery is almost complete and initial values are reached again. Remarkably is the drop in taxonomic diversity between two high waters. (Figure 6) Repeat measure ANOVA showed that there were significant effects of both Treatment (F=9.47, p<0.01) and Time (F=2.17, p<0.02) with respect to the total abundance (N). For average taxonomic diversity (Δ), any impacts of cleaning were minor in relation to temporal changes in the nematode assemblages during the progress of the experiment (F=4.08, p<0.02).

No changes, neither due to the cleaning nor temporal, were noted for Evenness (J') and ES(100). A statistically significant interaction Time x Treatment at the level of 5% was only noted for total abundance (F=1.45, p<0.01). (Table 1)
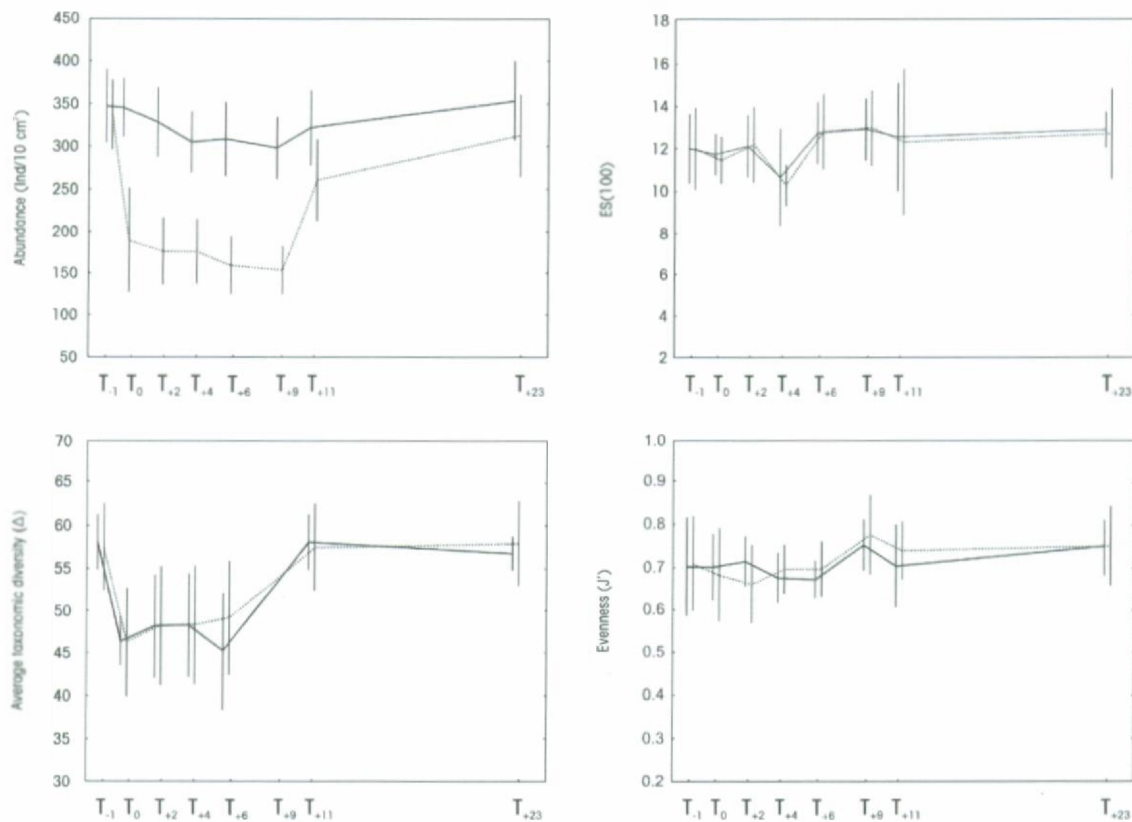
Figure 6: Means of the total abundance, ES(100), average taxonomic diversity (Δ) and evenness (J') plotted against hours after the experimental cleaning. Solid line: control plots, dotted line: cleaned plots. Vertical lines correspond to 95% confidence limits.

	df	F	p		df	F	p
Abundance (N)				**Evenness (J')**			
BLOCK	4	3.71	0.20	BLOCK	4	1.48	0.23
TREATMENT	1	9.47	<0.01	TREATMENT	1	3.10	0.09
TIME	7	2.17	<0.02	TIME	7	2.94	0.07
TIME x TREATMENT	7	1.45	<0.01	TIME x TREATMENT	7	1.21	0.32
Richness ES(100)				**Taxonomic diversity (Δ)**			
BLOCK	4	1.26	0.30	BLOCK	4	1.62	0.2
TREATMENT	1	0.28	0.60	TREATMENT	1	2.55	0.11
TIME	7	8.96	0.09	TIME	7	4.08	<0.02
TIME x TREATMENT	7	0.47	0.80	TIME x TREATMENT	7	0.97	0.45

Table 1: Results from the repeated measures analysis of variance of univariate indices.

Meiofaunal assemblages

Results from the two-way crossed ANOSIM showed no statistically significant block effect on the meiofaunal assemblages collected up to 23 hours after the beach-cleaning (R=0.194, p=0.09). The experimental treatment effect (averaged across all sampling dates; R=0.403, p<0.01) and the time of sampling collection (averaged across treatment groups; R=0.538, p<0.03) were statistically significant.

The one-way ANOSIM (Table 2) shows that differences in meiofaunal community structure collected at the cleaned plots were more pronounced than at the control plots. Pairwise comparisons derived from the ANOSIM test for each sampling occasion showed that highest dissimilarity between control and cleaned plots occurred within the first 9 hours after the experimental cleaning (Table 3). Dissimilarities were most distinct 4 hours after cleaning (48%). A higher value of R is indicative of larger relative differences between the fauna; thus, the decrease in the value of the R-statistic from T_4 onwards gives some indication of the recovery trajectory of the cleaned plots. The meiofaunal assemblages from the cleaned plots remained significantly different from the control plots until T_{11}, at which point they had recovered (R=0.115, p=0.231). At each sampling occasion (excepted T_{23}), the inter-variability is higher among cleaned assemblages, giving a negative value for the Index of Multivariate Dispersion, and thus indicating higher community stress. Highest negative IMD-values were noted within the first 2 to 4 hours after experimental cleaning. At T_{-1}, T_{11} and T_{23} IMD-values were close to zero implying negligible differences between control and cleaned samples.

	T_{-1}	T_0	T_2	T_4	T_6	T_9	T_{11}			T_{-1}	T_0	T_2	T_4	T_6	T_9	T_{11}
T_0	35*	-							T_0	29	-					
T_2	37*	22	-						T_2	30	18	-				
T_4	40*	30*	27	-					T_4	24	31*	27	-			
T_6	48*	37*	33	31	-				T_6	26	33	37	25	-		
T_9	34*	34	36	35	25	-			T_9	30*	25	22	26	25	-	
T_{11}	32	35*	33	23	34*	25	-		T_{11}	18	30	33	28	36*	29	-
T_{23}	35	34*	33*	31*	39*	32*	27		T_{23}	16	27	29	29	33	22	29

Table 2: Dissimilarities [%] on different sampling occasions based on square-root transformed species abundance data. *Significant differences at p<0.05 based on ANOSIM test. Cleaned plots (left), Control plots (right).

	Dissimilarity [%]	R	p	IMD
T_{-1}	21	0.042	0.451	-0.090
T_0	33*	0.531	0.029	-0.556
T_2	36*	0.771	0.029	-0.742
T_4	46*	0.801	0.001	-0.740
T_6	48*	0.586	0.037	-0.566
T_8	40*	0.548	0.010	-0.350
T_{11}	26	0.115	0.231	-0.118
T_{23}	20	0.240	0.810	+0.111

Table 3: Dissimilarities [%] and Index of Multivariate Dispersion (IMD) between cleaned and control plots on different sampling occasions based on square-root transformed species abundance data. *Significant differences at $p<0.05$ based on ANOSIM test.

According to the SIMPER-analyses (not shown) significant differences in assemblages within the hours after experimental cleaning mainly occurred as a result of reduced numbers of individuals from the dominant nematode species (*Theristus otoplanobius, Trissonchulus benepapilosus, Chromadorina germanica*) and Harpacticoid Copepod sp. in the cleaned plots.

