Macrobenthos abundance and distribution on a spatially patterned intertidal flat

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ABSTRACT: Natural ecosystems can show regular spatial vegetation patterns, which develop from small-scale ecological interactions. Some studies suggest that grazers can play a major role in controlling vegetation distribution in ecosystems with regular vegetation patterns, but the distribution of grazers and the effects of grazing on vegetation in spatially patterned ecosystems remains poorly understood. Here, we study how macrofaunal grazers are distributed on a spatially patterned intertidal flat and how they interact with benthic microalgae. The study was carried out on an intertidal flat where each year a regular spatial pattern of diatom-covered hummocks and water-filled hollows develops. In 2 consecutive years, benthic algal biomass was 5-fold lower in the hollows compared with the hummocks, whereas benthic macrofauna was equally abundant on both hummocks and hollows. In the laboratory we evaluated the interactive effect of landscape morphology (hummocks and hollows) and food abundance. Experiments with 2 abundant grazers, *Corophium volutator* and *Hydrobia ulvae* showed that food availability was the main driver for the spatial distribution of benthic herbivores rather than landscape morphology. Laboratory experiments, where we analyzed the grazing effects of *H. ulvae* and *C. volutator* on benthic algal biomass, revealed that both species increased biomass-specific primary production. This could indicate that benthic grazers can stimulate algal growth, which may explain the high grazer abundances in nearly bare hollows. Increased production of benthic algae may be a key factor uncoupling herbivore density from benthic algal biomass on a spatially patterned intertidal flat.

KEY WORDS: *Corophium volutator* · *Hydrobia ulvae* · Microphytobenthos · Intertidal flats · Landscape morphology

INTRODUCTION

Natural ecosystems can exhibit strikingly regular spatial patterns that develop from local feedback processes between organisms and the physical environment. Regular landscape patterns have been described in various ecosystems, among which tiger bush in arid ecosystems (Klausmeier 1999), striped oligotrophic peat lands in boreal regions (Eppinga et al. 2009) and mussel beds in intertidal systems (van

de Koppel et al. 2005) are well-known examples (reviewed by Rietkerk & van de Koppel 2008). In cases where pattern formation depends on interactions involving primary producers (e.g. benthic algae or vegetation), theoretical predictions suggest that grazers can have a profound effect on spatial patterns (Kéfi et al. 2007). This may result in irreversible shifts from a spatially patterned to a homogeneous state (Rietkerk et al. 2000, HilleRisLambers et al. 2001, Weerman et al. 2011). Such a shift can be

expected to feed back on the grazers, but despite the assumed role of herbivores in regularly patterned ecosystems, very little is known about the dynamics of grazers in these interactions.

On intertidal flats, regular spatial diatom patterns can develop in early spring (Weerman et al. 2010, de Brouwer et al. 2000, Paterson et al. 2000). These patterns develop because of an interaction between benthic algae and sedimentary processes (Weerman et al. 2010) and are characterized by regularly spaced, diatom-covered hummocks alternating with almost bare, water-filled hollows (de Brouwer et al. 2000, Weerman et al. 2010). These patterns have a scale of ~1 m and occur at muddy intertidal flats that lack a strong hydrodynamic regime (Weerman et al. 2010). Increased herbivore density, as the season progresses, results in rapid degradation as the ecosystem shifts into a homogenous tidal flat by both direct (removal of benthic algae) and indirect (e.g. bioturbation) effects of grazing (Weerman et al. 2011). It remains unstudied how macrobenthic herbivores are distributed in this patchy landscape of elevated diatom-covered hummocks, alternating with water-filled hollows. Moreover, in June the patterns disappear rapidly and benthic diatom abundances are low, hence macrofaunal abundances remain high (Weerman et al. 2011).

