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Processes limiting mussel bed restoration in the Wadden-Sea

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ABSTRACT

This paper reports on experimental restoration of mussel beds in the Wadden Sea and the processes that might limit successful restoration of this foundation species (i.e. substrate, predation, hydrodynamics). The importance of substrate, predation, hydrodynamic conditions and location on mussel restoration success was studied using artificially created mussel beds. Experimental beds established on a stable substrate (coir net) were compared with control beds established on sand, at three locations in the Wadden Sea. Their persistence was followed over time. The results revealed a near disappearance of all experimental beds in just over 7 months. Providing a stable substrate did not improve mussel survival. Predation could not explain the disappearance of the beds, as the maximal predation rate by birds was found to be insufficient to have a significant effect on mussel cover. Differences in wave conditions alone could also not explain the variation in decline of mussel cover between the locations. However, the gradual disappearance of mussels from the seaward side of the bed strongly suggested that hydrodynamic conditions (i.e. combined effects of waves and current) played an important role in the poor persistence of the artificial beds. Our results highlight the fact that restoration of mussel beds in dynamic areas cannot simply be implemented by mussel transplantation, particularly if additional measures to prevent wave losses are not taken, even when artificial substrate is provided to facilitate mussel adhesion.

1. Introduction

Estuarine ecosystems are threatened by both natural events and ever-increasing human pressure (Brierley and Kingsford, 2009; Durant et al., 2007; Halpern et al., 2008; Lotze et al., 2006). In many coastal environments, ecosystem integrity is strongly linked to the presence of ecosystem engineers (Christianen et al., 2014; Dankers and Koelemaij, 1989; Eriksson et al., 2010). The decline of several foundation species has resulted in a decrease of the ecosystem services provided by estuarine systems (Halpern et al., 2008). Bivalve beds, coral reefs, mangrove forests and seagrass meadows provide structured habitats for other species and protect the shoreline from erosion by stabilizing sediment and dampening waves (Bouma et al., 2009; Cocito, 2004). Historically, ecosystem engineers have been an important component of benthic communities in coastal areas (Beukema, 1976; Dame and Prins, 1997; Dijkema, 1991). Once considered seemingly inexhaustible, many coastal ecosystem engineer populations around the world have declined over the past two hundred years (Edgar and Samson, 2004; Eriksson et al., 2010; Gross and Smyth, 1946; Jackson et al., 2001). Because of the great economic and ecological value of the ecosystem services they provide by shaping their environment, restoring populations of foundation species can be a powerful way to restore the integrity and resilience of estuarine ecosystems (Borsje et al., 2011; Crain and Bertness, 2006; Eklof et al., 2011; Halpern et al., 2007; Peterson et al., 2003).

Restoration of habitats dominated by marine foundation species, such as seagrass meadows, mussel beds, oyster reefs or coral reefs, has been prioritized in many management policies aiming to improve estuarine ecosystem function (Byers et al., 2006; Carls et al., 2004; Crain and Bertness, 2006; Fortes, 1991; McLeod et al., 2012). However, the restoration of foundation species, such as; seagrasses, mussels and oysters, remains a challenge in many estuarine systems, since there are often thresholds that prevent establishment of these species in low numbers (Geraldi et al., 2013; Suding, 2011). Although a few projects have been successful (Green and Short, 2003; Schulte et al., 2009), Fonseca et al. (1998) highlighted that about 70% of seagrass transplantation trials

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have failed. A number of studies highlight that degradation of environmental conditions, such as turbidity, can limit reef establishment and influence restoration success (Badalamenti et al., 2006; Bouma et al., 2009; Hiddink, 2003; Lenihan and Peterson, 1998; Piersma et al., 2001). In order to set up a successful restoration project, it is important to identify and ameliorate these limiting factors. The use of artificial or alternative natural substrate has been put forward to reduce the effect of substrate instability and improve restoration success of ecosystem engineers (Bartol and Mann, 1997; Clark and Edwards, 1999; Fonseca et al., 1998). Yet, the majority of restoration projects have still failed, suggesting that other factors such as hydrodynamic stress or predation may be hindering restoration efforts (Christianen et al., 2014; Clark and Edwards, 1999; Luckenbach et al., 2005; van der Heide et al., 2014). It is therefore likely that restoration of ecosystem engineers may require a multifaceted approach that addresses the interplay between several limiting factors.

