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ORIGINAL PAPER

Gradients in biodiversity and macroalgal wrack decomposition rate across a macrotidal, ultradissipative sandy beach

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Abstract The decomposition process of, and the meiobenthic and nematode colonization on, stranded macroalgae were studied along a macrotidal, ultradissipative sandy beach gradient at De Panne (Belgium). The horizontal patterns of macro- and meiofaunal densities and diversity in this beach have been well-documented. Defaunated *Fucus* detritus was buried in situ in litter bags, 10–15 cm under the sediment surface, at seven stations across the beach profile. Colonization by (meio)fauna and organic matter decomposition rates measured as carbon, nitrogen, phosphorus and dry weight loss, were studied after 10, 21 and 52 days of incubation. Algal detritus was colonized mainly by nematodes dominated by Rhabditidae, *Sabatieria*, Dorylaimoidea, *Monhystera*, *Paracanthonchus* and *Daptonema*. Organic matter weight loss was slowest at the higher and lower shore and fastest in the mid-shore, in line with the horizontal pattern of nematode diversity in the beach sediment. However, there was no consistent relationship between nematode diversity inside the litter bags and organic matter weight loss, prohibiting an unequivocal conclusion on whether the observed parallel between extant nematode diversity and organic matter decomposition rate indicates a causal relationship or follows from the fact that both are governed by the same set of physicochemical conditions.

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Introduction

Effects of biodiversity—usually defined as species numbers—on ecosystem functioning are at the heart of a lively debate on whether and how current (high) species extinction rates may jeopardize ecosystem 'services' to man. To date, a majority of empirical studies on this issue have focused on terrestrial systems, with particular emphasis on the relation between plant species richness and (primary) productivity in grasslands (Hector et al. 1999; Kinzig et al. 2001; Loreau et al. 2001). Fewer studies have dealt with aquatic environments (Gessner et al. 2004), although these may have a number of unique features which are likely to bear on biodiversity-functioning relationships (Giller et al. 2004; Emmerson and Huxham 2004). There is thus an urgent need for both experimental and descriptive studies illustrating (cor)relations between species diversity and rates of selected ecosystem processes in aquatic environments.

Marine benthic systems tend to be characterized by (1) both high species density and diversity (Snelgrove 1997, 1999), (2) strong biogeochemical dynamics and gradients

(Valiela 1995), and especially in intertidal environments, (3) frequent disturbance, following often steep spatial gradients (Underwood 2000; Kaiser et al. 2005). Intertidal sandy beaches, for instance, typically show distinct horizontal gradients in both physical disturbance intensity and species density/diversity patterns (a.o. Brown and McLachlan 1990; McLachlan and Turner 1994; McLachlan and Jaramillo 1995; Degraer et al. 1999; Nicholas and Hodda 1999; Armonies and Reise 2000; Gheskiere et al. 2004; Defeo and McLachlan 2005). Whether and how this translates into beach ecosystem functioning, remains to be studied.

Sandy beaches are almost entirely supported by allochthonous inputs of carbon and organic matter (phytoplankton, macrophyte detritus, etc.) because only little primary production occurs on the beach itself (Brown and McLachlan 1990). In many coastal regions where the production of macrophytes is high, inputs of macroalgal wrack represent a major source of carbon (Griffiths et al. 1983; Dugan et al. 2003). By contrast, where such inputs of macrophytes are low or lacking, beaches are mainly fuelled by the deposition of suspended organic matter. Sandy beaches are classified as permeable marine sediments (i.e. those sediments that are sufficiently coarse-grained to allow measurable porewater flows when natural pressure gradients are applied) and provide essential ecological functions. The main feature of these systems is effective transport (i.e. diffusion, advection, dispersion and re-suspension). As a consequence, these sediments are biogeochemically active and participate importantly in the cycling of carbon and other elements, despite generally low organic matter concentrations and low standing stocks of reactants (Shum and Sundby 1996). Suspended particles, algae and bacteria are transported with the penetrating water into the sediment, where they become trapped in the pores (Huettel et al. 1996; Huettel and Rusch 2000) and processed by sediment-associated biota (McLachlan et al. 1981; McLachlan and Turner 1994). In addition, the direct water flows through permeable sediments enhance the decay of trapped organic particles by improving oxygen supply. Thus, large volumes of seawater penetrate the interstitial system by wave and tidal energy, and the associated organic matter is mineralized by interstitial organisms (McLachlan 1990; McLachlan and Turner 1994). Several studies, albeit mostly from estuarine habitats, have hinted at an enhancement of mineralization rates of organic matter and bacterial production in the presence of meiofauna (Coull 1999).

While on wrack-dominated beaches the structure, composition and diversity of macrofauna are closely linked to the input, size and fate of macrophyte wrack (Griffiths et al. 1983; Stenton-Dozey and Griffiths 1983; McLachlan 1985; Dugan et al. 2003; Olabarria et al. 2007), macrofauna on 'clean' beaches tends to increase in density, biomass and diversity from the high towards the low waterline (Brown and McLachlan 1990; Souza and Gianuca 1995; Degraer et al. 1999). Similarly, Koop and Griffiths (1982) reported on gradients in bacterial densities and biomass, with highest values at the low waterline. By contrast, the few studies which have hitherto investigated horizontal gradients of meiofaunal communities along dissipative tidal beach slopes highlight a discrepancy between density (showing basically similar patterns as for macrofauna) and diversity patterns, the latter typically showing a unimodal distribution with beach elevation (Armonies and Reise 2000; Gheskiere et al. 2004). Studies on horizontal zonation of ecosystem process rates, such as primary productivity and decomposition, on sandy beaches are scant and none refer to (ultra)dissipative beaches.

