CHAPTER 7
A LONG-TERM STUDY OF THE MACROBENTHOS RECOVERY FOLLOWING HYPOXIA-INDUCED MASS MORTALITY

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Abstract

Macrobenthos recovery after hypoxia-induced mass mortality was assessed during 3 years in replicated 16 m² plots located at an estuarine tidal mudflat (Paulinapolder, Westerschelde estuary, SW the Netherlands).

During the first 2 years, a Pearson-Rosenberg type of community recovery towards the control sediments took place along with the improving bottom water oxygen conditions. After 3 months, the spionid polychaetes *Pygospio elegans* and *Polydora cornuta* became superabundant (i.e. opportunistic peak), followed rapidly by a steep decline (i.e. ecotone point). Subsequently, a moderate increase in species richness and a steep increase in biomass, related to the growth of the long-lived species *Scrobicularia plana* and *Macoma balthica* occurred (i.e. transition region). Beyond this transition region, however, the recovering community diverged again from the ambient sediments. This divergence mainly resulted from the higher biomasses of *M. balthica* and *S. plana* in the recovering plots towards the end of our experiment. Enhanced recruitment success and subsequent growth of both species in absence of high interference from bioturbation during early recovery stages is hypothesized as the causal pattern for this biomass overshoot in the recovering community at the long-term. In particular, biomass of *Cerastoderma edule*, an important long-lived bioturbator at the study site, remained low in the recovering plots in comparison with the

ambient sediments due to a general, successive recruitment failure in 2006 and 2007.

The present study indicates that, despite community recovery may follow a more or less predictable pathway at early recovery stages (i.e. Pearson-Rosenberg recovery pattern), divergence may occur at the long term because biotic interactions at early recovery stages may become important at later recovery stages whenever the influence of the affected species becomes greatest. Consequently, such lagged effects may have important consequences for macrobenthos distribution, especially in areas which are frequently subjected to disturbances.

Keywords: *Macrobenthos, Recovery, Succession, Hypoxia, Tidal mudflat*

Introduction

Worldwide, about 85 % of the coastline (Airoldi & Beck 2007) is threatened by a wide range of anthropogenic disturbances (Halpern *et al.* 2007, 2008). For instance, enhanced anthropogenic nutrient inputs originating from increasing agricultural runoff and industrial sewage have resulted in depleted dissolved bottom water oxygen concentrations (DO) in shallow estuarine and coastal sediments. When DO declines below 0.5 mg l^{-1}, mass mortality of the macrobenthos may occur (Diaz & Rosenberg 1995). Soft-sediment macrobenthic communities provide important ecological goods and services. For example, estuarine tidal flat macrobenthos recycle nutrients (e.g. Lohrer *et al.* 2004), considerably alter sediment transport processes (e.g. Meysman *et al.* 2006, Solan *et al.* 2008) and represent an important trophic linkage, being a food source for epibenthic crustaceans, fish and birds (e.g. Hampel et al 2004) and by feeding on benthic algae and bacteria (e.g. Herman *et al.* 2000, Van Oevelen *et al.* 2006). Hence, depletion of the benthos can have dramatic consequences on estuarine ecosystem functioning. For environmental impact assessment and management it

is therefore important to gather knowledge on macrobenthic recovery dynamics after severe disturbance events (e.g. hypoxia).