The Wadden Sea is one of the largest intertidal areas in the world and has been included in the UNESCO's World Heritage list since 2009. It is recognized as a natural area of primary importance (Brinkman et al., 2002), characterized by high densities of various species of migrating birds that feed on the extensive stock of bivalves, worms, and crustaceans (Beukema, 1976, 1993). At the beginning of the 1980's, 23% of the biomass of benthic fauna living on intertidal flats of the Wadden Sea consisted of mussels (Dankers and Zuidema, 1995). However, by the end of the 1980's, almost all intertidal mussel beds had disappeared, probably due to a cumulative effect of mechanical dredging for mussels and cockles, poor recruitment on wild beds and cold winters (Brinkman et al., 2002; Higler et al., 1998). Since 1993, fishing restrictions have been imposed and from 2004 onwards-dredging activities have been banned from intertidal areas. Yet, despite these restrictions, mussel beds show slow recovery. Currently, only half of the mussel population has recovered, with recovery seemingly faster in the Eastern Dutch Wadden Sea than in the Western Dutch Wadden Sea. The limited recovery of intertidal mussel beds in the Wadden Sea can be caused by several factors. Firstly, disturbance of sediment resulting from past dredging activities may have caused degradation of habitats necessary for mussel settlement (Eriksson et al., 2010). Secondly, absence of sheltering structures such as older beds may have resulted in greater wave exposure limiting the opportunities for mussel larvae settlement. Thirdly, young newly settled mussel beds might be less resilient to wave disturbance than old stable beds, further slowing long term recovery. For mussel bed restoration efforts in the Wadden Sea to be successful, identification of the factors that limit mussel bed establishment and persistence is of crucial importance.

To test the feasibility of mussel bed restoration in the Wadden Sea and to assess the importance of limiting factors such as predation or hydrodynamic stress, artificial mussel beds were built near 3 islands in the Dutch Wadden Sea. In this experiment, we tested for the effect of providing substrate for attachment on mussel persistence in the form of coir nets. The cover of the artificial beds was followed over time as well as mussel attachment. The role of other factors such as predation (by birds and/or crabs) and wave conditions was also addressed. Finally, the relative importance of these factors for mussel bed persistence was discussed.

2. Materials and methods

2.1. Experimental set up

Between March and May 2011, artificial beds were set up near three islands of the Dutch Wadden Sea (Terschelling (53°19″7.00″N, 5°18″39.11″E), Ameland (53°25″59.69″N, 5°48″10.57″E), and Schiermonnikoog (53°28′3.43″N, 6°14′13.40″E) along an east–west line, (Fig. 1A)). At each of these sites, the presence of natural mussel beds evidenced habitat suitability. To ensure viable sites were chosen, the elevation of the existing natural mussel beds was measured using a Differential GPS (DGPS) and an experimental site within 1 km of this bed was chosen with an elevation equal to that of natural beds. This elevation varied between islands (Terschelling: elevation = −0.831 m ± 0.029 m, inundation time ≈ 85%, Ameland: Elevation = −0.663 m ± 0.032 m, inundation time ≈ 75%, Schiermonnikoog: elevation = −0.56 m ± 0.065 m, inundation time ≈ 70%).

At each of the 3 selected areas, 6 artificial mussel beds (20 × 20 m), parallel to the shoreline, were established. Beds were oriented to ensure similar wave exposure and were equally spaced with 40 m between each bed. Each of the groups of 6 beds consisted of 3 replicates built in a block design (3 blocks by island, 18 beds in total, Fig. 1B). Each block consisted of a control and a treatment bed. In each block, one of the two beds was allocated a substrate treatment consisting of an artificial stable substrate made of coir net (coconut fiber net), and the second served as a control with bare sediment. The coir net substrate served to mimic mason worm beds, which often provide a natural substrate for mussel spat to attach to (Bolam and Fernandes, 2003; Brinkman et al., 2002). A pilot set up of 3 × 2 m in a sheltered area with intertidal mussels showed that coir net was stable and that mussels were able to attach to it. To build the artificial beds with a coir net substrate, strips of coir net (3 × 20 m or 3 × 10 m) of a mesh size of 2 cm were used. The edges of each strip were dug 20 cm into the sediment for anchorage. As no motorized engines were allowed in the experimental locations, some of the work was done using horses and plows. To help prevent the coir net from being buried under sediment, 128 knotted burlap balls (10 cm diameter) were placed underneath the nets of each treatment plot.

After one week, 36,000 kg of adult mussels (size: 5.4 cm ± 6 cm) were obtained by mechanical dredging from a two-year-old natural subtidal mussel bed near Terschelling. Even though subtidal and intertidal mussel beds are considered as being the same habitat in the EU Habitats Directive (Directive, 1992), subtidal mussels were chosen for transplantation because their population is more important than the population of intertidal mussels. Mussels were manually placed on the earlier established test plots within 2 days of collection. Each artificial bed consisted in 25 circular mussel patches, with a diameter of about 2.5 m. Patches were regularly spaced (≈2 m), allowing the water (and food) to circulate between each patch (Fig. 1C). Within each artificial bed, the total cover of mussels was about 37%, with a local density of 16 kg/m^2 (about 6.4 million mussels) similar to that found on natural beds in the Wadden Sea.

2.2. Mussel bed persistence

To study the effect of coir net on mussel bed persistence, mussel cover on the artificial beds was surveyed over time. Mussel coverage was monitored after each storm (average wind > 6 Bft) during 7 months after setting up the experiment. The initial cover of the beds was estimated using 3D scans (Riegl VZ-400) of the plots during the first days of the experiment. Aerial pictures of the beds were taken after each storm (6 times) with a time-lapse camera mounted underneath a kite. Pictures were analyzed using ArcGIS 10.2. The outline of each mussel clump was delimited by hand on the image. Using this, a percentage of cover (persistence) could be estimated for each period and followed over time.

