



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

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Abstract

Spatial patterns of nematode community structure from two geographically spaced intermediate, micro-tidal 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/breakers 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.

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1. 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. Micro-tidal (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

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can develop, harbouring, as a consequence, a different benthic fauna (Wieser et al., 1974).

Most of the faunal research on sandy beaches has been principally concentrated on macrofauna (> 1 mm) (McLachlan and Jaramillo, 1995 and references therein) and more recently also birds (e.g. Cornelius et al., 2001). In contrast, sandy beach meiofauna (all metazoans between 1 mm and 38 μ m) 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 (Lamshead, 1993; Lamshead 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 (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). 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 (micro-tidal 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.

2. Material and methods

2.1. Study sites

Two micro-tidal 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 Gdańsk, Baltic Sea), at the end of the Hel Peninsula (Fig. 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.

(2) The beach at San Rossore, (43°42' N, 10°16' E, Italy) is situated in the San Rossore Massaciuccoli Natural Park (Fig. 1). This park occupies 30 km of flat coastal strip in northern–southern Tuscany (Ligurian Sea), between the provinces of Pisa and Lucca. San Rossore is a micro-tidal (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. 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.

The same beaches were also studied as 'control' sites in the framework of a superficial disturbance study on sandy beaches (Gheskiere et al., in press). However the disturbance study was based on the results of a different sampling campaign and followed a different sampling strategy.

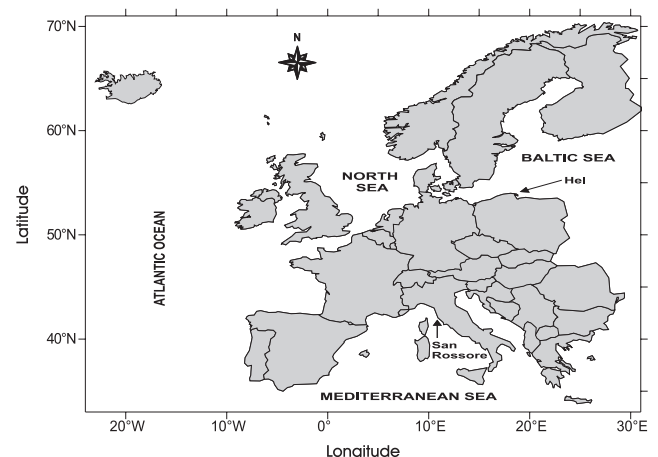


Fig. 1. Geographical location of the studied beaches.

Table 1
Environmental characteristics of the beaches studied

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

2.2. 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 breakers (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 cm^2) 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 ($70 \text{ }^\circ\text{C}$) 4% buffered formaldehyde water solution (Heip et al., 1985; Vincx, 1996).

2.3. 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 $38 \mu\text{m}$ 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). Shell-free sediment samples were oven-dried at $105 \text{ }^\circ\text{C}$ for 12 h and ashed at $500 \pm 50 \text{ }^\circ\text{C}$ for 2 h to determine the %TOM by loss of mass on ignition. 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 (ϕ , Quartile Deviation) and skewness were calculated as described by Dyer (1986).

2.4. Data analysis

Wave-dominated, micro-tidal beaches can be classified using three parameters – the modal breaker height in meters (H_b), modal wave period in seconds (T) and sediment fall velocity (W_s) in meters per second. 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 $\Omega = H_b/W_s T$ (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* (Masselinck 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, Clarke, 1993) was used to test for significant differences between beaches (across zones). One-way ANOSIM was subsequently applied to assess 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 addressed 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's HSD multi-comparison test for equal n was used in a pair-wise comparison (Zar, 1996). Statistical analyses were performed using the STATISTICA v6 software package (StatSoft, 2001).

