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Predation and habitat modification synergistically interact to control bivalve recruitment on intertidal mudflats

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ABSTRACT

Bivalves are key components of coastal ecosystems because they link pelagic and benthic food webs, and shape the landscape through habitat modification. Nevertheless, many bivalve stocks have dramatically declined, and recruitment failure due to (anthropogenically-) increased predation by mesopredators and loss of facilitation mechanisms have been separately hypothesized as underlying causes. Here, we tested the interactive effects of predation and habitat modification on bivalve recruitment in a large-scale experiment in the Wadden Sea, one of the world's largest intertidal soft-sediment ecosystems. We applied anti-erosion mats to simulate biotic attachment and substrate stabilization by commonly found tubeworm beds, crossed this with addition of adult mussels, and manipulated shrimp and crab predation using exclosures within these treatments. Epibenthic mussel recruits were only found in treatments with manipulated substrates, attached to either the anti-erosion mat or adult mussels. Three out of four endobenthic species were facilitated by the mat, but were inhibited by adult mussels. In contrast, invasive surf-dwelling American razor clams were inhibited by both substrate manipulations, indicating a preference for unstable sediments. These facilitation and inhibition effects, however, only clearly emerged when predators were excluded, demonstrating strong synergistic effects between predation and habitat modification. Our findings suggest that disturbance of trophic interactions and loss of habitat modifying species interactively affect bivalve recruitment dynamics in coastal ecosystems. We conclude that conservation and restoration of bivalves should focus on protecting and restoring internal facilitation mechanisms, and should simultaneously reduce excessive mesopredator predation by restoring natural food web dynamics, including the role of top-predators.

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1. Introduction

Over the last decades, about 30–50% of the Earth's coastal ecosystems have become severely degraded due to human impact, and losses are still continuing (Lotze et al., 2006; Barbier et al., 2008). Even though these areas make up only 4% of the Earth's surface, they are of great importance to marine biodiversity and human society (Costanza et al., 1997; Barbier et al., 2008). Bivalves are an important component for the functioning of these ecosystems. Reef-building species like mussels and oysters strongly modify their environment by creating complex structures that serve as a key-habitat for many species, attenuating currents and waves, enhancing water quality by filtering out large amounts of suspended particles and altering sediment conditions by depositing pseudofeces and stabilizing sediments (Widdows et al., 1998; Gutierrez et al., 2003; Schulte et al., 2009; Eriksson et al., 2010; van der Zee et al., 2012). Furthermore, both reef-building and free-living bivalves are important food sources for a wide range of animal species, like crustaceans, starfish, fish and birds (Hiddink et al., 2002; Beukema and Dekker, 2005; van Gils et al., 2006; Harley, 2011; van der Zee et al., 2012).

In conjunction with coastal ecosystems in general, various important bivalve species have declined or are under threat in a wide array of ecosystems, often with dramatic implications for associated species and overall biodiversity (Jackson et al., 2001; van Gils et al., 2006; Schulte et al., 2009; Eriksson et al., 2010). Natural recovery of bivalves – particularly those of epibenthic bivalves like mussels and oysters – is often slow, unpredictable or absent, and even active restoration has been proven difficult (Jackson et al., 2001; Schulte et al., 2009; Eriksson et al., 2010). This may in part be directly related to changes in abiotic conditions (Philippart et al., 2003), but altered biotic interactions may also play a major role in the failure of bivalve recovery. One potentially important biotic factor is increased predation by crustaceans (e.g., shrimp, crab) on bivalve spat. Outbreaks of crustaceans can, for instance, occur due to climate change (Philippart et al., 2003) or overfishing of predatory fish that feed on crustaceans – so-called mesopredator release (Worm and Myers, 2003). Second, declines of reef-forming species like mussels and oysters may reduce inter- and intraspecific facilitation mechanisms, further hampering bivalve recovery (Brinkman et al., 2002; Schulte et al., 2009; Troost, 2010; Donadi et al., 2013).

The intertidal flats of the Dutch Wadden Sea are areas where cockle (*Cerastoderma edule*) and mussel (*Mytilus edulis*) dredging caused severe declines of both species and of molluscivore birds preying on these bivalves (Brinkman et al., 2002; Verhulst et al., 2004; van Gils et al., 2006). Even after intertidal mechanical dredging was banned in 2004, the functioning of these Marine Protected Areas (MPAs) has remained threatened as recovery of cockles has been slow and unpredictable (Piersma et al., 2001; van Gils et al., 2006), and mussel beds have recovered only partly to this day (Eriksson et al., 2010). In this study, we therefore investigated the importance of predation, habitat modification and their interplay in explaining bivalve recruitment dynamics in the intertidal of the Wadden Sea. Predation during high tide by brown shrimp (*Crangon crangon*) and shore crab (*Carcinus maenas*) has been suggested to have a strong negative effect on bivalve recruitment in soft-sediment systems (van der Veer et al., 1998; Strasser, 2002). Next to predation, biotic habitat modification could be an important driver for recruitment as well, because such mechanisms can cause strong facilitation effects in coastal ecosystems (Bruno et al., 2003; Eriksson et al., 2010). Intraspecific facilitation may be especially important for epibenthic reef-building bivalves like mussels and oysters, as mussel and oyster beds provide both stable settlement substrate and protection from predators for their larvae in an otherwise unstable, sandy area (Brinkman et al., 2002; Schulte et al., 2009; Troost, 2010). Still, there are also indications that substrate stabilization and aboveground structure provided by other species like the tubeworms *Lanice conchilega* and *Pygospio elegans* enhance settlement of mussels (*Mytilus edulis*), cockles, Baltic tellins (*Macoma balthica*) and sand gapers (*Mya arenaria*) (Armonies and Hellwigarmonies, 1992; Brinkman et al., 2002; Bolam and Fernandes, 2003; Volkenborn et al., 2009; Donadi et al., 2013).