Analyses of changes in abundance over time for the seven most abundant species (accounting for >50% of the total number of individuals) are reported in table 4. Univariate analyses on the individual species elucidate that, with exception for Oligochaeta sp., the abundances were not significantly influenced by Time. Four out of seven species; *Theristus otoplanobius, Harpacticoida* sp., *Chromadorina germanica* and *Trissonchulus benepapilosus* were significantly influenced by the experimental cleaning (Treatment) and showed a significant Time x Treatment interaction. Multivariate analysis of variance (MANOVA) revealed that meiofauna species composition was not significantly affected by Time; however exhibit a significant effect of the experimental cleaning as well as a significant Time x Treatment interaction effect. The combination of both uni- and multivariate analyses demonstrated that there is evidence that; although there are no statistically significant changes in diversity measurements, there were changes in individual species abundances because of the experimental cleaning, *i.e.* the composition structure of the meiofaunal assemblage varies significantly in time because of the experimental cleaning. (Table 4)

The non-metric multi-dimensional scaling ordination plot clearly indicated a split between control and cleaned plots from immediately after the cleaning onwards and thus closely mirrored the results from the ANOSIM. Samples collected 11 hours and 23 hours after experimental cleaning clustered more or less together, suggesting a more similar (recovered) fauna. (Figure 7)

Univariate test	Time df	F	p	Treatment df	F	p	Time x Treatment df	F	p
Theristus otoplanobius	7	1.220	0.319	1	10.896	0.002	7	0.813	0.048
Harpacticoida sp.	7	6.673	0.613	1	3.728	<0.001	7	0.748	0.036
Onyx saggittarius	7	1.670	0.167	1	0.280	0.600	7	1.258	0.302
Oligochaeta sp.	7	14.251	<0.001	1	0.166	0.686	7	0.860	0.517
Chromadorina germanica	7	10.800	0.362	1	0.851	<0.001	7	0.597	0.002
Hypodontolaimus schuurmansstekhoveni	7	1.516	0.209	1	0.002	0.963	7	2.175	0.079
Trissonchulus benepapilosus	7	12.855	0.346	1	0.911	<0.001	7	1.034	0.013
Multivariate test	7	3.106	0.209	1	2.601	<0.001	7	1.214	<0.001

Table 4: Univariate and Multivariate ANOVA test based on square-root transformed abundance data for the 7 most abundant species.
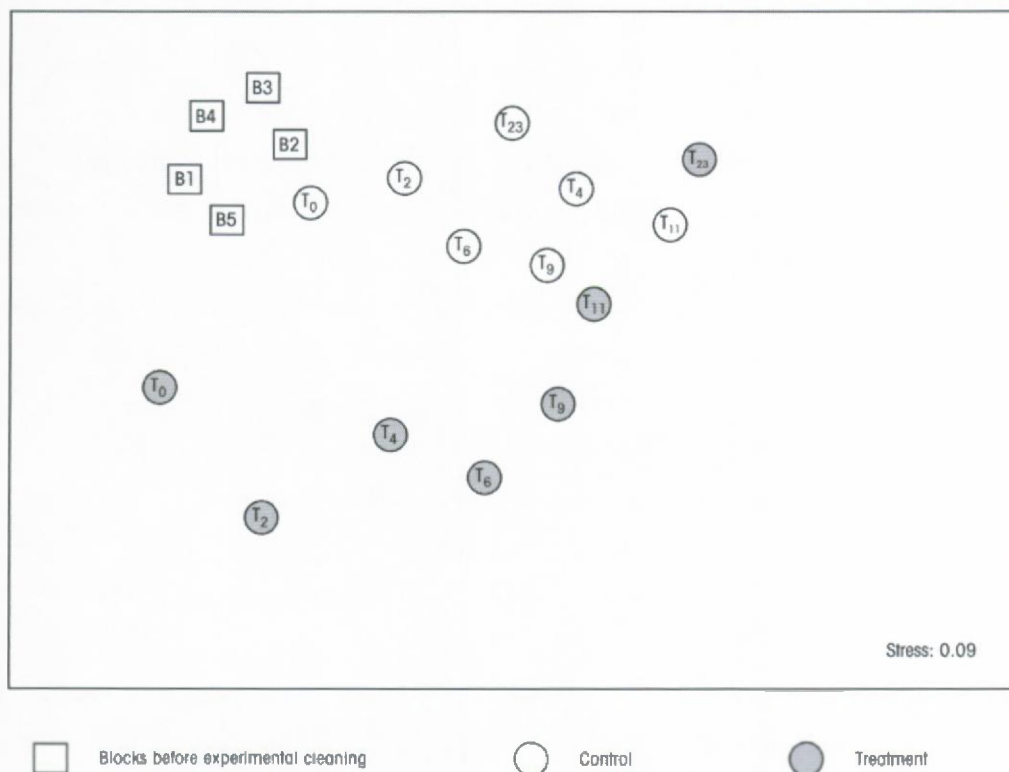

Figure 7: Non-parametric multidimensional scaling (MDS) ordination for meiofaunal assemblages collected from control and cleaned samples at several sampling occasions before and after experimental cleaning. (based on square-root transformed species abundance data) (n=5)

DISCUSSION

The strandline meiofaunal assemblages

Results from this study indicate that strandline-related meiofaunal assemblages are species rich, even with only the nematodes identified at species level. Recorded abundances at the un-cleaned control plots (on average 509 ± 60 Ind/10 cm^2) were seen to be equal over time, which is in contrast with literature where rapid increase after a new deposit of wrack is often reported. (*e.g.* McGwynne *et al.* 1988 report an average abundance of 1712 Ind/10 cm^2 on a sparse-wrack sandy beach in South Africa). Alkemade and Van Rijswijk (1993) stated that the number of nematodes associated with wrack is depending on the height on the beach and the Carbon/Nitrogen ratio. They recorded significant higher abundances as the nitrogen content increased relative to the carbon content and for material higher on the beach (the higher a wrack deposit is located on the beach, the longer it is presumably present on the beach). As the strandline and the stranded material studied in this paper were freshly deposited, we can assume C/N values are high and this may explain the general low nematode and meiofaunal abundances in comparison with other strandline studies. High C/N values may also explain the low densities of dipteral larvae in our samples compared other studies (Colombini *et al.* 2000).

At first sight the presence of oligochaetes as third-largest group seems unexpected as meiofaunal studies usually record oligochaetes only in very small numbers (Higgins and Thiel 1988). However, when searching the literature (Giere and Plannkuche 1982; Koop and Griffiths 1982, McLachlan 1985, McGwynne *et al.* 1988, Jedrzejczak 2002a, b) oligochaetes are generally found to be a high-abundance taxon in assemblages associated with decomposing wrack accumulations or in the sand beneath wrack. Giere (1975) and Koop and Griffiths (1982) indicate that the presence of high numbers of both nematodes and oligochaetes are directly related to the distribution of wrack, below which concentrations of Dissolved Organic Matter (DOM) can be high, and suggested that meiofauna use this as a direct food source. However, following McLachlan (1985), the possibility that the DOM is initially used by bacteria, which in turn are used a food source by the meiofauna cannot be precluded. Moens and Vincx (1996) assumed that meiofauna is not able compete for DOM with bacteria in view of their much longer turnover times. Jedrzejczak (2002a) suggested that oligochaetes feed on the metabolites of the other meiofaunal groups rather than directly on bacteria or DOM.

During this study, 55 different species of free-living nematodes were recorded in the strandline. 34 Species were only recorded sporadically or in very low abundances (0.1% of total recordings). *Theristus otoplanobius* (35%) was found to be the dominant nematode species and this is in concordance with earlier studies on this beach (Gheskiere *et al.* 2002). Little is known about the structure of the strandline nematode assemblages from other places with exception of the Antarctic strandline study of Alkemade and Van Rijswijk (1993) where eight nematode species were recorded. Only *Pelliodifis marina* and *Monhystera disjuncta* were found to be in common with this study. *P. marina* has a cosmopolitan distribution and is

typically associated with stranded decomposing wrack (Inglis and Coles 1961, Inglis 1966). Two other genera that are frequently reported in literature as 'associated with decomposing matter and/or high shore', namely *Diplolaimella* and *Diplolaimelloides* (Bouwman *et al.* 1984; Warwick 1976) were not recorded. The fact that strandline studied here was fresh and decomposition was thus in a very initial phase could possibly explain the low abundances of *P. marina* and the absence of the two above-mentioned genera. Nevertheless, it is remarkably that 55 different nematode species can coexist in such a narrow stripe on the beach. One explanation may be that the general high bacterial and protist diversity associated with the strandline deposited wrack (Olanczuk-Neyman and Jankowska 1998, Armstrong *et al.* 2000), combined with the high habitat heterogeneity and good water percolation, result in attractive and diverse bacterial '*aufwuchs*'. Seeing that nematodes are highly able to partition their environment extensively in various ways (*e.g.* food partitioning (Platt and Warwick 1980)), these bacterial '*aufwuchs*' can support species rich nematode assemblages.

Impact of cleaning

BACI designs have been widely used in environmental impact studies on the mean abundances of populations as well as on the community structure (*e.g.* Drabsch *et al.* 2001; Schratzberger *et al.* 2002). The principle of a BACI design is that a disturbance at the impacted plots will cause a different pattern of change from compared with natural change at the control plots (Underwood 1997). With the sampling intensity of this experiment, the power to detect specified changes in density, richness, evenness and taxonomic structure is generally high and therefore all are effective in detecting changes due to experimental cleaning. In other words, the risk of conducting a type II error (assuming no impact exists when in fact it does) is low. Beach cleaning (or beach grooming) is only a recent phenomenon in the coastal environment and so are the studies about the impacts. To date all studies have been concentrated on changes in abundance at macrofauna level (*e.g.* Davidson *et al.* 1991; Kirby 1992; Llewellyn and Shackley; 1996, Lavery *et al.* 1999; Dugan *et al.* 2003), whereas meiofauna have been largely neglected. After an extensive survey of 15 Californian strandlines Dugan *et al.* (2003) concluded that significant differences in community structure, including depressed species richness, abundance, and biomass of macrofauna were associated with beach grooming. This was most obvious for the typical wrack-associated herbivore taxa (talitrid amphipods, kelp flies and coleopterans) which are important prey for vertebrate predators, such as several species of shorebirds and insectivorous passerines. Malm *et al.* (2004) noted that the organic content of the sand (%TOM) was significantly reduced by beach cleaning, which is in accordance with our results. They suggested that the largest impact of beach cleaning seems to occur at the microbiological level, with a substantial reduction of the bacterial production and significantly less large ciliates at the cleaned beach, compared with the un-cleaned beach. Our cleaning experiment at the strandline of De Panne showed that there were no impacts of the beach cleaning on univariate measurements such as diversity, evenness and the taxonomic diversity. The only measurable impacts that could be attributed to the cleaning

were an immediate decrease in faunal density and change of assemblage structure. As the decrease in meiofaunal density relative to the control was 43%, this impact cannot be considered as ecologically significant. The multivariate species-dependent MDS ordination was seen to be more sensitive in discriminating the assemblages collected at both treatment and control plots, suggesting that the dominance relationships among species had changed at the treatment plots compared to the controls. The results of this study contrasted with the above-mentioned studies, which generally recorded, in addition to an immediate decreased number of individuals, a depressed biodiversity and even a complete disappearance of some species at cleaned sites compared to non-cleaned ones. These macrofauna studies, however, included many more taxa and a much wide range of size classes compared to the present study.

