



Tidal flat nematode responses to hypoxia and subsequent macrofauna-mediated alterations of sediment properties

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ABSTRACT: To assess the role of macrofauna-mediated sediment changes on nematode community recovery, we examined the temporal development of macrobenthos, nematode communities and sediment properties following hypoxia in 16 m² replicated plots over a 6 mo period. Hypoxia drastically changed nematode community composition (i.e. reduced diversity and abundances of all dominant nematodes, except *Odontophora* spp.), but complete mortality, as was the case for the macrobenthos, did not occur. Macrofauna diversity recovered slowly, but community composition approached that of control communities after several months. In contrast, nematode diversity recovered to control values within 1 mo but, subsequently, decreased again; hence, no clear convergence towards the control community composition was apparent. This diversity decline and lack of community recovery was mainly attributed to abundance overshoots of the epistrate feeding nematodes *Chromadora* spp., *Daptonema* spp. and *Ptycholaimellus ponticus* in the treatments, which dominated the treatment community after 2 mo. Nematode community reassembling was strongly related to the coupled macrobenthos-environmental temporal development. The dynamics of 2 sediment characteristics, which were both mediated by the colonizing macrobenthos, are presented as possible determinant factors for this relationship: (1) low nematode post-settlement resuspension resulting from stable sediments at early macrofauna recovery stages and (2) enhanced nematode reproduction and settlement success in a dense microphytobenthos mat in relation to the temporal variation in macrobenthos grazing pressure and bioturbation. In conclusion, the strong relationships between macrobenthos recovery, environmental development and nematode community development after hypoxia highlight the importance of macrobenthos–sediment interactions in the recovery and structuring of nematode communities.

KEY WORDS: Benthic community recovery · Macrofauna-meiofauna interactions · Sediment dynamics · Hypoxia · Intertidal mudflat · Westerschelde estuary · The Netherlands

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INTRODUCTION

Benthic communities of estuarine and coastal ecosystems are increasingly affected by disturbances. Besides physical disturbances, such as fishing, dredging and dredge disposal, which have adversely

impacted benthic communities over the last few decades (Newell et al. 1998, Thrush & Dayton 2002), shallow estuarine and coastal sediments worldwide are exposed to enhanced anthropogenic nutrient inputs, often resulting in permanent or seasonally depleted dissolved bottom oxygen (DO) concentrations, charac-

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terized by a high benthic mortality (Cloern 2001, Diaz 2001). While hypoxic ($DO < 2 \text{ mg l}^{-1}$) and anoxic ($DO = 0 \text{ mg l}^{-1}$) environments have existed throughout geological time, their occurrence in shallow coastal and estuarine areas appears to be increasing worldwide, most likely accelerated by human activities, e.g. agricultural runoff and industrial sewage (Wolanski 2007).

Research on the restoration of benthic communities from prolonged and/or seasonal periods of hypoxia has mainly been targeted on macrobenthos (e.g. Gamenick et al. 1996, Beukema et al. 1999, Van Colen et al. 2008), whereas recovery of meiobenthic organisms has been examined to a much lesser extent. Nematodes often constitute up to 90% of the meiobenthic community in intertidal flats (Soetaert et al. 1994) and are predators for meio- and microfauna, and serve as food source for macrofauna and juvenile fish (Heip et al. 1985, Coull 1990). In tidal flats, nematodes reach extremely high abundances in the upper centimeters ($>10^6 \text{ ind m}^{-2}$) (Steyaert et al. 2003), and their distribution is determined by sediment composition, salinity, organic content and oxygen (Soetaert et al. 1994, Steyaert et al. 2003). Furthermore, macrobenthic organisms have the potential to affect nematode communities, since macrobenthos can drastically change the physical and chemical characteristics of the sediment (i.e. bio-engineering capacity) (Reise 1983, Olafsson 2003 and references therein). Especially after disturbances causing severe benthic mortality (e.g. prolonged hypoxia), macrobenthos may be expected to influence nematode community structure considerably, since recolonizing macrobenthos is known to change physical and chemical sediment properties, often in a successional sequence (Pearson & Rosenberg 1978, Montserrat et al. 2008). Since nematodes have short generation times, they may be expected to respond rapidly to such macrobenthos-mediated changing environments. A few studies have examined macrobenthos and nematode community responses to disturbed tidal flat sediments simultaneously (e.g. Dittmann et al. 1999, Bolam et al. 2006) but the pattern and the importance of macrobenthos–nematode interactions during the recovery processes remains poorly understood.