We empirically tested the hypothesis that predation by crustaceans and inter- and intraspecific facilitation caused by habitat modification (substrate stabilization, attachment structure, predation shelter) synergistically interact to control bivalve recruitment in intertidal soft-sediment ecosystems. We manipulated predation pressure, substrate conditions, and presence/absence of adult epibenthic bivalves in a full factorial large-scale field experiment that was set up in the Dutch Wadden Sea just before the start of the reproductive season. We crossed the application of anti-erosion mats (to mimic tubeworm beds) with the addition of adult mussels in twelve large 20 × 20 m plots. Within these plots, we designated uncaged control areas and manipulated predation by placing exclosure cages. To test for possible cage effects, we also placed cage controls. After 2½ months, we ended the experiment and determined recruitment success of all bivalve species found.

2. Methods

2.1. Experimental setup

The experiment was conducted in 2011 on an intertidal mudflat at 0.5 m below mean water level (low water exposure time ~30%) in the eastern Dutch Wadden Sea, south of the island of Schiermonnikoog (53°28′3.43″N, 6°14′13.40″E). The site itself was characterized by bare sandy sediment, but was located relatively close (~500–1000 m) to three natural intertidal mussel beds with a similar depth and exposure time. In the study area, we set up twelve 20 × 20 m plots in a line parallel to the nearest tidal channel (distance from the channel ~100–150 m), with a distance of about 20 m between plots. The plots were divided over three blocks, with four plots within each block. Within each block we randomly designated one of four treatments to the plots: (1) control, (2) enhanced sediment stabilization and aboveground structure by application of a coco coir mat on the sediment surface, (3) addition of adult mussels, and (4) application of coir mat followed by addition of adult mussels (Fig. 1a).

We used anti-erosion coir mats to mimic sediment stabilization and habitat structure provided by tubeworm beds. Tubeworms are very common in the Wadden Sea where they stabilize the sediment and the aboveground parts of their tubes provide a fibrous substrate that is very suitable for bivalve settlement (Armonies and Hellwigarmonies, 1992; Brinkman et al., 2002; Bolam and Fernandes, 2003; Volkenborn et al., 2009; Donadi et al., 2013). In our experiment, we chose coir mats as a proxy for these biotic structures because, similar to tubeworm beds, the mats stabilize the sediment and provide a fibrous substrate that has been proven as a suitable settlement substrate for bivalves (Skidmore and Chew, 1985; Prou and Dardignac, 1993). The mats were made completely out of coconut fibre and are commonly used to prevent erosion of sediment and seeds on bare soil (e.g. on ski slopes, dikes). To still allow endobenthic burrowing bivalve recruits to dig into the sediment, we selected coir mats with mesh size of ~2 cm. The mats were applied by hand, fixed along the edges by digging them into a depth of ~20 cm (Fig. 1b) and in the middle by 15-cm long biodegradable pins. To prevent complete burial of the anti-erosion mats by deposition of suspended sediments, we added 128 knotted burlap balls (diameter ~10 cm) to each plot at regular distances underneath the mat, yielding small hummocks on which the mat was exposed and available as attachment substrate. Two-year old live mussels (shell length: 54 ± 6 mm; $n = 456$) were obtained from a natural subtidal mussel bed by mechanical dredging and transported to the site in the beginning of May. Within 2 days after collection, 25 circular mussel patches with a ~2.5-m diameter were created by hand at regular distances from each other within each plot, yielding a total cover of around 30% – a cover commonly found in natural mussel beds in the Wadden Sea.