Since meiofauna are among the smallest animals in benthic ecosystems and have very fast turnover times, they may be expected to show little responses to beach cleaning, as they are less susceptible to the brooms or mixers on the cleaners and can easily pass through the sieves (30 mm). Indeed, intuitively one may suspect that the susceptibility of species to beach cleaning/grooming is largely determined by their body size and turnover, with large slowly reproducing species being more susceptible than smaller, faster reproducing ones. In this respect, it is not unexpected that some of the larger nematode species like *Trissonchulus benepapilosus* (body length: 2.5-3.2 mm, Van der Heiden 1976) are significantly affected by the cleaning as they are probably crushed by the mixer. The fact that harpacticoid copepods are affected by the cleaning is also not unusual, as the crustacean meiofauna regularly seems to be the most affected in perturbation studies, mainly because of their fragile body parts (Coull 1988).

Resilience of ecosystems (*i.e.* the rate, manner and pace of restoration of initial structure and function in an ecosystem after disturbance), *sensu* Westman (1978) has become a subject of growing importance in stress ecology studies. Due to ever-increasing technology and greater risks of catastrophic human-induced disturbances, studies discovering the recovery rates of a variety of ecosystems are being actively explored (*e.g.* recovery after deposit of dredged material by Schratzberger *et al.* 2004a). Samples collected immediately after the high water following the cleaning (T_{11}) revealed that meiofaunal abundances were again at initial values. Such fast recolonization rates of meiofauna have been recorded frequently in literature. After a mechanically induced disturbance, Sherman and Coull (1980) observed that meiofaunal densities reached the same levels as those at the control sites after just 12 hours. Sun and Fleeger (1994) reported during an investigation of meiofaunal colonization into mimic sediment depressions that abundances of the dominant copepods showed no significant differences between experimental and control sediments after 24-48 h. Le Guellec (1988), working with exogenous sand, reported similar densities at experimental and control plots after two tidal cycles. All these studies suggest somewhat a restoring effect of the tides as it is indeed very unlikely that meiofaunal organisms can crawl distances in only hours (Schratzberger *et al.* 2004b). The tidal rise and fall across the intertidal region of a sandy beach produces an alternately land-directed and then seaward-directed hydraulic gradient at the frequency of the local tides. Following Darcy's law (describing the flow through a porous medium such as sand), this necessitates the flow of water into and out the beach (Manning 1997). Due to the ability of sea water on the upcoming tide to infiltrate vertically into a beach much more rapidly than it can drain nearer horizontally on the falling tide (Neilsen 1990), there is a tendency for elevation of the beach water table above the mean sea level. Water

input therefore only occurs when the elevation of the tide exceeds the elevation of the beach water table, thus water input occurs on the rising tide and water discharge mainly on the ongoing tide. As the beach of De Panne is an ultra-dissipative flat sandy beach, the ground water table is close to the sediment surface (Lebbe 1981, Gheskiere *et al.* 2004). Together with the elevation of the water table as the tide raises, probably also the interstitial meiofauna from deeper layers is elevated to the upper layers (*i.e.* passive vertical migration). This hypothesis is supported by the study of Van de Velde (2002) who noted during a survey of the vertical meiofaunal distribution of the same strandline that there are no significant differences in meiofaunal assemblage between the upper 0-5 cm layer and the 5-10 cm layer. Since the water table from the studied beach is known to harbour several terrestrial and brackish water nematodes (*e.g. Pellioditis marina, Aporcellaimus* sp.) (Gheskiere *et al.* 2004), this may explain the peak in taxonomic diversity in the samples immediately after the high tides (T_{-1}, T_{11}, T_{23}). At first thought, recolonization via water column migration seems also a possibility. Hagerman and Rieger (1981) and Savidge and Taghon (1988) gave evidence for this as they found that considerable portions of interstitial meiofauna were suspended in the water column by shoaling and breaking waves. Ullberg and Olafsson (2003a) suggest that settling of suspend marine, free-living, benthic nematodes is not entirely a random or passive process since several, particularly very small, species, belonging to different genera and families, were clearly able to choose settling points through active swimming. However, for this cleaning experiment it seems very unlikely that the recolonization occurred via water column modes, mainly because of two reasons. (1) Erosion of meiofauna from sediments by shoaling and/or breaking waves is in the first place controlled by the friction velocity or shear stress (Palmer and Gust 1985, Ullberg and Olafsson 2003b). Seeing the morphodynamics of the studied beach and the location of the experiment on the beach (the strandline), the erosive force imparted by the flowing water on the bottom sediments is assumed to be extremely low (Short 1999) as on this type of beach wave energy is dissipated at a considerable distance from the shore (on the subtidal sandbanks). (2) The meiofaunal community of a strandline is a very narrow and sharply defined community, characterised with species which are absent on very ambient parts of the beach (Gheskiere *et al.* 2004). Thus, if passive erosion of meiofauna from elsewhere (lower) on the beach should have occurred, a different meiofauna should be found in the cleaned plots after the tides. This was certainly not the case as the experimental plots were recolonized by exactly the same strandline-specific meiofauna.

However, an active upward migration of nematodes from deeper sediment layers during submersion cannot be fully excluded. Steyaert *et al.* (2001) observed such species-specific active vertical movements of Enoplid nematodes in their search for food on a hydrodynamically benign tidal sand flat in the Westerschelde.

CONCLUSIONS

Concluding, we have demonstrated that total density, species-specific densities and assemblage structure are all significantly, although not ecologically significant, influenced by mechanical beach cleaning while number of species and taxonomic richness suffer no direct impacts. We assumed that recolonization occurred via passive vertical migration, forced by the upcoming tide, from the underlying sediment layers. These findings are based on a once-only, limited, small-scale cleaning experiment. Therefore, it would be unwise to generalize that strandline meiofauna recover quickly from mechanical beach cleaning. Deeper, more catastrophic or repeated cleanings may certainly result in much slower recolonization rates.

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CHAPTER VI

General discussion and conclusions

INTRODUCTION

Two aspects of this doctoral thesis key issue will be discussed separately: (1) a discussion of the meio-nematofaunal biodiversity and zonation patterns on sandy beaches at different climatic and tidal conditions and (2) a synthesis of the human-related (or induced) disturbances to the sandy beach ecosystem.

MEIO-NEMATOFAUNAL BIODIVERSITY AND ZONATION PATTERNS ON SANDY BEACHES

Sandy shores generally consist of three components: nearshore zones, beaches and dunes which are linked by the interchange of material, particularly sand. Together they comprise a single geomorphic system, termed the littoral active zone (Tinley 1985). This is the part of the coast characterised by wave- and wind-driven sand transport and it lies between the outer seaward limit of wave effects on bottom stability and the landward limit of aeolian sand transport (*i.e.* the landward edge of the active dunes). Although the littoral active zone constitutes a single geomorphic system, ecologically it consists of two distinct ecosystems, a marine nearshore/intertidal/foreshore zone ecosystem and a terrestrial backshore/dune ecosystem which are interdependent and interacting (Brown and McLachlan 1990). The interstitial environment of these systems is directly determined by the sediment properties. Grain size, shape and sorting are cardinal factors in fixing porosity and permeability which influence water filtration or drainage. Permeability commonly increases with coarser sand and better sorting and also on steeper beaches (Short 1999). Filtration of water is the most important process involving the interstitial system and its inhabitants (McLachlan and Turner 1994). This water is introduced into sediment either by the tides, the pumping effects of waves or groundwater that seeps from the land into the sea through confined or unconfined aquifers and may often contain very high nutrient levels, thereby adding significantly to the nutrient pool of the beach. Water filtration is also critical in determining the moisture content, oxygen content and organic input and the depth of reduced layers.

