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SETBACKS AND SURPRISES

Incorporating facilitative interactions into small-scale eelgrass restoration—challenges and opportunities

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Marine ecosystem engineers such as seagrasses and bivalves create important coastal habitats sustaining high biodiversity and ecosystem services. Restoring these habitats is difficult due to the importance of feedback mechanisms that can require large-scale efforts to ensure success. Incorporating facilitative interactions could increase the feasibility and success of small-scale restoration efforts, which would limit pressure on donor sites and reduce costs and time associated with restoration. Here, we tested two methods for providing facilitation in small-scale eelgrass (*Zostera marina*) restoration plots across northern Europe: (1) co-restoration with blue mussels (*Mytilus edulis*, *M. trossulus*); and (2) the use of biodegradable establishment structures (BESEs). Eelgrass-mussel co-restoration showed promise in aquaria, where eelgrass growth was nearly twice as high in treatments with medium and high mussel densities than in treatments without mussels. However, this did not translate to higher shoot length or shoot densities in subsequent field experiments. Rather, hydrodynamic exposure limited both eelgrass and mussel survival, especially in the most exposed sites. The use of BESEs showed more potential in enabling small-scale restoration success: they effectively enhanced eelgrass survival and reduced mussel loss, and showed potential for enabling mussel recruitment in one site. However, eelgrass planted in BESE plots along with mussels had a lower survival rate than eelgrass planted in BESE plots without mussels. Overall, we show that though co-restoration did not work at small scales, facilitation by using artificial structures (BESEs) can increase early eelgrass survival and success of small-scale eelgrass and bivalve restoration.

Key words: ecosystem engineers, eelgrass, facilitation, interspecies interactions, mussels, restoration

Implications for Practice

- Incorporating facilitative interactions to overcome negative feedbacks could increase small-scale restoration success of coastal marine habitats such as seagrass meadows and bivalve reefs.
- Though mussels facilitated eelgrass growth in aquaria, this did not translate to increased survival in field transplantation, and mortality in small plots was very high, especially in exposed areas.
- BESEs enhanced eelgrass survival (through sediment stabilizing effects), limited mussel loss, and enabled mussel recruitment (through substrate provision), increasing the feasibility and short-term success of small-scale restoration efforts of these important ecosystem engineers.

Introduction

Ecosystem engineering species (Jones et al. 1994) such as seagrasses and mussels play an important role in shallow soft-bottom seas, creating structured habitats that ameliorate abiotic and biotic stress. These habitats provide numerous ecosystem services, including biodiversity provisioning (Nordlund et al. 2016; Hyman et al. 2019; Ysebaert et al. 2019), coastal protection (Fonseca & Cahalan 1992; van der Zee et al. 2012), and carbon sequestration (Fourqurean et al. 2012; Röhr et al. 2018). Ecosystem engineers are so-named for their ability to modify their surrounding environment, and many benefit from and rely on density-dependent positive feedbacks, which

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only appear beyond a certain threshold (van de Koppel et al. 2005; de Boer 2007; Rietkerk & van de Koppel 2008; Maxwell et al. 2017). Consequently, when a seagrass meadow disappears, re-establishment is difficult as the sediment becomes unstable due to the lack of belowground structure, increasing the probability of uprooted shoots (van der Heide et al. 2007). Moreover, unstable sediment is easily resuspended, reducing light availability (Adams et al. 2016; Carr et al. 2016). Mussel reefs also benefit from self-sustaining feedbacks, as established reefs provide critical substrate and structural complexity for recruits (van der Heide et al. 2014), thus their loss from a soft-substrate area limits successful recruitment (Wilcox et al. 2020). Positive interspecies interactions between ecosystem engineers also contribute to their stability (Fales et al. 2020; Gagnon et al. 2020; Reeves et al. 2020; Valdez et al. 2020). As habitat loss is often accompanied by regime shifts (Sorte et al. 2017), the lack of facilitating species can further limit natural recovery. The importance of self-sustaining feedbacks and facilitative interactions renders the initial phases of restoration difficult, and success rates (of seagrass restoration attempts remain low (survival rates of 37–38%; Bayraktarov et al. 2016; van Katwijk et al. 2016). Mussel reef restoration success has not been measured, but success rates for oyster reefs (in which similar feedback mechanisms occur) are estimated at 56% (Bayraktarov et al. 2016), and small-scale mussel restoration has proven especially difficult (de Paoli et al. 2015).

Despite low success rates, effective restoration and management of seagrass meadows can nevertheless improve conservation outcomes and reverse declines (de los Santos et al. 2019). Large-scale planting to overcome threshold limits improves restoration success (van Katwijk et al. 2016; Paulo et al. 2019), but large-scale transplantation has several disadvantages, notably the cost and time required, and higher impacts on donor populations. Incorporating facilitation into restoration efforts, for example using high-density transplanting units to take advantage of self-facilitation mechanisms (Paling et al. 2003; Bos & van Katwijk 2007) or co-transplanting seagrass with facilitative species (Bos & van Katwijk 2007; van Katwijk et al. 2009), could potentially reduce the effective transplant size needed and enable smaller-scale restoration efforts.