3. Results

3.1. 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 (Fig. 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 $>1000\text{ }\mu\text{m}$ 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 $>1000\text{ }\mu\text{m}$ were significantly higher in the swash/breaker zone at both beaches, a known feature caused by the wave-dominated character of these micro-tidal beaches (Short, 1999). %TOM was found to be significantly higher on the 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/breakers 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

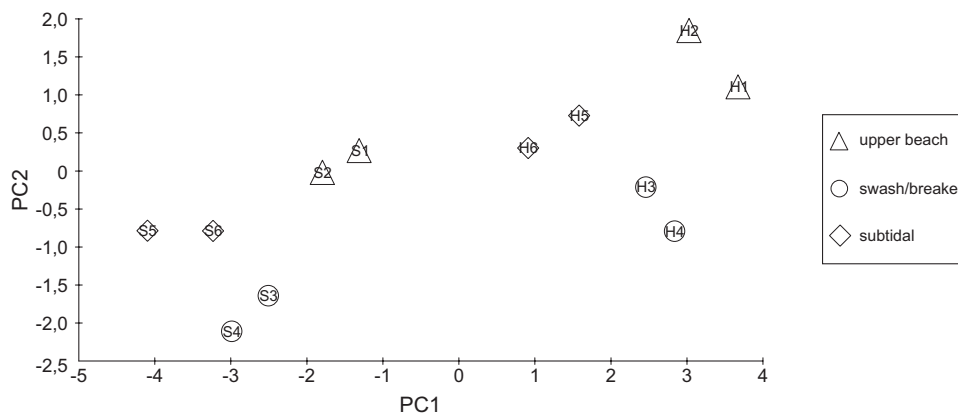


Fig. 2. Two-dimensional correlation-based principal-component analysis (PCA) of $\log(x + 1)$ transformed abiotic data from sampling stations ($n = 3$ per station) across the two beaches studied (San Rossore beach = S; Hel beach = H).

Table 2

Mean values (\pm standard deviation) of environmental variables and significance levels from one-way ANOVA tests for differences between the different zones across the beaches

	Upper beach (I)	Swash and breakers (II)	Subtidal (III)	<i>p</i>	Comparison
<i>San Rossore</i>					
Median grain size (μm)	433 \pm 10	564 \pm 20	522 \pm 8	<0.001	I < II > III
125–250 μm (%)	1.6 \pm 0.1	0.9 \pm 0.3	0.4 \pm 0.1	0.002	I > II, III
250–500 μm (%)	57.9 \pm 2.7	26.8 \pm 3.0	17.6 \pm 0.6	<0.001	I > II > III
500–1000 μm (%)	40.7 \pm 2.7	65.3 \pm 2.5	67 \pm 2.4	<0.001	I < II, III
> 1000 μm (%)	0.9 \pm 0.0	14.8 \pm 1.8	6.9 \pm 0.8	<0.001	I < II > III
Sorting (QD)	0.31 \pm 0.01	0.34 \pm 0.01	0.32 \pm 0.00	0.054	–
Temperature ($^{\circ}\text{C}$)	25.3 \pm 0.1	22.7 \pm 0.9	24.4 \pm 0.2	0.027	I > II
Salinity	27.8 \pm 0.22	35.9 \pm 0.7	37.1 \pm 0.1	0.001	I < II, III
%TOM	2.25 \pm 0.01	1.0 \pm 0.09	0.8 \pm 0.04	<0.001	I > II > III
Skewness	–0.35 \pm 0.17	–1.27 \pm 0.8	–3.73 \pm 1.15	0.975	–
<i>Hel</i>					
Median grain size (μm)	348 \pm 7	426 \pm 21	379 \pm 16	0.013	I < II > III
125–250 μm (%)	11.7 \pm 1.8	6.3 \pm 0.8	11.3 \pm 1.9	0.051	–
250–500 μm (%)	80.6 \pm 1.1	62.9 \pm 5.3	64.9 \pm 2.5	0.008	I > II, III
500–1000 μm (%)	7.2 \pm 0.4	27.7 \pm 4.7	22.1 \pm 3.7	<0.001	I < II, III
> 1000 μm (%)	0.7 \pm 0.3	3.1 \pm 0.4	1.8 \pm 0.8	0.041	I < II > III
Sorting (QD)	0.26 \pm 0.01	0.34 \pm 0.02	0.32 \pm 0.01	0.001	I < II, III
Temperature ($^{\circ}\text{C}$)	15.3 \pm 0.2	12.2 \pm 0.9	13 \pm 0.2	0.192	I > II
Salinity	5.2 \pm 0.5	7.3 \pm 0.02	7.4 \pm 0.01	<0.001	I < II, III
%TOM	2.11 \pm 0.04	1.4 \pm 0.09	0.95 \pm 0.02	<0.001	I > II > III
Skewness	–0.11 \pm 0.02	–0.21 \pm 0.02	–0.03 \pm 0.03	<0.001	I > II, II < III

Analyses performed on $\log(x + 1)$ transformed data. Significant differences evaluated with Tukey’s HSD multi-comparison test for equal *n*.