In order to investigate how macrofauna-mediated changes in sediment properties may affect nematode community recovery, we conducted a field experiment in which we simultaneously examined the temporal development of sediment properties and the macrobenthic and nematode community following hypoxia, over a 6 mo period. We specifically addressed the following questions: (1) How do nematodes respond to, and develop after, hypoxia in terms of diversity, abundance and community structure? (2) Are the temporal patterns of nematode recovery related to the temporal patterns in the coupled macrobenthos–environmental development?

MATERIALS AND METHODS

Experimental setup, sampling and laboratory treatment. The experiment was conducted at Paulinapolder, a tidal flat located along the southern shore of the polyhaline part of the Westerschelde estuary, the Netherlands ($51^{\circ} 21' 24'' \text{ N}$, $3^{\circ} 42' 51'' \text{ W}$). Nematodes constitute 81 to 98% of the meiobenthos abundance and occur predominantly (~65%) in the upper cm layer at the study site (C. Van Colen unpubl. data). Triple replicated $4 \times 4 \text{ m}$ treatment and control (i.e. undisturbed sediment) plots were randomly positioned within a $25 \times 25 \text{ m}$ homogeneous study site, at least 5 m apart. Hypoxic conditions were created by covering the treatment plot sediments by a water-proof polyethylene sheet (0.1 mm thick) and a tarpaulin sheet (140 g m^{-2}) and burying the edges 30 cm deep, following Beukema et al. (1999) and Dittman et al. (1999). After 40 d (30 March 2005), the plots were opened and biotic and abiotic samples were collected at low tide at a randomly selected subplot ($37.5 \times 37.5 \text{ cm}$) immediately after opening the plots (Day 0) and subsequently with a maximum interval of 2 wk, for 6 mo. Depending on the response variable, 1 (macrofauna, nematodes, organic matter, mud content and sediment stability) or 2 (bed level elevation, surface chlorophyll *a* [chl *a*], oxygen concentration, water content, nutrient pore water concentration) subplots were sampled in each plot. Nematode samples were collected from the upper cm using a Perspex corer (inner $\varnothing 3.6 \text{ cm}$, i.e. 10 cm^2) and subsequently fixed in a neutral 4% formaldehyde tapwater solution. Treatment plots were characterized by different macrofauna communities and sediment properties at Day 0, 28, 56, 98, 112 and 175 (Van Colen et al. 2008). Nematode samples from these sampling occasions were further processed in order to understand how nematode communities respond to and recover from hypoxia and how macrofauna-mediated environmental changes may affect this process. Nematodes retained on a $38 \mu\text{m}$ sieve were extracted from the sediment by centrifugation with Ludox (Heip et al. 1985). After staining with Rose Bengal, 120 nematodes were randomly selected, transferred to glycerine and mounted on slides for identification to species or genus level using the NEMYS database (Steyaert et al. 2005). For further information on the study site, experimental set up and abiotic and biotic sample processing, the reader is referred to Van Colen et al. (2008), Montserrat et al. (2008) and Rossi et al. (2008).

Statistical analyses. Two-way ANOVA was used to test for significant effects of the factors Time and Treatment (i.e. hypoxia vs. control) on univariate community characteristics (total nematode abundance, number of genera, Hill's N_1 diversity index and the abundances of the genera contributing most to the dissimilarity be-

tween control and treatment assemblages on each sampling occasion, as revealed by SIMPER analysis). Prior to the analyses, Bartlett's and Cochran's tests were used to test for homogeneity of variances, and data not meeting these criteria were appropriately transformed. Additionally, to assess recovery status, treatment effects within a sampling occasion were explored by 1-way ANOVA. In the context of the present study, we defined recovery of the affected plots as having occurred when the plots had attained a state that was no longer significantly different from the control plots.

A correlation based principal component analysis (PCA) using normalised Euclidean distance was performed to visualize treatment and temporal differences in the environmental variables. The effect of Treatment (averaged over time groups) and Time (averaged over treatment groups) on nematode community structure was examined using 2-way crossed analysis of similarity (ANOSIM) on square-root transformed abundance data and visualized using multidimensional scaling (MDS). Furthermore, dissimilarities between control and treatment nematode communities at each sampling occasion and the contribution of those genera responsible for the dissimilarity were determined using the similarities of percentage procedure (SIMPER). Finally, the RELATE routine was applied to examine whether the environmental, macrofaunal and nematode community development followed similar directional changes over time (i.e. seriation) and the BEST routine was applied in order to assess relations between the environmental, macrofaunal and nematode multivariate patterns.

Univariate statistical analyses were performed using Statistica 7.0 (Statsoft); multivariate analyses were performed using the Plymouth Routines In Multivariate Ecological Research (PRIMER) package, version 6 (Clarke & Gorley 2006). For a detailed analysis of the environmental and macrobenthos recovery pattern, the reader is referred to Van Colen et al. (2008) and Montserrat et al. (2008).