Grazers can affect plant biomass directly by reducing plant standing crop, but they also interact with plants indirectly by releasing nutrients or reducing light limitation (McNaughton 1979). This can have an important effect on plant production (McNaughton 1979). The concept of herbivore compensation suggests that at low grazing intensities, primary production increases and has a flow-on effect, which leads to a net increase in grazing intensity. This phenomenon has been described in both terrestrial (McNaughton 1979) and stream ecosystems (Gregory 1983). The feeding mechanism of herbivores could play a role in the effect they have on primary production. In this study, we test 2 abundant macrofaunal grazers, the amphipod *Corophium volutator* and the gastropod *Hydrobia ulvae*, with contrasting feeding modes. Both species are mainly deposit feeders and feed predominantly on benthic diatoms. They have significantly different feeding behaviours and therefore might affect their environment in different ways. *H. ulvae* mixes the sediment horizontally (Orvain et al. 2006) while browsing the sediment for diatoms (Jensen & Siegismund 1980, Levinton & Dewitt 1989). Feeding by *C. volutator* mixes the sediment vertically, as it feeds from semipermanent burrows in the sediment and gathers

sediment particles with its enlarged second antennae (Gerdol & Hughes 1994a,b, Hagerthey et al. 2002, Riisgård & Schotge 2007). These 2 feeding strategies might result in effects on pattern formation and primary productivity.

This study focuses on macrofauna distribution on a spatially patterned intertidal and the effects grazers can have on benthic microalgae. We expected that macrofauna species prefer the diatom-covered hummocks over almost bare hollows. We carried out a field survey in 2 successive years and measured macrobenthos and benthic algal abundance on the top of the hummocks and the adjacent hollows. To unravel the combined effect of landscape morphology and benthic algal abundance, we manipulated landscape morphology and benthic algal abundance in a laboratory experiment. Finally, in a second laboratory experiment, we investigated the hypothesis that herbivory stimulated benthic microalgal production, as a possible explanation of our field observation of high macrobenthic biomass in the almost bare hollows. Here, *Corophium volutator* and *Hydrobia ulvae* were added to benthic microalgae biofilms and their grazing effect on these biofilms was measured after several days. We hypothesized that these macrofauna species have species-specific effects on benthic biofilms as they apply different feeding mechanisms.

MATERIALS AND METHODS

Field sampling: spatial distribution of benthic microalgae and macrofauna

We measured the distribution of macrofauna and benthic algae on the intertidal flat Kapellebank. This is a muddy intertidal flat (51° 27' N, 3° 58' E) in the Westerschelde, The Netherlands. On this tidal flat, a spatial pattern of diatom-covered hummocks and alternating water-filled hollows develops each spring (Weerman et al. 2010). In both April 2007 and 2008, several samples were taken at random on both hummocks and adjacent hollows at the intertidal flat. At each sampling year, sampling was done at 2 different dates when spatial patterns were intact. On each sampling occasion, 5 paired samples for chlorophyll *a* (chl *a*) and 3 paired samples for macrofauna were taken. Chl *a* content was determined from the upper 2 mm of the sediment with a 100 ml cut-off syringe (36 mm inner ∅). During the fieldwork, chl *a* samples were placed on ice and upon arrival in the laboratory the samples were stored at −80°C. Pigment was extracted by adding 10 ml 90% acetone to lyophi-

lized sediment followed by chl *a* quantification by HPLC of the supernatant (Jeffrey & Humphrey 1975). Macrofauna samples were taken (n = 5) using a core (inner ∅ 11 cm, 20 cm deep) next to the samples for chl *a* content. The cores were sieved through 0.5 mm mesh and fixed with a neutralised 8% formalin solution. Prior to analysis, samples were stained using 0.01% Rose Bengal. The macrofauna obtained from the cores were identified to genus level.

