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MARINE ENVIRONMENTAL RESEARCH

Marine Environmental Research 61 (2006) 245-264

www.elsevier.com/locate/marenvrev

Are strandline meiofaunal assemblages affected by a once-only mechanical beach cleaning? Experimental findings

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Received 10 August 2005; received in revised form 24 October 2005; accepted 25 October 2005

Abstract

The increasing usage of sandy beaches as recreational resources has forced regional authorities of many tourist countries to remove all litter of fabricated origin and natural wrack from the beach. Consequently, a variety of heavy equipment has been developed during the last decades and is now used almost daily at many beaches. A field experiment, following a 'before–after-control-impact' (BACI) design, was conducted at the strandline of De Panne (Belgium) to investigate the impacts of mechanical beach cleaning on the strandline-associated meiofaunal assemblages, focus-sing on the free-living nematodes. Natural strandline assemblages were exposed to a one-off 5 cm deep mechanical beach cleaning and observed for 24 h. Differences between cleaned plots and those from control plots in terms of decreased percentage of organic matter, decreased total abundance and changed community structure were noticed from immediately after the experimental cleaning on species richness, Pielou's evenness and taxonomic diversity were shown to be minor in relation to the daily changes. Recolonization in the cleaned sediments is assumed to occur from the underlying sediments initiated by the elevated water table during the rising tide. © 2005 Elsevier Ltd. All rights reserved.

Keywords: Meiofauna; Free-living nematodes; Sandy beach; Mechanical beach cleaning; Disturbance; BACI; Recovery; North Sea

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1. Introduction

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

The deposition of manufactured debris on beaches has become a growing concern in many countries. Origins of this litter are both oceanic, e.g. from ships dumping at sea, and shore based, e.g. from rivers, sewage, or careless visitors. Stranded beach litter is more than a visible eyesore, causing a significant threat to many animal life forms (e.g. birds) through entanglement or ingestion (Laist, 1987) and, occasionally, the debris may become harmful to human health (Philipp, Pond, & Rees, 1997). The increasing usage of sandy beaches as recreational places has forced regional authorities of many tourist countries to remove all natural wrack and litter of fabricated origin (Ryan & Swanepoel, 1996). Consequently, a variety of cleaning techniques (front-end loaders, suction devices) have been developed in tourist coastal regions all over the world (Engelhard & Withers, 1997; Taylor, Owens, & Nordvik, 1994). The cleaning with large tractor-pulled sieving machines is seen as a cost-effective way of removing the "unwanted" strandline and has become an almost daily phenomenon on tourist sandy beaches (e.g. Gheskiere et al., 2005b). Along with the removal of wrack and litter almost every macroscopic item is removed from the sand as the beach cleaner shovels up the upper sediment layer with a fast-turning mixer or brush, replaces the sand after sifting and finally compresses the sediment with a dragged weight (personal observation). There is however, a growing concern about the use of these machines and their damaging impact on the overall strandlinerelated species diversity and abundance (Belpaeme, Kerckhof, & Gheskiere, 2004). On the invertebrate level this has already been documented extensively (e.g. Davidson et al., 1991; Dugan, Hubbard, McCraryc, & Pierson, 2003; Kirby, 1992; Llewellyn & Shackley, 1996; Weslawski, Stanek, Siewert, & Beer, 2000). However, these studies have focused on the larger macrofauna and habitat forming species, primarily because reductions in their abundance and species diversity are an important conservation issue. Studies dealing with the potential impacts on the meiofauna (all Metazoa $<38 \mu m$) of strandlines are lacking. Usually, free-living nematodes dominate the meiofauna of sandy beach sediments (e.g. Brown & McLachlan, 1990). Nematodes are generally considered as an excellent taxon to use as ecological indicators for benthic habitats and for studying the impacts of different kinds of natural and anthropogenic disturbances in the marine environment (Schratzberger, Gee, Rees, Boyd, & Wall, 2000; Gheskiere et al., 2005b). They reach high abundances, have a ubiquitous distribution, a high diversity (with a range from very tolerant to very sensitive species), short generation times and a continuous reproduction. Moreover, they are restricted to the sediments throughout their life.