The aim of this paper was to integrate biodiversity patterns and ecosystem process rates along a sandy beach slope. We, therefore, performed an in situ litter bag experiment to study the decomposition of buried macroalgae at seven stations along the slope of an ultra-dissipative sandy beach at the Belgian coast (De Panne), where horizontal patterns—in terms of density as well as species diversity—of both macrofaunal and metazoan meiofaunal communities have been well-documented (Degraer et al. 1999; Gheskiere et al. 2002, 2004).

Materials and methods

Study site

Our study site (51°05′30″N, 02°34′01″E) is located at De Panne, on the western part of the Belgian coast just a few hundred meters from the Belgian-French border, in front of the dune nature reserve 'Westhoek' (Fig. 1). The intertidal zone is approximately 440-m wide, with a beach slope of about 1:90 to 1:100 and mean spring and neap tide ranges of 4.97 and 3.02 m, respectively. The beach slope is 'crossed' transversely by several runnels which retain seawater on ebbing tide. More detailed descriptions of the study site can be found in Degraer et al. (1999) and Gheskiere et al. (2002, 2004).

The experimental stations along the beach slope were chosen as a function of inundation/exposure time: the uppermost station was situated just above the high waterline (just below MHWN level), the others followed the receding waterline at ca. 1-h intervals. In total, seven stations along the beach slope were selected (Fig. 1). No stations were located inside or on the edges of runnels. The experiment was started on 26 November 2001 upon high and low tide levels of +327 and +19 cm, respectively, relative to mean low water spring level. The distance between the

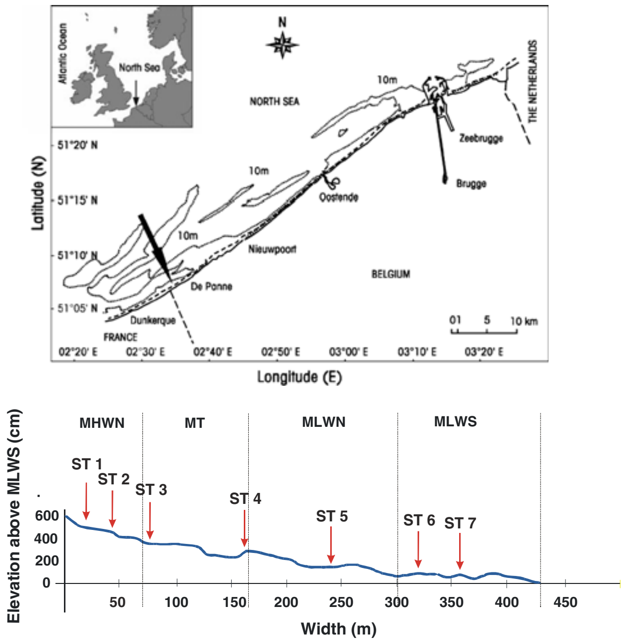

Fig. 1 Map of the study area and distribution of the sampling sites along the beach profile

higher- and lowermost station spanned ca. 353 m. As such, our stations roughly conform to S1–S7 in Gheskiere et al. (2004) and comprise the following zones: upper beach (S1, S2), drift-line (S3) and middle beach (S4 – S7).

Experimental strategy

We performed litter bag incubations with bags made up of mesh with a pore diameter of 250 µm, excluding most macrobenthos. Litter bags measured approximately 10 × 12 cm.

Litter bags contained 4 ± 0.5 g (dry weight) of fresh *Fucus* thalli collected elsewhere along the Belgian coast. Thalli were thoroughly rinsed with tap water, bathed in 70% ethanol for 15 min, rinsed again with tap water and dried to constant weight (60°C). They were partially re-hydrated on site just prior to the start of the experiment.

Because of strong hydrodynamical forcing, we chose to bury litter bags at a depth of approximately 10–15 cm to avoid their possible erosion. At each station, nine short 10- to 15-cm deep runnels, perpendicular to the waterline, were dug in a row parallel to the waterline. Separate runnels were interspaced by 50 cm. Each runnel received one litter bag. The runnels were closed again using the original sediment.

Sampling was performed after 10, 21 and 52 days of incubation by digging up the litter bags from three runnels per station. However, due to a period of strong (north-) westerly winds in the second half of December, the last sampling (52 day) was only successful at the higher- and lowermost station. At all other stations, most litter bags had been washed out. On the first sampling occasion (10 day), samples of station 4 were lost.

Sample processing: decomposition

Litter bags were carefully put in impermeable plastic bags on site and transported to the laboratory. There, the entire litter bag content was thoroughly washed with tap water over a stack of two sieves with mesh sizes of 500 and 38 µm, respectively. Prior to washing, litter bags were first submerged in a 7% $MgCl_2$ solution to anesthetize (meio)-fauna, which facilitates their release from the algal thalli (Hulings and Gray 1971).

Cleaned algal fragments retained on the 500- and 38-µm sieves were collected and dried (60°C) till constant weight, which allowed calculation of % dry weight loss. Dry samples were then ground to a powder using a Fritsch Pulverisette. Subsamples were used for C/N-analysis on a Carlo-Erba NA 1500 elemental analyzer, and for determination of phosphate concentration. Algal powder for phosphate analysis was subjected to acid digestion (2 h at 125°C) in a solution of 37% HNO_3 and 5.3% HCl. Phosphate concentrations were determined using a slightly modified version of the ascorbic acid method (Greenberg et al. 1992) on a SKALARSAN PLUS type ESD–1 automatic chain with photometric detection (simultaneously at 880 and 1,010 nm for optical matrix correction). Cumulative loss percentages of C, N and P were calculated following the equation:

$$\% E_{\mathrm{loss}} = 100 \times [(\mathrm{DWT}_0 \times \% E_0) - (\mathrm{DWT}_X \times \% E_X)]/(\mathrm{DWT}_0 \times \% E_0)$$

where DWT_0 and DWT_X are dry weight before and after the experiment and % E_0 and % E_X are the corresponding elemental concentrations (as %) in the remaining algal material.

