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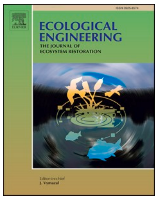

Initiating and upscaling mussel reef establishment with life cycle informed restoration: Successes and future challenges

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ABSTRACT

Worldwide, coastal ecosystems are rapidly degrading in quality and extent. While novel restoration designs include facilitation to enhance restoration success in stressful environments, they typically focus on a single life-stage, even though many organisms go through multiple life-stages accompanied by different bottlenecks. A new approach – life cycle informed restoration – was designed to ameliorate multiple bottlenecks throughout an organism's life cycle. It has successfully been tested on a small scale to facilitate intertidal bivalve reef formation in the Netherlands and Florida. Yet, it remains unknown whether this approach can be scaled to ecosystem-relevant scales. To test whether life cycle informed restoration is upscalable, we conducted a large-scale restoration experiment using blue mussel reefs as a model system. In our experiment, we used biodegradable structures to temporarily facilitate mussel reef formation by providing early-life settlement substrates, and subsequently, reduce post-settlement predation on an intertidal flat in the Wadden Sea, the Netherlands. The structures were placed in 10 × 20 m plots, mimicking bands found in natural mussel beds, spread out across 650 m, and were followed for two years. Our results show that the structures enhance mussel biomass (0.7 ± 0.2 kg DW m^{-2}), as mussels were absent in bare plots. However, biomass varied within plots; in intact structures it was 60 times higher (1.2 ± 0.2 kg DW m^{-2}) than in those that became buried (0.02 ± 0.009 kg DW m^{-2}). Next to burial, 18–46% of the structures were lost due to technical failure, especially during winters at this exposed site. We show that the life cycle informed restoration principle works, but we encountered technical challenges due to larger scale processes (e.g. sedimentation). Furthermore, environmental information is essential for site selection, and for restoration, the functioning of such structures should be tested under extreme conditions before upscaling.

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1. Introduction

Coastal ecosystems provide many important ecological and societal services, including shore protection, the provision of food and biodiversity (Grabowski et al., 2005; Coen et al., 2007; van der Zee et al., 2012). However, they are currently degrading and declining to a great extent, which affects their functioning and ecosystem services they provide. The cause lies often in human activities, such as overexploitation, climate change, eutrophication and land-use change (Lotze, 2005; Eriksson et al., 2010; Beck et al., 2011). As a consequence, epibenthic bivalve reefs, salt marshes, mangroves and seagrasses have strongly declined by 35–85% (Gedan et al., 2009; Waycott et al., 2009; Beck et al., 2011). To counteract this decline, restoration attempts aim to assist the recovery of coastal ecosystems and their ecological functions (Bayraktarov et al., 2016; Duarte et al., 2020; Saunders et al., 2020). However, these attempts often fail because positive species interactions that are typically important in harsh coastal systems (e.g. self-facilitation that leads to improved growing conditions, such as sedimentation or reduction of wave energy), are not included in restoration designs or are very expensive (Silliman et al., 2015; Bayraktarov et al., 2016; Saunders et al., 2020; Temmink et al., 2020).

In many coastal ecosystems, positive species interactions (i.e. self-facilitation) stimulate the resilience and colonization of such systems. For example, seagrass meadows, mangrove forests and salt marshes are able to attenuate hydrodynamic energy and trap sediment, which improves the growing conditions of the dominating ecosystem engineer (Bouma et al., 2007; Silliman et al., 2015; Maxwell et al., 2016). Following this, adult mussels provide settlement substrate for spat, because they prefer to settle on the byssus threads of adult mussels (Walters and Wethey, 1996; Reusch, 1998; Carl et al., 2012). In addition, spatial patterning of mussels on multiple scales makes mussel beds more resilient to storms and predation (Liu et al., 2014; de Paoli et al., 2017). On bare intertidal flats, by contrast, the lack of these feedbacks restricts natural settlement and survival, and frustrates restoration attempts. For instance, classic designs to restore salt marshes were based on reducing competition rather than including positive species interactions (Silliman et al., 2015). Silliman et al. (2015) showed that by including facilitation into restoration designs, restoration yields can be doubled. Building on these findings, Temmink et al. (2020) showed that facilitation can be artificially generated by mimicking emergent traits to both enhance survival of saltmarsh and seagrass transplants, and greatly reduce donor material.

