



Mussel beds are biological power stations on intertidal flats



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ABSTRACT

Intertidal flats are highly productive areas that support large numbers of invertebrates, fish, and birds. Benthic diatoms are essential for the function of tidal flats. They fuel the benthic food web by forming a thin photosynthesizing compartment in the top-layer of the sediment that stretches over the vast sediment flats during low tide. However, the abundance and function of the diatom film is not homogeneously distributed. Recently, we have realized the importance of bivalve reefs for structuring intertidal ecosystems; by creating structures on the intertidal flats they provide habitat, reduce hydrodynamic stress and modify the surrounding sediment conditions, which promote the abundance of associated organisms. Accordingly, field studies show that high chlorophyll *a* concentration in the sediment co-vary with the presence of mussel beds. Here we present conclusive evidence by a manipulative experiment that mussels increase the local biomass of benthic microalgae; and relate this to increasing biomass of microalgae as well as productivity of the biofilm across a nearby mussel bed. Our results show that the ecosystem engineering properties of mussel beds transform them into hot spots for primary production on tidal flats, highlighting the importance of biological control of sedimentary systems.

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1. Introduction

Benthic microalgae are important primary producers in intertidal soft-sediment habitats where they contribute up to 50% of total primary production (Underwood and Kromkamp, 1999). In these highly productive areas that have a great ecological and economical value across the globe (Heip et al., 1995), benthic microalgae fuel the benthic food web by forming extensive biofilms that support a vast array of organisms (Decho, 2000; Stal, 2003; Kromkamp et al., 2006; Markert et al., 2013; Rigolet et al., 2014). Resource availability and grazing play important roles in regulating benthic microalgae (Underwood and Kromkamp, 1999; Weerman et al., 2011a, 2011b). However, on tidal flats, large-scale heterogeneity in the abundance and productivity of benthic microalgae is commonly attributed to abiotic conditions, where increasing hydrodynamic stress decrease benthic microalgae biomass by resuspension of the sediment (de Jonge and van Beusekom, 1995; van

der Wal et al., 2010). Recently, we have recognized the importance of biological control over local hydrodynamic conditions on intertidal flats (van der Zee et al., 2012; Donadi et al., 2013a) and shown that the high abundances of benthic microalgae correlate strongly with the occurrence of mussel beds (Donadi et al., 2013b; Nieuwhof et al., 2016 personal communication).

Organisms that modify their habitats can facilitate complex food-webs by providing structural complexity and improving environmental conditions for many organisms (Olf et al., 2009; Kéfi et al., 2015; van der Zee et al., 2016). On tidal flats, above-ground aggregations of bivalves such as mussels or oysters can build extensive habitat-forming reefs (e.g. mussel beds). These structures are of fundamental importance for biological control of ecosystem structure and properties (Commito et al., 2008; Gutiérrez et al., 2011; van der Zee et al., 2012; Donadi et al., 2013a, 2015). By creating large emergent structures in the otherwise predominantly flat and soft-bottomed landscape, bivalve reefs generate habitat for many other species that live in or on the sediment (van der Zee et al., 2012; Nieuwhof et al., 2015). The reefs physically protect the surface sediment against erosion and resuspension, and furthermore increase organic matter content via

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suspension feeding and biodeposition (Widdows and Brinsley, 2002). The habitat modifying properties and ecosystem effects extend up to several hundred meters around reefs (van der Zee et al., 2012; Donadi et al., 2013a, 2013b, 2015; van de Koppel et al., 2015), which is reflected by a conspicuous increase of benthic microalgae biomass in the vicinity of intertidal mussel beds (Donadi et al., 2013b). Due to these impacts on a large spatial scale, it can be assumed that the interaction between benthic microalgae and intertidal bivalve reefs contribute significantly to coastal production. However, the assumed regulatory importance of bivalve reefs for microalgae biomass is based on observational data and statistical modelling only, while the causal link of (living) bivalves facilitating benthic diatoms have not been extensively examined. Consequently, we lack conclusive empirical evidence of the facilitation effect. In addition, due to limited measurements of actual productivity, we have a poor understanding of how the increased biomass of microalgae (commonly estimated by chlorophyll *a* concentration) around reefs relate to productivity of the system.

In this study, we tested the hypothesis that mussel beds increase the local biomass of benthic microalgae on a tidal flat. First, we showed that the biomass of benthic microalgae was consistently elevated across a mussel bed over several years and related this to higher primary productivity. We then used empirical evidence from a small-scale field experiment to demonstrate that the addition of live mussels to bare plots facilitates benthic microalgae.

