

# CHAPTER 6

## TIDAL FLAT NEMATODE RESPONSES TO HYPOXIA AND SUBSEQUENT MACROFAUNA-MEDIATED ALTERED SEDIMENT PROPERTIES

Adapted from:

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Tidal flat nematode responses to hypoxia and subsequent macrofauna-mediated altered sediment properties  
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### Abstract

To assess the role of macrofauna-mediated sediment changes on nematode community recovery, the temporal development of macrobenthos, nematode communities and sediment properties following hypoxia were examined in 16 m<sup>2</sup> replicated plots over a 6-months 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 to this, nematode diversity recovered to control values within one month but, subsequently, decreased again and 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 two months.

Nematode community reassembling was strongly related to the coupled macrobenthos-environmental temporal development. The dynamics of two 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, environmental and nematode community development after hypoxia highlight the importance of macrobenthos-sediment interactions in the recovery and structuring of nematode communities.

*Keywords: Benthic community recovery, Macrofauna – meiofauna interactions, Sediment dynamics, Hypoxia, Intertidal mudflat, Westerschelde estuary*

## 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 decades (Newell *et al.* 1998, Thrush & Dayton 2002), shallow estuarine and coastal sediments are worldwide exposed to enhanced anthropogenic nutrient inputs often causing permanent or seasonally depleted dissolved bottom oxygen (DO) concentrations characterized by a high benthic mortality (Cloern 2001, Diaz 2001). While hypoxic ( $\text{DO} < 2 \text{ mg l}^{-1}$ ) and anoxic ( $\text{DO} = 0 \text{ mg l}^{-1}$ ) environments have existed through 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 to macrobenthos (e.g. Gamienick *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 of meio- and microfauna and serve as a 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 ( $> 10^6$  ind.  $m^{-2}$ ) (e.g. Steyaert *et al.* 2003) and their distribution is determined by sediment composition, salinity, organic content and oxygen (e.g. 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) (e.g. 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 (e.g. Pearson & Rosenberg 1978, Montserrat *et al.* 2008). Since nematodes have relatively short generation times, they may be expected to rapidly respond 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 have simultaneously examined the temporal development of sediment properties, the macrobenthic and nematode community following hypoxia, over a 6-month period. We specifically addressed the following questions:

- How do nematodes respond to, and develop after, hypoxia in terms of diversity, abundance and community structure?
- Are the temporal patterns of nematode recovery related to the temporal patterns in the coupled macrobenthos-environmental development?

## Materials & methods

### Experimental set up, 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°21'24" N, 3°42'51" W). Nematodes constitute 81 – 98 % of the meiobenthos abundance and occur predominantly (~ 65 %) in the upper cm layer at the study site (C. Van Colen, unpublished data). Triple replicated 4 x 4 m treatment and control (i.e. undisturbed sediment) plots were randomly positioned within a 25 x 25 m homogeneous study site, at least 5 metres from each other. 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<sup>-2</sup>) and digging in the edges till 30 cm, following Beukema *et al.* (1999) and Dittman *et al.* (1999). After 40 days (30 March 2005), the plots were opened and biotic and abiotic samples were collected at low tide at a randomly selected subplot (37.5 x 37.5 cm) immediately after opening of the plots (day 0) and subsequently with a maximum interval of two weeks, during six months. Depending on the response variable, one (macrofauna, nematodes, organic matter, mud content and sediment stability) or two (bed level elevation, surface Chlorophyll *a*, oxygen concentration, water content, nutrient pore water concentration) subplots were sampled in each plot. Nematode samples were collected from the upper centimetre using a perspex corer (inner ø 3.6 cm, i.e. 10 cm<sup>2</sup>) and subsequently fixed in a neutral 4 % formaldehyde tap-water 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 analysis of variance 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 between control and treatment assemblages at each sampling occasion, as revealed by SIMPER analysis). Prior to the analyses, Bartlett's and Cochran's tests were used to verify 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 one-way analysis of variance. In the context of the present study we defined recovery of the impacted plots as having occurred when the impacted plots have attained a state that is 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 two-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, macrofauna 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, macrofauna and nematode multivariate patterns.

