

Can we enhance ecosystem-based coastal defense by connecting oysters to marsh edges? Analyzing the limits of oyster reef establishment

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ABSTRACT

Nature-based coastal defense schemes commonly value bivalve reefs for i) reducing coastal erosion in the intertidal and for ii) forming fringing reefs near salt marsh edges to protect them against lateral retreat. The capacity for a reef to reduce erosion increases at a higher position in the tidal frame as the lower over-lying water level magnifies the influence of the reef on wave attenuation. Unfortunately, ecological constraints on reef development typically limit their practical application in coastal protection schemes to the lower intertidal, as bivalves grow best with long inundation times. In micro-tidal areas this is a lesser problem, given the close proximity of lower and upper intertidal ecosystems in space. By contrast, in meso- and macro-tidal estuaries, bivalve reefs tend to form hundreds of meters away from existing marshes, nullifying any wave-protective benefits. In this study, we produce evidence that with the assistance of management measures, widespread reef formation is possible on open mudflats, including bordering the marsh edge in meso- and macro-tidal estuaries, where natural reef formation is normally strongly limited.

In four locations throughout the meso- to macro-tidal Dutch Scheldt estuary, we observed the presence of individuals of two major intertidal reef-forming bivalves, Pacific oysters (*Crassostrea gigas*) and blue mussels (*Mytilus edulis*), within low-lying *Spartina anglica*-dominated marshes. As these communities lie well outside of the expected range of reef formation, this observation suggests the existence of mechanisms that extend the habitable range of these bivalves. In a series of field experiments, we first demonstrate how the stabilization of shell-substrate within the marsh promotes successful establishment and adult survival. Secondly, by placing artificial stable substrate in transects from the subtidal up to the marsh edge, we demonstrate that bivalve establishment is possible throughout a much larger range of the intertidal than where natural reefs occur. The effectiveness of stable substrate in stimulating bivalve establishment is likely a consequence of bridging size-dependent thresholds that limit the effective range for natural reef formation on tidal flats. The success of this approach is tempered by a consistent decrease in reef size and growth at higher elevations, suggesting that the optimal reef position for utility in coastal defense lies at an intermediate tidal position, well above the observed range of natural occurrence, but below the maximum achievable upper limit of reef formation. Together this work provides a pathway forward concerning how artificial reefs may be fostered to increase their utility as a nature-based flood defense measure.

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1. Introduction

Mounting changes in the global climate are forecast to have a critical impact on the lives of the 37% of the world's population living along coasts (Syvitski et al., 2009; Knutson et al., 2010; Lin et al., 2012). Increases in sea level and storm-risk have called into question the viability of continuing to rely solely on grey infrastructure (i.e. dikes, storm-surge barriers, etc.) to protect coastal populations from flooding, because of rapidly rising management costs and negative ecological effects (van Slobbe et al., 2013; Temmerman et al., 2013; Hinkel et al., 2014). Implementation of nature-based flood defenses into coastal management schemes has had growing support due to the benefits coastal ecological systems provide over grey infrastructure. These benefits include their resiliency against sea-level rise and low maintenance requirements in the face of repeated disturbances from storms (Barbier et al., 2011; Feagin et al., 2015). In addition, they also provide ecosystem services beyond their immediate role in coastal protection (Morris et al., 2018, 2019, 2020), and mitigate negative socioeconomic (Hinkel et al., 2014) and environmental impacts (Bulleri and Chapman, 2010; Bishop et al., 2017; Heery et al., 2017) traditionally associated with grey infrastructure. The most effective ecosystems for coastal defense measures tend to be the vegetated foreshore ecosystems (a group that includes salt marshes, mangrove forests and vegetated dunes), due to their high position in the tidal frame (Bouma et al., 2014). Salt marshes have been demonstrated to reduce the risk of dike breaching and the magnitude of inland flood impacts when breaches do occur (Zhu et al., 2020). However, salt marshes are themselves vulnerable to cliff formation induced by wave forcing on their foreshore edge, which can initiate run-away landward erosion (van de Koppel et al., 2005; Bouma et al., 2016), which is the chief means of marsh loss in the Scheldt (van der Wal et al., 2008), and massively curtails their effectiveness for coastal protection (Barbier et al., 2008; Borsje et al., 2011).

Efforts that reinforce the marsh foreshore edge and maintain a broad tidal flat are important for maintaining a broad vegetated zone. Epibenthic bivalve reefs have recently been evaluated as key natural infrastructure for accomplishing these goals (Borsje et al., 2011; Bouma et al., 2014; Weaver and Zehnder, 2017; Chowdhury et al., 2019; Ysebaert et al., 2019). Nature-based coastal defense schemes commonly cite the role bivalve reefs play in both (1) reducing erosion on tidal flats (Walles et al., 2015a; Chowdhury et al., 2019) and (2) forming fringing reefs on the foreshore edge of salt marshes that protect the marsh against lateral-retreat induced by cliff-erosion (Meyer et al., 1997; Piazza et al., 2005; Ridge et al., 2017a). Reef building bivalves are regarded as ecosystem engineering organisms, in that they build structures that alter their physical environment. In terms of their utility for coastal protection, the rough vertical structure of bivalve reefs acts as a natural, rejuvenating break-water with potentially cost-saving characteristics due to its low maintenance requirements, ability to expand laterally over time and grow vertically alongside changing sea levels (Scyphers et al., 2011; Rodriguez et al., 2014; Walles et al., 2015b). However, a major weakness of pursuing nature-based coastal protection schemes that utilize bivalve reefs, is the inability to consistently incite reef-formation to optimize the impact of their services in key areas (as discussed in La Peyre et al., 2015; Walles et al., 2016a, Walles et al., 2016b).

For many ecosystem-engineering organisms living in frequently disturbed environments, establishment is only possible during 'windows-of-opportunity', wherein exceptionally calm periods allow for organisms to overcome size-dependent thresholds (Balke et al., 2011; Hu et al., 2015; Capelle et al., 2019). Auto-facilitation tends to be a key mechanism that enables the expansion of ecosystem engineers in frequently disturbed environments. Congregations of ecosystem engineers contribute communally to reducing the physical disturbances that limit the establishment of successive generations (Suding et al., 2004; Balke et al., 2014; Silliman et al., 2015). Within bivalve reefs, the provisioning of stable substrate by pre-existing bivalves creates a facilitative environment where self-sustained re-establishment is possible outside of

narrow windows of opportunity (Gutiérrez et al., 2003; Walles et al., 2016a; Capelle et al., 2019). While the re-establishment of larvae on top of existing reefs may occur semi-annually (Nestlerode et al., 2007; van den Ende et al., 2018), the initiation of a new reef on soft sediment appears to be a rare and stochastic phenomenon. This is likely because most available, naturally-occurring substrates in the intertidal, such as shells and shell fragments, overturn and are dislodged frequently by waves and tidal currents. This frequent overturning makes the substrate unsuitable for establishment except during periods where hydrodynamic forces remain calm for an exceptionally long period. Specifically, naturally-occurring reefs will only establish when the interval required for young bivalves to develop and stabilize their substrate with their own mass is shorter than the interval between substrate-disturbance events. This 'window of opportunity' framework thus predicts that there should be a bias for natural reefs to occur predominantly in regions where the growth rate is high, i.e. in the lower intertidal. This largely agrees with field observations (van den Ende et al., 2018; Walles et al., 2016c).

Management measures that artificially harness facilitative mechanisms to address size-dependent thresholds have been successful in inducing organism establishment in hostile environments (Silliman et al., 2015; Capelle et al., 2019; Temmink et al., 2020). The construction of artificial reef foundations has been a major avenue by which to overcome these size-dependent thresholds and initiate reef formation for decades (Butler, 1954; Nestlerode et al., 2007; Grabowski and Peterson, 2007; Beck et al., 2011; Walles et al., 2016a, 2016b, 2016c; Schotanus et al., 2020). However, the placement of artificial reefs has so far been generally restricted to intertidal levels that closely match where natural reefs already commonly form. Generating a deeper understanding of the establishment constraints and natural mechanisms that facilitate bivalve-reef establishment and survival may allow the development of artificial reefs to expand into areas where natural reef development usually would not occur on its own, but would be highly valuable for creating nature-based flood defenses.