These novel findings and approaches highlight the importance of including facilitation in restoration efforts to increase success rates (Gilby et al., 2021; Silliman et al., 2015; Renzi et al., 2019; Temmink et al., 2020; Temmink et al., 2021b, 2021a; Fivash et al., 2021b; van der Heide et al., 2021). They among with many other restoration approaches in the coastal realm, however, only focused on adult organisms; i.e. on a single life-stage. Examples of restoration approaches are the employment of settlement substrates for larvae of bivalves, or the transplantation of adult seagrass and cordgrass plants, or coral nubbins (Schulte et al., 2009; Marian and Orth, 2010; van der Heide et al., 2014; Angelini et al., 2015; Graham et al., 2017; Bersoza Hernández et al., 2018). Yet, almost all organisms show a complex life cycle during which they experience several bottlenecks. For instance, when organisms develop from seeds or larvae into juveniles, and from juveniles to adults (Balke et al., 2011; van der Heide et al., 2014; de Paoli et al., 2015). In a recent study, Temmink et al. (2021a) showed that bivalve reef restoration success can greatly benefit from artificially facilitating blue mussels during multiple life-stages; an approach named 'life cycle informed restoration'.

In life cycle informed restoration, restoration focuses on the life cycle of an organism, rather than a single stage. For example, many bivalve larvae depend on physical or chemical signals originating from healthy reefs and specific settlement substrates (Turner et al., 1994; Ritson-Williams et al., 2010; Carl et al., 2012; Villanueva et al., 2012). These signals act as settlement cues and larvae critically depend on adult organisms for successful settlement in a suitable habitat, as they provide suitable substrate for settlement (Villanueva et al., 2012). After establishment, and development into juveniles, they require ample food and protection from predation to further mature (van der Heide et al., 2014). Temmink et al. (2021a) showed that bivalve reef formation could be initiated by overcoming bottlenecks at two life-stages using complex biodegradable structures. Specifically, they showed that by stimulating early-life stage recruitment by the addition of fibrous coir rope as a preferable settlement substrate to a hard substrate, mussel recruitment was 12 times higher compared to the hard substrate alone. Next, the complexity of the structure reduced predation after settlement, which resulted in seven times higher mussel biomass compared to coir rope alone. Although their results are promising, their experiment took place on a 0.25–0.5m^2 scale, which is too small to restore epibenthic bivalve reefs on an ecosystem-relevant scale. Therefore, to explore the potential of life cycle informed restoration, it is important that this approach should be tested on a larger scale. Yet, larger scale restoration approaches could be affected by larger scale processes, such as coastal hydrodynamics and morphology (Bouma et al., 2007). This however, remains to be elucidated.

In this study, we focus on mussel bed restoration, because they i) have greatly declined in quality and extent, and ii) provide important ecological services, including shore protection, provisioning of food and biodiversity (Eriksson et al., 2010; van der Zee et al., 2012). We apply life cycle informed restoration on a larger scale than Temmink et al. (2021a) using biodegradable structures – named establishment structures – to test (1) whether this approach is upscalable and (2) how the structures behave and influence their environment on such a scale. To stimulate reef formation of the primary native reef-building bivalve (blue mussel, *M. edulis*) in the Netherlands, we use biodegradable establishment structures embedded with coir rope to overcome multiple establishment bottlenecks following Temmink et al. (2021a). In this way, we stimulate recruitment (early-life stage), and subsequently, lower predation through the complexity of the substrate (later-life stage, Temmink et al., 2021a). We executed a two-year experiment on the intertidal mudflat near Griend, an uninhabited island in the Wadden Sea of the Netherlands. We hypothesize that establishment structures enhance mussel reef development when applied on a larger spatial scale, because next to ameliorating establishment bottlenecks for mussels (Temmink et al., 2021a), the structures create more sheltered conditions by lowering waves and currents (Marin-Diaz et al., 2021; Fivash et al., 2021b).

2. Methods

2.1. Field site

Our experiment was carried out on the intertidal flats of the Dutch Wadden Sea from March 2017 till August 2019, south of the island Griend (53°14′24.97"N, 5°14′53.56″E, Fig. 1A-B). We selected this site, as the general abiotic environment could support mussel bed formation (inundation frequency, hydrodynamic conditions) and because mussel larvae are generally abundant in the water column in this part of the Wadden Sea. This is indicated by the yearly success of the floating mussel seed collectors (in Dutch *MosselZaadinvangsInstalaties*, MZI's, Capelle, 2021). The site was characterized by bare sandy sediment and was located 300 m west from a mussel bed that naturally established in 2016, but which had largely disappeared in the winter of 2017. For specifics regarding sediment dynamics, wind speed and wind direction, see Marin-Diaz et al. (2021).