Material collection and preparation for laboratory experiments

Sediment was collected at the Kapellebank. After collection, the sediment was mixed and defaunated by freezing it at −20°C for at least 24 h. Prior to the experiment, sediment was thawed and placed in the experimental units (see 'Grazing effects on benthic algae' below). Benthic algae were collected at the Kapellebank by scraping off the top layer of the sediment (~3 mm). Macrofauna and most of the meiofauna were obtained by sieving (150 µm mesh) the sediment with filtered seawater (0.45 µm). Benthic algae were mixed with filtered seawater to create a mixture of benthic algae, small sediment particles and other organic material. This suspension was sprayed on a defaunated sediment layer of 5 cm thickness. This setup was subsequently cultured for 1 wk to form a benthic microalgae biofilm. Adult *Corophium volutator* were collected at Kapellebank by sieving sediment (up to 10 cm depth; 1 mm mesh) and adult *Hydrobia ulvae* were collected 20 km east of the Kapellebank on an intertidal flat near Ritthem (51° 27′ N, 3° 39′ E) by sieving the top layer of the sediment (1 cm; 1 mm mesh). Both grazers were allowed to adapt to the experimental conditions for 2 wk. Experimental conditions were equal for all experiments. A tidal regime was applied (6 h low:6 h high) using filtered seawater. Light intensity was 120 ± 4 µW cm^{-2} (mean ± SEM), with a cycle of 12 h light:12 h dark, and temperature was set at 13°C in the laboratory.

Experimental design of the laboratory experiments

We conducted laboratory experiments to test whether the distribution of the grazers *Hydrobia ulvae* and *Corophium volutator* is affected by landscape morphology or food abundance. We created artificial hummocks, hollows and flat sediment, both in the absence and presence of benthic algae. Ten tidal tanks (30 × 40 × 10 cm) were established in a temperature-controlled room and filled with defaunated sediment. In each tank a randomized block design with a total of 30 patches (∅ ~5 cm) and 6 treatments was created. These treatments included 3 types of landscape morphology (hummock, hollow or flat) and 2 levels of food presence (absent or present). Hummocks were ~2 cm higher compared with the flat treatments and hollows were ~2 cm lower compared with the surrounding sediment. One hundred individuals of either *C. volutator* or *H. ulvae* were randomly added to the experimental tank. Preliminary experiments had shown that the settlement of *C. volutator* took longer compared with *H. ulvae*. Therefore, presence on the patches was counted after 1 h for *H. ulvae* and after 24 h for *C. volutator*. In total, 30 replicates of each treatment were applied. Animals could move freely between the patches. The video film in the supplement (www.int-res.com/articles/suppl/m440p095_supp/) shows the experimental setup and the movement of *H. ulvae* towards the food patches.

Grazing effects on benthic algae

Laboratory experiments were carried out to measure the effects of macrofaunal grazing on benthic algal biomass and production. Experimental units consisted of PVC cores (∅ 12.5, 10 cm height) filled with defaunated sediment. Benthic algae were scraped off the sediment in the benthic algae culture tanks and mixed with filtered seawater to create a mixture of benthic algae, small sediment particles and other organic material. During low tide, this mixture was sprayed on defaunated sediment in the experimental cores as a thin layer. Biofilms were allowed to grow for 7 d, after which grazers were added at different densities (0, 0.06, 0.19 and 0.38 ind. cm^{-2}). After 18 d, when the control cores had reached a steady state, we measured photosynthetic parameters in ungrazed und grazed biofilms using the Imaging Pulse Amplitude Modulated Fluorometer (Imaging PAM, Walz). Benthic algal biomass was measured as maximum fluorescence (F_m) after 15 min of dark adaptation of the biofilms (Kromkamp et al. 1998, Barranguet & Kromkamp 2000). There was a good correlation between the F_m values and the chl *a* concentration (mg C m^{-2}; Appendix 1); therefore, we converted the F_m values into chl *a* concentration. Fluorescence measurements were taken during the low-tide cycle. Diatoms in the laboratory did not