The Pearson-Rosenberg (PR) model is a generally applied method for examining macrobenthos community response to disturbance, based on the development of the community species richness, abundance and biomass (SAB) (Pearson & Rosenberg 1978). The model originally exemplified the changes in faunal community structure in a stable, subtidal muddy habitat along a gradient from excessive organic enrichment to 'normal' conditions but has been shown to hold for physical disturbance (Rhoads & Germano 1986) and recovery from oxygen deficiency (Rosenberg *et al.* 2002) as well. According to the PR model (Fig. 1), species richness, abundance and biomass are low at highest organic enrichment. A peak in abundance represents the point along the organic enrichment gradient were small-sized opportunists become superabundant and cause a secondary biomass maximum. This 'opportunistic peak' is followed by a steep decrease in abundance and a rapid increase in species richness, defined as the 'ecotone point'. Beyond this ecotone, a 'transition region' occurs where the long-lived fauna dominate the community and cause a primary peak in biomass due to moderate organic enrichment. Afterwards, the benthos declines to its background values. Furthermore, Pearson & Rosenberg (1987) stressed the availability of food as a structuring factor of their PR model and Nilsson & Rosenberg (1997) related the successional community changes along the disturbance gradient to a benthic habitat quality index, which takes the presence of (sub)surface biotic structures and the redox potential discontinuity (RPD) layer into account. The main advantage of the PR model is that the use of different simple univariate community characteristics allows for the definition of a general stress relationship, which can be compared across different ecosystems (Rakocinski *et al.* 2000). Moreover, the ratios between the different metrics in the model, have stimulated the development of different biotic indices (see Pinto *et al.* 2009 for a review).
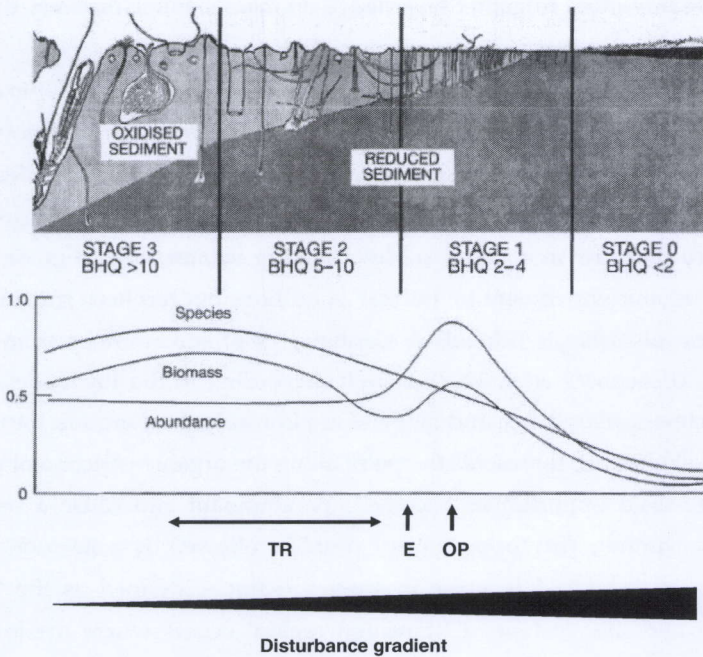
Fig. 1. Graphical model of infaunal succession stage distribution along a gradient of increasing environmental disturbance (after Pearson & Rosenberg 1978), and the associated benthic habitat quality (BHQ) index (after Nilsson & Rosenberg 1997). OP = peak of opportunists, E = ecotone point and TR = the transition region.

Despite the general applicability of the PR model, recovery studies in shallow water and tidal flat sediments have yielded variable results, not always in full accordance to a typical PR recovery pathway (Thrush & Whitlatch 2001). This may be ascribed to the limited temporal and spatial scale at which studies have been conducted: studies with a limited time frame may have been too short to identify full recovery, passing through all successional stages whereas small-scale studies will not identify different recovery stages due to the fast immigration of ambient organisms (Günther 1992). In accordance to the PR model, the two large-scale recolonisation studies in North-Western European

tidal flats which have lasted > 1 year (Beukema *et al.* 1999, Dittmann *et al.* 1999) indicate an abundance overshoot of typical opportunistic species and early colonizers. However, both studies are not consistent with the total model because not all metrics have been measured, e.g. biomass (Dittmann *et al.* 1999) or the total abundance remains high after an opportunistic peak due to very high abundances of later colonists (Beukema *et al.* 1999).

We assessed the recovery of a macrobenthic tidal mudflat community in large plots after complete mortality due to experimentally induced hypoxia. Previously, we described the macrobenthic early succession during the first recruitment season (i.e. 6 months, April – September) (Van Colen *et al.* 2008). In the present paper, we addressed whether the macrobenthic community reassembled to control conditions at the long term (i.e. three years) or not and whether this recovery occurred in accordance with to PR model, or not.

Materials & methods

Study site and sampling

Temporal variation within the macrobenthos after hypoxia-induced mass mortality was assessed in replicated 16 m² plots, located at the Paulinapolder tidal mudflat (median particle size = 65 μm, mud content = 51 %). This tidal flat is located in the polyhaline part of the Westerschelde estuary (SW the Netherlands), has a semi-diurnal local tidal regime with a mean tidal range of 3.9 m and salinity ranges from 16 PSU in winter to 27 PSU in summer (Ysebaert 2000). Hypoxic conditions were created by covering the sediment for 40 days with a water-proof polyethylene sheet (0.1 mm thick) and a tarpaulin sheet (140 g m⁻²) following Thrush *et al.* (1996), Beukema *et al.* (1999) and Dittman *et al.* (1999) which resulted in a total mortality of the macrobenthos community. At the opening of the plots, the sediment was hypoxic, characterized by a black surface and contained significantly higher NH_4^+ pore water concentrations in the upper