In addition to their indicator value, meiofauna play a key role in the functioning of beach ecosystems (e.g. mineralization of wrack). Wrack beach-cast material or natural flotsam refers to any organic debris of marine and terrestrial origin (Lord & Burger, 1984). Once wrack is cast ashore, it decomposes quickly as it undergoes physical processes of fragmentation and biological processes of decomposition and remineralisation (Koop &

Griffiths, 1982). We have therefore carried out a short-term, small-scale field experiment to investigate the potential impact of mechanical beach cleaning on strandline meiofauna.

This paper has three major aims:

(1) to describe the meiofaunal diversity of a freshly deposited strandline, (2) to asses the possible influence of a mechanical beach cleaner on the meio-nematofaunal diversity and community structure and (3) to asses the recovery of the assemblages after cleaning.

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

2. Material and methods

2.1. Study site

This study was performed at the beach of De Panne (51°05'30" N, 02°34'01" E) at the western Belgian coast, near the Belgian-French border, in front of the 'Westhoek' nature reserve. This beach is an undisturbed ultra-dissipative, macrotidal, fine-grained sandy beach with a natural, never cleaned strandline. During the experiment air temperature varied between 17.6 and 18.4 °C (Oceanographic Meteorological Service Zeebrugge) while interstitial temperature (measured at 2.5 cm depth) varied between 19.6 and 19.8 °C. Interstitial salinity was constant (34 PSU) during the experiment. Gheskiere, Hoste, Vanaverbeke, Vincx, and Degraer (2004) give detailed information about the nematode and meiofaunal species composition, the granulometry and morphodynamics of this beach.

2.2. Sampling strategy and techniques

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

Along with the removal of algae and wrack, the beach cleaner scrapes up the upper sand layer (5 cm) with a fast-turning wheel equipped with little shovels (540 rotations/ min) and replaces the sand after sifting. The machine was fitted with a 30 mm mesh sieve



Fig. 1. Experimental design on the beach of De Panne Westhoek (Belgium). (C = cleaned plots, U = un-cleaned control plots) (MLWS = Mean Low Water Spring).



Fig. 2. Time schedule of the experimental cleaning. Arrows indicate sampling occasions relative to tides and experimental beach cleaning. Numbers associated with the sampling occasion indicate the time (h) relative to the experimental beach cleaning.

allowing sand to pass and falling down on the beach again. Working speed was adjusted at 5 km/h. Settings of the beach cleaner were the default settings used for the daily cleaning on the Belgian tourist beaches. After experimental cleaning the machine's container contained parts of four different species of brown algae (*Fucus vesiculosus, Ascophylum nodo-sum, Sargassum muticum* and *Himanthalia elongata*), parts of *Rhizostoma* sp., several carapaces of *Carcinus maenas*, a dead *Pleuronectes platessa* and considerable amounts of razor shells (*Ensis* sp.).

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 and washed onto a 38-µm sieve. The residue from the 38-µm sieve was separated into heavy and light fractions using repeated decantation (10 times). The light fraction (containing the meiofauna) was centrifuged three times with

Ludox[©] HS40 (specific density is 1.18) and stained with Eosin (Heip, Vincx, & Vranken, 1985). The extract was then placed into a beaker, made up to a standard volume with filtered tap water and homogenized into suspension before a constant proportion (30%) of the sample was taken with a semi-automatic pipette. Per sub-sample all meiofauna was counted and identified at higher taxa level. All nematodes per sub-sample were picked out, transferred from formalin to glycerol through a series of ethanol–glycerol solutions and mounted on Cobb slides. Afterwards, nematodes were identified to the species level and classified, in order to use the taxonomic diversity index, according to the phylogenetic system proposed by De Ley and Blaxter (2003). Sediment samples were oven-dried at 105 °C for 12 h and ashed at 500 ± 50 °C for 2 h to determine the %TOM by loss of mass. The sediment fractions were defined according to the Wentworth scale (Buchanan, 1984); sediment-sorting coefficient and other granulometric characteristics were calculated as described by Dyer (1986).

