Caught in the middle: How predation, competition and ecosystem engineering interactively structure an intertidal bivalve population

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Abstract

Trophic interactions, competition and ecosystem engineering - the biotic modification of the physical environment - can all severely affect population dynamics. How these three mechanisms interact to shape ecological communities is, however, still unclear. Here, we studied the interactive effects of predation, competition and ecosystem engineering on common cockle (Cerastoderma edule) recruitment, growth and survival in the Wadden Sea, one of the world's largest intertidal ecosystems. In a predator-exclosure experiment, we manipulated cockle densities (100 vs. 1000 individuals m⁻²) and shorebird predation at a site engineered by blue mussels (Mytilus edulis) and at a sandy control site. We hypothesized that by facilitating high cockle numbers, mussels may alleviate predation-induced effects on cockle survival, and that this in turn may negatively affect competition among cockles. We found that bird predation strongly reduced recruit density, while mussels strongly facilitated recruits by reducing hydrodynamic stress. Cockle growth was reduced near mussels, but also in the high cockle density treatment outside exclosures. Adult cockle survival was enhanced near the mussel bed, while high cockle densities decreased adult cockle survival. Bird predation also decreased adult survival, but only at the control site. We conclude that ecosystem engineering by mussel beds can enhance cockle densities by reducing hydrodynamics and predation across different life stages, but may also reduce cockle growth, most likely by reducing hydrodynamics and by increasing inter-specific competition for food. Our study emphasizes the importance of ecosystem engineers in structuring intertidal communities and the necessity to integrate multiple interaction types into a single framework.

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Introduction

A substantial part of ecological theory concerns the role of interactions between organisms in determining population dynamics. Out of these interactions, predation, competition and their interactive effects received most attention, as they are believed to be crucial in structuring natural communities (e.g. Paine 1966; Schoener 1983; Chase et al. 2002). However, organisms can also affect each other indirectly through ecosystem engineering – the biotic modification of the physical environment (Jones et al. 1994) –, a type of interaction that has more recently been advanced as a critical interaction in many ecosystems as well (Bruno et al. 2003; Wright and Jones 2006). Therefore, it might be expected that ecological communities are often structured by an interplay of multiple interactions types (as emphasized by Olff et al. 2009).

Until now, most work on integrating ecosystem engineering into ecological interactions has focused on coupling ecosystem engineering to either trophic or competitive interactions among species. Previous studies revealed that ecosystem engineers can affect multiple trophic levels (e.g. Graham 2004; van der Zee et al. 2012), are able to modify predatory impact among other species (e.g. Grabowski 2004; Ransom 2011) and that ecosystem engineering and trophic processes are closely associated when a single species act as a predator and an engineer simultaneously (e.g. Wilby et al. 2001). Furthermore, facilitation through ecosystem engineering has been shown to affect competition as well (e.g. Palmer 2003; Ransom 2011). However, despite the fact that trophic interactions, competition, ecosystem engineering and their two-way interactions are all recognized as important structuring mechanisms in ecosystems, the combined effects of all three interaction types on population dynamics remain to be investigated to our knowledge.

Here we studied the interactive effects of ecosystem engineering by blue mussels (Mytilus edulis), predation by molluscivore shorebirds and competition on survival, recruitment and growth of the common cockle (Cerastoderma edule) in the Dutch Wadden Sea – one of the largest intertidal ecosystems in the world (Wolff 1983). Blue mussels are well-known ecosystem engineers that create hard substrate, reduce hydrodynamics and modify sediment conditions by depositing large amounts of (pseudo-)faeces (Kröncke 1996; Donadi et al. 2013). Especially in soft-bottom ecosystems like the Wadden Sea, effects on hydrodynamics and sediment conditions can extend far beyond the bed itself, up to distances of several hundreds of meters (Kröncke 1996; van der Zee et al. 2012; Donadi et al. 2013). In this surrounding area, cockle recruitment can be enhanced due to reduced hydrodynamic stress, yielding higher cockles densities (Donadi et al. 2013). Because recruitment is facilitated, cockles may experience enhanced competition for food with conspecifics due to increased densities (Jensen 1993), but also with the nearby mussel bed (Donadi et al. 2013). Additionally, the elevated cockle densities can lead to increased aggregation of
molluscivore shorebirds, such as oystercatchers (*Haematopus ostralegus*) (van der Zee et al. 2012) and red knots (*Calidris canutus*) (van Gils et al. 2005). Although higher bird densities can enhance predation pressure, the high cockle density and the presence of mussels as an alternative prey in the engineered area may at the same time mitigate the effects of increased bird densities by increasing giving up densities (GUDs) of predators on their prey (Charnov 1976; Brown 1988; Olsson and Molokwu 2007).