2.2. Experimental setup

To investigate whether the life cycle informed restoration approach can successfully initiate mussel bed formation (*M. edulis*) at a large scale,

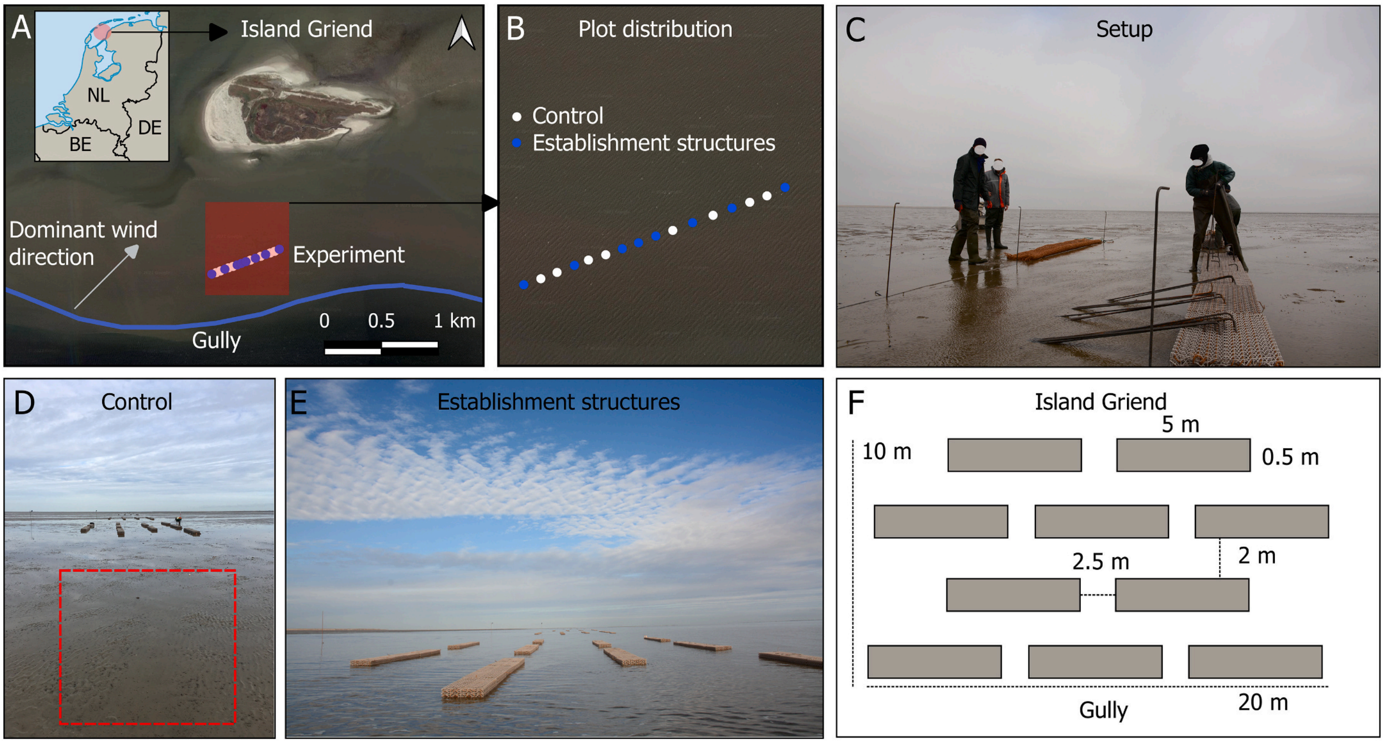

Fig. 1. Field site and experimental setup. The location of the field site (red circle) in the Netherlands and an aerial picture of the island Griend with the experimental area indicated by the circles. The gully is indicated by the blue line (A). The distribution of the experimental plots with (white circles, controls; blue circles, establishment structures are blue, B). The construction of the experimental plots (C). In the front; the establishment structures and the iron rebar that we used to anchor the structures onto the sediment. In the back; the coir mat that functions as the foundation of the structures to prevent gradual sinking into the sediment. The two experimental treatments were 1) bare sediment (red square, D) and 2) establishment structures embedded with coir rope as a settlement cue (E). Plots were spaced 20 m apart. We placed the establishment structures in such a way (F) to mimic the spatial organization normally found in natural mussel beds (Liu et al., 2014). Map on A: Natural Earth and B: Google Earth. Photos C-D: R.J.M.T. and E: M.J.A.C. (For interpretation of the references to colour in this fig. legend, the reader is referred to the web version of this article.)

by facilitating recruitment and reducing predation, we placed establishment structures on the intertidal flat near Griend. Sixteen plots were set out perpendicular to the nearest gully. Plots were placed pairwise ($n = 8$) and randomly designated to one of two treatments (1) *unmodified control* and (2) *establishment structures*. Each establishment structure consisted of eight stacked biodegradable sheets of BESE-elements (sheet dimensions: 91.5 × 45.5 × 2 cm [L × W × H]; BESE Ecosystem Restoration Products, Culemborg, The Netherlands) resulting in a 16-cm high module. Through each module, we braided 70 m of fibrous coir rope (Ø: 0.5–1 cm) to serve as a settlement cue for byssus-forming bivalves (Temmink et al., 2021a). A plot measured 20 × 10 m and consisted of 50 modules divided over 10 bands (width × length, Fig. 1F). We designed the layout of each plot in such way that we mimicked bands typically found in natural mussel beds (Liu et al., 2014). Each band was circa 5 m long and consisted of five modules that were placed on anti-erosion coir mats (circa 4 cm thick). Each module was secured using six 1.5 m long L-shaped rebar anchors. Control plots were completely bare and marked by buoys. Plots were established at 65% inundation frequency (−0.32 ± 0.003 m NAP, Fivash et al., 2021a) and were spaced 20 m apart over a line of circa 650 m.

