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Contrasting macrobenthic activities differentially affect nematode density and diversity in a shallow subtidal marine sediment

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ABSTRACT: By bioturbating and bio-irrigating the sea floor, macrobenthic organisms transport organic matter and oxygen from the surface to deeper layers, thereby extending the habitat suitable for smaller infauna. Next to these engineering activities, competition, disturbance and predation may also affect the spatial distribution of these smaller organisms. In a controlled laboratory experiment, we studied the effects of 3 functionally different macrobenthic species on the vertical distribution of nematodes. *Abra alba*, a suspension-deposit feeding bivalve reworking the sediment randomly, *Lanice conchilega*, a suspension-deposit feeding, tube-irrigating polychaete and *Nephtys hombergii*, a burrowing predatory polychaete, were added in single-species treatments to sediment from a coastal subtidal station in the Belgian part of the North Sea, sieved (1 mm) to remove macrofauna. After 14 d, the control treatment without macrobenthos was found to be detrimental to nematode density and diversity, which points to the importance of macrobenthic engineering to sustain the smaller components of the food web. Nematode densities were highest at the sediment surface in all treatments, but subsurface density peaks were observed in *A. alba* (to 3 cm depth) and *L. conchilega* (to 7 cm depth) microcosms. In the *A. alba* treatment, the dominant non-selective deposit feeders and the epistrate feeders shifted downwards probably to avoid disturbance and exploitative competition by the bivalve siphons at the surface, while they might have benefited from the faecal pellets deposited in the subsurface. In the *L. conchilega* treatment, the several dominant species were redistributed over depth layers, indicating polychaete-mediated habitat extension from surface into depth. Nematode communities seemed hardly affected by the presence of *N. hombergii*. These results reveal that functionally contrasting macrobenthic engineering effects shape nematode communities in different ways, which may maintain the role of nematodes in ecosystem functioning. The present study therefore highlights the need for conservation of macrobenthic functional diversity.

KEY WORDS: Bioturbation · Macrobenthos · Ecosystem engineering · Nematodes · Vertical distribution · Diversity · Density

INTRODUCTION

One of the major goals of ecology is to understand the distribution of species, populations and communities. Disentangling the drivers of these distributions is challenging since a wide variety of biotic and abiotic factors are recognised as being important in shaping biological communities. Gaining insight into these complex mechanisms has now become more pressing than ever in light of changing habitats and increasing rates of species extinctions. A key pathway by which one organism can affect others is by physically changing its abiotic environment, so-called ecosystem engineering (Jones et al. 1994). For example, macrobenthic

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organisms that inhabit marine soft sediments alter the distribution of high-quality organic matter (Graf 1989, Levin et al. 1997), oxygen and toxic metabolites in the sediment (Kristensen & Kostka 2005) through bioturbation and bio-irrigation activities (Aller 1988, Meysman et al. 2006) which, in turn, may influence the distribution of organisms that are too small to 'engineer' their own habitat, e.g. nematodes (Reise 1985) or bacteria (Mermillod-Blondin et al. 2004). The ecosystem-engineering concept is, however, controversial in that all organisms are affected by and change their abiotic environment to some extent (Reichman & Seabloom 2002). Consequently, the utility of the concept requires explicit effects of the ecosystem engineer on other organisms that differ from direct biotic interactions (Hastings et al. 2007).

Nematode vertical distribution in marine soft sediments is tightly coupled to (1) the prevailing geochemical properties, such as hydrogen sulfide and oxygen concentrations (e.g. Platt 1977, Hendelberg & Jensen 1993, Wetzel et al. 1995), and (2) food availability in the sediment (Franco et al. 2008a). These factors can be altered by bio-irrigation and bioturbation, not only by direct transport of solids and solutes, but also by stimulating biogeochemical processes along the burrow walls (Mermillod-Blondin et al. 2004). The sediments surrounding burrows likely support microbial communities that differ from those in the surficial sediments (Kristensen & Kostka 2005) and may therefore diversify the menu for nematodes. Further, macrobenthic faecal casts give rise to high bacterial activity due to a greater concentration of fine particles, rich in organic carbon and nitrogen, than in the surrounding sediment (Reise 1985). In addition, macrobenthos may affect nematode communities positively, by the construction of physical structures (e.g. polychaete tubes) that provide shelter from predation (Zühlke et al. 1998), or negatively, by depleting their food resources (Olafsson et al. 1993), and by direct physical disturbance due to regular bioturbation (Austen & Widdicombe 1998, Schratzberger & Warwick 1999).

Studies investigating the link between macro- and meiofauna (e.g. nematodes) are numerous (reviewed by Olafsson 2003, Dashfield et al. 2008, Bouchet et al. 2009) but evidence for the biogeochemical engineering effects of macrofauna on nematode distribution remains surprisingly scarce: the engineering mechanisms involved (i.e. altered environmental variables) are not always studied in detail (Olafsson et al. 1993, Austen et al. 1998, Austen & Widdicombe 1998, Austen & Thrush 2001) and therefore clear proof of interactions between macrobenthos, environmental variables and meiofauna are often lacking. Olafsson (2003) pointed out that enhancing the resolution in data collection, e.g. by taking the vertical distribution of the sediment into account and working at low(er) taxonomic levels, is crucial in determining macrofauna effects on nematodes. Moreover, the examination of whether macrofaunal species with a different functionality (in terms of bioturbation) differently affect nematode communities may help to identify the engineering mechanisms involved. Macrobenthic functional traits in terms of bioturbation are manifold and comprise (1) biodiffusers that rework the sediment at random, (2) gallery-diffusers that excavate and actively irrigate burrows, (3) upward-conveyors that remove sediment at depth in the substratum and expel it at the sediment-water interface, (4) downward-conveyors that cause 'active' transport of sediment through their gut from the sediment-water interface to their egestion depth and (5) regenerators that dig out sediment at depth and move it to the surface, where it is washed away and replaced by sediment from the surface (Gerino et al. 2003, Michaud et al. 2006). These differing traits have all been shown to make the biogeochemical sediment environment more heterogeneous (Mermillod-Blondin et al. 2004, Michaud et al. 2006, Braeckman et al. 2010) and thus potentially affect nematode vertical distribution.

