Creating a window of opportunity for establishing ecosystem engineers by adding substratum: a case study on mussels

JACOB J. CAPELLE [ID],[1,2,†] LENNET LEUCHTER,[1] MAURICE DE WIT,[1] EVA HARTOG,[1] AND TJEERD J. BOUMA[1,3,4]

[1]HZ University of Applied Sciences, Edisonweg 4, 4382 NW Vlissingen, The Netherlands
[2]Wageningen University and Research– Wageningen Marine Research, P.O. Box 77, 4400 AB Yerseke, The Netherlands
[3]Department of Estuarine and Delta Systems, Royal Netherlands Institute for Sea Research (NIOZ) and Utrecht University, P.O. Box 140, NL-4400 AC Yerseke, The Netherlands
[4]Faculty of Geosciences, Utrecht University, P.O. Box 80115, 3508 TC Utrecht, The Netherlands

Abstract. Ecosystem engineers typically exert positive feedback on their environment, which enhances their performance. Such positive feedback is lacking in the establishment phase, when densities are too low and/or patches are too small. There is a strong need to unravel the mechanisms for overcoming the resulting establishment thresholds, both for ecological restoration purposes and to be able to use their services. In the present study, we question whether providing a transient substratum can be used as tool to overcome establishment thresholds, by creating a window of opportunity for initial settlement, using mussels (*Mytilus edulis*) as a model system. Combining field and flume experiments, we study how biogenic substratum enrichment in the form of a shell layer on a soft mudflat affects the critical dislodgement thresholds and, thus, the chances of mussel establishment at different mussel densities and aggregation states. Flume results showed that the presence of a shell layer reduced dislodgement of mussel patches in low-energy environments but was conditional for establishment in high-energy environments. That is, in high-energy environments with shells, aggregation into clumps enhanced dislodgement, while dislodgement was reduced with increasing overall mussel biomass and overall mussel patch weight. Without shells, dislodgement was always 100%. These findings agreed with our field studies, which showed that coarse shell material reduced mussel losses (by a factor of 3), reduced aggregation (by a factor of 2.4), and increased attachment strength (by a factor of 2.4). Overall, our results show that the local presence of biogenic substratum increases the chance of mussel establishment by enhancing the critical hydrodynamic dislodgement threshold. Thus, the local addition of a biogenic substratum may create a window of opportunity to initiate settlement in more dynamic environments, to shift at a local scale from a bare mudflat state into an established biogenic reef state. Our findings have clear implications for how to approach restoration and management of ecosystem engineers dominated systems. For instance, when positive feedback of ecosystem engineers is lacking, (1) the transient offering of suitable settling substratum may be a necessary step to overcome establishment thresholds, and (2) this becomes increasingly important with increasing abiotic stress.

Key words: aggregation; density dependent; dislodgement; disturbance; flume; *Mytilus edulis*; positive feedback; stable state.

† E-mail: jacob.capelle@wur.nl

INTRODUCTION

To paraphrase John Donne (1624), no organism is an island entire of itself. Organisms interact with each other and with their environment. These interactions can eventually bring substantial changes to the environment around the organisms—often referred to as ecological

engineering—and significantly impact the functioning of the overall ecosystem (Jones et al. 1994). Ecosystem engineers are vital components in ecosystems and provide different goods and services to other organisms, including humans. Understanding this ecosystem engineering principle requires understanding of how the interaction of organisms with their environment alters the abiotic environment, and also how such changes in the abiotic environment affect the performance of the organism (Wright and Jones 2006). An important component within this context is that ecosystem engineers are able to exert positive feedback, which enhances their stability (Bertness and Leonard 1997, Jones et al. 1997). For example, macrophytes reduce hydrodynamic energy and drag within their environment, causing local accretion or wave attenuation that benefits expansion of the species (Bouma et al. 2005, Maxwell et al. 2017). Other examples are ants and termites that create biogenic structures that protect against threats and create optimal abiotic conditions for colony development (Jouquet et al. 2006). Reef-building organisms like corals, oysters, and mussels also exert positive feedback on their environments via their biophysical interactions (Coen et al. 2007, Norström et al. 2009).

Studies have found for various ecosystems that positive feedback such as that created by ecosystem engineers relates to alternative stable state dynamics (van de Koppel et al. 2001, Coco et al. 2006, Nyström et al. 2012). Alternative stable states in dynamic systems are characterized by the existence of multiple stable equilibria, with transitions occurring suddenly following a gradual change or large perturbation (Scheffer et al. 2001, Petraitis and Dudgeon 2004). The return to an initial state after a transition has taken place is inhibited by hysteresis effects (a condition wherein the reverse path is not the same as the forward path) that are inherent to alternative stable state dynamics (Scheffer et al. 2001, Folke et al. 2004). That is, merely returning to the external conditions that were present before a state shift occurred will not be enough to return to the original state. So, when a degraded state has been reached (i.e., when ecosystem engineers have been lost) after a catastrophic shift, it is inherently difficult to return to the original state.

Whereas ecosystem engineers rely on positive feedback to maintain their stable state, this positive feedback is typically absent when the ecosystem engineers have disappeared. Moreover, the positive feedback mechanisms that enhances the stability of ecosystem engineers are typically density and size dependent, which means that they are also lacking in the establishment phase (Bouma et al. 2009). As a result, the establishment of ecosystem engineers can be dependent on the occurrence of a specific short period with benign conditions, also referred to as a window of opportunity (Balke et al. 2014). Thus, a major question to answer in order to successfully restore degraded ecosystems by allowing ecosystem engineers to establish is: How can we successfully create windows of opportunity? In this study, we explore whether windows of opportunity might be created by the transient supply of settlement substratum.

A prerequisite for the initial establishment of reef-forming species like mussels, oysters, and corals is the availability of suitable settlement substratum. Here, the window of opportunity can be defined as the critical minimal duration that a suitable settlement substratum is available in the presence of recruits. For example, oyster reefs located at soft sediment locations require the presence of hard substratum for establishment. That is, the abiotic conditions might be suitable for oyster performance, but oysters cannot settle when hard substrata (such as an established oyster bed, stones, or shell banks) are lacking (Walles et al. 2016). Alternatively, where substrata are quickly buried, initial reef height in oysters in restoration efforts determines either the persistence or degradation of the reef (Jordan-Cooley et al. 2011, Colden et al. 2017). The overarching aim of the present paper is to improve current understanding of the role of spatial and temporal variable biogenic substrata on the establishment thresholds of ecosystem engineers, using the establishment of reef-forming mussels at soft-bottom environments as an ideal model species.

Mussels are reef-forming ecosystem engineers that generate environmental heterogeneity, which increases habitat diversity in coastal ecosystems (Arribas et al. 2014). Through their gregarious behavior, mussels self-organize in beds that form stable structures under a broad range of environmental conditions (Commito and Rusignuolo 2000, Hunt and Scheibling 2001, Van de Koppel

et al. 2005, Commito et al. 2014). Mussels attach themselves with collagenous byssus threads. Byssus threads can adhere to objects larger than 0.85 mm, which is equivalent to a size larger than coarse sand (Young 1983). Hence, mussels will attach to any hard structure: rocks (Hunt and Scheibling 2002); live or dead oyster shells (Fey et al. 2009); or any submerged material, such as rope (Dare and Davies 1975), wood, or steel (Seguin-Heine et al. 2014). Mussels are also found in soft sediment environments, where there is hardly any substratum large enough to attach to, making this the most challenging environment for mussel beds to become established (Commito and Dankers 2001, Büttger et al. 2008, Byers and Grabowski 2013).

In soft sediment environments, mussels attach to conspecifics to form dense mussel beds that can stretch out to a considerable scale (Van de Koppel et al. 2005, Commito et al. 2014, Christensen et al. 2015). Thus, established mussel beds exert positive feedback that stabilizes local sediment and increases mussel bed resilience (Meadows et al. 1998, Commito et al. 2005). Mussels adapt to increased environmental stress by increasing the number of byssal threads; for instance, attachment strength was found to be 15 times higher at the edges of the bed than at the middle (Witman and Suchanek 1984, Denny 1987, Bell and Gosline 1996).

