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Sandy beaches: state of the art of nematode ecology

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ABSTRACT

In this review, we summarize existing knowledge of the ecology of sandy-beach nematodes, in relation to spatial distribution, food webs, pollution and climate change. We attempt to discuss spatial scale patterns (macro-, meso- and microscale) according to their degree of importance in structuring sandy-beach nematode assemblages. This review will provide a substantial background on current knowledge of sandy-beach nematodes, and can be used as a starting point to delineate further investigations in this field. Over decades, sandy beaches have been the scene of studies focusing on community and population ecology, both related to morphodynamic models. The combination of physical factors (e.g. grain size, tidal exposure) and biological interactions (e.g. trophic relationships) is responsible for the spatial distribution of nematodes. In other words, the physical factors are more important in structuring nematodes communities over large scale of distribution while biological interactions are largely important in finer-scale distributions. It has been accepted that biological interactions are assumed to be of minor importance because physical factors overshadow the biological interactions in sandy beach sediments; however, the most recent results from *in-situ* and *ex-situ* experimental investigations on behavior and biological factors on a microscale have shown promise for understanding the mechanisms underlying larger-scale patterns and processes. Besides nematodes are very promising organisms used to understand the effects of pollution and climate changes although these subjects are less studied in sandy beaches than distribution patterns.

Key words: biodiversity, benthos, distribution patterns, food webs, climatic changes.

INTRODUCTION

Sandy beaches are dynamic ecosystems driven by prominent physical processes that shape the habitat for different functional and taxonomic groups. The term “sandy beach” can be used to describe a wide range of environments, from high-energy open-ocean beaches to sheltered estuarine sand flats (McLachlan 1983). Sandy beaches are, in general, dynamic environments occurring worldwide along ice-free coastlines, and located at the transition between the land and a waterbody such as oceans, seas or lakes. The beach sediment may be supplied by rivers or by the erosion of highlands adjacent to the coast, and the sea may also contribute to the sediment supply through input of biogenic

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structures (animal skeletons, coral and shell fragments) (adapted from McLachlan and Brown 2006). Here, the term sandy beach was used in a narrower context, applying only for high-energy open-ocean or pocket beaches ranging from the reflective to the dissipative extremes.

The sediment is mainly composed of quartz and/or carbonate sands of terrestrial and marine origin, respectively. Small amounts of feldspar, basalt and heavy minerals can also contribute to the sediment composition. Important features to characterize sediments are the grain size, the sorting coefficient and the angularity; all of them influence the porosity of sediments. The combination of permeability and penetrability determines the volume of water percolation, its drainage, and the oxygen penetration in sandy-beach sediments (McLachlan and Brown 2006).

The sandy beach ecosystem can be divided horizontally into different zones consisting of the foredune, backshore, swash/shoreline, surf zone and nearshore (Defeo and McLachlan 2005); vertically, it is represented by the pelagic and benthic systems. Sandy-beach endobenthic communities were largely neglected by ecologists until Remane (1933) initiated the first survey in Germany, with a focus on the benthic community. Today, sandy beaches are still less studied than most other coastal systems (Defeo and McLachlan 2011), and most research on intertidal sandy beaches has been concentrated on macrofauna and on birds (see Cornelius et al. 2001, Defeo and McLachlan 2005, for a review). The less-prominent sandy-beach meiofauna has received considerably less attention. For several years, meiofauna research on sandy beaches was dedicated to general surveys at higher taxonomic levels, and the first investigations focusing on the composition of sandy-beach nematode communities began only in the 1970s (Heip et al. 1985). More recent investigations have dealt with patterns of macro- (10^3m), meso- (m) and microscale (10^{-2}m) distributions and are more often framed in a context of coastal zone management. The macroscale pattern consists of differences between beach types and latitudes, the mesoscale pattern refers to distribution and community structure alongshore and across shore transects and finally the microscale pattern is related to distance between millimeters and few meters (McLachlan and Brown 2006). These three patterns of distribution are used in the context of this review and we chose to focus on nematodes because they are the most dominant group of the meiofauna in soft sediments and are supposed to act as a link for the flux of energy since they can be the food source for macrofaunal organisms and fishes (Esteves and Genevois 2006).

Although nematodes act as important nutritional resources for macroscopic organisms, the functional role of these organisms in sandy beach ecosystem is not well established since this environment is supposed to support three partially unconnected food-webs: a discrete food web consisting of interstitial organisms, a microbial loop and a macroscopic food web (McLachlan and Brown 2006). The relative importance of these three food webs is conceptually different among beach types; for instance, on cold-temperate sandy beaches, a diverse interstitial food web dominates on high wave energy while nematodes and the macroscopic food web are more important in dissipative shores (Menn 2002).

Beaches are squeezed between rising sea level on the marine side and expanding human population and development on the landward side (Schlacher et al. 2008). Therefore, this ecosystem faces numerous threats coming from both directions. Pollution, mining, disruption of sand transport and tourism development are threats mainly originated in the terrestrial side (Brown and McLachlan 2002) while the vulnerability to the impacts of the climate change is more related to the processes occurring in the sea side, such as sea level increase, shore erosion, acidification and increase of sea water temperature (McGlone and Vuille 2012).

The aim of this review is to summarize what is known for sandy-beach nematodes in terms of spatial distribution patterns, temporal variability, food webs, pollution, and climate change. We believe that this review will open a new niche for future researchers to fill gaps in the understanding of nematode ecology.

