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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.

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).

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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),