2.3. Bivalve reef formation

To determine mussel establishment in our experimental plots, each plot was subsampled using a custom-made metal soil sampler (surface area 0.018 m^2, diameter 15 cm, length: 48 cm) in August 2018 and 2019. The sampler was equipped with small teeth (height: 25 mm) to clean-slice through the structures, and a ball valve to extract samples under vacuum. In 2018, to gain insight into the spatial distribution of mussel recruitment, each band in every plot was sampled (10 × 8 samples) at the most representative part related to the structure height above the sediment (i.e. intact, mostly buried). We collected each sample in a plastic bag, after which we separated the mussels from the establishment structures. Next, as a first general metric of reef formation (Temmink et al., 2021a), we determined mussel (shell + soft tissue) dry mass. We measured the length of each mussel using a digital caliper with a 0.01 mm precision. Mussel dry mass (shell + soft tissue) was calculated based on a mussel length to dry mass calibration (1184 measurements of mussels collected in Netherlands, including the Griend area; Fig. S1):

$$\mathit{Mussel\ dry\ mass}\ (g) = 8.69^{-5} * x^{2.8832}$$

where x is the mussel shell length in mm.

In 2019, we additionally took two samples at each plot where the establishment structure was still present, and followed the same procedure as described above. We visually inspected control plots on mussel presence, but no mussels were observed here throughout the full experimental period.

2.4. Large-scale processes on biodegradable structures

To explore the effect of large-scale processes on burial and structural integrity of the establishment structures on landscape and within plot level, we used the mussel core samples ($n = 80$) collected in August 2018. We counted the number of layers that were present above the sediment (category intact). During the collection of mussels, we counted the total number of sheets in each sample and used this information to calculate the number of buried and lost sheets. The number of buried sheets was calculated by subtracting intact sheet number from total number. The number of lost sheets was calculated by subtracting the total number of sheets from the initially placed number (8 layers). Additionally, we determined the total area (m^2) of structure remaining in August 2018 and 2019 using drone imagery (Deltaquad Pro #Map, equipped with a Sony A7RIII, Vertical Technologies, the Netherlands, and Inspire 1 V2.0 equipped with a Zenmuse X5, DJI, China, Fig. S2). For this purpose, an image of each plot was loaded into ImageJ. The image colour threshold was adjusted to obtain clear contrasts between the sediment and the structure (hue: 0:255, saturation: 0:129, brightness 100:255 for 2018 and 50:100 for 2019), then the image was converted to a binary image. For each image, we set a scale using a known length to count the surface area of intact structures. Finally, we used the analyze particle function (including holes), summarized and exported the output.

2.5. Statistics

All analyses were performed in R: a language and environment for statistical computing using R studio (version 3.6.0, R Core Team, 2020). The difference in bivalve reef formation (proxy: mussel biomass) was analyzed for control vs establishment structure (ES) and for buried-ES vs non-buried-ES, non-parametrically using a Kruskal-Wallis test as assumptions for normality were not met. Structural integrity (proportion data) was analyzed per condition (lost, intact and buried) with a General Linear Model with a binomial distribution. Binomial models were checked for overdispersion, and if unsatisfactory, a quasibinomial model was used. All results are shown with their standard error of the arithmetic mean (±SE) and the significance level is assumed at $p < 0.05$.

3. Results

3.1. Bivalve reef formation

Establishment structures strongly facilitated reef development on the intertidal flats near Griend, while in bare controls no reefs developed. We found 0.7 ± 0.2 kg DW m^{-2} (4500 ± 1000 individuals m^{-2}) mussels in the plots with establishment structures and 0 ± 0 kg DW m^{-2} in the unmodified controls (Fig. 2, $\chi^2 = 12.886$, $p < 0.001$). Within the establishment structures, however, mussel biomass varied considerably depending on the structure height relative to the sediment ($R^2 = 0.12$, $p = 0.02$). In intact plots, mussel biomass was 60 times higher compared to structures that were buried, with 1.2 ± 0.2 kg DW m^{-2} (7800 ± 1800 individuals m^{-2}) in intact structures and only 0.02 ± 0.009 kg DW m^{-2} in buried structures (90 ± 42 individuals m^{-2}, $\chi^2 = 48.248$, $p < 0.001$, Fig. 3). Over the course of two growing seasons, mussel biomass continued to increase in intact establishment structures (from 0 at the start to 1.2 ± 0.2 in 2018 to 3 ± 0.4 kg DW m^{-2} in 2019), while mussels remained absent in controls (Fig. 2B).