MATERIALS AND METHODS

A bibliographic survey was done using Web of Science®, SCOPUS and Google Scholar considering works published until early 2015. Solely papers published in scientific journals and those with an ecological purpose related to meiofauna and nematode community from the intertidal region of sandy beaches were selected. Taxonomical articles and those ecological related to subtidal sampling design were largely excluded from the analysis. The selected studies were classified according to 1) type of benthic association (meiofauna or nematode), 2) pattern of distribution (macro-, meso- and microscale), 3) any other ecological approach including temporal variation, pollution, coastal management, colonization, natural impact, recreational activity, climate change and food web, 4) number of sampled beaches (Table I).

RESULTS AND DISCUSSION

In order to provide an overview of world investigations for meiofauna and nematode sandy-beach ecology, we have summarized this information in a world map showing where the studies were conducted (Fig.1) followed by the adopted approach (Table I). Of the 87 meiofauna studies, approximately 50% deal with nematodes (Table I). Our discussion is based on the main topics included in the built table and it was subdivided in the following sections.

PATTERNS OF NEMATODE DISTRIBUTION

Since the first scheme of horizontal faunal zonation was published by Mortensen (1921), several attempts have been made to define well-demarcated zones in sandy-beach sediments, by using physical factors (Salvat 1964, Pollock and Hummon 1971, McLachlan 1980), macroinvertebrates (Dahl 1952, Salvat 1964, 1967, McLachlan and Jaramillo 1995, Defeo and McLachlan 2005, for a recent review) or meiofauna (Blome 1983, Rodriguez et al. 2001, Gheskiere et al. 2004, 2005a, Kotwicki et al. 2005a, Gingold et al. 2010, Maria et al. 2013b, c).

The pattern of nematode distribution in sandy beaches is explained in detail in the following subsections. The variables are discussed below in relation to sandy-beach nematode communities.

Macroscale distribution of nematode communities

This topic has received relatively little attention. Two studies concerning the macroscale latitudinal distribution of sandy-beach nematodes and their diversity suggest that the present pattern follows the trend of increasing diversity toward the tropics (Nicholas and Trueman 2005, Lee and Riveros 2012). Macroscale nematode studies exploring the full range of beach types have not yet been undertaken, but the limited information available shows that nematode diversity is highest in coarse-grained, intermediate sandy beaches (Gheskiere et al. 2005a) or in sheltered conditions (Hourston et al. 2005, Urban-Malinga et al. 2005). It indicates that the a high diversity can be found in the full range of beach types, but the above mentioned references do not use the same methodological strategy what limited the interpretation of the results. A comprehensive understanding of the nematode diversity pattern among different beach types will be only possible when an equal sampling design would be adopted. For instance, the sampling design used to understand the distribution patterns of polychaetes in different beach types could be adopted (Di Domenico et al. 2008); in this study, it is indicated that reflective sandy beaches are more diverse than intermediate and dissipative ones.

TABLE I

Global overview of meiofauna and nematodes studies after 1970, with indication of the focus of the study and the number of beaches included. M: Meiofauna, N: Nematodes, CC: Climate change, Co: colonization, CM: Coastal management; DT: Patterns of Distribution, FW: Food webs P: pollution, TP: Temporal variation.

Code for fig. 1	Reference	Fauna	Focus	N of studied beach	Main Findings
1	Boaden and Platt 1971	M and **N**	DT	1	Daily tidal variations and biotic interactions affect the vertical distribution of meiofauna
2	Gray and Rieger 1971	M and **N**	DT	1	Highest meiofauna richness and diversity in less exposed (finer grain) beach
3	Harris 1972	M	DT	1	High temperatures in the upper beach is a limiting factor for meiofauna zonation
4	Ott 1972	**N**	DT	1	Presence of a typical nematofauna in sulfide systems
5	Hulings and Gray 1976	M	DT	89	Physical factors control the meiofauna abundance (e.g. wave, tide and currents) in tidal beaches while biological interactions (e.g. predation and competition) may control abundance in atidal beaches
6	McLachlan et al. 1977	M	DT and P	1	Meiofauna can occur down to 35 cm. Sewage can cause an increase of the meiofauna abundance, specially the nematode one
7	Platt 1977	**N**	DT	1	Horizontal distribution is driven by physical factors (e.g. grain size) and availability of food while vertical distribution is limited by oxygen availability
8	Munro et al. 1978	M	DT	2	Tropical beach shows higher respiration rates, less microbial production and meiofauna biomass when compared to a temperate one
9	Fricke et al. 1981	M and **N**	P	2	Harpacticoid copepods are more sensitive to oil pollution than nematodes; meiofauna can be recovered six months after an oil spill
10	McLachlan and Harty 1982	M	P	1	Oligochaetes are more sensitive to oil pollution than nematodes; meiofauna can be recovered five months after an oil spill
11	Ansari and Ingole 1983	M	DT	6	Meiofauna is more abundant in the upper 4 centimeters
12	Blome 1983	**N**	DT	1	Nematodes are more abundant in the oxic layers and shows a horizontal zonation; vertical migration is attributed to temperature variations
13	Sharma and Webster 1983	**N**	DT	2	Highest nematode density in well sorted medium grain size: most nematodes occur in the top 4 cm, but those that occur deeper seems to be tolerant to anoxic conditions
14	Ansari et al. 1984	M	DT	2	Highest density in the upper tide level for sheltered beach and highest density in the midtide level for exposed beach
15	Ansari et al. 1990	M	DT	6	Meiofauna abundance is reduced in zones of the beach exposed to desiccation
16	Pattnaik and Rao 1990	M	DT	1	Harpacticoid copepods are the dominant group; meiofauna is abundant in the midtide level occuring up to 20 cm deeper; their spatial distribution is controlled by physical factors.
17	Alongi 1990	**N**	TP	1	Highest nematode densities in austral autumn and winter and lowest densities in spring and summer
18	Ólafsson 1991	M	DT	4	Meiofauna is more abundant in the top 10 cm and nematodes show the most uniform vertical distribution in 95 cm deeper
19	Szymelfenig 1995	M	DT	10	The occurrence of meiofauna taxa is highly correlated to climatic characteristics of the habitats
20	Gourbault et al. 1995	M and **N**	DT	13	Harpacticoid copepods are more abundant than nematodes; this latter taxa shows higher diversity in coarse sediment
21	Long and Ross 1999	**N**	DT	1	Nematodes occur at 30cm deep and their vertical distribution is related to food availability