2.4. Data processing

Meiofauna species abundance data (N) (Ind/10 cm²) were used to calculate the diversity as the expected number of species per sample based on 100 individuals ES(100) (Sanders, 1968; Hurlbert, 1971) and Pielou's evenness (J'), the last index using Neperian logarithm in the formulation. Average taxonomic diversity (Δ) was calculated using only the nematode species data. Equal step-lengths between each taxonomic level were assumed for the calculation of the taxonomic indices, setting the path length ω to 100 for two species connected at the highest (taxonomically coarsest) possible level as stated by Warwick and Clarke (2001). Eight taxonomic levels were used (species, genus, family, superfamily, suborder, order, subclass and classis). 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 order), 87.5 (same class but different suborder), 75 (same subclass but different order), 87.5 (same class but different subclass) and 100 (different classes), respectively.

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

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

Major taxa densities mixed nematode species densities were used to produce Detrended Canonical Analysis (DCA) ordination plots (not shown) (Ter Braak, 1988) and non-metric Multi-dimensional Scaling (MDS) plots (Kruskal, 1964). Two-way crossed analysis of similarities (ANOSIM, Clarke, 1993) was carried out to test for a Block effect. Where none was found, two-way crossed ANOSIM was repeated with factors Time and Treatment and one-way ANOSIM (10,000 permutations) was carried out to test the significance in meiofaunal assemblages on different sampling occasions. The similarity of percentages programme (SIMPER, Clarke, 1993) was applied to determine the contribution of individual species and higher taxa towards the discrimination between samples. The Index of Multivariate Dispersion (IMD, Warwick & Clarke, 1993) has been applied here as a measure of community stress. The IMD is a measure of the increase in variability among replicate samples from cleaned versus control plots. The index contrasts the average rank of the dissimilarities among one set of samples (control) with the average rank among the other set (cleaned), re-ranking the full triangular matrix ignoring all between-group dissimilarities. The IMD is standardised to have a maximum value of +1 when all the dissimilarities among the control samples are higher than any dissimilarities among the cleaned samples and -1 when the reverse is true. All the above-described analyses involved constructing lower triangular similarity matrices from the square-root transformed abundance date using the Bray-Curtis similarity coefficient (Bray & Curtis, 1957). Transformation was chosen in order to limit the contributions of the most dominant species, and therefore allow the rarer species to influence the analyses (Elliot, 1971). Community analyses were performed using PRIMER version 5.2.9 (Clarke & Gorley, 2001). A significance level of p < 0.05 was used in all tests.

3. Results

3.1. Power analysis

Sandy sediment assemblages are known to be highly variable and detection of subtle changes in faunal communities is heavily dependent on the statistical power of the experimental design. Therefore, a power analysis was performed on the data for abundance, species diversity, taxonomic diversity and Pielou's evenness. This gives the probability of obtaining a statistically significant result for a given effect size based on our sampling design and sample variance from data collected from the control plots immediately after the experimental cleaning, and is simply based on the assumption that sample variability does not change over time (Cohen, 1988). The values of the biological responses at the treatment points are assumed to be lower than at the control sites immediately after the mechanical beach cleaning (i.e., at T_0). Moreover we assumed that values at cleaned sediments will be similar to control sediments the next or second next high water after the cleaning (Fig. 3). This assumption is based on the sediment disturbance experiment of Sherman and Coull (1980) which recorded recovery within two tidal cycles after disturbance. Generally, changes of <50% of the control mean are not considered ecologically meaningful in a dynamic and highly variable environment like shallow sandy sediments



Fig. 3. Probability of obtaining a statistically significant result given an assumed size of experimental treatment effect.

(Shaw, Moore, Kennedy, & Hill, 1994; Schratzberger, Dinmore, & Jennings, 2002), so we adapted that standard.

