

CHAPTER 5

BENTHOS-MEDIATED SEDIMENT DYNAMICS: IMPLICATIONS FOR GROWTH AND PRODUCTION OF JUVENILE RECRUITS

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Abstract

Recruitment success of the bivalves *Macoma balthica* and *Cerastoderma edule* and the polychaetes *Nereis diversicolor* and *Pygospio elegans* was investigated in response to macrobenthos community-mediated differences in sediment characteristics. Population and growth dynamics were inferred from a recolonisation field study after experimentally induced hypoxia where differences in macrobenthos community structure mediated differences in food supply (i.e. benthic primary production) and susceptibility to physical stress (i.e. erosion).

Species feeding on microphytobenthos grew significantly faster in hypoxic patches (i.e. treatments) where fresh food supply was higher and physical stress was lower as compared to control sediments. Moreover, differences in growth rate were positively related to the consumer-specific microphytobenthos contribution to its diet and suggest that the faster growth in the treatments relates to a lower interference competition for food. In addition to the enhanced growth, lower post-settlement dispersal in the more stable treatments is suggested to contribute substantially to the significant higher cohort production of *M. balthica*, *N. diversicolor* and *P. elegans*.

Because recruitment is the foundation upon which all subsequent interactions within the community take place, our results illustrate that biotic-physical interactions that affect benthic primary production and sediment stability are of

fundamental importance to tidal flat macrobenthic community distribution and functioning.

Keywords: *Recruitment success, Growth, Production, Interference competition for food, Post-settlement resuspension*

Introduction

Events affecting recruitment of macrobenthos may control benthic species diversity, and hence ecosystem functioning (Naeem *et al.* 2002) since these events determine (1) the magnitude of propagule arrival to the community (i.e. net input of new individuals) and (2) the survival of settlers to the benthic stage. For species with pelagic larvae, recruitment has five major components: input of propagules into the water column, propagule dispersal, planktonic mortality, settlement and post-settlement growth and survival (Jenkins *et al.* 1999). Recruitment limitation involves both pre and post-settlement events determining recruitment success but the relative importance of primary (i.e. pre-settlement) and secondary (i.e. post-settlement) recruitment limitation differs between substrate type, scale and species (Fraschetti *et al.* 2003). Stoner (1990) suggested that pre-settlement events influence distribution of recruits because these events operate at a larger scale, whereas post-settlement events (survival, growth and secondary dispersal) affect juvenile density at a local scale. In general, pre-settlement mortality is thought to limit benthic populations because planktonic larvae are considered the most vulnerable stage in the life cycle of marine invertebrates (Thorson 1950). However, recent evidence illustrates that secondary recruitment limitation cannot be neglected since post-settlement mortality may exceed 90% of the larvae settled (Gosselin & Qian 1997). In addition to interactions between established adults and recruits (e.g. predation, interference by bioturbation, competition for food and space), exposure to physical and hydrodynamic disturbance and food limitation may affect post-settlement growth and survival (Fraschetti *et al.* 2003).

In this paper, we evaluated whether differences in community-mediated sediment characteristics affected the post-settlement growth and production of four macrobenthic species. Population and growth dynamics were inferred from a recolonisation field study after experimentally induced hypoxia where differences in biological activity of a control, 'mature' community and a recovering community mediated differences in food supply (i.e. benthic primary production) and susceptibility to physical stress (i.e. erosion) (Van Colen *et al.* 2008, Montserrat *et al.* 2008). The polychaetes *Nereis diversicolor* and *Pygospio elegans* and the bivalves *Macoma balthica* and *Cerastoderma edule* were chosen because these species (1) differed in microphytobenthos (MPB) contribution to their diet, (2) settled at high densities and (3) are common and important contributors to the macrobenthic community, and hence, to the functioning of NW European tidal flats (Bachelet & Dauvin 1993, Ysebaert & Herman 2002, Ysebaert *et al.* 2003, Volkenborn & Reise 2007, Van Colen *et al.* 2008).

