Non-trophic Interactions Control Benthic Producers on Intertidal Flats

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ABSTRACT

The importance of positive effects of ecosystem engineers on associated communities is predicted to increase with environmental stress. However, incorporating such non-trophic interactions into ecological theory is not trivial because facilitation of associated species is conditional on both the type of engineer and the type of abiotic stress. We tested the influence of two allogenic ecosystem engineers (lugworms, *Arenicola marina* L. and cockles, *Cerastoderma edule* L.) on the main primary producers (microphytobenthos) of the tidal flats, under different abiotic stresses controlled by reefs of blue mussels (*Mytilus edulis* L.). We added 25,000 cockles or 2,000 lugworms to 5 × 5 m plots, both in a muddy site with high sedimentation rates located coastward of a mussel bed, and in a sandy site without mussels and characterized by high hydrodynamic stress. After a year, cockles increased algal biomass in the sandy area, but not in the mussel bed site, where high values were measured in all plots. However, lugworms did not affect algal biomass in any of the sites. Field measurements suggest that cockles outweighed negative effects of water currents in the site without mussels by locally increasing sediment stability, whereas mussels overruled the effects of cockles in the wake of the reefs through hydrodynamic stress alleviation and/or biodeposition. Our results suggest that non-trophic interactions by ecosystem engineering bivalves control primary production of intertidal areas, and that the sediment-stabilizing effect of cockles plays a crucial role where the overruling effects of mussel beds are not present.

Key words: ecosystem engineering; facilitation; hydrodynamic stress; microphytobenthos; *Cerastoderma edule*; *Arenicola marina*; *Mytilus edulis*; Wadden Sea.

INTRODUCTION

Ecosystem engineers can facilitate the survival of other species in hostile environments by modifying habitat conditions (Jones and others 1994; Bruno and Bertness 2001; Crain and Bertness 2006). The relative importance of facilitation is predicted to increase with environmental stress (Bertness and

Callaway 1994; Bruno and others 2003) and accordingly, studies from both marine and terrestrial ecosystems show that dominant interactions among species can shift from negative or neutral to positive when harshness of abiotic conditions increases (Callaway 1997; Callaway and Walker 1997; Bulleri and others 2011). Most of these studies have focused on foundation species, species which create and modify habitats through their own physical structure (Dayton 1972; Bertness and Callaway 1994; Crain and Bertness 2005). However, important facilitative effects in stressed environments also come from species that modify the environment through their activity rather than their physical shape, the so-called allogenic ecosystem engineers (Jones and others 1994; Reise 2002; Volkenborn and others 2007). Despite the broad literature on ecosystem engineers, experimental evidence of the relative importance of allogenic ecosystem engineering under different stress intensities is still scarce (but see Daleo and Iribarne 2009).

In the last decade, there has been an increased research effort to include habitat-mediated and other non-trophic interactions into ecological theory by developing ecological network analyses away from the traditional food-web studies that only include predator–prey interactions (Reise 2002; Bruno and others 2003; Olff and others 2009; Kefi and others 2012). Yet, understanding consequences of ecosystem engineering in natural ecosystems is not trivial, because facilitative effects in stressed environments vary with the engineering species under study and the nature of the stress factor involved (Choler and others 2001; Kawai and Tokeshi 2007; Maestre and others 2009). Ecosystems are often subjected to different types of abiotic stress and host engineering species that modify habitat conditions in contrasting ways. Therefore, facilitative effects of engineering species on local communities may alternate predictably along different stress gradients (Figure 1A). It is thus important to consider multiple ecosystem engineers and multiple abiotic stresses to better understand the importance of facilitation as a structuring force in natural communities.