show their natural migratory rhythm; therefore, the time of these measurements during the cycle did not influence the fluorescence signal. Following the F_m measurements, electron transport rate (ETR) measurements were carried out by exposing the biofilms to 10 different photon flux levels, ranging from 0 to 702 µmol m^{-2} s^{-1}. These ETR curves were fitted according to Webb et al. (1974), using the least squares method. In this method, the maximum rate of ETR, the initial slope and the light saturation parameter were calculated to estimate the photosynthetic productivity (mg C m^{-2} d^{-1}) of these biofilms according to Barranguet & Kromkamp (2000). Biomass-specific primary production was calculated by dividing the production (mg C m^{-2} d^{-1}) by the chl *a* concentration (mg C m^{-2}).

Statistical analysis

Field collection

The field data were analyzed using a paired *t*-test (2-tailed) to indicate significant differences in benthic algal biomass, *Corophium volutator* abundance, *Hydrobia ulvae* abundance or total macrofauna abundance on hummocks compared with adjacent hollows.

Laboratory experiments

The influence of benthic algal biomass and landscape morphology on *Corophium volutator* or *Hydrobia ulvae* abundance was analyzed using a 2-way ANOVA. Here, we tested for interactive effects of the fixed factors of food abundance (present or absent) and landscape morphology (hummock, hollow, flat). To overcome the problem of pseudoreplication, we used tank as a random categorical predictor. The data were checked for normality and homogeneity of variance; appropriate transformation was applied if these criteria were not met (Zar 1999).

Grazing effects

In the laboratory experiment, we analyzed the effects of grazing on benthic algal biomass, carbon production and biomass-specific production using linear regression. For all statistical analyses, we used R (www.R-project. org) significance levels were always set at p < 0.05.

RESULTS

Field observations

Benthic algal biomass was 4 times higher on the hummocks compared to the hollows (Fig. 1A, Table 1). We observed no effects of the benthic algal food abundance on macrofauna distribution, as total macrofaunal, *Corophium volutator* and *Hydrobia ulvae* densities were not significantly different between benthic algal-covered hummocks or almost bare hollows in either year (Fig. 1B–D, Table 1).

Laboratory experiments

We tested whether *Hydrobia ulvae* or *Corophium volutator* preferred specific landscape positions (hummock, hollow or flat) or whether they were generally attracted to food-enriched patches (p < 0.01). These experiments demonstrated the aggregation of both species in enriched food patches where they showed at least doubled abundances (Fig. 2, Table 2). Landscape morphology did not affect the distribution of *C. volutator* or *H. ulvae* (Fig. 2B).
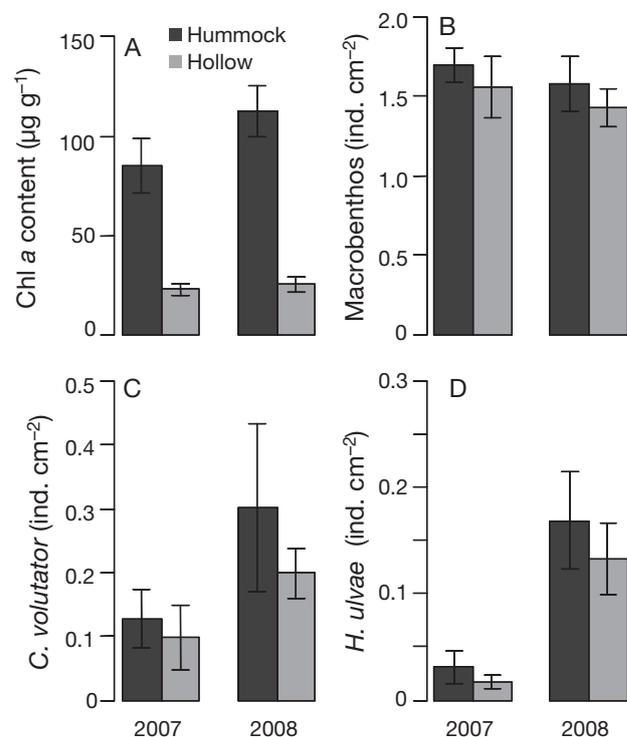