To test whether the coir net was used by the mussels, substrate use and attachment force were measured. The strength of attachment (attachment force, sensu Whitman and Suchanek (1984) and Bell and Gosline (1997)) of a mussel was measured as the perpendicular force needed to dislodge a mussel from the bed structure. Mussels were fixed within a metal clamp attached to a Wagner Force Dial™ FDK/FDN with peak force meter (WAGNER INSTRUMENTS, Greenwich, CT, USA). On Schiermonnikoog, 25 mussels were sampled at random over each treatment block. No more than 5 individuals were sampled on any circular mussel patch within the blocks. Substrate use, as defined in (wa Kangeri et al., 2014) was measured in situ for an additional 2

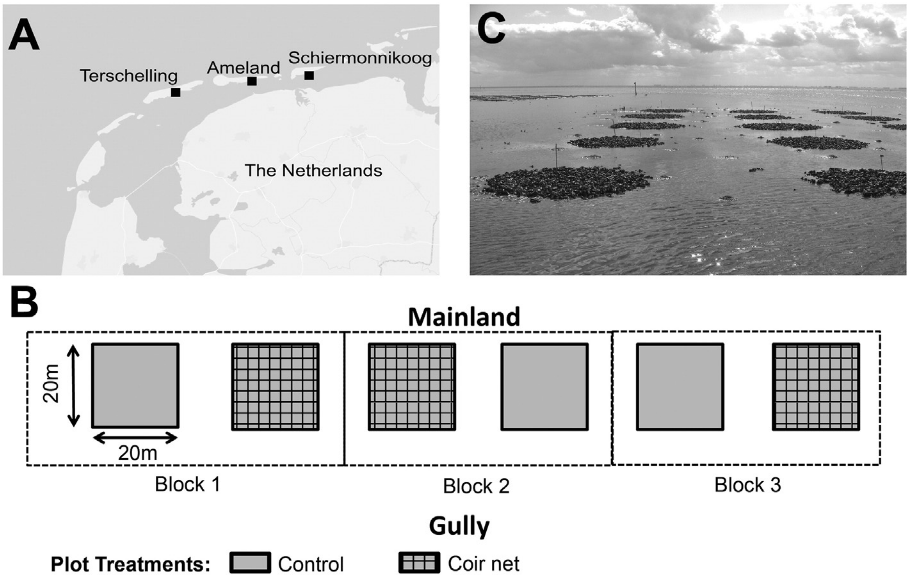

Fig. 1. Overview of the field site and the experiment. A: Map of the Dutch Wadden Sea showing the locations of the experiment (Terschelling, Ameland and Schiermonnikoog). B: Schematic view of the experiment on one island (Schiermonnikoog). Each block contains 2 artificial beds (experimental units). Bed treatments are randomly distributed inside the blocks. C: Picture of the experiment at day 1 on Schiermonnikoog. On each artificial bed, mussels were homogenously spread in 25 circles (2.5 m diameter).

individuals whereby substrate to which the mussel byssus were attached (shell material, other mussels, coir net, or other material) was recorded.

2.3. Predation survey

Oystercatchers (*Haematopus ostralegus*) and crabs (*Carcinus maenas*) were found to be the main predators on the experimental mussel beds, in agreement with observations by Elner (1978), Hilgerloh et al. (1997), Smallegange et al. (2009), and van der Zee et al. (2012). To estimate their predation effect, oystercatchers were counted and their feeding behavior studied on the artificial beds every two weeks over the course of 108 days after the experimental beds were created. Each of these survey sessions was done over the course of 5 tidal cycles during which the average number of birds on the plots and average individual food intake (mussels eaten/min/oystercatchers) were measured. Bird numbers on each plot were counted every 15 min during low tide and feeding behavior of a randomly selected bird was observed during 5 min in-between the counts. Based on these observations, the average food intake (mussel/day) was calculated using the following equation:

$$\begin{aligned}&\text{Average food intake}\\&\quad=\text{Average number of birds (individuals)}\\&\quad\times\text{Average food intake by an individual bird (mussel/bird/min)}\\&\quad\times\text{Emergence time every day (min)}.\end{aligned}$$

On Ameland, the survey was stopped after 60 days because all the mussels had disappeared. On the other locations, the survey continued over the entire 108 days.

To estimate predation pressure by crabs (*C. maenas*), pitfall traps were placed on the artificial beds at the end of July and beginning of August. These traps consisted of PVC tubes (30 cm diameter, 25 cm deep), and closed at the bottom. These were dug into the sediment within the artificial beds. After two tides, crabs trapped in the tubes were collected and counted. The experiment was replicated two times on Terschelling and Schiermonnikoog. On Ameland, no data were collected since all mussels had already gone by the end of June.