A key question for the use of reefs as coastal protection tools is how high in the intertidal it remains possible to place an artificial structure and still succeed in reef development. The position of the reef in the tidal frame is critical because it strongly determines the capacity for a reef to reduce erosion. Lower over-lying water levels magnify the influence of the reef on wave attenuation (Wiberg et al., 2019), and knock-on effects on sedimentation and erosion (d'Angremond et al., 1996). Unfortunately, bivalves tend to grow faster and form larger reef congregations in the lower intertidal and in subtidal areas where their role in coastal protection is strongly diminished (Spencer et al., 1978). Faster growing reef populations may also be more capable of displaying resilience in the wake of disturbances, be more effective at adjusting to sea-level changes, and expand more quickly to colonize and protect larger areas (Ridge et al., 2017a, 2017b). It is common to find that natural bivalve reef formation is strongest over a slim range of the lower intertidal (Walles et al., 2016c; van den Ende et al., 2018). In micro-tidal areas, the proximity of lower and upper intertidal ecosystems in space generally allow reef-forming bivalves to play a more substantial role in coastal protection (Ridge et al., 2017a). But in the larger intertidal areas that occur in meso- and macro-tidal estuaries, such as in the Dutch Scheldt Estuary in northern Europe, bivalve reefs tend to form hundreds of meters away from existing marshes (van den Ende et al., 2018), limited by their capacity to colonize areas that are less frequently inundated (Walles et al., 2016a & b). This nullifies key protective benefits provided by the reefs directly to the marshes.

In this study, we investigate to what extent it is possible to overcome establishment-limitations caused by the low growth-rates in higher intertidal areas, by artificially reducing the level of hydrodynamic disturbance experienced by the settlement substrate. Through the combination of an observational study and a suite of manipulative experiments, we provide evidence that demonstrates how low-lying *Spartina*-dominated saltmarsh vegetation appears to facilitate the

survival and establishment of reef-forming bivalves, Pacific oysters (*Crassostrea gigas*) and blue mussels (*Mytilus edulis*), as a consequence of the reduction of hydrodynamic disturbances within the vegetation. We show that the reduction in water movement within the vegetation lowers both the probability of adult oyster dislodgment and stabilizes shell substrate, which may facilitate settlement success. We then demonstrate how re-application of these same mechanisms onto the tidal flat using biodegradable artificial structures enables bivalve establishment well beyond its observed range. Overall, these findings provide a pathway forward concerning how artificial reefs may be fostered well beyond range of natural reef occurrence, thereby increasing their utility as a nature-based flood defense measure.

2. Methods

2.1. Study sites

The Western and Eastern Scheldt, originally two neighboring branches of a single historical delta in the Netherlands, have had diverging characteristics since becoming disconnected by historical land-reclamation. The Western Scheldt remains a meso- to macro-tidal estuary with a salinity gradient ranging from 32 to 10 ppt in the Dutch region (Damme et al., 2005) and a tidal range that varies from 4 m at the mouth to 6 m at its peak near the port of Antwerp (van Rijn, 2010).

By contrast, the Eastern Scheldt has been transformed from an estuary into an entirely marine system with a 3.25 m tidal range after losing its river connection (Smaal and Nienhuis, 1992). In the Eastern Scheldt intensive mussel culturing is practiced in the subtidal and in the intertidal, mixed reefs of Pacific oysters and blue mussels are widespread. Here, the two species commonly form mixed reefs in which the Pacific oyster creates the dominant structure, similar in character to the mixed novel communities documented throughout northern Europe where Pacific oyster invasions have occurred (Nehls et al., 2009; Troost, 2010; Eschweiler and Christensen, 2011; Herbert et al., 2016). Meanwhile, bivalve reefs are nearly absent from the Western Scheldt with the exception of two locations (see maps within van den Ende et al., 2018). Across both systems, only 2% of salt marsh area occurs deeper than an inundation frequency of 40% (as measured using aerial images supplied by the Dutch Ministry of Infrastructure and Water Management, Rijkswaterstaat), while bivalve reefs on the tidal flats can be found generally no higher than 50% (Walles et al., 2016c; van den Ende et al., 2018).

2.2. Observational study - bivalve reef formation within low-lying salt marshes

In an observational survey, we quantified the community of Pacific oysters (*Crassostrea gigas*) and blue mussels (*Mytilus edulis*) within four low-lying *Spartina*-dominated salt marshes in the Scheldt estuary. In

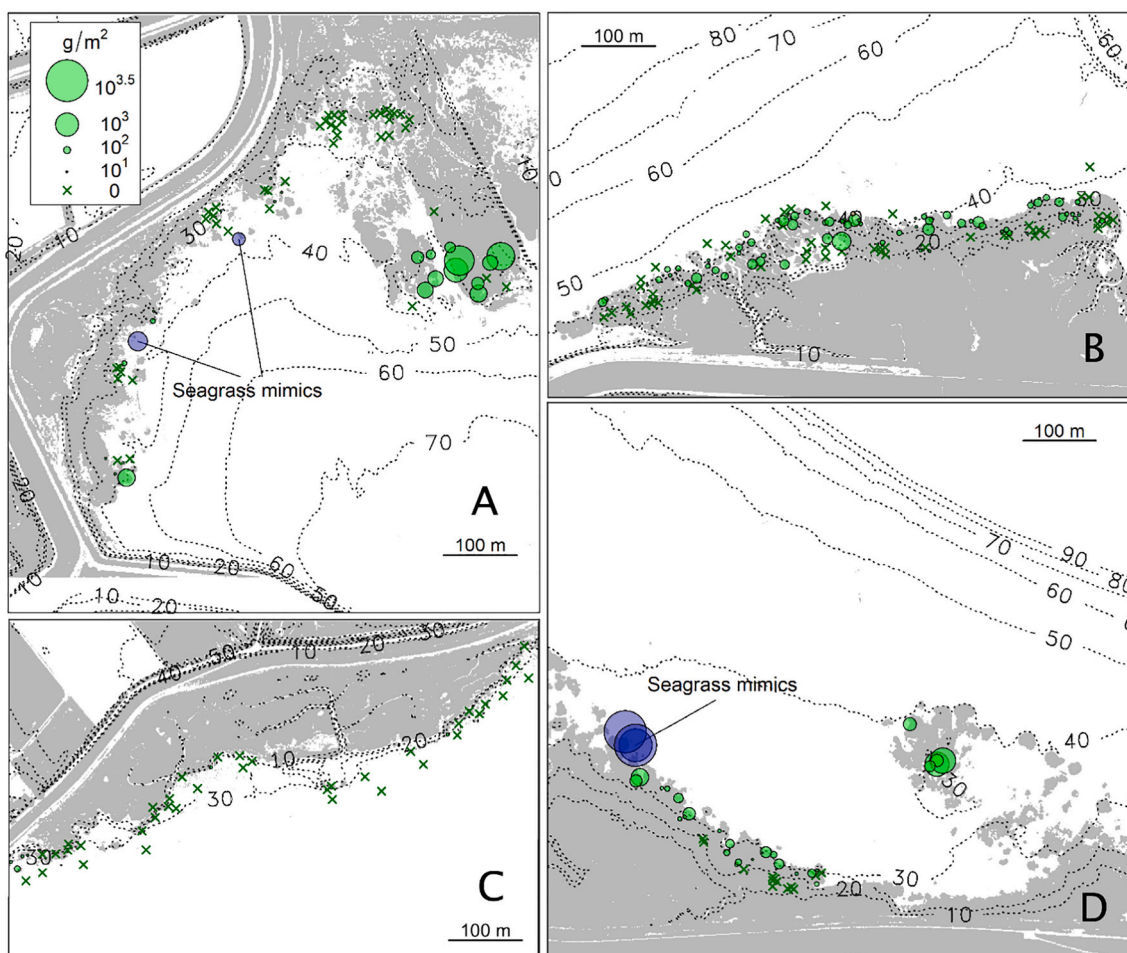


Fig. 1. Maps of bivalve occurrence within salt marshes (vegetated areas indicated in grey) at our four study sites in the Western and Eastern Scheldt: (a) Ritthem, (b) Hellegat, (c) Viane, & (d) Paulina. Both Pacific oysters and blue mussels appear across the landscape in proportion (see text for details), thus the displayed bivalve mass density of each sample quadrat (green circles, g dry mass m⁻²) includes both of these major reef-building species. Blue circles depict the position of the seagrass mimics, and bivalve density within them. Dashed contour lines depict the inundation frequency (%). Bivalves were found to appear in higher densities in lower-lying salt marsh areas, very rarely occurred outside of the vegetated zone, and were never found in the vegetation above the *Spartina*-dominated pioneer zone. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