10 cm as compared to the controls (i.e. > 30000 µg l^{-1} vs. ~ 4000 µg l^{-1}). After the opening of the plots (i.e. 30 March 2005), macrobenthos and environmental temporal development was monitored 21 times during the first 9 months (i.e. until 19 December 2005), and subsequently at every end of March and September until 26 March 2008. Furthermore, to assess recovery status of the reassembling macrobenthos community, samples were also collected from control (i.e. undisturbed) plots. For every sampling occasion, we randomly sampled in three replicated treatment and control plots. In March 2006, however, extra control samples taken in the immediate vicinity of the control and treatment plots indicated large differences from the 'original' control samples (i.e. average community dissimilarity = 30 % with significant lower abundances for *Pygospio elegans* (787 vs. 5174 ind. m^{-2}) and *Aphelochaeta marioni* (1521 vs. 2445 ind. m^{-2}) in the 'original' control samples). To enable a further, proper investigation of the colonization and recovery status, unbiased by effects due to the repeated sampling, we removed the March 2006 sampling point from the dataset and continued sampling in three 'new', control and treatment plots. The 'new' treatment plots were opened at the same time as the 'original' ones but were generally undisturbed. Macrobenthos was sampled with a core (inner ø 12.5 cm) to a depth of 40 cm and fixed with a neutralised 8% formalin solution. In the laboratory, the samples were sieved through a 0.5 mm mesh and the residual was fixed and preserved until processing using a neutralised 4 % formalin solution with 0.01 % Rose Bengal. All macrofauna was sorted, counted and identified to the species level, except for tubificid oligochaetes. Bivalve biomasses were obtained by determination of the ash free dry weight (4h combustion at 450°C of 24h, 60°C dried individuals) and the biomass of other macrobenthos was calculated by multiplying the organisms' blotted wet weight with a species-specific ISO certified wet weight-ash free dry weight conversion factor (Sistermans *et al.* 2007). For further details 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).
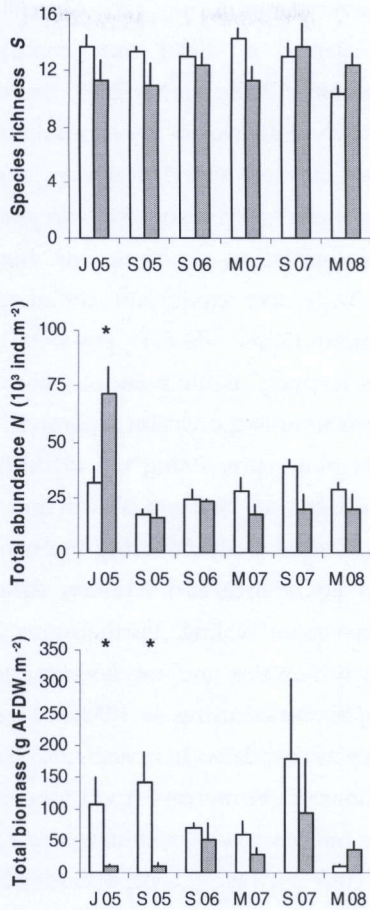
Fig. 2. *Mean + SEM temporal distribution of species richness (upper panel), total abundance (middle panel) and total biomass (lower panel) in control (white bars) and treatment sediments (grey bars). J, S and M refer to June, September and March, respectively. Asterisks denote significant differences between treatments according to Mann-Whitney-U testing.*

Statistical analysis

In order to analyze macrobenthos recovery patterns at the long term, community composition data representing different succession stages inferred from our

detailed short-term recovery monitoring (i.e. March 2005, June 2005 and September 2005; Van Colen *et al.* 2008) were completed with community composition data of September 2006, March 2007, September 2007 and March 2008. The temporal variation of species richness, total abundance, total biomass and the abundance of the four most abundant species at each sampling occasion in the treatment plots, was examined using one-way analysis of variance, after data were log(x+1) transformed in order to met homogeneity of variance (Bartlett-Cochran test). To detect significant differences between sampling occasions, Student-Neuman-Keuls (SNK) post-hoc tests were applied. Furthermore, we defined recovery as the point at which Mann-Whitney U-tests (MWU), performed at each sampling occasion separately, detected no significant differences between both plot types. Using the PRIMER v6 software package (Clarke & Gorley 2006), differences between control and treatment communities at each sampling occasion were analyzed using the one-way ANOSIM test on square root transformed abundance and biomass data and differences were visualized by multi-dimensional scaling. Furthermore, dissimilarities between treatment and control communities and the species that contributed most to these dissimilarities were identified using the SIMPER test. Finally, the Warwick statistic (W, Clarke 1990) was calculated to investigate changes in the community biomass/abundance relationship. W increases to +1 for communities with an even abundance across species but biomass is dominated by a single species, whereas W decreases to – 1 in the converse case (Clarke & Gorley 2006).