Sample processing: fauna

The faunal fractions retained on the 500- and 38-µm sieves were jointly preserved in buffered 4% formaldehyde and stained with Rose Bengal to facilitate counting and sorting. When significant amounts of sediment were present, samples were first centrifuged three times with Ludox HS40 at a specific density of 1.18 to elutriate all metazoan fauna (Vincx 1996). All fauna was then counted at higher taxon level under a stereomicroscope, and nematodes were sorted at random by hand and mounted on permanent glycerin slides. When less than 110 nematodes were obtained, they were all transferred onto slides; when more nematodes were present, the first 110 were picked up. Prior to slide preparation, nematodes were first transferred stepwise from formalin to glycerin through a series of ethanol–glycerin solutions (Vincx 1996). Nematodes were identified to genus level using pictorial keys (Platt and Warwick 1983, 1988; Warwick et al. 1998) and other relevant literature.

As a fixed number of individuals rather than a constant proportion of each sample was identified, three different diversity measures were calculated in order to compare genus richness and diversity between samples. Diversity was expressed as the N_1 diversity index (Hill 1973), which is a normalization of the Shannon–Wiener index H' and as such incorporates both a richness and an evenness component. We also calculated Margalef's index (d), which standardizes the number of genera against the number of individuals in a sample. Finally, the rarefaction index ES(x) (expected number of species), which provides an estimated number of species/genera present in a population of x individuals and is independent of sample size, was calculated (Hurlbert 1971). We used the expected number of species of a sample of 11 individuals [ES(11)], the lowest number of individuals identified in any single sample. All diversity indices were calculated with the software package PRIMER (version 5) (Clarke and Warwick 1994).

Data analysis

Cumulative losses of dry weight, C, N and P as well as C/N-ratios and total nematode or faunal densities were analyzed for differences between stations (seven stations) and times (two times, as the 52-day sampling only provided information on two of the seven stations) using two-way analysis of variance. Tukey's HSD-test was used for pairwise comparisons. Data were log(x+1) transformed where necessary (% nitrogen loss) to meet the assumptions of normality and homogeneity of variances. Spearman rank correlation analysis was performed to assess relationships between nematode density or diversity indices and organic matter weight loss. These analyses were performed using the software package STATISTICA, version 6.0.

ANOSIM based on the Bray–Curtis similarity matrix (Clarke 1993) (PRIMER version 5) was used to test for differences in nematode community structure in litter bags between study sites. Analyses were performed on standardized, square-root transformed nematode abundance data. Due to a lack of sufficient replicates on the second sampling ANOSIM was based on results from the first sampling only.

Turnover of nematode communities across the beach slope was assessed with a non-metric multidimensional scaling (nMDS) on standardized, double-root transformed nematode abundance data using Bray–Curtis similarities. Data from both sampling occasions (day 10 and day 21) were pooled for this analysis.

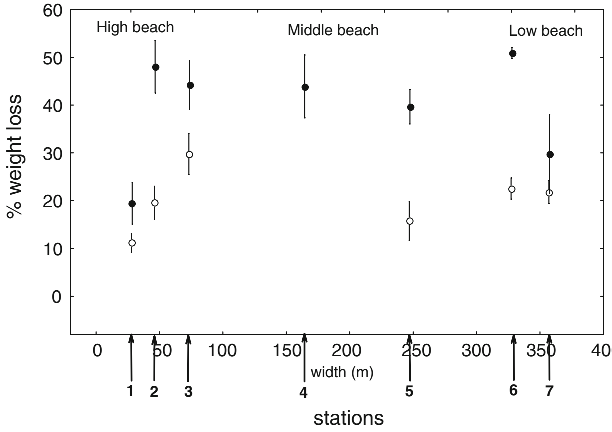

Fig. 2 % Dry weight loss across the beach slope after 10 and 21 days. Data are means ± 1SE of three replicates. *Open symbols* first sampling, *closed symbols* second sampling

Results

Dry weight and carbon loss

Dry weight loss (Fig. 2a, b) was significantly affected by time and site (both $P < 0.0005$). Weight loss typically more or less doubled from the first to the second sampling, indicating a fairly linear weight loss with time over the first 3 weeks of incubation. Site differences showed a 'unimodal' sort of pattern across the beach, with highest weight losses at stations 3–6 and lowest losses at the lower- and highermost stations. This pattern was more pronounced upon the second sampling, albeit on both sampling occasions the lowest weight losses were found at stations 1 and 7.

After 52 days of incubation, weight losses at sites 1 and 7 averaged 35.53 ± 6.36 and 46.71 ± 6.70%, respectively (data not shown).

The patterns of carbon loss matched those of dry weight loss very well and are therefore not depicted here. In brief, C-losses ranged from 17 (S1) to 37% (S3) on the first sampling, from 27 (S1) to 52% (S6) on the second sampling, and from 40 (S1) to 49% (S7) after 52 days. Over the first 21 days of the experiment, carbon losses at S1 and S7 were significantly lower than at all other stations ($P < 0.01$).

Nitrogen loss

At the first sampling, 50–60% of N had already disappeared from the algal thalli in all sites. This percentage increased, albeit moderately, after 21 days with only a minor further N-loss after 52 days. In addition to time ($P < 0.0005$)), site ($P < 0.001$) had a significant effect on cumulative nitrogen losses (Fig. 3a, b). Site differences

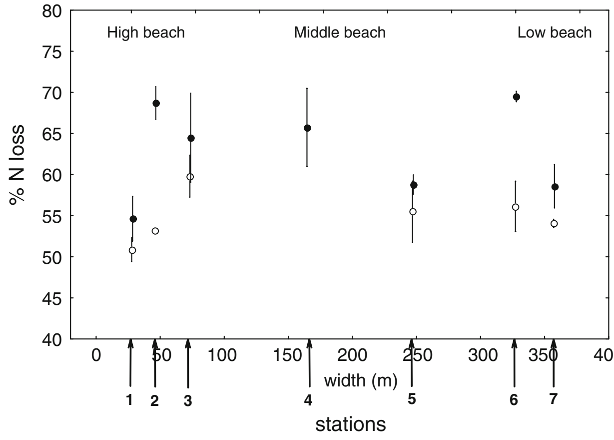

Fig. 3 % Nitrogen loss across the beach slope after 10 and 21 days. Data are means ± 1SE of three replicates. *Open symbols* first sampling, *closed symbols* second sampling

were broadly similar as for weight and carbon losses, but slightly less pronounced, losses at sites 3 and 6 being significantly higher than at all other stations.