Hence, we hypothesize that by facilitating high numbers of cockles, mussels can alleviate predation-induced effects on cockle survival. Both processes can in turn negatively affect inter- and intraspecific competition among cockles. Consequently, cockles are caught between the positive and negative effects of ecosystem engineering: cockle densities and survival are enhanced by reduced hydrodynamic stress and predation, but cockle growth is reduced due to interspecific competition with mussels and both growth and survival are reduced due to increased intraspecific competition among cockles. To test our hypothesis, we carried out a manipulative field experiment on the intertidal flats of Schiermonnikoog at a site engineered by a mussel bed and at a sandy control site. At both sites, we crossed two adult cockle densities with shorebird exclosure treatments, and added tagged cockles to monitor growth. After 1 year, we ended the experiment and determined cockle survival, recruitment and growth.

**Materials and methods**

**Experimental design**

The study was conducted at 0.5 m below mean water level (exposed during low tide for ~30% of time) in the eastern Dutch Wadden Sea, south of the island of Schiermonnikoog. The first out of two study sites was situated 100 meters coastward of a mussel bed (site Mussel, 53°28.127 N - 6°13.463’ E). This area was characterized by silty organic matter-rich sediment, and reduced hydrodynamic conditions (Donadi et al. 2013). The other site was located at ~500 m from the first site with the same tidal elevation, but out of the influence range of the mussel bed, and was therefore typified by sandy sediments and served as a control site (site Sand, 53°28.117 N - 6°13.938’ E) (Donadi et al. 2013). Both sites were chosen based on previous studies that demonstrate that this area is highly suitable to investigate the effects of ecosystem engineering by blue mussels on multiple interaction types (van der Zee et al. 2012; Donadi et al. 2013). At the start of the experiment in May 2010, the mean background cockle density was 65 n m⁻² at the mussel site and 0 n m⁻² at the sandy control site.

We manipulated predation pressure by establishing 12 1-m² bird exclosures and 12 control plots at both sites. Exclosure and control plots were paired with a
distance of 4 m between pairs and a distance of 10 m between replicates. Each exclosure consisted of 8 PVC-poles (0.5 m long) that were inserted in the sediment to a depth of 0.4 m and aligned in a square of 1 m². A nylon rope connected the tops of the poles thereby acting as a fence (Fig. 4.1A). Control plots were marked by two small PVC-poles. The plots were checked regularly in the following year and macroalgae and other fouling was removed if present.

Next, we crossed the exclosure treatments with two cockle densities by adding either 75 or 925 adult cockles (Fig. 4.1B) to each plot in May 2010, yielding a total of 6 replicates of each treatment per site. Cockles for the addition (> 3 yr old; > 25 mm shell length) were collected from a nearby mudflat by hand-raking. To monitor cockle growth, we also added 25 tagged young cockles to each plot, yielding a total of 100 and 1000 cockles m⁻² for both density treatments. The 1200 young cockles (~2 yr old; 12 to 26 mm shell length) needed for tagging were collected by hand-raking and immediately transferred to tanks with aerated natural seawater in the laboratory. Here, shell length of each individual was measured to the nearest 0.01 mm with a vernier caliper, and tagged with a polyethylene label (Hallprint glue-on shellfish tags, Australia; Fig. 4.1C) glued to the shell with cyanoacrylate glue. The tagged cockles were added to the experimental plots within 24 hours after collection.