total, we performed surveys of three marshes in the Western Scheldt known locally as Paulina, Hellegat, and Ritthem, and one marsh in the neighboring Eastern Scheldt known as Viane (see Fig. 1 for site details). At these four marsh sites, sampling positions were determined a priori by creating a list of GPS coordinates (n = Paulina: 50, Viane: 55, Ritthem: 80, Hellegat: 148) placed over the *Spartina*-dominated salt marsh edge where bivalve communities were known anecdotally to occur (Fig. 2a & b). These sampling coordinates were spread over an inundation frequency range between 5.5 and 47.5%. Alongside the marsh communities, we surveyed five seagrass mimic structures left in place in a long-term study over 10-years old, and subsequently colonized by reef-forming bivalves. These mimics are composed of an array of 50 cm-long plastic zip-ties anchored within a steel frame and were placed at the foreshore of the salt marshes at Paulina (n = 3) and Ritthem (n = 2) in 2001, experiencing an inundation frequency between 37 and 38% (Fig. 2c & d). At each specified sampling location, a 1 m² quadrat was used to sample the density of reef-forming bivalves. Within each quadrat, the shell length was measured of each living mussel and oyster. The mass of each individual bivalve was then calculated using a calibration between shell length and total individual dry mass (details in Fig. S1). The calibrated mass of each individual was then used to calculate the mass density (g dry biomass m⁻²) and explore the demographic makeup of these bivalve communities. For a randomly selected subset of the

oysters used for the biomass calibration (n = 129), the substrate on which each oyster was attached was also recorded. Additionally, at the saltmarsh, Hellegat, a survey of the salt marsh vegetation was performed within each of the sampling quadrats, in which a search was made for any settling oysters attached directly to the vegetation.

2.3. Observational study - bivalve reef formation in the lower intertidal

In order to draw a comparison between the density and demographic characteristics of bivalve communities living in the low salt marsh zone and more conventional reef communities in the lower intertidal, we performed a secondary survey on the mixed oyster-mussel reef at Ritthem. This reef is the largest existing bivalve reef in the Western Scheldt (51.45249, 3.661156), located 300 m from the salt marsh edge at an inundation frequency of $75.2 \pm 0.6\%$ (mean \pm se). Here, the reef was sampled at ten random pre-selected coordinates using a 15 cm diameter core. The individual sizes and total mass density of each sample was determined using shell lengths of all living bivalves as described above.

2.4. Observational study - shell substrate availability

In addition to surveying bivalve communities, we characterized the availability of shell substrate within and in front of the salt marsh. To do



Fig. 2. Photos of the various natural and artificial environments that supported bivalve reef formation in the upper intertidal, explored in this study: (a, b) the salt marsh of Hellegat; (c, d) seagrass mimics located <10 m from the saltmarsh edge at Paulina; (e, f) biodegradable 'BESE' lattice structures used in the transect experiment on the tidal flat in front of Paulina, in the Western Scheldt.

this, we collected a 3-cm depth sediment sample at a subset of coordinates ($n = 39$) within one of our four study sites, Hellegat. Sediment samples were freeze-dried for 72 h, then the shell material was separated from the sediment using a 1-mm sieve. The sediment shell content was calculated as the proportion of the total sediment mass contributed by the separated shell material. The inundation frequency of these sampling locations was determined using publicly available inundation frequency maps supplied by the Dutch Ministry of Infrastructure and Water Management (Rijkswaterstaat) for 2018. The distance of each sample coordinate to the nearest marsh edge was determined in reference to aerial photos of the Scheldt Estuary from 2018 supplied also by Rijkswaterstaat.

2.5. Manipulative experiment 1 - oyster & marked cockle shell transplantation

We performed a series of manipulative experiments to explore possible mechanisms that may explain the presence of bivalves in the high intertidal, solely within marsh vegetation. In the first experiment, we tested whether transplanted oysters have the physiological capacity

to survive in the infrequently inundated areas within salt marsh vegetation at Hellegat. In addition to this, we tested whether survival may be facilitated under marsh vegetation compared with that experienced on the nearby un-vegetated mudflat, chiefly through lowering dislodgement risk. This comparison was performed using both an exposed mudflat at the foreshore of the salt marsh, and a sheltered mudflat formed by a bare area within the marsh, encircled by pioneer vegetation (see Fig. 3d for visualization of the experimental design). For this experiment we purchased 200 2-yr old oysters, grown in subtidal culture, of 67.6 ± 0.1 g dry mass (mean \pm se, as calibrated from the shell length). These oysters were placed directly on the sediment surface, distributed amongst ten 1m^2 plots, each receiving 20 initial oysters (salt marsh: $n = 4$, exposed & protected mudflats: $n = 3$ each). Each experimental plot was located no farther than 70 m from any other plot, with an average inundation frequency of $34.4 \pm 2.15\%$. Oyster survival was then monitored over a period of 160 days. Beginning in May 2019, the disappearance of oysters from experimental plots (presumably due to dislodgement by hydrodynamic forces) and the death of oysters remaining within the plot (indicated by an oyster with an open valve and degrading or missing soft tissue) was recorded. Cause of death was not