After a 2-week adjustment period, we designated a control (uncaged) area and set up one exclosure and one partial (control) cage within each plot. Cages were similar in design as those used by Strasser (2002) near Sylt in the German Wadden Sea, but with a larger surface area. The cages were cylindrical with a 32-cm diameter and a height of 30 cm. The frame of the cages consisted out of three regularly interspaced 1.5-cm high PVC rings that were connected with three, regularly interspaced 2-cm wide PVC strips. The sides of the exclosures were completely covered with 1-mm mesh made out of PVC covered glass fibre (designed to keep predators out and allow settling bivalve larvae (~300 μm (Widdows, 1991)) in),
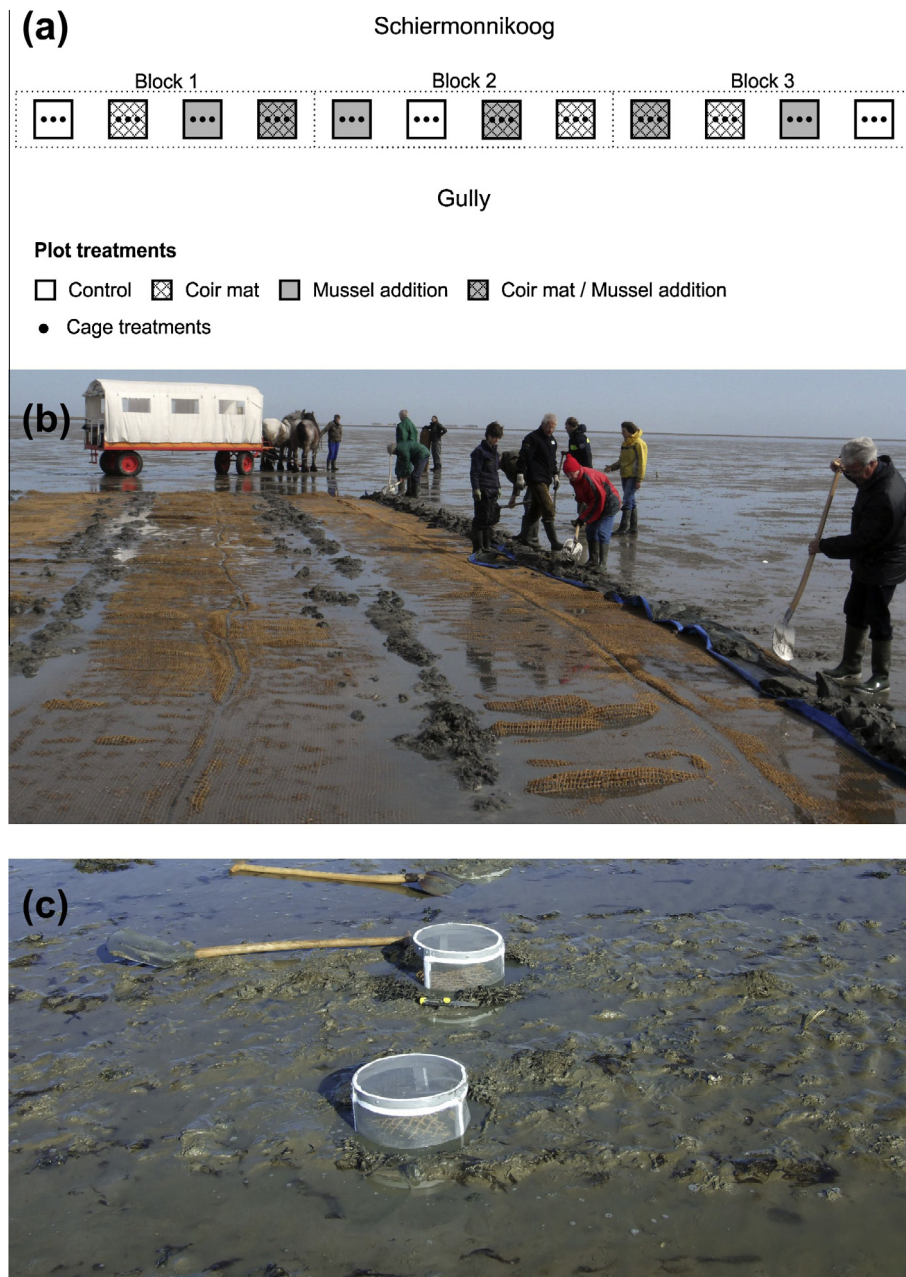
Fig. 1. (a) The experiment was set up in three blocks that included four treatments, with cage treatments (control, cage control and exclosure cage) nested within these treatments. (b) Coir mat and adults mussels on the 20 × 20 m plots were added by hand. (c) The 30-cm high cages were pushed 17 cm into the sediment.

while 1/3 of the sides of the partial cages were left open. The tops of all cages were fit with removable lids that consisted of a 1.5-cm PVC ring and 1-mm mesh. Cages were pushed about 17 cm into the sediment, in such a way that the middle ring was completely beneath the sediment surface (Fig. 1c). To minimize differences between control and exclosure cages, control cages were placed in such a way that the openings were located on the side of the cage that was most sheltered from currents and waves (north-east side). Because cages in coir mat plots were placed in areas without burlap balls, we added a small 5 × 5 cm piece of wood underneath the mat in the middle of the cages (and control areas) to prevent complete burial of the coir mat.

Over the course of the experiment, cages were cleaned and checked at least once every 2 weeks. Fouling on the cages turned out to be minimal and we found no evidence of breached or disturbed cages during the experiment. Two and a half months after

placement of the cages, the upper 15-cm layer of sediment in all cages and control areas was collected and passed through a 1-mm sieve. Everything remaining in the sieve, including adult mussels and coir mat, was stored in 4% formaldehyde solution for later analyses. Finally, we randomly collected sediment samples (top 5 cm) in each plot to determine the effects of adult mussels and coir mat on sediment grain size and organic matter content. Burial depth of the anti-erosion mats was determined with a ruler by 10 random measurements on each plot in areas without burlap balls.