One year after the start of the experiment (May 2011), all cockles were re-collected by hand-raking and afterwards the sediment of the plot was sieved over a 1 mm mesh. Shell length of recaptured tagged cockles was again measured to nearest 0.01 mm. Untagged individuals were divided into two age-classes – recruits (cockle juveniles that survived their first winter after settlement in 2010) and adults (> 3 yr old) – after which they were counted.

Although experimental setups with similar constructions have proven to work very well in excluding birds without changing abiotic conditions in the Dutch Wadden Sea (van Gils et al. 2003), we nevertheless tested for possible effects on hydrodynamic conditions by measuring % weight loss of plaster dissolution cylinders (Donadi et al. 2013). Next to possible exclosure effects, the placement of plaster cylinders on all treatments also allowed for the testing of cockle density and site effects. Cylinders (6.3 cm long, 2.4 cm diameter) were made by molding plaster (Knauf B.V., Utrecht, The Netherlands) around steel nails after which they were dried, weighted, and placed in the field for four consecutive tidal cycles in September 2010. Cylinders were placed randomly in the middle of four out of six plots per treatment. After collection, cylinders were again dried (24h, 30°C) and weighed. The loss of dry weight was used as a relative measure of hydrodynamic stress (Donadi et al. 2013).

Finally, molluscivore shorebird abundance was measured in a 25×100 m plot, surrounding each experimental study site. The two areas were marked with PVC poles and birds were counted from a distance of 150 m, using a telescope (zoom
Figure 4.1 Overview of a shorebird exclosure (A), treatment densities: 100 and 1000 cockles m\(^{-2}\) (B) and the added tagged cockles (C).
ocular 20–60 ×; ATM 80 HD, Swarovski, Absam, Austria). By counting half an hour after the water retreated from the plots until half an hour before the water inundated the plots again, we excluded shorebirds that foraged on pelagic or epibenthic species (i.e. shrimp, fish) and thereby focused only on endobenthic species as prey item. The number of feeding shorebirds was scored every 15 minutes during low water. Based on literature (Goss-Custard et al. 1977; Zwarts et al. 1996; Kubetzki and Garthe 2003; Folmer et al. 2010; Duijns et al. 2013) and personal observations (E. M. van der Zee), shorebirds species with cockles in their diet were divided in groups that prefer either adult cockles (>12 mm; oystercatchers (Haematopus ostralegus), herring gulls (Larus argentatus), common gull (Larus canus) and black headed gulls (Larus ridibundus)) or cockle recruits (<12 mm; red knots (Calidris canutus), dunlins (Calidris alpina), bar-tailed godwits (Limosa lapponica) and curlews (Numenius arquata)). Birds were counted during 8 tidal cycles between June 2010 and May 2011.

Statistical analysis
For statistical comparisons, changes in adult cockles numbers were expressed as proportions relative to the initial numbers at the start of the experiment. To compare growth rate of cockles, we used the Bertalanffy’s growth function (Von Bertalanffy 1938). In this function, growth rate \( \frac{dH_t}{dt} \) declines with an increase in size \( H_t \) (the shell height in 2010) in the following way:

\[
\frac{dH_t}{dt} = k (H_\infty - H_t)
\]  

(1)

where \( H_\infty \) is the mean maximum size and \( k \) is the growth constant. For each individual cockle we estimated \( k \) by taking \( \frac{dH_t}{dt} \) as the difference in shell length between May 2011 and May 2010, \( H_t \) as shell height in May 2010 and \( H_\infty \) as 45 mm (Cardoso et al. 2006). To deal with pseudoreplication (for having multiple cockles per exclosure) we averaged the growth constant \( k \) of cockles per plot.

