CHAPTER 2
BENTHIC COMMUNITY STRUCTURE, DIVERSITY AND TRAIT DISPLACEMENT ACROSS AN ESTUARINE TIDAL FLAT HYDRODYNAMIC STRESS GRADIENT

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Abstract

The intermediate disturbance hypothesis (IDH, Connell 1978) states that maximal diversity is maintained at intermediate disturbance or stress levels, and is perhaps one of the best accepted principles in ecology. However, recent research (Mackey & Currie 2001) highlights the lack of generality of the principle, indicating prudence in its overall application, e.g. in the development of ecosystem management plans. We investigated whether tidal mudflat macrobenthos community diversity and structure performed a unimodal response to the prevailing hydrodynamic stress gradient and whether this response is related to community-wide biological trait displacements.

Principal Component Analysis on the environmental characteristics of the sampling stations revealed the prevalence of one main 'hydrodynamic stress' axis (PC_{stress}: eigenvalue = 8.99, explanatory value = 74.9 %) which strongly correlated with cross-shore tidal current aspects and sediment composition. Sampling stations scores from PC_{stress} were retained to analyze diversity and community-wide patterns of biological traits in relation to the intertidal hydrodynamic stress gradient. Community structure differed significantly between stress levels and community species richness, diversity and evenness peaked at low hydrodynamic stress and were lowest at high hydrodynamic stress. Hence, our data did not support the IDH and suggest that competitive exclusion is not a main driver of macrobenthos diversity-stress relationships in highly stressed tidal flat habitats. Further, because additional stress components

(e.g. dessication, predation, access to food) may point in different directions and be different between functional groups, the detection of a unimodal community-wide diversity-stress response may be hampered and the IDH principle may therefore not be appropriate within the hydrodynamic stress range of our study site.

Suspension feeding peaked at intermediate hydrodynamically stressed stations, located in the mid intertidal where bottom shear stress is drastically lower as compared to the lower intertidal and submersion time, and consequently suspension feeding time, is slightly longer as compared to the high intertidal zone. In contrast, the proportional biomass and abundance of surface deposit feeders and the proportional abundance of species with a lecitotrophic larval development were lowest at intermediate hydrodynamically stressed stations. *Cerastoderma edule* is the most important suspension feeder, both in terms of biomass, biovolume and abundance at our study site and has been shown to affect benthic community structure negatively through disturbance of the benthic boundary layer. Given the surface dwelling life habit of surface deposit feeders and lecitotrophic non-pelagic larvae, these organisms may be expected as most vulnerable to the *C. edule* mediated disturbance in the upper sediment layer. This indicates that inhibitory benthos-physical interactions on ecosystem diversity, such as interference by bioturbation, should be incorporated in tidal flat biodiversity-stress models.

Keywords: *Intermediate disturbance hypothesis, Biological traits, Macrobenthos – environmental stress models, Bioturbation, Tidal mudflat, Westerschelde estuary*

Introduction

Understanding the factors and mechanisms that control patterns of diversity at a local scale is important since many ecosystems increasingly experience human disturbances which affect their species diversity (Hughes *et al.* 1997) and hence, ecosystem functioning and the resilience of ecosystems to environmental change

(Elliott *et al.* 2007, Naeem *et al.* 1994). The intermediate disturbance hypothesis (IDH, Connell 1978) predicts that sessile community diversity is maximized at intermediate levels of disturbance intensity and/or frequency because this state enables the coexistence of stress tolerant species and potential competitors, whereas competitively dominant species may exclude subordinate species at low disturbance and less tolerant species may directly be eliminated at high disturbance.

In marine benthic ecosystems, taxonomic community composition derived diversity measurements, such as species richness, diversity indexes (e.g. Shannon-Wiener) and taxonomic distinctness have traditionally been used to describe diversity in relation to different or changing environments or stress (e.g. Somerfield & Clarke 1995, Warwick & Clarke 1993). Species-specific ecological or functional characteristics (e.g. body size, feeding habit, mobility) have often, subsequently, been linked in order to determine indirectly the processes that underpin the observed diversity patterns. However, because the same two species may share characteristics but also differ in others, these species may interfere or not and react differently to stress (Ramsay *et al.* 1998), thereby hampering the detection of the driving ecological function of the stress response (Bremner *et al.* 2003). Therefore, regarding the two main drivers of the IDH, i.e. competitive exclusion and stress tolerance, a functional group approach, assigning species sharing the same biological traits into groups, regardless of the species composition, is expected to provide a more appropriate approach to unravel stress-diversity relations (e.g. Bremner *et al.* 2003).

