



The bivalve loop: Intra-specific facilitation in burrowing cockles through habitat modification [☆]



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ABSTRACT

Human exploitation of bivalve populations has changed intertidal landscapes worldwide. Many bivalves are ecosystem engineers that modify the physical environment, affecting the conditions for their survival. Here we argue that lack of recovery of overexploited intertidal bivalve beds may be partly caused by the loss of important biological feedbacks from depleted populations. In a large-scale experiment we investigated engineering effects of cockles (*Cerastoderma edule* L.) and lugworms (*Arenicola marina* L.) on juvenile cockles by adding high densities of either species to 5 × 5 m plots in areas with different hydrodynamic and sediment conditions in the intertidal flats of the Wadden Sea. We hypothesized that cockles would facilitate the new generations by increasing sediment stability, while lugworms would have negative effects on juvenile cockles through sediment disturbance. We found that in sandy areas with high wave and current energy cockles enhanced sediment accumulation and promoted local densities of young cockles, while lugworms did not have any effect on juvenile cockles. In muddy sites sheltered from the tidal currents by mussel reefs (*Mytilus edulis* L.), juvenile cockle densities were generally high, demonstrating the general importance of biological engineering for recruitment processes in the intertidal. We suggest that the acknowledgement of positive feedbacks between bivalves and sediment stability is essential to achieve long-term restoration goals in coastal ecosystems.

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1. Introduction

Overfishing and habitat destruction have led to dramatic reductions in bivalve populations worldwide (Airoldi and Beck, 2007; Jackson et al., 2001; Lotze et al., 2006 and references therein; van Gils et al., 2006). The rate of decline has accelerated dramatically within the last two hundred years, bringing several species close to collapse (e.g. Kirby, 2004; Lotze, 2005). Although the results of restoration efforts are encouraging (e.g. Arnold et al., 2005; Marsden and Adkins, 2009; Schulte

et al., 2009), large-scale restoration of shellfish stocks often remains difficult. Lack of recovery has been attributed to multiple, likely interacting factors such as food web changes (i.e. the arrival of new competitors or predators, Walters and Kitchell, 2001), habitat destruction (e.g. Lenihan and Peterson, 1998; Medina et al., 2007), climate change (e.g. Schückel and Kröncke, 2013), and pollution (Worm and Lotze, 2000). A possibly underestimated cause preventing re-establishment of former abundance levels is the loss of biological feedbacks from pre-existing populations. Many bivalve species act as ecosystem engineers that often modify their environment to their own benefit (Bertness and Leonard, 1997; Jones et al., 1994, 1997). The eradication of natural populations can break such positive feedbacks resulting in degraded habitat conditions that are hard to reverse (Nyström et al., 2012; Thrush et al., 2009).

Positive feedbacks have been suggested to be crucial for the stability and resilience of ecological communities (Gurney and Lawton, 1996; Scheffer and Carpenter, 2003), potentially leading to the occurrence of alternative stable states in ecosystems (May, 1977; Scheffer et al., 2001). In many species, habitat modification may affect the dynamics of future generations (“ecological imprint”) by increasing the probability of successful recruitment (Cuddington et al., 2009; Laland et al., 1999). This in turn may drive spatial segregation of species, resulting

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in self-organized spatial heterogeneity (Hui et al., 2004). Hence, positive feedbacks can strongly influence the distribution, persistence and dynamics of natural populations, emphasizing that appreciation of these mechanisms is crucial for conservation and restoration of ecosystem engineers (Boogert et al., 2006; Byers et al., 2006).

In this study, the effects of sediment-stabilizing bivalves (*Cerastoderma edule* – cockle) and sediment-destabilizing worms (*Arenicola marina* – lugworm) on juvenile cockles were investigated on the tidal flats of the Dutch Wadden Sea. Cockles live in the upper few cm of the sediment and can occur in dense assemblages of many thousands m^{-2} (Jensen, 1992). Although several studies emphasized the bioturbating effects of cockles (Flach, 1996; Neumeier et al., 2006), high densities of cockles can also increase sediment stability through the production of mucus-rich biodeposits and facilitation of sediment-binding diatom colonies (Ciutat et al., 2007; Donadi et al., 2013b). Sediment stabilization may affect cockle recruitment and post-larval processes (Bouma et al., 2001; Kater et al., 2006; Piersma et al., 2001), for instance by enhancing the ability of juvenile bivalves to anchor themselves to the substrate, thereby buffering negative effects of waves and currents (Armonies, 1996; Armonies and Hellwig-Armonies, 1992). Another common ecosystem engineer occurring in high abundances on tidal flats is the deposit-feeding lugworm *A. marina* (Flach and Beukema, 1994). Through bioturbation, lugworms increase erosion of fine particles thus decreasing sediment stability (Volkenborn et al., 2007). Moreover, sediment cohesiveness can be further reduced by the removal of diatom mats due to deposit feeding by the worms (Volkenborn et al., 2007). Consequently, lugworms likely decrease larval settlement and/or increase resuspension of macrozoobenthos recruits. Indeed, previous studies attributed observed negative effects of lugworms on juveniles of *C. edule* and several other species to sediment re-working activities and repeated burying by fecal castings (Brey, 1989; Flach, 1992).