In this study, we investigated the effects of two allogenic ecosystem engineers (lugworm: *Arenicola marina*, and common cockle: *Cerastoderma edule*) on microphytobenthos, under different abiotic stresses controlled by reefs of blue mussels (*Mytilus edulis*). Blue mussels form dense epibenthic reefs that enhance sedimentation of fine suspended matter by reducing water current velocities and by
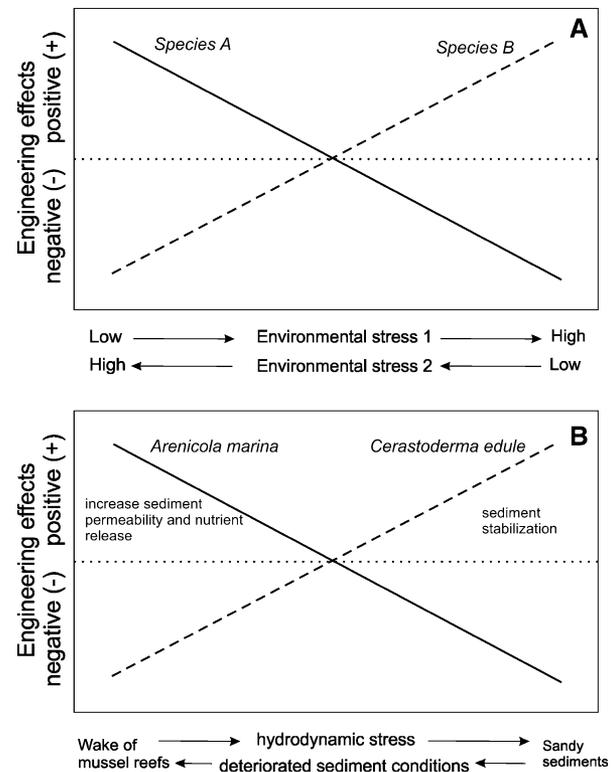

Figure 1. **A** Conceptual model illustrating a scenario where two ecosystem engineers (species A and species B) have opposite effects on the surrounding species under different abiotic stresses (stress 1 and stress 2) which covary along an environmental gradient. **B** The same conceptual model is used to illustrate our hypotheses: cockles (*C. edule*) have positive effects on microphytobenthos through sediment stabilization under high hydrodynamic stress, but not in the wake of mussel reefs, where low current velocities and biodeposition lead to deteriorated sediment conditions (low sediment permeability and rate of solute exchange). On the opposite, lugworms (*A. marina*) have positive effects on microphytobenthos under deteriorated sediment conditions by increasing sediment permeability and nutrient availability, but the effects are negative in high-energy environments.

biodeposition, thus creating a plume of fine cohesive sediments coastward of the reefs (Graf and Rosenberg 1997; van der Zee and others 2012; Donadi and others 2013). Previous studies showed that microphytobenthos biomass decreases with wave energy, which induces resuspension and subsequent transport by currents (de Jonge and van Beusekom 1995; van der Wal and others 2010), and is positively associated with fine sediments where both grazer pressure and resuspension are generally lower (de Jong and de Jonge 1995; Herman and others 2001). However, the

settlement of large amounts of fine particles can result in hypoxic sediments, with very low sediment permeability and rate of solute exchange (Winterwerp and Van Kesteren 2004). Thus, the presence or absence of mussel reefs exposes coastal soft-sediment habitats to different types of stresses: in areas with no mussel reefs high hydrodynamic energy triggers sediment erosion, whereas in the lee of mussel reefs low hydrodynamic energy and biodeposition cause deteriorated sediment conditions.

Cockles and lugworms are dominant species on tidal flats with opposite engineering effects on sediment stability. Cockles (*C. edule*) are filter-feeding bivalves that can decrease sediment grain size and increase sediment stability through the production of mucus-rich feces and pseudofeces (Andersen and others 2010). Lugworms are well-known sediment de-stabilizers which promote erosion of fine material through bioturbation (Volkenborn and others 2007). Furthermore, by flushing their burrows (bioirrigation) lugworms enhance the exchange of solutes between sediments and overlying water and influence the rates of benthic metabolism by increasing oxygen penetration in the substrata (Banta and others 1999). Recent studies have shown that positive effects on primary producers due to nutrient release by macrofaunal bioturbation can offset negative effects of grazing and subduction, especially in cohesive sediments where diffusion of solutes is slow (Lohrer and others 2004, 2010; Thrush and others 2006; Needham and others 2011).

To investigate if cockles and lugworms have contrasting effects on benthic primary producers and if these effects depend on hydrodynamic and sediment conditions, we performed a manipulative field experiment. In this experiment, we created a total of forty-eight 5 × 5 m plots with high densities of cockles, high densities of lugworms, or no manipulation (control). The experimental treatments were replicated in a muddy site sheltered from the tidal currents by a large mussel bed and in a sandy area without mussels on a tidal flat in the Wadden Sea. We hypothesize that at high levels of hydrodynamic stress (in the sandy site without mussels) cockles enhance algal biomass by increasing sediment stability, whereas lugworms hinder microphytobenthos growth by increasing sediment erosion. In deteriorated sediment conditions (in the wake of mussel reefs), we expect lugworms to increase algal abundances by increasing sediment permeability and nutrient availability and cockles to have negative effects on microphytobenthos through biodeposition (Figure 1B).