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

3.2. The abiotic environment

Generally, no significant granulometric differences (grain size, sorting, skewness, size class distribution) were noted between cleaned and control plots (data not shown). The sediments fell within the category of fine to medium sands, consisting on average of 7% shell fragments, 7% very coarse sand, 10% coarse sand, 33% medium sand, 56% fine sand and 1% very fine sand. Fig. 5 reveals the changes of percentage total organic matter (%TOM) at control and cleaned plots during the investigated period. Immediately following the experimental cleaning, the %TOM decreased to a level considerably lower at the cleaned plots than at the control plots. After the next high water (T_{11}) the %TOM raised again to more similar values compared to the control plots. Variation of %TOM at the control plots was negligible throughout the experiment. No block effects were recorded. Repeated measures analysis of variance indicated a significant effect of Time (p < 0.02), Treatment (p < 0.01) and Time × Treatment (p < 0.001).



Fig. 4. Power of the experimental design (for each biological response) corresponding to a hypothetical impact of p% on the first sampling occasion after experimental cleaning. The dotted line indicates the 5% significance level. Fifty percent is the ecologically significant change.



Fig. 5. Means of % total organic matter (%TOM) plotted against hours after the experimental cleaning. Solid line: control plots, dotted line: cleaned plots. Vertical lines correspond to 95% confidence limits. Arrows indicate the high tides (n = 5).

3.3. Abundance and richness measurements

13 Higher meiofauna taxa were recorded in the freshly deposited strandline dominated by nematodes (69% including 55 species), Harpacticoida + nauplii (14%), Oligochaeta (10%) and Turbellaria (4%). Other groups (3%) were present in low numbers or were found only sporadically; these included Polychaeta, Tardigrada, Diptera, Hydrozoa, Ostracoda, Cladocera, Gastrotricha, Aranea and Rotifera. The effect of the cleaning was manifested as a decrease in the total abundances in comparison to the control plots. Immediately after the experimental cleaning (T_0) the total abundance of the cleaned sediments, 338 ± 41 Ind/10 cm², is seen to decrease significantly to 191 ± 65 Ind/10 cm² until it raises again (at T_{11}) to 261 ± 48 Ind/10 cm². After the second high water, recovery is almost complete and initial values are reached again. The drop in taxonomic diversity between two high waters is remarkable (Fig. 6). Repeated measures ANOVA showed that there were significant effects of both Treatment (F = 9.47, p < 0.01) and Time (F = 2.17, p < 0.02) with respect to the total abundance (N). For average taxonomic diversity (Δ), any impacts of cleaning were minor in relation to temporal changes in the nematode assemblages during the progress of the experiment (F = 4.08, p < 0.02).

No changes, due to the cleaning nor temporal, were noted for Pielou's evenness (J') and ES(100). A statistically significant interaction Time × Treatment at the level of 5% was only found for total abundance (F = 1.45, p < 0.01, Table 1).



Fig. 6. Means of the total abundance, ES (100), average taxonomic diversity (Δ) and Pielou's evenness (J') plotted against hours after the experimental cleaning. Solid line: control plots, dotted line: cleaned plots. Vertical lines correspond to 95% confidence limits.

	df	F	р
Abundance (N)			
Block	4	3.71	0.20
Treatment	1	9.47	< 0.01
Time	7	2.17	< 0.02
Treatment × Time	7	1.45	< 0.01
Richness ES(100)			
Block	4	1.26	0.30
Treatment	1	0.28	0.60
Time	7	8.96	0.09
Treatment × Time	7	0.47	0.80
Pielou's evenness (J')			
Block	4	1.48	0.23
Treatment	1	3.10	0.09
Time	7	2.94	0.07
Treatment × Time	7	1.21	0.32
Taxonomic diversity (Δ)			
Block	4	1.62	0.2
Treatment	1	2.55	0.11
Time	7	4.08	< 0.02
Treatment × Time	7	0.97	0.45

Results from repeated measures analysis of variance for univariate indices of the strandline meiofaunal assemblage