Mussel beds are dynamic ecosystems that undergo cycles of disappearance and re-establishment (Theisen 1968). In general, the areas suitable for mussel bed occurrence greatly exceed the area where mature mussel beds are found, (Commito and Dankers 2001, Dankers et al. 2001, Airoldi and Beck 2007). Commonly, mussel beds re-establish after disasters (Dankers and Koelemaij 1989, Commito and Dankers 2001). Re-establishment is believed to be related to the presence of suitable substrata such as shell remains from old beds (Theisen 1968, Seed 1976, Dankers and Koelemaij 1989). This suggests that there is a link between substratum suitability and the critical dislodgement thresholds that hamper establishment. The effects of substrata in soft-bottom environments on critical dislodgement thresholds for the establishment of biogenic reefs have only been scarcely studied. The objective of the present study is to elucidate whether the addition of biogenic substratum on soft-bottom environments can be used to create a window of opportunity for establishment, by enhancing the critical hydrodynamic dislodgement threshold, with dislodgement being a major threshold to mussel bed establishment.

We hypothesize that in dynamic systems where the chances of establishment are low, the transient addition of substratum will act as a window of opportunity for establishing positive feedbacks for ecosystem engineers by lifting the establishment threshold.

Using mussel beds as a case study, we expect to find that (1) the spatial characteristics of a mussel bed on soft-bottom habitats are different when a biogenic substratum is provided, and the substratum will reduce conspecific aggregation and patch scale density; (2) with substratum the critical dislodgement threshold of mussels is elevated; (3) this effect increases with environmental energy, at lower mussel densities, and when mussels are not aggregated; (4) the effects of substratum on patch stability are that they provide a higher patch mass, provide increased anchorage points to the soft-bottom underlayer, and increase scouring, around the patch; (5) establishing a mussel bed with substratum makes it more resilient to disturbances and can thus be used to create a window of opportunity for the establishment of positive feedback in mussel beds.

MATERIALS AND METHODS

Process-based measurements were obtained from a lab experiment using a large racetrack flume. The results were validated in a field experiment. Treatments are summarized in Table 1.

Experimental design

We performed three different experiments in a flume to measure critical hydrodynamic dislodgement thresholds. In the first experiment, we tested effects of mussel biomass, aggregation time, and shells on dislodgement under a moderate and high flow speed. In the second experiment, we quantified effect of clump size and type of substratum on dislodgement thresholds of mussel clumps. In the third experiment, we measured the effect of mussels with and without shells on sediment transport.

The race track flume is situated at the Royal Netherlands Institute for Sea Research (NIOZ) in

Table 1. Overview of the different treatments applied in the flume and in the field experiment.

Experiment and response	Effect
Flume	
Dislodgement (%) at (1) high (0.6 m/s) and (2) moderate flow (0.4 m/s) speed	(1) Patch density (1, 2.5, and 10 kg/m^2)
	(2) Aggregation (aggregated into clumps and non-aggregated)
	(3) Substratum (shells, no shells)
Dislodgement threshold (m/s) at stepwise increase (steps: 0.05 m/s) of flow speed	(1) Underlayer (hard smooth, soft)
	(2) Waves at soft underlayer (yes, no)
	(3) Clump size (2, 4, 8, 16, and 32 mussels per clump)
	(4) Substratum (shells, no shells)
Sediment transport (cm^3)	(1) Clump area (variable, $n = 8$)
	(2) Substratum (shells, no shells)
Field	
(1) Attachment strength (N)	(1) Substratum (shells, no shells)
(2) Aggregation behavior	
(3) Change in patch density	
(4) Losses (%)	

Yerseke, the Netherlands (for details, see Bouma et al. 2005). The experiments were carried out on steel boxes with dimensions of 0.58 × 0.58 × 0.05 m filled with coarse sand. These sand-filled boxes fit exactly into a spacing so that they could be placed level with the floor of the flume. The mussels (*Mytilus edulis*) used in the experiment were between 20 and 40 mm in length. For the duration of the experiment, the mussels were kept in the Oosterschelde and were never used in more than two flume runs.

In a field experiment, we demonstrated the effect of substratum on the resilience of a newly established mussel bed and tested the effect of substratum on mussel aggregation, patch density, and attachment strength. Two treatments were applied in triplicate on six square plots with an area of 4 m^2 (2 × 2 m). On three randomly chosen plots, 2.5 kg/m^2 of coarse shell material and 2.5 kg/m^2 of mussel seed was homogeneously distributed. On the other three plots, the substratum remained unaltered (i.e., no shells

were added) and 2.5 kg/m^2 of mussel seed was homogeneously distributed.

The experiment was executed on an intertidal mussel lease site in the Oosterschelde (51°33′193″ N, 3°53′327″ E) between the 23 October 2014 and the 20 November 2014. Size class of the natural occurring sediment was measured from a 5 cm top layer of a random quadrant (0.25 m^2).

In order to minimize shore crab predation, a crab-proof fence was erected around the experimental area. The fence enclosed the experimental area with a buffer zone of 2 m around the plots; the fence design was based on fence type E, in Davies et al. (1980). The flow velocity inside and outside the fenced enclosure was measured for five days (13−17 November) 20 cm above the sediment with a Nortek Aquadopp profiler to determine the flow rate and test possible effect of the fence on the current velocity.

Mussel aggregation and mussel patch density

From the setup in the field, top-view photographs were taken at low tide, right after seeding the plots ($t = 0$), and at the end of the experiment ($t = 1$). Poles delimiting the edges of the plots were georeferenced using a D-GPS device to determine the exact position and scale of the plot photographs. Images were analyzed by converting mussel cover into polygons using ArcGIS 10. For each individual plot, the number of patches, individual size of all patches (m^2), perimeter per patch (m), and perimeter-to-area ratio (m^{-1}) were calculated. The density within patches was determined by dividing mussel density (n/m^2) by total patch area per plot. The factor of aggregation was calculated as: within-patch-density ($t = 1$)/within-patch-density ($t = 0$). Byssal attachment strength of a volumetric subsample (820 mL) of the mussels from each plot was taken and measured with a Newton meter. The Newton meter was connected to a plastic clamp that was then used to clutch single mussels. Conspecific attachment as well as attachment to associated flora fauna and debris (cockleshells on treatment plots) of the mussels was measured randomly.

Critical dislodgement threshold of mussel patches

The effects of a shell layer on mussel dislodgement were tested with mussel biomass and

pre-aggregation time as co-variables, at a moderate and high flow speed. In total, 48 runs of 24 duplicated treatments were performed in the flume. Mussels were tested in three different biomasses: 2500, 5000, and 10,000 g/m^2, based on Capelle et al. (2014). These biomasses represent the low-to-high range of the densities found on mussel bottom culture plots in this area. Half of all the biomasses were supplied with a 1:1 (mussel: shell) weight ratio of shells made out of intact cockle (*Cerastoderma edule* L.) shells. Since the coarse shell material was added in the same biomass as mussels, sediment coverage was comparable between the 2.5 and 5 kg m^2 with shells and the 5 and 10 kg m^2 without shells, respectively. Half of the treatments were exposed to the flow immediately after laying; the other half of the treatments were kept in the steel boxes for three days in large tanks with aerated sea water and were thus given time to aggregate before being exposed in the flume. Aggregation resulted in large strong patches at higher biomasses or in strong clumps at lower biomasses, while mussels that were not previously aggregated attached much more loosely to the nearest attachment substratum or to each other. The aggregation period of three days was chosen based on pretrials, which showed that aggregation behavior in the pre-treatment tanks was visually completed in three days. Twenty-four runs were performed using a five-minute exposure to a flow speed of 40 cm/s; the other 24 runs were performed using a five-minute exposure to a flow speed of 60 cm/s. Flow speed levels were based on flow speed measurements in the Oosterschelde that were carried out prior to the experiment (Appendix S1: Fig. S1) at mussel bottom culture plots, with 40 cm/s close to an average culture plot flow speed and 60 cm/s close to a maximum culture plot flow speed.