2.4. Hydrodynamic effects

To study the impact of wave action on the artificial beds, wave sensors (Wave Gauge, Ocean Sensor Systems, Coral Springs, USA) were simultaneously placed on each location for 15 days (3 sensors on Terschelling and Schiermonnikoog and 2 sensors on Ameland). The height of each of the pressure loggers above the sediment was recorded (10–20 cm). Bursts of pressure were collected at a sampling rate of 10 Hz for 5 min with a 5 min interval. Wave records were then processed to obtain significant wave height (mean wave height of the highest third of the waves) for each location. Data were processed in Matlab as per Christianen et al. (2013). Hourly weather condition data were provided by the Royal Netherlands Meteorology Institute (KNMI). During the deployment, wind conditions (2–6 Bft) and atmospheric pressure (1009–1027 hPa) were recorded. To quantify local and large scale hydrodynamic differences between the beds, significant wave heights were compared between islands.

2.5. Statistics

For each statistical test, normality and homogeneity of data or residuals and interaction between factors were tested beforehand. The development of mussel cover over time was fitted to two different models by minimizing the sum of squared residuals (ε) enabling an analysis of mussel loss over time (t) and its proportionality to A—Normalized area- (1) or P—Normalized perimeter- (2) of the mussel clusters.

$$\frac{dA}{dt}=\varepsilon_1\times A/A_0 \qquad (1)$$

$$\frac{dA}{dt}=\varepsilon_2\times P/P_0. \qquad (2)$$

The model best describing the mussel cover development over time was assessed using Akaike's Information Criterion (AIC) and performing a log likelihood ratio test (Johnson and Omland, 2004). A Generalized Linear Mixed Model (GLMM) was then performed on the fitted loss rates, ε_1 or ε_ν, of the best fitting models, using island and substrate as fixed factors, bird predation and wave height as covariates and block as random effect. To fulfill requirements of normality, residuals were log transformed. Tukey posthoc tests were used to test for differences between islands. The effects of location on bird numbers and wave height were tested in a Generalized Linear Model (GLM), with the factor island and the variables bird number and wave height. Differences in attachment force were analyzed using an Analyses of Variance (ANOVA) with time and substrate as factors and attachment force as dependent variable. Attachment force data were $\log_{10}$ transformed for homogeneity and normality. As data for crab predation were only available on Terschelling and Schiermonnikoog, a student *T*-test was utilized. All statistical tests were run in SPSS 22.

3. Results

3.1. Mussel bed persistence

All the artificial beds disappeared within 200 days (Fig. 2A). Local conditions were found to have a significant effect on mussel bed persistence (Table 1, $p < 0.001$). On Ameland, a fast and close-to-constant decrease (−1.105 ± 0.06% per day) could be observed until the beds disappeared after 108 days. The decline of the experimental beds on this island was significantly faster than of the beds on the two other islands (Tukey, $p < 0.001$). The survival trends on Schiermonnikoog (−0.63 ± 0.04% per day) and Terschelling (−0.495 ± 0.03% per day) were similar (Tukey, $p = 0.22$). However, on Schiermonnikoog, a sudden disappearance of the beds occurred after 120 days. On all locations, the loss of mussels was proportional to the perimeter of the transplanted patches (area: $\mathrm{AIC} = -490.5$, perimeter: $\mathrm{AIC} = -649.38$, $\chi = 317.84$, $p < 0.001$), suggesting that the mussels were dislodged from the edges of the patches.

Comparison of the loss of bed cover did not reveal any significant effect of substrate on the persistence of the beds (Fig. 2B). The decreasing trend (slope) was not significantly different for the beds built on coir net compared to the control beds (Table 1, $p = 0.06$). However, after 208 days, the remaining cover of mussels on the control beds was on average 1.3 ± 0.9%, while on the beds with coir fiber net an average cover of 2.9 ± 2.4% remained.

After 2 months, only 5.1 ± 2% of byssal threads were attached to the coir net, showing that this substrate was poorly used by mussels. Mussels were mainly attached to conspecifics (26.6–29.4% ± 3.5–3%) or to shell material (59.8–53.5% ± 3.9–3.2%). No differences were found in attachment force between treatments (Table 1, $p = 0.09$). However, attachment force was found to decrease significantly over time (Table 1, $p = 0.02$, Fig. 3). Mussels present on coir net showed a mean attachment force of 12.09 ± 0.6 N after 36 days and 9.6 ± 0.4 N after 88 days. Mussels on the control beds showed a mean attachment force of 13.1 ± 0.7 N after 36 days of experiment and 10.04 ± 0.4 N after 88 days.

Table 1
Summary table of the results of the different test used in this study.