METHODS

Field Experiments

The study was conducted on the intertidal flats south of the island of Schiermonnikoog (Dutch Wadden Sea). On these tidal flats, cockles and lugworms commonly co-occur at the local scale (<0.1 m), whereas mussels typically form large (>1 ha) epibenthic reefs. Pilot surveys conducted in 2009 in the study area showed relatively stable densities of 20–40 lugworms per m^2 and a patchy distribution of cockles, with abundances ranging from 0 to several hundreds individuals per m^2. These values are in agreement with natural occurring densities of cockles and lugworms typically found on the tidal flats of the Wadden Sea (Beukema and Devlas 1979; Jensen 1992). To evaluate the effects of these species on microphytobenthos, a large-scale experiment was set up in May 2010 in two selected sites: the first one located at about 350 m coastward of a large mussel bed (53°28′2″N, 6°10′59″E) and characterized by fine sediment (muddy) and lower current velocities; the second one at 500 m from the first site, at the same tidal elevation (53°28′7″N, 6°11′33″E), and characterized by coarser sediment (sandy) and higher current velocities. At each site, twenty-four 5 × 5 m experimental plots grouped in two blocks were randomly assigned to one of the following treatments: (i) addition of high densities of cockles (1,000 per m^2); (ii) addition of high densities of lugworms (80 per m^2); and (iii) no addition (control). Treatment densities of cockles and lugworms were chosen to mimic maximum observed densities in the study area. Cockles were collected from a nearby intertidal flat by professional fishermen through hand-raking and were 2–4 years old (mean mm length ± SE = 32.40 ± 0.78, $n = 15$). Lugworms were harvested by a commercial lugworm fishery company (Arenicola BV, Oosterend, The Netherlands) from an intertidal flat in the Western Wadden Sea (mean g. dry weight ± SE = 0.97 ± 0.12, $n = 20$). Persistence of transplanted specimens was monitored throughout the experiment by periodic counts of cockles (one replicate per plot) and lugworm fecal casts (three replicates per plot) within a 0.5 × 0.5 m frame. Abundances of both cockles and lugworms were always significantly higher in enriched plots compared to the other treatments, the only exception being lugworm abundances in the mussel bed site in July 2011, when there was no difference between the treatments (Appendix A in Electronic supplementary material).

To estimate microphytobenthos biomass in the experimental plots, we analyzed chlorophyll *a* content of the sediment, a commonly used proxy for algal biomass. Two replicates per plot of the upper sediment layer (2 mm depth) were collected by means of cut-off disposable syringes (2.4 cm internal diameter) in May, June, and July 2011. Samples from all plots of both sites were taken within a few hours on the same day and stored in a dark and cold place. After freeze-drying the sediment, chlorophyll *a* content was determined by acetone extraction following Jeffrey and Humphrey ([1975](#)).

Hydrodynamic stress was estimated in the experimental plots in June 2011 as % weight loss of plaster dissolution cylinders. Laboratory experiments showed that the dissolution rate of plaster is a good (relative) measurement of water flow speed (Thompson and Glenn [1994](#)). However, under field conditions the loss of plaster may also indicate the magnitude of the abrasion effect by sediment suspended in the water column, and is therefore a general proxy for the erosive power of the currents. Dissolution cylinders (6.3 cm long; 2.4 cm diameter) were molded with model plaster (Knauf Modelgips, Knauf B.V., Utrecht, The Netherlands), dried, weighed (mean g. dry weight $\pm$ SE = 41.22 $\pm$ 1.54, $n = 48$) and placed in the center of each plot for four tidal cycles (about 46 h), after which they were retrieved and dried until constant weight. To account for differences in the exposure time between sites, plaster weight loss values were divided by the average tidal submersion time of each site (mean minutes $\Delta t \pm$ SE = 406 $\pm$ 4 coastward of the mussel bed; $\Delta t \pm$ SE = 370 $\pm$ 6 in the sandy site, $n = 3$), estimated in June 2011 by means of Sensus Ultra pressure loggers (Reefnet, Missisauga, Canada).

To investigate effects of ecosystem engineers on sediment accumulation and erosion, we assessed changes in bed level using a Trimble Spectra Precision LL500 Laser Level (Trimble, California, USA). At each site, measurements were calibrated against fixed reference metal poles. Five replicates were randomly taken in all plots in July 2010 and July 2011, and averages per plot were calculated. The difference of the averages between the 2 years was computed to evaluate bed level change over time (from here on *bed level change*), whereas the averages of July 2011 were used as a measurement of relative bed level at the time of the experimentation (from here on *relative bed level height*). Measurements of erodibility estimated in the sandy sites in September 2011 by means of a cohesive strength meter (CSM, Partrac, Glasgow, UK) following Tolhurst and others ([1999](#)) showed a positive correlation between critical erodibility stress (CSM jet pressure at which sediment erosion occurs) and relative bed level height ($r = 0.51$, $P = 0.018$, $n = 21$), and between critical erodibility stress and bed level change ($r = 0.65$, $P = 0.001$, $n = 21$). These results, combined with the evidence that differences in relative bed level height were due to sediment accumulation or erosion in the experimental plots rather than to the site topography (see ''[Results](#)''), suggest that bed level height can be reasonably considered as a good proxy for sediment stabilization or erosion.