Sieved samples were stained with Rose Bengal in the laboratory. All fauna were identified to species level and all bivalves were counted. Sediment organic matter content in dried sediments (24 h at 70 °C) was estimated as weight loss on ignition (5 h at 550 °C). Silt (<63 µm) content of the sediment was measured on freeze-dried samples by laser diffraction on a Beckman Coulter particle size analyser.

2.2. Statistical analyses

Prior to model fitting, all data were checked for normality using Shapiro–Wilk tests ($p = 0.05$). Based on this test, sediment organic matter and silt content were analysed using ANOVA models with a Gaussian error distribution and block as random factor. Recruitment data could not be analysed with Gaussian models and these data were therefore fitted to models more suitable for count data. For each bivalve species, we started by comparing uncaged areas with cage controls to identify possible cage effects. Next, when we found no significant differences ($p < 0.05$) between cage treatments (i.e., no cage effect), exclosures were compared to the mean of uncaged areas and partial cages. Exclosure cages were compared to cage controls in case of significant cage effects (Hindell et al., 2001). The above analyses were first run using Generalized Linear Mixed Models (GLMM) with which we tested two distributions – Poisson and negative binomial, respectively. Blocks were included as random factor with cage treatments nested within plot. To test for significance of the random effects, we repeated the above procedure using Generalized Linear Models (GLMs). We finally selected negative binomial models without random effects for all bivalve species based on AIC comparisons (using identical AIC algorithms for each model). All analyses were carried out in R 2.15.1 & RStudio 0.96 for Mac. GLMMs were constructed with the *glmmadmb* function in the *glmmADMB* package. Negative binomial GLMs were built with the *glm.nb* function from the *MASS* package. GLMs with Poisson distribution and Gaussian models were constructed using the *glm* and *aov* functions from the *Stats* package, respectively.

3. Results

As expected, the anti-erosion mat increased suspended sediment deposition, burying the mat under a 33 ± 6 (mean ± SD; $n = 6$) mm layer of sand. The mat only remained available as attachment substrate on small hummocks created by the burlap balls and wooden blocks that were added underneath the mat (Fig. 2a). The coir mat did not significantly effect either silt (control: $4.4 \pm 1.7\%$; coir: $4.8 \pm 2.3\%$) or organic matter content (control: $0.8 \pm 0.2\%$; coir: $0.9 \pm 0.3\%$) in the sediment (silt: $F_{1,6} = 0.5$, $p = 0.516$; organic matter: $F_{1,6} = 1.1$, $p = 0.329$).

Apart from providing hard substrate, adult mussels significantly modified sediment conditions. Silt content doubled from 2.9 ± 0.8 (mean ± SD; $n = 6$) to 6.3 ± 0.8 % ($F_{1,6} = 44.2$, $p < 0.001$), and organic matter increased with a factor 1.6 from $0.6 \pm 0.1\%$ to $1.0 \pm 0.2\%$ ($F_{1,6} = 30.5$, $p = 0.001$; no significant interactions with the coir mat treatment). The density of adult transplanted mussels in uncaged areas was 439 ± 110 (mean ± SD; $n = 6$) individuals/m², which was lower than in partial cages (564 ± 72 ind./m²; $\chi^2 = 7.5$, $p = 0.006$). Partial cages, however, did not differ significantly from exclosures (576 ± 78 ind./m²; $\chi^2 = 0.1$, $p = 0.798$) and we also found no significant effect of the coir mat on adult mussel density ($\chi^2 = 0.3$, $p = 0.609$) or any significant interactions.

We found that 5 bivalve species settled in our plots: blue mussels, common cockles, Baltic tellins, sand gapers, and American razor clams (*Ensis directus*). Of these species, only mussels showed a significant cage effect ($\chi^2 = 9.6$, $p = 0.002$; no significant interactions). However, the increased settlement in the partial cage could only explain between 2% (on bare sediment) and 10% (on coir with mussel addition) of the difference between exclosures and control areas.

Mussel recruits were found almost exclusively attached to either the coir mat or adult mussels and predominately in the predator exclosures (Figs. 2 and 3; Table 1). Similar to mussel recruits, spat numbers of endobenthic, burrowing cockles, Baltic tellins, sand gapers and razor clams were significantly higher in predator exclosures. Cockle densities were highest in sediments of exclosures stabilized by a coir mat ($\sim$21,000 m⁻²), but numbers were also high in exclosures on bare sediment ($\sim$6000 m⁻²), resulting in a $\sim$3-cm thick multilayer mat of cockles in these two treatments (Fig. 2). In contrast with cockles, Baltic tellins and sand gapers that were all significantly enhanced in coir mat-stabilized sediments, numbers of razor clams were much lower here compared to exclosures on bare sediment (Fig. 3). Finally, spat numbers of cockles, sand gapers and razor clams were all significantly lowered by the presence of adult mussels in the exclosures. Baltic tellins were also significantly lowered in the presence of adult mussels, but only in the coir mat treatment.