Test	Factor	Variable	Df	N	F/t	p value
GLMM	Island	Cover decrease	2	18	49.15	0.00
GLMM	Substrate	Cover decrease	1	18	4.55	0.06
GLMM	Block	Cover decrease	2	18	0.56	0.6
GLMM	Wave height	Cover decrease	1	18	3.21	0.10
GLMM	Bird number	Cover decrease	1	18	0.92	0.35
GLM	Island	Bird	2	18	24.2	0.00
GLM	Island	Waves	2	18	28.16	0.00
ANOVA	Substrate	Attachment force	1	300	2.9	0.09
ANOVA	Time	Attachment force	1	300	5.2	0.02
Student test	Island	Crab number	1	23	1.7	0.11

3.2. Predation survey

Significant between island differences in oystercatcher numbers were found, with Terschelling having the highest number of oystercatchers (28.1 ± 1.30) compared to the other islands (Fig. 4A). On Schiermonnikoog, the number of oystercatchers was the lowest (2.5 ± 0.23) and on Ameland, the situation was intermediate (16.15 ± 1.14). However, this trend was reversed in terms of feeding efficiency. On Schiermonnikoog, the individual food intake (0.39 mussel/bird/min ± 0.09) was significantly higher than the food intake on Terschelling (0.11 mussel/bird/min ± 0.02), with Ameland having an intermediate position (0.19 mussel/bird/min ± 0.05). On Schiermonnikoog, the number of oystercatchers was low but constant with in average 2.5 ± 0.23 individuals present on the experiment. On Terschelling and Ameland, however, the number of oystercatchers present decreased over time. The number of mussels eaten by birds over the entire experiment was about 2185 mussels/day. Bird predation was not found to be an explanatory variable for the rapid disappearance of the mussels (Table 1, $p = 0.35$).

No significant differences in crab densities (Fig. 4B, Table 1, $p = 0.11$) were found. On Schiermonnikoog, 19 ± 3 crabs were trapped around each artificial bed after 2 tides. On Terschelling, 13.3 ± 1.7 crabs were trapped. As previously mentioned in Section 2.3, no data was collected on Ameland, as the mussel beds had already disappeared before crab traps were deployed.

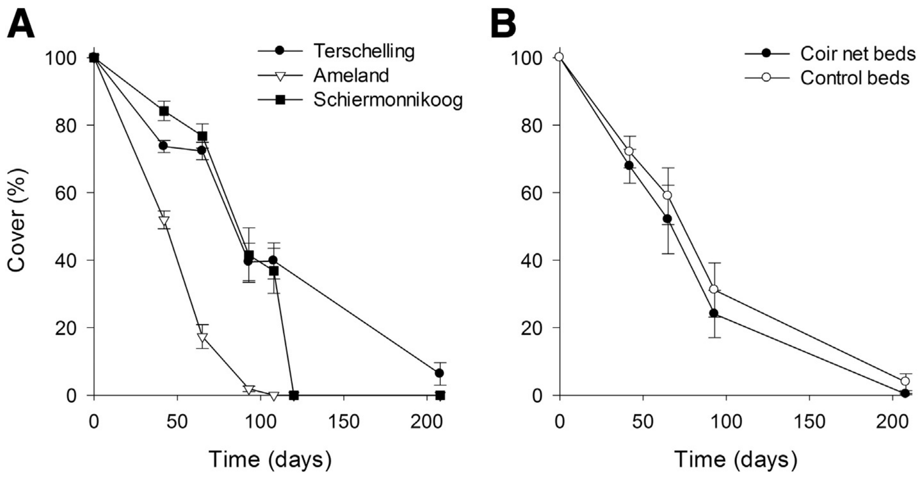

Fig. 2. Persistence of the artificial mussel beds over time. A: Average persistence over time per island (N = 18, mean ± SE). B: Persistence over time on the different substrates (N = 18, mean ± SE).

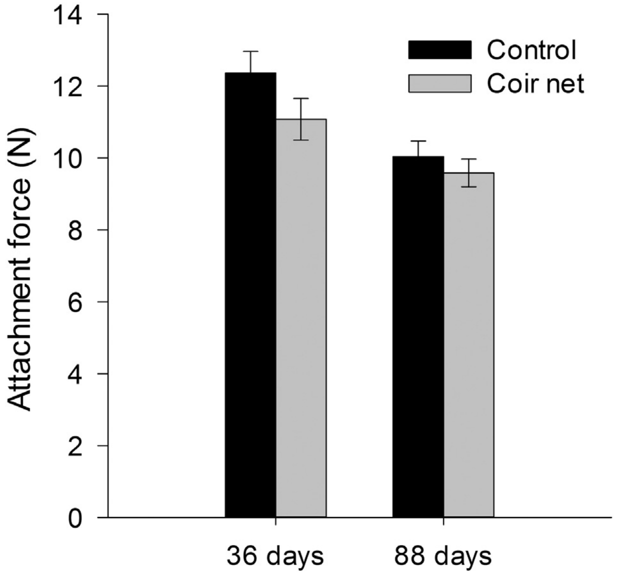

Fig. 3. Average attachment force of mussels on coir net and on bare mudflat (control) after 36 and 88 days of the experiment (N = 300, mean ± S.E.).