The present work explores for the first time the nematode community response to functionally contrasting macrobenthic activities in shallow subtidal sediments, both on a detailed taxonomic level and with respect to their vertical distribution. We introduced 3 functionally different macrobenthic species in single-species treatments into microcosms containing (subtidal) sediment with the same natural nematode communities but devoid of the natural macrobenthic population. The 3 species are dominant representatives of the *Abra alba–Kurtiella bidentata* community in the Belgian part of the North Sea (Van Hoey et al. 2004). Both the bivalve *A. alba* and the polychaete *Nephtys hombergii* rework the sediment at random (i.e. they are biodiffusers), though the first species is a suspension-deposit feeder while the latter is a predator. The tube-irrigating, suspension-deposit feeding polychaete *Lanice conchilega* is sedentary and has limited impact on sediment turnover once the tubes are established. Its piston-pumping (Forster & Graf 1995) stimulates microbial activity and enhances benthic mineralisation, whereas the biodiffusers *A. alba* and *N. hombergii* do not irrigate their burrows or feeding pits, resulting in a limited stimulation of benthic mineralisation rates (Braeckman et al. 2010).

We tested whether the presence of macrobenthos affects the vertical profile of environmental variables and nematodes, and whether different functional groups of macrobenthos have a contrasting effect on the vertical profile of environmental variables and nematodes.

MATERIALS AND METHODS

Study site and sampling. The experimental set-up required sediment containing the natural vertical distribution of nematodes excluding abundant macrofauna. Therefore, sediment from a sandy coastal station off the coast of Oostende (51°19.27'N, 2°52.09'E, 18 m depth, 9 km offshore) was collected with a Reineck boxcorer from the RV 'Zeeleeuw'. Sediment median grain size at the study site is 215 ± 0.22 µm with a mud fraction (<63 µm) of 5.8 ± 0.2%. The macrobenthic community present belongs to the *Abra alba–Kurtiella bidentata* community (Van Hoey et al. 2004). The sediment was sliced into 0–1 cm, 1–3 cm, 3–5 cm, 5–8 cm, 8–end cm sections, wet-sieved to remove macrofauna (>1 mm) and brought to a temperature-controlled laboratory (18°C) 7 d before the start of the experiment (Day –7). The naturally oxygenated 0–1 cm section was aerated overnight. During this sampling campaign, 3 cores of 3.6 cm internal diameter (i.d.), obtained from replicate deployments of the Reineck boxcorer, were sliced in 1 cm sections to serve as a field control (FC). Macrobenthos inhabiting these FC slices was retained on a 1 mm mesh. On Day –6, the sediment column (8 cm) was reconstructed by stacking subsequent sediment horizons in cylindrical microcosms of 10 cm i.d. The microcosms were left to acclimatise in the dark for 4 d at 18°C, covered with 20 cm of natural seawater of salinity 32.

Lanice conchilega was collected in the intertidal area by means of metal frames (Rabaut 2009) and subsequently introduced into the microcosms within its tube as described in Ziegelmeier (1969) at a natural density of 637 ind. m^{-2} (corresponds to 5 animals introduced into each microcosm). To check the fitness of the animals, the fringed tube end was cut after introduction to the sediment. The next day, all animals had rebuilt a new crown of fringes. *Abra alba* and *Nephtys hombergii* were sampled from the subtidal with the RV 'Zeeleeuw' and introduced at a density of 764 ind. m^{-2} (7 animals introduced) and 382 ind. m^{-2} (3 animals introduced) respectively, which is within the ranges of their natural density (Degraer et al. 2006). *N. hombergii* and *A. alba* specimens that did not burrow within 30 min were replaced by more active individuals.

Experimental set-up and slicing. Twelve microcosms were attributed to 4 experimental treatments in triplicate: 3 experimental control (C) microcosms where reconstructed sediment was incubated without macrofauna; and 3 microcosms each with *Abra alba*, *Lanice conchilega* and *Nephtys hombergii.* Three additional reconstruction controls (RC) served as a procedural control for possible disturbance during and after microcosm reconstruction (homogenisation and compaction of the sediment). Microcosms were incubated at constant room temperature of 18°C for 14 d. The overlying water in the microcosms was continuously aerated and replaced every 2 d to avoid accumulation of NH_x. The 3 RC were sliced on Day 1 in 1 cm sections. On Day 14, all experimental microcosms were sliced in defined vertical sections as described above ('Study site and sampling'), but with higher resolution in the first 2 cm for closer inspection of nematode species response (0–0.5, 0.5–1, 1–1.5 and 1.5–2 cm). The sediment from each slice was homogenised and subsamples were taken for nematode density and community analysis (5 ml in 0.5 cm slices and 10 ml in 1 cm slices) and stored in a buffered 4% formalin solution. Meiofauna was extracted by centrifugation with Ludox (Heip et al. 1985). All nematodes were hand-picked, mounted onto slides and identified to genus or species level according to the pictorial key of Warwick et al. (1998). Sediment subsamples (10 ml) were dried at 60°C and median grain size and silt content was determined with a Malvern Mastersizer using laser diffraction. Sediment subsamples for pigment analyses (10 ml) were stored at –80°C until analysis and sediment water content was calculated from the difference in weight between frozen and freeze-dried sediment. The freeze-dried sediment was extracted with 10 ml of 90% acetone and pigment (chlorophyll *a* [chl *a*], phaeophytin *a* and phaeophytin *a*-like) concentrations in the supernatant were determined using HPLC (Gilson) analysis (Wright & Jeffrey 1997).

Data analysis. A fully crossed 3-factor design was performed in PERMANOVA with random factor replicate (Rep) nested in the fixed factor treatment (TR), next to the fixed factor slice (Sl). The interaction term TR × Sl informs us about the difference in depth profiles of nematode uni- or multivariate measures or environmental variables among treatments. Since a PERMANOVA test can show significant differences between groups, but does not distinguish between a difference due to location (factor effects) or dispersion (variance), homogeneity of multivariate dispersion was tested with PERMDISP, using distances among centroids calculated both within Rep(TR) groups (averaged depths) and in TR × Sl (averaged replicates) groups. The PERMDISP test was never significant, indicating equally dispersed distances to centroids, hence a difference due to location (TR × Sl interaction, hence 'profile'). In case of significant TR × Sl interactions, pairwise tests of TR within TR × Sl were performed to investigate in which slice the treatments differed or vice versa. With only significant single-factor effects, pairwise tests within each factor were carried out. Because of the restricted number of possible permutations in pairwise tests, p-values were obtained from Monte Carlo samplings (Anderson & Robinson

2003). The 3-factor design was used for both multivariate and univariate analyses since PERMANOVA allows us to perform univariate ANOVAs with p-values obtained by permutation (Anderson & Millar 2004), thus avoiding the assumption of normality. A Euclidean distance and Bray-Curtis based resemblance matrix was used for univariate and multivariate measures. The TR effect on the vertical structure of the nematode community was tested on (1) standardised (to account for differences in total nematode abundances among treatments) and square root-transformed data (to reduce the importance of dominant species) and on (2) raw data to take differences in species/genus abundance into account.