TABLE I (continuation)

Code for fig. 1	Reference	Fauna	Focus	N of studied beach	Main Findings
22	Nicholas and Hodda 1999	**N**	DT	1	Higher nematode abundance in the mid and high tide level of the beach; persistence of nematode zonation during a short period (24h and under calm conditions
23	Armonies and Reise 2000	M	DT	1	Turbellarian is the dominant taxa; highest meiofauna richness at midtide level
24	Nicholas 2001	**N**	DT	1	Nematodes occur at 60 cm deep; highest densities in the warmer months of the year
25	Rodriguez et al. 2001	M	DT	3	Highest density of the meiofauna in reflective beach and at upper and midtide level
26	Gheskiere et al. 2002	M and **N**	DT	1	Increase in meiobenthic density towards low tide level; presence of nematode horizontal zonation
27	Menn 2002	M	DT and FW	2	Nematodes are an important food sources for higher trophic level in intermediate beaches while macrofauna plus nematodes are the food sources in dissipative beaches
28	De Oliveira and Soares-Gomes 2003	M	P	1	No relationship between sewage disposal and meiofauna
29	Moellmann and Corbisier 2003	M	P	2	Nematodes migrate to the deeper layers of the sediment in intense trampling areas
30	Souza-Santos et al. 2003	M	DT	1	Physical factors (e.g. grain size, chl*a*, phaeopigments, sediment skewness) are the main factors structuring the meiofauna community seasonally
31	Rodríguez et al. 2003	M	DT	10	Richness and biomass of meiofauna increases toward very exposed and coarse beaches
32	Gheskiere et al. 2004	**N**	DT	1	Higher nematode density in the low tide level of the beach; high richness in the midtide level; presence of nematode zonation
33	Rodriguez 2004	M	DT	1	Highest meiofauna density in the midtide level
34	Urban-Malinga et al. 2004	M and **N**	DT	1	Turbellarian is the dominant meiofauna taxa; sheltered beach showed a higher meiofauna density and respiration rates than exposed beach
35	Gheskiere et al. 2005a	**N**	DT	2	Highest nematode density and diversity in coarse-grained sandy beach; presence of isocommunities only in the upper beach
36	Kotwicki et al. 2005a	M	DT	5	Meiofauna show high density in the upper 5 cm; high densities in the midtide level or in the lower tide level; presence of horizontal zonation
37	Calles et al. 2005	M and **N**	DT	2	Turbellarian is the dominant taxa in the sheltered beach; high meiofauna density in the exposed beach; no difference between meiofauna diversity of sheltered and exposed beaches
38	Kotwicki et al. 2005b	M	DT	13	Nematodes are dominant in warmer regions of the globe while turbellarian are dominant in cold water regions; no latitudinal trend was found for meiofauna density or diversity
39	Lee and Correa 2005	M	P	12	Reduction of density and diversity in sites impacted by mine tailing.
40	Gheskiere et al. 2005b	M and **N**	DT and P	4	Lowest species diversity in the upper tide level, especially in touristic beaches
41	Hourston et al. 2005	**N**	DT	3	Highest density in the sheltered habitat, but declining during winter; weak zonation reflecting the presence of a small tidal range
42	Nicholas and Trueman 2005	**N**	DT	3	Richness increases with decreasing latitude

TABLE I (continuation)