3.2. Large-scale processes on biodegradable structures

Large-scale processes negatively affected structural integrity of the establishment structures, defined as intact structures, throughout the experimental period because part of the structures were buried or lost. The experiment was placed in a line of circa 650 m, and on a landscape scale, the data revealed that the number of intact sheets differed from west to east ($\chi^2 = 14.5$, df. = 7, $p < 0.05$), while the number of buried (~42%) and lost (~28%) sheets did not differ along this east-west gradient (Fig. 4, for buried sheets $\chi^2 = 7.7$, df. = 7, $p = 0.36$, for lost sheets $\chi^2 = 6.7$, df. = 7, $p = 0.46$). On a plot scale however, structure conditions differed greatly (Fig. 5). Bands that were situated closest to the gully were buried the least (~25%), while bands behind this first row in a northwestern direction were buried most deeply (~60–70%, Fig. 5). Over the course of the experiment, drone imagery revealed that the amount of intact structures decreased from 20.9 ± 0 m^2 per plot (100 ± 0%) in March 2017 to 12.2 ± 1 m^2 (58 ± 6%) in August 2018 and 5.1 ± 1 m^2 (24 ± 4%) in August 2019.

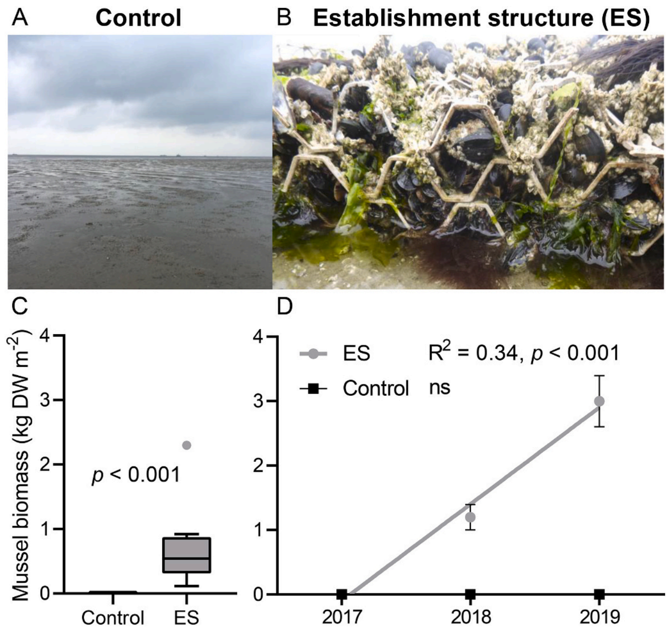

Fig. 2. Effect of establishment structures on reef development. Controls without mussels (A) establishment structures with mussels (B). Boxplots depict mussel biomass in controls and plots with establishment structures in August 2018 (C, kg DW m^{-2}, $n = 8$). Mussel biomass through time in controls and plots with establishment structures (D, $n = 8$ for all controls and all treatments at the start of the experiment in 2017, for ES data; $n = 46$ for 2018 and $n = 15$ for 2019). Boxplots show the median (middle line), quartiles (boxes), 1.5 times the interquartile range (IQR) (whiskers), and extreme values (dots). Error bars in D represent SEs. 2018 only displays data from intact structures to allow comparison with 2019 data. Photos: R.J.M.T.

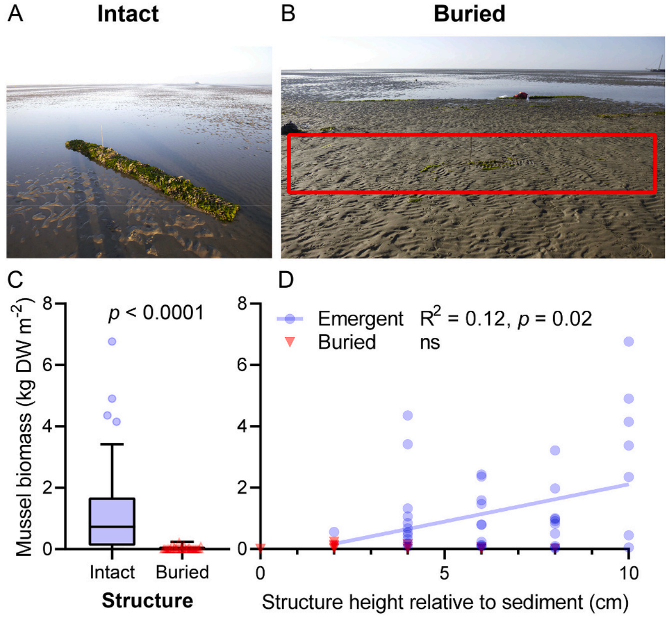

Fig. 3. Effect of burial on mussel biomass. Intact (A) and buried bands – row of structures (B) in the field in August 2018. Impact of burial on mussel biomass in intact and buried bands (C), and the relation between mussel biomass and structure height relative to the sediment (D, kg DW m^{-2}, $n = 46$ for intact bands). Boxplots show the median (middle line), quartiles (boxes), 1.5 times the interquartile range (IQR) (whiskers), and extreme values (dots). Photos: R.J.M.T.