C/N-ratio

C/N-ratio differed significantly with time ($P < 0.005$) and site ($P < 0.05$). It increased from an initial value of 11.2 to values between 15 and 20 at all stations after 10 days, with a subsequent small but statistically significant ($P < 0.01$) decrease at the second and third (only data on sites 1 and 7 available) sampling event (Fig. 4a, b). The pattern of C/N-ratio across the beach was more or less the inverse of that for weight, carbon and nitrogen losses, with highest values at the upper beach but with much less pronounced differences. The only significant pair-wise difference was that between sites 1 and 3 ($P < 0.05$).

Orthophosphate loss

Orthophosphate concentrations did not significantly vary with time, although the main trend (an increased concentration with time) resembled that of nitrogen concentration; they did, however, show significant site differences ($P < 0.05$) (data not shown). Lowest phosphate concentrations were found at the upper beach, but pair-wise comparisons yielded at best borderline significant differences ($0.05 < P < 0.10$) between sites 1 (lowest) and 3 (highest).

Fauna

Faunal densities remained relatively low in most litter bags. Macrofauna—mostly large oligochaetes, some insect larvae and polychaetes—were only occasionally encountered (1–4 ind. per bag recorded at the first and second sampling event at stations S5–S7). Nematodes and oligochaetes were the only meiofauna. Oligochaete densities were extremely variable, ranging from 0 in many samples to a maximum of 234 ind. at the second sampling occasion. High oligochaete densities coincided with high nematode densities and were limited to the highermost station (S1). At other stations oligochaetes were only occasionally found (≤3 ind. per litter bag). Nematodes were present in all litter bags, with densities ranging from 11 to 3,559 ind. At the first sampling, meiofaunal densities were low at all sites (from 16 ± 3.6 ind. per bag at S2 to 149 ± 156 ind. per bag at S6) (Fig. 5). They subsequently stabilized or even decreased at some sites, but strongly increased at the highermost station (S1), where average densities after 52 days exceeded 1,164 ind. per litter bag. Generally, the lowest nematode densities after the first sampling event were recorded at stations 2–3 (on average 16 and 20 ind. per bag,

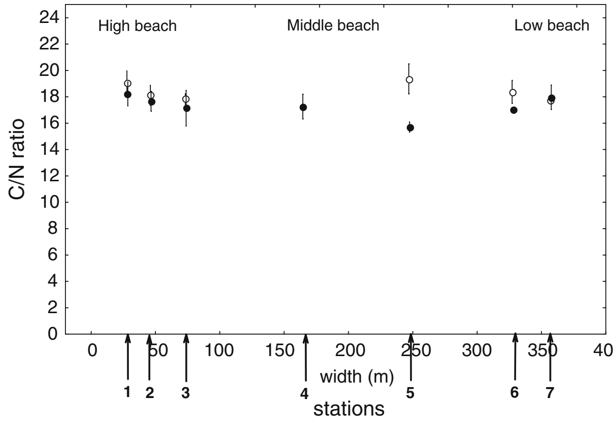

Fig. 4 C/N-ratio across the beach slope after 10 and 21 days. Data are means ± 1SE of three replicates. *Open symbols* first sampling, *closed symbols* second sampling

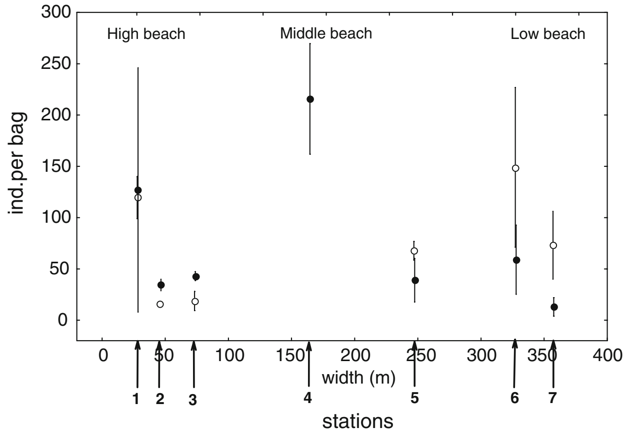

Fig. 5 Total meiofaunal densities across the beach slope after 10 and 21 days. Data are means ± 1SE of three replicates. *Open symbols* first sampling, *closed symbols* second sampling

respectively), and the highest at S1 and S6 (119 and 149 ind. per bag, respectively). After the second sampling event the lowest nematode densities were noted at S5 and S7 (on average 39 and 13 ind. per litter bag, respectively) and the highest at S1 and S4 (127 and 216 ind. per bag, respectively). Because the data from the last sampling event were omitted from the statistical analysis, there was no significant overall effect of time. However, site had a highly significant effect on nematode densities, which were on average higher at S1. The lowest overall densities were found at the lowermost station. All pair-wise comparisons between S1 and the other stations were significant ($P < 0.05$), whereas differences between S6 + S5 and S7 were borderline significant ($0.05 < P < 0.06$). In addition, the interaction factor time * site was significant ($P < 0.005$), illustrating the different temporal evolution of nematode numbers at S1 compared to the other stations.