Results

Univariate analyses

Table 1 presents the temporal variation of NH_4^+ pore water concentrations in the upper 10 cm, Chl a concentration in the upper 3 mm and mud content in the upper first cm sediment layer of control and treatment plots. After recovering sediments initially developed higher Chl a and mud content values as compared

to the controls, these variables returned to ambient levels in September 2005 (Table 1)(Montserrat et al. 2008, Van Colen et al. 2008). The NH_4^+ pore water concentrations in the upper sediment layers (0-1-2-3 cm) returned to ambient levels in September 2005, whereas such recovery in the deeper sediment layers took longer (i.e. March 2007).

In the treatments, highest species richness and total biomass was found in September 2007 (i.e. 2.5 yr after opening of the plots), whereas the total abundance peaked in June 2005. These general community characteristics all exhibited a significant temporal variation but recovery to control values was variable-specific (Fig. 2). Mann-Whitney-U tests (MWU) performed for each sampling occasion separately depicted (1) no significant differences in species richness from June 2005 onwards, (2) a significantly higher abundance in June 2005 and (3) no biomass recovery before September 2006.

The temporal variation in abundance of the four most dominant species at each sampling occasion, is presented in Fig. 3. These species comprised > 70 % of the total macrobenthic abundance at each sampling occasion and all, except *Hydrobia ulvae*, displayed a significant temporal variation (p < 0.05; one-way analysis of variance). Dominant species in June 2005 were the bivalve *Macoma balthica* and the polychaetes *Nereis diversicolor, Heteromastus filiformis, Polydora cornuta* and *P. elegans*, comprising together > 95 % of the total abundance; the spionid polychaetes *P. elegans* and *P. cornuta* showed a significant abundance overshoot (MWU p < 0.05) and the other species were no longer significantly different from the controls. Further, the abundance of all dominant species in June 2005 was significantly reduced at all later sampling occasions (SNK post-hoc test p < 0.05) but, nonetheless, still dominated the community in September 2005 (i.e. > 80 % of the total abundance). Contrary, significantly higher abundances as compared to June 2005 were found for tubificid oligochaetes from September 2006 onwards and for *A. marioni* from March 2007 onwards (SNK post-hoc test p < 0.05). Nevertheless, in comparison with the controls, a significantly lower abundance of the tubificid oligochaetes still remained in March 2008 (MWU p < 0.05).
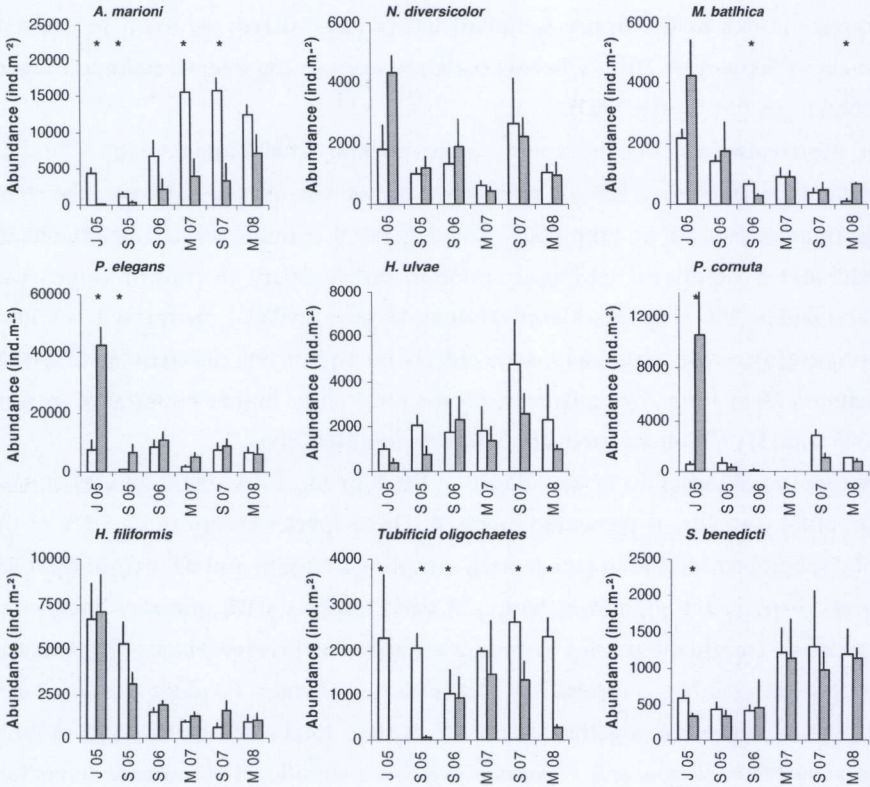
Fig. 3. Mean + SEM *temporal distribution of the abundance of* Aphelochaeta marioni, Pygospio elegans, Heteromastus filiformis, Nereis diversicolor, Hydrobia ulvae, tubificid oligochaets, Macoma balthica, Polydora cornuta *and* Streblospio benedicti *in control (white bars) and treatment sediments (grey bars). J, S and M refer to June, September and March, respectively. Asterisks denote significant differences between treatments according to Mann-Whitney-U testing.*