RESULTS

Nematode response to, and recovery from, hypoxia

Total nematode abundance, total number of genera and Hill's N_1 diversity index were significantly reduced in the treatment plots at Day 0 (Fig. 1). According to the SIMPER analysis, differences between the control and treatment communities at Day 0 mainly resulted from significantly reduced abundances of *Oncholaimellus* sp.1 (-61%) and species belonging to the genera *Chromadorita* (-87%), *Viscosia* (-70%),

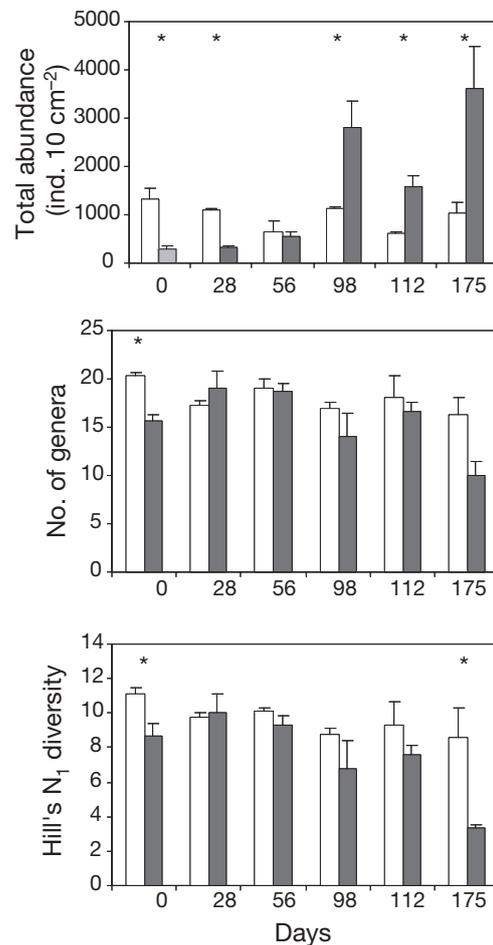


Fig. 1. Temporal variation in general univariate community characteristics in control (white) and treatment (grey) plots: total abundance, total number of genera and Hill's N_1 diversity. Error bars are + SE. *Significant treatment effects for sampling occasions, deduced from 1-way ANOVA

Daptonema (-80%) and *Neochromadora* (-100%). Next to *Neochromadora*, only less abundant genera (i.e. <18 ind 10 cm⁻² in control plots at Day 0) were absent at Day 0 in the treatment plots. Large but non-significant reductions in abundances of other species and genera in the treatment plots were found for *Ptycholaimellus ponticus* (-59%), *Anoplostoma viviparum* (-37%), *Sphaerolaimus* spp. (-58%), *Sabatieria* spp. (-38%) and *Paramonhystra* spp. (-24%). The only abundant genus not reduced after hypoxia was *Odonotophora* (28 ± 14 ind 10 cm⁻², mean ± SE; + 3%). Highest abundances in the treatment plots were reached for *Anoplostoma viviparum*, *Oncholaimellus* sp.1 and *Paramonhystra* spp. (58 ± 23, 49 ± 22 and 41 ± 17 ind. 10 cm⁻², respectively). However, these species were more abundant in the control plots.

Two-way ANOVA indicated a significant Time and significant Treatment effect for the total number of

genera and Hill's N_1 diversity index, whereas only a significant Time effect was found for the total nematode abundance (Table 1). Total nematode abundance recovered at Day 56, followed by a significant overshoot in the treatment plots, whereas the total number of genera and Hill's N_1 diversity index had already recovered at Day 28. However, the latter variables were consistently lower in the treatment plots from Day 56 onwards, as compared to the controls; at Day 175, Hill's N_1 diversity index was significantly lower in the treatment plots (Fig. 1). Results of 2-way ANOVA revealed a significant Time and Treatment effect for *Chromadora* spp. and *Ptycho-*

laimellus ponticus, whereas only significant Treatment effects were found for *Oncholaimellus* sp.1, *Viscosia* spp. and *Anoplostoma viviparum* and a significant Time effect was apparent for *Daptonema* spp. (Table 1). All these species and genera had recovered or showed an abundance overshoot in the treatment plots at Day 175. Abundance overshoots in the treatment plots were noticed for *Daptonema* spp., *Ptycholaimellus ponticus* and *Chromadora* spp. from Day 56 onwards (Fig. 2). The contribution of the juveniles to the total abundance of *Daptonema* spp. remained quite stable in the treatment plots during the course of the experiment, whereas this variable