Finally, to investigate sediment properties, two sediment samples were taken from each plot in June and in July 2011. Sediment was collected to a depth of 5 cm using a PVC corer (3 cm internal diameter) and average organic matter content was estimated from oven-dried (48 h, 75°C) samples as loss on ignition (LOI; 4 h, 550°C). Silt content of sediment samples (fraction < 63 μm) collected in July 2011 was determined with a Malvern particle size analyzer (Malvern Particle Sizer 2000, United Kingdom) after freeze-drying the sediment samples. The concentration of ammonium, which is one of main limiting nutrients for microphytobenthos and a proxy for anaerobic conditions, was measured from pore-water samples collected in July 2011 in airtight 50 ml syringes using ceramic soil moisture samplers (Eijkelkamp Agrisearch Equipment, The Netherlands). Average pore-water reduction–oxidation potential (redox) was estimated from two samples collected in each plot in March 2011 and September 2011 with a Sentix ORP probe connected to a Multi 340i voltmeter (WTW, Germany).

Data Analysis

Effects of cockles, lugworms, and mussels on all measured parameters were evaluated with statistical linear models including the fixed factors engineer addition (three levels: cockle addition, lugworm addition, no addition), site (two levels: mussel bed site, sandy site), and their interaction. Effects on average chlorophyll *a* content ($n = 6$), average bed level change ($n = 5$), and average redox potential ($n = 4$) were assessed by general linear models, whereas effects on % plaster weight loss, silt content, average % organic matter content ($n = 2$), and ammonium concentration were estimated by generalized least squares (GLS) to account for heteroscedasticity (Zuur and others [2009](#)). Independence of observations taken within the same block was investigated by comparing models with and without a residual compound

symmetry correlation structure (Zuur and others 2009). The addition of a correlation structure led to a significant improvement only in the analysis of % silt content, therefore mixed-effect models were used to assess the significance of fixed factors. Treatment effects on relative bed level height were assessed separately per each site, as measurements were calibrated against two different reference poles (see above). A linear model was used for this analysis including engineer addition and block as fixed factors, as the number of levels for block in the site-separated analysis did not allow us to include it as a random factor. The normality assumption was checked with the Shapiro-Wilks test ($P = 0.05$) and homoscedasticity was assessed with the Bartlett test ($P = 0.05$) and by comparing GLS models with or without a residual variance structure (Zuur and others 2009). Independence, normality, and homogeneity of variance of residuals were further confirmed by graphical validation of the final models. When needed, multiple comparisons to identify the source of any significant differences were performed using Fisher's LSD post hoc test.

To investigate the relationship among primary producer biomass, hydrodynamic stress and sediment accumulation, correlations between chlorophyll *a* content and plaster weight loss, and between chlorophyll *a* content and relative bed level height were calculated using Pearson correlation coefficient and Spearman's rank correlation coefficient for parametric, and non-parametric data, respectively. When the Pearson correlation coefficient was significant, the parameters of the functional relationship between variables were estimated using standard major axis regression (SMA), as both variables were random and measured with error (Legendre and Legendre 1998). All statistical calculations were carried out in R (CRAN, R: A language and environment for statistical computing. 2010. R Foundation for Statistical computing. Vienna, Austria).