4. Discussion

Recruitment failure is an important factor driving bivalve declines in soft-sediment ecosystems and both predation and loss of facilitation mechanisms have been separately suggested as potential underlying causes (Olafsson et al., 1994; Gosselin and Qian, 1997; Schulte et al., 2009; Eriksson et al., 2010; Donadi et al., 2013). In this study, we experimentally show that recruits of the four most important native bivalve species in the Wadden

Fig. 2. Top views of a control cage (a) and an exclosure cage (b) on a coir mat plot (cage lids removed) at the end of the experimental period. The addition of wooden blocks underneath the mat created small hummocks where the mat remained available as attachment substrate (a). The combination of predator exclusion and substrate stabilization yielded high numbers mussel recruits attached to the mat (black patch in the middle of b) and cockles (white shells) in the surrounding sediment.
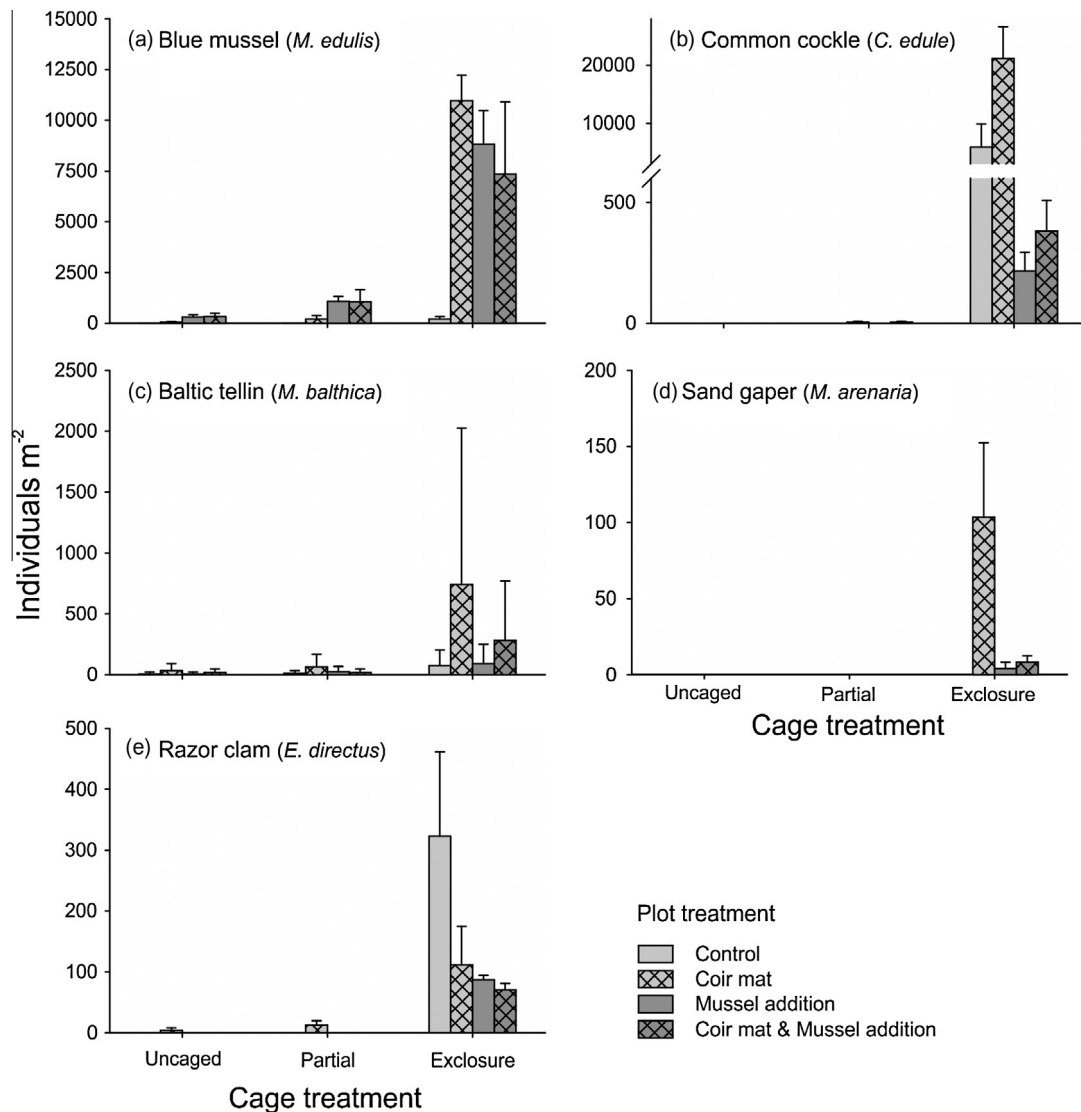
Fig. 3. Mean number of recruits per treatment for all five bivalve species found at the end of the experimental period. Error bars denote standard errors.

Table 1
Chi-square values and significance levels for all treatments and their interactions per bivalve species.