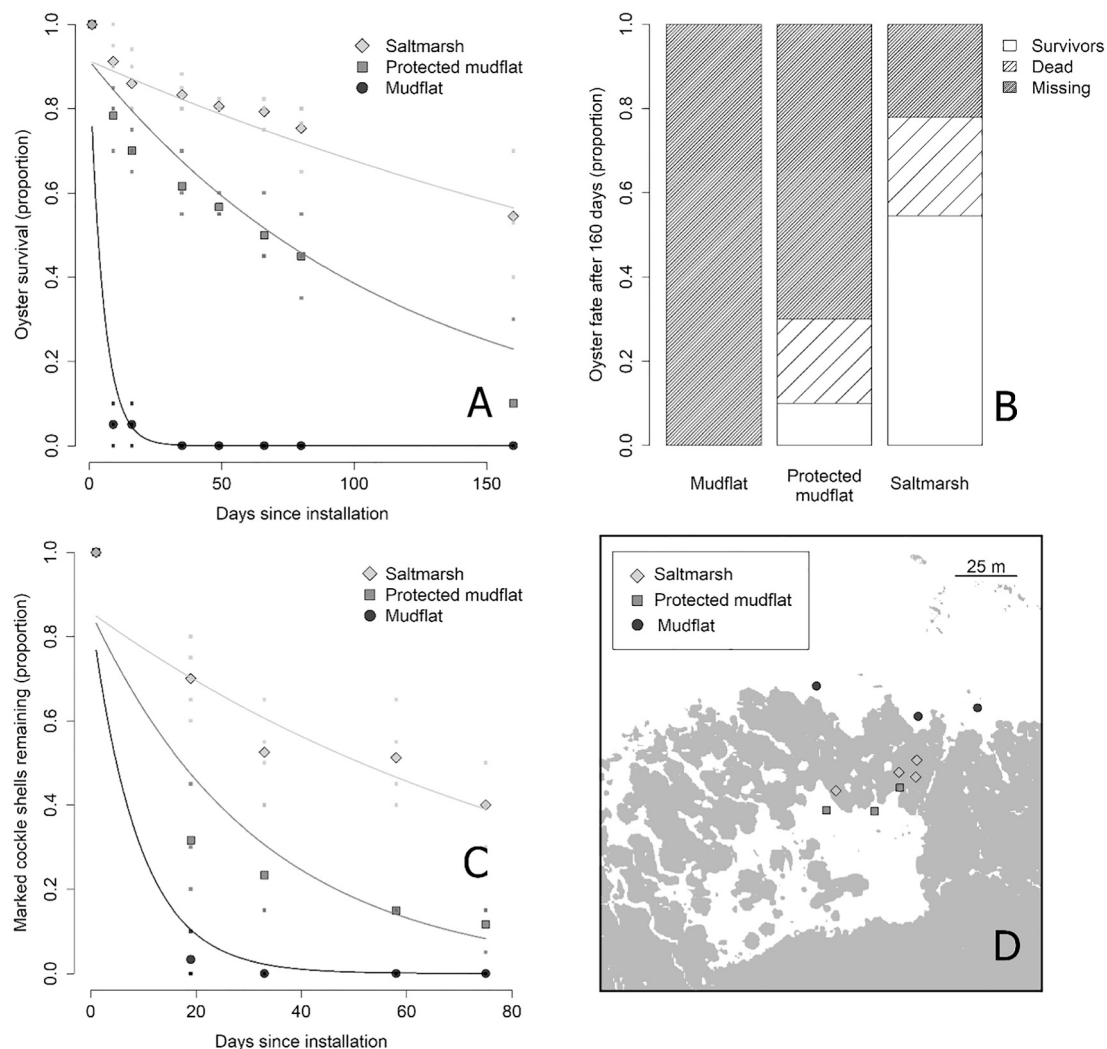


Fig. 3. Results of the manipulative experiments using transplanted adult oysters (a, b) and marked cockles, which represent a common settlement substrate (c). A map of the experiment has also been included (d). Transplanted oysters showed strong survival throughout the study period 160 days despite the infrequently inundated conditions within the *Spartina*-dominated marsh pioneer zone. Oysters had a much lower likelihood of being dislodged from the study area by hydrodynamic forces when placed underneath the vegetation canopy. Similar hydrodynamic-sheltering was also extended to the marked cockle shells. Infrequent dislodgement in the vegetated zone may facilitate the establishment of settling bivalves. Evidence was also found that physiological survival of transplanted oysters was higher underneath the vegetation (see text for details).

determined.

In a coupled experiment, we tested to what extent the vegetation canopy plays a role in stabilizing shell substrate within the marsh. In this experiment, 200 shell valves (4.3 ± 0.2 cm in length) from the common cockle (*Cerastoderma edule*), the most common form of naturally-occurring settlement substrate in the marsh, were collected from the surroundings and marked with red nail polish. Marked shells were distributed in sets of 20 amongst the ten experimental plots used in the oyster survival trials. This was done to detect differences in the likelihood of substrate dislodgment between vegetated and un-vegetated areas, that could indicate a facilitative mechanism driving the establishment of settling bivalves exclusively underneath the marsh canopy. The retainment of marked cockle shells within the plots was monitored periodically over a period of 75 days.

2.6. Manipulative experiment 2 - oyster establishment on settlement plates

To test if the establishment of young oyster spat was possible within the marsh, and whether the marsh vegetation played some role in amplifying the intensity of this establishment, twenty-two oyster settlement plates (as described in Walles et al., 2016b) were placed along a transect ranging from the uppermost extent of the *Spartina*-dominated pioneer zone on the marsh at Hellegat, down the intertidal gradient to a maximum of 67% inundation frequency (see Fig. 4b for visualization of the experimental design). These 'settlement plates' are two roughened Plexiglass plates (20×18 cm) anchored within a steel frame, partially protected against predation by a layer of plastic netting encasing the frame. The plates were placed at even distances of between 10 and 15 m along a transect with a total length of 230 m, at the onset of the major annual spawning event between July and September in this region. The four uppermost structures were placed under the canopy of marsh vegetation. In addition to the main transect line, a parallel transect of four settlement plates was placed that travelled through the sheltered mudflat within the marsh pioneer zone to detect any effects of marsh vegetation on settlement independent of the position in the tidal frame. Originally placed in July, the settlement plates were removed in November, after a period 120 days. Settled oyster spat were removed from the plates and dried at 60°C for 72 h. The cumulative mass of all settled oysters on each structure, including those attached directly to the

metal frame, was weighed and divided by the total area of the structure to calculate the mass density of settlement (in g dry biomass m^{-2}).

2.7. Manipulative experiment 3 - reef formation on artificial stable-substrate

Lastly, we performed a long-term experiment in order to test to what extent the provisioning of stable substrate could facilitate bivalve reef formation over the entire region of the intertidal gradient between the subtidal channel and the vegetation edge. In this experiment, we deployed biodegradable lattice structures along a transect near the salt marsh, Paulina, in the Western Scheldt. These structures, known as BESE-elements (BESE, Culemborg, the Netherlands; see Temmink et al., 2020 for details, Fig. 2e & f) have the dimensions $50 \times 100 \times 10$ cm and are made of biodegradable potato-waste derived Solanyl C1104M (Rodenburg Biopolymers, Oosterhout, the Netherlands). In total, eleven structures were anchored to the tidal flat at even intervals along an inundation frequency gradient ranging between 40 and 85%, over a transect 350 m in length. These structures remained in place for two growing seasons from March 2017 until removal in November 2018. A 15-cm diameter core sample was removed from each of the structures, except for the four structures highest in the intertidal, which were sampled in their entirety. Within these samples, the shell length of each living mussel and oyster was measured from which the individual dry mass was calculated via calibration as in the observational survey. The elevation of each structure in both the short-term settlement plate study and this long-term experiment was measured using an RTK-dGPS (Topcon Hiper SR & FC-5000, Topcon Positioning Systems Inc., Tokyo, Japan) to an accuracy of 2 cm. The inundation frequency experienced by each structure was then calculated based on a local water level time series provided by Rijkswaterstaat, measured at the nearest sampling station (Terneuzen for Hellegat & Paulina, and Stavenisse for Viane).

2.8. Statistical analyses

Differences in transplanted adult oyster survival and marked shell retainment were compared at the conclusion of the experiment using binomial generalized linear mixed effects models where the plot number