Intertidal habitats experience pronounced gradients in environmental stress (Raffaelli & Hawkins 1996) and, hence, provide a good opportunity to test hypotheses on local scale community diversity in relation to stress or disturbance. Most of the knowledge in this field has accumulated by using rocky shore habitats as model systems, since the relatively small size of the intertidal organisms, together with the stress gradients that occur across short distances, facilitate observational and experimental research (Menge & Branch 2001, Scrosati & Heaven 2007). In the soft-sediment intertidal, diversity tends to peak at intermediate (Beukema 1976) to low intertidal levels (Degraer *et al.* 1999,

Armonies & Reise 2000, Giménez *et al.* 2005, 2006, Harriague & Albertelli 2007, Honkoop *et al.* 2006) on sandy beaches and sandflats, whereas comparable detailed information on cross-shore species diversity is limited for sheltered intertidal mudflats.
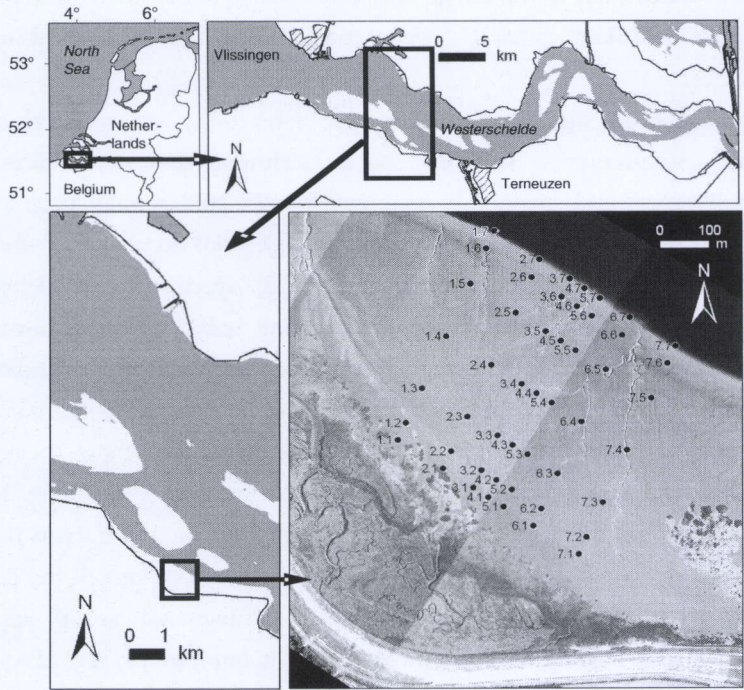
Fig. 1. *Location of the intertidal study site with indication of the seven cross-shore transects. Sampling stations are depicted as bullets with their label.*

In this study, the macrobenthic community across a full intertidal gradient on a single tidal mudflat was used to investigate how diversity, biological traits and community structure vary in relation to the prevailing hydrodynamic stress gradient. Given the general idea that sets of traits are related to species abilities to cope with stress, a functional group approach was used to give insight in the underlying drivers of the community-wide responses to changing hydrodynamical stress.

In particular, we addressed the following questions:

i.   Does benthic species diversity exhibit a unimodal hydrodynamic stress response, congruous the IDH?

ii.   Does the macrobenthos community structure differ in relation to hydrodynamic stress?

iii. Do community-wide biological trait shifts occur along the hydrodynamic stress gradient, which may explain the observed stress response?