First, the difference between FC, RC and C profiles in terms of nematode density and community composition was tested. Further analyses considered experimental treatments only. The effect of macrobenthos on the totals and depth profiles of densities, diversity indices (species richness [S], evenness [J'], and Hill's indices N_1 and N_∞) and depth profiles of environmental variables was analysed. Sample sizes varied between levels of depth (5 ml for 0.5 cm slices, 10 ml for 1.0 cm slices). As samples vary proportionally, a non-linear relationship between sample volume and number of species cannot be excluded. Thus for all statistical analyses on nematode community structure and diversity indices that include depth horizons through the whole core (0 to 8 cm), 0.5 cm slice samples were combined into 1.0 cm slices to give comparable sample sizes, and separate analyses were run on the upper 2 cm samples at 0.5 cm discrimination.

Within the multivariate analyses, a SIMPER analysis was selectively carried out on the slices that differed significantly among treatments in nematode community composition. A second-stage MDS plot with additional ANOSIM visualises the correlation between the vertical profiles of the nematode community composition. DISTLM (DISTance Based Linear Models) is a routine for analysing and modeling the relationship between a multivariate data cloud and one or more predictor variables. This analysis was carried out to identify the environmental parameter (1 cm scale) with the greatest influence on the variance distribution of the nematode community composition. After elimination of highly correlated (i.e. $|r| > 0.8$) variables (i.e. %silt with median grain size), this analysis was performed on the normalised variables chl *a*, phaeophytin *a*, phaeophytin *a*-like pigment, %silt and water content using a global BEST selection procedure with Bayesian Information Correction (BIC). A generalised linear model (GLM) calculated the amount of variation in the nematode univariate measures (Poisson distribution was assumed) explained by combinations of environmental variables. If the residual variance exceeded the degrees of freedom, the data were 'overdispersed', and one of the assumptions of GLMs was violated. In this case, a compensation of the significance values was included in the models (Breslow 1984). The GLM accompanying adjusted D^2 is reported, which is a measure (equivalent to adjusted R^2 in least squares models) that resembles the fit of the model and increases with an increasing number of observations (n) or a decreasing number of parameters in the model (Guisan & Zimmermann 2000).

All analyses were performed within PRIMER v6 with PERMANOVA add-on software (Clarke & Gorley 2006, Anderson et al. 2008). Exceptions were the 1-way ANOVAs on the difference in total nematode densities and diversity indices among treatments with additional Tukey HSD post hoc tests and the GLM carried out in R 2.6.0 software (www.r-project.org). Results are expressed as mean ± SE of triplicates.

RESULTS

Procedural controls

Macrobenthos resident in the FC was very scarce, consisting of 1.3 ± 0.4 *Nephtys* sp. juveniles 10 cm^{-2} and 0.3 ± 0.4 *Aonides* sp. juveniles 10 cm^{-2} concentrated in the upper 2 cm.

The total nematode density in the FC, RC and C did not differ significantly (1-way ANOVA: $F_{2,6} = 2.71$, $p = 0.15$). The vertical profiles of the nematode densities, however, were distinct (Fig. 1; Table S1 in the Supplement at www.int-res.com/articles/suppl/m422p179_supp.pdf). Nematode densities in the FC increased gradually to a depth of 3 cm, below which they decreased again with depth, while in both C and RC this gradual pattern was replaced by a sharp decline in nematode densities below 1 cm. Significant differences between C and RC were observed in the deepest sediment layers: the RC had a significantly higher nematode density at depth than the FC and C. Also in terms of nematode community structure, in the FC the vertical structure was distinct from the C, but mainly in terms of abundance of dominant species (as detected by the higher pseudo-F value in the PERMANOVA analysis on raw data vs. standardised and square root-transformed data) (Table S2 in the supplement). The differences between FC and RC must be linked to manipulations during reconstruction, i.e. sieving and homogenising, and sediment compaction due to removal of particles and fauna >1 mm. In contrast, apart from a lower nematode density in the deepest layer in C probably due to anoxia-related mortality, nematode communities in C did not differ from those in RC. Thus, maintaining the microcosms in experimental

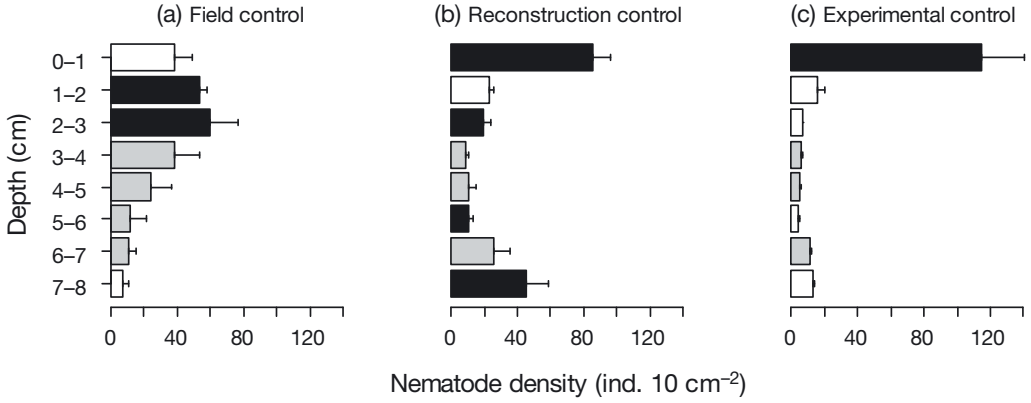

Fig. 1. Nematode density profiles in field (a), reconstruction (b) and experimental (c) controls. The higher (black bar) and lower (white bar) nematode density of each pair according to pairwise tests of TR within TR × Sl and slices not significantly different from other slices (grey bar) are indicated. Error bars indicate SE

Table 1. PERMANOVA results for environmental variables, general univariate community variables and the 5 most abundant nematode species. N: nematode abundance; *S*: species richness; *J'*: evenness; ns: not significant. P-values obtained by permutation