Several studies in beach environments have shown that the variation in macrofaunal density and diversity is partly related to composite abiotic characteristics such as morphodynamic state and wave exposure (*e.g.* McLachlan and Jaramillo 1995). Studies on the influence of these composite factors on meiofauna are scarce. In relation to wave exposure, pioneer studies of McIntyre (1971) and McLachlan *et al.* (1981) suggested that meiofauna in sandy beaches is not as negatively affected by the increases in wave exposure as with the macroinfauna. In relation to morphodynamics, McLachlan and Turner (1994) predicted that optimum conditions for the development of diverse and abundant meiofauna are likely to occur on intermediate beaches. Their prediction is based on the fact that the intermediate morphodynamics represent an equilibrium state between organic inputs which increases towards the dissipative beach state and aerobic

interstitial conditions which increases towards the reflective beach state. The study in **Chapter III** agreed with McLachlan and Turner's prediction. All studied zones across the coarse-grained Italian beach yield higher meiofaunal densities (average beach density: 870 ± 59 Ind/10 cm²) and species richness (average ES(100): 18 ± 2) than the finer grained Polish beach (beach density: 215 ± 34 Ind/10 cm², average ES(100): 10 ± 4), except for the species diversity in the upper beach zone. The upper beach zone on the Polish beach nevertheless showed a higher number of species as a result of the occurrence of several free-living terrestrial nematodes. Given the much lower salinity on the Polish beach (in contrast to the Italian beach) this was not unexpected. Higher densities and diversities towards the reflective beaches are in contrast with the worldwide trend within the macrofauna which tend to have highest diversities on fine-grained (dissipative) beaches (McLachlan and Jaramillo 1995). The opposite trends observed for macro- and meiofauna are related to the fact that the greater the grain size and the higher the exposure rate, the higher flushed and oxygenated the interstitial space will be (Short 1999). The concentration of interstitial oxygen is one of the most relevant physical factors affecting the presence of meiofauna (Giere 1993; Moodley *et al.* 1997). Therefore, while the meiofauna inhabiting tide-dominated and/or fine grain size beaches are confined to the oxygenated upper few centimetres, the meiofauna of wave-dominated and/or coarse grain size beaches can reach deeper into the sediment (Olafsson 1991), avoiding the surface effect of currents and wave action. On the contrary, macrofauna is generally not limited by oxygen concentration due to bioturbation of the sediment and the life habits of the species, mostly occupying the first centimetres or sediment surface. The fact that most macrofaunal species show a direct dependence of feeding activity on the sediment surface makes them commonly negatively affected by the increasing environmental severity along the morphodynamic continuum from dissipative to reflective conditions. Short (1999) showed that grain size becomes coarser, erosion-accretion dynamics more intense, and swash frequency and velocity increase as morphodynamic conditions change from dissipative to reflective extremes. Brazeiro (2001) proposed, based on a intensive survey of sandy beaches in Chile, that these environmental factors, although physically interrelated, may have independent influences on the macrobenthic species as coarser sediment reduces the burrowing capacity, more intense erosion-accretion dynamics induces a higher risk of being removed and higher swash frequency can reduce the feeding time. This also supports the concept of McIntyre (1969, 1971) and McLachlan (1977 b) of two quite distinct metazoan faunas on sandy beaches controlled by different factors additionally to the differences in size and different micro-habitats occupied by meio-and macrofauna. The distinction between these two faunal components is coupled with differences in metabolic rates, generation times and turnover. However, despite of the distinction between meio- and macrofauna, there are also links and biological interactions between them (Aarnio 2001). Nevertheless, this study only comprises two beaches, one intermediate-reflective and one intermediate-dissipative. Comparison of the Mediterranean and Baltic beach with the ultra-dissipative North Sea beach of De Panne (average beach density: 1775 ± 809 Ind/10 cm², average ES(100): 18 ± 6) seems difficult as this beach is subjected to a macrotidal regime which has a significant controlling impact on the faunal density and diversity. A different sampling strategy (more sampling points) was also followed. More similar studies, covering a complete spectrum from fully reflective to fully dissipative states within the same tidal regime, are certainly needed to further validate these trends.

Across a beach several horizontal environmental gradients exist (*e.g.* salinity, exposure, temperature, organic matter, …) with increasingly or decreasingly harsh environmental conditions for certain animals. In combination with the chemical (vertical) gradients in the sediment these horizontal and vertical gradients generate a complex three dimensional spatial matrix of living conditions (Fenchel *et al.* 1967). The faunal response to this complex matrix of living gradients is zonation, both vertical and horizontal. Vertical meiofaunal distribution patterns are believed to be mainly related to the degree of drainage and oxygenation of the sediment (McLachlan 1977a, b), but this falls out of the scope of this thesis. Meiofauna abundance commonly decreases drastically in the RPD and reduced layers and consequently a deep vertical distribution only occurs on coarse beaches where reduced layers are absent. Different species and higher taxa show well-defined vertical distribution patterns related to differing tolerances to reducing conditions (Giere 1993). Horizontal faunal zonation patterns are a distinctive and well described feature of intertidal zones, intensively studied by macrobenthic ecologists worldwide (reviewed by McLachlan and Jaramillo 1995) while studies on the meiofaunal zonation patterns are scarce. As a consequence of the dynamic environment of the beach, and their general invisibility in the sand, horizontal zonation on sandy beaches is not nearly as visible as on rocky shores. In the first review of sandy beach ecology, Hedgpeth (1957) suggested that zonation on sandy beaches was almost as pronounced as on rocky shores. He mentioned a scheme of Mortensen (1921) dividing the shore into two zones, the foreshore or beach with supra littoral species exposed mainly to air, and the intertidal with its inhabitants living primarily in water. The first general zonation scheme for invertebrates on sandy shores was proposed by Dahl (1952). He noted an increase in diversity downwards the beach and proposed three zones, based entirely on biological parameters defining these zones in terms of their dominant crustaceans as: subterrestrial fringe, a midlittoral zone and a sublittoral fringe. Another general horizontal tidal zonation scheme for sandy shores was proposed by Salvat (1964, 1967). This scheme is entirely based on physical parameters; it was subsequently adapted by Pollock and Hummon (1971) and McLachlan (1980). In this scheme four zones are defined:

a zone of drying or dry sand above the normal high tide mark and wetted only by spray (high oxygen content, highly variable temperature),

a zone of retention below this, reached by all tides but losing "gravitational" (capillary) water as the tide recedes, so that the sediment remains damp, but not wet, during the low tide period (high oxygen content, variable temperature)

a zone of resurgence, which experiences discharge of water during the ebb tide and is characterized by interstitial water flow in and out of the sediment with the tide (moderate to low oxygen content, stable temperature),

a zone of saturation where the sand is permanently saturated with water and limited interstitial water flow occurs (low to very low oxygen content, very stable temperature)

In Chapter II and III meiofaunal assemblages (with emphasis on the free-living nematodes) across beaches were studied. Apart from the extensive study on an open sea dissipative beach in Sylt by Blome (1974, 1982, 1983) zonation studies based on meiofaunal 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 maybe important biological factors. At the macrotidal ultra-dissipative beach in De Panne, four nematode species associations reflecting the tidal zonation were discerned by multivariate analysis showing some affinities with the general zonation scheme of Salvat (1967) and the studies on Sylt. A very distinct meiofaunal community was found in association with the strandline (Chapter II, V). The microtidal beaches in the Baltic and the Mediterranean region were both found to harbour three meiofaunal species assemblages. These assemblages are associated with the upper beach, swash/breaker and subtidal zones. The upper parts of the studied beaches possess a set of characters defined by the interactions between the physical contrasts of the adjacent ecological systems (sea/land) and consequently a unique microhabitat is created. Therefore these upper beaches can be seen as the transition zone (an ecotone) where nematode species from both pure terrestrial and pure marine ecosystem co-exist. On the beach of De Panne this ecotone is disturbed by the presence of a concrete dyke which results in the complete absence of terrestrial species on the upper beach. Thorson (1957) for macrofauna and Por (1964) for meiofauna both stated that 'parallel level-bottom communities' or 'isocommunities' are typical for benthic environments and are defined as ecological parallel assemblages: 'the same types of bottoms are everywhere inhabited by species of parallel animal communities in which different species, of the same genera, replace one another as the characterising species". Several twin-species (*i.e.* pairs of species that show slight morphological differences but have widely separated areas of distribution and are ecological counterparts) were detected between both microtidal upper beaches suggesting that the isocommunities concept is fully supported for this zone. Also the nematofaunal composition on upper beach zone of De Panne suggests the existence of isocommunities as *Pellioditis marina* was also found in the upper zone of the ultra-dissipative beach of Sylt (Blome 1974, 1982, 1983) and *Trissonchulus benepapilosus* was recorded on the Polish beach. On the much coarser beach in Italy, *T. benepapilosus* was replaced by *Trissonchulus oceanus*. *Pellioditis marina* was found on the upper zones of all beaches studied. One may argue that this is a cosmopolite species and not a truly twin-species. However, recent research (Derycke unpublished) observed a large amount of differentiation (cryptic species) within this species.

Summarizing we conclude that coarser and more physically controlled beaches harbour higher meiofaunal densities and diversities than fine grained chemically controlled ones. Isocommunities only exist on the upper beach parts, which are important ecotones between the terrestrial and the marine environment.