3.4. Meiofaunal assemblages

Results from the two-way crossed ANOSIM showed no statistically significant block effect on the meiofaunal assemblages collected up to 23 h after the beach-cleaning (R = 0.194, p = 0.09). The experimental treatment effect (averaged across all sampling dates; R = 0.403, p < 0.01) and the time of sampling collection (averaged across treatment groups; R = 0.538, p < 0.03) were statistically significant. The one-way ANOSIM (Table 2) shows that differences in meiofaunal community structure collected at the cleaned plots were more pronounced than at the control plots. Pairwise comparisons derived from the ANOSIM test for each sampling occasion showed that highest dissimilarity between control and cleaned plots occurred within the first 9 h after the experimental cleaning (Table 3). Dissimilarities were most distinct 4 h after cleaning (48%). A higher value of R is indicative of larger relative differences between the fauna; thus, the decrease in the value of the *R*-statistic from T_4 onwards gives some indication of the recovery trajectory of the cleaned plots. The meiofaunal assemblages from the cleaned plots remained significantly different from the control plots until T_{11} at which point they had recovered (R = 0.115, p = 0.231). At each sampling occasion (except T_{23}), the inter-variability is higher among cleaned assemblages, giving a negative value for the Index of Multivariate Dispersion, and thus indicating higher community stress. Highest negative IMD-values were noted within the first 2–4 h after experimental cleaning. At T_{-1} , T_{11} and T_{23} IMD-values were close to zero implying negligible differences between control and cleaned samples.

According to the SIMPER-analyses (not shown) significant differences in assemblages within the hours after experimental cleaning mainly occurred as a result of reduced

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Table 1

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

Table 2 Dissimilarities [%] on different sampling occasions based on square-root transformed abundance data

 T_0 is immediately after experimental cleaning, T_2 is 2 h after experimental cleaning, etc.

* Significant differences at p < 0.05 based on ANOSIM test.

Table 3

Dissimilarities [%] and index of multivariate dispersion (IMD) between cleaned and control plots on different sampling occasions based on square-root transformed species abundance data

	Dissimilarity [%]	<i>R</i> -value	<i>p</i> -Value	IMD
T_{-1}	21	0.042	0.451	-0.090
T_0	33*	0.531	0.019	-0.556
T_2	46*	0.771	< 0.001	-0.742
T_4	48*	0.801	0.001	-0.740
T_6	41*	0.586	0.020	-0.566
T_9	40*	0.548	0.025	-0.350
T_{11}	26	0.115	0.231	-0.118
T_{23}	20	0.240	0.810	+0.111

* Significant differences at p < 0.05 based on ANOSIM test. T_0 is immediately after experimental cleaning, T_2 is 2 h after experimental cleaning, etc.

numbers of individuals from the dominant nematode species (*Theristus otoplanobius*, *Trissonchulus benepapilosus*, *Chromadorina germanica*) and Harpacticoid Copepod sp. in the cleaned plots.

Analyses of changes in abundance over time for the seven most abundant species (accounting for >50% of the total number of individuals) are reported in Table 4. Univariate analyses on the individual species elucidate that, with exception of Oligochaeta sp., the abundances were not significantly influenced by Time. Four out of seven species; *T. otoplanobius, Harpacticoida* sp., *C. germanica* and *T. benepapilosus* were significantly influenced by the experimental cleaning (Treatment) and showed a significant Time × Treatment interaction. Multivariate analysis of variance (MANOVA) revealed that meiofauna species composition was not significantly affected by Time; however it exhibited a significant effect of the experimental cleaning as well as a significant Time × Treatment interaction effect. The combination of both uni- and multivariate analyses showed that, although there are