Code for fig. 1	Reference	Fauna	Focus	N of studied beach	Main Findings
43	Urban-Malinga et al. 2005	**N**	DT	2	Oligochaete is the dominant taxa; highest diversity in sheltered beaches; density increases towards the low water level
44	Moreno et al. 2006	M and **N**	DT	1	Highest density and diversity in the swash level
45	Harriague et al. 2006	M	DT	1	Higher density in the surfzone than in the swash level
46	Gheskiere et al. 2006	M	CM	1	There is no reduction in density or diversity of mechanical cleaning areas.
47	Urban-Malinga and Moens 2006	M	FW	2	Fastest carbon remineralization in exposed coarse sandy beach
48	Nicholas 2006	M and **N**	DT	1	Nematodes occur at 60 cm deep
49	Albuquerque et al. 2007	M	DT	1	Tardigrades are the most dominant taxa; highest density in the midtide level
50	Papageorgiou et al. 2007	M	FW	1	Bacteria are a potential food source for meiofaunal organisms
51	De Jesús Navarette 2007	**N**	DT	2	Highest richness in coarse-grained beach
52	Mundo Ocampo 2007	**N**	DT	2	Highest density and diversity in the coarse-grained beach
53	Rodríguez et al. 2008	M	DT	10	Eh and water content are the best environmental variables that explains meiofaunal densities
54	Harriague et al. 2008	M	DT	6	Food availability is a key role in structuring meiofauna community
55	Liu et al. 2008	**N**	DT	1	Physical factors (e.g. temperature, chl*a* and grain size are responsible for the nematode community structure
56	Maria et al. 2008	**N**	DT	3	Highest richness in very coarse sandy beach
57	Urban-Malinga et al. 2008	**N**	DT	1	Fastest organic matter weight loss in the highest diverse habitat of the beach - midtide level
58	Delgado et al. 2009	M	DT	23	Gravel and organic matter are best correlated to meiofauna composition and abundance; absence of pattern in meiofaunal abundance along a degree of exposure
59	Grzelak et al. 2009	M	NI	3	Fast recover of meiofauna community after a Tsunami event
60	Gomes and Rosa Filho 2009	M	DT	1	Highest density and diversity in the midtide level; presence of zonation
61	Urban-Malinga and Burska 2009	M	DT	1	Wrack-associated meiofauna community and density from upper and lower shores are similar
62	Veiga et al. 2010a	M	P	9	Low densities in exposed sandy beaches contaminated by polycyclic aromatic hydrocarbons
63	Veiga et al. 2010b	M	DT	2	Highest density in the top 5 cm; oxygen is the limiting factor especially for copepods and ostracods
64	Yamanaka et al. 2010	M	DT	3	Positive correlation between meiofauna abundance and exposure index
65	Gingold et al. 2010	**N**	DT	1	Highest diversity in the midtide level; presence of similar zonation patterns in topographical heterogeneous habitat

TABLE I (continuation)

Code for fig. 1	Reference	Fauna	Focus	N of studied beach	Main Findings
66	Gingold et al. 2011	**N**	DT	1	Patch distribution is more prone to occur in the runnel habitat than in the sandbar
67	Nanajkar and Ingole 2010	**N**	P	1	Highest density in organically polluted sites
68	Barnes et al. 2011	M	DT	6	Highest density in the mid and lower tide level; diversity decreases towards the tropics
69	Maria et al. 2011a	M and **N**	FW	1	Benthic diatoms are the preferential food source of meiofaunal organisms
70	Maria et al. 2011b	**N**	Co	1	Polychaetes seems to facilitate the colonization of azoic sediments by nematodes
71	Riera et al. 2011	M	TV	1	Total abundance and community structure are similar along a year of study
72	Lee and Riveros 2012	**N**	DT	66	Richness decreases with increasing latitude
73	Mantha et al. 2012	M	DT	5	Harpacticoid copepods are thedominanttaxa
74	Maria et al. 2012	M and **N**	DT and FW	1	Biological factors are important in controlling the vertical distribution of nematodes; interstitial and macrofaunal food webs seems do not compete for food sources
75	Riera et al. 2012	M and **N**	DT	2	Copepods are dominant in medium sand while nematodes are dominant in fine sand, i.e. grain size influences in the meiofauna composition
76	Gingold et al. 2013	**N**	CC	1	Temperature increase shows a negative impact on dominant predator species
77	Maria et al. 2013a	**N**	Co	1	Polychaetes did not affect the colonization of azoic sediments by nematodes
78	Maria et al. 2013b	**N**	DT	1	Runnels and sandbar harbors different communities showing different zonation patterns
79	Maria et al. 2013c	**N**	DT	2	Highest density in the upper tide level; gravel is the most important variable that explains the nematode community
80	Schlacher and Hartwig 2013	M	FW	1	Meiofauna community is strongly influenced by sediment grain size; the density of nematodes and ostracod is controlled by bottom up processes
81	Kang et al. 2014	M and **N**	P	1	Reduction of density in oil polluted sites; meiofauna can be recovered one month after an oil spill
82	Kotwicki et al. 2014	M	DT	7	Mean grain size and sorting coefficient showed great influence on meiofauna variation
83	Cooke et al. 2014	M	DT	3	Patch distribution of the meiofauna in the upper tide level, especially harpacticoid copepods and gastrotrichs
84	Netto and Meneghel 2014	M	FW	1	Surfzone diatoms are an important food source for meiofaunal organism of high-energy sandy beaches
85	Sun et al. 2014	M	P	5	Anthropogenic disturbed beaches showed high meiofauna abundance reflecting high chl *a* and dissolved oxygen levels
86	Venekey et al. 2014a	**N**	DT	1	Lowest density in dry months; no influence of the tidal cycle in the nematode density
87	Venekey et al. 2014b	**N**	DT	1	Seasonal and spatial variation of nematode communities in a tropical sandy beach