Materials & methods

Site description and sampling

Samples were collected on 17, 19 and 23 April 2002 at Paulinapolder tidal flat, which is located along the south bank of the lower, polyhaline part of the Westerschelde estuary (SW the Netherlands) (Fig. 1). The flat has a semi-diurnal tidal regime with a mean tidal range of 3.9 m and an average salinity of 24 PSU (Ysebaert *et al.* 2003). The sediment material generally consists of mud (average median particle size = 65 μm, average mud content = 51 %) but the sand fraction increases linearly down the flat, associated with the prevailing stronger currents towards the estuarine main channel (Table 1). The established macrofauna community is rich, consisting of 21 species characterized by a wide variety of biological traits (Table 2).

Macrobenthos samples were collected with a stainless corer (inner ø 11 cm) to a depth of 40 cm along seven intertidal transects. Each transect consisted of seven sampling stations, covering a complete cross-shore gradient from the marsh edge towards the subtidal estuarine main channel (Fig. 1). The macrobenthos samples (n = 1 sampling station^{-1}) were washed over a 0.5 mm mesh-sized sieve and the residual organisms were fixed in a buffered 4% formalin-seawater solution. In the laboratory, the retained organisms were sorted, counted and identified to

species level (except for oligochaetes), after staining with Rose Bengal. At each sampling station, the first sediment layer was sampled, freezedried and stored at $-20°C$, and subsequently processed in the laboratory for granulometry using Malvern laser diffraction analysis. Further environmental characteristics were extracted at the sampling stations in a Geographical Information System, based on maps from Rijkswaterstaat, the Dutch Ministry of Transport, Public Works and Water Management (Graveland 2005). Elevation data were obtained from a laseraltimetry survey of 2001 for the intertidal zone, combined with a multibeam survey for the subtidal zone. Spatial information on current velocity, i.e. the maximum current velocity during flood and ebb on spring and mean tides, were derived from simulations (using the 2001 elevation data) with SCALWEST, a numerical flow model developed for the Westerschelde. The 2001 elevation data were also combined with water level information from 2002 from the nearby tide gauge station Terneuzen (Fig. 1) to calculate inundation duration at the sampling stations at spring and mean tide, respectively.

Parameter	Minimum-maximum	PC_{stress}		Tidal elevation	
		r	p	r	p
Maximal ebb current velocity mean tide (cm.s^{-1})	6 - 45	-0.98	< 0.001	-0.97	< 0.001
Maximal flood current velocity mean tide (cm.s^{-1})	11 - 49	-0.95	< 0.001	-0.93	< 0.001
Maximal ebb current velocity spring tide (cm.s^{-1})	11 - 51	-0.98	< 0.001	-0.97	< 0.001
Maximal flood current velocity spring tide (cm.s^{-1})	16 - 58	-0.98	< 0.001	-0.97	< 0.001
Median particle size (µm)	37.4 – 131.8	-0.88	< 0.001	-0.80	< 0.001
Mud content (% < 63 µm)	14.4 – 75.2	0.87	< 0.001	0.79	< 0.001
Very fine sand fraction (% 63-125 µm)	19.7 – 42.6	-0.84	< 0.001	-0.74	< 0.001
Fine sand fraction (% 125-250 µm)	3.0 – 44.8	-0.87	< 0.001	-0.80	< 0.001
Medium sand fraction (% 250-500 µm)	0 – 10.9	-0.28	0.057	-0.29	0.040
Sorting coefficient (φ)	1.1 – 3.3	0.68	< 0.001	0.55	< 0.001
Submersion duration at spring tide (hrs)	4.8 – 10.8	-0.96	< 0.001	-1.00	< 0.001
Submersion duration at mean tide (hrs)	4.6 – 12.0	-0.96	< 0.001	-1.00	< 0.001

Table 1. Minimum and maximum values for each parameter and Spearman rank correlations with the first principal component (PCstress) and elevation (cm above Dutch Ordnance Datum NAP) of sampled variables across the intertidal flat at Paulinapolder. Relations with PCstress are significant at p < 0.004 after Bonferroni correction.