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 $^{\circ}\text{C}$, Italy 25.3 $^{\circ}\text{C}$) followed by a very slight decrease towards the swash/breaker zones and an increase in the subtidal zones.

3.2. 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% (two-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 (Fig. 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 two-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. One-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 (77–57%) 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 (82–78%). 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

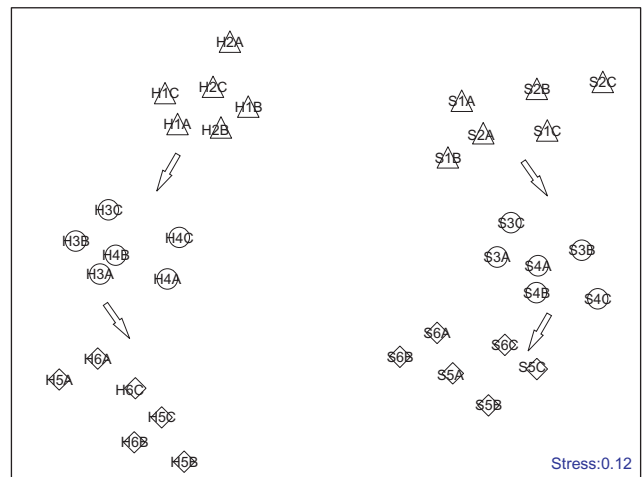


Fig. 3. Nematode assemblages: output of non-metric Multi-Dimensional Scaling (MDS) on square-root transformed species abundance data (three replicates per sampling station) with indication of the different zones (symbols as in Fig. 2) across the beaches (stress: 0.12).

Table 3

Results of the one-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)

Zones compared	San Rossore			Hel		
	Dissimilarity (%)	<i>R</i>	<i>p</i>	Dissimilarity (%)	<i>R</i>	<i>p</i>
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

Percentage of Bray–Curtis dissimilarity as calculated from the SIMPER analyses. All analyses performed on square-root transformed data.

(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). *Enoplolaimus enoploidiformis* seems to be an important predator in all zones across the Italian beach.

Two-way ANOVA indicated significant differences ($p < 0.01$) for all investigated indices between beaches, zones and beach \times zone interaction (table not shown). Nematode density and total species richness per zone are illustrated in Fig. 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

breakers 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). At both beaches average taxonomic distinctness (Δ^*) showed more or less similar patterns: a step 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 (Fig. 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 (Fig. 5A). Changes in evenness (J') and N_∞ (Fig. 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_∞ , a higher dominance of some species (*Epsilonema pustulatum* and *Theristus heterospiculum* in Italy;

Table 4

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

Zones	San Rossore			Hel		
Upper beach	<i>Aporcelaimus</i> sp1	23%	2B	<i>Aporcelaimus</i> sp2	20%	2B
	<i>Theristus aculeatus</i>	20%	1A	<i>Tripylloides archeriusus</i>	17%	2B
	<i>Enoplolaimus enoploidiformis</i>	10%	2B	<i>Chromadorita</i> nsp1	13%	2A
	<i>Trileptium subterraneum</i>	10%	2B	<i>Aporcelaimellus</i> sp3	12%	2B
	<i>Aporcelaimellus</i> sp2	6%	2B	<i>Leptolaimus</i> nsp.1	6%	1A
Swash/breakers	<i>Epsilonema pustulatum</i>	37%	1B	<i>Trissonchulus benepapilosus</i>	40%	2B
	<i>Theristus heterospiculum</i>	24%	1A	<i>Bathylaimus stenolaimus</i>	31%	1B
	<i>Dracognomus simplex</i>	15%	1B	<i>Tripylloides archeriusus</i>	10%	2B
	<i>Axonolaimus tirrenicus</i>	10%	1B	<i>Chromadorita</i> nsp1	6%	2A
	<i>Enoplolaimus enoploidiformis</i>	7%	2B	<i>Anoplostoma exceptum</i>	4%	1B
Subtidal	<i>Theristus heterospiculum</i>	12%	1A	<i>Ascolaimus elongatus</i>	26%	1B
	<i>Epsilonema pustulatum</i>	10%	1B	<i>Metadesmolaimus</i> nsp1	22%	1B
	<i>Enoplolaimus enoploidiformis</i>	9%	2B	<i>Trissonchulus benepapilosus</i>	11%	2B
	<i>Platycoma sudaficana</i>	7%	1A	<i>Enoplolaimus balgensis</i>	10%	2B
	<i>Theristus inermis</i>	7%	1B	<i>Metachromadora remanei</i>	8%	2B