	M05	J05	S05	S06	M07	S07	M08
Control							
NH_4+ 0-1cm	3643 ± 198	7787 ± 892	4386 ± 2552	10048 ± 2394	1548 ± 180	5306 ± 576	2725 ± 261
NH_4+ 1-2 cm	4205 ± 586	12996 ± 693	6436 ± 2507	9730 ± 3073	3093 ± 487	4774 ± 106	3473 ± 857
NH_4+ 2-3 cm	3521 ± 1169	16846 ± 3874	4641 ± 696	6783 ± 589	2520 ± 376	2568 ± 369	2436 ± 926
NH_4+ 3-5 cm	4328 ± 1424	16259 ± 1197	3731 ± 2215	6603 ± 2158	1853 ± 320	3118 ± 840	1931 ± 344
NH_4+ 5-10 cm	4124 ± 176	6597 ± 268	2871 ± 714	3904 ± 707	1852 ± 187	3757 ± 542	3424 ± 1079
Chl a 0-3 mm	6.7 ± 0.4	9.3 ± 0.7	9.4 ± 1.2	16.8 ± 4.1	3.8 ± 0.7	15.2 ± 2.2	3.5 ± 1.5
% Mud 0-1 cm	40.7 ± 1.8	36.8 ± 2.8	42.3 ± 5.2	35.6 ± 1.3	29.9 ± 4.3	38.8 ± 1.6	39.6 ± 2.6
Treatment							
NH_4+ 0-1cm	51338 ± 20684	7829 ± 2295	4960 ± 1702	8309 ± 1387	1826 ± 289	3864 ± 205	2562 ± 64
NH_4+ 1-2 cm	46477 ± 20196	5039 ± 182	6566 ± 1611	10554 ± 3253	2208 ± 539	3191 ± 441	2130 ± 465
NH_4+ 2-3 cm	40772 ± 18479	4463 ± 593	6798 ± 1947	8040 ± 1461	2345 ± 737	3500 ± 1179	1612 ± 220
NH_4+ 3-5 cm	35089 ± 15214	5292 ± 2209	6638 ± 1993	3022 ± 51	2899 ± 660	2516 ± 478	1202 ± 52
NH_4+ 5-10 cm	26683 ± 9838	9816 ± 4506	4382 ± 2648	3877 ± 750	1826 ± 196	2117 ± 290	2611 ± 455
Chl a 0-3 mm	4.7 ± 0.5	10.5 ± 0.8	17.5 ± 4.1	16.0 ± 4.5	3.8 ± 0.8	18.5 ± 5.4	6.0 ± 4.0
% Mud 0-1 cm	44.7 ± 2.2	47.9 ± 0.7	40.9 ± 1.0	37.9 ± 2.8	24.9 ± 6.9	41.6 ± 2.0	36.9 ± 0.8

Table 1. Averaged ± SE (n = 3) NH_4^+ pore water concentrations in the upper 10 cm, Chl a concentration in the upper 3 mm and mud content in the upper first cm sediment layer of control and treatment plots. J, S and M refer to June, September and March, respectively.

Multivariate biotic analyses

Based on both species biomasses and abundances, the temporal variation of the change in the dissimilarity between treatment and control communities illustrated a clear community recovery until September 2006-March 2007 (Table 2). Overall, a faster convergence during this recovery period was found for analyses based on species abundances than for analyses based on species biomasses. According to their *R*-statistic, control and treatment communities were no longer clearly separable in September 2006 and March 2007 ($R < 0.25$), which is further illustrated by their overlap in de MDS ordination diagram (Fig. 4a, c). Later on, the averaged community dissimilarity based on biomass increased again, indicating a divergence between control and treatment