Variable	Treatment				Slice				Treatment × Slice			
	df	MS	Pseudo-*F*	p	df	MS	Pseudo-*F*	p	df	MS	Pseudo-*F*	p
Median grain size	3	29.75	2.83	ns	9	31.04	7.97	<0.001	27	6.18	1.59	ns
%Silt	3	29.30	1.38	ns	9	35.37	9.37	0.001	27	6.00	1.59	ns
Water content	3	1.28	2.37	ns	9	79.382	8.82	<0.001	27	3.17	2.18	0.005
Chlorophyll *a*	3	59.78	1.75	ns	9	95.69	8.56	<0.001	27	18.15	1.62	0.001
Phaeophytin *a*	3	0.00	1.02	ns	9	0.01	20.53	<0.001	27	0.00	1.94	0.014
Phaeophytin *a*-like pigment	3	0.02	1.28	ns	9	0.01	13.26	0.001	27	0.00	1.21	ns
N	3	1133.40	4.10	ns	9	19825	54.54	<0.001	27	1566.70	4.31	<0.001
S (whole core, cm scale)	3	92.40	13.44	0.003	7	464.92	49.28	<0.001	21	19.43	2.06	0.017
S (upper 2 cm, 0.5 cm scale)	3	33.5	8.46	0.009	3	211.33	16.63	<0.001	9	34.72	2.73	0.020
J' (whole core, cm scale)	3	0.09	1.31	ns	7	0.04	1.23	ns	21	0.02	0.69	ns
Hill's N_1 (whole core, cm scale)	3	37.98	23.35	0.006	7	81.38	18.50	<0.001	21	9.66	2.20	0.011
N_1 (upper 2 cm, 0.5 cm scale)	3	22.04	17.67	<0.001	3	19.406	4.19	0.016	9	10.98	2.37	0.042
Hill's N_∞ (whole core, cm scale)	3	1.84	4.32	ns	7	2.67	3.02	0.009	21	1.45	1.64	ns
N_∞ (upper 2 cm, 0.5 cm scale)	3	4.52	15.66	0.005	3	1.92	1.90	ns	9	1.44	1.43	ns
Richtersia inaequalis	3	87.37	1.47	ns	9	2343.70	36.83	<0.001	27	139.58	2.19	0.006
Sabatieria celtica	3	53.54	3.29	ns	9	85.27	5.56	<0.001	27	30.77	2.01	0.013
Sabatieria punctata	3	18.41	0.89	ns	9	13.94	1.53	ns	27	11.66	1.28	ns
Dichromadora cucullata	3	9.43	4.09	ns	9	462.45	74.62	<0.001	27	40.13	6.47	<0.001
Microlaimus conothelis	3	20.30	0.80	ns	9	58.78	4.72	0.001	27	32.35	2.60	0.004

conditions did not introduce large differences into the systems, and the patterns observed among experimental treatments can be linked to the effect of macrobenthic presence.

Experimental treatments

Survival of added macrobenthos

All added macrobenthos except 1 *Abra alba* individual were recovered live on slicing. *A. alba* individuals were found between 1.5 and 7 cm depth and mainly (77%) between 2 and 4 cm depth. *Nephtys hombergii* resided between 1 and 6 cm depth, with 76% in the 2 to 5 cm layer. *Lanice conchilega* tubes extended to the very bottom of the microcosms (8 cm).

Environmental variables

The macrobenthic functional groups did not affect the depth profiles of sediment median grain size and silt content (i.e. no interaction effect of TR × Sl) and there was only a significant 'Slice' effect (Table 1): sediment median grain size was smaller and silt content higher in the top centimetre in all experimental treatments. The water content of the sediment was sig-

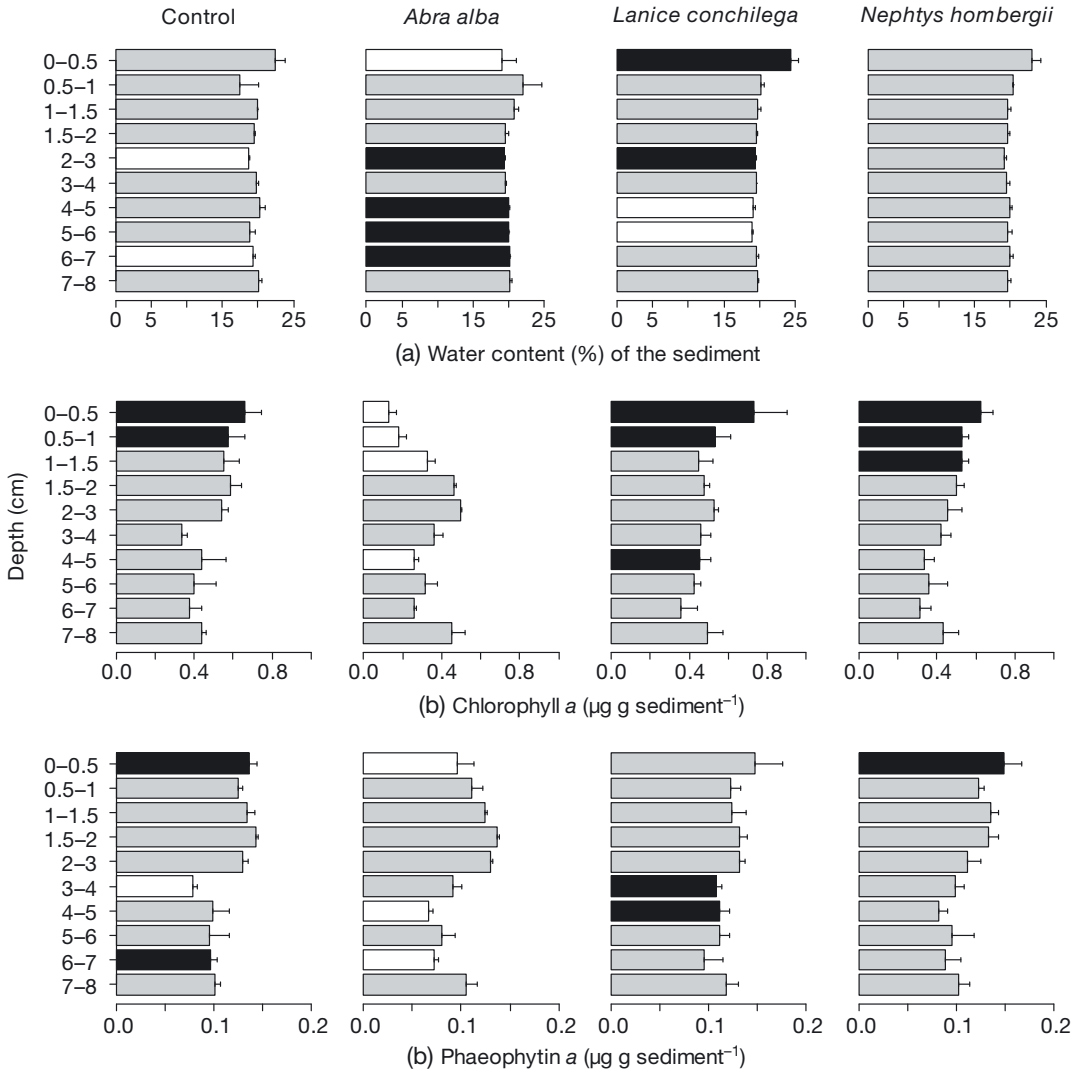

Fig. 2. (a) Water content, (b) chlorophyll *a* and (c) phaeophytin *a* profiles in control, *Abra alba*, *Lanice conchilega* and *Nephtys hombergii* treatments (from left to right). Grey shades as in Fig. 1. Error bars indicate SE