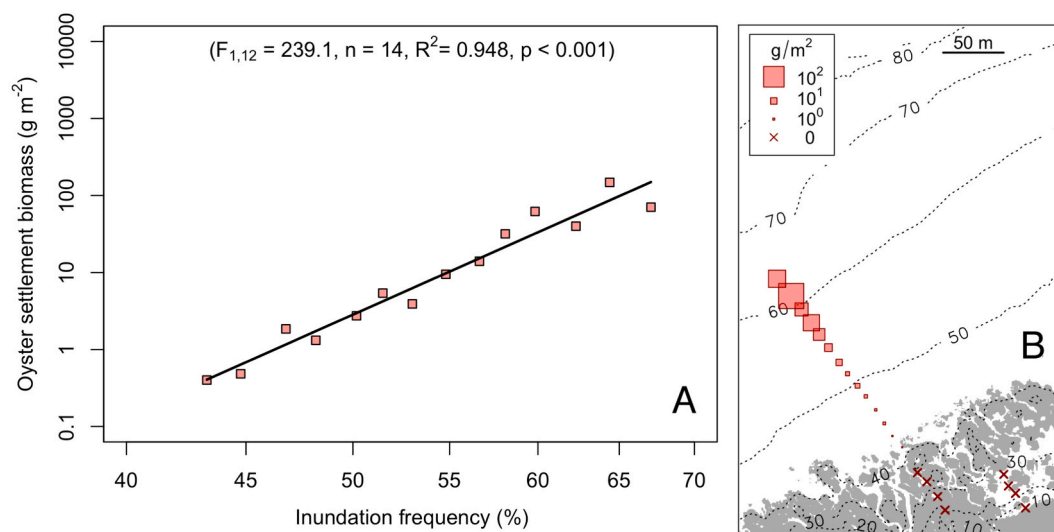


Fig. 4. Recruitment of juvenile Pacific oysters on settlement plates along a transect across the intertidal at Hellegat displays a strong correlation with inundation frequency, defined by a power-law scaling relationship (a). Note the log-scale x- and y-axes. A map of the experimental design is provided (b). The size of the red squares indicate the oyster mass density established on the structures after a period of 120 days. Although juvenile oysters were found to occur within the vegetation naturally, no establishment on settlement plates occurred in this study above the marsh boundary. The position of settlement plates where oysters did not establish are indicated in the map diagram (b), but were not used in the regression due to the log-log fit. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

was included as a random variable. The mass density of mussels and oysters were correlated against inundation frequency through linear regression after log-transforming both variables. This model was selected as the best fitting choice after comparison against linear and exponential models using AIC model comparisons. The same model choice was used to measure the correlation between bivalve mass density and inundation across the marsh survey, the oyster settlement experiment and the artificial structure experiment. The correlation between (1) oyster and mussel mass density across the salt marsh survey and the transect of artificial structures, and (2) bivalve density and sediment shell content were also compared using this approach. Species-specific differences in the cause of variation in mass density (driven either by change in the individual number or average individual size) were determined by comparing the coefficients of determination between these two components. All analyses were performed in R version 3.6.0 (R Core Development Team, 2008).

3. Results

3.1. Status and characteristics of bivalve communities within low-lying salt marshes

The field survey demonstrates that bivalve communities frequently occur within low-lying *Spartina*-dominated salt marsh vegetation throughout the Scheldt estuary, as living bivalves were found to inhabit all sampled sites (Fig. 1). The intensity of establishment varied heavily both between and within the four marshes. The mass density of bivalve communities was highest in the most low-lying regions of the marshes (see the lower lying regions of Ritthem: Fig. 1a, and Paulina: Fig. 1d, linear regression in Fig. 5). The mass density of Pacific oyster and blue mussel communities correlated roughly with one another across the entire survey ($F_{1,84} = 26.4$, $R^2 = 0.23$, $p < 0.0001$, $n = 181$). Less than 1.5% of living bivalves occurred farther than 30 m into the marsh from the vegetation edge at any location. Where very little low-lying *Spartina* vegetation was present, such as in Viane, which is an eroding marsh-remnant where the lowest vegetation extent reaches 33% inundation, almost no bivalves occurred (averaging $3.3 \pm 1.5 \text{ g m}^{-2}$; mean \pm se). Control measurements directly in front of the salt marsh edge found

living bivalves on the unvegetated nearby mudflat in only 0.6% of all samples as opposed to 52.2% in samples within the vegetated zone. Neither bivalve species were ever found to occur on raised marsh platforms. A survey of the attachment substrate of 129 oysters sampled from within the vegetation determined that oysters were predominantly attached to either shell fragments (32.5%) or other living oysters (67.5%). A further survey of the salt marsh vegetation concluded that there was so far no evidence of oysters attaching directly to salt marsh shoots in this region.

3.2. Protective benefits of marsh canopy on oyster survival

Transplantation of adult oysters into the marsh was successful, as $54.5 \pm 6.1\%$ of oysters remained alive after 160 days, indicating that the marsh is a physiologically suitable environment for survival, despite the stress of infrequent inundation (Fig. 3). We furthermore found that salt marsh vegetation plays a protective role by reducing the probability of oyster dislodgment under hydrodynamic forces. Oyster retainment within the transplantation plots was significantly greater within salt marsh vegetation than that seen on either the exposed mud flat and on the sheltered internal mud flat on Hellegat, encircled by vegetation ($\beta = -2.9$, $\text{SE} = 0.6$, $z(197) = -5.0$, $p < 0.0001$, Fig. S2b). While after 160 days, only 22% of oysters had been dislodged from their positions within salt marsh vegetation, 95% of the oysters placed on the nearby exposed mud flat had already disappeared after 9 days in the field (Fig. 3a). Benefits provided by the marsh to support the oyster's physiological health were less pronounced, however a significantly smaller fraction of the remaining oysters experienced physiological death within salt marsh vegetation than on the sheltered mudflat after 160 days: 30% against 66% ($\beta = -1.5$, $\text{SE} = 0.6$, $z(78) = -2.7$, $p = 0.007$, Fig. S2c).

3.3. Substrate stabilization by salt marsh vegetation

The retainment trials of marked shells also demonstrated the role vegetation plays in retaining and stabilizing shell material. This shell material is expected to be an important substrate that facilitates both mussel and oyster bivalve establishment. On our experimental site at Hellegat, the shell content at the edge of the vegetation was as high as

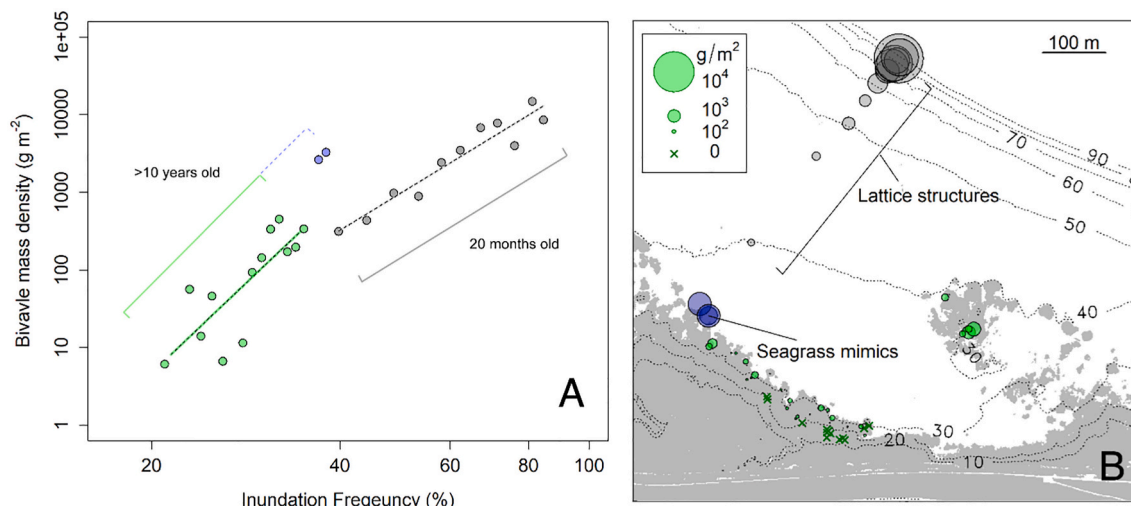


Fig. 5. Bivalve mass density (g m^{-2}) measured across our transect of artificial structures (grey circles), including also bivalve communities living in the salt marsh (green circles) and seagrass mimics (blue circles) at Paulina (a). Note that the communities within the lattice structures contrast strongly in age (20 months) with those found in the salt marsh and seagrass mimic habitats (> 10 years). A strong correlation is found between the bivalve mass density and inundation frequency across habitat types, captured by a power-law scaling relationship. Note the log-scale x- and y-axes. A map of the experimental study site is provided (b). Dashed-contour lines in this map depict inundation frequency (%). These results demonstrate that bivalve reef formation and development is possible throughout most of the intertidal gradient, although it is strongly diminished at higher tidal positions. The fact that bivalve reefs are not observed to occur naturally on tidal flats at these levels indicates the presence of factors limiting the formation of reefs on tidal flats, which are not present within the marsh vegetation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