Here we focus on two ecosystem engineers, eelgrass *Zostera marina* and blue mussels *Mytilus edulis/M. trossulus*, that are widely distributed and often co-occur across the temperate North Atlantic, but are in decline in many areas (Short et al. 2011; Christie et al. 2020). Seagrass cover has decreased by at least 30% globally over the past 50 years (Waycott et al. 2009), and many northern European eelgrass populations were eliminated in the 1930s due to eelgrass wasting disease (Muehlstein et al. 1988; Muehlstein 1989). Eutrophication, algal blooms, and coastal development further reduced eelgrass cover (Erftemeijer & Lewis 2006; Burkholder et al. 2007), while trophic cascades caused by overfishing, climate change, and heat waves threaten survival and growth (Baden et al. 2010; Duarte et al. 2018). Similarly, overfishing has led to mussel population declines (Christianen et al. 2017; Christie et al. 2020), while extreme climatic events can cause mass mortality events, especially in conjunction with pathogens such as *Vibrio* spp. (Polsenaere et al. 2017). Coastal development and dredging also physically damage and smother mussel reefs (Eriksson et al. 2010), while shifting hydrodynamic patterns can reduce larval supply (Franz et al. 2019), and increased sedimentation inhibits settlement (Westerbom & Jattu 2006).

Eelgrass and blue mussels are known to facilitate each other (Gagnon et al. 2020 and references therein). Mussels can facilitate eelgrass both at large and small scales: the former by reducing water turbidity through filtration (Wall et al. 2008) and the latter by increasing sediment nutrient availability through biodeposition of pseudo-feces (Worm & Reusch 2000; Vinther & Holmer 2008) which are rich in nitrogen and phosphorus (Kautsky & Evans 1987). Eelgrass can facilitate mussels by offering protection from physical disturbances (Reusch & Chapman 1995), while particle trapping can promote larval settlement (Reusch 1998) and food availability (Ruckelshaus et al. 1993). A first attempt at co-restoring these species found that short-term eelgrass survival was higher with mussels, but all transplants died after several months due to unsuitable hydrodynamic conditions (Bos & van Katwijk 2007), indicating the importance of exposure in driving restoration success. Kristensen et al. (2015) also experimented with restoring eelgrass meadows adjacent to mussel reefs but concluded that the mussel density used was too low to have any significant effects, suggesting that high mussel densities may be necessary for facilitation. The use of artificial structures can also promote the early survival of transplanted ecosystem engineers. Hessian bags (Kidder et al. 2015), subsurface meshes (Wendländer et al. 2020), and biodegradable polymers (Temmink et al. 2020) can increase seagrass restoration success by stabilizing sediment, while artificial structures can increase mussel survival (Bertolini et al. 2018; Schotanus et al. 2020*a*, 2020*b*).

The aim of this study was to explore strategies for increasing small-scale eelgrass restoration success by incorporating facilitative interactions that could potentially aid eelgrass to cross the establishment threshold in small restoration plots. We first tested whether mussel addition facilitated eelgrass growth in aquaria, which could accelerate establishment and spread in a restoration context. We then tested whether transplanting eelgrass and blue mussels together in the field would increase the survival of either or both species in sheltered and exposed sites. Finally, we tested whether adding artificial biodegradable establishment structures increased restoration success by temporarily stabilizing sediment for eelgrass and providing substrate for mussels. In cold temperate areas, winter conditions (strong hydrodynamics, cold temperatures, low light intensity, ice scouring) can be a major stressor for both eelgrass and bivalves, thus we observed responses over a growing season, as well as after one to two winter seasons. We predicted that mussels would increase eelgrass growth and survival through fertilization, while eelgrass would facilitate mussel retention by protecting them from disturbance. Furthermore, we predicted that biodegradable establishment structures would increase the survival of both species.

Methods

Field Survey

In order to provide baseline densities for the experiments, we sampled natural densities of eelgrass and blue mussels in eight

eelgrass meadows in Finland in September 2016. At each site, we took five 5-cm deep sediment cores (Ø 25 cm), and measured eelgrass shoot density and dry weight, and mussel abundance and biomass (wet and dry weight).

Aquarium Experiment

The 5-week aquarium experiment was run in July 2017, using 76-L flowthrough aquaria (58 cm L × 27 cm w × 50 cm h) in the Korpoström Archipelago Centre (Korpo, Finland) semi-outdoor aquarium facility, with natural light and seawater at ambient temperature (18–20°C) and salinity (approximately 6). We used 16 aquaria, with four replicates of four treatments: (1) Eelgrass; (2) Eelgrass with low mussel density; (3) Eelgrass with medium mussel density; and (4) Eelgrass with high mussel density. Each aquarium contained a 6-cm deep layer of fine sand (organic content approximately 0.4%) sieved through a 1-mm mesh to remove detritus, and 50 eelgrass shoots (shoot length: approximately 15 cm, rhizome length: approximately 6 cm, shoot density: approximately 320 shoots/m^2). The mussel treatments included three different mussel densities (low: 75 g wet weight, approximately 470 g/m^2, approximately 60 mussels; medium: 150 g, approximately 950 g/m^2, approximately 125 mussels, high: 300 g, approximately 1,900 g/m^2, approximately 250 mussels). The eelgrass density was similar to natural Finnish meadows, while the medium mussel density corresponded to the highest recorded mussel density (i.e. our highest density was higher than could be found in nature to correspond to "mussel addition"). The sediment and eelgrass shoots were collected from a nearby eelgrass meadow (Ängsö; Table 1), while mussels were collected from nearby rocks and piers (mussel length 1–3 cm). The shoots were planted and left undisturbed for 5 days to acclimate before adding mussels. We then took one sediment core (Ø 2.5 cm corer) from the center of each aquarium to determine initial sediment organic content.