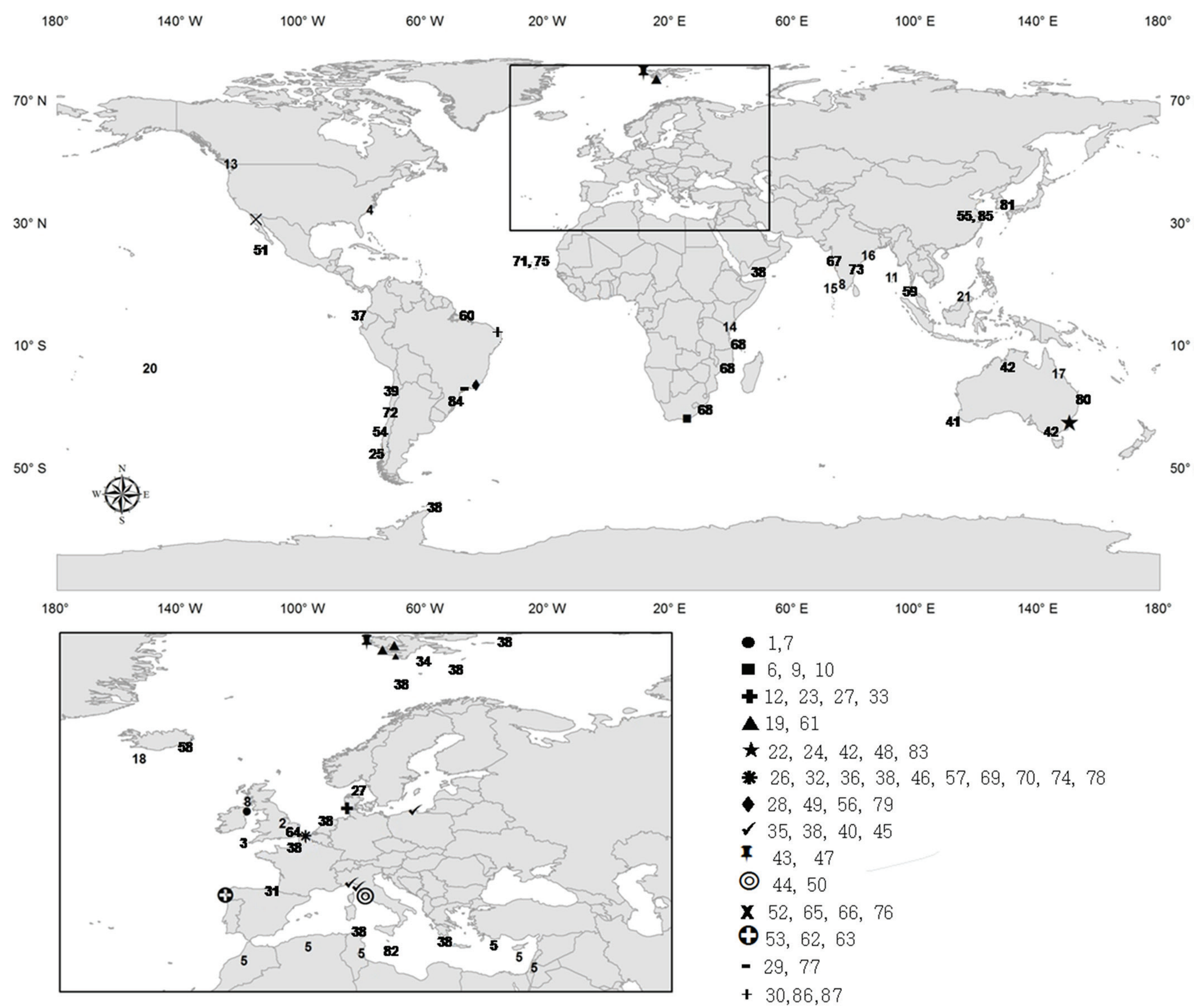

Figure 1 - Global distribution of sandy beach meiofauna studies after 1970 (for studies before 70' see Heip et al. 1985). See Table I for authors and a detailed information of the studies.

Mesoscale distribution of nematode communities

Concerning the horizontal zonation in across-shore transect on a single beach, granulometry, organic input, temperature and salinity are the key factors governing the horizontal nematode distribution (Platt 1977, Gheskiere et al. 2004, Urban-Malignа et al. 2005, Moreno et al. 2006, Maria et al. 2012), whereas biological interactions between macro- and meiofauna and/or among meiofauna organisms have only an indirect effect (Maria et al. 2011b, 2012, 2013a). High diversity is often found where there is an optimal balance of these variables, i.e., physical and chemical conditions are intermediate (Gheskiere et al. 2004, Hourston et al. 2005, Gingold et al. 2010). However, some, more heterogeneous beaches display intertidal sandbars intercalated by depressions, which retain water when tides recedes, across their wide intertidal zone (Masselink et al. 2006); this habitat is therein called runnel and those beaches that bear it are so-called macrotidal ridge-and-runnel beach. On these beaches, for example De Panne Beach in Belgium, studied by Maria et al. (2013b), the two microhabitats (runnels and sandbars) contain different nematode communities, which are reflected in dissimilar across-shore zonation. Three nematode associations (upper, middle and lower beach) are much more evident in the sandbars than in the runnels. These three biological zones on the sandbars were in accordance with the tidal zonation previously observed by Gheskiere et al. (2004) in the same study are contradicting the previous knowledge that the horizontal nematode zonation may just persist for short intervals of time and under calm conditions (Nicholas and Hodda 1999). The main difference between the two most recent studies is that the latter excluded the runnel microhabitat. The inclusion of the runnels by Maria et al. (2013b) showed that the shift over three horizontal nematode communities found in the sandbar was interrupted by the runnel communities. These results contrast somewhat with the results of Gingold et al. (2010) for a macrotidal ridge-and-runnel beach in the Gulf of California, where both sandbars and runnels showed the same pattern of across-shore zonation. We can conclude that next to the horizontal mesoscale, the presence of runnels may influence the nematode zonation. Although both habitats (sandbars and runnels) are horizontally distributed over the sandy beach interface and did not show consistent differences in grain size or chlorophyll *a* content, they were not under the same horizontal gradient of air exposure during low tide.

Based on these results, it is not so much the combination of a physical characteristic that determines the nematode community structure, but rather the degree of variation of these physical factors that affect the nematode horizontal distribution in the intertidal zone.