Fig. 1. Field measurements of densities of (A) benthic microalgae biomass, (B) total macrofauna, (C) *Corophium volutator* and (D) *Hydrobia ulvae* expressed as individuals per cm^2. Black and grey bars indicate abundances on hummocks and in hollows, respectively. Means ± SE

Table 1. Paired *t*-test for the field data on benthic algal biomass, and abundances of *Corophium volutator*, *Hydrobia ulvae*, and total macrofauna in April 2007 and 2008 tested for the influence of landscape morphology (hummocks and hollows)

Parameter	Year	Landscape morphology		
		t	df	p
Benthic algal biomass	2007	4.37	9	<0.01
	2008	6.01	9	<0.001
Total macrofauna abundance	2007	0.39	6	0.70
	2008	0.63	5	0.55
C. volutator abundance	2007	0.76	6	0.48
	2008	0.78	5	0.46
H. ulvae abundance	2007	0.79	5	0.46
	2008	0.63	5	0.55

However, in the presence or absence of food, these grazers showed different preferences for landscape morphology, and the interaction term was significant for both *C. volutator* and *H. ulvae* (Table 2).

Grazing effects

Our laboratory grazing experiments revealed an influence of grazers on benthic algal biomass and production. As expected, increasing grazer abundance reduced benthic algal biomass (Fig. 3A, Table 3). At the highest densities, both grazers reduced algal standing stock by 50%. Although similar grazer concentrations showed similar effects on benthic algae removal, primary production was affected differently by species. Carbon production did not
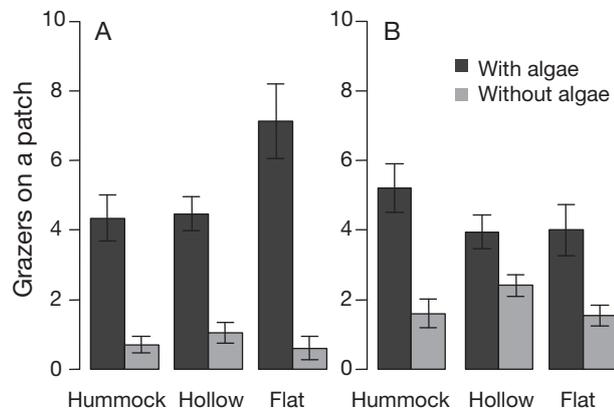

Fig. 2. Abundances of (A) *Hydrobia ulvae* and (B) *Corophium volutator* on food-enriched (black bars) and non-food-enriched patches (grey bars) with the different landscape morphology treatments (hummock, hollow and flat). Means ± SE

Table 2. Two-way ANOVA for influence of landscape morphology, food abundance (benthic algae) and landscape morphology × food abundance on *Corophium volutator* and *Hydrobia ulvae* abundances. ns: not significant (p > 0.05)

Grazer Factor	SS	df	MS	*F*	p
C. volutator					
Food abundance	33.36	1	33.35	71.79	<0.001
Landscape morphology	1.226	2	0.613	1.320	ns
Landscape × Food	6.894	2	3.447	7.419	<0.001
H. ulvae					
Food abundance	66.69	1	66.68	139.98	<0.001
Landscape morphology	0.467	2	0.233	0.491	ns
Landscape × Food	2.883	2	1.441	3.026	<0.001

change with increasing *Corophium volutator* abundance, whereas for *Hydrobia ulvae* a slight but significant decrease was found in primary production with increasing grazer densities (Fig. 3B, Table 3). Biomass-specific production increased similarly with grazing of *C. volutator* and *H. ulvae* (Fig. 3C, Table 3).