	Feeding habit	Development mode
Arenicola marina	Subsurface deposit feeder	Direct
Aphelochaeta marioni	Surface deposit feeder	Lecitotrophic
Anaitides mucosa	Omnivore/Scavenger	Planktotrophic
Abra tenuis	Surface deposit feeder	Direct
Cerastoderma edule	Suspension feeder	Planktotrophic
Capitella capitata	Subsurface deposit feeder	Lecitotrophic
Corophium volutator	Surface deposit feeder	Direct
Eteone longa	Omnivore/Scavenger	Planktotrophic
Heteromastus filiformis	Subsurface deposit feeder	Planktotrophic
Hydrobia ulvae	Surface deposit feeder	Planktotrophic
Macoma balthica	Surface deposit feeder	Planktotrophic
Mysella bidentata	Suspension feeder	Planktotrophic
Nephtys cirrosa	Omnivore/Scavenger	Planktotrophic
Nereis diversicolor	Omnivore/Scavenger	Lecitotrophic
Oligochaeta	Subsurface deposit feeder	Direct
Polydora cornuta	Surface deposit feeder	Planktotrophic
Pygopsio elegans	Surface deposit feeder	Planktotrophic
Retusa obtusa	Omnivore/Scavenger	Planktotrophic
Streblospio benedicti	Surface deposit feeder	Lecitotrophic
Scrobicularia plana	Surface deposit feeder	Planktotrophic
Spio sp.	Surface deposit feeder	Planktotrophic

Table 2. *List of macrobenthic species of the Paulinapolder mudflat, recorded in this study with indication of their biological traits. Feeding habits are based on Fauchauld & Jumars 1979 and Van Colen et al. 2008, development modes are based on Eckert 2003, Dekker & Beukema 1999 and <https://www.marlin.ac.uk/>.*

Characterization of the environmental stress gradient

Principal Component Analysis (PCA, Goodall 1954) was carried out on the environmental characteristics of the sampling stations (Table 1). PCA revealed the prevalence of one main 'hydrodynamic stress' axis (PC_{stress}; eigenvalue = 8.99; explanatory value = 74.9 %), which strongly correlated with tidal current aspects and sediment composition after Bonferroni correction (Table 1). Decreasing values of PC_{stress} indicate a lower intertidal position with an increased submersion time, increased current velocity during ebb and flood and a substrate

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composed of less sorted, less muddy sediment. Because we aimed to study tidal flat macrobenthos diversity, community structure and community-wide patterns of biological traits in relation to hydrodynamical stress *sensu lato*, we retained sampling stations scores from the first PCA axis for further analysis. Stations were characterized as low, medium and highly stressed according to their distribution within the upper (PC_{stress} > 0.4), middle (-2.9 > PC_{stress} < 0.4) and lower (PC_{stress} < -2.9) third of the PC_{stress} axis.

Data analysis: species diversity and biological traits

Species richness and diversity have often been used as synonyms in past studies and in the context of the IDH, both terms have been used interchangeably (e.g. Menge & Sutherland 1987, Bertness 2007). However, since diversity depends on the number of species in the community and the degree of similarity in abundance among species (i.e. evenness), their patterns in relation to environmental stress may differ (e.g. Kimbro & Grosholz 2006). Hence, we calculated species richness (i.e. total number of species), species diversity (Shannon-Wiener diversity index, H'(e)) and evenness (Pielou's evenness, J') for each sampling station. Further, to delineate insights in the underlying drivers of the diversity and community structure stress response, the influence of hydrodynamical stress on the community-wide proportional biomass and abundance of the feeding habits (surface deposit feeder, subsurface deposit feeding, filter feeding, omnivore/scavenging) and the community-wide proportional abundance of the species' development modes (lecitotrophic, planktotrophic, benthic development) was analyzed. Species-specific traits and the respective references, upon which they are based, are presented in Table 2. The influence of hydrodynamical stress on community-wide diversity and biological traits was assessed using linear and quadratic models (GLMs, Statistica 7.0). The first PCA axis was used as the continuous factor, reflecting hydrodynamic stress *sensu lato*, whereas species richness, diversity, evenness and the arcsine transformed proportional abundance and biomass data were used as dependent variables. Extreme outliers were excluded from the analysis (casewise

plot of residuals ± 3 sigma, Statistica 7.0) to achieve normality of residuals. Akaike's information criterion (AIC)(Johnson & Omland 2004) revealed that quadratic models were, overall, more reliable as compared to the linear regressions, and consequently these models were retained and presented in this manuscript. One sampling station (5.1), which contained only three individuals of two different species, was omitted from all analyses because it consistently behaved as an outlier in the GLM. One-way analysis of similarity (Anosim, Clarke & Gorley 2001) was applied to investigate difference in community structure based on log (x+1) transformed, non-standardized abundance data and the species contributing most to the dissimilarities were identified using similarity of percentages analysis (Simper, Clarke 1993).