RESULTS

We observed a reduction of the erosive power of the water currents coastward of the mussel bed compared to the sandy area, as indicated by lower plaster weight loss in the lee of the reefs (Site effect: Likelihood Ratio test statistic = 20.23, $P < 0.001$, Figure 2A). Bed level measurements revealed that cockles and lugworms influenced sediment stability in opposite directions, but only in the absence of mussel reefs (interaction effect between engineer addition and site, Table 1). Cockles significantly favored sediment
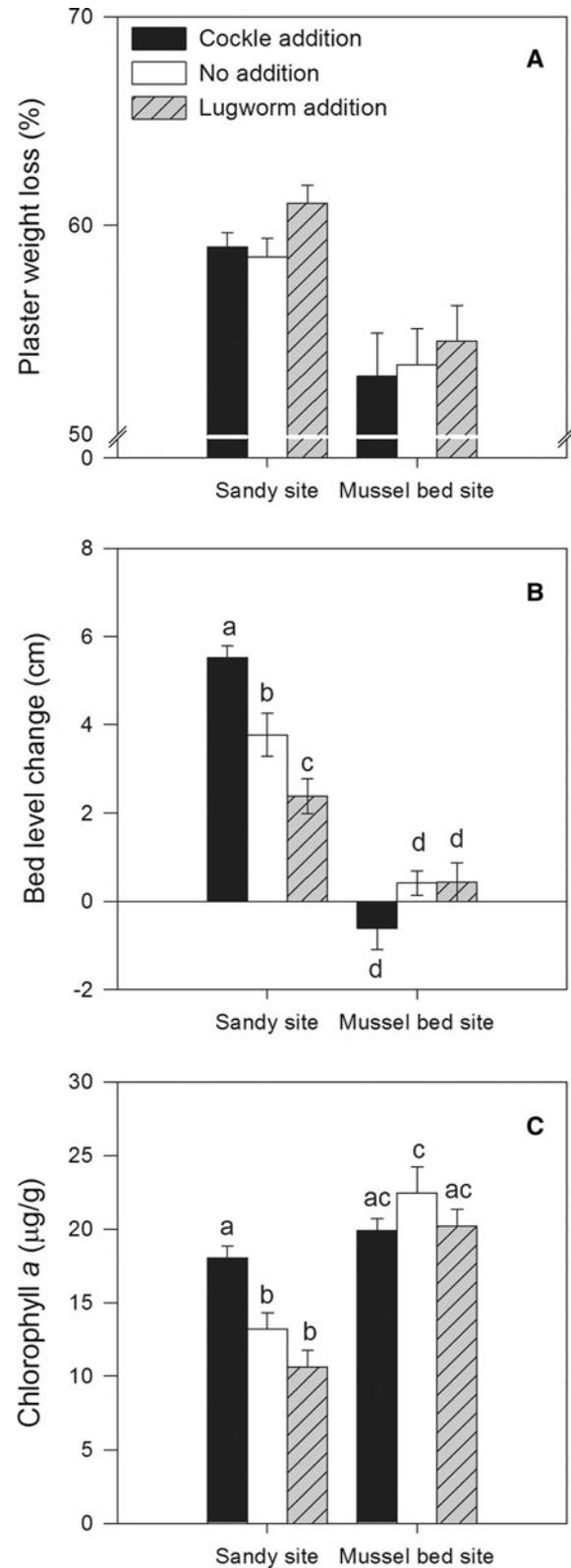

Figure 2. **A** Plaster weight loss, **B** bed level change, and **C** chlorophyll *a* content measured in cockle-addition, lugworm-addition, and no-addition plots in a sandy site and coastward of a mussel bed. Mean ± SE ($n = 8$).

Table 1. Statistical Results of Linear Models Examining Effects of Mussel Bed Vicinity (Site) and High Densities of Cockles and Lugworms (Engineer Addition) on Chlorophyll *a* Content and Bed Level Change

Source of variation	Df	Bed level change			Chorophyll *a*			Redox potential		
		MS	F	P	MS	F	P	MS	F	P
Site	1	173.96	134.85	**<0.001**	569.54	51.87	**<0.001**	3464	41.641	**<0.001**
Engineer addition	2	4.50	3.49	**0.039**	53.30	4.85	**0.012**	68	0.812	0.451
Site * engineer addition	2	18.11	14.03	**0.002**	75.89	6.91	**0.002**	7	0.084	0.920
Residuals	42	1.29			10.98			83		

Significant P values are highlighted in bold.
Significance level (α) was set at 0.05 of probability.

Table 2. Statistical Results of Linear Models Examining Effects of High Densities of Cockles and Lugworms (Engineer Addition) and Block on Relative Bed Level Height in the Sandy Site and in the Mussel Bed Site

Source of variation	Df	Relative bed level height Sandy site			Relative bed level height Mussel bed site		
		MS	F	P	MS	F	P
Engineer addition	2	41.89	28.41	**<0.001**	0.08	0.10	0.905
Block	1	1.33	0.90	0.353	17.95	20.18	**<0.001**
Block * engineer addition	2	4.08	2.76	0.089	0.83	0.93	0.411
Residuals	18	1.47			0.89		