Materials & methods

Data collection

Benthic recruits were collected with a 12.5 cm inner diameter corer from six replicated 4 x 4 m sediment patches at the Paulinapolder tidal flat (Westerschelde estuary, SW the Netherlands) during Spring and Summer 2005. Biweekly, from March 30th – August 3th, one sample was randomly taken from each patch, fixed with a neutralized 8 % formalin solution and subsequently sieved over a 500 µm mesh size. Three of these patches were disturbed by severe hypoxia for 40 days until March 30th (i.e. treatments) and three patches were left undisturbed (i.e. controls). Hypoxia was induced by covering the sediment surface by thick plastic sheets and resulted in a complete mortality of the macrobenthic community. Subsequently, macrobenthos recovery developed through different succession stages characterized by clear biotic and abiotic shifts (Van Colen *et al.* 2008). As a result of the low grazing pressure during the first month of recovery, benthic

primary production – which was made up by > 80 % of diatoms (F. Montserrat, unpublished data) - strongly exceeded control values in the treatment patches during early recovery stages and returned to control levels after three months, along with an enhanced grazing and bioturbation impact, characterizing later succession stages (Fig. 1). Further, whereas the control patches constantly eroded during May and June, the bed level of treated patches remained more or less stable, most probably due to the combined effect of the dense diatom mat, the dense patches of tube-building polychaetes and the relatively low bioturbation disturbance during that period (Montserrat *et al.* 2008).

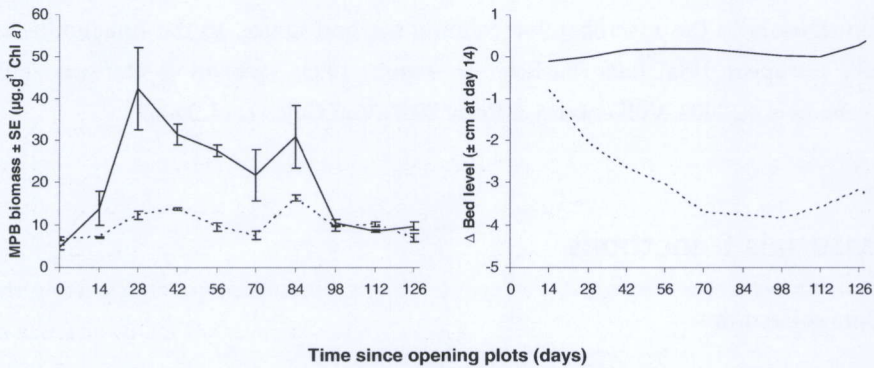


Fig.1. Temporal variation in microphytobenthos biomass \pm SE (left panel) and difference in bed level height (right panel), as compared to the first measurement (i.e. day 14) in control (dashed line) and treated patches (solid line). Curve fits for Δ bed level height are running averages (period = 2 sampling occasions).

In similar treatment plots, used in a parallel experiment, Rossi & Middelburg (in prep.) quantified the MPB contribution to the consumers' diet by comparing the consumers' $\Delta\delta^{13}\text{C}$ (i.e. the increment of $\delta^{13}\text{C}$ due to a PLFA biomarker uptake, as compared to natural background values) to the MPB $\Delta\delta^{13}\text{C}$: $\Delta\delta^{13}\text{C}_{\text{consumer}} / \Delta\delta^{13}\text{C}_{\text{resource}}$ (i.e. Δ -ratio). This approach revealed that *M. balthica* juvenile recruits relied primarily on MPB carbon, reaching a Δ -ratio close to 100 %, whereas benthic microalgae contributed less to the diet of *P. elegans* and *N. diversicolor* (Δ -

ratio ~ 30 %). No label uptake was found in juvenile *C. edule* which supports the well-known filter feeding behavior on phytoplankton of this species (Herman *et al.* 2000, Rueda & Smaal 2002). For more details on MPB isotope tracking, information on the study site, experimental set-up and sample processing, the reader is referred to Van Colen *et al.* (2008), Montserrat *et al.* (2008) and Rossi *et al.* (2008).