nificantly altered by the macrobenthic treatments (Table 1, Fig. 2) and was significantly enhanced in the *Lanice conchilega* treatment in the upper 0.5 cm (compared to the *Abra alba* treatment) and in the 2–3 cm layer (compared to control). Water content in the *A. alba* treatment was higher in the 2–3 cm and 6–7 cm layers (compared to control) and the 4–6 cm layer (compared to *L. conchilega*) (Table S3 in the supplement). Chl *a* profiles were also significantly structured by the macrobenthic treatments (Table 1, Fig. 2): the chl *a* content of the *A. alba* treatments was depleted in the upper 1.5 cm, and also the 4–5 cm layer of this treatment had a lower chl *a* content than the same slice in the *L. conchilega* treatment (Table S3). The profile of the chl *a* degradation products differed among treatments for phaeophytin *a*, but not for phaeophytin *a*-like pigment (Table 1). Phaeophytin *a* content followed a similar pattern to chl *a*, although less pronounced, being significantly lower in the surface layer of the *A. alba* treatment.

Nematode density and diversity

The average total number of nematodes per treatment (over the entire microcosm of 8 cm depth) was 233 ± 18 ind. 10 cm^{-2}. Nematode densities differed among treatments (Table S4 in the supplement) and were significantly higher in *Lanice conchilega* microcosms than in control microcosms (Tukey HSD post hoc: $p = 0.033$). As the proportion of juveniles was equal in all treatments, this difference should be attributed to mortality in the controls. The macrobenthic species belonging to 3 different functional groups had contrasting structuring effects

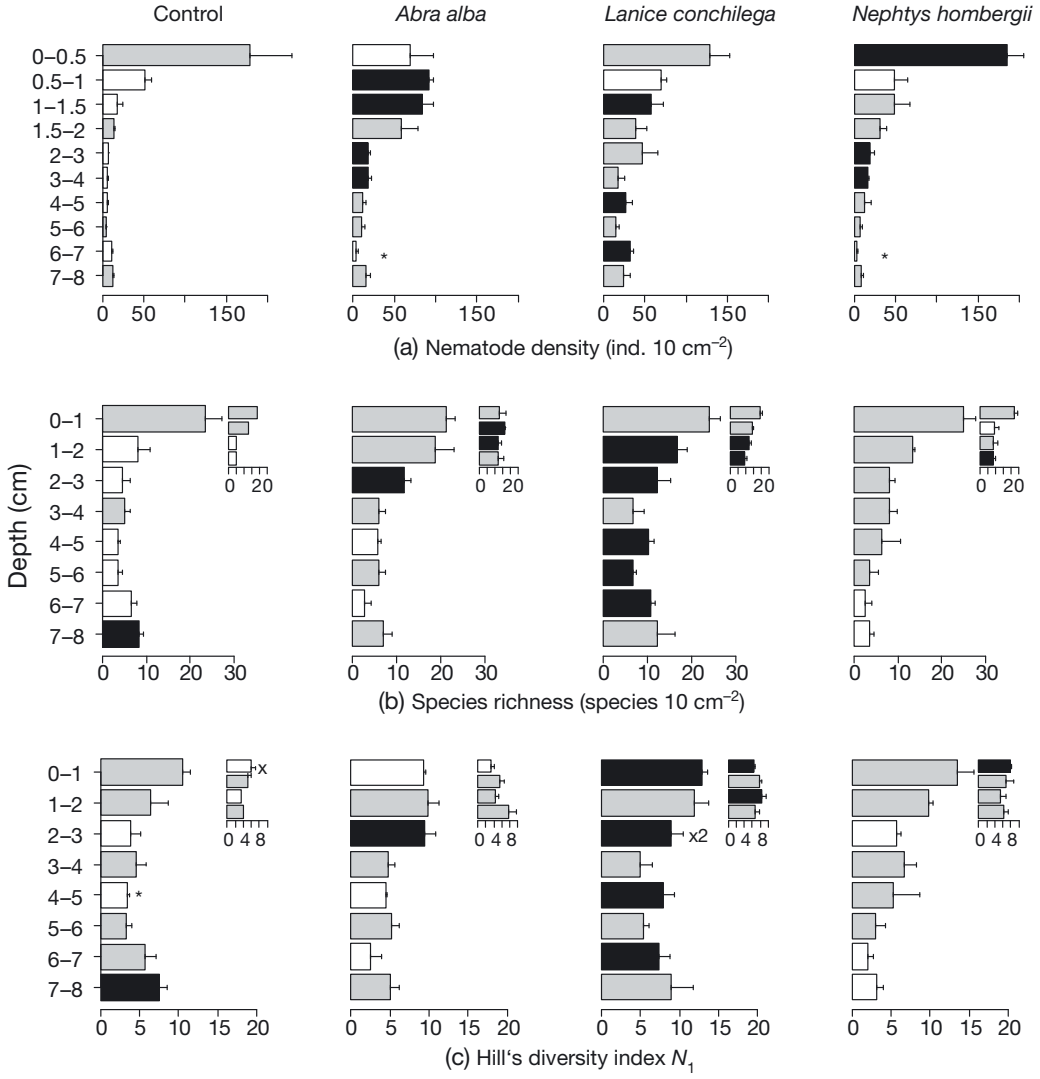

Fig. 3. Nematode (a) density and (b,c) diversity (b: species richness; c: Hill's diversity index N_1) profiles in control, *Abra alba*, *Lanice conchilega* and *Nephtys hombergii* treatments (from left to right). Main graphs indicate analyses on whole core (cm scale); inset graphs show analyses on the upper 2 cm (0.5 cm scale). *Significantly lowest values. x: N_1 of the control 0–0.5 cm slice was only lower than the 0–0.5 cm slice of *N. hombergii*. x2: N_1 of the *L. conchilega* 2–3 cm layer was only higher than N_1 of the control 2–3 cm layer. Grey shades as in Fig. 1. Error bars indicate SE

on the vertical distribution of the nematodes (Table 1, Fig. 3). Whereas nematode densities declined rapidly below 0.5 cm in the control treatment, significant subsurface peaks were observed (Fig. 3, Table S5 in the supplement) in *Abra alba* (0.5 to 1.5 cm, 2 to 4 cm) and *Lanice conchilega* (1 to 1.5 cm, 4 to 5 cm, 6 to 7 cm) treatments. In the *Nephtys hombergii* microcosms, nematodes were likewise found somewhat deeper than in the control microcosms (2 to 3 cm, 3 to 4 cm, 6 to 7 cm). Nematode abundance in the upper 0.5 cm in the *A. alba* treatments was significantly lower than in the *N. hombergii* treatments, whereas in the 0.5–1 cm layer it was significantly higher than in all other macrobenthic treatments.