Significant P values are highlighted in bold.
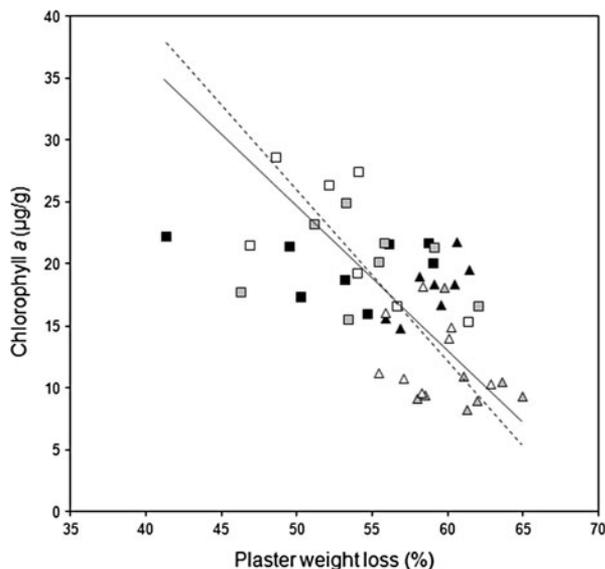*Significance level (α) was set at 0.05 of probability.*

Figure 3. Scatter plot of chlorophyll *a* content and plaster weight loss measured in cockle-addition, lugworm-addition, and no-addition plots in a sandy site and coastward of a mussel bed (*n* = 47). *Black symbols* Cockle-addition plots, *gray symbols* lugworm-addition plots, and *white symbols* no-addition plots. *Squares* Plots from the mussel bed site, *triangles* plots from the sandy site. SMA regression lines indicate significant correlations in the lugworm-addition (*solid line*) and no-addition plots (*dashed line*).

accumulation in the sandy area compared to lugworm-addition plots (Fisher LSD post hoc test; $P < 0.001$) and no-addition plots (Fisher LSD post hoc test; $P = 0.003$), whereas lugworms enhanced sediment erosion (Fisher LSD post hoc test; lugworm addition vs cockle addition in sandy site, $P < 0.001$; lugworm addition vs no addition in sandy site, $P = 0.019$; Figure 2B). This resulted in a more elevated substrate in the cockle-addition plots: on average 4.6 ± 1.4 cm (mean $\pm$ SD; $n = 8$; Fisher LSD post hoc test; $P < 0.001$) and 2.7 ± 1.7 cm (mean $\pm$ SD; $n = 8$; Fisher LSD post hoc test; $P < 0.001$) higher than in the lugworm-addition and no-addition plots, respectively (Table 2).

We found a significant effect of the interaction between engineer addition and site (Table 1) on chlorophyll *a*: in the sandy area, cockle addition resulted in a 70 and 37% higher microphytobenthos growth compared to lugworm-addition (Fisher LSD post hoc test; $P < 0.001$) and no-addition plots (Fisher LSD post hoc test; $P = 0.005$), respectively, whereas lugworms did not significantly decrease algal biomass (Figure 2C). In the muddy site in the wake of the mussel bed, chlorophyll *a* content was overall 49% higher than in the sandy site, but we did not detect any effects of either cockles or lugworms (Figure 2C; Table 1).
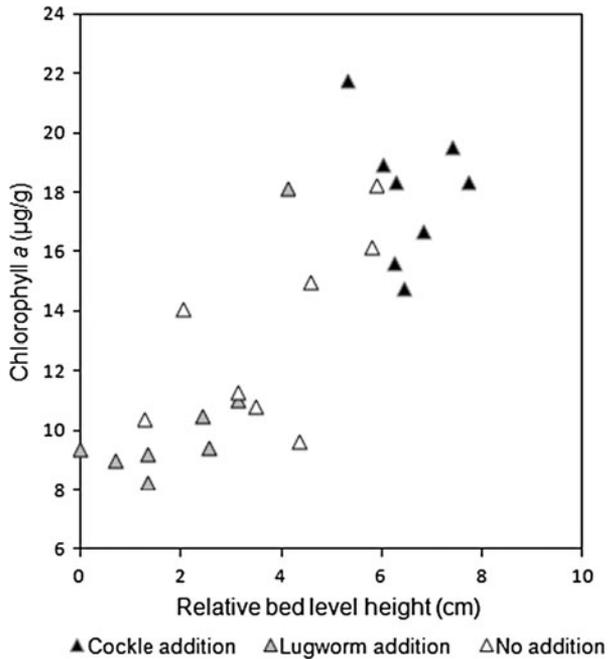
Figure 4. Scatter plot of chlorophyll *a* content and relative bed level height measured in cockle-addition, lugworm-addition, and no-addition plots in the sandy site (*n* = 24). Bed level measurements are relative values to the minimum, which was set as zero. *Black triangles* Cockle-addition plots, *gray triangles* lugworm-addition plots, and *white triangles* no-addition plots.