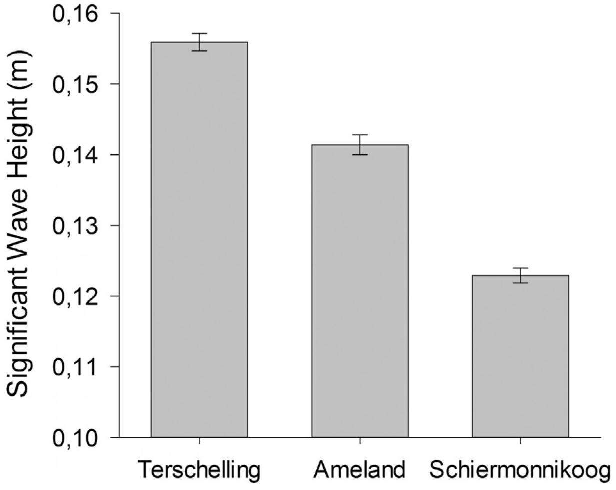

Fig. 5. Average wave height on the islands of Terschelling, Ameland and Schiermonnikoog. Measurements were conducted during 15 days in average wind conditions (2–6 Bft). Mean ± SE.

3.3. Hydrodynamic effects

Measurements of wave forcing could not explain variation in persistence between islands. Wave data clearly showed a significant decrease of wave height along the west–east gradient (Fig. 5). These differences did not, however, coincide with differences in persistence between islands. Terschelling was significantly more exposed than Ameland and Schiermonnikoog (Table 1, $p < 0.001$). The average significant wave height was greatest on the western most island, Terschelling (15.6 cm ± 0.1), decreasing eastwards with intermediate heights on Ameland (14.1 cm ± 0.1 cm), and the lowest on the Eastern most island, Schiermonnikoog (12.3 cm ± 0.1 cm). Despite the obvious importance of wave action in the decline of the mussel beds, differences in wave forcing cannot explain why mussels disappeared faster on Ameland compared to the other islands (Table 1, $p = 0.1$).

4. Discussion

The results of the mussel bed restoration experiment highlighted the difficulty of restoration of mussel beds by means of mussel transplantation. They show that mussels transplanted into the intertidal mudflats were not able to persist for longer than a few months on the experimental plots. Even when mussels were provided with an artificial substrate for attachment, none of the beds persisted for more than a few months. Clear differences in persistence were found between the experimental locations (islands). However, we were unable to provide a clear explanation of the factors limiting the persistence of the mussel beds on the intertidal mudflats. The rapid disappearance of the experimental mussel beds was neither explained by either bird or crab predation, nor by overall predation. Even though the importance of wave action on mussel bed persistence has been pointed out frequently in literature (Capelle et al., 2014), the wave measurements on the plots could not explain mussel bed disappearance.

Over all locations mussel loss was proportional to the perimeter of the transplanted clusters. This suggests that hydrodynamic forces acting on the bed edges gradually eroded individual mussels from the patches. Upon reaching a critical minimum size, erosion caused a complete collapse of the patches. These observations are further supported by data from the aerial images. These showed a gradual disappearance of mussels from the seaward edge (Fig. 6). Hence, it is most likely that extensive wave action, possibly in interaction with currents, was the main cause of the loss of the mussel beds. On Schiermonnikoog, the disappearance of the beds was sudden and could not be related to any

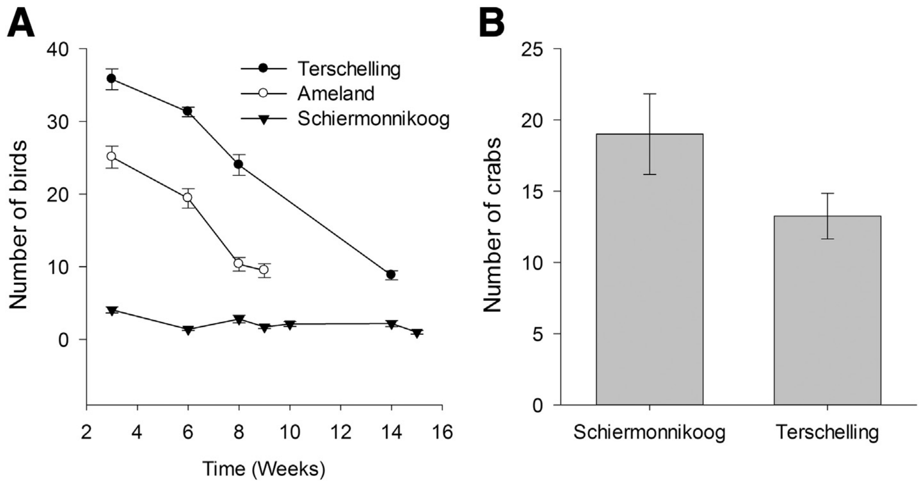

Fig. 4. Estimation of predation on the experiment. A: Number of oystercatcher on the experiment. The counts were made every 5 min during a tide (N = 18, mean ± SE). B: Number of crabs on the experiment. The counts were made on each artificial bed after 2 tides (N = 12, mean ± SE).