Univariate statistical analyses were performed using Statistica 7.0 (Statsoft, Inc. 1984-2004), multivariate analyses were performed using the Plymouth Routines In Multivariate Ecological Research (PRIMER) package, version 6  $\beta$  (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 %), *Daptonema* (-80 %) and *Neochromadora* (-100 %). Next to *Neochromadora*, only less abundant genera (i.e. < 18 ind. 10cm<sup>2</sup> 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 *Paramonhystera spp.* (-24 %). The only abundant genus, not reduced after hypoxia, was *Odontophora* (28  $\pm$  14 ind. 10cm<sup>2</sup>  $\pm$  SE; + 3 %). Highest abundances in the treatment plots were reached for *Anoplostoma*

*viviparum*, *Oncholaimellus sp.1* and *Paramonhystra spp.* ( $58 \pm 23$ ;  $49 \pm 22$  and  $41 \pm 17$  ind.  $10\text{cm}^{-2} \pm \text{SE}$ , respectively). However, these species were more abundant in the control plots.

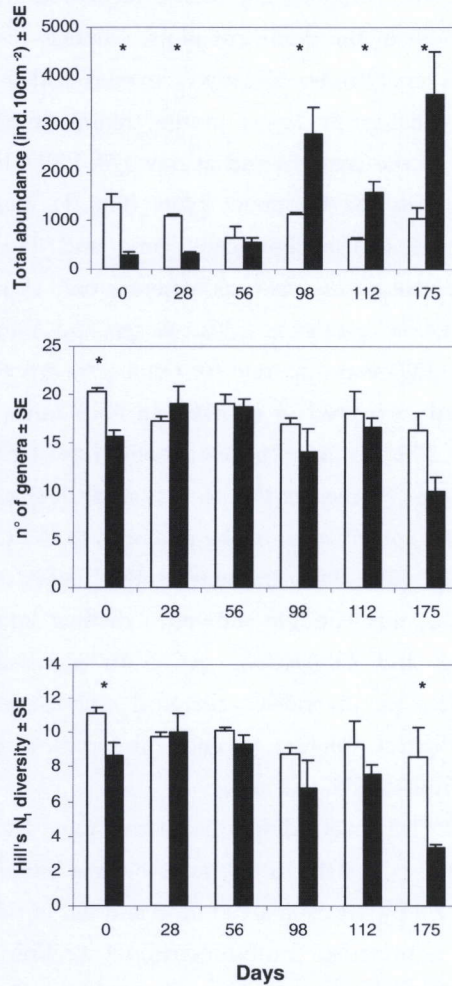


Fig. 1. Temporal variation of general univariate community characteristics in control (white) and treatment (black) plots: Total abundance, total number of genera and Hill's  $N_1$  diversity. \* significant treatment effects for sampling occasions, deduced from one-way analysis of variance.

Two-way analysis of variance 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 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 and at day 175, Hill's  $N_1$  diversity index was significantly lower in the treatment plots (Fig. 1). Results of two-way analysis of variance revealed a significant Time and Treatment effect for *Chromadora spp.* and *Ptycholaimellus 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 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 (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 attributed 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 relatively most to the dissimilarity from day 98 onwards.

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

**Table 1.** Two-way analysis of variance tests for univariate nematode community characteristics and dominant nematode genera (df = 1, 5; respectively for treatment and time). Values in bold are significant terms (p < 0.05). Assumptions for homogeneity of variances were met for all variables (Bartlett-Cochran test; p > 0.05). Analysis performed on square root (†) and log(x+1) (‡) transformed data.