HUMAN-INDUCED DISTURBANCES TO THE SANDY BEACH

ECOSYSTEM

Physical disturbance is one of the key factors controlling the spatial and temporal composition of marine soft sediment communities (Hall 1994), which are subjected to a range of natural and anthropogenic perturbations. It refers to any discrete event in time that disrupts ecosystem, community, population structure and changes resources, substratum availability, or the physical environment (Picket and White 1985). In addition, biological disturbances occur as a result of processes such as foraging by predators (Kenny and Rees 1996), bioturbation (Schratzberger and Warwick 1999) and other biotic interactions that cause changes to habitat properties such as sediment stability and permeability. The effects of physical disturbance in soft sediments are manifested as the partial or complete defaunation of disturbed patches through direct mortality and physical damage, as well as through the displacement of species to nearby unfavourable habitats leading to increased vulnerability and mortality to predation (Hall 1994). In addition there are numerous effects of disturbance on sediment properties (*e.g.* sediment stability) which in turn can induce changes in hydrodynamics (Short 1999). In many soft-sediment habitats human-induced physical disturbances far outweigh the natural or biological disturbances (Grant 1981). Human-related perturbations vary from beach to beach; however, structures or activities that impede natural sand transport or alter the sand budget commonly lead to severe erosion, often of a permanent nature. An increasing pressure of physical disturbances in the coastal zone is assumed in the future as both human-induced and natural disturbances (as a result of global change) are expected to increase. Especially the expected rise in sea level, if coupled with an increase in the frequency and/or intensity of storms, as predicted for some regions, is likely to lead to escalating erosion and consequent loss of habitat (Brown and McLachlan 2002). As a consequence, disturbances by human interferences on sandy beaches may also rise as an increase of coastal defences with, irrefutable, destruction of natural dune-beach transitions is expected (Nordstorm *et al.* 2000). Beach nourishment is likely to become more widely practised (Peterson *et al.* 2000). Many sandy beaches also suffer intermittent or chronic pollution, and direct human interference includes off-road vehicles, mining, trampling, bait collecting and beach cleaning. Additionally, beach management focussing on the value of beaches as important recreation places may increase as sandy beaches are subjected to ever-increasing pressure from recreational activities as people enjoy more leisure time and higher standards of living. Consequently, there is the necessity in many tourist countries to provide accommodation and facilities for the growing tourism; while this is clearly a top priority (in view of the socio-economics) it is not always done wisely or with the aim of protecting the ecosystem in mind. The recreational value of sandy beaches can hardly be over-exaggerated. Recreational activities such as swimming, wading, surfing, running, dog walking, picnicking, ball games, horseback riding, sand sailing, wave kites, cooking and building sand castles, must all have some impact, although this has never been quantified. In general, recreational pressures decrease sand stability and increase its mobility (Carter 1975; Artukhin 1990).

Inevitable, all these anthropogenic disturbances in the coastal areas impinge on habitats and assemblages of conservation interest such as important bird feeding grounds (*e.g.* strandlines) or juvenile fish habitats. Human-induced disturbances, especially multiple events such as tourism that occur in rapid succession, are recognized as cardinal initiators of shifts in community structure (Sousa 1984; Hall 1994). Such shifts are increasingly possible as the rate and severity of the physical and human-induced disturbances increase. Despite these concerns, the intensity and extent of the disturbances have continued to increase, particularly over the last few decades and multiple disturbance effects have come together in the very popular tourist sandy shorelines all over the world. Tourism is a continuously adapting industry, responding to changing demographic and economic conditions as well as to new demands and technologies. On the other hand, tourism and related activities have always played a marginal role in discussions on biodiversity as tourism was known as a clean industry (Bundesamt für Naturschutz 1997). Only recently, some important progress has been made in this respect, as sustainable tourism has been included as one of the themes for further implementation of Agenda 21. The Commission on Sustainable Development has been assigned to develop an action-oriented international program of work to be defined in cooperation with the Conference of the Parties to the Convention on Biological Diversity, together with other relevant organizations, including the World Tourism Organization (WTO), the United Nations Conference on Trade and Development (UNCTAD) and the United Nations Environment Program (Van der Duim and Caalders 2002). The presence of mass tourism and related activities had marked effects on the meiofauna (Gheskiere *et al.* 2005b). In Chapter IV we have demonstrated, based on a geographically replicated survey of tourist and nearby pristine beaches, that mass tourism and related activities have marked effects on the community composition of the interstitial meiofauna and that such shifts in community structure are indeed not temporary. In two different coastal systems (Mediterranean and Baltic), we found that tourism related activities are particularly affecting the upper beach meio-nematofauna, the specific ecotone in which many meiofauna species from both the marine and the terrestrial environment congregate and contribute to higher community stress, lower taxonomic range and species diversity of the nematode assemblages compared to nearby pristine locations. The tourist upper beach zones are characterized by lower meiofauna diversities and low mature nematode assemblages consisting of taxonomically closely related species with *r*-strategist features. We were able to demonstrate the effect of 'tourism on the whole' but when trying to assess which activities cause loss of biodiversity and the shift in communities the study shows its weakness. The composition of tourism generally complicates measuring its impacts (Dietvorst and Ashworth 1995; Tremblay 1998). In its most simple form, it consists of accommodation and recreational activities. When trying to measure its relationships with biodiversity, one should take into account the impacts of both construction and maintenance of tourism infrastructure as well as the use of these facilities by tourists. Typically, for many of these elements, the impact will vary from one tourist to another depending on activity patterns and general behaviour. Impacts on biodiversity can be, direct or indirect, temporary or lasting and can vary in scale from global to local. The lack of knowledge on the functioning and dynamics of natural beach systems is also a problem. This means, for example, that it is not clear to what extent variation in biodiversity and species assemblages is a natural phenomenon (Brown and McLachlan 1990). The self-recuperative power (resilience) of the beach ecosystem, the limit to the extent to which a beach can be exploited, is poorly understood, as are the related

time-scales. The carrying capacity can be defined as the maximum use that the biota or the physical processes of the beach can withstand before becoming unacceptably or irreversibly damaged. As any use of the beach ecosystem induces change, the decision as to what level of use will cause unacceptable change is to a large extend subjective. The fact that such questions cannot yet be clearly answered leads to uncertainties about the kinds of species that should be monitored in order to have accurate information about the state of the beach ecosystem. It also creates doubt about the effectiveness of measures to protect biodiversity. However, even if a relation between tourism and a change in biodiversity is shown, the question as to whether these changes are ecologically significant or not still remain. This necessitates value judgements concerning the coastal zone management (Van der Duim and Philipsen 1995).

The increasing use of sandy beaches as recreational resources has forced regional authorities of many tourist countries to remove all natural wrack and litter of man-made origin to give their beaches an aesthetic look (Ryan and Swanepoel 1996). Litter left behind on the beach and in the dunes by human visitors has become an escalating problem (Moore *et al.* 2001). As a consequence a variety of cleaning techniques (front-end loaders, suction devices, sand rakes ...) has been developed in attractive coastal areas all over the world, particularly during the last two decades (Taylor *et al.* 1994; Engelhard and Withers 1997). Especially the cleaning with large tractor-pulled sieving machines has been seen as a cost-effective way of removing the unwanted strandline and has become an almost daily phenomenon on tourist sandy beaches. However, any legislation for the use of these machines is lacking. Cleaning commonly takes the form of clearing the beach not only of debris left behind by visitors, but also of kelp, wrack and other dead or stranded biota. Strandlines and upper beaches have traditionally been considered to be interface environments that process organic matter derived from the sea (Pearse *et al.* 1942; Brown 1964) so frequently cleaning deprives the ecosystem of valuable nutritional input. Generally, studies on the impacts of beach-cleaning are scarce (see **Chapter V**). Our study showed that meiofaunal densities and assemblage structure are significantly influenced immediately after the mechanical beach cleaning while number of species and taxonomic richness suffer no direct impacts from the experimental cleaning. We have demonstrated rapid recolonization rates of meiofaunal densities and assemblage structure of the cleaned parts of the strandline with fauna from underlying sediments within the two high waters following the experimental cleaning. However, these findings are based on a once-only, limited, small-scale cleaning experiment. Therefore it would be unwise to generalize that strandline meiofauna recover quickly from mechanical beach-cleaning. Further research should include, deeper, more catastrophic or repeated cleanings replicated on different strandlines and on dry parts of the beach, in different seasons, using different sieving machines to further elucidate the impact of these cleaning machines on the beach biota.

It is difficult to asses the contribution of beach cleaning activities to the noticed decrease in diversity on the above-mentioned tourist upper beaches as beach cleaning is only a part of the human-induced disturbances on these tourist beaches (next to human trampling, destruction of dunes, ...). However, as tidal induced recovery of the cleaned sediments is expected to be negligible (*cfr.* microtidal to nearly atidal regime), frequent (daily?) beach-cleaning is pushed forward as perhaps the main cause for the recorded decrease in meiofaunal density and diversity on these tourist beaches. Unfortunately data about the frequency of cleaning activities, depth and used mesh sizes on the mentioned beaches are not on hand.

Concluding, one should remember that the strandline and the washed ashore flotsams on the upper beach are in the main a result of natural processes. It is seen as a problem in tourist sites mainly because of the man-made litter it incorporates. Origins of this litter are both oceanic, *e.g.* from ships dumping at sea, and shore based, *e.g.* from rivers, sewage, or careless visitors. Seaweed and natural flotsam in itself are not rubbish, do no harm and provide a very special home for a range of both animal and plant life. The natural breakdown of seaweed and flotsam by the sea provides enough humus to allow flowering plants to survive. This is the beginning of sand dune formation. Sand dunes are important as landscape features and for natural coastal protection. They are also a specialist habitat and therefore of high wildlife value.