DISCUSSION

In this study, we have investigated the effects of macrobenthic herbivores on primary productivity on an intertidal flat. The enhancement of biomass-specific production and resource heterogeneity could explain the spatial distribution of macrobenthic herbivores. Although clear differences in benthic algal biomass were observed, total macrobenthos abundance was similar on diatom-covered hummocks compared with the adjacent relatively bare hollow. Even though the spatial scale of this study is limited to 1 intertidal flat, similar patterns of macrobenthic herbivores surviving at apparent low benthic algal biomass have been observed in similar systems (Montserrat et al. 2008, de Brouwer et al. 2000). A possible explanation for this phenomenon could be the increased biomass-specific production of benthic algae, induced by both *Hydrobia ulvae* and *Corophium volutator* grazing. High primary production rates prevent macrobenthic herbivores from entirely depleting the algae. This compensated production seems to be essential in the apparent insensitivity of benthic herbivores to spatial and temporal variation in the availability of their resources.

Laboratory experiments revealed a clear preference of both *Corophium volutator* and *Hydrobia ulvae* to concentrate in patches of high algal biomass,
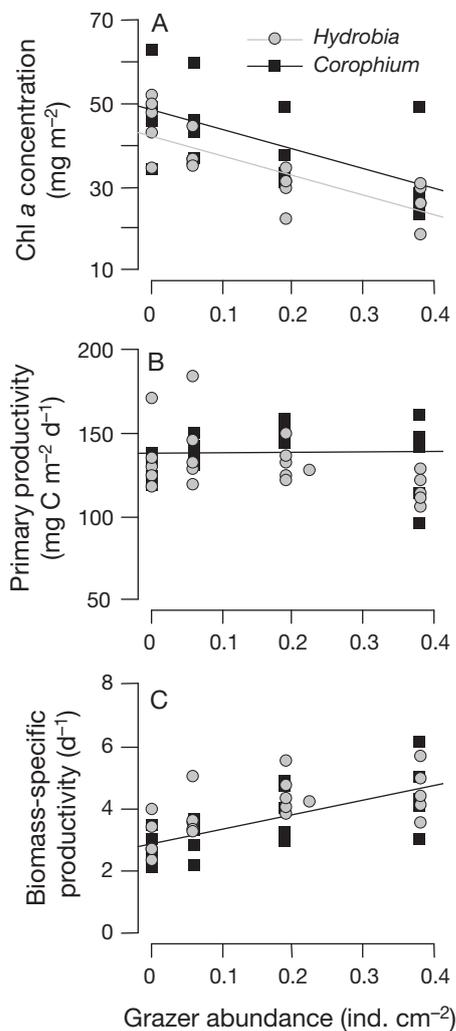
Fig. 3. Laboratory experiment on the grazing effects of *Hydrobia ulvae* (grey lines; circles) and *Corophium voluta- tor* (black lines; squares) on (A) benthic algal biomass (μg chl *a* g⁻¹ sediment), (B) carbon production (g C yr⁻¹) and (C) biomass-specific production (area-specific production/algal biomass)

Table 3. Test statistics and p-values for the linear regression analysis of benthic algal biomass, carbon production and bio-mass-specific production on grazer (*Corophium volutator* and *Hydrobia ulvae*) abundance. ns: not significant ($p > 0.05$)

	a	b	r^2	p
C. volutator				
Benthic algal biomass	152.70	−14.41	0.34	<0.01
Carbon production	137.65	0.4909	0.05	ns
Biomass-specific production	0.9119	0.144	0.41	<0.01
H. ulvae				
Benthic algal biomass	134.51	−15.14	0.61	<0.001
Carbon production	141.26	−5.88	0.17	<0.05
Biomass-specific production	1.070	0.120	0.32	<0.01

even though food concentrations were 5 times higher on top of the hummocks. Field data from a similar intertidal flat showed that benthic macrofauna reached highest densities at intermediate food densi-ties (van der Wal et al. 2008). This suggests that, above a certain minimum benthic algal biomass, macrofauna abundance is relatively independent of algal biomass.