Treatments	Mytilus	Cerastoderma	Macoma	Mya	Ensis
Coir	14.3***	7.8**	17.4***	16.9***	2.9
Mussels	36.8***	69.0***	1.7	9.1**	10.5**
Predation	63.6***	221.1***	42.7***	25.1***	88.8***
Coir × mussels	33.8***	0.9	3.8*	4.5*	1.8
Coir × predation	0.0	1.3	2.0	0.0	6.9**
Mussels × predation	6.8**	4.9*	0.0	0.0	2.6
Coir × muss. × pred.	0.5	0.0	0.0	0.0	0.0

Degrees of freedom: 24 in total; 16 residual.
* Significance level: $p < 0.05$.
** Significance level: $p < 0.01$.
*** Significance level: $p < 0.001$.

Sea appear strongly, but species-specifically, controlled by the complex interplay between predation, facilitation and interspecific inhibition. Mussel spat was only found in significant amounts in predator exclosure cages attached to either coir mat or adult mussels, illustrating its dependence on both low predation pressure and a suitable attachment substrate. Free-living burrowing cockles, Baltic tellins and sand gapers were similarly dependent

on low predation levels, and were facilitated by the anti-erosion mat – most likely due to its sediment stabilizing effects. In contrast to mussel spat, however, adult mussels inhibited settlement of these endobenthic species. Since there is no evidence of selective predation on larvae by filter-feeding mussels (Troost, 2010), we suggest that the physical presence of adult mussels may have inhibited burrowing and/or that altered sediment conditions caused by pseudofeces deposition inhibited recruitment of these endobenthic bivalves (Diaz and Rosenberg, 1995; Graf and Rosenberg, 1997). Strikingly, recruitment of invasive razor clams (introduced in the late 1970s) was positively affected by exclusion of predation, but negatively affected by both adult mussels and coir mat, illustrating that these clams may benefit from unstable sediment conditions (Armonies, 2001).

Apart from manipulating predation pressure, cages may also alter hydrodynamics and larval settlement because of their physical structure. For instance, lowered hydrodynamic intensity in the cages may lead to reduced sediment disturbance, in turn enhancing larval settlement (Strasser, 2002). Nevertheless, our analyses revealed little evidence of cage artefacts. Although we found some evidence for cage effects on mussel spatfall, these effects seem small as the total amount of mussel recruits in the partial cages was only 6% of the number of recruits in the closed

cages. Moreover, we found no indication at all for similar artefacts in any of the other bivalve species. Possibly, the byssally attaching mussel larvae used the cage structure as a primary attachment substrate, subsequently allowing recruits to move onto the substrate inside the cages. Also, in the mussel addition treatments, the enhanced mussel recruitment in the partial cages compared to controls may (in part) be explained by increased facilitation due to the somewhat higher adult densities. Hence, although we were not able to gather direct observations of high tide shrimp and crab predation in and around the cages (the waters are too murky in our system), we conclude that predation by crustaceans is the most likely explanation for our experimental results as cage artefacts are unlikely to have contributed importantly.

Marine bivalves typically have an opportunistic reproductive strategy, releasing large numbers of eggs per individual (>1 million) into the water column (mainly in spring), where they are externally fertilized (Honkoop and van der Meer, 1998). The settlement location and subsequent survival of the bivalves in the following months, are notoriously unpredictable and variable between years in soft-sediment systems like the Wadden Sea (van der Veer et al., 1998; Brinkman et al., 2002). Apart from environmental factors (e.g., temperature, hydrodynamics, substrate conditions), it has been suggested that biotic interactions like chemical cues are important to initiate settlement (Dobretsov and Wahl, 2001; Liu et al., 2011). Once settled, overall recruitment success of bivalves in intertidal areas is considered to be depend on many different factors, including abiotics, predation and facilitation effects (van der Veer et al., 1998; Brinkman et al., 2002; Strasser, 2002; Schulte et al., 2009; Troost, 2010). Our experimental findings suggest that these factors are not only important, but that they can strongly interact to control bivalve recruitment dynamics, potentially explaining in part the difficulties in predicting bivalve recruitment success in soft-sediment systems.

Our findings have important implications for management of soft-sediment ecosystems as they indicate that disturbance of trophic interactions and loss of habitat modifying species can severely hamper bivalve recruitment. Over the last decades, large-scale declines of bivalve stocks have occurred in North-America, Australia and Europe (including the Wadden Sea) due to mechanical dredging for commercially exploitable species like oysters, mussels and cockles (Schulte et al., 2009; Eriksson et al., 2010). Apart from the physical removal of adult bivalves, mechanical dredging also removes hard substrates (e.g., dead shells, tubeworm structures) and destabilizes the sediment (Ferns et al., 2000; Piersma et al., 2001). Our results show that recruitment of native bivalves in the Wadden Sea is negatively affected by these activities. Contrastingly, the invasive American razor clam, originally an inhabitant of the lower surf-zone, but now strongly increasing in the Wadden Sea, may actually be facilitated as this species profits from unstable sediments (Armonies, 2001). Apart from deteriorated substrate conditions, predation pressure by crustaceans is increasing in many coastal areas, often due to overfishing of top-predators resulting in mesopredator release (Worm and Myers, 2003). In the Dutch Wadden Sea, shrimp numbers are over twice as high compared to other European coastal waters (Tulp et al., 2012), peaking in summer at over 100 individuals/m^2 on intertidal flats (van der Veer et al., 1998). Furthermore, shore crab densities increased over 10-fold since 1995, with numbers still rising (Tulp et al., 2012). At present, the underlying causes are unknown, but our results suggest that high predator numbers now hamper bivalve recruitment.