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APPENDIX I

Free-living nematode species list

from the studied beaches

PHYLUM NEMATODA (Rudolphi, 1808)

Classification following De Ley and Blaxter 2003

Incertae sedis:
<u>ORDER BENTHIMERMITHIDA</u>
Family Benthimermithidae
<u>ORDER RHAPTOTHYREIDA</u>
Family Rhaptothyreidae

CLASS ENOPLEA
SUBCLASS ENOPLIA

<u>ORDER ENOPLIDA</u>
Incertae sedis: Family Andrassyidae
Suborder Enoplina
Superfamily Enoploidea
Family Enoplidae
Family Thoracostomopsidae
  Enoploides aff. *brunetti* Gerlach, 1953
  Enoploides spiculohamatus Schulz, 1932
  Enoploides tyrrhenicus Brunetti, 1949
  Enoplolaimus attenuatus Brunetti, 1949
  Enoplolaimus balgensis Skwarra, 1921
  Enoplolaimus conicollis Gerlach, 1952
  Enoplolaimus litoralis Schulz, 1936
  Enoplolaimus longicaudatus (Southern, 1914)
  Enoplolaimus propinquus de Man, 1922
  Enoplolaimus subterraneus Gerlach, 1952
  Enoplolaimus villosus Gerlach, 1953
  Epacanthion enoploidiforme Warwick, 1970
  Mesacanthion africanthiforme Warwick, 1970
  Mesacanthion diplechma (Southern, 1914)
  Mesacanthion hirsutum Gerlach, 1953
  Mesacanthion sp.
  Trileptium subterraneum (Gerlach, 1952)
Family Anoplostomatidae
  Anoplostoma exceptum Schulz, 1935
  Chaetonema riemanni Platt, 1973
Family Phanodermatidae
  Phanodermopsis sp.1
Family Anticomidae
  Anticoma sp.
Suborder Trefusiina
Superfamily Trefusioidea
Family Simpliconematidae
Family Trefusiidae
  Trefusia sp.1
Family Lauratonematidae
  Lauratonema adriaticum Gerlach, 1953
  Lauratonema reductum Gerlach, 1953
Family Xenellidae
Suborder Oncholaimina
Superfamily Oncholaimoidea

Family Oncholaimidae
    Adoncholaimus sp.1
    Calyptronema maxweberi (DE MAN, 1922)
    Calyptronema sp.
    Metaparocholaimus sp.1
    Metoncholaimus sp.1
    Oncholaimellus calvadosicus DE MAN, 1890
    Oncholaimus conicauda FILIPJEV, 1929
    Oncholaimus dujardinii DE MAN, 1876
    Oncholaimus oxyuris DITLEVSEN, 1911
    Oncholaimus sp.
Family Enchelidiidae
    Pareuystomina sp.
    Thoonchus inermis GERLACH, 1953
    Viscosia cobbi FILIPJEV, 1918
    Viscosia sp.
    Viscosia sp.1
Suborder Ironina
Superfamily Ironoidea
Familie Ironidae
    Dolicholaimus sp.
    Syringolaimus sp.1
    Trissonchulus benepapilosus (SCHULZ, 1935)
    Trissonchulus oceanus COBB, 1920
    Trissonchulus sp.
    Trissonchulus sp.1
Family Leptosomatidae
    Platycoma sp.
    Platycoma sudafricana INGLIS, 1966
Family Oxystominidae
    Halalaimus cirrhatus GERLACH, 1953
    Paroxystomina sp.
Suborder Tripyloidina
Superfamily Tripyloidoidea
Family Tripyloididae
    Bathylaimus capacosus HOPPER, 1962
    Bathylaimus inermis DITLEVSEN, 1918
    Bathylaimus paralongisetosus STEKHOVEN & DE CONINCK, 1933
    Bathylaimus stenolaimus STEKHOVEN & DE CONINCK, 1933
    Tripyloides acherusius GERLACH, 1952
    Tripyloides gracilis (DITLEVSEN, 1918)
    Tripyloides marinus (BÜTSCHLI, 1874)
Suborder Campydorina
Superfamily Campydoroidea
Family Campydoridae
Suborder Alaimina
Superfamily Alaimoidea
Family Alaimidae

ORDER TRIPLONCHIDA

Suborder Diphtherophorina
Superfamily Diphtherophoroidea
Family Diphtherophoridae
Family Trichodoridae
Suborder Tobrilina
Superfamily Tobriloidea
Family Tobrilidae

Family Triodontolaimidae
Family Rhabdodemaniidae
Family Pandolaimidae
Superfamily Prismatolaimoidea
Family Prismatolaimidae
Suborder Tripylina
Superfamily Tripyloidea
Family Tripylidae
Family Onchulidae

SUBCLASS DORYLAIMIA
ORDER DORYLAIMIDA
Dorylaimida sp.
Suborder Dorylaimina
Superfamily Dorylaimoidea
Family Dorylaimidae
       Mesodorylaimus sp.
       Mesodorylaimus sp.1
Family Aporcelaimidae
       Aporcellaimellus sp.1
       Aporcellaimellus sp.2
       Aporcellaimellus sp.3
       Aporcellaimus sp.1
       Aporcellaimus sp.2
       Aporcellaimus sp.3
       Aporcellaimus sp.4
Family Qudsianematidae
Family Nordiidae
Family Longidoridae
Family Actinolaimidae
Superfamily Belondiroidea
Family Belondiridae
Superfamily Tylencholaimoidea
Family Leptonchidae,
Family Tylencholaimidae
Family Aulolaimoididae
Family Mydonomidae
Suborder Nygolaimina
Superfamily Nygolaimoidea
Family Nygolaimidae
       Nygolaimus sp.1
Family Nygellidae
Family Aetholaimidae
Family Nygolaimellidae

ORDER MONONCHIDA
Suborder Bathyodontina
Superfamily Cryptonchoidea
Family Bathyodontidae
Family Cryptonchidae
Superfamily Mononchuloidea
Family Mononchulidae
Suborder Mononchina
Superfamily Anatonchoidea
Family Anatonchidae
Superfamily Mononchoidea
Family Mononchidae

Family Mylonchulidae
ORDER ISOLAIMIDA
Superfamily Isolaimoidea
Family Isolaimiidae

ORDER DIOCTOPHYMATIDA
Suborder Dioctophymatina
Family Dioctophymatidae
Familiy Soboliphymatidae

ORDER MUSPICEIDA
Suborder Muspiceina
Family Muspiceidae
Family Robertdollfusiidae

ORDER MARIMERMITHIDA
Family Marimermithidae

ORDER MERMITHIDA
Suborder Mermithina
Superfamily Mermithoidea
Family Mermithidae
Family Tetradonematidae

ORDER TRICHINELLIDA
Superfamily Trichinelloidea
Family Anatrichosomatidae
Family Capillariidae
Family Cystoopsidae
Family Trichinellidae
Family Trichosomoididae
Family Trichuridae

CLASS CHROMADOREA
SUBCLASS CHROMADORIA

ORDER DESMOSCOLECIDA
Suborder Desmoscolecina
Superfamily Desmoscolecoidea
Family Desmoscolecidae
Family Meyliidae
Family Cyartonematidae

ORDER CHROMADORIDA
Suborder Chromadorina
Superfamily Chromadoroidea
Family Chromadoridae
      Chromadorella sp.
      Chromadorina germanica (BÜTSCHLI, 1874)
      Chromadorina sp.1
      Chromadorita abnormis KREIS, 1928
      Chromadorita nana LORENZEN, 1973
      Chromadorita sp.1
      Dichromadora abnormis GERLACH, 1953
      Dichromadora brevisetosa (GERLACH, 1953)
      Dichromadora cephalata (STEINER, 1916)

Dichromadora hyalocheile De CONINCK & STEKHOVEN, 1933
Dichromadora microdonta KREIS, 1929
Dichromadora sp.1
Dichromadora sp.2
Hypodontolaimus mediterraneus BRUNETTI, 1949
Hypodontolaimus schuurmansstekhoveni GERLACH, 1951
Neochromadora trichophora STEINER, 1921
Parachromadorita sp.1
Prochromadorella ditlevensi (DE MAN, 1922)
Ptycholaimellus ponticus (FILIPJEV, 1922)
Spilophorella candida GERLACH, 1951
Spilophorella sp.
Family Ethmolaimidae
Family Neotonchidae
Neotonchus sp.1
Family Achromadoridae
Family Cyatholaimidae
Nannolaimus sp.1
Paracanthonchus thaumasius (SCHULZ, 1932)
Paracanthonchus tyrrhenicus (BRUNETTI, 1949)
Paracyatholaimoides multispiralis GERLACH, 1953
Paracyatholaimoides sp.1
Paracyatholaimus pentodon RIEMANN, 1966
Paracyatholaimus sp.1
Pomponema elegans LORENZEN, 1972
Pomponema multipapilatum (FILIPJEV, 1922)
Pomponema sp.
Pomponema sp.1
Praeacanthonchus punctatus (BASTIAN, 1865)
Family Selachinematidae
Choanolaimus psammophilus DE MAN, 1880
Choniolaimus sp.1
Gammanema conicauda GERLACH, 1953
Gammanema sp.
Gammanema sp.1
Halichoanolaimus lanceolatus VITIELLO, 1970
Halichoanolaimus sp.1
Richtersia sp.
Synonchiella riemanni WARWICK, 1970

ORDER DESMODORIDA

Suborder Desmodorina
Superfamily Desmodoroidea
Family Desmodoridae
Chromaspirina inglisi WARWICK, 1970
Chromaspirina parapontica LUC & DE CONINCK, 1959
Chromaspirina pontica FILIPJEV, 1918
Leptonemella aphonothecae GERLACH, 1950
Metachromadora remanei GERLACH, 1951
Onyx perfectus COBB, 1891
Onyx sagittarius GERLACH, 1950
Pseudonchus deconincki WARWICK, 1969
Sigmophoranema rufum (COBB, 1933)
Spirinia laevis (BASTIAN, 1865)
Spirinia parasitifera (BASTIAN, 1865)
Spirinia sp.