To assess sediment fertilization by mussels, we took one sediment core and one porewater sample (using rhizon 10-cm soil moisture samplers) from the center of each aquarium at the end of the experiment. Sediment organic content (loss on ignition; LOI) was analyzed by homogenizing the sediment, drying 3 days at 100°C, then combusting 3 hours at 520 °C. We then calculated the change in organic content between the start and end of the experiment. Porewater nutrient concentrations (ammonium and phosphate) were analyzed in an accredited laboratory using continuous flow analysis. We also measured eelgrass growth (by puncturing and marking shoots 1 week prior to the end of the experiment; Short & Duarte 2001) and length of two random shoots in each aquarium. We then collected all remaining eelgrass, separated shoots, roots, and rhizomes, dried (60°C for 48 hours) and weighed each section separately, and calculated the aboveground:belowground ratio of each aquarium. We also measured the condition index of 10 mussels from each aquarium (flesh dry weight/shell dry weight × 100; Davenport & Chen 1987).

We analyzed shoot, root, and rhizome biomass, aboveground: belowground ratio, porewater ammonium and phosphate, and change in organic content using generalized linear models with Treatment (mussel density, four levels) as the fixed factor. For porewater nutrients, we used gamma distribution with log link function, while for all other variables we used normal distribution. For eelgrass growth, shoot length, and mussel condition index, we ran linear mixed models (with normal distribution) with Aquarium added as a random factor to account for multiple sampling within each aquarium. Distributions were selected based on inspection of quartile–quartile plots and residual plots. We used the "aov," "glm," and "lmer" functions ("lmer" from the *lme4* package; Bates et al. 2015) in R version 3.6.2, then post hoc Tukey tests when necessary to determine which treatments were significantly different from each other.

Field Experiment I

The first field experiment was set up in May–June 2017 in six sites across three countries: one sheltered and one exposed site in Estonia, Finland, and Norway (Fig. 1A, Table 1). Eelgrass and mussels were collected from nearby sites with similar environmental conditions. In each site, we set up 30 plots at 2–5 m distance, consisting of six replicates of five treatments: control ("Control"), procedural control with mesh ("Mesh"), mussels ("M"), eelgrass ("Z"), and eelgrass + mussel ("Z + M"). The control plots were bare sand, while the procedural control plots included the buried plastic mesh (25 × 25 cm, mesh size 5 cm) as in the mussel and eelgrass plots. The mussel plots included the mesh with 1 L of adult mussels (wet weight approximately 300 g, mussel length: 1–3 cm in Baltic Sea, 3–5 cm in North Sea), and the eelgrass plots included the mesh with 16 shoots attached with cable ties (shoot length: 10–20 cm, rhizome length: 5–10 cm), and the eelgrass + mussel plots included 16 shoots with mussels added between shoots (Fig. 1B). The meshes were buried under approximately 1 cm of sediment and anchored with two metal pins.

The planted eelgrass density (400 shoots/m^2) was an average density for the region, while the mussel biomass (4,800 g/m^2) was an order of magnitude higher than natural mussel biomass (2.5 times higher than the highest density in the aquarium experiment), as we expected that high densities would be necessary for facilitation, and that not all mussels would likely succeed in attaching themselves in the plots. Eelgrass and mussels were collected 1–3 days prior to setup from nearby sites, rinsed, and stored in flowthrough aquaria until needed. The plots were sampled in September 2017 (3 months), May/June 2018 (12 months), and September 2018 (15 months), at which time we measured eelgrass shoot density and mussel percent cover in each plot. In Estonia and Finland, we took additional samples at 3 months: a sediment core from the center of each plot to determine organic content (LOI), eelgrass growth and length (1–2 shoots per plot), and mussel condition index (2–10 mussels per plot). Some plots could not be found due to low visibility or lost plot markers, especially in 2018. If there had been no eelgrass or mussels during the previous sampling, we assigned a value of zero to the plot. However, if there had been eelgrass or mussels during the previous sampling, we considered it as a missing value (4 plots in 2017, 17 in 2018).