	Time			Treatment			Time × Treatment		
	df	F	р	df	F	р	df	F	р
Univariate test									
Theristus otoplanobius	7	1.220	0.319	1	10.896	0.002	7	0.813	0.048
Harpacticoida sp.	7	6.673	0.613	1	3.728	< 0.001	7	0.748	0.036
Onyx sagitarius	7	1.670	0.167	1	0.280	0.600	7	1.258	0.302
Tardigrada sp.	7	14.251	< 0.001	1	0.166	0.686	7	0.860	0.517
Chromadorina germanica	7	10.800	0.662	1	0.851	< 0.001	7	0.597	0.002
Hypodontolaimus schuurmansstekhoveni	7	1.516	0.209	1	0.002	0.963	7	2.175	0.079
Trissonchulus benepapilosus	7	12.855	0.346	1	0.911	< 0.001	7	1.034	0.413
Multivariate test	7	3.106	0.319	1	2.601	< 0.001	7	1.214	0.209

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

no statistically significant changes in diversity measurements, there were changes in individual species abundances because of the experimental cleaning, i.e. the composition of the meiofaunal assemblage varies significantly in time because of the experimental cleaning (Table 4).

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

4. Discussion

4.1. The strandline meiofaunal assemblages

Results from this study indicate that strandline-related meiofaunal assemblages are species rich, even with only the nematodes identified at the species level. Alkemade and Van Rijswijk (1993) stated that the number of nematodes associated with wrack depends on the height on the beach and the Carbon/Nitrogen ratio. They recorded significantly higher abundances as the nitrogen content increased relative to the carbon content and for material higher on the beach (the higher a wrack deposit is located on the beach, the longer it is presumably present on the beach). As the strandline and the stranded material studied in this paper were freshly deposited, we can assume C/N values are high and this may explain the generally low nematode and meiofaunal abundances in comparison with other strandline studies. These assumed high C/N values may also explain the low densities of dipteral larvae in our samples compared to other studies (Colombini, Aloia, Fallaci, Pezzoli, & Chelazzi, 2000).

Meiofaunal studies usually record oligochaetes only in very small numbers (Higgins & Thiel, 1988), therefore the presence of oligochaetes as third-largest group was unexpected. However, when searching the literature (Giere & Pfannkuche, 1982; Jedrzejczak, 2002a, 2002b; Koop & Griffiths, 1982; McGwynne, McLachlan, & Furstenberg, 1988; McLachlan, 1985) we found oligochaetes generally to be a high-abundance taxon in assemblages associated with decomposing wrack accumulations or in the sand beneath wrack. Giere (1975) and Koop and Griffiths (1982) indicate that the presence of high numbers of both

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Table 4



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

nematodes and oligochaetes are directly related to the distribution of wrack, below which concentrations of Dissolved Organic Matter (DOM) can be high, and suggested that meiofauna use this as a direct food source. However, following McLachlan (1985), the possibility that the DOM is initially used by bacteria, which in turn are used as food source by the meiofauna cannot be precluded. In view of their much longer turnover times, Moens and Vincx (1996) assumed that meiofauna are not able to compete for DOM with bacteria. Jedrzejczak (2002a) suggested that oligochaetes feed on the metabolites of the other meiofaunal groups rather than directly on bacteria or DOM.

During this study, 55 different species of free-living nematodes were recorded in the strandline. 34 Species were only recorded sporadically or in low abundances (0.1% of total recordings). *T. otoplanobius* (35%) was found to be the dominant nematode species and this is in concordance with earlier studies on this beach. Little is known about the structure of the strandline nematode assemblages from other places with the exception of the Antarctic strandline study of Alkemade and Van Rijswijk (1993) where eight nematode species were recorded. Only *Pellioditis marina* and *Monhystera disjuncta* were found to be in common with this study. *P. marina* has a cosmopolitan distribution and is typically associated with stranded decomposing wrack (Inglis & Coles, 1961; Inglis, 1966). Two other genera that are frequently reported in literature as 'associated with decomposing matter and/or high shore', namely *Diplolaimella* and *Diplolaimelloides* (Bouwman, Rameyn, Kremer, &

Van Es, 1984; Warwick, 1976) were not recorded. The fact that the strandline studied here was fresh and decomposition was thus in an initial phase could possibly explain the low abundances of *P. marina* and the absence of the two above-mentioned genera. Nevertheless, it is remarkably that 55 different nematode species can coexist in such a narrow stripe on the beach. One explanation may be that the generally high bacterial and protist diversity associated with the strandline deposited wrack (Olanczuk-Neyman & Jankowska, 1998; Armstrong, Rogerson, & Leftley, 2000), combined with the high habitat heterogeneity and good water percolation, result in attractive and diverse bacterial '*aufwuchs*'. Seeing that nematodes are highly able to partition their environment extensively in various ways (e.g. food partitioning (Platt & Warwick, 1980)), the bacterial '*aufwuchs*' can support species rich nematode assemblages.