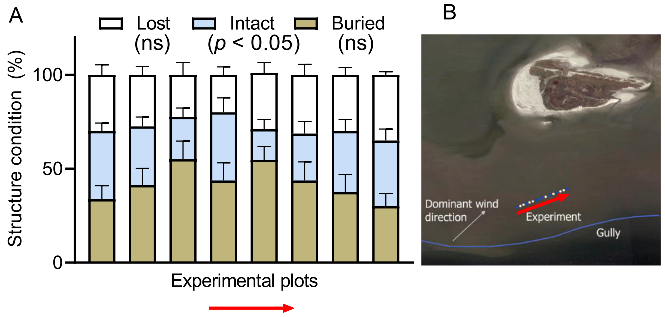

Fig. 4. Structural integrity of establishment structures for all experimental plots. Structure condition of all experimental plots in August 2018 (A, % buried [brown], intact [blue] and lost [white] sheets, $n = 10$). Error bars represent SEs. The plots follow the red line on the map (B). The gully is indicated by the blue line. ns stands for non-significant. B: Google Earth. (For interpretation of the references to colour in this fig. legend, the reader is referred to the web version of this article.)

4. Discussion

To successfully counteract the degradation of coastal ecosystems dominated by habitat modifiers, novel approaches are required that include important positive interactions in restoration designs (Silliman et al., 2015; Temmink et al., 2020; Temmink et al., 2021a; Fivash et al., 2021b). While a number of restoration efforts does take positive interactions into account, they only focus on one specific life-stage, while other important stages are still overlooked. Here, we upscaled mussel bed restoration using a life cycle informed restoration approach, in which multiple bottlenecks at different life-stages are mitigated using biodegradable establishment structures (Temmink et al., 2021a). We showed that life cycle informed restoration can indeed result in intertidal reef formation when applied at larger spatial scales, in line with our hypothesis. Contrasting to our hypothesis, upscaling resulted in burial of specific structures within a plot, and also increased physical stressors on the structures at this exposed site, which indicates the necessity for choosing optimal environmental conditions based on environmental data. The scaled-up restoration experiment at this dynamic site showed that at larger scales, sedimentation – partly induced by the structures – plays an important role and negatively influence nearby plots and thus restoration. We conclude that the method used will most likely be applicable to facilitate reef building bivalves after structure optimization and taking into account larger-scale processes (e.g. sedimentation). Furthermore, life cycle informed restoration is a promising restoration approach for mussel reef establishment, which may also be applicable to other ecosystems in which adult organisms facilitate the survival and growth of conspecifics by alleviating bottlenecks throughout their life cycle, such as in mangrove forest, seagrass meadows or coral reefs.

4.1. Bivalve reef formation using life cycle informed restoration

The establishment structures, incorporated with a fibrous substrate to stimulate settlement of blue mussels, resulted in successful reef formation as opposed to the unmodified controls, in which no mussel establishment occurred. Blue mussels preferentially settle on substrates