Another uncommon way to analyze the mesoscale distribution of nematodes is to examine an along-shore transect in the intertidal zone. In this case, samples that are far from each other are more heterogeneous (Nicholas and Hodda 1999, Gingold et al. 2011); however, if the beach has different microhabitats along the across-shore transect, as in the case of a macrotidal ridge-and-runnel beach, the degree of patchiness is more accentuated in the microhabitat with calmer conditions (Gingold et al. 2011).

Microscale distribution

In relation to microscale vertical distribution, desiccation and oxygen availability are considered to be ultimate factors controlling the vertical distribution of the meiofauna (McLachlan 1978, Coull 1988, Maria et al. 2012). Oxygen is a significant limiting factor only in sheltered beaches. In this habitat, marine nematodes are restricted to the first centimeters of the sediment (McLachlan 1978), while in more exposed conditions, nematodes can be distributed more deeply (Urban-

Malinga et al. 2004). This phenomenon has led to the use of vertically undivided cores in meiofauna sandy-beach sampling, or the use of cores divided into large intervals of cm (i.e., larger than 1cm) (Blome 1983, Sharma and Webster 1983, Long and Ross 1999, Urban-Malinga et al. 2005). Moreover, samples are usually taken during low tide. This is a sampling strategy initially adopted for the macrofauna to avoid contamination by tidal migrants. It is however, also known that nematodes can migrate downward (Boaden and Platt 1971) or upward (McLachlan et al. 1977, Maria et al. 2012) in the sediment column at high tide. Therefore, to better understand the vertical distribution of nematodes, a finer-scale sampling scheme should be adopted, using cores subdivided into thin layers of a few centimeters, when dealing with protected and dissipative sandy beaches. Joint et al. (1982) has already demonstrated that nematodes showed different vertical distribution patterns at mm scale in an intertidal sandflat.

The relationship between the vertical distribution of sandy-beach nematodes and the tidal cycle was demonstrated by Boaden and Platt (1971) and McLachlan et al. (1977). These two studies were rather contradictory. The former authors showed that nematodes move down in the sediment, escaping from the upper layers and thus avoiding being washed away by the turbulent conditions. McLachlan et al. (1977) demonstrated that meiofauna living above the depth of the permanent water table undergoes vertical movements coupled with the tidal cycle, i.e., move up during submersion and vice-versa. Since the depth fluctuation of the groundwater level is directly linked to the different tidal stages (Urish and McKenna 2004), the upward movements of the meiofauna are closely linked to the tidal cycle. Indeed, the vertical distribution of many nematode species in the upper sediment layers of De Panne Beach during submersion was mainly explained by upward passive transport from deeper layers. Downward movements during emersion were explained by a combination of passive and active transport (Maria et al. 2012). Passive transport could be attributed to the drop in the underground water level, while active migration would occur to avoid harsh conditions created by drying of surface layers (McLachlan et al. 1977).

Although the investigation of the importance of the tidal cycle for the vertical distribution of the nematodes by Maria et al. (2012) was restricted to the upper five centimeters of the middle beach level, these results could be extrapolated to the other intertidal beach levels by combining the observations of the groundwater discharge in the beach sediments during the different tidal stages. The water table is very close to the sediment surface toward the low-water line during low tide. Therefore, here the vertical rise of the water table during the incoming tide would be more discrete than toward the high-water line. Consequently, upward passive transport of nematodes in the low intertidal beach would be less likely, so that nematodes would not dramatically modify their vertical distribution over the tidal cycle in this part of the beach. On the other hand, changes in the nematode vertical distribution over the tidal cycle would be more evident in the upper beach.

Biological interactions may also affect the vertical distribution of nematodes in the sediment, and may occur among different sizes of organisms. The role of biological interactions, such as competition and predation, in regulating macrofauna zonation remains little known (McLachlan and Jaramillo 1995). From the point of view of the meiofauna, biological interactions were only suggested to be important for atidal beaches (Hulings and Gray 1976), but Maria et al. (2012) showed that the species-specific vertical distribution of nematodes over a tidal cycle is clearly driven by biological interactions. The importance of predation was evidenced by the predacious nematode *Enoplolaimus litoralis*. This species was recorded in the layers just above the deposit-feeder *Daptonema normandicum*, which inhabited the subsurface 2-5-cm layers during submersion (Maria et al. 2012). The same pattern of predator-prey segregation was also observed in the coarsest sediments (<170µm and less than 5% silt) of a mudflat under high hydrodynamic stress, and was explained by food preferences (Steyaert et al. 2003). During exposure in De Panne Beach, *E. litoralis* was no longer restricted to the 1-3-cm layers as during submersion, but was found deeper in the sediment. This change may be the consequence of active migration, since another thoracostomopsid nematode, *Enoploides longispiculosus*, has shown high motility to actively catch deeper-living prey when the surface sediment was not water-saturated and the groundwater level was lowered (Steyaert et al. 2001). This migration took place during ebb tide, and also coincided with a low abundance of suitable prey species within the upper 5cm.

The importance of competition in driving the vertical distribution of species is confirmed to some extent by the vertical segregation of nematode species in the sediment. Species with a more ^{13}C-enriched diet, such as *Sigmophoranema rufum,* were abundant in the upper two centimeters of the sediment, whereas species belonging to epistrate (2A) and non-selective feeder (1B) groups that exploit a more ^{13}C-depleted diet showed higher densities in the subsurface layers - 2 to 3 cm - (Maria et al. 2012). The importance of food competition between *S. rufum* and 1B/2A nematodes was supported by the results of an enrichment experiment, since the diatom uptake of epistrate nematodes was highest when the same food sources (diatoms) were offered to the nematode community. This may indicate that 2A nematodes are better competitors (Maria et al. 2011a).