Interactions between mussel clump size and the underlayer

Mussel clumps were created in densities of two, four, eight, 16, and 32 mussels per clump. In half of the clumps, mussels were mixed with the same biomass of empty cockleshells. Mussels were kept in aerated seawater for three days and molded by hand every day to stimulate aggregation. Aggregated mussels clumps were placed in the middle of the flume. Flow velocity was increased in a stepwise manner using 60-s time steps, starting with a flow speed of 25 cm/s and increasing with steps of 5 cm/s. The critical hydrodynamic dislodgement threshold (i.e., hydrodynamic energy needed to displace a mussel patch) was reordered.

Treatments were applied in triplicate on a coarse sand substratum without waves, then repeated on smooth hard substratum (Trespa material) on which the mussels were not able to attach, and then finally repeated on coarse sand substratum with waves. Mussel clumps were exposed to flow immediately after placement on the substratum. The maximum flow speed that could technically be achieved was 70 cm/s without waves. With waves, the maximum flow speed was 45 cm/s (without orbital velocity). Above these speeds, water spillage became too extensive. We imposed regular waves that were 10 cm high and had a period of 1 s.

Patch morphology was measured prior to placing them into the flume, by taking top and frontal images of patches with a scale bar. In ImageJ, the following parameters were retrieved: mussel patch density (i.e., five levels: two, four, eight, 16, and 32 mussels/patch); maximum height (mm) of a mussel patch; stability index (defined as the ratio between patch area [mm^2] and maximum patch height [mm]), mussel-to-substratum (coarse shell material) ratio (|two levels: 1 or 0); mussel patch mass (g) including shell substratum.

In addition, in eight mussel patches, with and without substratum sediment transport was measured. Due to time constraints, we chose a practical approach by taking an average clump size of eight mussels, two clumps with shells and two clumps without shells. The clumps with shells corresponded with an area of ~20 mussels without shells, and the clumps without shells with clumps of four mussels with shells (properties summarized in Appendix S2: Table S1). These patches were placed in the flume in the middle of an experimental box filled with soft substratum and exposed to a laminar flow of 35 cm/s for 15 min. Erosion and sedimentation after 15-min exposure were quantified by mapping the sediment morphology using a PVC beam with a small hole every cm (diameter = 3 mm). An iron rod (diameter = 2.5 mm) was carefully lowered through each hole until

the top of the sediment at a 1 × 1-cm grid. The pieces of rod extending the PVC beam were measured to the nearest millimeter. All measurements were presented relative to a reference height taken before exposure. The result is a 1 × 1 cm x-y grid with length in the z direction that relates to erosion when negative or to sedimentation when positive. Total sediment transport (cm^3) was calculated as the net difference between sedimentation (cm^3) and erosion (cm^3).

In situ validation

In the field experiment, we weighed and counted the mussels from each plot at the start and at the end of the experiment. Mussel density per plot was calculated by dividing mussel biomass per plot by plot area. The loss percentage for each plot during the four weeks was calculated as $(n_{end}\ m^{-2})/(n_{start}\ m^{-2}) \times 100$.

Data analysis

Flume experiments.—Data of the first experiment were analyzed for high (60 cm/s) and low (40 cm/s) flow speed levels, respectively. Dislodgement ratio was modeled as a function of the explanatory factors and their interaction using a logistic regression model with proportions. Underdispersion (low-energy level = 0.15, high-energy level = 0.12) was corrected for with a quasibinomial error distribution (Geyer 2003). Model simplification was achieved by stepwise reduction in model parameters, starting with the highest-order interactions. Parameters were retained when removal resulted in a significant difference between original and simplified model in an F-test. Pairwise comparisons were carried out using Wald chi-square tests. Results from the logistic regression models were back-transformed to dislodgement ratio as: $e^y/[1 + e^y]$. Model assumptions were interpreted with a binned residual plot (Gelman and Su 2018).

The effect of cluster morphology on dislodgement on soft substratum with and without waves and on hard substratum in flume experiment 2 was right-censored and analyzed with Tobit regression using the VGAM package in R (Yee 2007). Measured variables were maximum patch height, patch mussel biomass, patch weight, patch area, and patch frontal area. These variables show

an initial high level of multicollinearity. For that reason, variables in the analysis were limited to index of stability (g/mm), defined as patch area divided by patch frontal area, patch weight, and mussel: substratum ratio (2 levels: 1,0); index of stability and patch weight were only weakly correlated (ρ: 0.2). The minimal adequate model was achieved by a stepwise reduction of a full model with all explanatory variables included. Homogeneity and normality of variance were evaluated by residual plotting, following Yee (2007).

Field experiment.—The factors of aggregation, seed loss, and attachment strength were analyzed by testing for the difference between the means of the two treatments with a Kruskal-Wallis test. The third spatial parameter (P/A), as well as the condition index, was tested for the difference between means of treatments in a one-way ANOVA. Normal distribution of residuals was tested with a Shapiro-Wilk test. Homogeneity of residual variance was tested with a Bartlett test.

All tests were performed using a significance level of 0.05 and carried out in R, 3.1.2 (R Core Team 2013).

RESULTS

Mussel aggregation and mussel patch density

The attachment strength (Fig. 1A) of mussels on shell treatment plots (2.06 N) was, on average, 2.44 times higher than the attachment of mussels on a control plot (0.85 N; $P < 0.001$). Density within patches in the field experiment on culture plots with shells as treatment (4847 mussels/m^2) was lower ($H = 3.8571$, $P = 0.4953$) than patch density on control mussel-only plots (8667 mussels/m^2). That is, the density within patches for control treatment was 1.79 times higher than when coarse shell material was applied. Mussels on plots where shell material was applied prior to relaying aggregated less ($H = 3.8571$, $P = 0.04953$, Fig. 1B) than mussels on unaltered substratum. Aggregation on culture plots lacking coarse shell material increased by a factor of 2.42, while aggregation appeared to remain constant on plots with prepared substratum showing an aggregation factor of 1.06. The ratio of perimeter to area (P/A) at the end of the experiment is lower on shell treatment plots (45.32 m) than the P/A on control plots (66.74 m; $F = 20.24$, $P = 0.0108$, Fig. 1C).

Critical dislodgement threshold of mussel patches

A high flow speed of 60 cm/s resulted in substantially higher mussel dislodgement (84.42%) than a moderate flow speed of 40 cm/s (14.45%, $P < 0.001$). At the high flow speed, more mussels were dislodged after three days of pre-aggregation (X^2 (1, $n = 24$) = 13.7, $P < 0.001$) than mussels that were exposed immediately after placement in flume (Fig. 2). In addition, a shell layer resulted in lower dislodgement than treatments without shell layer (X^2 (1, $n = 24$) = 5.4, $P = 0.02$), as 100% of the mussels dislodged in the treatment without shell layer. There was no significant effect of mussel biomass, and there were no significant interactions. The average proportions of dislodged mussels for significant factors (back-transformed results of the logistic regression model) are summarized in Table 2.