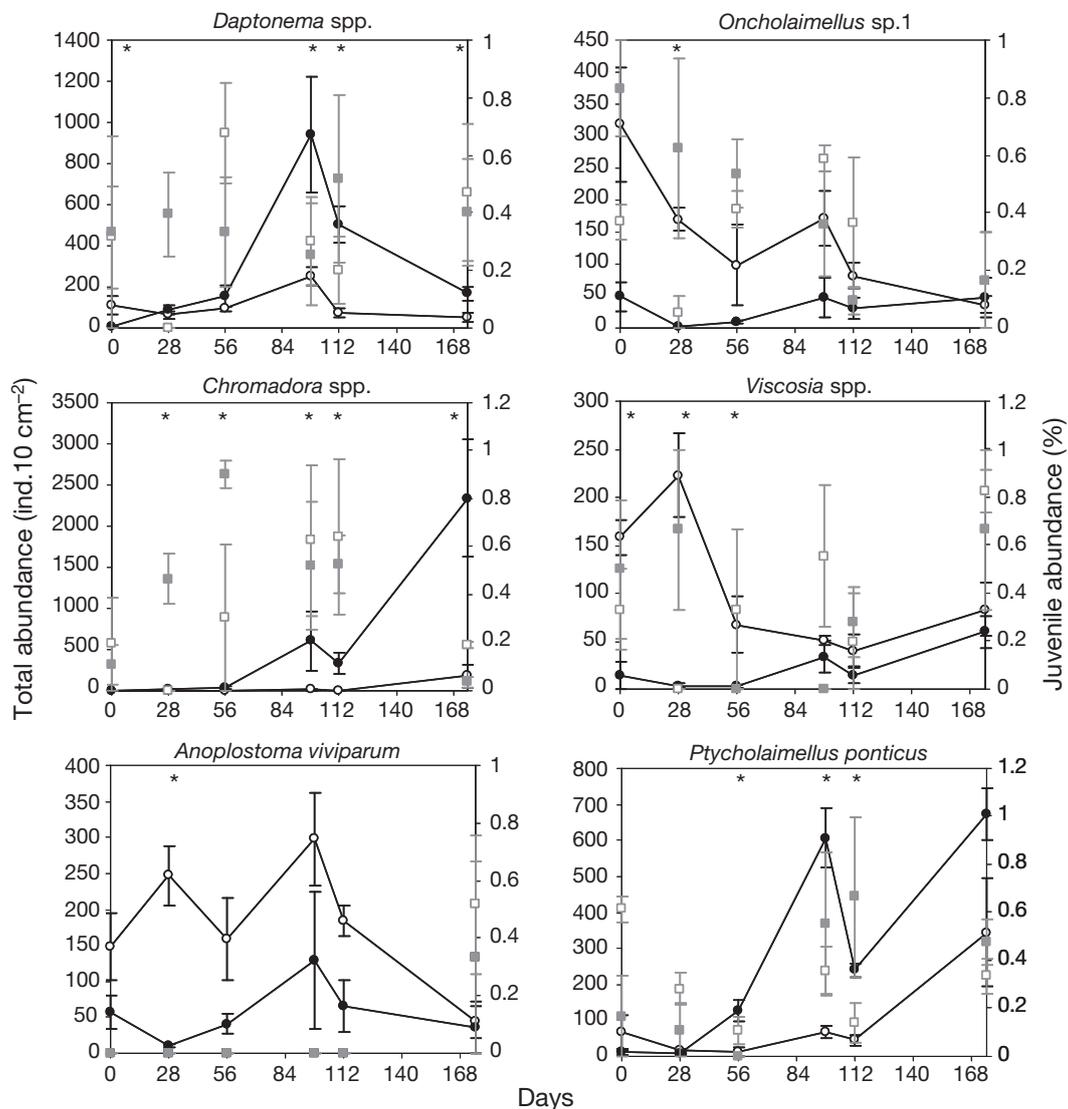


Fig. 2. Temporal variation in the total abundance (mean ± SE) of the dominant nematodes *Daptonema* spp., *Chromadora* spp., *Anoplostoma viviparum*, *Oncholaimellus* sp.1, *Viscosia* spp. and *Ptycholaimellus ponticus* in control (○) and treated (●) plots. The contribution of juveniles to the total abundances (%), mean ± SE is given on the secondary y-axis (control = □, treatment = ■).

*Significant treatment effects for the total abundance per sampling occasion, deduced from 1-way ANOVA

showed a distinct temporal pattern for *Ptycholaimellus ponticus* and *Chromadora* spp. An increase in the relative abundance of *Chromadora* spp. juveniles occurred during the second month after hypoxia, while the highest relative juvenile abundances of *Ptycholaimellus ponticus* were present from Day 98 onwards.