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

**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.

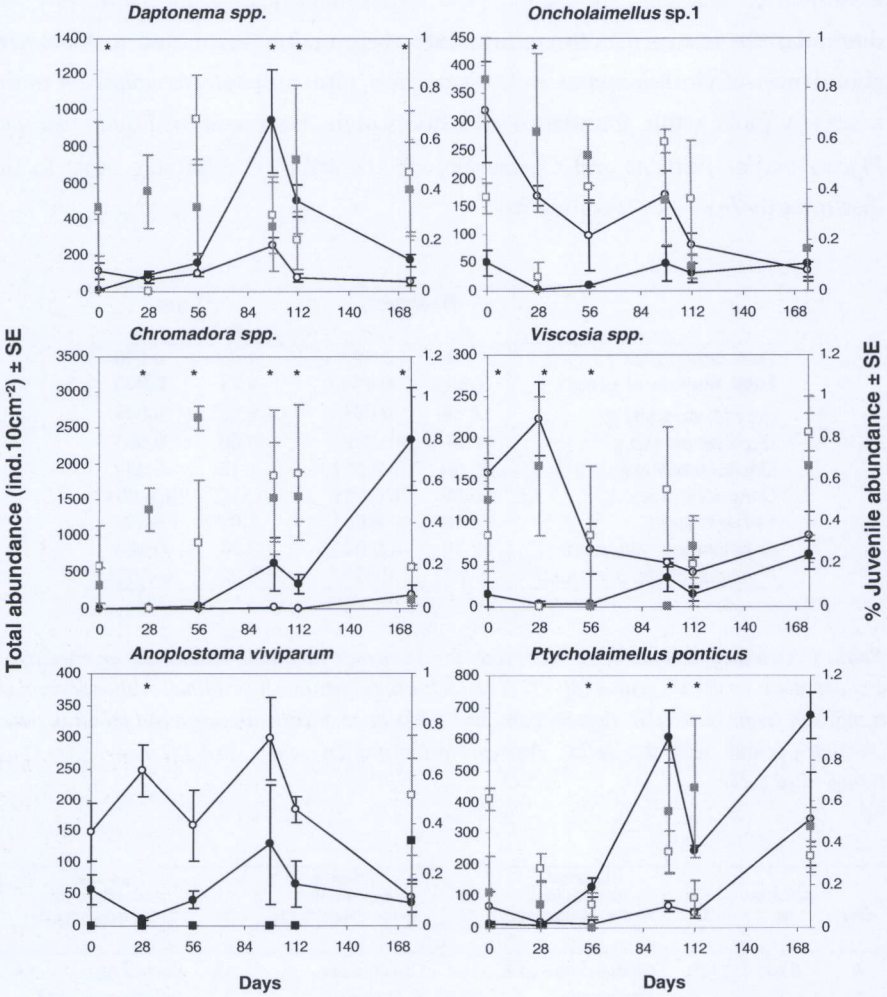


Fig. 2. Temporal variation of the total abundance of the dominant nematodes *Daptonema spp.*, *Chromadora spp.*, *Anoplostoma viviparum*, *Oncholaimellus sp.1*, *Viscosia spp.* and *Ptycholaimellus ponticus* in control (open circles) and treated (filled circles) plots. The contribution of juveniles to the total abundances is given on the secondary y-axis (control = open grey squares, treatment = filled grey squares). Asterisks indicate significant treatment effects for the total abundance per sampling occasion, deduced from one-way analysis of variance.

### 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 was explained by four macrobenthic species: *Cerastoderma edule*, *Heteromastus filiformis*, *Macoma balthica* and *Pygospio elegans* ( $\rho = 0.879$ ,  $\rho = 0.952$ ; for their 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 chlorophyll  $a$  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 ( $\rho = 0.879$ ).