communities (Table 2, Fig. 4c, d). Species that contributed most to the community dissimilarity before September 2006 were the spionid polychaetes *P. elegans* and *P. cornuta* for analyses based on abundances and the bivalves *Cerastoderma edule* and *M. balthica* for analyses based on species biomasses (Table 2). From September 2006 onwards, differences in abundances were mainly due to *A. marioni* and Oligochaeta which only partly recovered. For biomass, *C. edule* remained low in the treatment plots throughout the study period, whereas distinct, however not significantly, higher biomasses were observed in the treatments for *Srobicularia plana* in September 2007 and March 2008 and for *M. balthica* in March 2008 (Fig. 5). In general, despite a small drop in March 2007, an increase of the Warwick-statistic was apparent throughout the course of the experiment (Fig. 6). This indicates a shift from a community dominated by a few small-sized short-lived species in June 2005 (e.g. *P. elegans* and *P. cornuta*) towards a community where the biomass is dominated by a few large, long-lived species, represented by rather few individuals in March 2008 (e.g. *S. plana* and *M. balthica*) (Table 2, Fig. 6).

Discussion

Along with improving bottom water oxygen conditions, as indicated by the decrease in ammonium pore water concentrations, macrobenthos species richness, abundance and biomass (SAB) recovery performed a clear nonlinear pattern, as is summarized in Fig. 6. In June 2005, a few opportunistic species became superabundant, causing a distinct abundance peak (Van Colen *et al.* 2008, this study). Subsequently, a moderate increase in species richness and a steep increase in biomass, related to the growth of the long-lived species *M. balthica* and *S. plana*, occurred from September 2005 to September 2006. Until September 2006-March 2007, the macrobenthos thus, in general, reassembled in concordance with the Pearson-Rosenberg species-abundance-biomass curves (Pearson & Rosenberg 1978) and the associated successive zones in benthic habitat quality

(BHQ) (Nilsson & Rosenberg 1997) (Fig. 1, 6). Yet, a significant increase in species richness and a clear drop in the total biomass at the ecotone point, where later colonists replace the dominance of early colonizing opportunists was lacking. At the study site, the majority of the species spawn in spring and subsequently pass through a pelagic larval stage and therefore were able to settle rapidly into the treatment plots in late spring or summer (i.e. within 3 months after hypoxia)(Van Colen *et al.* 2008). Recovery of the few species without a pelagic larval phase (*A. marioni* and tubificoid oligochaetes) took longer and resulted in a modest extra increase in species richness after June 2005. This finding corroborates with the general idea that species colonization at a large scale, and thus recovery time, is mainly dependent on postlarval settlement by pelagic recruits because these stages can disperse over large areas (e.g. Günther 1992, Whitlatch *et al.* 1998). Further, the absence of a significant biomass drop is presumably related to the combined effect of (1) the very low body mass of the small-sized opportunists *P. elegans* and *P. cornuta* (Anger *et al.* 1996, Zajac 1991) and (2) the growth of the long-lived species *M. balthica*, *H. filiformis* and *N. diversicolor*, which had already settled at high abundances before the ecotone point. In concordance with the PR model, biomass recovery was slow which corroborates Beukema *et al.* (1999) who found no biomass recovery during their 4 year monitoring period because > 4 year old *Mya arenaria* were present in the control sediments. Furthermore, beyond biomass recovery at the end of the transition period (i.e. September 2006), we observed a marked temporal variation in total community biomass with a maximum biomass in September 2007, flanked by steep drops in March 2007 and March 2008 (Fig. 2, 6). These dips corresponded with the biomass decreases of the large bivalves *C. edule* and *S. plana* (Fig. 5). In contrast to *M. balthica*, *C. edule* and *S. plana* are extremely vulnerable to low (winter) temperatures (Guerreiro 1998, Strasser *et al.* 2001). Therefore, besides biomass increase during the growing season (i.e. spring-summer), the temporal variation in biomass seems also related species-specific winter mortality. In addition to the seasonal peak in availability of dispersive benthic settlers, this temporal variation in biomass further highlights the importance of seasonality in the interpretation of recovery patterns, in general.
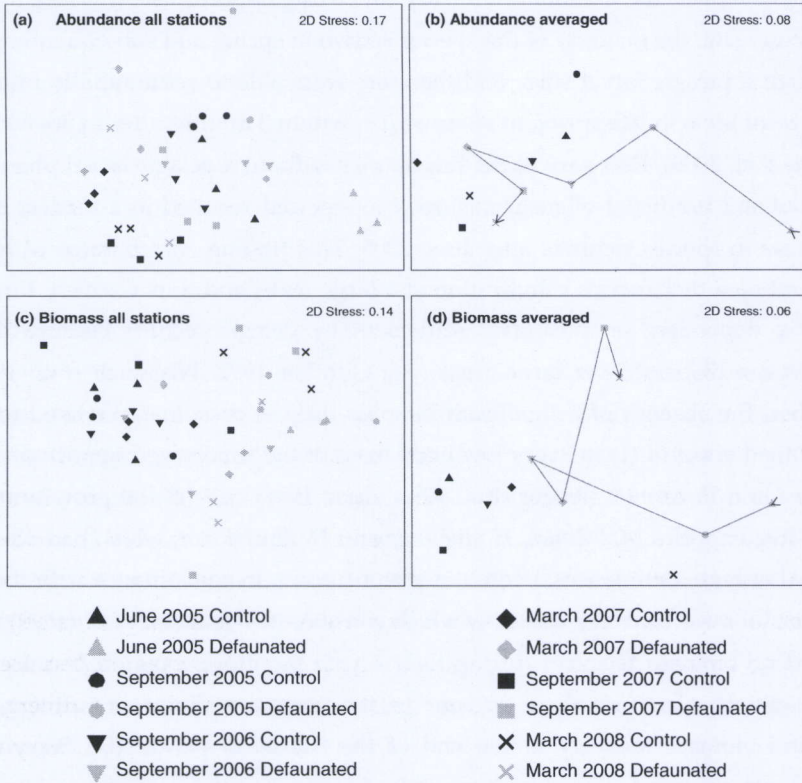
Fig. *4.* *Multi-dimensional scaling showing the changes in benthic community structure from June 2005 to March 2008, based on squareroot transformed abundance (a, b) and biomass (c, d) data. The line in b and d indicates the averaged recovery trajectory.*