Recently, there is an increasing amount of evidence pointing at the key importance of the interplay of habitat modification and biotic interactions in structuring soft-sediment marine ecosystems like mudflats and seagrasses (Weerman et al., 2011; van der Heide et al., 2012a,b). Our study clearly demonstrates that such interactions are equally important for bivalve recruitment dynamics in intertidal soft-sediment ecosystems and that knowledge of the interaction between predation and facilitation mechanisms is key to understanding how these ecosystems can be managed sustainably. Overall, we conclude that it is of utmost importance to protect existing bivalve beds and conserve their internal facilitation effects. Furthermore, restoration efforts should focus on reducing (anthropogenic) disturbances, and the simultaneous recovery of lost facilitation mechanisms and natural food web dynamics.

References

Armonies, W., 2001. What an introduced species can tell us about the spatial extension of benthic populations. Mar. Ecol. – Prog. Ser. 209, 289–294.

Armonies, W., Hellwigarmonies, M., 1992. Passive settlement of *Macoma baltica* spat on tidal flats of the Wadden Sea and subsequent migration of juveniles. Neth. J. Sea Res. 29, 371–378.

Barbier, E.B., Koch, E.W., Silliman, B.R., Hacker, S.D., Wolanski, E., Primavera, J., Granek, E.F., Polasky, S., Aswani, S., Cramer, L.A., Stoms, D.M., Kennedy, C.J., Bael, D., Kappel, C.V., Perillo, G.M.E., Reed, D.J., 2008. Coastal ecosystem-based management with nonlinear ecological functions and values. Science 319, 321–323.

Beukema, J.J., Dekker, R., 2005. Decline of recruitment success in cockles and other bivalves in the Wadden Sea: possible role of climate change, predation on postlarvae and fisheries. Mar. Ecol. – Prog. Ser. 287, 149–167.

Bolam, S.G., Fernandes, T.F., 2003. Dense aggregations of *Pygospio elegans* (Claparede): effect on macrofaunal community structure and sediments. J. Sea Res. 49, 171–185.

Brinkman, A.G., Dankers, N., van Stralen, M., 2002. An analysis of mussel bed habitats in the Dutch Wadden Sea. Helgol. Mar. Res. 56, 59–75.

Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. Trends Ecol. Evol. 18, 119–125.

Costanza, R., dArge, R., deGroot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., Oneill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., vandenBelt, M., 1997. The value of the world's ecosystem services and natural capital. Nature 387, 253–260.

Diaz, R.J., Rosenberg, R., 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. In: Ansell, A.D., Gibson, R.N., Barnes, M. (Eds.), Oceanography and Marine Biology – An Annual Review, vol. 33. UCL Press Ltd., London, pp. 245–303.

Dobretsov, S., Wahl, M., 2001. Recruitment preferences of blue mussel spat (*Mytilus edulis*) for different substrata and microhabitats in the White Sea (Russia). Hydrobiologia 445, 27–35.

Donadi, S., van der Heide, T., van der Zee, E.M., Eklöf, J.S., van de Koppel, J., Weerman, E.J., Piersma, T., Olff, H., Eriksson, B.K., 2013. Cross-habitat interactions among bivalve species control community structure on intertidal flats. Ecology 94, 489–498.

Eriksson, B.K., van der Heide, T., van de Koppel, J., Piersma, T., van der Veer, H.W., Olff, H., 2010. Major changes in the ecology of the Wadden Sea: human impacts, ecosystem engineering and sediment dynamics. Ecosystems 13, 752–764.

Ferns, P.N., Rostron, D.M., Siman, H.Y., 2000. Effects of mechanical cockle harvesting on intertidal communities. J. Appl. Ecol. 37, 464–474.

Gosselin, L.A., Qian, P.Y., 1997. Juvenile mortality in benthic marine invertebrates. Mar. Ecol. Prog. Ser. 146, 265–282.

Graf, G., Rosenberg, R., 1997. Bioresuspension and biodeposition: a review. J. Mar. Syst. 11, 269–278.

Gutierrez, J.L., Jones, C.G., Strayer, D.L., Iribarne, O.O., 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos 101, 79–90.

Harley, C.D.G., 2011. Climate change, keystone predation, and biodiversity loss. Science 334, 1124–1127.

Hiddink, J.G., Marijnissen, S.A.E., Troost, K., Wolff, W.J., 2002. Predation on o-group and older year classes of the bivalve *Macoma balthica*: interaction of size selection and intertidal distribution of epibenthic predators. J. Exp. Mar. Biol. Ecol. 269, 223–248.

Hindell, J.S., Jenkins, G.P., Keough, M.J., 2001. Spatial and temporal variability in the effects of fish predation on macrofauna in relation to habitat complexity and cage effects. Mar. Ecol. – Prog. Ser. 224, 231–250.

Honkoop, P.J.C., van der Meer, J., 1998. Experimentally induced effects of water temperature and immersion time on reproductive output of bivalves in the Wadden Sea. J. Exp. Mar. Biol. Ecol. 220, 227–246.