For the 3-month sampling, we analyzed eelgrass growth, shoot length, sediment organic content, and mussel condition index using generalized linear mixed models with Plot treatment and

Table 1. Coordinates and characteristics of field sites used in the two field experiments. Note that the plots at Tagalaht (Estonia) were buried within 1 month of planting, so the experiment was restarted at Kihelkonna Bay. Tagalaht was subsequently not used in any of the analyses, and we did not calculate the wave exposure for this site. Note that only sites used in experiment I were assigned a categorical sheltered versus exposed value. Mean fetch was measured at each site from eight directions. Wave exposure values are based on the simplified wave exposure model (Isæus et al. 2004; Isæus & Rygg 2005; Nikolopoulos & Isæus 2008). Eelgrass and mussels were collected from nearby sites at similar depths to the experimental sites.

Country	*Site Name*	*Coordinates*	*Exp*	*Exposure Category (Exp I)*	*Wave Exposure (m^2/s)*	*Mean Fetch (km)*	*Max Fetch (km)*	*Sediment*	*Existing Eelgrass at Site*	*Eelgrass Donor Site, Coordinates, and Distance*	*Mussel Donor Site, Coordinates, and Distance*
Denmark	Limfjorden	56.7874°N, 9.0273°E	II		n/a	2.4	13	Coarse sand	Small patches	Limfjorden (same site)	Limfjorden, 56.71°N, 9.18°E (~13 km)
Estonia	Soela Strait	58.6420°N, 22.6030°E	I	Exposed	152,767	14	~200	Fine sand	Large patchy meadow	Küdema Bay, 58.53°N, 22.24°E (~30 km)	Küdema Bay (~25 km)
	Tagalaht*	58.4198°N, 22.0929°E	I*	Sheltered	n/a*	7.0	~175	Fine sand	Small patches	Küdema Bay (~30 km)	Küdema Bay (~30 km)
	Kihelkonna Bay	58.3799°N, 21.9601°E	I, II	Sheltered	104,622	2.5	~200	Medium sand	Large patchy meadow	Kihelkonna Bay (same site)	Küdema Bay (~35 km)
Finland	Ängsö	60.1092°N, 21.7106°E	I	Exposed	11,274	1.9	15	Coarse sand, some gravel	Large patchy meadow	Ängsö (same site)	Korporström, 60.11°N, 21.60°E (~6 km)
	Sackholm	60.1228°N, 21.8686°E	I	Sheltered	4,834	0.6	5	Fine sand and silt	Small patches	Ängsö (~9 km)	Korporström (~15 km)
	Fårö	59.9193°N, 21.7958°E	II		12,322	3.6	36	Fine sand	Large continuous meadow	Fårö (same site)	Korporström (~24 km)
Norway	Olbergholmen South	59.0070°N, 10.1322°E	I, II	Exposed	145,000	12	~100	Fine sand	Medium patchy meadow	Olbergholmen South (same site)	Vikeroysundet, 59.04°N, 10.14°E (~4 km)
	Olbergholmen North	59.0088°N, 10.1311°E	I	Sheltered	1,250	0.2	1.5	Coarse sand, some stones	Medium patchy meadow	Olbergholmen South (200 m, opposite side of peninsula)	Vikeroysundet (~4 km)
	Varildsfjorden	59.0487°N, 10.1574°E	II		2,610	0.5	1.6	Muddy	Large continuous meadow	Flatholmen, 59.04°N, 10.13°E (1.7 km)	Vikeroysundet (300 m)

Exposure as fixed factors, and Country as a random factor. We used gamma distribution for eelgrass growth and sediment organic content, and normal distribution for shoot length and mussel condition index. For sediment organic content, we compared all treatments, for eelgrass growth and shoot length we compared eelgrass versus eelgrass + mussel plots, and for mussel condition index we compared mussels versus eelgrass + mussel plots. For shoot density and mussel cover, we analyzed each time point (3 months, 12 months, 15 months) separately, due to the high number of missing values in the late time points, and changes in the error distribution. We used general linear mixed models with Plot treatment and Exposure as fixed factors, and Country as a random factor. For shoot density at 3 months and 12 months, we used Poisson distribution, while for shoot density at 15 months, and all mussel cover time points, we used negative binomial distribution, based on inspection of quartile–quartile plots and residual plots. For shoot density we compared eelgrass versus eelgrass + mussel plots, while for mussel cover we compared mussel versus eelgrass + mussel plots. We used "lmer," "glmer," and "glmer.nb" functions in the *lme4* package (Bates et al. 2015) in R version 3.6.2, then post hoc Tukey tests when necessary to determine which treatments differed significantly from each other.

Field Experiment II

The second field experiment was set up in June–July 2018 (August in Norway) in five sites across four countries: one in Denmark, one in Estonia, one in Finland, and two in Norway (Fig. 1A, Table 1). These sites were chosen as they were considered to potentially benefit from sediment stabilization. Having observed mussel loss in almost every site during the first experiment, we used biodegradable elements for starting ecosystems (BESE-elements, hereafter BESEs) as a substrate for mussel attachment. The BESEs (www.bese-products.com) are composed of a biodegradable polymer made from potato-waste Solanyl C110 4M (Rodenburg Biopolymers, Oosterhout, The Netherlands), which should biodegrade in 10–20 years. Here, each BESE unit was 30 cm L × 30 cm w × 6 cm h, with a 10-cm-diameter circle cut in the center for planting eelgrass. Temmink et al. (2020) showed that these BESEs are effective in increasing eelgrass restoration success by stabilizing the sediment when placed belowground. To test both the stabilizing effect and the potential for facilitating mussels, we half-buried the BESEs (3 cm under the sediment, 3 cm above), and anchored them using two 40-cm-long L-shaped steel rebar anchors in two corners.