50.2% of the sediment's mass, tapering off progressively with distance from the edge both seaward and landward (Fig. 6d). However, bivalve occurrence did not clearly follow patterns in substrate availability ($F_{1,24} = 0.31$, $R^2 = -0.028$, $p = 0.58$, $n = 26$). While shell content peaked at the salt marsh margin, the bivalve mass density was highest 12 m into the vegetation (Fig. 6e). Additionally, although the shell content on the exposed mud flat directly in front of the marsh is quite high ($0.14 \pm 0.05\%$ shell by mass, Fig. 6d), our shell-retainment trial demonstrated that the turn-over rate of these shells occurs on the scale of days (Fig. 3c). On the exposed mudflat, 96.6% of all marked shells had disappeared after 19 days. By contrast, within the vegetation, 60% of marked shells could be found within the plots at the final sampling point, at the last monitoring point after 75 days, representing a significant difference in shell retention ($\beta = 2.0$, $SE = 0.4$, $z(200) = 5.0$, $p < 0.0001$). Overall, this suggests that a major driver of bivalve establishment within salt marsh vegetation is the retainment and stabilization of shell material in the understory, rather than simply serving as a deposition site for large but potentially unstable congregations of shell material.

3.4. Evidence of bivalve establishment within the marsh

Direct evidence of bivalve establishment within the marsh, which could explain the presence of the naturally occurring communities is mixed. None of the settlement plates placed within the marsh or within the protected mudflat above the inundation frequency of 43% experienced any oyster establishment. Below this level in the tidal frame, however, the total mass density of the settled oysters on each structure grew consistently alongside increasing inundation frequency ($F_{1,12} = 239.1$, $R^2 = 0.948$, $p < 0.01$, $n = 14$), growing by approximately ten times with every 10% increase in inundation frequency. The demographic makeup of the naturally-occurring bivalve communities suggests the capacity for successful establishment within the salt marsh is likely, due to the presence of extremely small individual oysters within the marsh (as small as 0.001 g dry biomass, see Fig. S3), predominantly establishing on the shells of larger oysters. While settlement on the experimental structures only occurred up to 43% inundation, the highest naturally-occurring oysters in the Hellegat marsh occurred at an inundation frequency of 9% (Fig. 4).

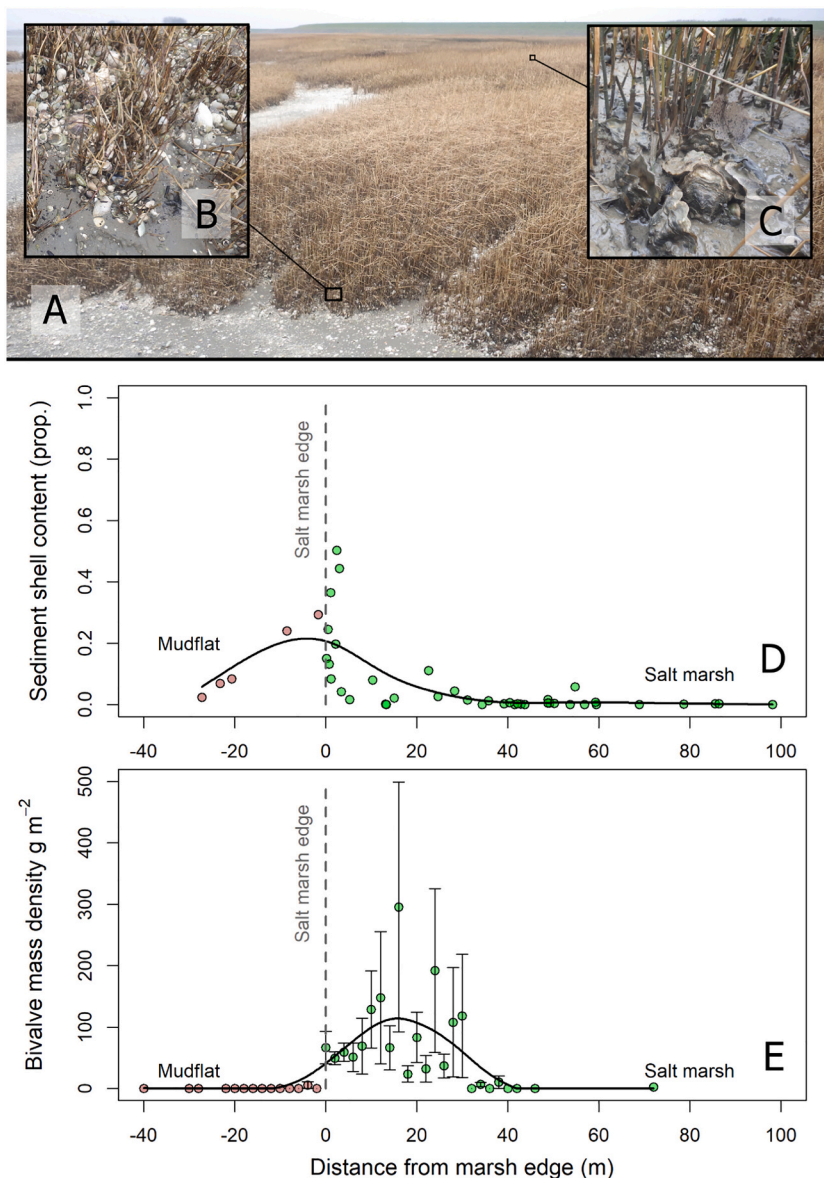


Fig. 6. The entrapment of shell material at the saltmarsh foreshore edge is depicted in photos (a, b) and as measured in our survey at the saltmarsh, Hellegat (d), matched against the distribution of living bivalves in the marsh (c, e), with respect to the marsh edge. Shell content increases toward the vegetation boundary both on the tidal flat (brown), and within the marsh vegetation (green). Data is fit with smooth spline for visualization. Shell material, which is a major substrate for bivalve recruitment in early-life, is imported from the tides and collects at the vegetation margin likely due to the abrupt lowering of flow velocity and wave energy within the vegetation, and further entrapment by the vegetation structure. However, the distribution of living bivalves is highest 18 m behind the vegetation edge. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.5. Reef formation on artificial structures

Given the evidence found in these marsh communities that bivalve establishment, growth and survival is possible very high in tidal frame, we finally sought to determine whether the installation of stable substrate on the tidal flat could initiate reef-formation across the breadth of the intertidal gradient. In our last experiment, the provisioning of hard stable-substrate, in the form of biodegradable lattice structures, was effective in stimulating bivalve reef development. Just as was seen in the oyster settlement experiment, the total mass density of the developing reef on the artificial structures occurred according to a consistent pattern throughout the intertidal gradient that can be predicted very well by the inundation frequency ($F_{1,9} = 100.6$, $R^2 = 0.91$, $p < 0.0001$, $n = 11$, Fig. 5a). It is notable, that the same general pattern in bivalve mass density, controlled by inundation frequency, can also be observed within the marsh. The seagrass mimics, which were artificial structures that had been in place for at least ten years, supported much greater reef mass-densities than appeared naturally within the marsh or within the younger (20 month-old) artificial structures at comparable (35–40%) inundation frequency (i.e., 630 ± 97 g in the seagrass mimics against 159 ± 33 g in the marsh and 187 ± 31 g in the lattice structures).