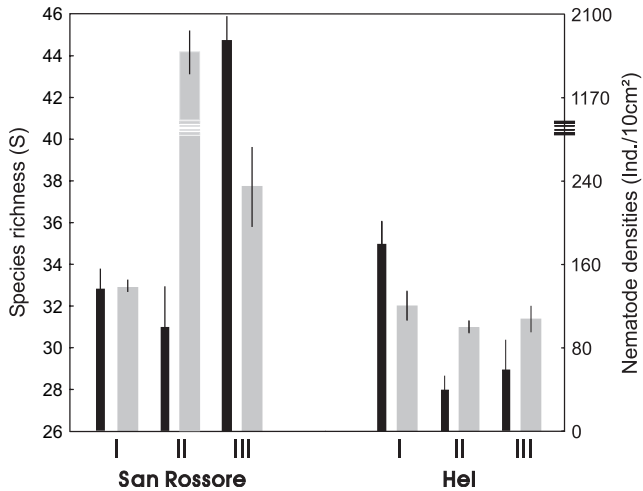


Fig. 4. Mean nematode species richness (black bars \pm standard errors, left ordinate) and total nematode densities (grey bars \pm standard errors, right ordinate). All calculated by pooled variance of replicates per zone and per beach. I = upper beach, II = swash/breaker zone and III = subtidal zone.

Trissochulus benepapilosus and *Bathylaimus stenolaimus* in Poland). Fig. 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. Fig. 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 are 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 shared between the upper beaches 17% and 27%, respectively.

4. 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 $> 1000 \mu\text{m}$ and sediment sorting coefficient. On the Polish beach, highest correlation ($\sigma = 0.523$) was found with %TOM.

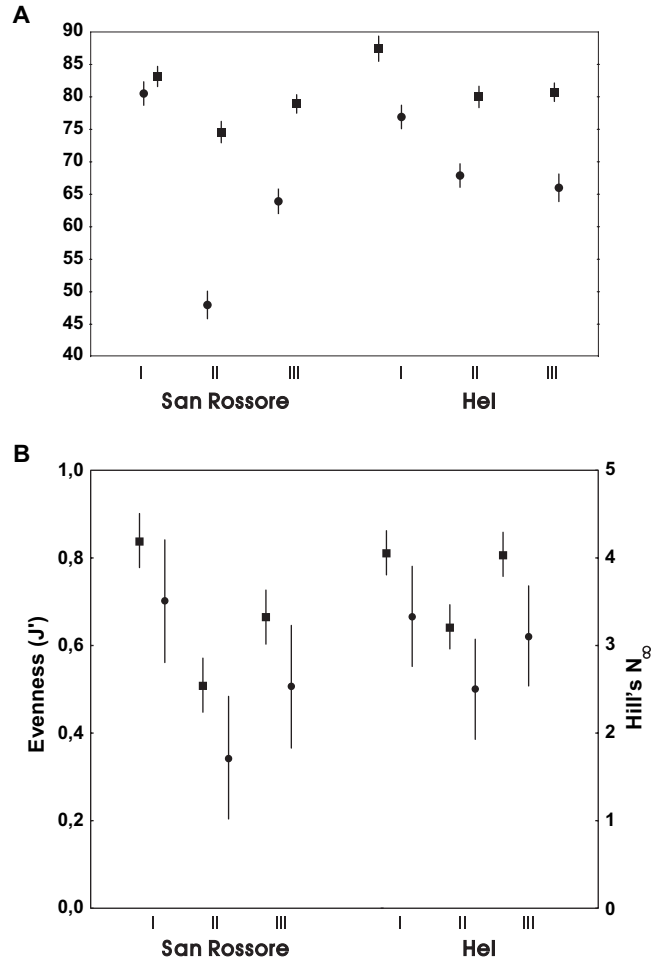


Fig. 5. Various diversity indices across the beaches (zones as in Fig. 4). (A) Average taxonomic distinctness (■) and Average taxonomic diversity (●). (B) Evenness (J') (■) and Hill's N_∞ (●). All calculated by pooled variance of replicates \pm standard errors.