A total of 80 nematode species was identified, with *Richtersia inaequalis*, *Sabatieria celtica*, *S. punctata*, *Microlaimus conothelis* and *Dichromadora cucullata* the 5 most abundant. Total species richness (S) and evenness (J') over the entire depth range did not differ among treatments, but Hill's indices N_1 and N_∞ were different (Table S4) and N_∞ was significantly higher in the *Nephtys hombergii* treatment than in the *Abra alba* (Tukey post hoc: p = 0.02) and control (Tukey post hoc: p = 0.04) treatments. This indicates that the commonest species (i.e. *R. inaequalis*) was less dominant in the *N. hombergii* treatment. For N_1, no significant pairwise tests were found. Evenness (J') depth profiles were similar in all treatments, whereas profiles of species richness (S) and Hill's diversity index N_1 differed significantly among treatments (Table 1, Fig. 3). Species richness (S) was enhanced in the 0.5–1.5 and 2–3 cm

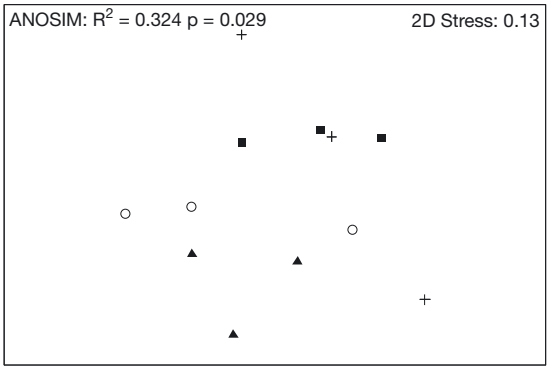

Fig. 4. Second-stage MDS plot of Spearman rank correlations between nematode community profiles on whole core (cm scale and raw data) in control (■), *Abra alba* (▲), *Lanice conchilega* (+) and *Nephtys hombergii* (○) treatments

layer of the *A. alba* treatment and in several depth layers between 1 and 7 cm depth in the *Lanice conchilega* treatment (Table S5). Similarly, Hill's diversity index N_1 was enhanced in several depth layers of the *L. conchilega* treatment (Fig. 3, Table S5) and in the 2–3 cm layer of the *A. alba* treatment.

Nematode community

The vertical structure of the nematode community composition in the whole core was different among experimental treatments when analysed with raw data as well as with standardised, square root-transformed data (Table S6 in the supplement). Pairwise tests on raw data (whole core) showed a significant difference among treatments in nematode community composition in the 3–4 cm horizon between control and *Abra alba* treatment ($t = 1.94$; Monte-Carlo p = 0.042). SIMPER analyses (Table S7 in the supplement) indicated that this difference could be accounted for by higher densities of *Sabatieria punctata* and *Spirinia* spp. at that depth in the *A. alba* treatment compared to control, while *Richtersia inaequalis* was completely absent in that horizon of the *A. alba* treatment. The analysis on the upper 2 cm only showed differences in vertical nematode community structure when analysed with raw data (Table S6). Pairwise tests on these raw data indicated a significant difference among treatments in community composition in the 0.5–1 cm horizon between the *A. alba* and *Nephtys hombergii* treatment (t = 1.80; Monte-Carlo p = 0.049). SIMPER analyses (Table S7) showed that *R. inaequalis*, *Dichromadora cucullata* and to a lesser extent *Microlaimus conothelis* occurred in higher densities in the *A. alba* treatment of this horizon, while *Sabatieria celtica* and *Sabatieria punctata* were more dominant in the *N. hombergii* treatment of this horizon. Only the ANOSIM on the whole core based on raw data showed significantly different nematode community profiles among treatments (visualised in the second-stage MDS plot in Fig. 4), which implies that the major nematode community changes take place over the entire depth range and are mainly a result of the response of the dominant species.

Dominant species

The vertical distribution of *Richtersia inaequalis* differed significantly among treatments (Table 1, Fig. 5a). The difference was mainly due to the significantly higher densities in the 0.5–2 cm horizons of the *Abra alba* treatment. Whereas the profiles of *Sabatieria punctata* were unaffected by the macrobenthic treatment, the profiles of its congener *S. celtica* (Table 1, Fig. 5b) differed significantly among treatments. *Microlaimus conothelis* (Fig. 5c) and *Dichromadora cucullata* (Fig. 5d) profiles also differed among macrobenthic treatments (Table 1) mainly due to higher densities in deeper layers of the *Lanice conchilega* (*S. celtica*, *M. conothelis*) and *A. alba* treatments (*S. celtica*), and differences in the surface layers (*D. cucullata*, *M. conothelis*).

Correlation between environmental variables and nematode distribution

The DISTLM routine with global BEST analysis and BIC correction revealed that the combination of phaeophytin *a* (9.15% of the variation explained) and water

Table 2. Results of regression model, corrected for overdispersion, between nematode univariate measures and environmental variables that are significantly affected by macrobenthic presence. *N*: nematode abundance; *S*: species richness; N_1: Hill's diversity index; ns: not significant

Variable	p-values		Water content	Adjusted D^2
	Chl *a*	Phaeophytin *a*		
N	<0.001	<0.001	<0.001	0.50
S (whole core, cm scale)	0.023	<0.001	<0.001	0.39
S (upper 2 cm, 0.5 cm scale)	ns	ns	<0.001	0.31
N_1 (whole core, cm scale)	ns	<0.001	0.016	0.26
N_1 (upper 2 cm, 0.5 cm scale)	ns	ns	ns	ns
Richtersia inaequalis	<0.001	<0.001	ns	0.40
Sabatieria celtica	ns	<0.001	ns	0.33
Sabatieria punctata	ns	ns	ns	ns
Dichromadora cucullata	0.007	<0.001	ns	0.33
Microlaimus conothelis	0.015	<0.001	ns	0.17