At a moderate flow speed (40 cm/s), the presence of a shell layer resulted in a lower
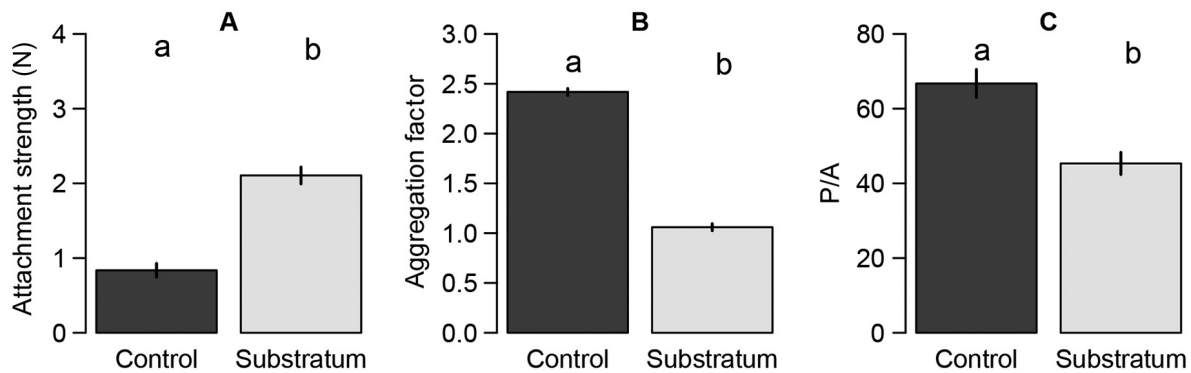

Fig. 1. Mussel response parameters (±standard error) as measured at the end of a field experiment on soft sediment without predation over a five-week period with ($n = 3$) and without ($n = 3$) shell layer: (A) mussel attachment strength (N, $n_{control} = 182$, $n_{shells} = 201$), (B) aggregation factor ($n_{control} = 3$, $n_{shells} = 3$), and (C) perimeter-to-area (P/A) ratio ($n_{control} = 3$, $n_{shells} = 3$). Letters indicate significant differences. Attachment strength was measured with a Newton meter connected to a plastic clamp, which was then used to clutch single mussels. The aggregation factor was measured as within-patch-density ($t = 1$)/within-patch-density ($t = 0$), with higher numbers indicating a higher compaction over time. The perimeter-to-area (P/A) ratio indicated the compactness of a clump, with lower numbers indicating more compact clumps, and was measured as area of a patch (m^2)/ perimeter a patch (m).
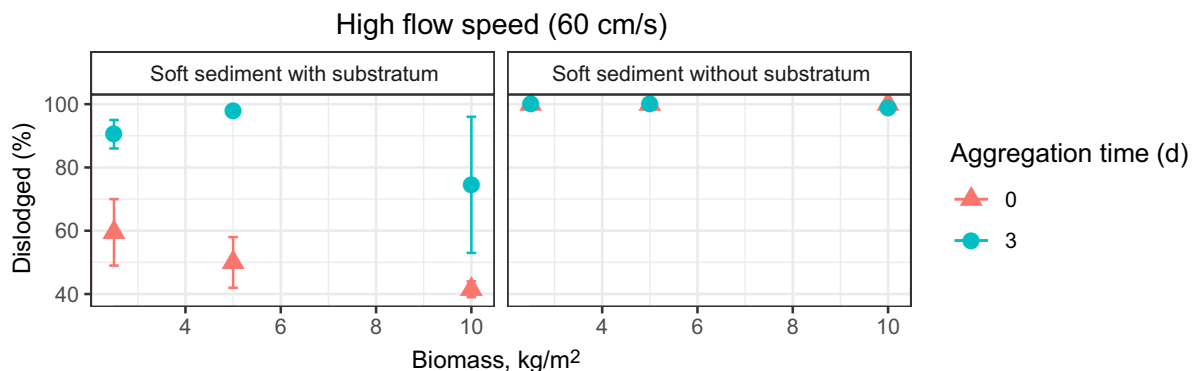

Fig. 2. Percentage of mussel biomass dislodged (±standard error, $n = 24$) after a single exposure to a flow speed of 60 cm/s for mussels placed in three different biomasses (2.5, 5, and 10 kg/m^2) with and without a pre-aggregation period and with and without a shell layer.

dislodgement ratio (X^2 (1, $n = 24$) = 9.8, P = 00.02). Dislodgement decreased with mussel biomass (X^2 (2, $n = 24$) = 19.2, $P < 0.001$; Fig. 3). In addition, more mussels are displaced after three days of aggregation than mussels that were exposed without pre-aggregation time (X^2 (1, $n = 24$) = 24.8, $P < 0.001$; Fig. 3). There is an interaction between presence of shell material and pre-aggregation time (X^2 (1, $n = 24$) = 23, $P < 0.001$), and between biomass and pre-aggregation time (X^2 (2, $n = 24$) = 11.4, $P = 0.003$). The average proportions of dislodged mussels for significant factors (back-transformed results of the logistic regression model) are summarized in Table 3.

The results so far indicate that biomass has a large effect on mussel dislodgement and that presence of a shell layer further reduces mussel dislodgement. Mixing mussels with shells at a 1:1 biomass ratio increased the biomass by 100%. Increasing biomass can reduce dislodgement based only on a higher mass. To test this assumption, we repeated the analysis for the 40 cm/s

treatment, replacing only mussel biomass with total (mussel + shell) biomass. As expected, an increase in total biomass reduces mussel dislodgement, but mussel dislodgement remains lower on a shell layer compared to a similar biomass on bare sediment (Table 4).

Interactions between mussel clump size and the underlayer

The results clearly show that adding shells into the patches increased the dislodgement threshold on all underlayers (Table 5). The regression lines in Fig. 4 indicate that the dislodgement threshold was about 5 cm/s higher with shells than without shells. Of the patch morphology parameters, only patch weight was negatively related to dislodgement in all treatments. The index of stability, which we defined as the patch area divided by the patch frontal area, could not be related to the dislodgement threshold in all substrata treatments.

In the soft sediment treatment, not all mussel patches with shells were dislodged, even at the maximal flow velocity of 70 cm/s (Fig. 4A). On the smooth hard substratum, the dislodgement threshold was much lower than on soft sediment, and all mussel patches without shells and with shells were dislodged at 35 and 45 cm/s, respectively (Fig. 4B). The impact of waves on mussel dislodgement on soft sediment was not very different to the impact without waves, in that not all mussel patches with shells could be displaced even at the maximal hydrodynamic forcing (i.e., 45 cm/s flow plus waves; Fig. 4C). The results

Table 2. Back-transformed results of the final logistic regression model at 60 cm/s, showing average proportions of dislodged mussel biomass.

Shells	No[†]		Yes[†]	
Aggregation time (d)	0[‡]	3[‡]	0[‡]	3[‡]
Proportion displaced	1	1	0.51	0.87

† $n = 12$.
‡ $n = 6$.

Moderate flow speed (40 cm/s)
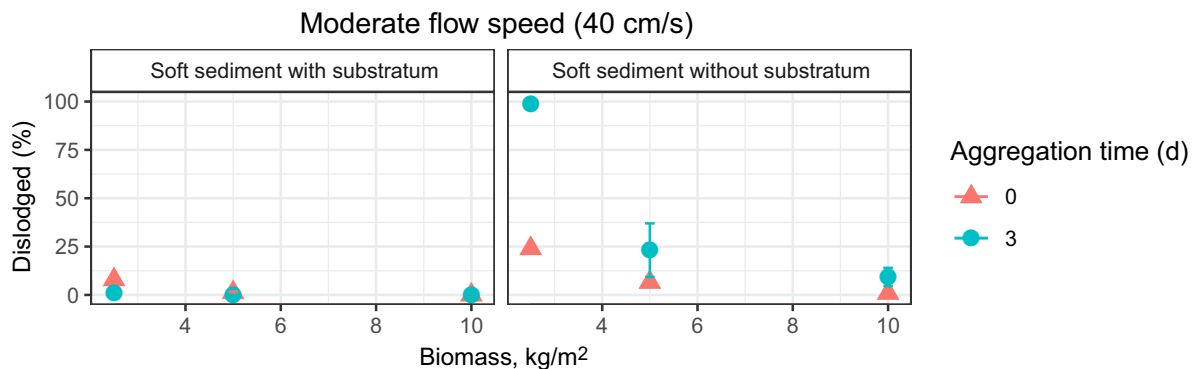
Fig. 3. Percentage of mussel biomass dislodged (±standard error, $n = 24$) after a single exposure to a flow speed of 40 cm/s for mussels placed in three different biomasses (2.5, 5, and 10 kg/m²) with and without a pre-aggregation period and with and without a shell layer.