Here, we hypothesize that (1) adult cockles can facilitate recruitment of juvenile conspecifics and that (2) lugworms could disrupt these positive feedbacks via habitat-modification. As the intensity of ecosystem engineering by cockles and lugworms likely depends on environmental conditions (Montserrat et al., 2009; Volkenborn et al., 2007), we tested our hypotheses by adding a total of 800,000 cockles and 64,000 lugworms to 5×5 m plots in habitats with contrasting hydrodynamic and sediment properties caused by the nearby presence or absence of blue mussel (*Mytilus edulis*) reefs. In addition, to explore the relative importance of ecosystem engineering by cockles and lugworms versus the effects of the local species, half of the plots were defaunated before the additions.

2. Methods

2.1. Experimental treatments

The study was conducted on the intertidal flats of Schiermonnikoog, in the Dutch Wadden Sea. On these tidal flats, blue mussels form several large (>1 ha) epibenthic reefs, cockles are often found in dense assemblages within the sediment of hundred to thousand individuals m^{-2} and lugworms occur in populations with relatively stable densities of 20–40 individuals m^{-2} (Beukema and Devlas, 1979; Jensen, 1992), as confirmed by pilot surveys conducted in 2009 in the study area (*pers. obs.*).

We used a large-scale experiment to investigate the effects of cockles and lugworms on recruitment success of juvenile cockles, defined here as the result of settlement and survival of 3 to 6 month individuals. In March 2010, a total of ninety-six 5×5 m plots arranged in a randomized block design were assigned to two muddy sites ($53^{\circ}28'8.15''N$, $6^{\circ}13'27.95''E$; $53^{\circ}28'2.44''N$, $6^{\circ}10'59.83''E$) located 100 and 350 m coastward of two mussel beds, and two sandy sites ($53^{\circ}28'7.42''N$, $6^{\circ}13'55.95''E$; $53^{\circ}28'7.54''N$, $6^{\circ}11'33.48''E$) far from the influence of mussel reefs, at the same tidal elevation, respectively. Previous

research highlighted the engineering effects of the same mussel reefs considered in the current study by showing strong spatial gradients of increasing organic matter and silt content, and decreasing pore water redox potential and current velocities in the direction of the reefs (Donadi et al., 2013a; van der Zee et al., 2012). This evidence together with the absence of any macroscopic topographical features in the area assured us that the differences in sediment composition between muddy and sandy sites were due to engineering effects of the mussel beds (e.g. biodeposition, shelter from tidal currents). In each site we set up two blocks of twelve plots with a random full factorial combination of (1) defaunation treatment (two levels) and (2) engineer addition (three levels) (Fig. 1). The defaunation treatment consisted of an anoxia-induced kill off of macrobenthos in half of the plots by covering the sediment with plastic tarps for a period of 28 days (April 2010). After this period, the tarps were removed and the absence of living macrobenthic organisms was confirmed by the collection of sediment cores. Ten days after the removal of the tarps, we performed the engineer addition: one-third of all plots was enriched with high densities of cockles (1000 individuals m^{-2}), one-third with high densities of lugworms (80 individuals m^{-2}) and the remaining plots served as a control (no addition). As effects of ecosystem engineers are strongly dependent on the densities and the spatial extent of the engineer populations and considering the highly patchy distribution of cockles on intertidal areas, treatment densities of cockles and lugworms were chosen to mimic maximum adult densities in the study area, as estimated within a 0.5×0.5 m frame during several pilot surveys conducted between March and October 2009 (*pers. obs.*). Cockles were collected from a nearby intertidal flat by professional fishermen through hand-raking and were 2 to 4 years old (mean mm length \pm 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 \pm SE = 0.97 ± 0.12 , $n = 20$).

Total abundance of engineers was monitored every six months by counting 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 generally decreased after the additions (also because of a winter freeze between 2010 and 2011) but remained considerably higher in enriched plots compared to the other treatments (Figs. 2 and 3), the only exception being lugworm abundances in September 2011, when there was mostly no difference between cockle- and lugworm-addition plots (Fig. 3).

2.2. Juvenile cockles and sediment conditions

Abundance of juvenile cockles (3–12 mm long, ~3–6 months-old) was estimated within a 0.5×0.5 m frame which was randomly placed on each plot in September 2010, March 2011, July 2011 and September 2011. Cockles commonly settle in the Wadden Sea in late spring (May–June) and in late autumn (October–November, van der Veer et al., 1998; R. Dekker, *pers. comm.*). At each sampling time, juvenile cockles were counted after sieving the upper sediment layer (0–3 cm depth) through a 1-mm mesh. To minimize sampling effects, the sediment was put back in place after sieving and leveled with the surrounding bed level.

To investigate engineering effects of transplanted species on sediment accretion and erosion we estimated bed level height in March 2011 and September 2011 using a Trimble Spectra Precision LL500 Laser Level (Trimble, California, United States of America). At each site, measurements were calibrated against fixed reference metal poles. At each sampling time, five replicates per plot were collected and averaged and the differences between the two dates were used to calculate bed level changes (a proxy for net sediment accumulation or erosion) during the summer, when bioengineering activity of cockle and lugworms is more conspicuous.

To explore effects of cockles and lugworms on sediment properties, sediment samples were collected in September 2010, March 2011 and

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