Results

Species diversity and community structure

Overall species richness, diversity and evenness peaked at low hydrodynamic stress levels (Fig. 2, Table 3). Fig. 2 shows that the peak of the latter variable is less pronounced as compared to the species richness and diversity. Anosim revealed a significant difference between low, medium and highly stressed stations (low-medium; R = 0.478 p < 0.001, low-high; R = 0.897 p < 0.001, medium-high; R = 0.639 p < 0.001), with different species comprising the majority of the community (Table 4). *Pygospio elegans*, Oligochaeta spp. and *Cerastoderma edule* contributed most to the dissimilarity between highly stressed and low - medium stressed communities, whereas differences between low and medium stressed communities were attributable to contributions of the surface deposit feeders *Aphelochaeta marioni*, *Hydrobia ulvae*, *Streblospio benedicti* and *P. elegans* (Table 4).

(a) Species richness

(b) Shannon-Wiener diversity
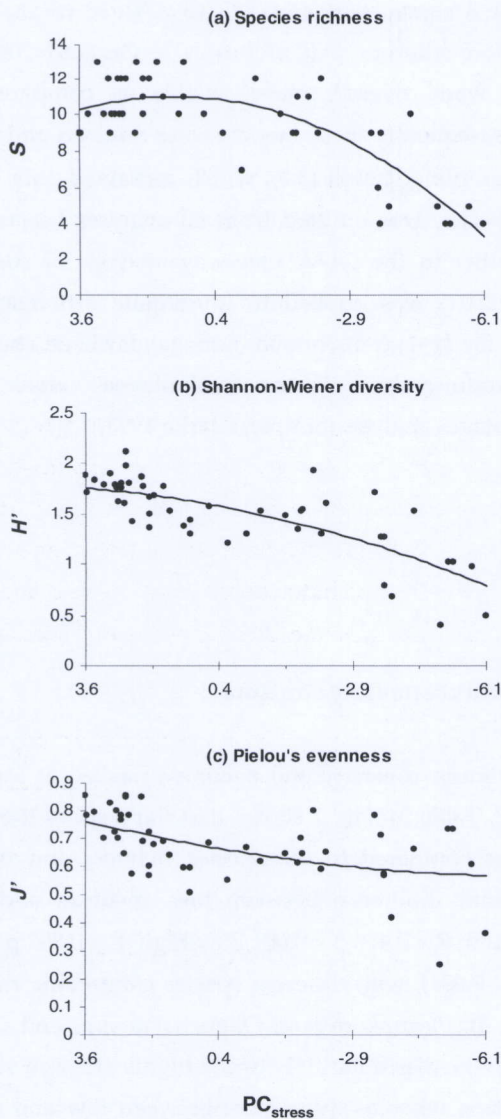
(c) Pielou's evenness

PC_{stress}

Fig. 2. Relationship between overall (a) species richness, (b) Shannon-Wiener diversity, (c) Pielou's evenness and the degree of hydrodynamic stress across the intertidal gradient. The principal component scores derived from a principal component analysis of station-specific habitat characteristics (PC_{stress}) are used to indicate the degree of hydrodynamic stress along the x-axis.