Table 3. Back-transformed results of the final logistic regression model at 40 cm/s, showing average proportions of dislodged mussel biomass.

Shells	No[†]		Yes[†]	
Pre-aggregation time (d)	0[‡]	3[‡]	0[‡]	3[‡]
Biomass (g/m^2)				
2500[§]	0.25	0.99	0.07	0.01
5000[§]	0.06	0.23	0.02	<0.01
10,000[§]	<0.01	0.09	<0.01	<0.01

[†] $n = 12$.
[‡] $n = 6$.
[§] $n = 8$.

Table 4. Back-transformed results of the final logistic regression model at 40 cm/s, showing average proportions of dislodged mussel biomass, when replacing only mussel biomass with total biomass (mussels + shells).

Shells	No[†]		Yes[†]	
Pre-aggregation time (d)	0[‡]	3[‡]	0[‡]	3[‡]
Biomass (g/m^2)				
5000[§]	0.09	0.43	0.01	0.09
10,000[§]	<0.01	0.03	<0.01	<0.01

[†] $n = 12$.
[‡] $n = 6$.
[§] $n = 8$.

clearly show that mussel patches interact with their substratum, as persistence on smooth hard substratum is limited by a lack of friction, while on soft substratum it was observed that scouring resulted in a lowering (and thereby stabilization) of the mussel patch by undercutting. Results from the sedimentation and erosion measurements showed that scouring was related to the weight of the mussel patch and was not enhanced by the presence of shells (Fig. 5).

In situ validation

The grain size analysis revealed that the substratum in the location of the experiment was composed of 93.4% fine sand (0.25 mm), silt, and clay (≤0.63 mm). Particles that were big enough for *M. edulis* to attach to (>0.85 mm) were estimated between 1 and 2%. The observed flow ranged between 0 and 0.3 m/s and did not show differences of flow velocity between the inside and outside of the enclosure.

Table 5. Results of final Tobit regression model for flume experiment 2: cumulative exposure of mussel patches to increasing flow speed, on soft sediment, hard sediment, and soft sediment with waves, all treatments were carried out in triplicate ($n = 15$ with and $n = 15$ without substratum).

Factor	Response: mussel dislodgement threshold mussel clump (m/s)			
	Estimate	Standard error	z	P
Soft substrate				
Shells	1.30	0.33	3.89	<0.001
Patch weight	0.01	0.004	3.02	0.003
Hard substrate				
Shells	0.60	0.20	2.95	0.003
Patch weight	0.006	0.002	2.88	0.004
Soft substrate with waves				
Shells	0.74	0.14	5.29	<0.001
Patch weight	0.007	0.002	3.03	0.003

The field experiments (where predation was excluded) confirmed our flume findings that loss of mussels (Fig. 6) is lower when substratum was prepared with shell material (6.09 mussels·d^{-1}·m^{-2}) than for unprepared substratum (18.99 mussels·d^{-1}·m^{-2}, $H = 3.8571$, $P = 0.04953$). Most of the washed-away mussels were retained at the basis of the crab-proof fences, so that only 3.5% of the mussels were lost and could not be accounted for.

DISCUSSION

Ecosystem engineers typically face establishment thresholds due to a lack of positive feedback in the early phase. We found that transient substratum addition diminishes the establishment threshold by decreasing the risk of hydrodynamic dislodgement, thereby creating a window of opportunity that has been defined as a short time frame where conditions are temporarily favorable, thus allowing establishment.

Role of substratum in thresholds for dislodgement in mussels and other ecosystem engineers

Mussels are not sedentary like most other ecosystem engineers; instead, they aggregate actively. Due to required substratum sizes for
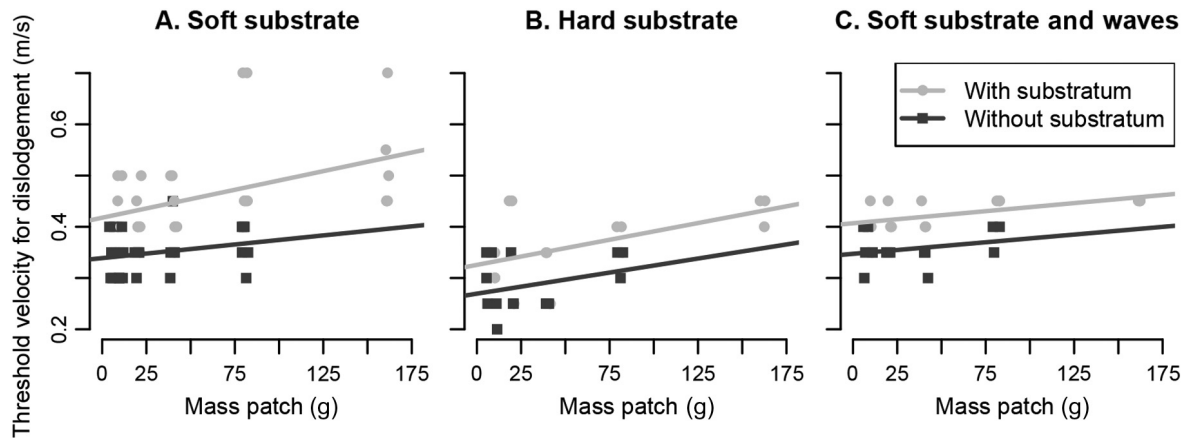
Fig. 4. Threshold velocity for dislodgement for different sized mussel clumps with ($n = 15$, per substratum) and without ($n = 15$, per substratum) shells as substratum exposed to increasing flow speeds on (A) soft underlayer (censored at 0.7 m/s, without substratum, $y = 0.0003x + 0.34$; $R^2 = 0.03$; with substratum, $y = 0.0007x + 0.42$; $R^2 = 0.15$), (B) hard underlayer (without substratum, $y = 0.0005x + 0.27$; $R^2 = 0.02$; with substratum, $y = 0.0007x + 0.33$; $R^2 = 0.23$), and (C) soft underlayer with waves (flow speed without orbital velocity and censored at 0.45 m/s, without substratum, $y = 0.0003x + 0.35$; $R^2 = 0.001$; with substratum, $y = 0.0003x + 0.41$; $R^2 = 0.26$).
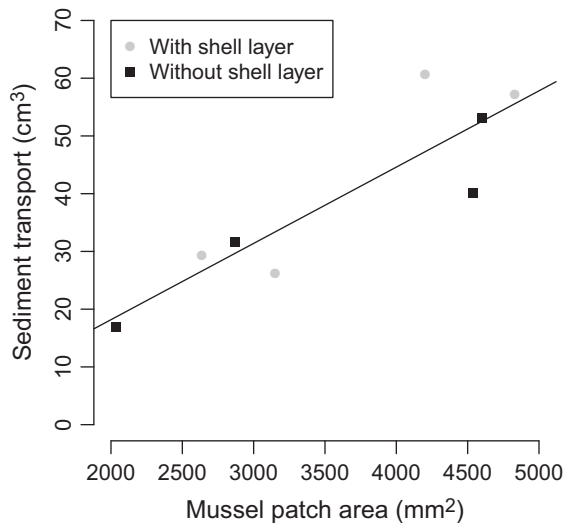

Fig. 5. Relation between sediment transport (s) and mussel patch area (A) ($s = 0.013A-8.24$, $P = 0.004$, $R^2 = 0.75$, $n = 8$) after exposure to a laminar flow of 35 cm/s for 15 min. Sediment transport was measured by taking the difference between average erosion (expressed as negative values) and sedimentation (expressed as positive values) under and around a mussel patch.