In each site, we set up 32 plots at 2–5 m distance consisting of four replicates of two crossed treatments (Fig. 1C): sand or BESE crossed with four plot treatments: control without organisms, eelgrass ("Z"), mussel ("M"), and eelgrass + mussel ("Z + M"). The sand plots (i.e. without BESEs) consisted of six eelgrass shoots attached to a u-shaped metal anchor using natural fiber string, and/or 1 L (approximately 300 g) of loose mussels added to bare sand. For the BESE plots, six eelgrass shoots were planted in the central hole using the same technique as the sand plots, and/or 1 L of mussels were added to each BESE. The mussels were added in an aquarium approximately 1 week prior to planting so they could form byssus threads and attach to the

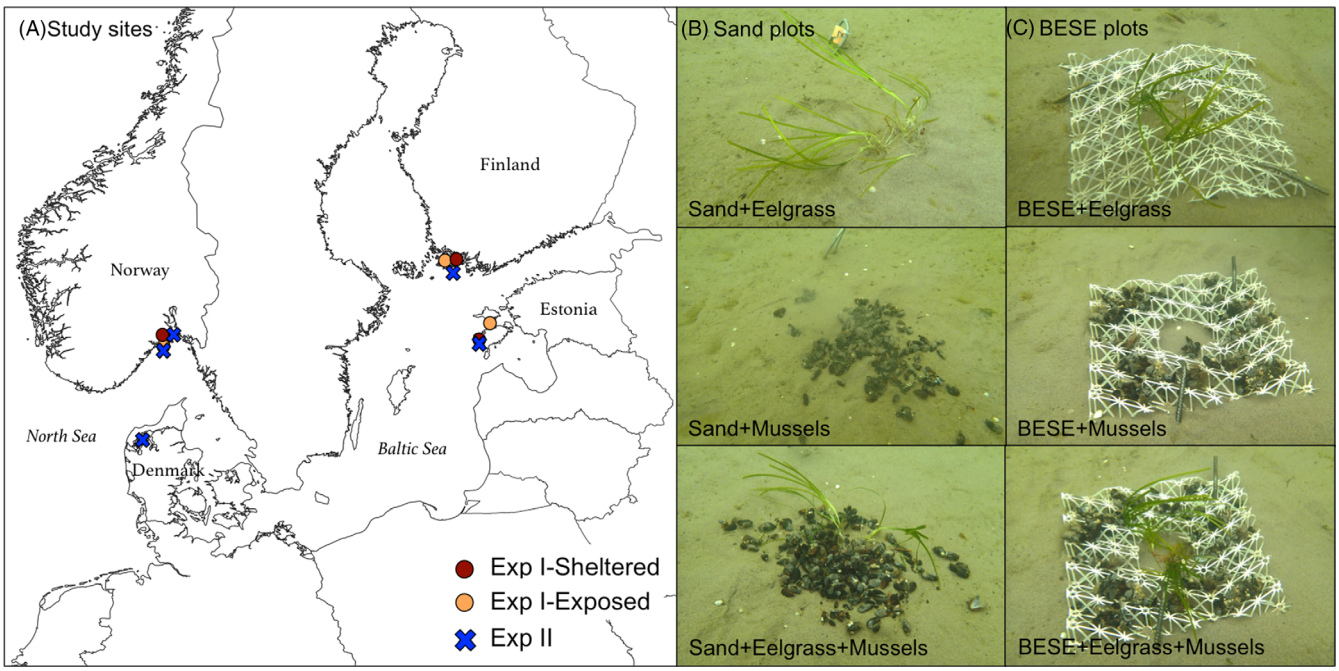

Figure 1. Left: Map of study sites in northern Europe (dark circles: Sheltered sites in field experiment I, light circles: Exposed sites in experiment I, blue crosses: Sites in field experiment II). See Table 1 for site coordinates and descriptions. Right: Pictures of plots from experiment II (left column: Eelgrass, mussel, and eelgrass + mussel plots without BESEs; right column: Eelgrass, mussel, and eelgrass + mussel plots with BESEs). All pictures by Karine Gagnon, from the Finnish experimental site in experiment II (Fårö).

BESE surface, and then transported to the field site submerged in water. We measured eelgrass shoot density and mussel percent cover in each plot in September/October 2018 (3 months), May 2019 (12 months), and September/October 2019 (15 months).

We analyzed shoot density and mussel cover separately at each sampling point using generalized linear mixed models with BESE (sand, BESE) and Plot (eelgrass, mussel, eelgrass + mussel) treatments as fixed factors, and Site as a random factor. We used negative binomial distribution for both shoot density and mussel cover, based on inspection of quartile–quartile plots and residual plots. For shoot density we compared the treatments with eelgrass, while for mussel cover we compared treatments with transplanted mussels. We used the "glmer.nb" functions in the *lme4* package (Bates et al. 2015) in R version 3.6.2, then post hoc Tukey tests when necessary to determine which treatments differed significantly from each other.