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293, 629–638.

Liu, G.X., Stapleton, E., Innes, D., Thompson, R., 2011. Aggregational behavior of the blue mussels Mytilus edulis and Mytilus trossulus: a potential pre-zygotic reproductive isolation mechanism. Mar. Ecol. – Evolution. Perspect. 32, 480–487.

Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby, M.X., Peterson, C.H., Jackson, J.B.C., 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312, 1806–1809.

Olafsson, E.B., Peterson, C.H., Ambrose, W.G., 1994. Does recruitment limitation structure populations and communities of macroinvertibrates in marine soft sediments? The relative significance of presettlement and postsettlement processes. Oceanogr. Mar. Biol. 32, 65–109.

Philippart, C.J.M., van Aken, H.M., Beukema, J.J., Bos, O.G., Cadee, G.C., Dekker, R., 2003. Climate-related changes in recruitment of the bivalve Macoma balthica. Limnol. Oceanogr. 48, 2171–2185.

Piersma, T., Koolhaas, A., Dekinga, A., Beukema, J.J., Dekker, R., Essink, K., 2001. Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea. J. Appl. Ecol. 38, 976–990.

Prou, P., Dardignac, M.J., 1993. Recruitment of mussels in the Pertuis Breton (France) in these last years. A preliminary analysis on the influence of temperature and sunshine. In: 2nd Workshop on Spatfall and Recruitment of Mussels and Cockles, Yerseke, Netherlands (11–12 March 1993). Yerseke.

Schulte, D.M., Burke, R.P., Lipcius, R.N., 2009. Unprecedented restoration of a native oyster metapopulation. Science 325, 1124–1128.

Skidmore, D., Chew, K.K., 1985. Mussel Aquaculture in Puget Sound. Washington Sea Grant Program, College of Ocean and Fishery Sciences, University of Washington, Seattle.

Strasser, M., 2002. Reduced epibenthic predation on intertidal bivalves after a severe winter in the European Wadden Sea. Mar. Ecol. – Prog. Ser. 241, 113–123.

Troost, K., 2010. Causes and effects of a highly successful marine invasion: case-study of the introduced Pacific oyster Crassostrea gigas in continental NW European estuaries. J. Sea Res. 64, 145–165.

Tulp, I., Bolle, L.J., Meesters, E., de Vries, P., 2012. Brown shrimp abundance in northwest European coastal waters from 1970 to 2010 and potential causes for contrasting trends. Mar. Ecol. – Prog. Ser. 458, 141–154.

van der Heide, T., Eklof, J.S., van Nes, E.H., van der Zee, E.M., Donadi, S., Weerman, E.J., Olff, H., Eriksson, B.K., 2012a. Ecosystem engineering by seagrasses interacts with grazing to shape an intertidal landscape. Plos One 7.

van der Heide, T., Govers, L.L., de Fouw, J., Olff, H., van der Geest, M., van Katwijk, M.M., Piersma, T., van de Koppel, J., Silliman, B.R., Smolders, A.J.P., van Gils, J.A., 2012b. A Three-stage symbiosis forms the foundation of seagrass ecosystems. Science 336, 1432–1434.

van der Veer, H.W., Feller, R.J., Weber, A., Witte, J.I.J., 1998. Importance of predation by crustaceans upon bivalve spat in the intertidal zone of the Dutch Wadden Sea as revealed by immunological assays of gut contents. J. Exp. Mar. Biol. Ecol. 231, 139–157.

van der Zee, E.M., van der Heide, T., Donadi, S., Eklof, J.S., Eriksson, B.K., Olff, H., van der Veer, H.W., Piersma, T., 2012. Spatially extended habitat modification by intertidal reef-building bivalves has implications for consumer-resource interactions. Ecosystems 15, 664–673.

van Gils, J.A., Piersma, T., Dekinga, A., Spaans, B., Kraan, C., 2006. Shellfish dredging pushes a flexible avian top predator out of a marine protected area. PLoS Biol. 4, 2399–2404.

Verhulst, S., Oosterbeek, K., Rutten, A.L., Ens, B.J., 2004. Shellfish fishery severely reduces condition and survival of oystercatchers despite creation of large marine protected areas. Ecol. Soc. 9.

Volkenborn, N., Robertson, D.M., Reise, K., 2009. Sediment destabilizing and stabilizing bio-engineers on tidal flats: cascading effects of experimental exclusion. Helgol. Mar. Res. 63, 27–35.

Weerman, E.J., Herman, P.M.J., Van de Koppel, J., 2011. Top-down control inhibits spatial self-organization of a patterned landscape. Ecology 92, 487–495.

Widdows, J., 1991. Physiological ecology of mussel larvae. Aquaculture 94, 147–163.

Widdows, J., Brinsley, M.D., Bowley, N., Barrett, C., 1998. A benthic annular flume for in situ measurement of suspension feeding/biodeposition rates and erosion potential of intertidal cohesive sediments. Estuar. Coast. Shelf Sci. 46, 27–38.

Worm, B., Myers, R.A., 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. Ecology 84, 162–173.