Growth and production estimates and analysis

Species size-frequency analyses were performed for all sampling occasions for each replicate plot (n = all individuals in a replicate sample with a maximum of n = 50 individuals for *P. elegans*). Size classes were 1 mm shell width for *M. balthica* and *C. edule* and 0.05 mm and 0.2 mm 5th setiger width for *P. elegans* and *N. diversicolor*, respectively. These analyses revealed the occurrence of one clear juvenile cohort for *M. balthica* and *C. edule* throughout the sampling period, whereas no unimodal pattern for *P. elegans* and *N. diversicolor* was apparent. Consequently, size, standard deviation and density of juvenile cohorts of the latter two species were determined according to Bhattacharya (1967) using the Fisat II software (Gayaniilo *et al.* 1996). This approach revealed the occurrence of several juvenile cohorts throughout the monitoring period for both of these species. Only data of the first appearing cohort of both species was used in this study.

Cohort growth rate and production – which takes both survival and growth into account - were used as indicators of recruitment success. Average daily cohort growth was estimated for each replicate treatment (n = 3) as the difference in mean size of the individuals of an identified cohort between the last and first appearance in the samples, normalized per unit time (size increment day⁻¹). A power function enabling conversions from body size (S , mm), i.e. 5th setiger width for polychaetes and shell width for bivalves, to biomass (W , g) was assessed from size and biomass measurements from the same complete individuals: $W_{N. diversicolor} = 0.001S^{2.6913}$, $r = 0.96$, $n = 50$; $W_{P. elegans} = 0.0004S^{1.9039}$, $r = 0.76$, $n = 49$; $W_{M. balthica} = 3.10^{-5}S^{1.8954}$, $r = 0.91$, $n = 156$; $W_{C. edule} = 2.10^{-5}S^{2.3193}$, $r = 0.84$, $n = 153$).

Bivalve biomass was obtained by determination of the ash free dry weight (4h combustion at 450°C of 24h, 60°C dried individuals) and polychaete biomasses were calculated by multiplying the organisms' blotted wet weight with a species-specific ISO certified wet weight-ash free dry weight conversion factor (Sistermanns *et al.* 2007). Cohort production for each replicate treatment (n=3) was estimated using the weight increment method (Crisp 1971) (Table 4, a-d in Appendix 3). After data transformation in order to meet homogeneity of variances (Levene test) and normality (Shapiro-Wilks test) assumptions, Student t-tests were applied to analyze differences in initial settlement density and size, cohort growth rate and production between treatments and controls.