5. 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 micro-tidal 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 (0.2–2.5 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

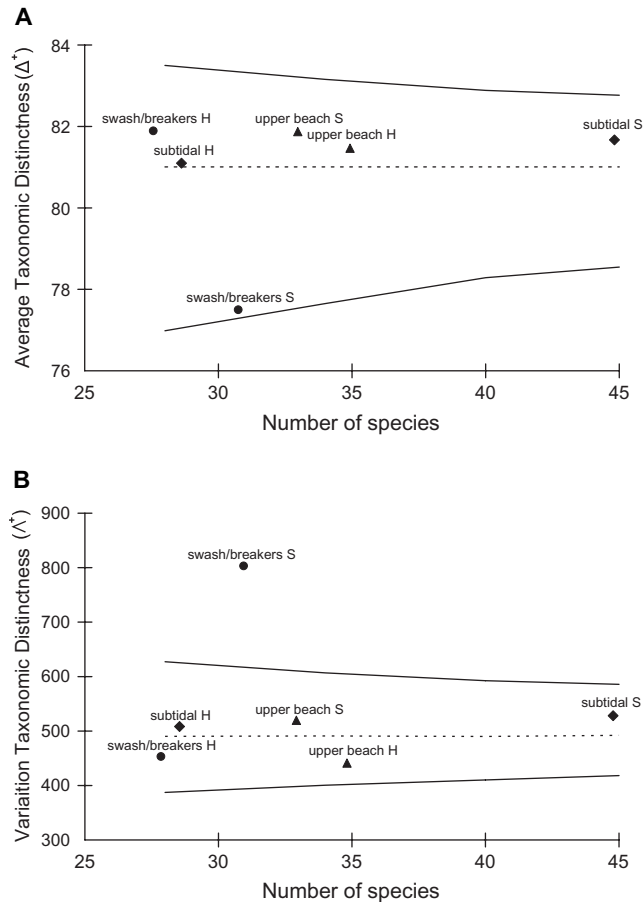


Fig. 6. The 95% probability funnels for average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+) plotted against the number of species for the different nematode assemblages on the two beaches studied. Dashed lines indicate the simulated mean Δ^+ and Λ^+ from 5000 random selections from the master list of 108 nematode species from this study for each sublist size.

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, characterised 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 exists 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, 1977; 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 causing them to break 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 may be 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

Table 5

Bray–Curtis similarities as calculated from the SIMPER analyses at different taxonomical resolutions between corresponding zones on the two beaches studied

	Species (%)	Genus (%)	Family (%)
Upper beach	17	27	37
Swash/breakers	2	16	27
Subtidal	5	19	40

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 (Crooker, 1977; Alexander et al., 1993).

The severe climatological 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 (Heip et al., 1985). Concerning the low salinities, benthic communities in brackish-water have fewer nematode species than either pure marine or pure freshwater communities (Heip et al., 1995). Some of the nematodes (e.g. *Viscosia viscosa*, *Tripyloides archeruisus*, *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 these 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 nematofauna assemblages of other non-tidal 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*, *Enoplolaimus enoploidiformis*, *Enoplolaimus attenuatus*, *Enoplolaimus villosus*, *Viscosia cobbi*, *Leptolaimus setiger* on the Italian beach were found to have *Trissonchulus benepapilosus*, *Axonolaimus spinosus*, *Enoplolaimus*

balgensis, *Enoplolaimus propinquus*, *Viscosia viscosa* and *Leptolaimus* nsp2 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, Vanavaerbeke 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, micro-tidal 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.

It is concluded that across intermediate, micro-tidal 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 were noted on both upper beaches. The latter is considered to be important ecotones between the terrestrial and marine environment with nematode species from both adjacent ecosystems.

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