Nematoda: taxonomic composition and diversity

In total, 54 nematode genera were recorded in the litter bags (42, 38 and 16 after 10, 21 and 52 days, respectively, but note that the third sampling event only included two stations) (Electronic Supplementary Material, Table 1). The uppermost station was dominated by Rhabditidae (probably the genus *Pellioditis*) and *Monhystera*. These together constituted 81, 96 and 98% of the nematode community in litter bags at S1 after 10, 21 and 52 days of incubation, respectively, but were much less prominent at other stations, where *Sabatiera*, *Paracanthonchus, Daptonema* and Dorylaimoidea were generally the most abundant nematodes. Exceptions were S5 and S7 where Rhabditidae and *Monhystera* were again prominently present (up to 58 and 47% of the community, respectively) (ESM, Table 1).

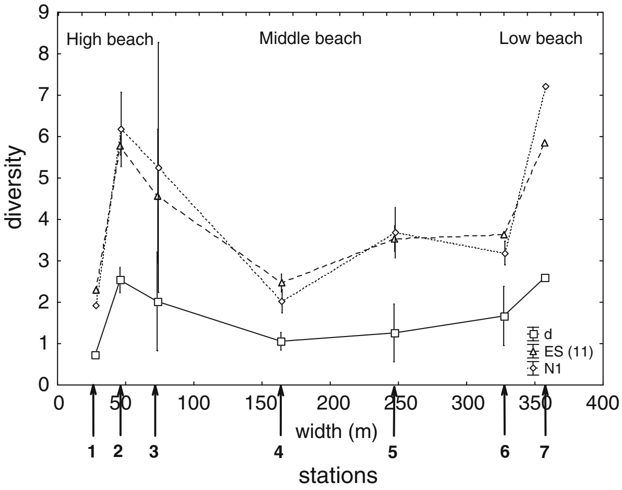

Fig. 6 Average (mean ± SD) nematode diversity (*d* Margalef's index; *ES(11)* expected number of species; *N1* Hill's diversity index) in litter bags after 21 days of incubation

The pattern of nematode diversity in litter bags was highly variable and differed with time ($P < 0.05$), but the lowest nematode diversity was always recorded at S1 (Fig. 6). A strong increase of nematode density with time at S1 (except for one replicate of the second sampling containing no nematodes) was accompanied by a slight decrease of nematode diversity. Similarly, nematode diversity at other stations across the beach slope generally showed a tendency to decrease with time (data not shown).

No overall correlation was recorded between nematode diversity (N1) inside litter bags and organic matter decomposition rate, but some positive trends were observed between diversity and organic matter weight loss after the first sampling event (Fig. 7a). A negative correlation was found between nematode densities in individual litter bags and the organic matter weight loss at the different stations along the beach slope ($r = -0.44$, $P = 0.03$, $n = 28$) (Fig. 7b), albeit at the second sampling event only. A negative relationship was also recorded between organic matter weight loss and densities of Rhabditidae on both sampling occasions ($r = -0.47$, $P = 0.04$, $n = 19$ after 10 days, and $r = -0.66$, $P = 0.007$, $n = 15$ after 21 days) and of *Paracanthonchus* at the second sampling (21 days, $r = -0.72$, $P = 0.014$, $n = 11$), whereas densities of *Sabatieria* were positively correlated with weight loss ($r = 0.63$, $P = 0.002$, $n = 22$) (Fig. 7c).

ANOSIM rejected the null hypothesis that there were no differences in nematode community composition in the litter bags at different study sites ($R = 0.53$, $P = 0.1\%$). nMDS on nematode genus composition inside litter bags, however, revealed no pronounced turnover of nematode communities across the beach slope (Fig. 8). Apart from a few outliers and from the lowermost station (S7), all samples of drift-line and middle beach stations were mixed. Only samples of the upper beach station 1 were clearly separated.

The pattern of organic matter weight loss across the beach is very similar to that of nematode diversity on this beach (Gheskiere et al. 2004) (Fig. 9).

Discussion

Decomposition rates

Horizontal variability in organic matter decomposition rates can be caused by a number of abiotic and biotic factors that change across the beach gradient. Tide-associated differences in temperature, salinity, moisture, oxygen, sediment stability, etc. generate both horizontal (physical) and vertical (chemical) gradients on the beach (Brown and