To test for the effects of predation, density and site, we used general and generalized linear models. Prior to model fitting, all data were checked for normality and homogeneity of variance using Shapiro-Wilk tests \( (P = 0.05) \) and Bartlett’s tests \( (P = 0.05) \) respectively. Therefore, we applied models with a Gaussian residual error distribution to changes in adult density, growth rate and plaster loss. Changes in adult cockle density were logit-transformed to obtain normality. Cockle recruitment could not be fitted to a Gaussian model. These data were therefore fitted to a Poisson regression model and a negative binomial model after which we selected the first model based on AIC comparisons. Furthermore, to test for significance of the random effect the exclosure-control pairs, we first ran all above analyses with linear mixed-effects models (GLMM’s) and repeated these procedures with linear models (GLM’s) without the random effect pair. We selected models without random effects
for all response variables based on AIC comparisons. For adult density, growth rate and plaster loss, we than used ANOVA tests. When applicable, we applied Tukey’s HSD for post-hoc comparisons. Finally, bird observation data were analyzed with Chi-square tests.

All statistical analyses were carried out in R (CRAN, R: A language and environment for statistical computing. 2013. R Foundation for Statistical computing. Vienna, Austria). GLMMs were constructed with the glmmadmb function in glmmADMB package. GLMs with negative binomial distributions were built with the glm.nb function from the MASS package. GLMs with Poisson error distributions, ANOVA models, post-hoc comparisons and Chi-squared test were constructed using the glm, aov, TukeyHSD and chiq.test functions from the Stats package (R Core Team).

Results

Adult cockle survival was significantly reduced by both high densities of cockles and predation by birds (Fig. 4.2A). However, whereas cockle survival was overall lowered by 19% in the high density treatment compared to low density treatment irrespective of both exclosure treatment and site (main effect of density: F = 78.69, n = 24, P < 0.001; $\bar{X}_{1000}$±SE = 25.9±5.3% vs. $\bar{X}_{100}$±SE = 44.6±9.1%), predation only negatively affected survival at the sandy site (interaction effect of site × exclosure: F = 5.19, n = 12, P = 0.03; Tukey’s HSD post-hoc test: site Sand, P < 0.001; site Mussel, P = 0.11) (Fig. 4.2A).

Growth rate of the tagged cockles was affected by site, density and predation (Fig. 4.2B). Cockle growth was 9% higher at the sandy site compared to the mussel site (main effect of site: F = 19.99, n = 24, P < 0.001; $\bar{X}_S$±SE = 0.56±0.01 k vs. $\bar{X}_M$±SE = 0.51±0.01 k). Growth rates were significantly lower in the 1000 cockle m$^{-2}$ than in the 100 cockle m$^{-2}$ plots, but only in the presence of predation (interaction effect of density×exclosure: F = 10.17, n = 12 P = 0.003 ; Tukey’s HSD post-hoc test: predation in control plots, P = 0.014; predation in exclosure plots, P = 0.55).

Cockle recruitment was significantly correlated with predation and site, but not with density (Fig. 4.2C). Cockle recruit densities were 69% lower in the control than in the exclosure plots (main effect of exclosure: $\chi^2$ = 33.2, df = 1, P < 0.001; $\bar{X}_c$±SE = 1.1±0.2 n m$^{-2}$ vs. $\bar{X}_e$±SE = 3.6±0.7 n m$^{-2}$) and 63% lower at site Sand compared to site Mussel (main effect of site; $\chi^2$ = 26.6, df = 1, P < 0.001; $\bar{X}_S$±SE = 1.3±0.3 n m$^{-2}$ vs. $\bar{X}_M$±SE = 3.5±0.7 n m$^{-2}$).