4.2. Impact of cleaning

BACI designs have been widely used in environmental impact studies on the mean abundances of populations as well as on the community structure (e.g. Schratzberger et al., 2002). The principle of a BACI design is that a disturbance at the impacted plots will cause a different pattern of change compared with natural change at the control plots (Underwood, 1997). With the sampling intensity of this experiment, the power to detect specified changes in density, richness, Pielou's evenness and taxonomic structure is generally high and therefore all are effective in detecting changes due to experimental cleaning. In other words, the risk of conducting a type II error (assuming no impact exists when in fact it does) is low. Beach cleaning (or beach grooming) is only a recent phenomenon in the coastal environment and so are the studies about the impacts. To date all studies have been concentrated on changes in abundance at the macrofauna level (Davidson et al., 1991; Kirby, 1992; Llewellyn & Shackley, 1996; Lavery, Bootle, & Vanderklift, 1999; Dugan et al., 2003), whereas meiofauna have been largely neglected. After an extensive survey of 15 Californian strandlines Dugan et al. (2003) concluded that significant differences in community structure, including depressed species richness, abundance, and biomass of macrofauna were associated with beach grooming. This was most obvious for the typical wrack-associated herbivore taxa (talitrid amphipods, kelp flies and coleopterans) which are important prey for vertebrate predators, such as several species of shorebirds and insectivorous passerines. Malm, Råbarg, Fell, and Carlsson (2004) noted that the organic content of the sand (%TOM) was significantly reduced by beach cleaning, which is in accordance with our results. They suggested that the largest impact of beach cleaning seems to occur at the microbiological level, with a substantial reduction of the bacterial production and significantly less large ciliates at the cleaned beach, compared with the un-cleaned beach. Our cleaning experiment at the strandline of De Panne showed that there were no impacts of the beach cleaning on univariate measurements such as diversity, Pielou's evenness and the taxonomic diversity. The only measurable impacts that could be attributed to the cleaning were an immediate decrease in faunal density and change of assemblage structure. As the decrease in meiofaunal density relative to the control was 43%, this impact cannot be considered as ecologically significant. The multivariate species-dependent MDS ordination was seen to be more sensitive in discriminating the assemblages collected at both treatment and control plots, suggesting that the dominance relationships among species had changed at the treatment plots compared to the controls. The results of this study contrasted with the above-mentioned studies, which generally recorded, in addition to an immediate decrease in number of individuals, a depressed biodiversity and even a complete disappearance of some species at cleaned sites compared to non-cleaned ones. These macrofauna studies, however, included many more taxa and a much wider range of size classes compared to the present study.

Since meiofauna are among the smallest metazoan animals in benthic ecosystems and have fast turnover times, they may be expected to show little responses to beach cleaning, as they are less susceptible to the brooms or mixers on the cleaners and can easily pass through the sieves (30 mm). Indeed, intuitively one may suspect that the susceptibility of species to beach cleaning/grooming is largely determined by their body size and turnover, with large slowly reproducing species being more susceptible than smaller, faster reproducing ones In this respect, it is not unexpected that some of the larger nematode species like T. benepapilosus (body length: 2.5-3.2 mm, Van der Heiden, 1976) are significantly affected by the cleaning as they are probably crushed by the mixer. Although this study was not designed to assess chronic impacts, it is likely that turn-over rates are potentially more important in affecting the longer-term maintenance of populations following repeated beach cleaning. Nematodes in dynamic environments such as the beaches, generally exhibit morphological adaptations (e.g body ornamentation which provide an anchorage) to high turbulence and shifting sediments (Gheskiere et al., 2005a). These morphological adaptations together with physiological adaptations and population growth rates can be expected to contribute significantly to the high resilience of the studied nematode assemblages to mechanical beach cleaning. The fact that harpacticoid copepods are affected by the cleaning is also not unusual, as the crustacean meiofauna regularly seems to be the most affected in perturbation studies, mainly because of their fragile body parts (Coull, 1988).