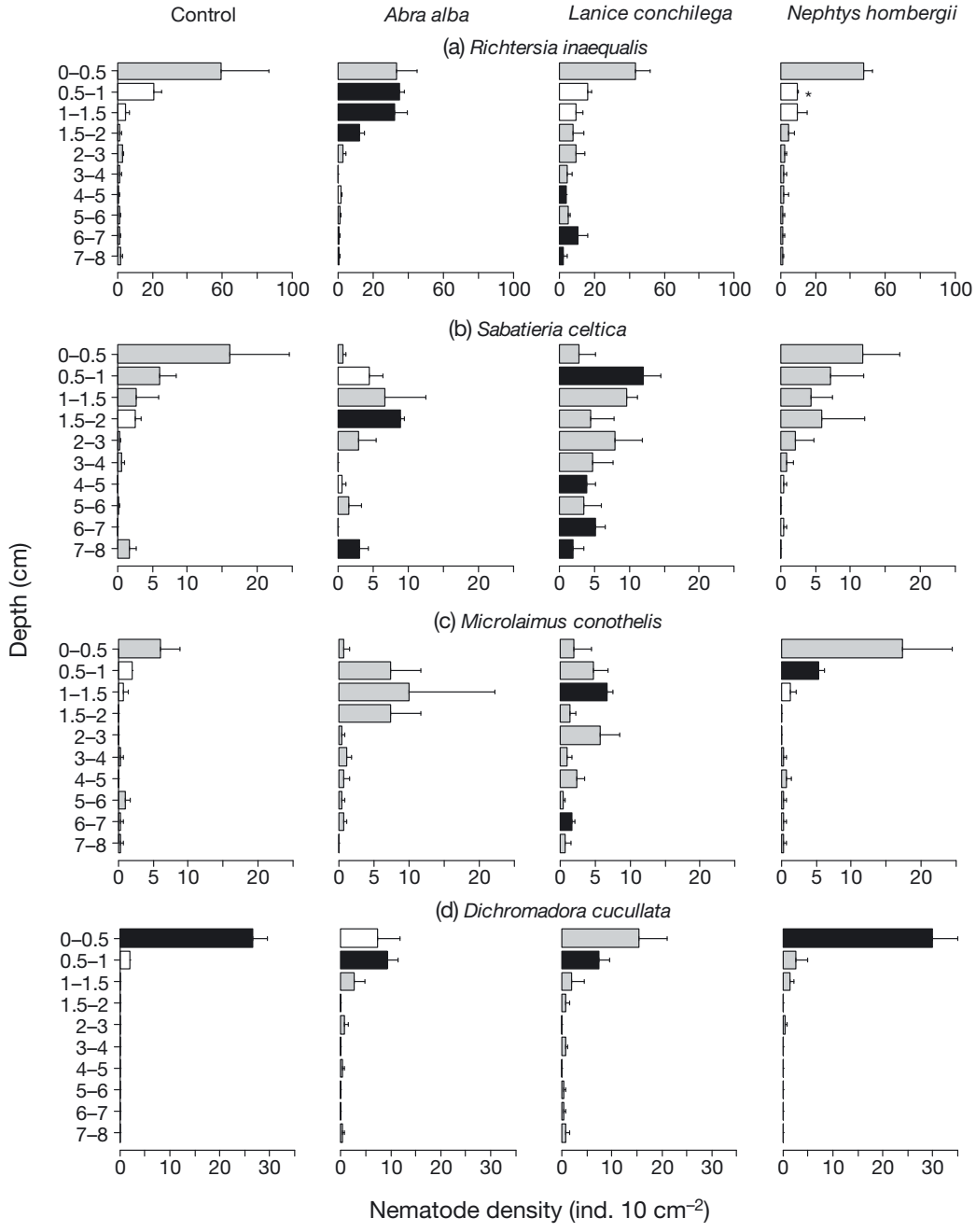

Fig. 5. (a) *Richtersia inaequalis*, (b) *Sabatieria celtica*, (c) *Microlaimus conothelis* and (d) *Dichromadora cucullata* density profiles in control, *Abra alba*, *Lanice conchilega* and *Nephtys hombergii* treatments (from left to right). *Significantly lowest values. Grey shades as in Fig. 1. Error bars indicate SE

content (6.87 % of the variation explained) explains the structure in the multivariate data set (whole core, raw data) the best. However, this correlation is quite low (R^2 = 0.138). In contrast, the GLM model using combinations of environmental variables explains the variation in the univariate measures of the nematode community by between 17 and 50 %, except for N_1 (2 cm) and *Sabatieria punctata* (Table 2).

DISCUSSION

The present laboratory study demonstrates a significant effect of macrobenthos on the vertical distribution of nematodes, in terms of density, diversity and community composition, corroborating earlier observations on the structuring effect of macrobenthos on nematode communities (Olafsson 2003, Pinto et al. 2006, Dash-

field et al. 2008). However, by identifying nematodes to the lowest taxonomic level and resolving their vertical profile, we revealed that (1) these nematode community responses are due to increased densities of the dominant non-selective deposit-feeding (*Richtersia inaequalis* and *Sabatieria celtica*) and epistrate-feeding (*Dichromadora cucullata* and *Microlaimus conothelis*) species at certain depths, and that (2) the type of response depends on the macrobenthic functional traits (in terms of bioturbation and bio-irrigation). Furthermore, the densities of the nematode species most responsible for the changes in community structure were related to the environmental variables altered by the resident macrofauna (i.e. water content and photopigments), suggesting ecosystem-engineering effects of macrofauna on nematodes. Yet, these environmental variables did not fully explain the vertical structure of the nematode community composition (cf. the low R^2 value in the DISTLM analysis). (1) This may point at missing measurements of important structuring factors such as oxygen penetration depth (Steyaert et al. 2005). (2) It may indicate a uniform response of the nematode species to the altered environmental variables, as reflected in the higher correlation with the univariate measures nematode density and diversity. (3) It demonstrates that apart from engineering the environmental variables, biotic interactions might play a role in the vertical structure of nematode community composition.

Nematodes experienced higher mortality in the control sediment without macrofauna, and those that survived concentrated in the upper centimetre of the sediment, apparently because bioturbation and bio-irrigation were lacking, which reduced subsurface oxygen concentrations and increased concentrations of toxic metabolites (Steyaert et al. 2003, 2005, 2007, Franco et al. 2008b). In addition, nematode diversity in these controls was impoverished in several depth layers compared to the sediments with macrofauna present. Widdicombe et al. (2003) pointed out that bioturbation is essential for species diversity by producing heterogeneity or complexity within the sediment. Importantly, the significantly different treatment effects suggest differing underlying mechanisms (as hypothesised in the following subsections) for the observed nematode community responses depending on macrofaunal functional identity.