Results

Field Survey

In the Finnish pilot field survey, eelgrass and mussel abundance were highly variable: mean eelgrass densities varied from 150–800 shoots/m^2 and mean mussel densities from 90–4,000 individuals/m^2 and 50–1,000 g wet weight/m^2.

Aquarium Experiment

In the aquarium experiment, eelgrass growth was approximately twice as high in the high and medium mussel density treatments than in the treatment without mussels ($F = 4.34_{[3,12]}$, $p = 0.027$; Fig. 2; Table S1). Porewater ammonium ($F = 16.12_{[3,12]}$, $p = 0.001$) and phosphate ($F = 18.95_{[3,12]}$, $p = 0.0003$) concentrations were nearly four times higher in the high mussel density treatment than in other treatments (Fig. 3; Table S1), indicating mussel biodeposition. There were no significant differences between treatments for other variables (eelgrass dry weight, ag:bg ratio, sediment organic content, eelgrass shoot length, mussel condition index; Table S1).

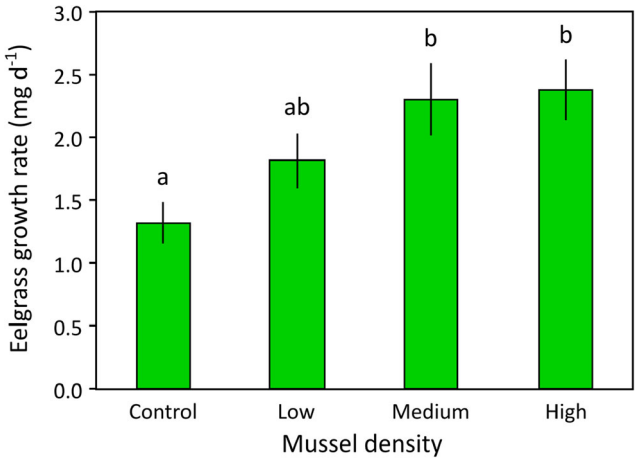

Figure 2. Eelgrass growth rate (mean ± SE) in aquarium experiment with four different mussel densities. Letters indicate significant differences ($p < 0.05$).

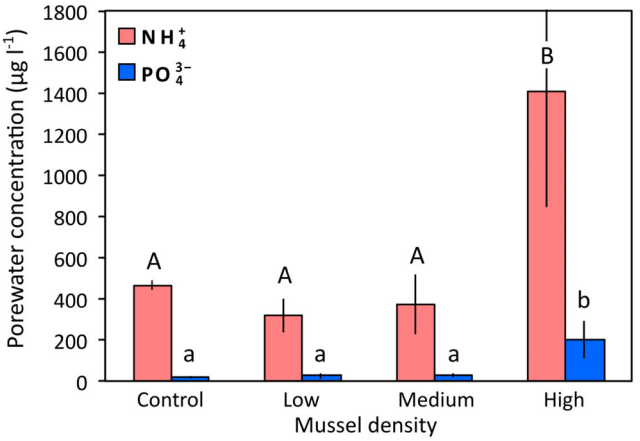

Figure 3. Porewater ammonium (red) and phosphate (blue) concentrations (mean ± SE) in aquaria with four different mussel densities in aquarium experiment. Letters (uppercase: ammonium, lowercase: phosphate) indicate significant differences ($p < 0.05$).

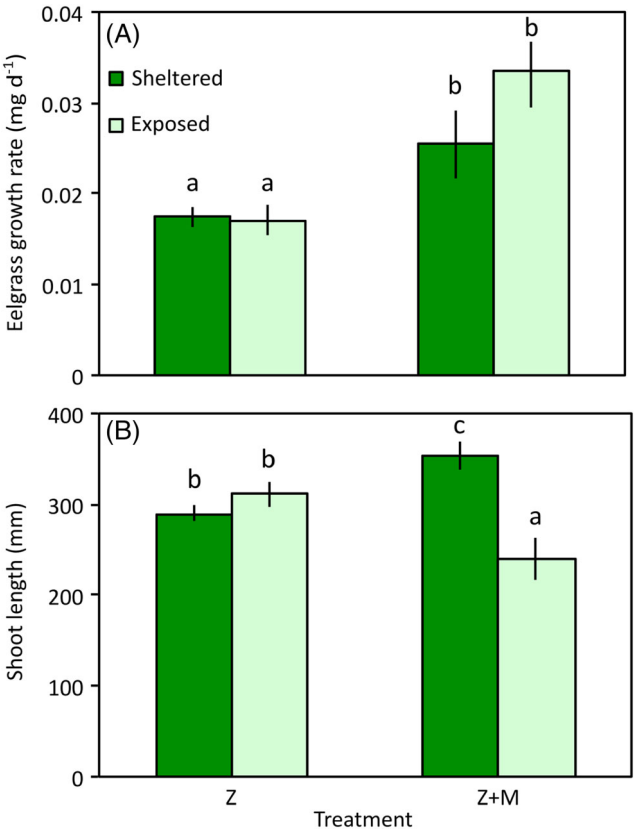

Figure 4. (A) Eelgrass growth and (B) shoot length (mean ± SE) in eelgrass (Z) and eelgrass + mussel (Z + M) plots in sheltered (dark) and exposed (light) sites 3 months post-transplantation (September 2017) in field experiment I. Means were calculated for two shoots per plot. Letters indicate significant differences ($p < 0.05$).