Accordingly, we found an overall negative correlation between chlorophyll *a* and plaster weight loss ($r_s = -0.54$, $P < 0.001$, $n = 47$), supporting the idea that erosion by currents limits microphytobenthic growth in the intertidal flats where we conducted our study. However, although hydrodynamic stress and sediment transport negatively affected microphytobenthos growth in a similar way in the lugworm-enriched plots ($r = -0.62$, $n = 16$, $P = 0.011$, SMA slope = -1.16, 95% confidence interval: -1.80 to -0.75) and in the no-addition plots ($r = -0.71$, $n = 15$, $P = 0.003$, SMA slope = -1.38, 95% confidence interval: -2.07 to -0.92), such a negative relationship was not detected in the cockle-addition plots ($r_s = 0.01$, $n = 16$, $P = 0.969$; Figure 3). In the sandy area, higher values of algal biomass were found in more elevated plots, as shown by the positive correlation between chlorophyll *a* content and relative bed level height ($r_s = 0.83$, $n = 24$, $P < 0.001$; Figure 4).

Contrary to our expectations, cockle and lugworm addition did not have any significant effect on organic matter, silt content, pore-water ammonium concentration, and redox potential. Yet, organic matter and silt content were at least three and four times higher, respectively, in the mussel bed area than in the sandy

site (site effect on organic matter content: likelihood ratio test statistic = 83.34, $P < 0.001$; Appendix B in Electronic supplementary material; site effect on silt content: likelihood ratio test statistic = 19.03, $P < 0.001$; Appendix B in Electronic supplementary material), pointing to accumulation of biodeposits in the wake of the mussel reefs. Ammonium concentration was higher in the mussel bed site than in the sandy site, although this difference was only marginally significant (site effect: likelihood ratio test statistic = 3.80, $P = 0.051$, Appendix B in Electronic supplementary material). Also, we found a significant effect of site on pore-water redox potential, with lower values coastward of the mussel reefs suggesting oxygen depletion in the mussel biodeposition plume (Table 1; Appendix B in Electronic supplementary material).

DISCUSSION

We demonstrate that cockles facilitate benthic primary producers on intertidal flats by increasing sediment stability, but this effect is conditional on hydrodynamic and sediment conditions. At high levels of hydrodynamic stress, high densities of cockles accumulated sediment and thereby compensated for the negative effects of waves and currents on microphytobenthos, leading to increased chlorophyll *a* content in the sediment. Cockles have been primarily described as a bioturbating species, which increases sediment disturbance and erodibility (Flach 1996; Neumeier and others 2006; Ciutat and others 2007; Montserrat and others 2009). We are the first to show through a large-scale manipulation that high densities of cockles can actually enhance sediment stability (as recently suggested by Andersen and others 2010) and that this in turn favors primary producers. At lower hydrodynamic stress in the wake of a mussel bed, cockles and lugworms neither affected sediment parameters nor algal biomass. In the lugworm-addition plots, this might be due to low lugworm abundances measured at the end of the experimental period. However, in the cockle-addition plots high cockle abundances rather point to the overwhelming effects of the mussel bed, which likely enhanced algal biomass by a combination of hydrodynamic stress alleviation and biodeposition. Hence, the vicinity of a mussel bed shifted the balance between abiotic and biotic control, overriding engineering effects of cockles. In fact, interactions between primary producers and cockles shifted from facilitative far from the mussel bed to neutral coastward of the mussel bed, where environmental conditions were more benign. Thus, our large-scale

manipulation demonstrates that not only foundation species but also allogenic ecosystem engineers play an increasingly important role at higher intensities of environmental stress. As the intertidal flats of the Wadden Sea host relatively few mussel beds if compared with historical data, the persistence of cockle populations likely contributes significantly to maintain a high level of productivity in these habitats. In light of this consideration, we suggest that the simultaneous exploitation of mussels and cockles in the Wadden Sea and the consequential decline of their abundance over the last half century (Lotze and others 2005; Kraan and others 2011) might have contributed to a decrease in benthic primary production (Eriksson and others 2010). Because benthic primary producers (such as algae and seagrasses) play an important role as sediment stabilizers (Widdows and Brinsley 2002; van der Heide and others 2007) and constitute an essential source of food for many birds and benthic species (for example, Nacken and Reise 2000; Lebreton and others 2011), their loss may entail severe consequences for the habitat and for different trophic levels of coastal ecosystems.