Community-wide biological traits

Statistics of the relationships between PC_{stress} and community-wide feeding and development traits are shown in Table 5 and the significant relationships are presented in Fig. 3. The relation between PC_{stress} and proportional suspension feeding abundance and biomass revealed an intermediate optimum across the hydrodynamic stress gradient. The proportional subsurface deposit feeder abundance and biomass and the proportional biomass of omnivore/scavengers increased with increasing hydrodynamic stress (i.e. lower PC_{stress} values), whereas the opposite pattern was found for the proportional surface deposit feeding abundance and biomass (Fig. 3). Furthermore, a differing trait pattern was also apparent for development mode: lecitotrophic development showed a U-shaped distribution pattern across the hydrodynamic stress gradient, whereas direct benthic development peaked at medium stress levels and the proportional abundance of species with a planktotrophic larval development mode slightly increased towards less hydrodynamically stressed environments (Fig. 3).

	Df numerator	Df denumerator	F	p	Adjusted R^2
Species richness	2	45	39.167	< 0.001	0.62
Shannon-Wiener diversity	2	45	31.616	< 0.001	0.57
Pielou's evenness	2	45	7.866	0.001	0.23

Table 3. Quadratic regression statistics of the relation between PC_{stress} and total species richness, Shannon-Wiener diversity and Pielou's evenness.

Discussion

The present study primarily aimed to test whether tidal mudflat macrobenthos diversity performs a unimodal response to hydrodynamic stress, as predicted by the IDH (Connell 1978). In agreement with the IDH, low overall species richness,

diversity and evenness was found at high hydrodynamically stressed stations in the low intertidal. However, diversity, evenness and species richness peaked at low hydrodynamic stress occurring in the high intertidal, and hence, no diversity optimum at intermedium hydrodynamical stress was found. Consequently, overall, our data provide no support for the IDH.

Species	Average Abundance	Average Abundance	Contribution to the dissimilarity	Cumulative percentage
	Low stressed	Medium stressed		
Aphelochaeta marioni	3065 ± 639	453 ± 120	13.97	13.97
Hydrobia. ulvae	745 ± 195	53 ± 24	11.46	25.43
Streblospio benedicti	487 ± 93	53 ± 28	10.26	35.68
Pygospio elegans	4207 ± 1415	1358 ± 195	9.88	45.56
Oligochaeta	9491 ± 2443	5740 ± 1405	8.61	54.17
Cerastdorma edule	663 ± 88	1000 ± 215	8.53	62.7
	Low stressed	High stressed		
Pygospio elegans	4207 ± 1415	278 ± 153	15.15	15.15
Oligochaeta	9491 ± 2443	5790 ± 1405	14.06	29.21
Cerastoderma edule	663 ± 88	0 ± 0	10.34	39.55
Streblospio benedicti	487 ± 93	0 ± 0	8.51	48.06
Macoma balthica	550 ± 44	67 ± 33	8.41	56.46
Aphelochaeta marioni	3065 ± 639	1158 ± 354	8.31	64.77
	Medium stressed	High stressed		
Oligochaeta	5740 ± 1405	5790 ± 1405	15.85	15.85
Cerastoderma edule	1000 ± 215	0 ± 0	14	29.85
Pygospio elegans	1358 ± 195	278 ± 153	13.37	43.22
Macoma balthica	463 ± 83	67 ± 33	8.94	52.16
Aphelochaeta marioni	453 ± 120	1158 ± 354	8.93	61.09