A further remarkable fact that appears from this study is that, with respect for biomass community (dis)similarities, control and treatment communities diverged again beyond the transition period. This pattern mainly resulted from the higher biomasses of *S. plana* in September 2007 and March 2008 and of *M. balthica* in March 2008 in the treatments due to a significant higher recruitment in

the treatments of *M. balthica* in 2005 and of *S. plana* in 2006 and 2007 (Fig. 5, Van Colen *et al.* 2008). As most probably, the surface deposit feeding juveniles of these two species has benefited from the low bioturbation of *C. edule* in the treatments throughout the course of the experiment. After the moderate recruitment in 2005, *C. edule* abundances declined in both control and treatments which corresponded with its observed recruitment failure in 2006 and 2007 in the whole Westerschelde estuary (Kesteloo *et al.* 2007, 2008). *C. edule* is a suspension feeding bivalve which crawls through the superficial sediment layers, thereby affecting both the abiotic and biotic parts of its environment (Ciutat *et al.* 2007, Flach 1996) and is considered an important bioturbator at our study site (Chapter 8). Interference by bioturbation is recognised as an important process affecting benthic recruitment success (Fraschetti *et al.* 2003). Moreover the inhibitory impact of *C. edule* on benthic recruitment success has been demonstrated by Flach (1996) and lowered macrobenthic post-settlement growth has been observed in areas with higher *C. edule* biomasses (Chapter 5). This community divergence indicated that macrobenthic community recovery should not necessarily be convergent and deterministic at the long term because biotic interactions at early recovery stages may give rise to community divergence at later stages whenever the impact of the affected species becomes greatest. Hence, in addition to changes in environmental variables, community divergence resulting from a lagged effect of biotic interactions during early recovery may explain macrobenthic patchiness within one tidal flat which is subjected to relatively small-scale disturbances (e.g. hypoxic conditions resulting from algal bloom decomposition; Bolam & Fernandez 2002, Norkko & Bonsdorff 1996, Reise 1985) and/or differences in community structure between disturbed and non-disturbed sites at a larger scale.