Two-way crossed ANOSIM revealed significant treatment ($R = 0.748$, $p = 0.01$) and temporal ($R = 0.6$, $p = 0.01$) differences on the nematode community structure, as is also shown by the clear separation and temporal variation of both communities in the non-metric multidimensional scaling (MDS) (Fig. 3). Temporal variation in the treatments was greater as compared to the controls, but no apparent convergence of the treated community towards the control community occurred throughout the experiment. Consequently, at Day 175 both communities were still clearly different

Table 1. 2-way ANOVA for univariate nematode community characteristics and dominant nematode genera (df = 1,5; respectively for treatment and time). Values in bold are significant ($p < 0.05$). Assumptions for homogeneity of variances were met for all variables (Bartlett-Cochran test; $p > 0.05$)

	Treatment		Time	
	F	p	F	p
Total abundance ^a	0.29	0.592	4.06	0.006
Total number of genera ^b	7.56	0.010	4.25	0.005
Hill's N ₁ diversity ^b	12.34	0.001	5.93	0.001
<i>Daptonema</i> spp. ^b	1.06	0.312	6.00	0.001
<i>Oncholaimellus</i> sp.1 ^b	22.80	<0.001	1.15	0.359
<i>Chromadora</i> spp. ^b	60.30	<0.001	15.67	<0.001
<i>Viscosia</i> spp. ^b	24.14	<0.001	1.07	0.396
<i>Anoplostoma viviparum</i> ^a	21.19	<0.001	2.35	0.066
<i>Ptycholaimellus ponticus</i> ^b	6.60	0.016	9.32	<0.001

Analysis performed on (a) square root and (b) log(x+1) transformed data

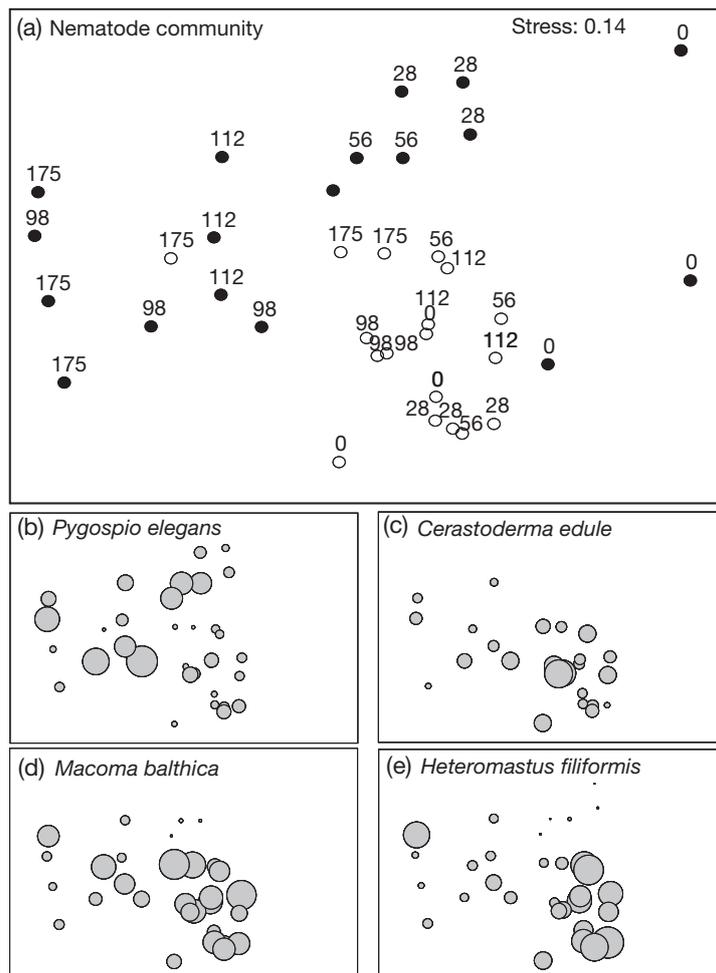


Fig. 3. (a) Multidimensional scaling ordination diagram based on square root transformed data of nematode genera abundances in treatment (●) and control plots (○) on the sampling occasions. To visualize the relationship with the macrobenthos recovery and resemblance to control plots, abundances of (b) *Pygospio elegans* and (c) *Cerastoderma edule* and biomasses of (d) *Macoma balthica* and (e) *Heteromastus filiformis* are superimposed on the ordination as circles whose sizes reflect the magnitude of these variables

Table 2. Results of ANOSIM and SIMPER analysis based on square-root transformed nematode genera abundances indicating the strength of separation between the communities (Anosim R) and the total dissimilarity (% D) between control and treated communities at each sampling occasion and the contribution of the most discriminating genera to this dissimilarity. Italicized values indicate higher genera abundances in the treatment plots