Table 4. Contribution of species to > 60 % dissimilarity between low, medium and high hydrodynamically stressed sampling stations using Simper analysis based on Bray-Curtis similarity of log (x+1) species abundance data. Presented abundances ± standard errors (ind.m^{-2}) are not transformed.
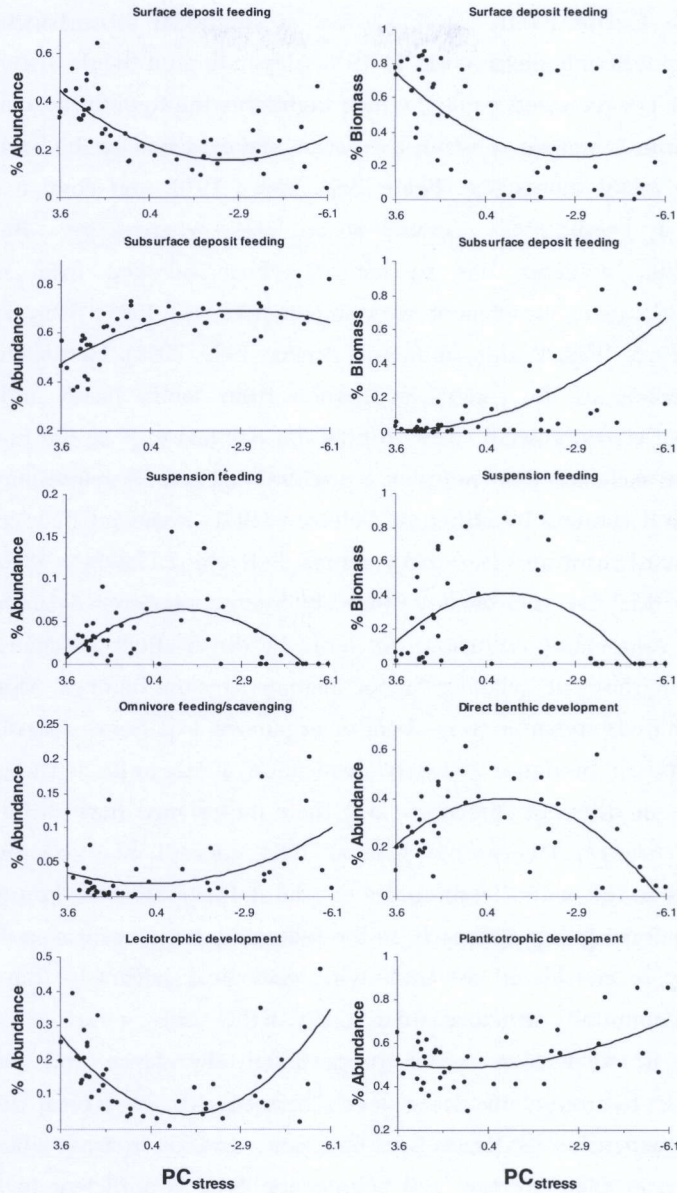
Fig. 3. Relationship between the proportional community biomass and/or abundance of species exhibiting surface deposit feeding, subsurface deposit feeding, suspension feeding, omnivore feeding/scavenging, lecitotrophic development, direct benthic development, planktotrophic development and the degree of hydrodynamic stress along the x-axis (i.e. PCstress).

Mackey & Currie (2001) revealed that a unimodal disturbance-diversity relationship was only observed in 11-19 % (depending on the diversity measure applied) of 116 reviewed papers, which highlights the hypothesis status of the IDH principle. In marine substrates, experimental evidence for the IDH has been shown for rocky shores (e.g. Paine 1966, Sousa 1979) and coral reef studies (Aronson & Precht 1995, Connell *et al.* 2004) whereas for soft-sediment environments, evidence has so far only been invoked from mesocosm disturbance/organic enrichment experiments (Austen 1998, Schratzberger & Warwick 1998, 1999, Widdicombe and Austen 1999, 2001). Hence, the present study corroborates the general suggestion from sandy beach and sandflat surveys that environmental stress in tidal flat habitats may be too high so that competitive exclusion does not play a predominant role in determining species diversity and community structure. Peterson (1991) reviewed that, contrary to intertidal hard substrates (e.g. rocky shores, Raffaelli & Hawkins 1996), benthic zonation in tidal flats is rarely determined by intense interference competition for space (i.e. competitive exclusion) but more by direct effects of changes in the physical environment, whether or not mediated by the benthos. Moreover, in addition to hydrodynamic stress, benthic organisms experience also other stress components, e.g. predation pressure, dessication, access to food. These stressors may point in different directions and their importance may differ between functional groups. Hence, the general IDH concept may simply not be appropriate to the benthic community of tidal flat habitats. Based on the results of the functional group approach, in the following, we present some processes which may be considered the underlying ecological drivers for the observed pattern in community structure and diversity in this study.