2. Material and methods

2.1. Set-up transects

We set up two parallel transects spanning a distance of 1 km each on a tidal flat south of the island Schiermonnikoog (latitude 53.47° N, longitude 6.23° E, Friesland, The Netherlands; Fig. A.1a–b; Table A.1). This tidal flat is a mudflat with varying sediment grain types ranging from fine mud to sand. During low tide, the flat falls completely dry and the tidal range is about 3.5 m. The two transects were 300 m apart and perpendicular to the coast. One transect crossed a *Mytilus edulis* (blue mussel) reef that was ca. 100 m wide and extended for approximately 250 m along the coast; the other one was in a habitat without mussels present. The mussel bed is elevated and exhibits spatial self-organization on two scales: (1) a banded pattern with mussels on top of several meter large hummocks of accumulated sediment and small pools of 1–2 m in diameter, that are void of mussels and retain water during low tide (Liu et al., 2012), and (2) a labyrinth-like banded pattern of small mussel clusters that aggregate on the 5–10 cm scale (van de Koppel et al., 2008), but that changes into a thick homogenous cover of mussels at peak densities on the hummocks. We established the first point of each transect 350 m coastward of the mussel bed (about 500 m from the shore) and placed subsequent points every 50 m in seaward direction up to 100 m behind the mussel bed (last point ca. 1000 m from the shore). The transect points were selected to cover a visible plume of muddy sediment that extended around the mussel bed.

In June 2012, we sampled chlorophyll *a* concentration at six transect points in both transects (–300 m, –200 m, –100 m, 0 m, +100 m, +150 m distance to the mussel bed/the corresponding tidal elevation in the no mussel bed habitat, where negative values mean distances coastward of the mussel bed/the corresponding tidal elevation in the no mussel bed habitat and positive distances seaward of the mussel bed/the corresponding tidal elevation in the no mussel bed habitat). Distance to the mussel bed is hereafter referred to collectively as distance to the mussel bed in both habitats. Sampling was replicated spatially, by including samples 50 m to the right and 50 m to the left of each

transect point (N = 36). In 2015–16, we took chlorophyll *a* and organic matter samples at five similar transect points in both transects (–350 m, –200 m, –100 m, 0 m, +100 m distance to the mussel bed, where negative distances are coastward and positive distances are seaward of the mussel bed), but instead of two spatial replicates we repeated the sampling six times in total (October 2015, October 2016, April 19, 2016, April 29, 2016, May 2016, June 2016). Due to unexpected weather conditions, we could not sample the two last transect points for the no mussel bed habitat in October 2015 (0 m, +100 m) and had to abandon the last sampling point (+100 m) in both habitats in April 2016 (N = 56).

We measured photosynthetic yield of the sediment as proxy for benthic microalgae productivity at two different time points. In June 2012 and June 2016, we took triplicate samples in five transect points per habitat.

2.2. Set-up field experiment

We designed an experiment to analyze the local effects of mussel presence on benthic microalgae in small-scale plots of 0.5 m² (Fig. A.2a). Thus, we did not simulate the hierarchical spatial structure of intertidal mussel beds (as described above; see also Snover and Commito, 1998; Kostylev and Erlandsson, 2001; Commito et al., 2006), or their long-range effects (Donadi et al., 2013a, 2013b; van de Koppel et al., 2015). Our experiment allowed us to assess the effect of mussels at the plot scale, avoiding possible confounding effects that different environmental factors could have when including multiple spatial scales in the experimental design (Wiens, 1989; Commito et al., 2006).

We set up the mussel facilitation experiment in three different sites on the same tidal flat as the transects, south of Schiermonnikoog island (Fig. A.1a, c). The three sites were placed at the same tidal elevation, meaning that all plots fell dry at the same time during low tide, but along a gradient of influence by mussel beds which also means that they differ in sediment erosion, organic matter content and infauna community composition (van der Zee et al., 2012; Donadi et al., 2013b, 2015). Site 1 was placed in the transect without a mussel bed; Site 2 coastward of the mussel bed included in the mussel bed transect (300 m to the east of Site 1); and Site 3 coastward of another larger mussel bed that is 100–200 m wide and extends almost 1000 m along the coast (2000 m east of Site 1; Fig. A.1a).

In each site, we tested the effects of adding mussels on benthic microalgae biomass. For this, we prepared four different treatments with three replicates in each site, leading to 36 experimental units (plots) in total. Each individual plot had an area of 0.25 m² (plot dimension: 0.5 m by 0.5 m) and each corner of the plot area was marked with a plastic pole. The poles were 66 cm long and inserted about 30 cm deep into the sediment. The distance between the plots was 5 m on each side.

The experiment combined two mussel addition treatments and two controls in a factorial design with: a fenced control (FC; Fig. A.2b), a fenced mussel addition treatment (FM; Fig. A.2c), a semi-caged control (CC; Fig. A.2d), and a semi-caged mussel addition treatment (CM; Fig. A.2e). For the two mussel addition treatments (FM, CM), we collected live *Mytilus edulis* and distributed them evenly in the plots so that the surface of the entire plot was covered. After the addition, the mussels organized themselves in the plots overnight by creating a spatial pattern of 5–10 cm banded aggregations (Fig. A.2e). Placing experiments on an intertidal flat may lead to critical artifacts because of changes to water flow caused by equipment rather than treatments, but also because of changed predation rates since the experiment may hinder or attract natural predators. This is critical when placing bivalves on the tidal flat, since they become islands of food for both birds and crabs that

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