Fig. 6. Mussel losses (±standard error) after five weeks in a field experiment on 4-m^2 plots ($n_{control} = 3$, $n_{shells} = 3$) on soft sediment without predation over a five-week period with and without shell layer. Letters indicate significant differences.

attachment (Young 1983), in soft sediment environments the (secondary) external attachment substratum for mussels is limited to existing reefs, shell remains, and each other (Theisen
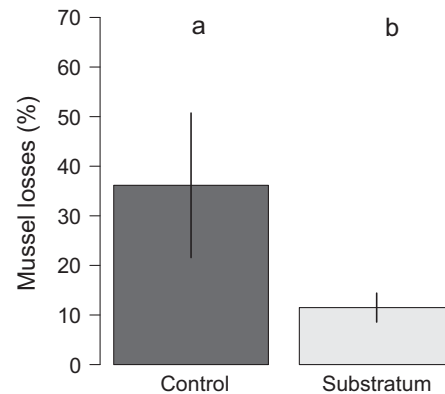
1968, Commito et al. 2005, 2014). In the absence of external attachment substrata, mussels aggregate into higher biomass patches than in situations with attachment substratum (Fig. 1). Aggregation is regarded as a facilitating process that provides protection against dislodgement and predators (Hunt and Scheibling 2001). For example, spatial patterning of soft-bottom mussel beds can partly be explained by a trade-off between this facilitation and the effect of

interspecific competition (Van de Koppel et al. 2005, Van De Koppel et al. 2008). However, experimental evidence on the facilitating effect of mussel aggregation is scarce. In the flume, we observed that the stability (dislodgement threshold) was highest in high-biomass pre-aggregated patches. Stability decreased when mussels without substratum to attach to the underlayer were pre-aggregated into small clumps at lower densities, which started rolling by the flow. Thus, mussel bed resilience to disturbances can be expected to be enhanced above the threshold density when mussel configuration changes from clumps into a reticulate network, as was predicted by Liu et al. (2014) from model analysis.

Stability increased when non-aggregated mussels were exposed to flow because part of the mussels that were dislodged were caught by mussels of shells in the distal part of the patch. At the end of the experiment, incidental wedge-shaped heaps of mussels remained on the sediment. The occurrence of this effect increased with mussel and shell biomass. The effect where mussels dislodged from the frontal area are retained distally might also occur on natural mussel beds. Therefore, stability on the bed scale can be much higher than on the patch scale. This phenomenon may result in patterns of mussel patches on wild beds, which are the result of accumulated mussels by flow or wave forcing, a pattern that has been found in different areas in the world (Morales et al. 2006, Donker et al. 2012, Commito et al. 2014).

Aggregation increases patch density, which increases competition between mussels (Capelle et al. 2014). In our in situ experiment, within-mussel-patch density increased by a factor 2.5. However, mussel patch density did not change after relay when a shell layer was added. The benefit of reduced competition did not reduce the facilitation effect: The flume study showed the stabilizing effect of a shell layer, which facilitates better anchoring of mussels to the underlayer. At a flow speed of 60 cm/s (representing high environmental stress levels), shells were conditional for establishment: Dislodgement without shells was always 100%. A reduction in losses caused by dislodgement in situ validated this effect. Furthermore, apart from competition for food, aggregation also increases competition for space. Individuals will try to climb on top of each other to reach favorable positions, which weakens the attachment strength through discontinuity (Christensen et al. 2015). The addition of shells reduces aggregation and results in a continuous attachment, which explains the stronger attachment strength that was found in the presence of shells.

Adding attachment substratum can also reduce mussel bed performance. For instance, Bertolini et al. (2017) suggested that a limited aggregation that follows the addition of shells (in *Modiolus modiolus*) is not helping restoration purposes because it reduces density-dependent recruitment. However, when the establishment of such positive feedback (as density-dependent recruitment) is prevented by disturbances in high-energy environments, the availability of a substratum can be more important (Geraldi et al. 2013). Also, for oysters it was suggested that the increased substratum complexity of empty shells improves recruitment by providing a refuge for spat against predation (Carroll et al. 2015).

Widdows et al. (2002) showed that erodibility (reducing stability) increases at low mussel densities because of scour around patches and reduced sediment protection from less mussel interconnection. The density-dependent dislodgement we observed was not due to a reduction in erodibility. The dislodgement threshold was lower on smooth hard substratum (to which the mussels could not attach) than on soft substratum. On smooth hard substratum, there was no interaction with the sediment (no sediment transport). Our results suggest that regardless of patch size, scour around the patches did in fact have a stabilizing effect. Sediment transport provides shelter through typical erosion around the patch and sedimentation after the patch, which substantially reduces the height above the sediment. Interestingly, the mussels themselves also act as substratum and several studies have shown that epibenthic growth on mussels, specifically by macroalgae, can greatly affect the drag on the mussels and dependent on the circumstances induce or reduce dislodgement (Witman and Suchanek 1984, O'Connor et al. 2006, O'Connor 2010).

Substrata that affect dislodgement thresholds have also been observed in other ecosystem engineers. For example, mangrove seedling substratum anchorage occurs with roots whose length is

proportional to the dislodgement risk (Balke et al. 2011). Establishment of oysters also appears to be limited by substratum and hydrodynamic conditions and not by the presence or absence of larvae (Francis et al. 1995, Geraldi et al. 2013).

Windows of opportunity for the establishment of positive feedback increase stability and resilience

Persistence of ecosystem engineers in dynamic systems is dependent on strong feedback between biotic factors and the physical environment (Jones et al. 1997, Suding et al. 2004). In populations of ecosystem engineers, such as mussels (Meadows et al. 1998), oysters (Campbell 2015), and macroalgae (England et al. 2008), population losses increase with tidal energy. Storms and strong currents are highly responsible for structuring the distributions of ecosystem engineers in coastal ecosystems (Theisen 1968, Witman and Suchanek 1984, Witman 1987, Nehls and Thiel 1993, O'Connor et al. 2006). In such dynamic environments, ecosystem engineers are dependent on positive feedback for their own resilience against disturbances; for example, bivalve beds stabilize the sediment. Many studies have addressed the feedback of established soft-bottom ecosystem engineers, such as on salt marshes (Bouma et al. 2005, 2009), sea grass beds (Maxwell et al. 2017), oyster reefs (Coen et al. 2007), Sabellaria reefs (Godet et al. 2011), and mussel beds (Prins et al. 1997, Van de Koppel et al. 2005).

In ecosystem engineers, vulnerability to disturbances is greater in the establishment phase than in mature reefs (Liu et al. 2014). For example, adult mussels provide stability against dislodgement and shelter against predation (Wilcox and Jeffs 2017). Furthermore, expansion of mature beds is stimulated through a positive resource-mediated feedback, where shell production is enhanced through recruitment (Gutierrez et al. 2003). Shells become part of the mussel bed and will gradually be buried by the silt that accumulates underneath the bed. Once reefs have disappeared, shells in highly dynamic systems are removed or buried, which may shift community dynamics into an alternative state (Petraitis and Dudgeon 2004) where mussels are simply not able to settle due to the lack of substrata. A return to the initial state where reefs are present might be dependent on the occurrence of a window of opportunity to push conditions beyond the bifurcation point (Balke et al. 2014), which seldom occurs in such highly dynamic systems (Suding and Hobbs 2009, Kraan et al. 2011). Moreover, the lack of positive feedback of ecosystem engineers in the establishment phase creates a threshold that limits the chance of establishment. This is a cause of great concern, since the worldwide state of biogenic reefs are considered very poor (e.g., Figure 1 in Beck et al. 2009); reefs are among the ecosystems with the highest cumulative human impact (Halpern et al. 2008).

Using mussels as a model species, we found evidence that with adding transient substratum, a window of opportunity is created that enhances the chance of establishment in dynamic systems. Our results implicate that when positive feedback of ecosystem engineers (e.g., by providing biogenic settling substrata or reducing environmental stress; Widdows et al. 1998, Donker et al. 2012, Walles et al. 2014) is lacking, the transient offering of suitable settling substratum may be a necessary step to overcome establishment thresholds, and this is increasingly important with increasing abiotic stress (in our case hydrodynamic forcing) of the systems. This approach may be expected to be widely applicable for restoring ecosystem engineers, beyond our case study of mussels.