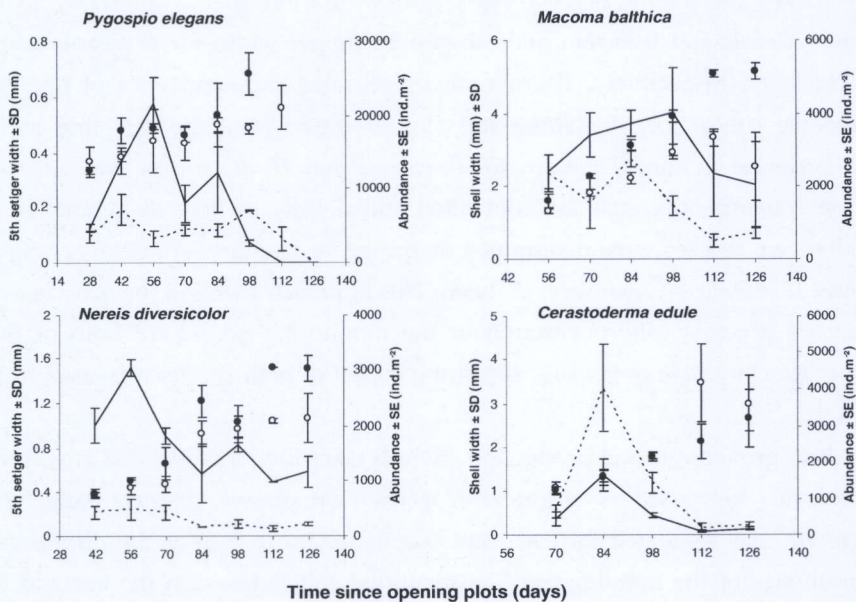


Fig. 2. Temporal variation of mean size \pm SD (circles, left y-axis) and density \pm SE (lines, right y-axis) of the identified juvenile cohorts of *Pygospio elegans*, *Nereis diversicolor*, *Macoma balthica* and *Cerastoderma edule* in control (open circles, dashed line) and treatment patches (closed circles, solid line).

Results & discussion

Temporal variation of mean cohort size and density are presented in Fig. 2. Settlement size (i.e. mean cohort body size at first appearance in samples) did not differ significantly between treatments and controls for all species (t-test, $df = 4$, $p > 0.05$). Juvenile *M. balthica*, *P. elegans* and *N. diversicolor* treatment cohorts grew significantly faster as compared to the controls (+ 31.0 $\mu\text{m day}^{-1}$ shell width for *M. balthica*, + 2.2 $\mu\text{m day}^{-1}$ 5th setiger width for *P. elegans* and + 5.4 $\mu\text{m day}^{-1}$ 5th setiger width for *N. diversicolor*), whereas growth rates were not significantly different between control and treatment sediments for *C. edule* (Fig. 3a, Table 1). Furthermore, differences in growth rate between control and treatment patches were positively related to the microphytobenthos contribution to the consumers' diet: +102% for *M. balthica*, which almost completely feed on MPB; + 77 %, for *P. elegans* (feeding less on MPB, i.e. ~30%); + 67 % for *N. diversicolor* (feeding less on MPB, i.e. ~30%) and no significant difference for *C. edule*, which does not feed on MPB.

Taking into account the species-specific microphytobenthos contribution to the macrobenthos diet (Herman *et al.* 2000, Rossi & Middelburg in prep.) and assuming a net growth efficiency of 60 % and 75 % for macrobenthos and epistrate feeding nematodes, respectively (Van Oevelen *et al.* 2006), one can estimate that 17.3 % of the produced microalgal carbon during the 126-day experimental period is consumed by the macrobenthos and epistrate feeding nematodes in the control sediments, whereas grazing of these organisms only account for 3.5 % of the produced microalgal carbon in the treatments. One can expect that an organism feeds more efficiently, and thus spends less energy, in a more stable environment where there is less interference with other organisms. Hence, the faster growth in the treatment cohorts presumably relates to a lower interference competition for food (i.e. microalgal carbon). Furthermore, differences in grazing pressure and bioturbation intensity have been shown to alter benthic diatom community composition (e.g. Hagerthey *et al.* 2002). Therefore, alterations in diatom species-specific nutritional value or cell wall characteristics, affecting the benthos' digestion efficiency (e.g. Kawamura *et al.*

1995), may have affected differences in growth rate between controls and treatments. Differences in body size became clearly more pronounced at the end of the study period. In addition to their deposit feeding behaviour, large *M. balthica* also filterfeed and this filterfeeding behaviour is known to increase with body size (Herman *et al.* 2000, Rossi *et al.* 2004). As a result of their enhanced initial growth, the threshold body size which enables proper filterfeeding (i.e. 3 mm, Herman *et al.* 2000) was more rapidly reached by *M. balthica* juveniles in the treatments as compared to the controls. Consequently, additional food intake via the filterfeeding pathway may have contributed to the large difference in *M. balthica* body size between controls and treatments at the end of the experiment.