The peak in suspension feeder proportional abundance and biomass at intermediate hydrodynamic stress levels corroborates the typical distribution pattern of suspension feeders in tidal flats: concentration in areas where bottom shear stress is relatively low and submersion time is sufficient to feed long enough to meet energetic requirements (Beukema 1976, Herman *et al.* 1999). These conditions are best in the mid intertidal region of our study site, where tidal currents, and thus bottom shear stress, are drastically lower as compared to

the lower intertidal and submersion time is slightly longer as compared to the highest intertidal region. The common edible cockle, *Cerastoderma edule*, is the most important suspension feeder, both in terms of biomass, biovolume and abundance in the upper 5 cm at our study site (Ysebaert & Herman 2002, Van Colen *et al.* 2008, Montserrat *et al.* 2008, this study) and has been shown to affect the benthic boundary layer significantly by increasing bottom shear stress due to the physical structure of its shell and by biodiffusion due to its movement (Ciutat *et al.* 2007, Montserrat *et al.* 2008). Interference by bioturbation of large macrofauna adversely affect juvenile recruitment success, and benthic community stucture in general, directly (e.g. by predation; Hiddink *et al.* 2002) and/or indirectly (e.g. by destabilisation of the sediment, inhibition of microphytobenthos development; Ólafsson 1989, Ólafsson *et al.* 1994, Flach 2003). Consequently, given the feeding habit and surface dwelling life habit of surface deposit feeders and lecitotrophic non-pelagic larvae, these organisms may be expected as most vulnerable to the cockle mediated disturbance in the upper sediment layer. The low proportional abundance of surface deposit feeders and species with a lecitotrophic development in this study support and generalize the findings of Flach (1996), who showed a severe negative effect of *C. edule* densities on juvenile recruitment of the surface deposit feeders *P. elegans*, *M. balthica* and the lecitotrophic surface deposit feeder *A. marioni*. Therefore, the suspension feeding optimal stress response at intermediate hydrodynamic stress presumably enhances the overall surface dwelling organisms' stress due to interference by bioturbation, which may have contributed to the overall community diversity peak at low hydrodynamically stressed habitats in the high intertidal. Additionally, at muddier high intertidal habitats, overall benthic diversity, and surface dwelling species in particular, may benefit from (1) lower hyperbenthic predation pressure due to shorter submersion times and (2) higher benthic primary production (de Jong & de Jonge 1995, van de Koppel *et al.* 2001), despite some possible adverse effects due to enhanced desiccation stress and avian predation pressure.

Increased awareness of the importance of benthos-physical interactions, determining overall benthic community structure and diversity (e.g. Kimbro &

Grosholz 2006, Rabaut *et al.* 2007, Thrush *et al.* 2008, Van Colen *et al.* 2008), have led to the incorporation of facilitative interactions into recently updated environmental stress models (Bruno *et al.* 2003, Scrosati & Heaven 2007). Additionally, the results of the present study indicate that inhibitory benthos-physical interactions on overall ecosystem diversity such as interference by bioturbation (this study, Solan *et al.* 2008) should be incorporated in tidal flat biodiversity-environmental stress models, as well.

	Df numerator	Df denumerator	F	p	Adjusted R²
% Abundance surface deposit feeders	2	45	17.826	< 0.001	0.41
% Abundance subsurface deposit feeders	2	44	14.805	< 0.001	0.38
% Abundance suspension feeders	2	44	8.839	< 0.001	0.26
% Abundance omnivore/scavengers	2	42	1.432	0.250	0.02
% Biomass surface deposit feeders	2	45	8.362	< 0.001	0.24
% Biomass subsurface deposit feeders	2	45	27.602	< 0.001	0.53
% Biomass suspension feeders	2	44	7.730	0.002	0.23
% Biomass omnivore/scavengers	2	41	4.843	0.012	0.15
% Abundance planktotrophic development	2	45	5.801	0.006	0.17
% Abundance lecitotrophic development	2	44	18.856	< 0.001	0.44
% Abundance direct benthic development	2	45	14.004	< 0.001	0.36

Table 5. Quadratic regression statistics of the relation between PCstress and the arcsine transformed proportional community biomass and/or abundance of the biological traits surface deposit feeding, subsurface deposit feeding, suspension feeding, omnivore/scavenger feeding habit, planktotrophic development, lecitotrophic development and direct benthic development.

Acknowledgements