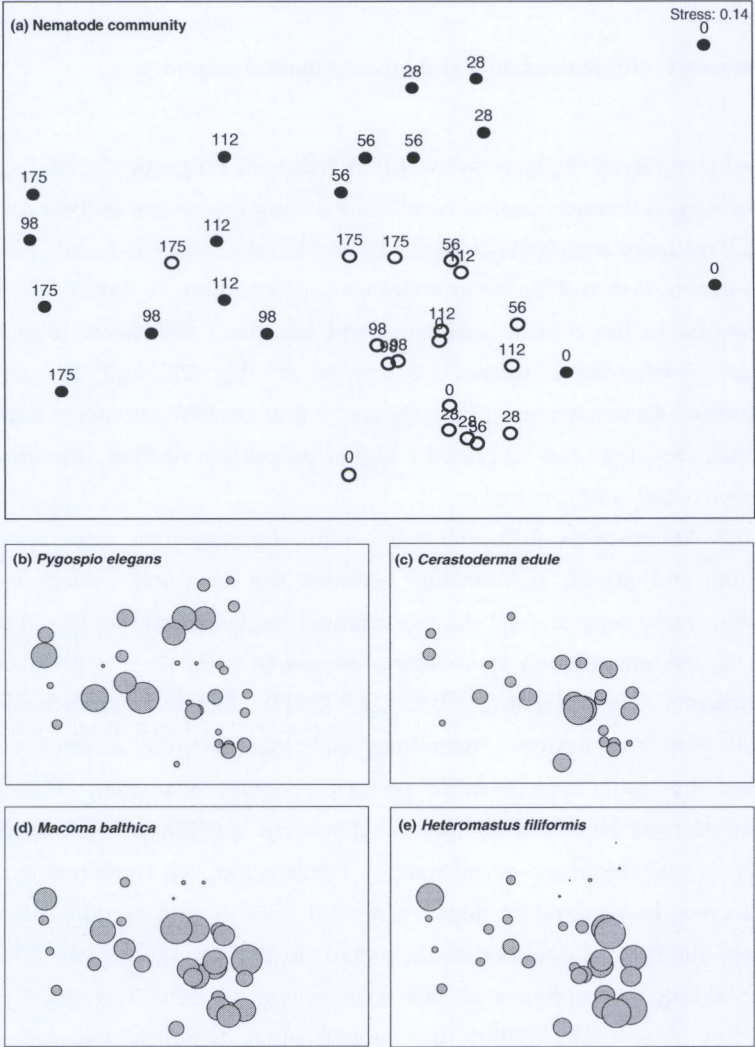
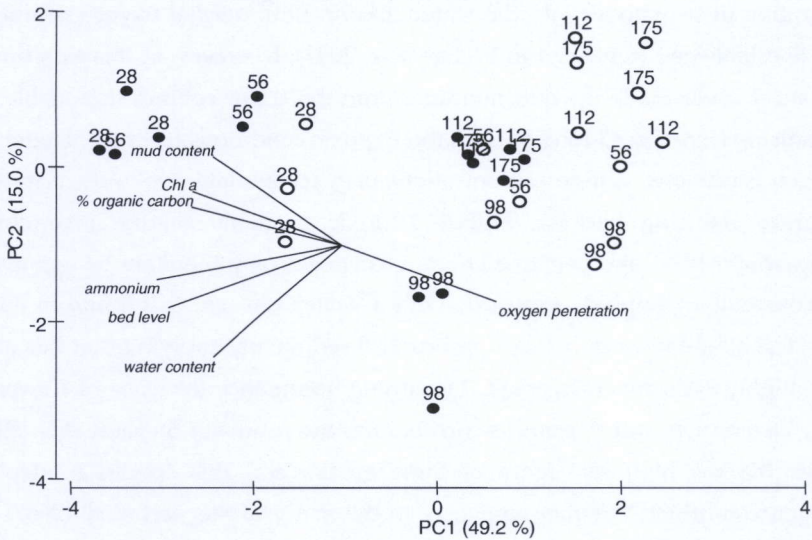


Fig. 3. (a) MDS ordination diagram based on square root transformed data of nematode genera abundances in treatment (filled circles) and control plots (open circles) at the sampling occasions. To visualize the relationship with the macrobenthos recovery and resemblance to control plots, abundances of *P. elegans* (b) and *C. edule* (c) and biomasses of *M. balthica* (d) and *H. filiformis* (e) are superimposed on the same ordination, using circles which sizes reflect the magnitude of these variables.