Literature Cited

Airoldi, L., and M. W. Beck. 2007. Loss, status and trends for coastal marine habitats of Europe. Oceanography and Marine Biology: an Annual Review 45:345–405.

Arribas, L. P., L. Donnarumma, M. G. Palomo, and R. A. Scrosati. 2014. Intertidal mussels as ecosystem engineers: their associated invertebrate biodiversity under contrasting wave exposures. Marine Biodiversity 44:203–211.

Balke, T., T. J. Bouma, E. M. Horstman, E. L. Webb, P. L. A. Erftemeijer, and P. M. J. Herman. 2011. Windows of opportunity: thresholds to mangrove seedling establishment on tidal flats. Marine Ecology Progress Series 440:1–9.

Balke, T., P. M. J. Herman, and T. J. Bouma. 2014. Critical transitions in disturbance-driven ecosystems: identifying Windows of Opportunity for recovery. Journal of Ecology 102:700–708.

Beck, M. W., et al. 2009. Shellfish reefs at risk: a global analysis of problems and solutions. The Nature Conservancy, Arlington, Virginia, USA.

Bell, E., and J. Gosline. 1996. Mechanical design of mussel byssus: Material yield enhances attachment strength. Journal of Experimental Biology 199:1005–1017.

Bertness, M. D., and G. H. Leonard. 1997. The role of positive interactions in communities: lessons from intertidal habitats. Ecology 78:1976–1989.

Bertolini, C., N. R. Geraldi, W. I. Montgomery, and N. E. O'Connor. 2017. Substratum type and conspecific density as drivers of mussel patch formation. Journal of Sea Research 121:24–32.

Bouma, T. J., M. B. De Vries, E. Low, G. Peralta, I. C. Tánczos, J. van de Koppel, and P. M. J. Herman. 2005. Trade-offs related to ecosystem engineering: a case study on stiffness of emerging macrophytes. Ecology 86:2187–2199.

Bouma, T. J., M. Friedrichs, B. K. Van Wesenbeeck, S. Temmerman, G. Graf, and P. M. J. Herman. 2009. Density-dependent linkage of scale-dependent feedbacks: a flume study on the intertidal macrophyte *Spartina anglica*. Oikos 118:260–268.

Büttger, H., H. Asmus, R. Asmus, C. Buschbaum, S. Dittmann, and G. Nehls. 2008. Community dynamics of intertidal soft-bottom mussel beds over two decades. Helgoland Marine Research 62:23–36.

Byers, J. E., and J. H. Grabowski. 2013. Soft-Sediment Communities. Pages 227–249 *in* M. D. Bertness, J. F. Bruno, B. R. Silliman, and J. J. Stachowicz, editors. Marine community ecology and conservation. Sinauer Associates Inc., Sunderland, Massachusetts, USA.

Campbell, D. 2015. Quantifying the effects of boat wakes on intertidal oyster reefs in a shallow estuary. Dissertation. University of Central Florida, Orlando, Florida, USA.

Capelle, J. J., J. W. M. Wijsman, T. Schellekens, M. R. van Stralen, P. M. J. Herman, and A. C. Smaal. 2014. Spatial organisation and biomass development after relaying of mussel seed. Journal of Sea Research 85:395–403.

Carroll, J. M., K. Riddle, K. E. Woods, and C. M. Finelli. 2015. Recruitment of the eastern oyster, *Crassostrea virginica*, in response to settlement cues and predation in North Carolina. Journal of Experimental Marine Biology and Ecology 463:1–7.

Christensen, H. T., P. Dolmer, B. W. Hansen, M. Holmer, L. D. Kristensen, L. K. Poulsen, C. Stenberg, C. M. Albertsen, and J. G. Støttrup. 2015. Aggregation and attachment responses of blue mussels, *Mytilus edulis*—impact of substrate composition, time scale and source of mussel seed. Aquaculture 435:245–251.

Coco, G., S. F. Thrush, M. O. Green, and J. E. Hewitt. 2006. Feedbacks between bivalve density, flow, and suspended sediment concentration on patch stable states. Ecology 87:2862–2870.

Coen, L. D., R. D. Brumbaugh, D. Bushek, R. Grizzle, M. W. Luckenbach, M. H. Posey, S. P. Powers, and S. G. Tolley. 2007. Ecosystem services related to oyster restoration. Marine Ecology Progress Series 341:303–307.

Colden, A. M., R. J. Latour, and R. N. Lipcius. 2017. Reef height drives threshold dynamics of restored oyster reefs. Marine Ecology Progress Series 582:1–13.

Commito, J. A., E. A. Celano, H. J. Celico, S. Como, and C. P. Johnson. 2005. Mussels matter: postlarval dispersal dynamics altered by a spatially complex ecosystem engineer. Journal of Experimental Marine Biology and Ecology 316:133–147.

Commito, J. A., A. E. Commito, R. V. Platt, B. M. Grupe, W. E. D. Piniak, N. J. Gownaris, K. A. Reeves, and A. M. Vissichelli. 2014. Recruitment facilitation and spatial pattern formation in soft-bottom mussel beds. Ecosphere 5:1–26.

Commito, J. A., and N. M. J. A. Dankers. 2001. Dynamics of spatial and temporal complexity in European and North American soft-bottom mussel beds. Pages 39–59 *in* K. Reise, editor. Ecological comparisons of sedimentary shores. Springer, Berlin, Heidelberg, Germany.

Commito, J. A., and B. R. Rusignuolo. 2000. Structural complexity in mussel beds: the fractal geometry of surface topography. Journal of Experimental Marine Biology and Ecology 255:133–152.

Dankers, N., A. G. Brinkman, A. Meijboom, and E. Dijkman. 2001. Recovery of intertidal mussel beds in the Waddensea: use of habitat maps in the management of the fishery. Hydrobiologia 465:21–30.

Dankers, N., and K. Koelemaij. 1989. Variations in the mussel population of the Dutch Wadden Sea in relation to monitoring of other ecological parameters. Helgolander Meeresuntersuchungen 43:529–535.

Dare, P. J., and G. Davies. 1975. Experimental suspended culture of mussels (*Mytilus edulis* L.) in Wales using spat transplanted from a distant settlement ground. Aquaculture 6:257–274.

Davies, G. P., P. J. Dare, and D. B. Edwards. 1980. Fenced enclosures for the protection of seed mussels (*Mytilus edulis* L.) from predation by shore-crabs (*Carcinus maenas* L.). Fisheries Research Technical Report 56, Great Britain Directorate of Fisheries Research, Lowestoft, UK.

Denny, M. W. 1987. Lift as a mechanism of patch initiation in mussel beds. Journal of Experimental Marine Biology and Ecology 113:231–245.

Donker, J. J. A., M. van der Vegt, and P. Hoekstra. 2012. Wave forcing over an intertidal mussel bed. Journal of Sea Research 82:54–66.

England, P. R., J. Phillips, J. R. Waring, G. Symonds, and R. Babcock. 2008. Modelling wave-induced disturbance in highly biodiverse marine macroalgal communities: support for the intermediate disturbance hypothesis. Marine and Freshwater Research 59:515–520.

Fey, F., N. Dankers, J. Steenbergen, and K. Goudswaard. 2009. Development and distribution of the non-indigenous Pacific oyster (*Crassostrea gigas*) in the Dutch Wadden Sea. Aquaculture International 18:1–15.

Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology, Evolution, and Systematics 35:557–581.

Francis, X. O., P. B. Heffernan, and R. L. Walker. 1995. Preliminary recruitment studies of the eastern oyster, *Crassostrea virginica*, and their potential applications, in coastal Georgia. Aquaculture 136:231–242.

Gelman, A. and Y.-S. Su. 2018. arm: data Analysis Using Regression and Multilevel/Hierarchical Models. https://CRAN.R-project.org/package=arm

Geraldi, N. R., M. Simpson, S. R. Fegley, P. Holmlund, and C. H. Peterson. 2013. Addition of juvenile oysters fails to enhance oyster reef development in Pamlico Sound. Marine Ecology Progress Series 480:119–129.