3.6. Species-specific constraints on growth and maximum size in the upper intertidal

Throughout the artificial structures, the positive correlation in mass density between mussels and oysters was consistent ($F_{1,9} = 28.53$, $R^2 = 0.73$, $p = 0.0005$, $n = 11$), reflecting a looser pattern seen earlier in the marsh survey. However, the drivers of reef size, as measured by the total

bivalve mass density (a metric that combines both the individual number and the average size), appear to vary between mussels and oysters (Fig. 7). Across the transect of artificial structures, increases in mussel individual mass were driven predominantly by an increase in the total number of individuals within an area. Variation in the number of mussel individuals explained 93% of the variance in mass density, against 21% explained by changes in the average mussel size. By contrast, oyster mass density increased mostly as a consequence of individuals growing to a larger average size. Here, changes in average oyster size explained 65% of the variance in mass density, against 32% explained by the variation in the individual number. This suggests that the growth rate of oysters diminishes with increasing position in the tidal frame. Oysters found within the salt marsh vegetation were also found to achieve a substantially smaller maximum size (182 g, Fig. S3d) than that of the oysters found in the lower intertidal reef (521 g, Fig. S3a). By contrast, the individual size of the population of mussels within the salt marsh were statistically indistinguishable from those that occurred in the lower intertidal reef ($F_{1,176} = 1.107$, $p = 0.29$, $n =$ low intertidal: 18, salt marsh: 163).

4. Discussion

In this study, mechanisms found to facilitate bivalve settlement and survival in low-lying marshes were artificially recreated through the provisioning of artificial settlement substrates. This provoked reef development on the tidal flat at elevations beyond where bivalve reefs are observed to naturally occur on soft sediment. When provisioned with stable substrate, both Pacific oysters (*Crassostrea gigas*) and blue mussels (*Mytilus edulis*) had the potential to form reefs across most of the

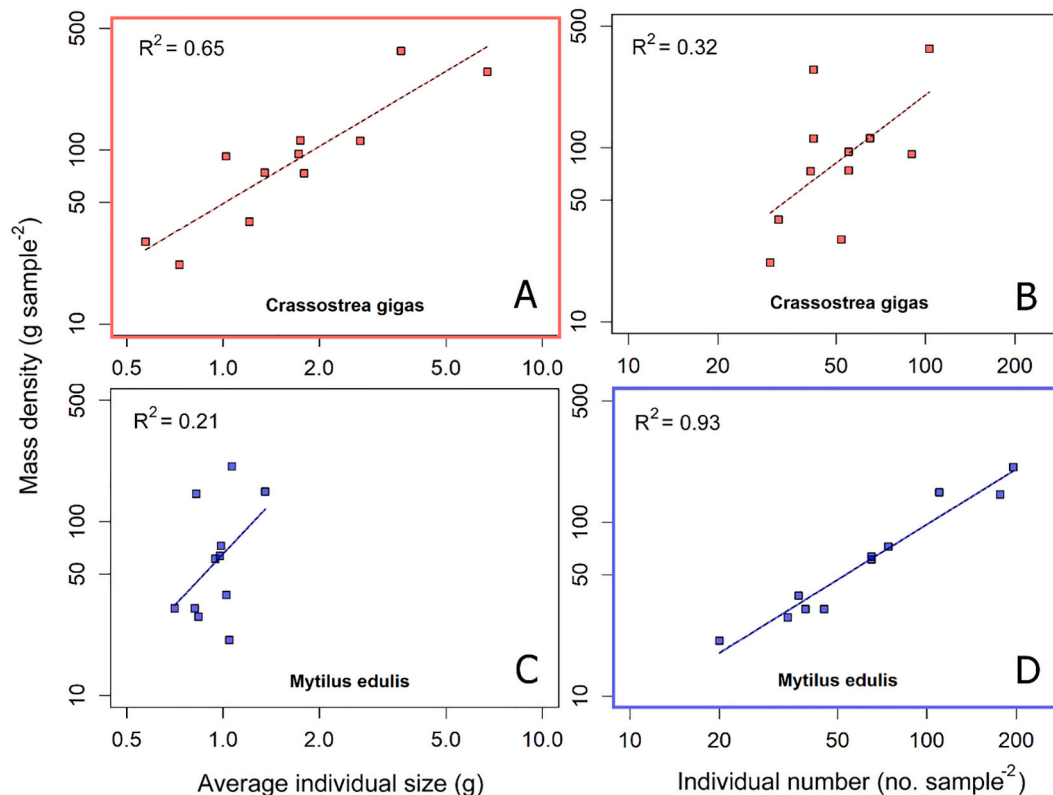


Fig. 7. The respective contribution of individual number and average individual size to mass density (the overall metric of population size) is displayed for both Pacific oysters and blue mussels within the long-term transect experiment. It appears that the driving components behind the increase in mass density is driven by different factors for each species: Oysters tend to predominantly increase in size (a), and to a lesser degree increase in number (b); while mussel mass density is almost entirely driven by the individual number (d) and the average individual size remains fairly constant (c). This may be driven in part by the comparatively low maximum size of an individual mussel (~10 g), compared to oysters (~1000 g, see Fig. S3). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

intertidal gradient. The mechanistic explanation for this, provided within the ‘window of opportunity’ framework is that, in a setting prone to hostile levels of substrate mobility, establishing juveniles survive despite their lower growth rate because artificial stable-substrate removes the risk of substrate dislodgment under hydrodynamic forcing during this vulnerable period (Fig. 8). Most importantly, the conceptual validation presented in our study extends the potential utility of artificial reefs for coastal defense, by demonstrating that reef initiation is possible on high intertidal mudflats even in the region near the salt marsh edge where protective fringing reefs (which do not occur naturally in this region) could protect the marsh against cliff-erosion.

4.1. Management to foster establishment by understanding natural mechanisms

In general, the management of coastal ecosystems to develop nature-based infrastructure and defense schemes is constrained by our understanding of how ecosystems initiate and perpetuate themselves. Many of the most important ecosystem engineers in coastal settings have developed positive feedback systems to mitigate the destruction wrought by natural disturbances in the dynamic coastal setting (van Wesenbeeck et al., 2008; van der Heide et al., 2011; Nyström et al., 2012). However, when the biotic feedback mechanisms are missing, as is typically the case early in the developmental process, there are only rare occasions when the environmental circumstances will allow successful establishment and growth to occur (Balke et al., 2014). Thus, provoking establishment in ‘window of opportunity’-driven systems will require either vast patience or the intervention of active restoration measures. Such restoration measures must typically approach the problem from one of two angles: i) temporarily reducing environmental stresses to engineer an artificial ‘window of opportunity’ that would otherwise be very unlikely to occur (Kamali and Hashim, 2011) or ii) temporarily mimicking

the positive feedbacks that enable established organisms to persist despite the hostile environment (Temminck et al., 2020). This study, which could be interpreted in either light, provides a demonstration of how such approaches can be effective. Additionally, the use of biodegradable substrates in place of permanent installations made of stone, cement, metal, or even plastic structures more commonly used in artificial reefs (Butler, 1954; Nestlerode et al., 2007; Grabowski and Peterson, 2007; Beck et al., 2011; Walles et al., 2016a), creates the possibility for artificial reefs to transition to reefs with a fully natural character. In the best-case scenario, biodegradable structures can support reef initiation in the essential early stage, but as the structures degrade, biological feedbacks will step-in to support continued establishment so that the reef no-longer depends on the artificial reef foundation.

4.2. Limitations and trade-offs in the construction of high-intertidal reefs

Although reef initiation may be possible in otherwise uncolonized regions of the tidal flat, when stable-substrate is provisioned, reef development in the high intertidal remains limited by the physiological constraints of infrequent inundation (Spencer et al., 1978). When the inundation frequency is too low, the sustainable maximum size of the reef may be too small to have utility in coastal defense. Slow-growing reefs may also have impoverished resilience in the wake of disturbances (Housego and Rosman, 2016; Colden et al., 2017), and may expand both laterally and vertically at slower rates (Ridge et al., 2015; Ridge et al., 2017a, 2017b). Ultimately, the total reef size is a major component of its contribution to wave attenuation for coastal defense (Borsje et al., 2011). Therefore, finding a position in the tidal frame that optimizes the costs and benefits attributed to intertidal position and reef productivity represents a crucial design trade-off problem in the construction of bivalve reefs for coastal defense.