**Fig. 4.** Principal component analysis ordination (PCA) based on normalised environmental data, showing the temporal changes in the control (open circles) and treatment plots (filled circles). 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.

## 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, consistently with Josefson & Widbom (1988) and Mödigg & Olafsson (1998), indicates a higher resistance of nematodes to hypoxic conditions as compared to the macrobenthos. Nonetheless, hypoxia adversely impacted the nematode community, i.e. reduced number of genera and abundances causing a less diverse community, in general. 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 to die. Under low oxygen conditions, sulfide concentrations may accumulate due to the activity of sulphate reducing bacteria. Sulfide is toxic to many marine invertebrates (Baggarinao 1992) and negative effects of hypoxia may therefore be aggravated by concomitant sulphide exposure. Only *Odontophora* spp. was found in almost identical abundances in hypoxic and control sediments, implying that this genus was highly resistant to hypoxia. The strong abundance decrease of *Daptonema* spp., *Viscosia* spp. and *P. ponticus* corroborates the results of Steyaert *et al.* (2007), indicating the high sensitivity of these genera and this species to depleted oxygen conditions. Another similarity to the study of Steyaert *et al.* (2007) was that *Sabatieria* abundances were moderately 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). Further, no significantly higher abundances were noticed for any genus, indicating that, in hypoxic conditions, no nematode species belonging to a certain genus could take advantage of the reduced abundances of others.

### **Nematode recovery and relation with the coupled macrofauna - environmental recovery**

Nematode diversity recovery occurred fast (i.e. within one month) in comparison with macrofauna diversity recovery, indicating the higher resilience of nematodes as compared to the macrofauna. Macrobenthos diversity recovery took six months 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 attributable to

strong currents in these areas. Commito and Tita (2002) found that suspended nematodes 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 strong abundance increase of the epistrate feeders *Ptycholaimellus ponticus* and *Chromadora spp.* and the facultative epistrate feeder *Daptonema spp.* in the treatments occurred concomitantly with the sediment erosion in the control plots between day 28 and day 98, which suggests that recolonisation via the resuspension pathway is an important recovery mechanism in the present study. Moreover, the strong abundance overshoots of these epistrate feeding nematodes in the treatments (1) resulted in a diversity decrease in the treatment community from two months after opening of the plots onwards and (2) largely contributed to the lack in community recovery (i.e. lack of directional nematode reassembling towards the controls). Nematode reassembly 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 (*P. elegans*, *M. balthica*, *C. edule* and *H. filiformis*), all identified to mediate 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 two 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 (*P. elegans*, *Polydora cornuta*) and the low biomass of biodestabilizing species (*M. balthica*, *C. edule* and *H. 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 Thrush *et al.* (1997) 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 microcosm feeding experiments Moens & Vincx (1997) concluded that species belonging to this genus also feed on diatoms. High abundances for *Daptonema* spp., *P. ponticus* and other chromadorid nematodes have been reported from different recolonisation 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 onwards. Evidence for such active settlement in a diatom biofilm was found by Ullberg and Olafsson (2003). However, it should be noted that the results from the referred 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 and Tita (2002). As far as we know, evidence for active habitat choice of nematodes from field experiments is still lacking.

The dominance of *Ptycholaimellus ponticus* and *Chromadora* spp. in the treatment community was also maintained after the decline of tube-building populations and microphytobenthos biomass resulting in the recovery of the sediment stability at day 98 – 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 *H. filiformis* and growth of *M. 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 yet recovered after six months. 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.

## Conclusion

This study shows that, in comparison with the macrobenthos, nematode communities are much more resistant to hypoxia. Following severe hypoxia,

nematode community reassembly was strongly related to the recovery of the macrobenthos community and the concomitant changes in sediment properties. The dynamics of two 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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