Family Epsilonematidae
     Epsilonema pustulatum (GERLACH, 1952)
Family Draconematidae
     Dracognomus simplex (GERLACH, 1954)
Superfamily Microlaimoidea
Family Microlaimidae
     Bolbolaimus crassiceps (GERLACH, 1953)
     Calomicrolaimus honestus (DE MAN, 1922)
     Calomicrolaimus monstrosus GERLACH, 1953
     Calomicrolaimus parahonestus (GERLACH, 1950)
     Calomicrolaimus sp.
     Microlaimus conspicuus LORENZEN, 1973
     Microlaimus microseta GERLACH, 1953
     Microlaimus ostracion STEKHOVEN, 1935
     Microlaimus sp.
     Microlaimus sp.1
Family Aponchiidae
Family Monoposthiidae
     Monoposthia costata (BASTIAN, 1865)
     Monoposthia mirabilis SCHULZ, 1932
     Monoposthia thorakista (SCHULZ, 1935)

ORDER MONHYSTERIDA

Suborder Monhysterina
Superfamily Monhysteroidea
Family Monhysteridae
     Diplolaimella sp.1
     Diplolaimella stagnosa LORENZEN, 1966
Superfamily Sphaerolaimoidea
Family Xyalidae
     Ammotheristus sp. 1
     Cobbia sp.
     Daptonema hirsutum (VITIELLO, 1967)
     Daptonema normandicum (DE MAN, 1890)
     Daptonema sp.
     Daptonema sp.1
     Daptonema sp.2
     Daptonema sp.3
     Daptonema sp.4
     Daptonema stylosum LORENZEN, 1973
     Daptonema tenuispiculum (DITLEVSEN, 1918)
     Metadesmolaimus aversicula GERLACH, 1953
     Metadesmolaimus gelana WARWICK & PLATT, 1973
     Metadesmolaimus pandus LORENZEN, 1972
     Metadesmolaimus sp.
     Metadesmolaimus sp.1
     Monhystera disjuncta (BASTIAN, 1865)
     Monhystera sp.
     Paramonhystera sp.
     Paramonhystera sp.1
     Promonhystera faber WIESER, 1956
     Promonhystera sp.1
     Rhynchonema sp.
     Rhynchonema sp.1
     Theristus aculeatus SCHULZ, 1936
     Theristus denticulatus WARWICK, 1970
     Theristus heterospiculoides GERLACH, 1953

          Theristus heterospiculum (ALLGÉN, 1932)
          Theristus inermis GERLACH, 1953
          Theristus interstitialis WARWICK, 1970
          Theristus otoplanobius GERLACH, 1951
          Theristus pertenuis BRESSLAU & STEKHOVEN, 1935
          Theristus pictus GERLACH, 1951
          Theristus sp.
          Theristus sp.1
          Theristus sp.2
          Trichotheristus mirabilis (STEKHOVEN & DE CONINCK, 1933)
          Trichotheristus sp.1
          Xenolaimus sp.1
          Xyala striata COBB, 1920
Family Sphaerolaimidae
          Sphaerolaimus sp.
Suborder Linhomoeina
Superfamily Siphonolaimoidea
Family Siphonolaimidae
          Siphonolaimus sp.1
Family Linhomoeidae
          Desmolaimus sp.
          Eumorpholaimus sabulicosus SCHULZ, 1932
          Metalinhomoeus sp.
          Metalinhomoeus sp.1
          Paralinhomoeus sp.1
          Terschellingia sp.1
Family Fusivermidae

ORDER ARAEOLAIMIDA
Superfamily Axonolaimoidea
Family Axonolaimidae
          Ascolaimus elongatus (BÜTSCHLI, 1874)
          Axonolaimus helgolandicus LORENZEN, 1971
          Axonolaimus hexapilus WIESER & HOPPER, 1967
          Axonolaimus orcombensis WARWICK, 1970
          Axonolaimus spinosus (BÜTSCHLI, 1874)
          Axonolaimus tirrenicus BRUNETTI, 1941
          Odontophora ornata LORENZEN, 1972
          Odontophora phalarata LORENZEN, 1972
          Odontophora rectangula LORENZEN, 1971
Family Comesomatidae
          Cervonema sp.
          Comesoma warwicki PLATT, 1982
          Hopperia sp.
          Sabatiera sp.1
          Sabatieria celtica SOUTHERN, 1914
          Sabatieria longispinosa LORENZEN, 1972
Family Diplopeltidae
          Araeolaimus sp.
          Southerniella sp.1
Family Coninckiidae
          Coninckia sp.1

ORDER PLECTIDA
Superfamily Leptolaimoidea
Family Leptolaimidae
          aff. *Camacolaimus* sp.

Camacolaimus barbatus WARWICK, 1970
Camacolaimus longicauda DE MAN, 1922
Leptolaimoides sp.1
Leptolaimus ampullaceus WARWICK, 1970
Leptolaimus setiger STEKHOVEN & DE CONINCK, 1933
Leptolaimus sp.1
Leptolaimus sp.2
Stephanolaimus elegans DITLEVSEN, 1918
Stephanolaimus gandavensis JENSEN, 1976
Stephanolaimus jayasreei PLATT, 1983
Stephanolaimus sp.1
Family Rhadinematidae
Family Aegialoalaimidae
Aegialoalaimus sp.1
Cyartonema elegans JAYASREE & WARWICK, 1977
Family Diplopeltoididae
Family Paramicrolaimidae
Paramicrolaimus spirulifer WIESER, 1959
Family Ohridiidae
Family Bastianiidae
Family Odontolaimidae
Family Rhabdolaimidae
Rhabdocoma sp.1
Rhabdodemania coronata GERLACH, 1952
Rhabdodemania sp.
Rhabdodemania sp.1
Superfamily Ceramonematoidea
Family Tarvaiidae
Tarvaia angusta GERLACH, 1953
Tarvaia sp.1
Family Ceramonematidae
Ceramonema chitwoodi DE CONINCK, 1942
Family Tubolaimoididae
Superfamily Plectoidea
Family Plectidae
Plectidae sp.
Plectus sp.
Plectus sp.1
Family Chronogasteridae
Family Metateratocephalidae
Superfamily Haliplectoidea
Family Peresianidae
aff. *Manunema* sp.
Family Haliplectidae
Haliplectus minimus GERLACH, 1967
Haliplectus sp.
Setoplectus sp.
Setoplectus sp.1
Family Aulolaimidae

ORDER RHABDITIDA
Incertae sedis: Family Teratocephalidae, Family Chambersiellidae, Family Brevibuccidae
Suborder Spirurina
Incertae sedis: Superfamily Dracunculoidea
Family Dracunculidae
Family Philometridae
Family Phlyctainophoridae

Family Skrjabillanidae
Family Anguillicolidae
Family Guyanemidae
Family Micropleuridae
INFRAORDER GNATHOSTOMATOMORPHA
Superfamily Gnathostomatoidea
Family Gnathostomatidae
INFRAORDER OXYURIDOMORPHA
Superfamily Thelastomatoidea
Family Thelastomatidae
Family Travassosinematidae
Family Hystrignathidae
Family Protrelloididae
Superfamily Oxyuroidea
Family Oxyuridae
Family Pharyngodonidae
Family Heteroxynematidae
INFRAORDER RHIGONEMATOMORPHA
Superfamily Rhigonematoidea
Family Rhigonematidae
Family Ichthyocephalidae
Superfamily Ransomnematoidea
Family Ransomnematidae
Family Carnoyidae
Family Hethidae
INFRAORDER SPIRUROMORPHA
Superfamily Camallanoidea
Family Camallanidae
Superfamily Physalopteroidea
Family Physalopteridae
Superfamily Rictularoidea
Family Rictulariidae
Superfamily Thelazoidea
Family Thelaziidae
Family Rhabdochonidae
Family Pneumospiruridae
Superfamily Spiruroidea
Family Gongylonematidae
Family Spiruridae
Family Spirocercidae
Family Hartertiidae
Superfamily Habronematoidea
Family Hedruridae
Family Habronematidae
Family Tetrameridae
Family Cystidicolidae
Superfamily Acuarioidea
Family Acuariidae
Superfamily Filarioidea
Family Filariidae
Family Onchocercidae
Superfamily Aproctoidea
Family Aproctidae
Family Desmidocercidae
Superfamily Diplotriaenoidea
Family Diplotriaenidae
Familiy Oswaldofilariidae

INFRAORDER ASCARIDOMORPHA
Superfamily Ascaridoidea
Family Heterocheilidae
Family Ascarididae
Family Raphidascarididae
Family Anisakidae
Superfamily Cosmocercoidea
Family Cosmocercidae
Family Atractidae
Family Kathlaniidae
Superfamily Heterakoidea
Family Heterakidae
Family Aspidoderidae
Family Ascaridiidae
Superfamily Subuluroidea
Family Subuluridae
Family Maupasinidae
Superfamily Seuratoidea
Family Seuratidae
Family Cucullanidae
Family Quimperiidae
Family Chitwoodchabaudiidae
Family Schneidernematidae
Suborder Myolaimina
Superfamily Myolaimoidea
Family Myolaimidae
Suborder Tylenchina
INFRAORDER PANAGROLAIMOMORPHA
Superfamily Panagrolaimoidea
Family Panagrolaimidae
Superfamily Strongyloidoidea
Family Steinernematidae
Family Strongyloididae
Family Rhabdiasidae
Family Alloionematidae
INFRAORDER CEPHALOBOMORPHA
Superfamily Cephaloboidea
Family Cephalobidae
      Acrobeles ciliatus LINSTOW, 1877
      Acrobeles sp.
Family Elaphonematidae
Family Osstellidae
Family Alirhabditidae
Family Bicirronematidae
INFRAORDER TYLENCHOMORPHA
Superfamily Aphelenchoidea
Family Aphelenchidae
Family Aphelenchoididae
Superfamily Criconematoidea
Family Criconematidae
Family Hemicycliophoridae
Family Tylenchulidae
Superfamily Sphaerularioidea
Family Anguinidae
Family Sphaerulariidae
Family Neotylenchidae
Family Iotonchidae
Superfamily Tylenchoidea