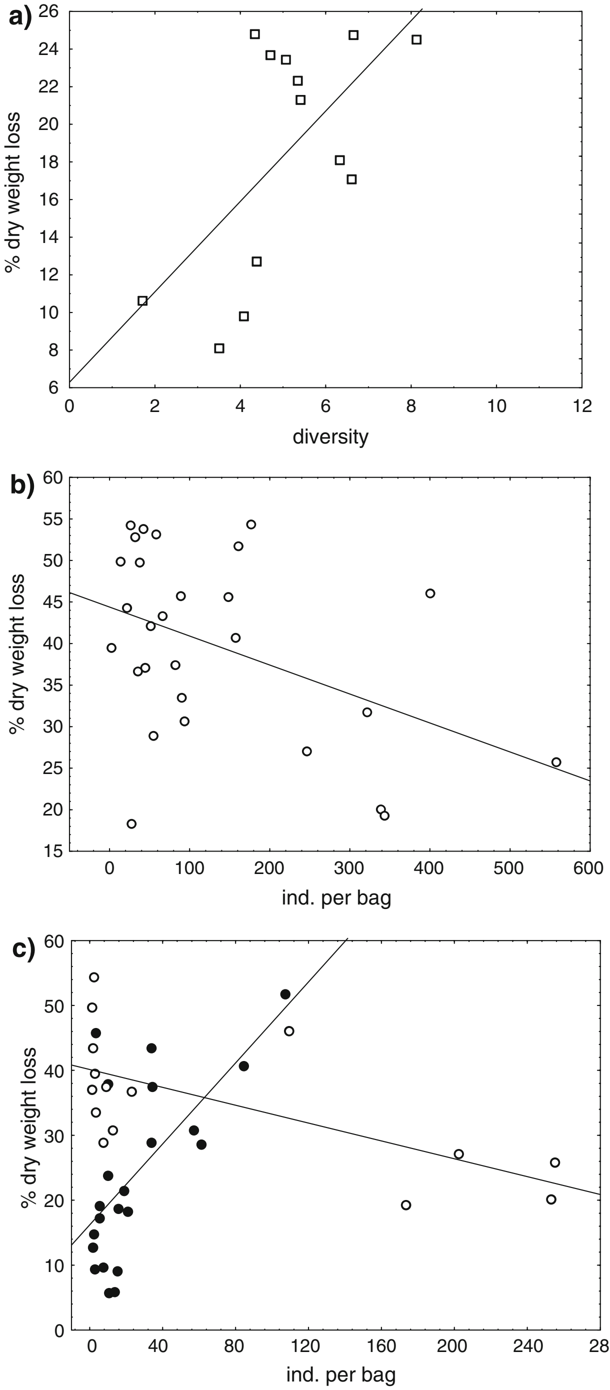

Fig. 7 Relationship between organic matter weight loss and **a** nematode diversity in litter bags after 10 days of incubation, **b** total nematode densities in litter bags after 21 days of incubation, **c** densities of *Sabatieria* and Rhabditidae (probably *Pellioditis marina*) in litter bags; *filled circles* represent *Sabatieria*, *empty circles* represent Rhabditidae; *lines* indicate significant correlation

McLachlan 1990; McLachlan and Turner 1994; McLachlan and Jaramillo 1995; Armonies and Reise 2000). Horizontal gradients in turn ensue a specific zonation of beach fauna (Fenchel et al. 1967; Armonies and Reise 2000), which is

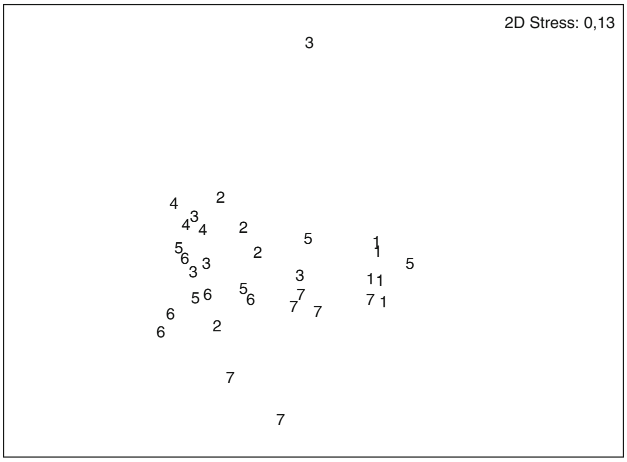

Fig. 8 nMDS (non-metric multidimensional scaling) of nematode communities inside litter bags across the De Panne beach. Numbers conform to station numbers

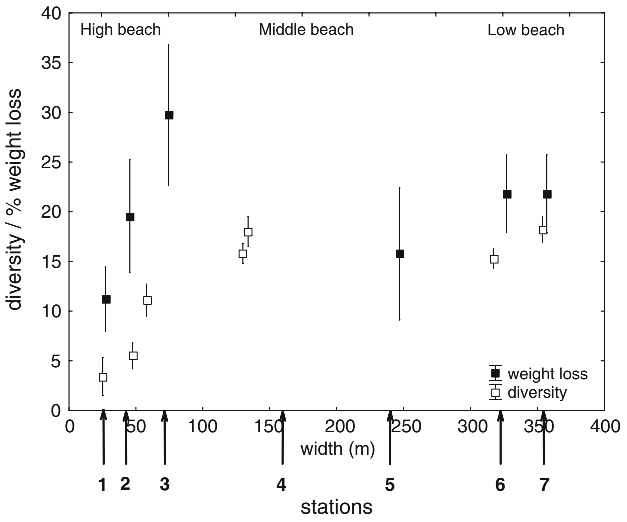

Fig. 9 Patterns of organic matter weight loss (this study) and extant nematode diversity (Gheskiere et al. 2004) across the beach slope. Data are means ± 1SD of three replicates

dependent on beach morphology, degree of exposure and tidal regime (McLachlan and Jaramillo 1995; Kotwicki et al. 2005). On dissipative beaches, an optimal balance between organic supply, oxygenation and water retention at or near the mid-shore may favor a high faunal diversity compared to the lower and higher shore (Armonies and Reise 2000). A similar pattern has been reported for the nematode species diversity on the beach at De Panne which we selected for the present study, albeit from a different time of year (late summer vs. winter in the present study) (Gheskiere et al. 2004). Interestingly, the horizontal variability of organic matter decomposition rates recorded here followed the same pattern. This analogy may suggest either that diversity and ecosystem process (decomposition) rates are governed by the same set of physicochemical factors, or that there is a tight connection between (nematode) species diversity and decomposition rates.

The latter assumption is particularly appealing since a significant role of nematodes in decomposition processes has been well-documented (Gerlach 1978; Findlay and Tenore 1982; Alkemade et al. 1992a, 1993; Lillebø et al. 1999; De Mesel et al. 2003). Nematodes may enhance organic matter decomposition rates mainly through (1) bioturbation, improving vertical fluxes of oxygen and nutrients (Aller and Aller 1992; Alkemade et al. 1992b), and (2) effects on the activity and/or composition of the microbial community (De Mesel et al. 2004; Moens et al. 2005). However, while several studies have reported a positive relationship between nematode densities and decomposition rates (Findlay and Tenore 1982; Alkemade et al. 1992a; Alkemade et al. 1993), we are aware of only one study that directly links marine nematode species diversity with their effect on the decomposition process. That particular study found a statistically significant but largely unpredictable relationship between nematode species diversity and their effect on organic matter decomposition in a microcosm experiment (De Mesel et al. 2006).