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

horizontally on the falling tide (Neilsen, 1990), there is a tendency for elevation of the beach water table above the mean sea level. Water input therefore only occurs when the elevation of the tide exceeds the elevation of the beach water table, thus water input occurs on the rising tide and water discharge mainly on the outgoing tide. As the beach of De Panne is an ultra-dissipative flat sandy beach, the ground water table is close to the sediment surface (Gheskiere et al., 2004; Lebbe, 1981). Together with the elevation of the water table as the tide raises, the interstitial meiofauna from deeper layers is probably elevated to the upper layers (i.e. passive vertical migration). This hypothesis is supported by the study of Van de Velde (2003) who noted during a survey of the vertical meiofaunal distribution of the same strandline that there are no significant differences in meiofaunal assemblage between the upper 0-5 cm layer and the 5-10 cm layer. Since the water table from the studied beach is known to harbour several terrestrial and brackish water nematodes (e.g. P. marina, Aporcellaimus sp.) (Gheskiere et al., 2004), this may explain the peak in taxonomic diversity in the samples immediately after the high tides (T_{-1}, T_{11}, T_{23}) . At first thought, recolonization via water column migration seems also a possibility. Hagerman and Rieger (1981) and Savidge and Taghon (1988) gave evidence for this as they found that considerable portions of interstitial meiofauna were suspended in the water column by shoaling and breaking waves. Ullberg and Olafsson (2003a) suggest that settling of suspend marine, free-living, benthic nematodes is not entirely a random or passive process since several, particularly very small, species, belonging to different genera and families, were clearly able to choose settling points through active swimming. However, for this cleaning experiment it seems very unlikely that the recolonization occurred via water column modes, mainly because of two reasons. (1) Erosion of meiofauna from sediments by shoaling and/or breaking waves is in the first place controlled by the friction velocity or shear stress (Palmer & Gust, 1985; Ullberg & Olafsson, 2003b). Seeing the morphodynamics of the studied beach and the location of the experiment on the beach (the strandline), the erosive force imparted by the flowing water on the bottom sediments is assumed to be extremely low (Short, 1999) as on this type of beach wave energy is dissipated at a considerable distance from the shore (on the subtidal sandbanks). (2) The meiofaunal community of a strandline is a very narrow and sharply defined community, characterised by species which are absent on ambient parts of the beach (Gheskiere et al., 2004). Thus, if passive erosion of meiofauna from elsewhere (lower) on the beach should have occurred, a different meiofauna assemblage should be found in the cleaned plots after the tides. This was certainly not the case as the experimental plots were recolonized by exactly the same strandline-specific meiofauna.

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

5. Conclusions

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

Acknowledgements

The Institute for the Promotion of Innovation through Science and Technology in Flanders (IWT-Vlaanderen) and Ghent University (UGent) financially supported the first author.

The local authority of De Panne is acknowledged for facilitating sampling opportunities and use of the mechanical beach cleaner. Several persons assisted in the field and in the laboratory; thanks to R. Verstraete (driving the beach cleaner), B. van de Velde, H. Hampel, M. Raes, G. De Smet (sampling), A. Van Kenhove (nematode slides) and D. Schram (granulometry and %TOM analyses).

Dr M. Schratzberger (CEFAS, UK) and Prof Dr S. Van Aelst (UGent) are acknowledged for advice on power analyses. We are also grateful for the constructive comments and suggestions of three anonymous referees and the editor (JW) which have improved the manuscript.

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