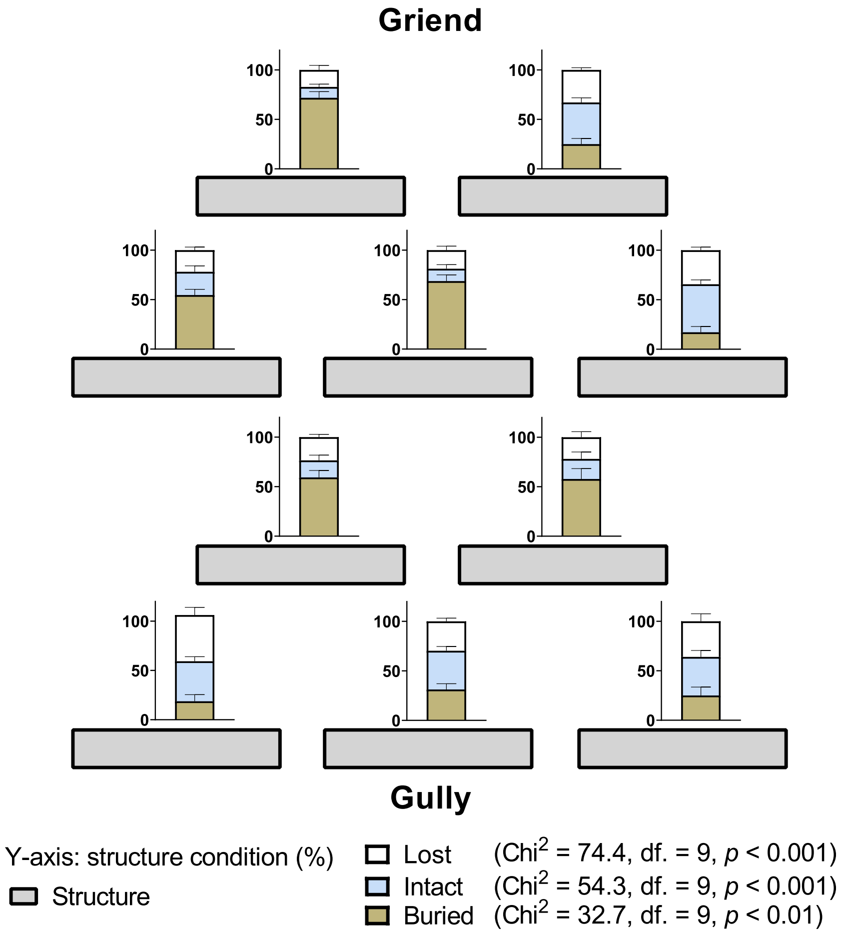

Fig. 5. Structural condition within experimental plots. % buried [brown], intact [blue] and lost [white] sheets in August 2018 ($n = 8$, error bars represent SEs). Gray rectangles represent strips of establishment structures. (For interpretation of the references to colour in this fig. legend, the reader is referred to the web version of this article.)

that closely resemble characteristics of established mussel reefs (Dobretsov and Wahl, 2001; Carl et al., 2012; Temmink et al., 2021a). Such reefs consist of hard mussel shells intertwined with fibrous byssal threads, which was mimicked in our experiment by coconut fibre and the hard structure. This structure has been shown to reduce predation pressure (Temmink et al., 2021a), which is known to be an important bottleneck for mussel bed establishment (van der Heide et al., 2014).

We found large differences in mussel biomass between structures that became buried over time compared to structures that remained exposed, most likely because burial significantly reduced their mussel holding capacity. In natural mussel beds, mussels trap sediment and accumulate pseudofeces up to 10 cm yr^{-1} (ten Brinke et al., 1995; van Leeuwen et al., 2010), thereby elevating their environment compared to the surrounding intertidal flat (Widdows and Brinsley, 2002; Gutiérrez et al., 2003). During sedimentation processes, buried mussels are able to climb up to 6 cm in a day. However, older mussels gradually lose the ability to move and may be buried by sediment or younger mussels (Widdows and Brinsley, 2002). In our experiment, we observed sedimentation invoked by and inside the establishment structures (1.8, 7, 4.3 cm yr^{-1} for the minimum, maximum, and average sedimentation rate, respectively; rate is based on burial of the structure from March 2017 till August 2018, Fig. 5), which was in the same order of magnitude as the maximum rate of 10 cm yr^{-1} in natural reefs (ten Brinke et al., 1995, van Leeuwen et al., 2010). The lack of (young) mussels in the buried structures may be explained either by i) a rapid sedimentation event that killed the mussels, or ii) - that the complex 3D-structure prevented the repositioning of the mussels during gradual sedimentation, leading to near-zero mussel survival. Our intertidal experimental site was rather exposed and the strong hydrodynamics may well have facilitated this burial by enhancing concentrations of suspended sediment that were subsequently deposited in and around the establishment structures (Marin-Diaz et al., 2021). Consequently, repeating this experiment at a more sheltered location would most likely result in a reduction of burial.

Establishment structures strongly facilitate mussel settlement, and even though yields are lowered when plots are buried, they are still successful as no reef initiated on the bare mudflat (Fig. 3). Interestingly, total mussel biomass was higher in 2019 compared to 2018 (1.2 ± 0.2 kg DW m^{-2} in 2018 vs. 3 ± 0.4 kg DW m^{-2} in 2019) even though only 24 ± 4% of the plot area was intact. For comparison, mussel biomass in natural beds older than 2 years range from 4.5 to 8 kg DW m^{-2} (unpublished data, following the same method as described in the methods section). Our work clearly demonstrates that epibenthic bivalve reefs can be restored from early life-stages using structures that mitigate bottlenecks, and thus do not require adult transplants (de Paoli et al., 2015).

4.2. Large-scale processes on biodegradable structures

Our large-scale experiment was stretched over a distance of circa 650 m and the size of experimental plots measured 20 × 10 m, allowing us to study the upscaling of the life cycle informed restoration approach and larger scale processes (e.g. on morphology). Within each plot, we clearly observed habitation modification (i.e. sedimentation) by the structures on a plot-scale (Fig. 5, S3). When placing relatively high structures on a bare flat (20 cm: structures and the coir mat) it can be expected that they alter local morphology (Marin-Diaz et al., 2021; Bouma et al., 2007). In our case, the structures increased the sediment bed level within the plot (20 × 10 m), resulting in significant burial of part of the bands in each plot (> 50%). Such an effect only emerged because of the large-scale of the experiment, and indicates the importance of executing larger-scale restoration experiments in dynamic ecosystems to obtain crucial knowledge for successful restoration at ecosystem-relevant scales.