Nematode densities in the litter bags showed a more or less inverse gradient across the beach compared to that described for the surrounding sediment (Gheskiere et al. 2004): highest densities of nematodes in litter bags, but lowest numbers in sediment, were found at the uppermost station. Conversely, the lowest densities in our litter bags were found at the lowermost station, where Gheskiere et al. recorded highest densities (up to 3,000 ind. 10 cm^{-2}). Nematode density was significantly negatively correlated with organic matter weight loss, but this correlation disappeared when data from S1 were omitted from the analysis. Litter bags in S1 were characterized by high densities of bacterivorous rhabditid and monhysterid nematodes, which are well-known opportunistic colonizers of algal deposits in littoral habitats (Warwick 1987; Bongers et al. 1991; De Mesel et al. 2003). Grazing rates of the rhabditid *Pellioditis marina* (probably the dominant species in our litter bags at S1) on bacteria can be as high as 2.9 (Moens et al. 1999) to 4.3×10^7 cells $\mathrm{adult}^{-1}\ \mathrm{d}^{-1}$ (Tietjen et al. 1970), and this species has been shown to reduce bacterial densities and activity in controlled microcosm experiments (Moens et al. unpubl.). Hence, the comparatively low organic matter weight losses at S1 may well result from a top-down control on bacterial activity by rhabditids and monhysterids. In controlled laboratory experiments, De Mesel et al. (2003, 2004) found a similar top-down grazing pressure by another bacterivorous nematode, *Panagrolaimus paetzoldi*, on bacterial activity and diversity, albeit that this effect was probably caused by the extremely high nematode densities rather than by high individual grazing rates.

At the same time, such effects are highly nematode species-specific (De Mesel et al. 2003, 2004)—in the present study densities of *Sabatieria*, for instance, were positively correlated with organic matter weight loss—and depend on nematode species diversity, albeit in a very unpredictable way (De Mesel et al. 2006). These observations are in line with those from terrestrial ecosystems which suggest that properties of individual species and community composition significantly impact soil ecosystem processes, whereas the effects of diversity per se are weak and inconsistent (Mikola et al. 2004). The parallel between decomposition rate and nematode species diversity in extant sediments across the De Panne beach, however, does suggest a link between diversity and decomposition rate. The pool of potential colonizer species is larger at higher nematode diversity in the surrounding sediment, enhancing the probability of colonization by species which affect decomposition. The dominance of known bacterial-feeding genera which may negatively affect decomposition rate was highest at the low-diversity station S1. *Sabatieria* and *Paracanthonchus* were the most abundant genera in litter bags at the drift-line and middle beach stations. These genera are usually classified as, respectively, deposit-feeders and epistrate-feeders (Wieser 1953; Moens and Vincx 1997), but unfortunately, there is little empirical information on their actual food sources and life strategies. Their stoma morphology potentially allows uptake of particulate organic matter of larger size than bacteria, but whether and how—for instance by detritivory, a hitherto poorly documented phenomenon for nematodes, but see Riemann and Helmke (2002)—they may affect litter decomposition is unclear. However, inspite of a positive correlation at the first sampling, there was no overall significant relationship between decomposition rates and nematode genus diversity inside the litter bags. Hence, trends and correlations illustrated here between nematode diversity and decomposition rate may equally indicate that both nematode diversity and organic matter breakdown on the beach are governed by the same set of physicochemical factors.

Moisture regime and leaching were the main factors explaining differences in organic matter decay rates in field experiments on a non-tidal beach (Jedrzejczak 1999, 2002). In our study, the strongest fluctuations in moisture regime at the uppermost station were indeed accompanied both by the highest densities of bacterivorous nematodes inside litter bags and by the slowest decomposition. However, decomposition rates at intermediate stations (e.g., stations 2–3) also exposed to relatively long periods of desiccation upon tidal exposure were relatively intense, whereas decomposition at the nearly permanently water-saturated lowermost station was comparatively slow. The latter may be related to a shift from aerobic to predominantly anaerobic decomposition (Pollock and Hummon 1971; McLachlan 1980).

We can only speculate on the generality of the observed patterns across seasons. However, the suggested top-down effect of rhabditid and monhysterid nematodes at the upper beach is likely to be consistent. The genus *Pellioditis* is dominant here both in summer and winter (Gheskiere et al. 2004; Moens unpubl.), and can cope with a fairly broad range of temperature and salinity conditions (Moens and Vincx 2000, and refs. therein), provided suitable substratum (decomposing algae) is present. For Monhysteridae, the picture is less straightforward, since there are large differences in temperature ranges tolerated by different species (Heip et al. 1985; Moens and Vincx 2000). *Halomonhystera disjuncta*, for instance, by far the most common monhysterid colonizer of algal wrack in the nearby Westerschelde Estuary, can still reproduce at temperatures down to 3°C, but suffers increased mortality when exposed to temperatures above 25°C (Moens unpubl.), even for very short periods (several hours). In this respect, it is worth noticing that Gheskiere et al. (2004) did not find Monhysteridae in extant sediment of the upper beach in their summer survey. The exact identity and hence environmental tolerances of the Monhysteridae recovered in our litter bags are, however, unknown. Similarly, functional effects of dominant species (e.g. *Sabatieria*) in other stations across the beach slope may vary with seasonal fluctuations of these particular species, and diversity-dependent effects may vary with seasonal shifts in species richness, but unfortunately we lack seasonal data on nematode genus composition and diversity at the De Panne beach to properly assess this issue.