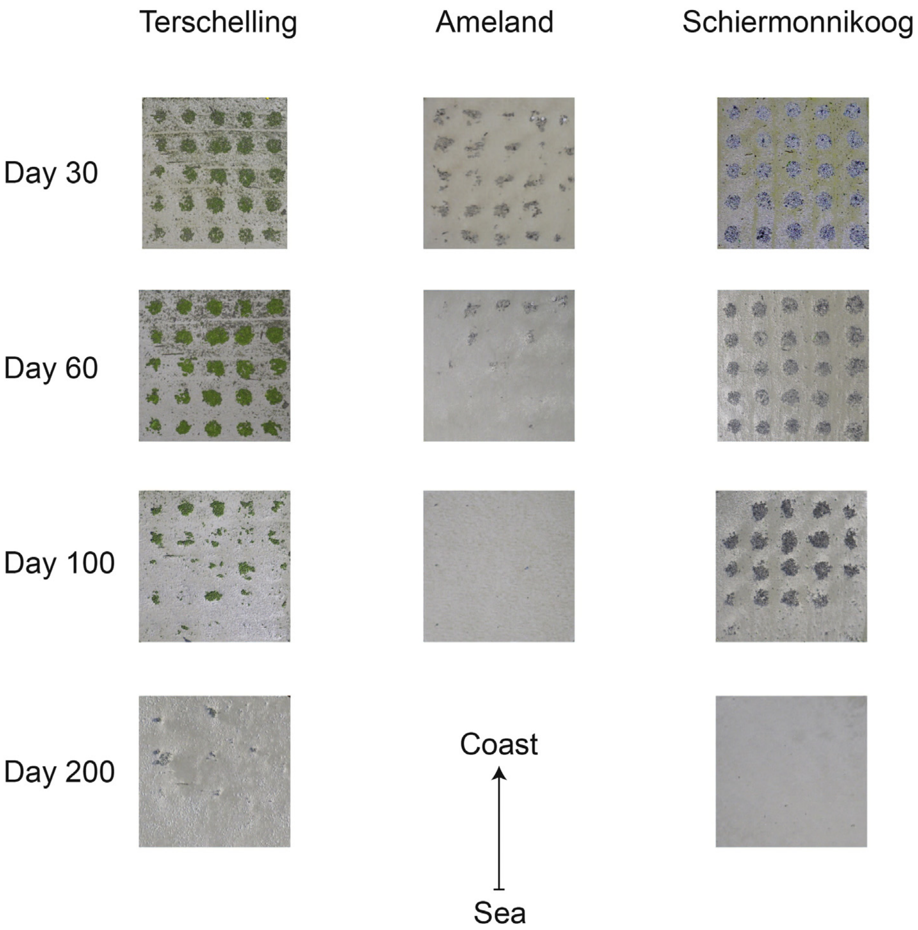

Fig. 6. Evolution of mussel covers over time. One artificial bed by island was chosen as an example on this figure. The pictures suggest that mussels gradually disappear from the seaward edge of the beds.

storm events. Even though these areas were closed for boat activity, the sudden disappearance can only be explained by human activity.

The results revealed that coir nets, provided as an artificial substrate, had little effect on mussel persistence. Mussels made little use of the substrate and no difference in attachment force or persistence of mussel patches was found between beds built on the net or on bare sediment. This could potentially be explained by the rapid burial of the coir net underneath 2–3 cm of sediment prior to placement of mussels on the plot. This burial was likely the result of the combined effect of lugworm activity and sedimentation. The consequence of this burial was the inaccessibility of the net for the epibyssal mussels that tend to interact with materials directly accessible at the surface, particularly when generating new byssus attachment, as was the case here. Although artificial substrates, such as coir net, concrete mats were successfully used in mangrove and coral restoration (Clark and Edwards, 1995; Hashim et al., 2010), using coir net as an artificial substrate for mussel bed restoration on sediment proved to be of little use. During our experiment, the coir substrate was vulnerable to burial by sediment as a result of water current, wave action and/or bioturbation. These effects could be avoided by placing the mussels on the bed immediately after placement of the net. In this case, mussels would have had the opportunity to become attached to the coir before burial in sediment allowing more secure anchorage to be achieved.

Although many studies have pointed to bird and crab predation as a result of major limitation on mussel bed persistence (Hilgerloh et al., 1997; Nehls et al., 1997), predation rate in the present study was low and did not seem to be the main cause of rapid collapse of the experimental beds. The predation pressure by oystercatchers (around 0.03%/day over the entire experiment) was low compared to the total amount of mussels present on the experimental beds. This low predation pressure might be explained by the size of mussels used in the experiment. On natural mussel beds, small mussels are usually more vulnerable to predation. Most of the mussels that were used to create the restoration plots were larger than 5 cm potentially making them more difficult pray to handle than those the birds are accustomed to on natural intertidal beds where mussels are on average under 5 cm (Hilgerloh et al., 1997; Smallegange et al., 2009).