Apart from burial, 18–46% of the structures were lost due to technical failure, especially during winters. Structure loss was most likely caused by wind-driven waves and ice floats (winter 2017–2018) that come together in this dynamic intertidal area, since the most exposed structures – those closest to the gully – showed the highest losses (~40%, Fig. 5). Interestingly, high losses coincided with the lowest burial rates and resulted in the highest mussel biomass. Overall, technical failure – sheet loss – most likely resulted in lower mussel biomass in the establishment structure, because i) mussels attached to the lost sheets were removed from the plots and cannot contribute to reef formation, and ii) mussels protected by the uppermost sheets suddenly become exposed to predators, such as crabs and birds.

Although the material used is biodegradable, the loss of sheets and the littering of the mudflat is an unwanted effect that simultaneously can affect the public opinion towards the applied restoration approach. It is therefore vital to minimize the loss of biodegradable structures to safeguard a high restoration success, minimize negative environmental impacts and motivate the public for future restoration projects (Suding, 2011; Suding et al., 2015). While sheet loss likely reduced mussel biomass, we still found 3.0 ± 0.4 kg DW mussels m^{-2} at the end of our two-year experimental period, which is two times higher compared to an earlier smaller scale experiment near the island Ameland in the Dutch Wadden Sea (1.5 ± 0.3 kg DW mussels m^{-2}, Temmink et al., 2021a), showing the potential of upscaling life cycle informed restoration.

4.3. Upscaling and restoration

Suding et al. (2015) introduced four conditions which have to be met when planning restoration: 1) restoration increases ecological integrity, 2) restoration is informed by the past and future, 3) restoration is sustainable in the long-term, and 4) restoration benefits and engages society. We here tested a new method for mussel bed restoration, and moved from small to larger scale using the concept of life cycle informed restoration. To obtain greater restoration success, we used knowledge about the functioning of natural mussel beds, such as the inclusion of banded patterning of mussel beds that increases resilience (Liu et al., 2014; de Paoli et al., 2017), as well as preferred substrates for settlement and attachment (Walters and Wethey, 1996; Reusch, 1998; Carl et al., 2012; van der Heide et al., 2014; Temmink et al., 2021a). However, our data shows that larger scale processes become vital when scaling up restoration measures in dynamic areas (e.g. sedimentation on an exposed site as in this study) and should be taken into account for the scaled up approach to become sustainable in the long-term. Lastly, natural mussel reefs provide various ecosystem services such as biodiversity, food and shore protection. In our experiment, we found that the establishment structures acted like a barrier as evidenced by the sedimentation in its wake (Fig. S3, Marin-Diaz et al., 2021, Fivash et al., 2021b), and found that they enhanced mussel biomass. However, after successful establishment, information about the quality and functioning of such a reef is important to determine their ecological value (e.g. food for birds, enhanced biodiversity, van der Zee et al., 2012). In conclusion, upscaling of life cycle informed restoration seems to be feasible for mussel bed restoration, but large-scale processes should be taken into account especially at exposed and dynamic sites. Specifically, optimization of these structures are required to increase restoration success and prevent littering.

4.4. Conclusion and outlook

We learned valuable lessons by performing this large-scale restoration experiment. While bare controls did not show any mussel settlement, mussel biomass could strongly increase when we artificially facilitated multiple life-stage of the blue mussel by providing a settlement cue (coir rope) combined with a hard substrate that lowers predation pressure. However, overall results depended on larger-scale processes such as on burial and structural integrity. In a broader context, this implies that i) environmental information with respect to the target habitat modifying species at relevant scale is always needed for site selection (e.g. sediment movement, wave heights, spat availability) and ii) for large scale restoration, technical failure of structures need to be addressed at scale. As both points are critical for restoration success, projects should always include site research, piloting, but also monitoring to learn from successes and mistakes to further ecological restoration on a large-scale (Gann et al., 2019), which is often not the case. By using novel facilitation-based restoration approaches that are scalable (Temmink et al., 2020, 2021a; Fivash et al., 2021b), such as life cycle informed restoration, and combining them with lessons learned in the past (van der Heide et al., 2014; de Paoli et al., 2015), we gear towards successful bivalve reef restoration. These science-based restoration approaches are crucial to restore degraded ecosystems worldwide, which is also emphasized by the UN declaring this decade the 'decade on ecosystem restoration'.

Data statement

Data available via the Data Archiving and Networked Services (DANS) EASY (https://doi.org/10.17026/dans-xp8-ncmh) (Temmink et al., 2021c).

Sample CRediT author statement

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Declaration of Competing Interest

None.

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Appendix A. Supplementary data

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