Family Hoplolaimidae
Family Meloidogynidae
Family Tylenchidae
Family Belonolaimidae
Family Pratylenchidae
Family Dolichodoridae
Superfamily Myenchoidea
Family Myenchidae
INFRAORDER DRILONEMATOMORPHA
Superfamily Drilonematoidea
Family Drilonematidae
Family Ungellidae
Family Homungellidae
Family Pharyngonematidae
Family Creagrocercidae
Suborder Rhabditina
INFRAORDER BUNONEMATOMORPHA
Superfamily Bunonematoidea
Family Bunonematidae
Family Pterygorhabditidae
INFRAORDER DIPLOGASTEROMORPHA
Superfamily Cylindrocorporoidea
Family Cylindrocorporidae
Superfamily Odontopharyngoidea
Family Odontopharyngidae
Superfamily Diplogasteroidea
Family Pseudodiplogasteroididae
Family Diplogasteroididae
Family Diplogasteridae
Family Neodiplogasteridae
Family Mehdinematidae
Family Cephalobiidae
INFRAORDER RHABDITOMORPHA n. infraorder
Incertae sedis: Family Carabonematidae, Familie Agfidae
Superfamily Mesorhabditoidea
Family Mesorhabditidae
Family Peloderidae
Superfamily Rhabditoidea
Family Diploscapteridae
Family Rhabditidae
> *Pellioditis marina* (BASTIAN, 1865)
> *Rhabditidae* sp.
> *Rhabditis* sp.
Superfamily Strongyloidea
Family Heterorhabditidae
Family Strongylidae
Family Ancylostomatidae
Family Trichostrongylidae
Family Metastrongylidae
Family Diaphanocephalidae
Family Heligmosomidae
Family Molinidae

APPENDIX II

Publication list Tom Gheskiere

(As on 28 February, 2005)

A1 PUBLICATIONS

VANAVERBEKE J, GHESKIERE T, VINCX M (2000) The meiobenthos of subtidal sandbanks on the Belgian Continental Shelf. Estuarine, Coastal and Shelf Science 51:637-649

VANAVERBEKE J, GHESKIERE T, STEYAERT M, VINCX M (2002) Nematode assemblages from subtidal sandbanks in the Southern Bight of the North Sea: effect of small sedimentological differences. Journal of Sea Research 48:197-207

URBAN-MALINGA B, KOTWICKI L, GHESKIERE T, JANKOWSKA K, OPALINSKI K, MALINGA M (2004) Composition and distribution of meiofauna, including nematode genera, in two contrasting Arctic beaches. Polar Biology 27:447-457

GHESKIERE T, HOSTE E, VANAVERBEKE J, VINCX M, DEGRAER S (2004) Horizontal zonation patterns and feeding structure of marine nematode assemblages on a macrotidal, ultra-dissipative sandy beach (De Panne, Belgium) Journal of Sea Research 52:211-226

GHESKIERE T, VINCX M, URBAN-MALINGA B, ROSSANO C, SCAPINI F, DEGRAER S (2005) Nematodes from wave-dominated sandy beaches: diversity, zonation patterns and testing of the isocommunities concept Estuarine, Coastal and Shelf Science 62:365-375

GHESKIERE T, VINCX M, WESLAWSKI JM, SCAPINI F, DEGRAER S (2005) Meiofauna as descriptor of tourism-induced changes at sandy beaches. Marine Environmental Research 60:245-265

KOTWICKI L, DE TROCH M, URBAN-MALINGA B, GHESKIERE T, WESLAWSKI JM (SUBMITTED) Horizontal and vertical distribution of meiofauna on sandy beaches of the North Sea (The Netherlands, Belgium, France) Helgoland Marine Research

GHESKIERE T, VINCX M, PISON G, DEGRAER S (SUBMITTED) Are strandline meiofaunal assemblages affected by mechanical beach cleaning? – Experimental findings. Marine Ecology Progress Series.

SPEYBROECK J, BONTE D, COURTENS W, GHESKIERE W, GROOTAERT W, MAELFAIT JP, MATTHYS M, PROVOOST S, SABBE K, STIENEN EWM, VAN LANCKER V, VINCX M, DEGRAER S (SUBMITTED) Beach nourishment: An ecologically sound coastal defence alternative? Aquatic Conservation: Marine and Freshwater Ecosystems

URBAN-MALINGA B, GHESKIERE T, DEGRAER S, MOENS T (IN PREP) Gradients of biodiversity and ecosystem process rates along a macrotidal, ultradissipative sandy beach

DEGRAER S, BEYST B, GHESKIERE T, VINCX M (IN PREP) Benthos research on Belgian sandy beaches: an overview

A2 PUBLICATIONS

GHESKIERE T, HOSTE E, KOTWICKI, DEGRAER S, VANAVERBEKE J, VINCX M (2002) The sandy beach meiofauna and free-living nematodes from De Panne (Belgium) Bulletin of the Royal Belgian Institute of Natural Sciences, Biology Suppl. 72:53-57

A4 PUBLICATIONS

GHESKIERE T, DEGRAER S, VINCX M (2003) Vrijlevende mariene nematoden, ongekende bewoners van het zandstrand ecosysteem. De Strandvlo 23:58-67

B2 PUBLICATIONS

GHESKIERE T, DE SMET G, VANREUSEL A, VINCX M (2003) Fadenwürmer (Nematoda) In: HOFFRICHTER R (Ed): Das Mittelmeer: Fauna, Flora und Ökologie, Band II/1, Spektrum Akademischer Verlag Heidelberg, Berlin, Germany, 602-627 (in German)

C1 PUBLICATIONS

VINCX M, DEGRAER S, BEYST B, VOLCKAERT A, HOSTE E, DE BACKER A, GHESKIERE T (2001) Stranden, niet alleen voor toeristen! VLIZ special publication 4:69-74

GHESKIERE T, VINCX M (2002) Interactions between nematode biodiversity and anthropogenic disturbances on European sandy beaches. In: MEES J, SEYS J (Eds): VLIZ Young Scientists' Day. VLIZ special publication 7:35

DEGRAER S, BEYST B, GHESKIERE T, VINCX M (2002) Onbekend is onbemind: De mariene fauna van Vlaamse stranden. VLIZ special publication 9:1-10

GHESKIERE T, DEGRAER S, VINCX M (2003) Nematode diversity and zonation patterns on sandy beaches In: MEES J, SEYS J (Eds): VLIZ Young Scientists' Day. VLIZ special publication 12:39

BELPAEME K, KERCKHOF F, GHESKIERE T (2004) About "clean" beaches and beach cleaning in Belgium, In: Green DR *et al.* (Eds) (2004). Littoral 2004: Delivering sustainable coasts: connecting science and policy, proceedings volume II:749-751

BELPAEME K, KERCKHOF F, GHESKIERE T (2005) About "clean" beaches and beach cleaning in Belgium, In: MEES J, SEYS, J (Eds) VLIZ Young Scientists' Day. VLIZ Special Publication, 20:21

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GHESKIERE T (2000) Interactie tussen biodiversiteit van het meiobenthos (*in casu* Nematoda) en toerisme op drie Europese zandstranden Onderzoeksproject ter aanvraag van een IWT-specialisatiebeurs 1ste termijn (2000/2002), 28 p

GHESKIERE T (2002) Interactie tussen biodiversiteit van het meiobenthos (*in casu* Nematoda) en toerisme op drie Europese zandstranden Onderzoeksproject ter aanvraag van een IWT-specialisatiebeurs 2de termijn (2002/2004), 25 p

GHESKIERE T (2003) Interactie tussen biodiversiteit van het meiobenthos (*in casu* Nematoda) en toerisme op drie Europese zandstranden Tussentijds verslag 2de termijn IWT-specialisatiebeurs (2002/2004) na 3de beursjaar, 23 p

SPEYBROECK J, BONTE D, COURTENS W, GHESKIERE T, GROOTAERT P, MAELFAIT JP, MATTHYS M, PROVOOST S, SABBE K, STIENEN EWM, VAN LANCKER V, VINCX M, DEGRAER S (2004) Studie over de impact van zandsuppleties op het ecosysteem. Dossiernr. 202.165 In opdracht van: Ministerie van de Vlaamse Gemeenschap Departement leefmilieu en infrastructuur, Administratie Waterwegen en Zeewezen, afdeling Waterwegen Kust, 201 p

SPEYBROECK J, BONTE D, DASSEVILLE R, GHESKIERE T, GROOTAERT P, LIONARD M, MAELFAIT JP, SABBE K, STIENEN EWM, VAN DEN BROECK K, VAN DE WALLE M, VAN LANDUYT W, VERCRUYSSE E, VINCX M, DEGRAER S (2004). Biologische evaluatie van elf strandzones langs de Vlaamse kust, B.E.S.T. AMINAL – afdeling Natuur – cel Kustzonebeheer. Contractnummer AN.GKB/2002/nr.2 Final report, 179 p