Field Experiment I

After 3 months, eelgrass growth was approximately 50% higher in eelgrass + mussel plots than eelgrass plots in both sheltered and exposed sites (treatment $X^2 = 9.44$, $p = 0.002$; Fig. 4A, Table S2). Shoot length was approximately 10% higher in eelgrass + mussel plots than eelgrass plots in the sheltered sites, but approximately 30% lower in the exposed sites (interaction $X^2 = 17.34$, $p < 0.001$; Fig. 4B, Table S2). Sediment organic content was approximately 40% higher in the sheltered than exposed sites, and approximately 10% higher in the eelgrass plots than all other treatments (exposure $X^2 = 217.31$, $p < 0.001$; treatment $X^2 = 16.54$, $p = 0.002$; Fig. S1, Table S2). Eelgrass shoot density at 3 months varied by treatment and exposure (interaction $X^2 = 30.50$, $p < 0.001$; Fig. 5A, Table S2). In the exposed sites, it was higher in the eelgrass than eelgrass + mussel plots, and the eelgrass plots were the only treatment in which eelgrass shoot density increased, while there was approximately 50% shoot loss in the eelgrass + mussel plots. In the sheltered sites, there was approximately 50% shoot loss in both. After 12 months, shoot density was significantly higher in the sheltered sites though survival was <50% in most sites (exposure $X^2 = 61.39$, $p < 0.001$; Fig. 5A, Table S2). After 15 months, shoot density had increased to nearly twice the planted density in the sheltered sites, but no shoots remained in the exposed sites (exposure $X^2 = 109.41$, $p < 0.001$; Fig. 5A, Table S2).

Mussel condition index at 3 months did not differ among treatments (Table S2). Mussel retention at 3 months was higher in the sheltered (approximately 40% retention) than exposed (20% retention) sites (exposure $X^2 = 19.76$, $p < 0.001$) with no differences between plot treatments (Fig. 5B, Table S2). After 12 months, >90% and approximately 70% of mussels were lost in the exposed and sheltered sites, respectively (exposure $X^2 = 21.23$, $p < 0.001$; Fig. 5B, Table S2). After 15 months, mussels had disappeared from exposed sites, and only approximately 5% remained in sheltered sites (exposure $X^2 = 12.01$, $p < 0.001$; Fig. 5B, Table S2).

Field Experiment II

After 3 months, eelgrass shoot density was slightly (approximately 5%) higher in BESE than sand plots, but there was no difference between treatments with and without mussels (BESE $X^2 = 5.32$, $p = 0.021$; Fig. 6A, Table S3). After 12 months, the only plots with multiple surviving shoots were the BESE + eelgrass plots (BESE $X^2 = 11.15$, $p < 0.001$; Plot $X^2 = 5.50$, $p = 0.019$; Fig. 6A, Table S3) with 4 surviving plots in Estonia, 3 in Denmark, and 2 in Finland. After 15 months, overall shoot

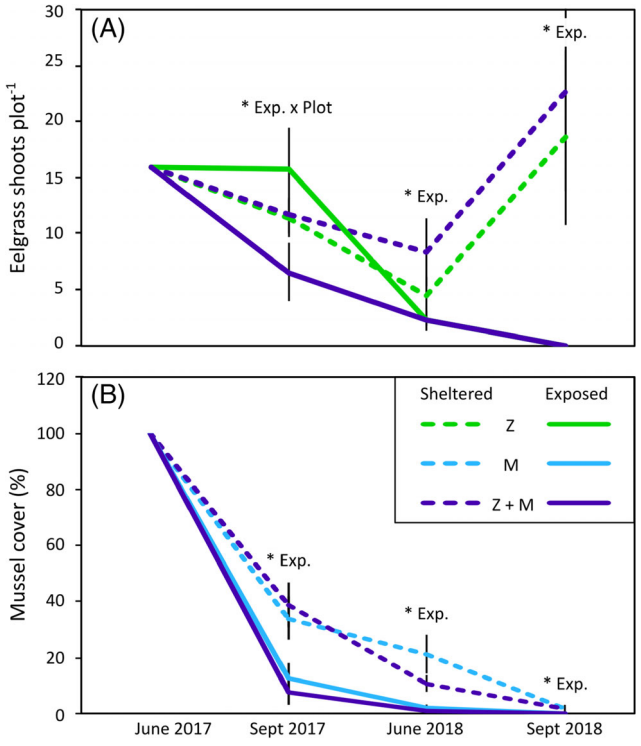

Figure 5. (A) Eelgrass shoot density and (B) mussel percent cover (mean ± SE) 3, 12, and 15 months post-transplantation in eelgrass (Z), mussel (M), and eelgrass + mussel (Z + M) plots. Field experiment I, abbreviations above each time point indicate which fixed factors or interactions were significant (*$p < 0.05$) at that time (Exp. = exposure, plot = plot treatment).