Abra alba: exploitative competition and disturbance at the surface vs. faecal pellets in subsurface

Nematode density was significantly lower in the surface layer reworked by *Abra alba*. Nematodes seemed to have migrated downwards, resulting in higher densities between 0.5 and 4 cm sediment depth, which was particularly clear for the dominant species *Richtersia inaequalis*, *Dichromadora cucullata* and *Sabatieria celtica*, as shown by the different community profile of the *A. alba* treatment based on raw data (whole core, response of dominant species not weighed down; Fig. 4). Despite the substantial bioturbation activity of *A. alba* (Braeckman et al. 2010), its activity is probably limited to sediment reworking and does not consist of deep organic-matter burial (Graf 1989, Levin et al. 1997). During the present experiment, most of the labile organic matter was consumed by *A. alba* (emptied chl *a* profile in Fig. 2) and little to none was left for subsurface transport. Hence, the downward migration of nematodes cannot be linked to transport of food from the surface to depth. It therefore presumably relates to the depletion of food resources (diatoms) of the non-selective deposit- and epistrate-feeders sensu Wieser (1953) due to deposit-feeding activities of *A. alba* at the surface. In addition, the sediment-sucking siphons may have caused a substantial physical disturbance in the first 0.5 cm, thereby chasing the nematodes downwards. Direct predation seems unlikely as the size of particles taken up by *A. alba* siphons is smaller than the size of nematodes (Austen et al. 1998). The enhanced water content and thus related interstitial space around the bivalve might have facilitated the mobility of nematodes (McIntyre 1969). Furthermore, the downward shift of *R. inaequalis* and *D. cucullata*, both known to be intolerant to oxygen stress (Steyaert et al. 2007, Franco et al. 2008b), suggests the presence of small oxygen pulses into the sediment in close vicinity of the bivalve, likely facilitating the deeper survival of these species (Bouchet et al. 2009). Reise (1983) related an increased turbellarian density in close vicinity of the deposit-feeding bivalve *Macoma balthica* to the subsurface creation of micro-oxic zones and nutrient-stimulated micro-organism growth. Similarly, in the present experiment, the downward shift of the nematodes was concentrated between 0.5 and 3 cm, which lies exactly in the working area of *A. alba*, where it creates feeding pits (Maire et al. 2007) and deposits faecal pellets (Amouroux et al. 1989), both potentially sustaining bacterial populations (Solan & Wigham 2005).

Nephtys hombergii: no effect

Our data indicate no engineering effects of *Nephtys hombergii* on nematodes. Apart from a lower dominance of species (N_∞ in Table 1, Table S4), the vertical structure of the nematode community composition was not different from the pattern found in the control sediments. Further, the total nematode density was not affected, which excludes predation of this poly-

chaete on the nematodes (Tita et al. 2000). Moreover, *N. hombergii* did not alter the environmental variables measured and does not introduce oxygen into the sediment (Braeckman et al. 2010), thereby precluding engineering effects on nematodes via modification of sediment characteristics.

Lanice conchilega: deep sediment oxygenation

The higher survival of nematodes and the redistribution of several dominant species in the *Lanice conchilega* treatment suggest that this polychaete has engineering capacities that facilitate nematodes to dwell in deeper layers (Tita et al. 2000, Pinto et al. 2006). In contrast to *Abra alba*, *L. conchilega* did not deplete the chl *a* and phaeophytin *a* repository at the surface (and even slightly enhanced chl *a* and phaeophytin *a* concentrations at depth when compared to the *A. alba* treatment) (Fig. 2). In addition, regular and deep oxygen pulses along the tube walls (Forster & Graf 1995, Braeckman et al. 2010) may be beneficial to nematode survival as well. The recorded high nematode density at depth was mainly visible in *Sabatieria celtica* and to a lesser extent in *Microlaimus conothelis* and *Richtersia inaequalis* profiles. Whereas it is generally accepted that *S. punctata* and *S. pulchra* are resistant (Jensen 1981, 1983, Steyaert et al. 2005) to anoxia and associated elevated hydrogen sulphide concentrations, observations on the distribution of *S. celtica* on the one hand and *M. conothelis* on the other are less clear: Soetaert et al. (1994, 1995) showed a deep and opportunistic distribution of *S. celtica*, whereas Jensen (1983) and the control treatment in the present study point to a preference for oxygenated layers. Similarly, Heip et al. (1985), Wetzel et al. (1995) and Steyaert et al. (1999) point towards a deep distribution of *M. conothelis*, whereas the control treatment in the present study showed avoidance of deep layers. Consequently, the presence of the long and slender nematode species *S. celtica* and *M. conothelis* in the deep layers of the *L. conchilega* treatment might be linked to the regular oxygen pulses that reach this depth while at the same time these species can tolerate anaerobic non-irrigated intervals (Reise & Ax 1979). The presence at depth of the stout species *R. inaequalis*, which is probably vulnerable to oxygen diffusion limitations due to its large body width (Wetzel et al. 1995, Soetaert et al. 2002), further illustrates the *L. conchilega*-induced oxygenation of deeper sediment layers. In addition to the oxygenation of deep sediment layers, deposit-feeding nematodes may profit from the stimulation of bacterial populations in the mucus linings of the tube (Ziegelmeier 1952) or/and in the sediment surrounding the tubes (Solan & Wigham 2005).

CONCLUSIONS

The control treatment was detrimental to nematode survival compared to the *Lanice conchilega* treatment, most probably due to compaction of the sediment, lack of irrigation and associated shallower oxygen penetration depth in the absence of bioturbating macrofauna. In contrast, *Abra alba* and *L. conchilega* showed ecosystem-engineering capacities that extended the possible habitat area to a depth of respectively 3 and 7 cm, probably through removal of sulphide and ammonia and possibly also by stimulation of bacteria as food sources (in faecal pellets and along tube walls, respectively). This indicates again that ecosystem-engineering macrobenthos is essential for the survival of lower parts of the food web, such as foraminifera (Bouchet et al. 2009) and nematodes (Van Colen et al. 2009). It is important to note, however, that the outcome of our experiment is likely strongly habitat-dependent and the results presented should therefore strictly be interpreted in terms of subtidal fine-sandy habitats under a regular hydrodynamic regime. For instance, muddy sediments are subjected to slow diffusive pore-water transport while advective transport dominates in coarse sediments. Organisms in the first sediment type will therefore benefit from additional macrobenthic engineering of pore water flows, while physical forces may overrule macrobenthic engineering effects in sandy sediments (Olafsson 2003, Meysman et al. 2006). Furthermore, depletion of food resources may be less prevalent in biofilm-covered tidal-flat sediments (Kennedy 1993) or during the seasonal mass input of phytodetritus in subtidal sediments (Franco et al. 2010). Overall, our results reveal that functionally contrasting macrobenthic identities shape nematode communities in different ways. Such different engineering effects may maintain the role of nematodes in ecosystem functioning (Yeates et al. 2009) and the present study therefore highlights the need for the conservation of macrobenthic functional diversity.

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