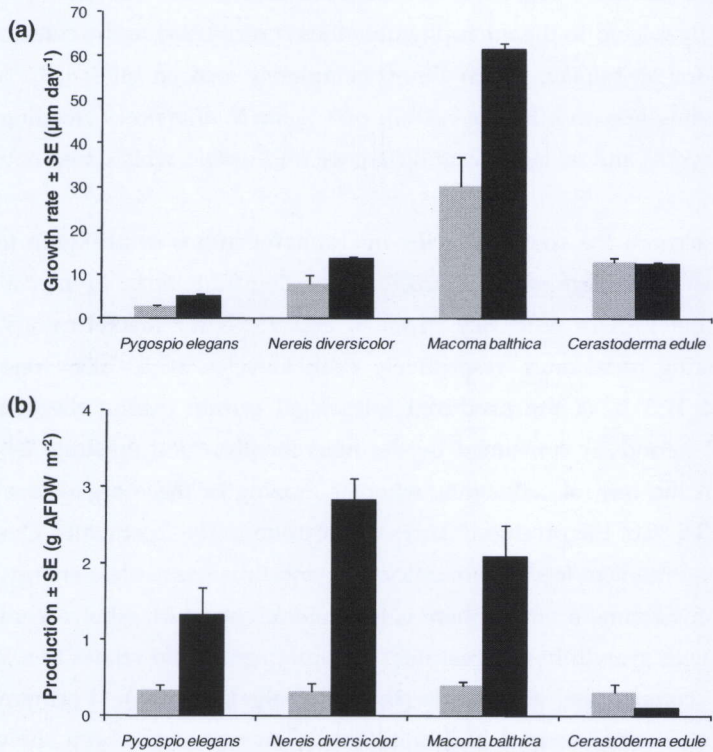


Fig. 3. (a) Mean growth rate \pm SE and (b) production \pm SE of *Pygospio elegans*, *Nereis diversicolor*, *Macoma balthica* and *Cerastoderma edule* in control (grey bar) and treatment patches (black bar).

In addition to their faster growth in the treatment plots, distinctly higher post-settlement densities of *P. elegans*, *N. diversicolor* and *M. balthica* in the treatments (Fig. 2) resulted in a significantly higher production of these species in the treatments (Fig. 3b, Table 1). In contrast to the eroding control sediments, treatment sediments were found to be more stable, presumably due to the stabilizing effect of a dense diatom mat and the dense aggregations of polychaete tubes (Montserrat *et al.* 2008). Consequently, enhanced accumulation due to a lower resuspension of settled recruits is hypothesized to primarily cause the higher abundances of *P. elegans*, *N. diversicolor* and *M. balthica* in the treatments.

	t-statistic	Df	p	Transformation
Growth rate				
<i>Pygospio elegans</i>	-2.983	4	0.041	Log (x+1)
<i>Nereis diversicolor</i>	-2.891	4	0.045	Log (x+1)
<i>Macoma balthica</i>	-4.640	4	0.010	Arcsine (x)
<i>Cerastoderma edule</i>	0.763	4	0.488	Log (x+1)
Production				
<i>Pygospio elegans</i>	-2.811	4	0.048	Log (x+1)
<i>Nereis diversicolor</i>	-8.720	4	0.001	Log (x+1)
<i>Macoma balthica</i>	-5.279	4	0.006	Log (x+1)
<i>Cerastoderma edule</i>	1.843	4	0.139	Log (x+1)

Table 1. Student *t*-test results for difference in growth rate and production of the identified cohorts between control and treatments.

Conclusion

In summary, the present study shows that the growth rate and production of microphytobenthos feeding macrobenthos juveniles is enhanced in a community with low bioturbation intensity. The available data suggest that this enhanced recruitment success resulted both from a lower post-settlement resuspension and lower interference competition for food due to an initially higher primary production. Consequently, because recruitment is the foundation upon which all

subsequent interactions within the community take place (Woodin *et al.* 1995), biotic-physical interactions that affect primary production and sediment stability are of fundamental importance to tidal flat macrobenthic community structure and functioning.

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