Day	Anosim R	% D	Species contribution to the dissimilarity (%)					
0	0.63	46.8	<i>Oncholaimellus</i> sp.1	10.3	<i>Chromadorita</i>	8.8	<i>Viscosia</i> spp.	8.7
28	1	52.4	<i>Viscosia</i> spp.	12.2	<i>Anoplostoma viviparum</i>	11.7	<i>Oncholaimellus</i> sp.1	10.9
56	0.74	37.5	<i>Ptycholaimellus ponticus</i>	10.3	<i>Oncholaimellus</i> sp.1	9.0	<i>Viscosia</i> spp.	8.7
98	0.74	36.5	<i>Chromadora</i> spp.	19.1	<i>P. ponticus</i>	14.7	<i>Daptonema</i> spp.	13.2
112	1	40.5	<i>Chromadora</i> spp.	16.3	<i>Daptonema</i> spp.	14.1	<i>P. ponticus</i>	8.8
175	0.59	41.8	<i>Chromadora</i> spp.	29.1	<i>P. ponticus</i>	6.2	<i>Paramonhystera</i>	5.6

(ANOSIM $R = 0.593$, averaged dissimilarity = 41.8%, Table 2). Species contributing most to the community dissimilarity changed throughout the experiment (Table 2). Until Day 56, dissimilarities between both communities were mainly attributable to the lower abundances of *Oncholaimellus* sp.1, *Viscosia* spp. and *Anoplostoma viviparum* in the treatment plots, while abundance overshoots in the treatments of *Daptonema* spp., *Ptycholaimellus ponticus* and *Chromadora* spp. contributed most to the dissimilarity from Day 98 onwards.

Relationships with macrofauna and environmental recovery

Principal component analysis showed that sediment properties in the treatment plots converged towards control conditions during the course of the experiment (Fig. 4). Treatment sediments at Day 0, 28 and 56 were more reduced (lower free oxygen penetration and higher ammonium concentration, i.e. lower PC1 values) as compared to the control sediments and treatment sediments from Day 98 onwards. Furthermore, treated sediments at Day 28 and 56 could be distinguished from later sampling occasions and control sediments, since they had higher elevation and contained a higher proportion of mud, organic carbon and chl a (i.e. lower PC1 values).

From Day 28 onwards, RELATE test within the treatment plots revealed a significant and strong relationship between the temporal variation of the nematode community and (1) the macrofauna species biomasses ($\rho = 0.830$; $p = 0.043$), (2) the macrofauna species abundances ($\rho = 0.782$; $p = 0.020$) and (3) environmental development ($\rho = 0.572$; $p = 0.035$). BEST analysis revealed that maximal matching between nematode and macrobenthic assemblages

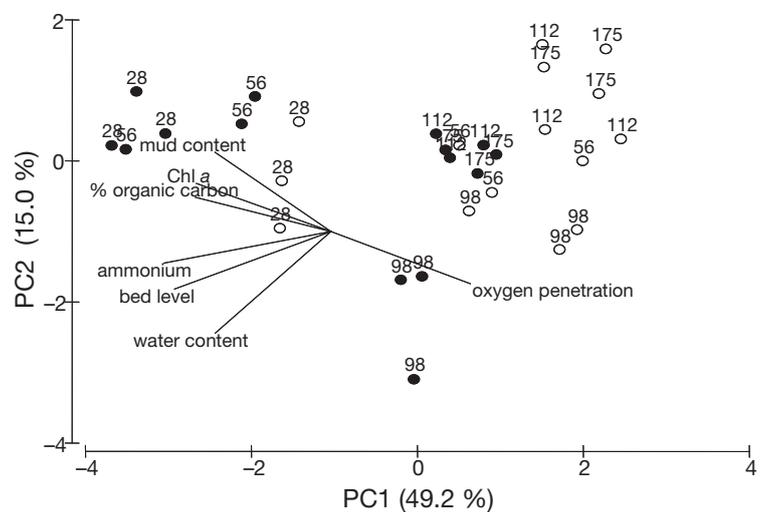


Fig. 4. Principal component analysis (PCA) ordination based on normalised environmental data, showing the temporal changes in the control (O) and treatment plots (●). Vectors presenting the environmental variables relative to PC1 and PC2 are superimposed. Note that sampling occasion Day 0 (extreme high ammonium concentrations in the treatments) is omitted to enhance visualisation

was explained by 4 macrobenthic species: *Cerastoderma edule*, *Heteromastus filiformis*, *Macoma balthica* and *Pygospio elegans* ($\rho = 0.879$, $\rho = 0.952$, abundance and biomass, respectively). Furthermore, a combination of the variables oxygen penetration depth, sediment stability and organic carbon best explained the multivariate nematode pattern in the treatment plots (BEST, $\rho = 0.964$). Adding chl a to this combination resulted in a slightly lower correlation ($\rho = 0.952$). Within the control plots, temporal variation of the nematode community was only, but to a lesser extent, related to the temporal variation in environmental characteristics ($\rho = 0.572$, $p = 0.035$). BEST revealed that a combination of water content, bed level and sediment stability best explained the multivariate nematode pattern in the control plots ($\rho = 0.879$).