Although the survey of crab densities did not allow us to quantify predation, comparison between two islands was possible. The results of the survey showed no differences between the number of crabs present on Schiermonnikoog and Terschelling. The role of crab predation is likely to have been low, since the size of mussels used in our artificial beds (5.4 cm ± 6 cm). This is greater than the size mussels require to achieve refuge from crab predation (4 cm) (Kraeuter and Castagna, 2001; Leonard et al., 1999).

Differences in wave forcing could not sufficiently explain differences in mussel persistence either. The mussel beds persisted longer at Terschelling (west) and at Schiermonnikoog (east) compared to Ameland (Middle). However, the hydrodynamic measurements suggest a west–east gradient in intensity of wave action, being strongest at Terschelling and weakest at Schiermonnikoog. Since both the number of birds and wave heights were the highest on Terschelling and the lowest on Schiermonnikoog, the lower mussel bed persistence on Ameland cannot be explained by predation or the general wave conditions. It is likely that other parameters not taken into account here, like current velocity, or food availability may provide insight into the losses. Importantly, while no storms were recorded during the experimental period, extreme events, like localized storms, were not taken into account. Since waves in the Wadden Sea are locally generated (Donker et al., 2013), and since the specific conditions with regard to wave orientation can play a determinant role in erosion, the transplantation failure may not necessarily be linearly related to the average conditions. In the past, other studies have suggested that in the Wadden Sea, mussels seem to recover better in the East than in the West (Brinkman et al., 2002; Folmer et al., 2014). These papers suggest the gradient of recovery was influenced by both higher hydrodynamic stress and by a higher number of birds in the Western Wadden Sea, neither of which were found to be significant in this study. However, the hydrodynamic measurements, done under average weather conditions (wind force 2–6 Bft), did not provide information about wave forcing during more severe wind conditions. Extended monitoring periods capturing local storms might have been key to understanding the relationship between wave forcing and bed persistence.

While external factors did not provide us with a satisfactory explanation for the limited success of the experiment, intrinsic factors, such as the use of subtidal mussels for transplantation likely played an important part. A previous pilot study showed that mussels sourced from an intertidal site quickly attached to the coir net. Moreover, three other one m^2 pilot plots again using intertidal mussels, close to the bed of Schiermonnikoog, persisted for over 2 years before disappearing. As it makes little sense to restore one intertidal mussel bed by destroying another, the mussels used for this experiment were sourced from a subtidal bed. Such translocation of organisms has been extensively used in restoration projects (Bajomi et al., 2010; Bolden and Brown, 2002; Fariñas-Franco and Roberts, 2014; Fariñas-Franco et al., 2013). However, mussels exhibit extensive phenotypic variation, which can limit restoration success (Seed, 1968; Fariñas-Franco et al., 2014). Subtidal mussels are less adapted to intertidal conditions. In intertidal areas, mussels experience extensive wave action directly after settlement, while in subtidal ecosystems, predation by starfish is the most important cause of mortality (Saier, 2001). Consequently, subtidal mussels might have morphological and behavioral adaptations that are disadvantageous to survival in intertidal environments. These differences may explain why the mussels did not successfully attach to coir net on the plots. The presence of natural mussel beds in the proximity of the experiments on each island, suggests that the failure of mussel restoration was, at least in part due to maladaptation of subtidal mussels to the conditions they face on intertidal flats.

While the density used on the plots was similar to the density found on natural mussel beds in the Wadden Sea, the beds faced significant losses already at the start of the experiment. Thus the remaining density on the experimental plots would be lower than what might be found in a natural bed and might have been too low to allow persistence of the bed. The use of a higher initial density of mussels (allowing for initial losses) might increase the chances of success of such an experiment. In addition to local patch density, the relatively low coverage used (in part due to logistical limitations), meant that the surface area to edge ratio was relatively low. Since erosion of mussels occurred primarily along patch edges, the high rate of loss may have been exacerbated by a greater number of mussels being located on patch edges.

Although restoration of coastal communities by transplantation proves challenging, the use of recruits to rebuild a new population could be considered as a fruitful alternative. In the Wadden Sea, a recent study showed that predation and lack of suitable substrate are limiting mussel-spat establishment (van der Heide et al., 2014). The use of artificial biodegradable structures, which could be used by mussel recruits both as settlement substrate and for protection from predation, may provide a more promising avenue for restoration. However, further investigations and pilot studies are needed to test how to implement such a strategy to restore mussel beds in a dynamic coastal system. Our study may provide interesting prospects for successful restoration of mussel beds in the future, both in the Wadden Sea and in other intertidal systems. Moreover, guidelines have been recently published on bivalve restoration that can be helpful in designing new techniques of mussel bed restoration (Baine, 2001; Pérez et al., 2012). Hence, there may still be interesting prospects for success restoration of mussel beds in the future, both in the Wadden Sea and in other intertidal systems. This viewpoint corroborated with recently published guidelines on bivalve restoration that can be helpful in designing new techniques of mussel bed restoration (Baine, 2001; Pérez et al., 2012).

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