Furthermore, as expected because of differences in exposure to waves and currents (see Donadi et al. 2013), the effect of site was significant, with a higher relative weight loss at site Sand compared to site Mussel (main effect of site: F = 28.73, n = 8 P < 0.001; $\bar{X}_S$±SE = 44.6±0.4% vs. $\bar{X}_M$±SE = 36.1±0.8%). We found no
significant effects on plaster loss of exclosures (main effect of exclosure: $F = 0.02$, $n = 8$, $P = 0.89$; $X_{c} \pm SE = 40.2 \pm 1.8\%$ vs. $X_{ex} \pm SE = 40.4 \pm 1.9\%$) and cockle density (main effect of density: $F = 0.004$, $n = 8$, $P = 0.954$; $X_{100} \pm SE = 40.3 \pm 1.7\%$ vs. $X_{1000} \pm SE = 40.4 \pm 1.9\%$).

Observations of shorebirds foraging on adult-sized cockles resulted in a cumulative total density of 424 birds ha$^{-1}$ over 8 tides, with a density of 304 birds ha$^{-1}$ (63%
oystercatchers, 32% herring gulls, 1% common gulls and 4% black headed gulls) at the mussel site and a density of 120 birds ha\(^{-1}\) (20% oystercatchers, 7% herring gulls, 10% common gulls and 63% black headed gulls) at the sandy site (\(\chi^2 = 40.99, \text{df} = 1, P < 0.001\)). The density of shorebirds foraging on recruit-sized cockles was 504 birds ha\(^{-1}\), with a density of 244 birds ha\(^{-1}\) (16% red knots, 58% dunlins, 13% curlews and 13% bar-tailed godwits) at the mussel site and 260 birds ha\(^{-1}\) (23% red knots, 6% dunlins, 2% curlews and 69% bar-tailed godwits) at the sandy site (\(\chi^2 = 0.19, \text{df} = 1, P = 0.66\)).

**Discussion**

Although trophic interactions, competition and ecosystem engineering and their two-way interactions have been recognized as important structuring mechanisms in ecosystems, the interplay between the three types of interaction on population dynamics have not been investigated to our knowledge. In this study, we demonstrate that cockles, one of the most common and trophically important bivalve species in the Wadden Sea (e.g. Verwey 1981; van Gils *et al.* 2006; Compton *et al.* 2013), are caught between ecosystem engineering-induced processes that affect survival, growth and predation risk across different life stages. Our experimental results show that cockles have higher recruit and adult survival in the vicinity of mussels, most likely due to reduced hydrodynamics (see also Donadi *et al.* 2013). Moreover, despite the generally higher abundance of shorebirds foraging on adult cockles at the mussel site, high adult cockle densities (i.e., caused by the enhanced recruitment and adult survival) in combination with high densities of other potential prey (i.e., mussels) at this site seem to mitigate potential predation effects of this increased shorebird abundance, resulting in a lower predation pressure on adult cockles at the mussel site. Apart from these positive effects, ecosystem engineering by mussels negatively affected relative growth rates of cockles, an effect that is most likely caused by reduced water flow (and hence lower food availability) (Frechette *et al.* 1989) and by indirectly affecting inter-specific competition for food (Donadi *et al.* 2013) through the facilitation of cockles.

The low impact of predation on adult cockles at the mussel site compared to the control site can be explained by earlier studies arguing (Charnov 1976; Olsson and Molokwu 2007) or showing (Brown 1988) that predators have higher GUDs in higher quality foraging environments. At the mussel site, with high cockle densities and mussels nearby as an alternative prey for molluscivore shorebird that forage on adult-sized cockles, higher intake rates may induce higher GUDs and a reduced predation effect compared to the site not affected by mussel beds. Our results corresponds to this explanation by showing that numbers of remaining cockles in the control plots at the mussel site were higher for both manipulated densities (\(\bar{X}_{100} \pm \text{SE} \)).
= 43±4 and $\bar{X}_{1000±SE} = 260±16$ m$^{-2}$; see Fig. 4.2A) compared to numbers of remaining cockles in the control plots at the sandy site ($\bar{X}_{100±SE} = 34±1$ and $\bar{X}_{1000±SE} = 150±23$ m$^{-2}$; see Fig. 4.2A). However, since oystercatchers, the main avian predator of adult-sized cockles, can have very low GUDs for adult cockles (<25 m$^{-2}$; Zwarts et al. 1996), it is suggested that the actual GUD may not be reached yet for both sites, especially not in the high density treatments.