DISCUSSION

Nematode response to hypoxia

The induced hypoxic conditions did not result in complete nematode mortality. Such severe mortality was however observed for the macrobenthos (see Van Colen et al. 2008), which, consistent with the findings of Josefson & Widbom (1988) and Mödigi & Olafsson (1998), indicates a higher resistance of nematodes to hypoxic conditions as compared to the macrobenthos. Nonetheless, hypoxia adversely affected the nematode community, i.e. it reduced the number of genera and abundances, causing a generally less diverse community. Such effects have commonly been noticed after hypoxic events and have been attributed to migration of nematodes into the water column until normal oxygen conditions are re-established (reviewed in Wetzel et al. 2001). However, in this experiment, the sheet cover made upward migration into the water column impossible, and organisms were forced to cope with the hypoxic conditions or die. Under low oxygen conditions, sulfide concentrations may accumulate due to the activity of sulphate reducing bacteria. Sulfide is toxic to many marine invertebrates (Bagarinao 1992) and negative effects of hypoxia may therefore be aggravated by concomitant sulphide exposure. *Sabatieria* abundances were reduced, although species belonging to this genus have often been shown to resist hypoxic events (e.g. Bouwman et al. 1984, Wetzel et al. 2002). Only *Odontophora* spp. was found in almost identical abundances in hypoxic and control sediments, implying that this genus was highly resistant to hypoxia. Further, no significantly higher abundances were noticed for any genus, indicating that in hypoxic conditions no nematode species or genus could take advantage of the reduced abundances of others.

Nematode recovery and relation to coupled macrofauna–environmental recovery

Nematode diversity recovery occurred fast (i.e. within 1 mo) in comparison with macrofauna diversity recovery, indicating the higher resilience of nematodes as compared to the macrofauna. Macrobenthos diversity recovery took 6 mo and was strongly dependant on successful colonization of juvenile macrobenthos (Van Colen et al. 2008). In contrast, both juvenile and adult recruitment were important nematode recovery mechanisms in this study (Fig. 2). Fast nematode recovery has often been found in tidal flats (e.g. Savidge & Taghon 1988, Atilla & Fleeger 2000) and is probably mainly attributed to strong currents in these areas. Commito & Tita (2002) found that suspended nema-

todes in the water column of an intertidal flat are in particular epistrate feeders, most probably because they are more susceptible to erosion-induced sediment transport. In this experiment, the large increase in abundance of the epistrate feeders *Ptycholaimellus ponticus* and *Chromadora* spp., and the facultative epistrate feeder *Daptonema* spp. in the treatments occurred concomitant with the sediment erosion in the control plots between Day 28 and Day 98, which suggests that recolonization via the resuspension pathway is an important recovery mechanism in the present study. Moreover, the large abundance overshoots of these epistrate feeding nematodes in the treatments (1) resulted in a diversity decrease in treatment community from 2 mo after opening of the plots and (2) largely contributed to the lack of community recovery (i.e. lack of directional nematode reassembling towards the controls).

Nematode reassembling was strongly related to the development of both macrofauna and environmental characteristics following hypoxia, whereas the temporal variation in the control plots was only related to environmental temporal variation. Moreover, a subset of species (*Pygospio elegans*, *Macoma balthica*, *Cerastoderma edule* and *Heteromastus filiformis*), all determined to have affected sediment properties significantly in this experiment (Van Colen et al. 2008, Montserrat et al. 2008), best 'matched' the nematode development following hypoxia. Macrobenthos-mediated physical–biological interactions have been shown to influence nematode communities (Olafsson 2003 and references therein), and 2 types of such interactions are hypothesized as structuring factors of the nematode community recovery in this experiment: (1) sediment bio(de)stabilization and post-settlement resuspension and (2) the development and decomposition of a dense microphytobenthos mat due to temporal variation in macrobenthic grazing and bioturbation.