Next to food abundance, we also tested the influ-ence of landscape morphology on the distribution of grazers. We did not find a clear preference of either grazer for hummock, hollows or flat landscapes. However, there was an interaction effect with food availability that indicates that, depending on food availability, both organisms prefer a different land-scape type. Previous studies have shown that macro-fauna preferably occupy hollows (Barros et al. 2004, Ramey et al. 2009). However, these studies were con-ducted in the field, which makes it very difficult to distinguish the direct effects of elevation from other factors such as variations in hydrodynamic forcing, silt content and food availability between crests and troughs (Lanuru et al. 2007). Our controlled experi-ments showed that the prime determinant of species distribution was resource availability and that there were no effects of landscape morphology. We should acknowledge that the field sampling was conducted during low water and during the laboratory ex-periments high water was simulated. The difference in mobility of the species can be important, as it is not known how they behave during inundation in the field. Even though neither species responds to landscape morphology, they can change landscape morphology (Mouritsen et al. 1998, Weerman et al. 2011). Both species have been shown to increase erodibility of the sediment (Daborn et al. 1993, Andersen et al. 2002, Orvain et al. 2004), thereby dis-turbing diatom–sediment feedbacks that are respon-

indicating that food availability was the prime deter-minant of the spatial distribution of these grazers. It is known that both species accumulate in patches with high food abundance (Morrisey 1988a, Lawrie et al. 2000). Mud snails move slower once they have reached high-density food patches (Forbes & Lopez 1986); along with the ability to follow mucus trail of others (Bretz & Dimock 1993), this results in a rapid assembly of large groups on abundant food resour-ces. Previous studies also concluded that *C. volutator* aggregates towards patches with higher food abun-dance (Lawrie et al. 2000, Hamilton et al. 2006). Nev-ertheless, in the field we could not observe prefer-ence for macrofauna between hummocks or hollows

sible for the hummock–hollow landscape structure (Weerman et al. 2011).

The feeding mode of grazers is an important aspect of the effects that herbivores have on plant primary production (Carpenter 1986, McClanahan 1994). The browser *Hydrobia ulvae* and the central place forager *Corophium volutator* have different feeding mechanisms and although the highest grazer abundance we applied in our laboratory study is still quite low compared with peaks in natural abundances, both species reduced diatom biomass in our laboratory experiment (Fig. 3). *H. ulvae* and *C. volutator* are known to have a strong effect on benthic algal biomass even at low grazer concentrations (López-Figueroa 1988, Morrisey 1988b, Gerdol & Hughes 1994a). Both species also enhanced the biomass-specific production, which indicates that the growth of benthic algae was stimulated by grazing. Initially, we expected that *C. volutator* grazed biofilms would enhance production more compared with *H. ulvae* grazed biofilms. *C. volutator* mixes and ventilates the sediment much deeper than *H. ulvae* (Meadows et al. 1990, Orvain et al. 2004). This ventilation may enhance the flux of nutrients to the sediment surface. Because we did not find a difference on biomass-specific productivity between the 2 feeding mechanisms, it is likely that our biofilms were not nutrient limited. Therefore, it is likely that other mechanisms caused the increased biomass-specific productivity, such as changes in taxonomic composition of the benthic algae (Kaehler & Froneman 2002) or shading (Hill et al. 1995). *H. ulvae* is a grazer on sub-dominant species, whereas *C. volutator* consumes mostly dominant taxa, which increases species richness (Hagerthey et al. 2002). Both strategies result in a different benthic algae consortium, which can affect biomass-specific productivity.