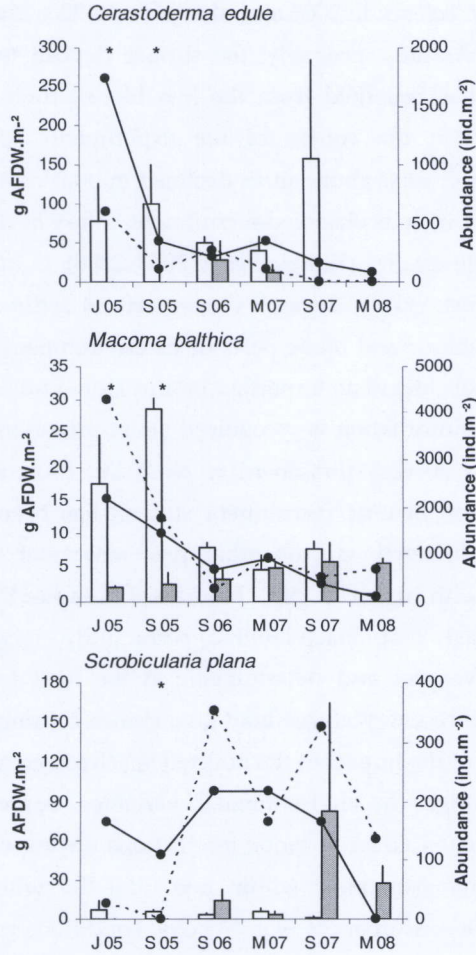
Fig. 5. *Mean + SEM temporal distribution of the biomass of* Cerastoderma edule *(upper panel),* Macoma balthica *(middle panel) and* Scrobicularia plana *(lower panel) in control (white bars) and treatment sediments (grey bars). J, S and M refer to June, September and March, respectively. Averaged abundance in controls (solid line) and treatments (dashed line) is presented on the right y-axis. Asterisks denote significant biomass differences between treatments according to Mann-Whitney-U testing.*
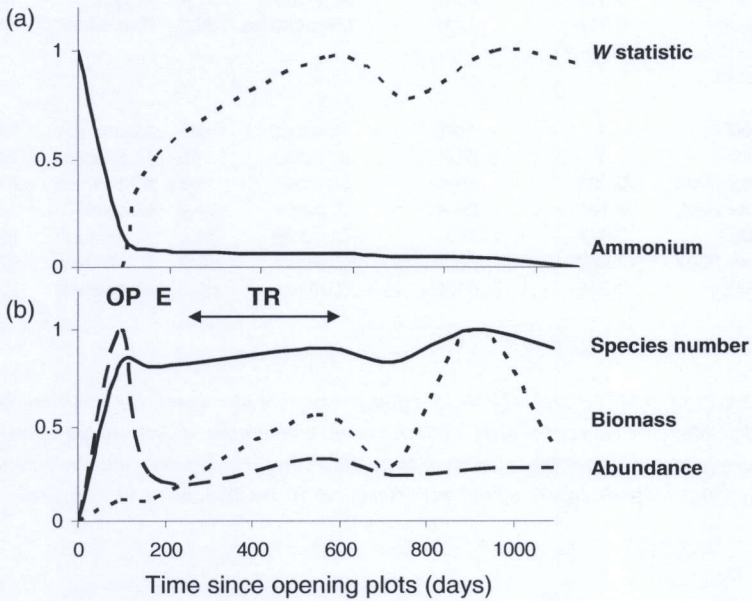
Fig. 6. *Temporal variation of (a) the ammonium pore water concentration at the 3-5 cm sediment layer and the Warwick (W) statistic, and (b) species richness, total abundance and total biomass. Data points are normalized and OP, E and TR refer to the peak of opportunists, the ecotone point and the transition region of the Pearson-Rosenberg model (1978).*

	R-value	Dissimilarity (%)	Species	D%	Species	D%
(a) Abundance						
March 2005	1	100	*H. filiformis*	25.5	*A. marioni*	13.6
June 2005	1	36.3	*P. elegans*	<u>26.2</u>	*P. ligni*	<u>17.6</u>
September 2005	0.63	27.4	*P. elegans*	<u>23.6</u>	Oligochaeta	17.2
September 2006	-0.037	11.3	*A. marioni*	32.4	*P. elegans*	<u>11.5</u>
March 2007	0.185	17.3	*A. marioni*	39.2	*P. elegans*	<u>16.6</u>
September 2007	0.519	20.5	*A. marioni*	31.4	*P. ligni*	9.6
March 2008	0.519	17.6	Oligochaeta	20.3	*A. marioni*	17.9
(b) Biomass						
March 2005	1	100	*C. edule*	39	*M. balthica*	13.6
June 2005	1	61.4	*C. edule*	45	*M. balthica*	14.5
September 2005	0.926	56.4	*C. edule*	53	*M. balthica*	20.6
September 2006	0.185	20.3	*S. plana*	<u>24.2</u>	*C. edule*	23.6
March 2007	0.074	16.6	*C. edule*	54.2	*A. marioni*	10.2
September 2007	0.222	56.3	*C. edule*	50.9	*S. plana*	<u>32.6</u>
March 2008	0.519	41.4	*S. plana*	<u>54.3</u>	*M. balthica*	<u>13.9</u>

Table 2. Results of SIMPER and ANOSIM analysis based on abundance (a) and biomass (b), indicating the difference between control and treatment communities at each sampling occasion and the two species which contributed most to these differences. Underlined contributions to the dissimilarity (%D) indicate higher abundances/biomasses in the treatments as compared to the controls.

Acknowledgements