Geyer, C. J. 2003. Generalized linear models in R. http://www.stat.umn.edu/geyer/5931/mle/glm.pdf

Godet, L., J. Fournier, M. Jaffré, and N. Desroy. 2011. Influence of stability and fragmentation of a worm-reef on benthic macrofauna. Estuarine, Coastal and Shelf Science 92:472–479.

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

Halpern, B. S., S. Walbridge, K. A. Selkoe, C. V. Kappel, F. Micheli, C. D'agrosa, J. F. Bruno, K. S. Casey, C. Ebert, and H. E. Fox. 2008. A global map of human impact on marine ecosystems. Science 319:948–952.

Hunt, H. L., and R. E. Scheibling. 2001. Patch dynamics of mussels on rocky shores: integrating process to understand pattern. Ecology 82:3213–3231.

Hunt, H. L., and R. E. Scheibling. 2002. Movement and wave dislodgment of mussels on a wave-exposed rocky shore. Veliger 45:273–277.

Jones, C. G., J. H. Lawron, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946–1957.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Pages 130–147 Ecosystem management. Springer, New York, New York, USA.

Jordan-Cooley, W. C., R. N. Lipcius, L. B. Shaw, J. Shen, and J. Shi. 2011. Bistability in a differential equation model of oyster reef height and sediment accumulation. Journal of Theoretical Biology 289:1–11.

Jouquet, P., J. Dauber, J. Lagerlöf, P. Lavelle, and M. Lepage. 2006. Soil invertebrates as ecosystem engineers: intended and accidental effects on soil and feedback loops. Applied Soil Ecology 32:153–164.

Kraan, C., A. Dekinga, and T. Piersma. 2011. Now an empty mudflat: past and present benthic abundances in the western Wadden Sea. Helgol Mar Res 65:51–58.

Liu, Q.-X., P. M. J. Herman, W. M. Mooij, J. Huisman, M. Scheffer, H. Olff, and J. van de Koppel. 2014. Pattern formation at multiple spatial scales drives the resilience of mussel bed ecosystems. Nature 5:5234.

Maxwell, P. S., J. S. Eklöf, M. M. van Katwijk, K. R. O'brien, M. de la Torre-Castro, C. Boström, T. J. Bouma, D. Krause-Jensen, R. K. F. Unsworth, and B. I. van Tussenbroek. 2017. The fundamental role of ecological feedback mechanisms for the adaptive management of seagrass ecosystems–a review. Biological Reviews 92:1521–1538.

Meadows, P. S., A. Meadows, F. J. C. West, P. S. Shand, and M. A. Shaikh. 1998. Mussels and mussel beds (*Mytilus edulis*) as stabilizers of sedimentary environments in the intertidal zone. Geological Society, London, Special Publications 139:331–347.

Morales, Y., L. J. Weber, A. E. Mynett, and T. J. Newton. 2006. Effects of substrate and hydrodynamic conditions on the formation of mussel beds in a large river. Journal of the North American Benthological Society 25:664–676.

Nehls, G., and M. Thiel. 1993. Large-Scale distribution patterns of the mussel *Mytilus edulis* in the Wadden Sea of Schleswig-Holstein: Do storms structure the ecosystem? Netherlands Journal of Sea Research 31:181–187.

Norström, A. V., M. Nyström, J. Lokrantz, and C. Folke. 2009. Alternative states on coral reefs: beyond coral–macroalgal phase shifts. Marine Ecology Progress Series 376:295–306.

Nyström, M., A. V. Norström, T. Blenckner, M. de la Torre-Castro, J. S. Eklöf, C. Folke, H. Österblom, R. S. Steneck, M. Thyresson, and M. Troell. 2012. Confronting feedbacks of degraded marine ecosystems. Ecosystems 15:695–710.

O'Connor, N. E. 2010. Shore exposure affects mussel population structure and mediates the effect of epibiotic algae on mussel survival in SW Ireland. Estuarine, Coastal and Shelf Science 87:83–91.

O'Connor, N. E., T. P. Crowe, and D. McGrath. 2006. Effects of epibiotic algae on the survival, biomass and recruitment of mussels, *Mytilus* L. (Bivalvia: Mollusca). Journal of Experimental Marine Biology and Ecology 328:265–276.

Petraitis, P. S., and S. R. Dudgeon. 2004. Detection of alternative stable states in marine communities. Journal of Experimental Marine Biology and Ecology 300:343–371.

Prins, T. C., A. C. Smaal, and R. F. Dame. 1997. A review of the feedbacks between bivalve grazing and ecosystem processes. Aquatic Ecology 31:349–359.

R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature 413:591.

Seed, R. 1976. Ecology. Pages 13–16 *in* B. L. Bayne, editor. Marine mussels: their ecology and physiology. Cambridge University Press, Cambridge, UK.

Seguin-Heine, M.-O., A.-A. Lachance, B. Genard, B. Myrand, C. Pellerin, I. Marcotte, and R. Tremblay. 2014. Impact of open sea habitat on byssus attachment of suspension-cultured blue mussels (*Mytilus edulis*). Aquaculture 426–427:189–196.

Suding, K. N., K. L. Gross, and G. R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. Trends in Ecology & Evolution 19:46–53.

Suding, K. N., and R. J. Hobbs. 2009. Threshold models in restoration and conservation: a developing framework. Trends in Ecology & Evolution 24:271–279.

Theisen, B. F. 1968. Growth and mortality of culture mussels in the Danish Wadden Sea. Medd. Danm. Fiskeri og Havunders 6:47–78.

van de Koppel, J., P. M. J. Herman, P. Thoolen, and C. H. R. Heip. 2001. Do alternate stable states occur in natural ecosystems? Evidence from a tidal flat. Ecology 82:3449–3461.

Van De Koppel, J., J. C. Gascoigne, G. Theraulaz, M. Rietkerk, W. M. Mooij, and P. M. J. Herman. 2008. Experimental evidence for spatial self-organization and its emergent effects in mussel bed ecosystems. Science 322:739–742.

Van de Koppel, J., M. Rietkerk, N. Dankers, and P. M. J. Herman. 2005. Scale-dependent feedback and regular spatial patterns in young mussel beds. American Naturalist 165:66–77.

Walles, B., J. Salvador de Paiva, B. C. van Prooijen, T. Ysebaert, and A. C. Smaal. 2014. The ecosystem engineer *Crassostrea gigas* affects tidal flat morphology beyond the boundary of their reef structures. Estuaries and Coasts 37:1–10.

Walles, B., K. Troost, D. van den Ende, S. Nieuwhof, A. C. Smaal, and T. Ysebaert. 2016. From artificial structures to self-sustaining oyster reefs. Journal of Sea Research 108:1–9.

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

Widdows, J., J. S. Lucas, M. D. Brinsley, P. N. Salkeld, and F. J. Staff. 2002. Investigation of the effects of current velocity on mussel feeding and mussel bed stability using an annular flume. Helgoland Marine Research 56:3–12.

Wilcox, M., and A. G. Jeffs. 2017. Is attachment substrate a prerequisite for mussels to establish on soft-sediment substrate? Journal of Experimental Marine Biology and Ecology 495:83–88.

Witman, J. D. 1987. Subtidal coexistence: storms, grazing, mutualism, and the zonation of kelps and mussels. Ecological Monographs 57:167–187.

Witman, J. D., and T. H. Suchanek. 1984. Mussels in flow: drag and dislodgement by epizoans. Marine Ecology Progress Series 16:259–268.

Wright, J. P., and C. G. Jones. 2006. The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. BioScience 56:203–209.

Yee, T. W. 2007. Vector generalized linear and additive models: with an implementation in R. Springer, New York, New York, USA.

Young, G. A. 1983. The effect of sediment type upon the position and depth at which byssal attachment occurs in *Mytilus edulis*. Journal of the Marine Biological Association of the United Kingdom 63:641–651.

Supporting Information