Interaction 1: macrofaunal bioturbation and post-settlement resuspension

In comparison with the controls, treatment sediments remained at the same intertidal height, were more stable and consisted of a higher proportion of mud during the second and third month after hypoxia (Montserrat et al. 2008). This presumably resulted from the combined effect of the dense aggregations of opportunistic biostabilizing tube-building polychaetes (*Pygospio elegans*, *Polydora cornuta*) and the low biomass of biodestabilizing species (*Macoma balthica*, *Cerastoderma edule* and *Heteromastus filiformis*) during early macrobenthic recovery stages (Fig. 3). These conditions may reduce the boundary shear stress so that fine

particles (e.g. nematodes) are less easily suspended after settlement (Eckman 1983). Hence, lower resuspension in the treatments may explain the enhanced accumulation of mud particles and nematodes as compared to eroding control sediments. These findings corroborate with Thrush et al. (1996), who found increased sediment instability after the experimental removal of the tube-building polychaete *Boccardia syrtis* from a New Zealand sandflat.

Interaction 2: macrobenthos grazing, bioturbation and microphytobenthos

The development of a dense microphytobenthos bloom, resulting from the low grazing pressure by macrofauna during the first month, might have favoured nematodes with the reproductive potential to take advantage of an organic enrichment, such as *Ptycholaimellus ponticus* and *Chromadora* spp. (Gee & Warwick 1985, Schratzberger & Warwick 1998, Schratzberger et al. 2004). Juvenile abundance contributes largely to the total abundance overshoots of the diatom-feeding nematodes *P. ponticus* and *Chromadora* spp. Moreover, for *P. ponticus* it was particularly clear that initial colonization predominantly occurred through adult recruitment, while the proportion of juveniles of this species became larger at a later stage. Further, significantly higher abundances in the treatment plots were also found for the non-selective deposit feeder *Daptonema* spp. Based on observations from mesocosm feeding experiments, Moens & Vincx (1997) concluded that species belonging to this genus also feed on diatoms. High abundances for *P. ponticus*, *Daptonema* spp. and chromadorid nematodes have been reported from different recolonization studies (Wetzel et al. 2002, Schratzberger et al. 2004) indicating the opportunistic behaviour of these nematodes.

In addition to a lower post-settlement mortality and enhanced reproduction due to the favourable conditions during the second and third month, enhanced settlement may have contributed to the significant abundance overshoot in the treatment plots from Day 98 onward. Evidence for such active settlement in a diatom biofilm was found by Ullberg & Olafsson (2003). However, it should be noted that the results from that study are deduced from a still-water laboratory experiment, while active habitat choice becomes presumably less important at higher hydrodynamic conditions (i.e. field conditions), as suggested by Commito & Tita (2002). As far as we know, evidence for active habitat choice of nematodes is still lacking from field experiments.

The dominance of *Ptycholaimellus ponticus* and *Chromadora* spp. in the treatment community continued even after the decline of tube-building poly-

chaetes and microphytobenthos biomass, characterizing the shift between intermediate and later macrobenthos succession stages. These changes coincided with the enhanced grazing pressure of surface deposit feeding macrofauna populations and enhanced sediment disturbance resulting from the colonization of *Heteromastus filiformis* and the growth of *Macoma balthica* and *Nereis diversicolor* (Van Colen et al. 2008) and resulted in the recovery of the sediment stability between Day 98 and Day 112 (Montserrat et al. 2008). These changes, characterizing the shift between intermediate and later macrobenthos succession stages were related to the enhanced grazing pressure of surface deposit feeding macrofauna populations and enhanced sediment disturbance resulting from the colonization of *Heteromastus filiformis* and growth of *Macoma balthica* and *Nereis diversicolor* (Van Colen et al. 2008). However, macrobenthos grazing pressure and disturbance due to bioturbation remained lower as compared to the controls, since macrobenthos biomass had not recovered after 6 mo. Further, some epistrate-feeding nematodes can also feed on mineralized material (i.e. trophic plasticity) (Moens & Vincx 1997, Danovaro & Gambi 2002). Therefore, in addition to a lower competition with macrofauna, *P. ponticus* and *Chromadora* spp. probably also benefit from the subsequent decomposition of the microphytobenthos bloom by bacteria.

CONCLUSIONS

This study shows that, in comparison with the macrobenthos, nematode communities are much more resistant to hypoxia. Following severe hypoxia, nematode community reassembling was strongly related to the recovery of the macrobenthos community and the concomitant changes in sediment properties. The dynamics of 2 sediment characteristics, which were both mediated by the colonizing macrobenthos, were suggested as determinant factors for these relationships: (1) low post-settlement resuspension resulting from low macrobenthic bioturbation impact at early macrofauna recovery stages and (2) the development and subsequent decomposition of a dense microphytobenthos mat in relation to the temporal variation of macrobenthos grazing pressure and bioturbation.

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