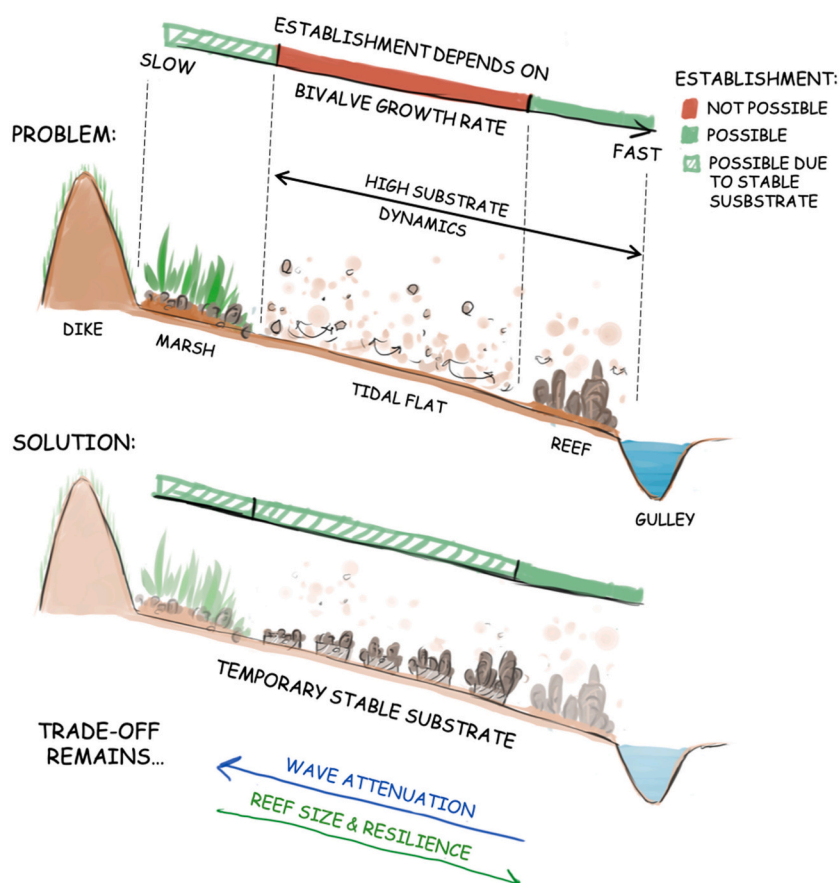


Fig. 8. Conceptual figure visualizing how substrate turn-over creates size-dependent thresholds that limit bivalve reef formation on tidal flats. Natural reef formation occurs only where the growth rate is high enough to overcome frequent substrate disturbance, unless substrate is stabilized, as within the marsh. By introducing stable substrate onto tidal flats, reefs may be artificially initiated across the intertidal gradient, including areas of lower growth. Once established, a reef's size remains constrained by its tidal position, indicating the presence of a management trade-off between a reef's resilience (which is strongest in the low intertidal) and its contribution to coastal protection (which is strongest at high intertidal position).

There is of course only an indirect relationship between inundation frequency and reef mass density. This correlation is driven by a suite of under-lying mechanisms, which likely include the period available for feeding, which is counter-balanced against the food quantity in the water column, physiological costs associated with anaerobic respiration during low tide, and the accessibility of the site to predators (Spencer et al., 1978, Crosby et al., 1991, Johnson and Smeets, 2014, Byers et al., 2015, Walles et al., 2016c). However, we have found that these multiple factors seem ultimately to produce a tight correlative relationship over the breadth of the intertidal, defined by a power-law scaling equation. There does not appear to be a clear upper threshold where it is no longer possible for bivalve establishment to occur over the intertidal gradient. Instead, both the probability of establishment and the rate of growth progressively decline as the inundation frequency decreases until any bivalve establishment becomes nearly impossible to detect.

Thanks to the consistent manner of establishment on artificial substrate across the intertidal gradient, the methodology provided here may be useful for determining the effective upper limit where reef formation on the tidal flats is most cost-effective, when balancing benefits of increased height in the intertidal frame, against the costs to the reef's projected mass density and productivity. Although an arbitrarily high tidal position may not be appropriate for artificial reef construction due to these physiological consequences, it is quite likely that initiating reefs at positions on the tidal flat above the natural band of reef-development will prove to be of greater utility for coastal defense.

4.3. Other potential mechanisms to facilitate reef development

In addition to the mechanical effects of the marsh structure, there may be further mechanisms that support the physiological health of bivalves in the vegetated zone. The presence of such additional mechanisms was suggested by the greater physiological survival of oysters in our experimental study under the marsh canopy compared to the hydrodynamically sheltered internal mudflat. Additionally, we observed anecdotally that bivalve communities living within and attached directly to the blades of the seagrass mimics appeared only within the shaded understory of the structures, occupying only a fraction of the available settlement surface (this can be seen in Fig. 2c & d). Mechanisms to consider as potential contributors to the success of reef development within the marsh and marsh-like environments include shade-induced temperature buffering and enhanced water storage. Similar mechanisms have been earlier demonstrated to play important roles in buffering physiological stress and mortality during heat waves in other intertidal environments (Crosby et al., 1991; Harley, 2008). Gagnon et al. (2020) presents an exhaustive list of known facilitative mechanisms between reef-forming bivalves and marine and freshwater vegetation, many of which may be relevant in this setting. It is also conceivable that the complexity of these environments (both natural and artificial) also reduces the risk of predation (as suggested by Humphries et al., 2011, Bertolini et al., 2018). Further investigation and integration of any of these additional facilitative mechanisms into the design of artificial reefs may help to further ameliorate some of the physiological costs related to living at a high intertidal position, and thus boost the potential for reefs to appear and grow more quickly at higher tidal positions.

4.4. Novel ecosystem

It is not lost on the authors that we describe an environment that could be classified as 'novel' given that it has been colonized by two non-native species (*Crassostrea gigas* and *Spartina anglica*), neither of which have existed in the Netherlands for much longer than half a century (Gray and Benham, 1990, Ruesink et al., 2005). Given that the native varieties, *Spartina maritima* and *Ostrea edulis* (the European flat oyster) have much more limited intertidal ranges (Reise, 2005), it is likely that the potential for the ranges of oyster reefs and salt marshes to overlap in

the Dutch mesotidal estuaries has only become possible in the past few decades, since the introduction of these invasive species. Whereas this may be of great benefit for coastal defense, future invasions should for obvious reasons be avoided as much as possible. Additionally, as foundational ecosystem engineers, the establishment of bivalve reefs causes significant changes to the nature of their local environment, which impacts the food web composition locally (Borst et al., 2018) and at a long-distances (Donadi et al., 2013). Although net changes to biodiversity tend to increase as a consequence, it is important to recognize that in the process of facilitating reef ecosystems for the purposes of coastal protection, tidal flats and the communities that rely upon them will be displaced. That said, coastal defense management that utilizes solely grey infrastructure tends to instigate ecological consequences that are considerably more drastic (Bulleri and Chapman, 2010; Bishop et al., 2017; Heery et al., 2017).

5. Conclusion

Bivalve reefs have the potential to play an important role in coastal protection schemes, but their utility is limited by our ability to initiate reef formation according to need. By studying atypical environments where bivalve communities naturally occur (such as within salt marsh vegetation), we can uncover mechanisms that can extend the habitable range of reef formation. Here we show that, when provided with artificial stable-substrate, bivalve reefs can form at intertidal heights beyond where naturally-occurring reefs can be found. The utility of this approach is tempered by the fact that the optimal tidal position for reef construction remains constrained by reef growth-rates, which diminish with increasing tidal position, even as the reef's potential to effect over-lying water movement grows. Based on an understanding of this essential trade-off, it should be possible to optimize the placement of artificial reefs higher on intertidal mudflats than where natural reefs tend to form, so as to maximize their utility in coastal protection.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoleng.2021.106221>.

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