The patterns of decomposition rates across the beach slope observed here on a dissipative beach where macroalgal wrack inputs are relatively sparse will likely differ from those on wrack-dominated beaches. Regular deposition of substantial amounts of wrack on the beach shore may lead to anoxic conditions in the sediment, which in turn may locally inhibit meiofauna (McGwynne et al. 1988). Hence, meiofaunal density and diversity patterns across wrack-dominated beach slopes can be strongly affected by the distribution of macroalgal wrack, which in turn depends on beach morphology. Furthermore, while micro- and meiofauna have an important role in the decomposition of macroalgal detritus on wrack-loaded beaches (McLachlan and Brown 2006), the abundant and highly diverse wrack-associated macrofauna like amphipods, isopods and insects may also be very important in wrack decomposition. Macrofauna are often the first effective colonizers of stranded macroalgae (Inglis 1989; Olabarria et al. 2007) and may feed directly on the wrack and its epiphytes (McLachlan and Brown 2006). As such, while their numbers, diversity and succession patterns depend on the amount and quality of wrack deposits (Olabarria et al. 2007), they can in turn affect wrack decomposition rates. In our study, the mesh size of the litter bags excluded most macrofauna. At the same time, however, macrofauna were almost equally sparse on litter bags with larger perforations incubated in parallel (data not shown), which indicates that at the site, time and sediment depth of our study, macrofaunal colonization of algal wrack was very limited.

Composition of the associated community

Stations selected in the present study cover three nematode species associations characteristic for the beach in De Panne (Gheskiere et al. 2004): S1–S2 represent the upper beach, S3 refers to the strandline and S4–S7 belong to the middle beach association. Despite discrepancies in the exact location of the sampling stations and in the seasonal timing of the samplings between the present study and the one by Gheskiere et al. (2004), there were obvious similarities in nematode community composition between both studies. For instance, 35 out of a total of 64 nematode genera recorded by Gheskiere et al. (2004) were found in our litter bags, and the majority of the remaining 29 genera were not very abundant in the extant sediment community. In turn, 19 out of 54 genera found in the litter bags were not recorded by Gheskiere et al. (2004), but their abundance in the litter bags was consistently very low (<1%), except for *Oncholaimus* (ESM, Table 1).

Since we buried litter bags at 10- to 15-cm depth, and Gheskiere et al. sampled down to 15 cm, some of the 'new' genera in our study may have originated from deeper sediment layers. For instance, a high proportion of Dorylaimoidea in the litter bags at all stations contrasts with their total absence in the study by Gheskiere et al. (2004). Dorylaimid nematodes are effectively terrestrial and freshwater inhabitants that are often abundant in, and in front of, dunes (Wall et al. 2002; Gheskiere et al. 2005). Because groundwater from the dunes percolates into the beach and into the shallow subtidal zone, dorylaimid nematodes are probably common in deeper sediment layers. Nevertheless, their abundance in the litter bags seems at odds with the presumed low colonization ability of Dorylaimoidea (Johnson et al. 1974; Zullini 1976). Similarly, the dominance of *Sabatieria* in litter bags at S2, while being virtually absent from the surrounding sediment, may indicate migration from deeper layers. *Sabatieria* is well-known to migrate to spots of decaying organic matter (Gerlach 1977; Heip 1995), although it is not clear whether it feeds primarily as a bacterivore, detritivore or even a predator of ciliates and flagellates. Hence, we can only speculate on causes for the positive correlation between *Sabatieria* densities and organic matter weight loss.

Although the diversity pattern of nematodes across the beach was very similar to that noted by Gheskiere et al. (2004), nematode diversity in the litter bags was generally lower than in the surrounding sediment (Shannon–Wiener index of 0.7–2.0 vs. 1.1–2.9). Generally, litter bag communities were characterized by a dominance of only few genera, which did not necessarily belong to the dominant genera of the local sediment community. With the exception of S1, those predominant genera were pretty much the same for all stations, indicating that *Fucus* detritus was colonized by similar nematode genera regardless of its location on the beach profile and of the dominance structure of the local community. For instance, while the predominance of rhabditid nematodes in litter bags at S1 corresponds to that in surrounding sediment, the fairly high abundances of Rhabditidae, Dorylaimoidea, *Sabatieria* and *Monhystera* in litter bags at other stations does not conform to extant community composition at those stations. Among the predominant nematode genera in our litter bags at S2–S7, *Daptonema* and *Paracanthonchus* were the only ones that were also abundant in the surrounding sediment (Gheskiere et al. 2004). In fact, whereas the clear separation of upper beach, drift-line, middle and lower beach associations in an nMDS of the extant sediment communities (Gheskiere et al. 2004) is evidence of a high turnover of species along the beach slope, such a separation was not found in an nMDS of the nematode communities in our litter bags (Fig. 8), indicating a limited and undirected species turnover along the beach slope. Only the upper beach station 1 was clearly separated from the other stations on this beach.

Conclusions

We observed a remarkable parallel between decomposition rates and nematode genus diversity in sediments across the beach gradient, which may suggest a relationship between meiobenthic diversity and decomposition rates. However, the diversity of the nematode community associated with the decomposing organic matter was not significantly correlated with decay rates, and the community composition of nematodes inside litter bags did not follow the same zonation as in extant sediments. Our experiments therefore do not allow an unequivocal conclusion on whether the observed parallel between extant nematode diversity and organic matter decomposition rate indicates a causal relationship or follows from the possibility that both may be governed by the same set of physicochemical conditions. Future field studies should consider patterns in productivity and community composition of bacteria, the principal decomposers in this ecosystem, across the beach slope, and should be complemented by controlled incubations in which effects on bacteria of varying physicochemical conditions are contrasted with effects of varying (in terms of abundance, species composition and diversity) meiobenthic communities. Such a combination of approaches will allow a better understanding of the mechanisms underlying the correlations between meiobenthic (nematode) species diversity and ecosystem process rates observed in this study and—even more pronounced—in an assessment of a large set of data on deep-sea meiofauna and microbiota (Danovaro et al. 2008).

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