Nematode Communities in Beach Food Webs

Food webs in sandy beaches differ with the beach type, and particularly with the degree of coupling between the beach and the surf zone (McLachlan and Brown 2006). Two distinct ecosystems are recognized: (1) beaches with little or no surf zone (reflective beaches), which are dependent on food input from the sea; and (2) beaches with extensive surf zones (dissipative beaches), which have high primary production from the surf diatoms that shows a vertical migration from the sediment deep in the surf zone to the water (McLachlan and Brown 2006). This ecosystem may support three partially unconnected food webs: the interstitial food web, the microbial loop (which is restricted to the surfzone and has been little investigated), and the macroscopic food web (Heymans and McLachlan 1996).

There are two studies that investigated the importance of nematodes in sandy beach food webs. Menn (2002) showed that a high wave energy beach has an impoverished food web due to a more diverse meiofauna while a less dynamic sandy beach showing a high dominance of nematodes in the meiofauna community can support a richer food web.

The second study assessed the integrative food web of the middle part of De Panne Beach by means of stable isotope analyses (Maria et al. 2012). Vascular plants were not included as a possible food source, since they are important primary producers of the supralittoral zone of Belgian sandy beaches (Speybroeck et al. 2008) and were assumed to be of less importance for the middle beach of De Panne, where a concrete dike separates the dunes from the beach (Gheskiere et al. 2004). Most of the meiobenthic species (nematodes and copepods) utilize more carbon-enriched food sources than the macrofaunal organisms, indicating that there was no competition for food between these two classes of organisms. Phytoplankton and suspended detritus seem to be more important food sources for macrobenthic organisms on dissipative and reflective sandy beaches (Bergamino et al. 2011, Maria et al. 2012), while microphytobenthos

(MPB) is utilized as a carbon source by nematodes, copepods, turbellarians and a few macrofaunal species, such as two species of the amphipod *Bathyporeia* (Maria et al. 2012). Laboratory experiments also indicated a higher uptake of benthic diatoms by these organisms (Maria et al. 2011a). Nonetheless, MPB is considered a limiting food source for sandy-beach organisms due to its low primary productivity, probably because of the strong hydrodynamic forces acting on the beach interface (McLachlan and Brown 2006); the preference for benthic over planktonic diatoms, as demonstrated by Maria et al. (2011a), leads to us to speculate that the absence of a diatom biofilm in sandy beaches, a condition extremely common on tidal flats, can be attributed to the rapid consumption of diatoms by benthic sandy-beach organisms.

Although some field investigations and experimental approaches demonstrated that nematodes may serve as food source for large organisms, such as shrimps and fishes (see Coull 1990, for a revision), there was no explicit trophic link between macrofaunal and nematode species evidenced by isotopes analysis (Maria et al. 2012). It can be easily explained by the few numbers of species investigated in the study.

POLLUTION

A large set of features, including ease of sampling, omnipresence, high diversity, short generation time, and absence of a planktonic stage, make nematodes an excellent tool to evaluate the ecological condition of different environments (Giere 2009); however, very few studies have dealt with nematodes at lower taxonomic resolution (e.g. Fricke et al. 1981, Gheskiere et al. 2005b, Nanajkar and Ingole 2010). This may be related to the difficulty and tedium of species identification; therefore, pollution studies tend to use broader taxonomic categories and the two numerically dominant groups, nematodes and copepods, are the main focus of such studies.

As seen in Table I, the four pollution-related studies focusing on sandy-beach nematodes dealt with different subjects: oil, recreational activities, and sewage discharge. In terms of oil pollution, the nematode density was still similar to reference sites when the sediment of the polluted site was not mechanically removed (Fricke et al. 1981). This finding contradicts the expected pattern of reduction in density at sites where an oil spill occurred (Wormald 1976, Giere 1979, Danovaro et al. 1995, Kang et al. 2014), but other field and experimental studies have indicated that nematodes are insensitive to oil pollution (Boucher 1980, Warwick et al. 1988, respectively). On the other hand, a mechanical treatment of the oil-polluted sediment had more impact in the nematode density than the pollution by oil *per se,* and more individuals were found in the deeper layers (Fricke et al. 1981).

There is little controversy around the time required for meiofauna recovery in areas subjected to oil spills. Fricke et al. (1981) found that meiofauna had recovered six months after an oil spill on the coast of South Africa (SA), while this time period was not enough for meiofauna recovery in three beaches located on the coast of Galicia (GC) (Veiga et al. 2010a). The lack of a similar response here is probably related to the difference in the magnitude of the oil spill (31,000 tons in SA *x* 50,000 tons in GC), and the local hydrodynamics (exposed in SA and under intermediate conditions in GC). *In situ* experiments have shown that sandy-beach meiofauna can recover their density and community composition one month after an oil spill when very small quantities of oil are spilled (Kang et al. 2014).

The discharge of domestic sewage onto sandy beaches is a common problem in coastal areas, especially in developing countries, where a large part of the population may develop coastal areas in an unregulated manner. Nanajkar and Ingole (2010), studying the impact of chronic sewage discharge on a tropical sandy beach, observed that nematodes responded to the organic enrichment with an increase in density and dominance of one genus (*Daptonema*) in the areas closest to the sewage outflow. These authors believed that the non-selective deposit-feeding activity of *Daptonema* aided the bioremediation of the site.