Cockles facilitated microphytobenthos by stabilizing the sediment at hydrodynamic conditions where sediment erosion otherwise limited microphytobenthic growth. Previous evidence demonstrated that waves and currents can drastically reduce microphytobenthos biomass through sediment resuspension and subsequent transport (de Jonge and van Beusekom 1995; van der Wal and others 2010). Accordingly, we observed a negative correlation between plaster weight loss and chlorophyll *a* content, where high chlorophyll *a* values corresponded to low erosive power of water currents coastward of the mussel bed. However, such a relationship was not significant on cockle-addition plots, demonstrating that high densities of cockles overruled hydrodynamic control of the primary producer community. Production of feces and mucus by high densities of cockles can reduce vulnerability to erosion (Ciutat and others 2006), and might have promoted sediment accretion in the cockle-addition plots in the sandy area, as suggested by the positive correlation between critical erosion threshold and bed level change. Alternatively, enhanced nutrient availability (Swanberg 1991) and/or reduced sediment resuspension due to cockle biodeposition might have favored diatom growth, which in turn further decreased vulnerability to erosion and promoted sediment accumulation (Widdows and others 2004; Andersen and others 2010). Also, protruding shells of cockles from the sediment might have slowed down current velocity, causing local sediment accretion. Although our experiments clearly show

that cockles can positively affect sediment stability, they do not allow the separation of structural and functional effects of cockles, and further experiments are needed to unravel the mechanisms underlying facilitation of microphytobenthos by cockle beds.

Our study suggests that cockles trigger positive feedbacks among sediment accumulation, microphytobenthos growth, and the cockles themselves. Positive feedbacks are essential for high benthic primary production in intertidal soft-bottom ecosystems (Van De Koppel and others 2001). Indeed, productive tidal flats might persist through positive feedbacks (1) between microphytobenthos growth and sediment accumulation: low water content in locally elevated areas on tidal flats allows the persistence of colloidal carbohydrates, water-soluble diatom excretions which bind sediment particles (Blanchard and others 2000; Weerman and others 2010); (2) between diatoms and cockles, as microphytobenthos constitutes a food source for cockles (Sauriau and Kang 2000; Filgueira and Castro 2011); (3) between cockles and sediment stability, as coarser sediment may attract smaller densities of bivalve spat (Thrush and others 1996; Piersma and others 2001; Beukema and Dekker 2005). This suggests that removal of cockles or sediment disturbance on large scales following anthropogenic activities may entail severe and unexpected consequences for the ecosystem functioning.

The high levels of algal biomass measured in the surface sediments coastward of the mussel bed together with the negative correlation between chlorophyll *a* and plaster erosion and the observed reduction of erosive energy coastward of the reefs suggest that mussels facilitated microphytobenthos by alleviating hydrodynamic stress. However, also intense biodeposition indicated by high sediment organic matter and silt content and high ammonium concentration in the mussel bed site might have contributed to enhance microphytobenthos growth. Besides decreasing the suspended sediment concentration and therefore the erosive power of water currents, filter feeding and production of mucus-rich biodeposits can result in (1) higher cohesiveness of the substrata (Widdows and others 1998), (2) lower sediment grain size (Ysebaert and others 2009), as confirmed by our results, which in turn alleviates grazer pressure and sediment disturbance by bioturbators (Herman and others 2001), (3) increased light availability for primary producers (see Newell and Koch 2004 for review), and (4) enhanced nutrient availability (Bracken 2004). Therefore, both hydrodynamic stress alleviation and biodeposition by mussel reefs are likely to play a role in the facilitation of

microphytobenthos, and their relative contribution remains to be confirmed by further studies providing conclusive experimental evidence of such mechanisms as well as spatial replication of the patterns observed.

In previous studies, we showed that engineering effects of mussel reefs on hydrodynamic and sediment properties extend far from the reefs, thereby affecting the distribution of benthic species as well as bird populations at long distances (van der Zee and others 2012; Donadi and others 2013). In the current study, we found that microphytobenthos growth was facilitated several hundred meters coastward of a mussel bed, suggesting that mussel reefs may influence multiple trophic levels at large spatial scales. Thus, our results highlight both the general importance of non-trophic interactions for ecosystem function, as well as the specific importance of sediment-stabilizing bioengineers in conserving and promoting the primary productivity of soft-bottom intertidal ecosystems. Our findings are critical to improve coastal management and conservation policies of intertidal flats, eventually leading to the preservation and restoration of healthy and productive ecosystems.

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