In contrast to predation on adult cockles, we found no significant site effect of predation on recruits (i.e. no interaction between site and exclosure on recruit densities). As the number of cockle recruits were relatively low at both sites, it seems likely that a lack of alternative prey for birds specifically feeding on this size class, results in lower GUDs at both sites, causing the observed differential result between recruits and adult cockles. Another explanation for this result might be that red knots, which are important avian predators of small cockles, have much larger home ranges (van Gils and Piersma 1999), than oystercatchers (Schwemmer and Garthe 2011). This suggests that the notion that environments differ between both sites may only hold for oystercatchers and not for red knots. For this reason, one would only expect a differential predation effect between sites for adult cockles, but not for recruits. The overall low densities of cockle recruits further indicates low survival during the first months after settlement, most likely due to predation by crustaceans (crabs and shrimps) that were able to enter the exclosures and are known to strongly reduce cockle spat numbers (e.g. Strasser 2002).

Apart from apparent interspecific competition for food between mussels and cockles (Donadi et al. 2013), we found a significant effect of cockle density on adult cockle survival and growth. The lower survival of adult cockles in the high density treatments is most likely caused by intraspecific interference competition for space (Peterson and Andre 1980) and/or by density-dependent predation by crabs (Seitz et al. 2001) and not by density-dependent predation by shorebirds because we did not detect a difference in density-dependent survival between the exclosure and control plots. The density-dependent effect on growth under normal condition (i.e. including predation), however, cannot solely be explained by intraspecific competition for food. The lack of a density-effect in predator exclosures indicates that the 1-m$^2$ plots were probably too small to cause significant differences in food depletion between the high and low density treatment (Kamermans et al. 1992, but see for example Peterson 1982) or that treatment densities were too low to see an effect of food depletion (Jensen 1992; 1993). We therefore suggest that the density-dependent effect on growth in the presence of predators and the lack of this effect in the absence of predators is a behavioural mechanism in response to predators (Brown and Kotler 2004 and references therein) rather than an effect of food depletion. Possibly, cockles in the exclosure plots burry less deeply, as there is no need to escape predation (but see Zwarts and Wanink 1989; Griffiths and Richardson 2006). A more shallow position would make it easier to filter-feed and by reducing
burrowing activities, less encounters with conspecifics would occur, resulting in longer feeding times (Peterson and Andre 1980). This effect can especially increase growth rate in the high densities plots with high encounter rates, thereby neutralizing the density-dependent effect of 1000 versus 100 cockles per m². Other behavioural responses of cockles to shorebird predation might be an extension of their valve closure time during low tide and/or the investment in thicker shelves (Irlandi and Peterson 1991; Smith and Jennings 2000). The absence of these responses when avian predators are excluded might neutralize the density-dependent effect on growth as well, but only if shorebird predation is density-dependent. For this hypothesis, however, we did not find evidence, since density-dependent survival did not differ between the exclosure and control plots (but see for example Goss-Custard 1977). Overall, we demonstrate that predation increases the strength of intraspecific competition.

Recently, integration of multiple interaction types into so-called “interaction networks” has been gaining attention, but the studies addressing this issue have mostly remained of a theoretical nature (e.g. Goudard and Loreau 2008; Kefi et al. 2012). Our empirical results clearly show that predation, competition and ecosystem engineering can interactively control population dynamics in a real ecosystem, which emphasizes the need to integrate multiple ecological interaction types into a single framework (Olff et al. 2009). Finally, our study shows that communities in intertidal soft-sediment ecosystem can be strongly structured by ecosystem engineers. We therefore argue that conservation and restoration of habitat-forming species like mussels, oysters and seagrasses is crucial for protecting the health and overall functioning of these ecosystems.

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