From the point of view of beach management, this ecosystem has great socio-economic value as a recreational area and is therefore considered a key tourist destination during holiday periods. The recreational use of sandy beaches has a significant impact in terms of reduction of meio- and nematofauna diversity, which responds by shifting to a large number of species with small size, rapid growth and high rates of reproduction (r-strategists). Nevertheless, this reduction may only be associated with the upper beach, which can be mechanically cleaned daily (Gheskiere et al. 2005b). On the other hand, in intense trampling activity in the intertidal area leads the meiofauna to migrate downward to layers deeper than 5cm (Moellman and Corbisier 2003).

Climate Change

Concerns about global warming have dramatically increased and it is widely understood that sandy beaches will be drastically affected, especially by sea-level rise. To date, very few studies have dealt with this subject (e.g. Kont et al. 2003, Lock et al. 2011, Mead et al. 2013). In terms of nematodes, only the study of Gingold et al. (2013) has concentrated on this group in sandy-beach environments. Laboratory microcosm experiments have shown that high temperatures lead to loss of important predacious and omnivorous nematodes that are important for the top-down control of the community, consequently leading to a change in the food web.

Concerning sea-level rise, the nematode intertidal community will be immersed more often or will become permanently submersed; therefore, we can speculate that many intertidal species will be unable to withstand long periods submerged. This may eliminate many of these species and consequently reduce biodiversity in areas where the nematode biodiversity is presently very high. Besides, the rapid sea level rise will move beaches towards a more reflective morphodynamic state which is characterized by low meiofauna abundances (Yamanaka et al. 2010). In both cases, the reduction in nematode abundance may lead to a lost in ecosystem functioning. However, this topic requires further investigation.

CONCLUSIONS

Sandy beach ecosystems are one of the less studies coastal ecosystems; it can be easily exemplified by a simple search in the Web of Science which the number of studies in this environment correspond to 10% and 25% of those realized in estuaries and mangroves, respectively. The current state of knowledge shows us that over the decades, sandy beaches have been the scene of studies focusing on community and population ecology, both in relation to morphodynamic models. The combination of physical factors (e.g. grain size, tidal exposure and degree of drainage) and biological interactions (e.g. trophic relationships and competition) is responsible for the spatial distribution of nematodes. The degree of importance of these factors is related to the kind of distribution pattern analyzed; physical factors are more important in structuring nematodes communities over large scale of distribution (e.g. macro- and mesoscale) while biological interactions are largely important in finer-scale distributions.

Although nematodes are the dominant meiofauna group and are largely used as indicator of environmental conditions it is of primordial importance to understand the natural relationship between the environment and these organisms. Therefore, to understand better the ecological processes driving the sandy-beach nematode community is necessary to increase the efforts in understanding latitudinal and beach type patterns also taking into account the environmental heterogeneity.

In terms of energy, nematodes are considered an important link between micro- and macrofaunal organisms; however, isotopic studies showed that there is a clear separation between the interstitial and macrofaunal food webs at least for temperate sandy beaches.

Even though the nematode diversity is related to physical and biological interactions, it is also related to the degree of impact occurring in the environment; under disturbed conditions (i.e., organic pollution, oil pollution, beach cleaning or trampling) the diversity decreases and the density of some dominant species (especially deposit feeders) increases, the natural recovery depends on the amount and duration of the impact.

And last but not the least, the relationship between nematodes and climate change is a promising research area, which many aspects must still be evaluated for sandy-beach organisms, but a common believe is that the nematode density must decrease.

This review elucidates the current knowledge of sandy-beach nematodes and as this ecosystem is easily reached and occurs worldwide we should stimulate more and more studies that can provide a more comprehensive approach toward a better understanding of the physical and biological interactions among sandy-beach organisms. This is essential in order to understand the possible effects of key human pressures on the beach ecosystem.

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RESUMO

Nessa revisão, reunimos o conhecimento existente sobre a ecologia dos nematódeos de praias arenosas, em relação à distribuição espacial, teias tróficas, poluição e mudanças climáticas. Tentamos discutir os padrões em escala especial (macro-, meso- e microescala) conforme o seu grau de importância na estruturação das associações de nematódeos em praia sarenosas. Esta revisão fornece uma base substancial sobre o conhecimento atual dos nematódeos de praias arenosas e poderá ser usada como um ponto de partida para futuras investigações nesse campo da Ciência. Por décadas, as praias arenosas têm sido objeto de estudos enfocando a ecologia de comunidade e populacional, ambas relacionadas aos modelos morfodinâmicos. A combinação dos fatores físicos (p. ex., tamanho do grão, nível de exposição às marés) e os fatores biológicos (p. ex., relações tróficas) é responsável pela distribuição espacial dos nematódeos. Em outras palavras, os fatores físicos são mais importantes na estruturação das comunidades de nematódeos em grandes escalas, enquanto que as interações biológicas são mais relevantes em escalas menores de distribuição. Tem sido aceito que as interações biológicas seriam de menor importância porque os fatores físicos ocultam as interações biológicas nos sedimentos de praias arenosas; no entanto, estudos experimentais mais recentes (*in-situ* e *ex-situ*) sobre o comportamento e os fatores biológicos (em microescala) têm mostrado resultados promissores para a compreensão dos mecanismos subjacentes aos processos e padrões em maior escala. Além disso, os nematódeos são organismos muito promissores para serem utilizados a fim de compreender os efeitos da poluição e das mudanças climáticas, ainda que esses dois tópicos sejam menos estudados em praias arenosas do que os padrões de distribuição.

Palavras-chave: biodiversidade, bentos, padrões de distribuição, teias tróficas, mudanças climáticas.

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