The results presented in this study show some interesting similarities with the concept of grazing lawns in terrestrial studies. In grazing lawns, herbivory leads to increased plant production and therefore favours grazing-tolerant species. As a consequence, the independence of herbivores from food biomass is enhanced by the increase of biomass-specific production rate as an indirect effect of grazing. This interaction results in a mosaic of heavily grazed patches surrounded by inaccessible bushes (McNaughton 1984). In our intertidal system, grazing was found to stimulate primary production in a similar way. The dense diatom mats on the hummocks in the patterned state could be equivalents to the terrestrial inaccessible bush vegetation. The hollows could be equivalents to the heavily grazed

parts where biomass-specific production is increased. However, the analogy with terrestrial systems breaks down in the long run. The bioturbation of macrobenthic organisms disrupts the biophysical feedbacks between diatom growth and sedimentation of fine-grained materials, leading to a dramatic collapse of both benthic algal biomass and the resulting landscape morphology on intertidal mudflats (Weerman et al. 2011). This suggests that by their insensitivity to food abundance, at least in the short term, herbivores can have a profound impact on the spatial structure of ecosystems, similar to what is found in terrestrial ecosystems (Iacobelli & Jefferies 1991, Jefferies et al. 1994).

Our results revealed that macrofaunal distribution in a patchy landscape is mainly driven by food availability rather than the topography of the sediment. Initially, we expected that macrofauna species preferred the diatom-covered hummocks over almost bare hollows in the field. Surprisingly, we did not find a significant difference in macrofauna biomass on the diatom-covered hummocks compared with almost bare hollows. We then investigated, in a laboratory experiment, the hypothesis that herbivory stimulated microalgal production, providing a possible explanation of the observation of high macrobenthic biomass at locations with low benthic microalgae biomass. These results, combined with our previous work in this ecosystem (Weerman et al. 2010, 2011), revealed that the interactive effects of resource heterogeneity and grazing-induced enhancement of benthic algae production provided a possible explanation for the spatial distribution of macrobenthic grazers on a patterned intertidal flat.

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Appendix. Relationship between maximal fluorescence F_m and chlorophyll *a* concentration

The relationship between F_m values and chl *a* concentration (mg C m^{-2}) was estimated by analyzing chl *a* content and F_m values of different aged biofilms. These biofilms were grown as described in 'Materials and methods'. Chl *a* samples were taken from these biofilms by using the contact core method, where a metal disc was used to take a sediment sample, ~2 mm deep, for chl *a* concentration analysis. A detailed description of this contact core method can be found in Honeywill et al. (2002). The sediment samples were freeze dried for 48 h. These freeze-dried samples were analyzed in the laboratory to determine chl *a* concentration. Chl *a* content was determined spectrophotometrically after 48 h of 90% acetone extraction (Jeffrey & Humphrey 1975). Data were analyzed using linear regression in R (www.R-project.org).

F_m values were positively correlated with chl *a* concentration in the top 2 mm of the sediment (p < 0.001; Fig. A1). These results are in agreement with similar studies that correlated F_m values measured with a Pulse Amplitude Modulated Fluorometer (PAM) with chl *a* content (Honeywill et al. 2002, Kromkamp et al. 2006).
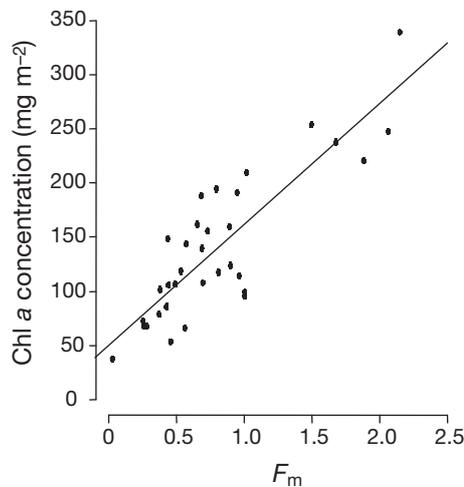

Fig. A1. Relationship between F_m (relative units) and chl *a* concentration (mg; linear regression, p < 0.001, $R^2 = 0.73$)