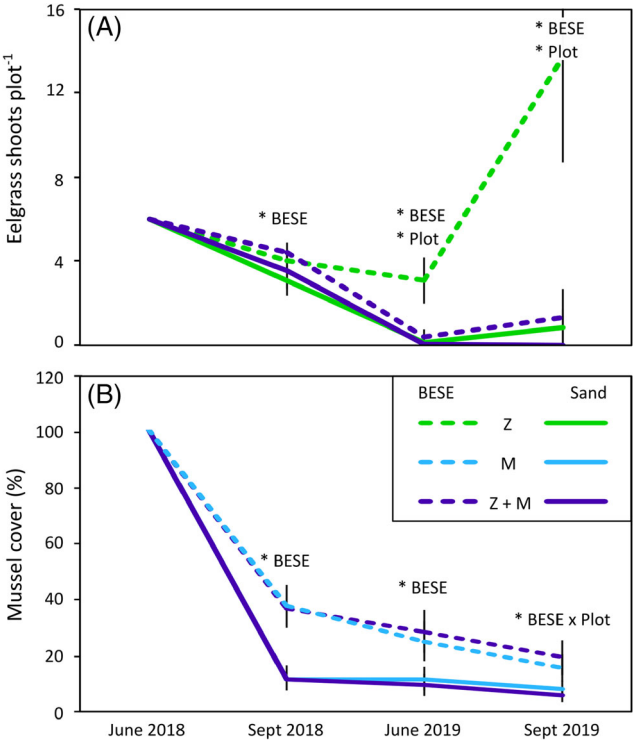

Figure 6. (A) Eelgrass shoot density and (B) mussel percent cover (mean ± SE) 3, 12, and 15 months post-transplantation in eelgrass (Z), mussel (M), and eelgrass + mussel (Z + M) plots in field experiment II. BESE = BESE treatment (sand or BESE), plot = plot treatment, abbreviations above each time point indicate which fixed factors or interactions were significant (*$p < 0.05$) at that time.

density in the BESE + eelgrass plots had increased substantially to more than twice the planted density (BESE $X^2 = 123.76$, $p < 0.001$; Plot $X^2 = 131.99$, $p < 0.001$; Fig. 6A; Table S3), indicating very high expansion in those plots that survived the first winter.

The BESEs had a positive effect on mussel retention: after 3 months, there was approximately 40% retention on BESE plots, but only 10% on sand plots (BESE $X^2 = 8.66$, $p < 0.001$; Fig. 6B; Table S3). These differences remained over time, with approximately 30% and 25% retention in BESE plots after 12 and 15 months, respectively, and 10% and 5% retention in sand plots after 12 and 15 months, respectively (BESE $X^2 = 8.66$, $p = 0.0033$, interaction $X^2 = 13.70$, $p < 0.001$; Fig. 6B; Table S3). We also noticed high juvenile mussel recruitment onto all BESEs at the Finnish site (these recruits were not included in the analyses). However, there were important site differences: in Denmark all mussels on BESEs were lost due to predation by green crabs *Carcinus maenas* (pers. obs.), while all mussels were presumably washed away in one of the Norwegian sites (Olbergholmen South).

Discussion

Our aim was to explore the potential for incorporating facilitative interactions into small-scale eelgrass restoration, through (a) co-restoration of eelgrass and blue mussels, and/or (b) the use of artificial biodegradable ecosystem engineering structures (BESEs). We hypothesized that these two ecosystem engineering species would facilitate each other, and that the BESEs would further facilitate survival by stabilizing sediment for eelgrass and providing substrate for mussels. Though the mussel-eelgrass interaction showed promise in facilitating eelgrass in a pilot aquarium experiment, this did not translate to facilitation in the field. We did find that BESEs were effective in ensuring both eelgrass and mussel survival (and recruitment of the latter) in the field, though not in a co-restoration context. In addition, we found that, in both experiments, rapid expansion of eelgrass shoots was only apparent during the second growing season, in plots that survived the first winter season, showing the importance of multi-year monitoring of restoration efforts.

The aquarium experiment supported the idea that mussels can promote eelgrass growth through biodeposition, as evidenced by higher nutrient concentrations in sediment porewater. However, attempts to apply this in the field have proven difficult. The first field experiments showed that mussels increased growth rates in the field (at least over the first growing season), but that this did not result in longer shoots or increased shoot density in the short or long term. Indeed, both with and without mussels, eelgrass mortality was high, especially in the exposed sites. Though initial growth was lower in the sheltered sites, shoot density in these sites eventually surpassed the exposed sites. As eelgrass loss in the Experiment I sites was due to hydrodynamic forces (uprooting and erosion of plots in Norway and the exposed Estonian site, drifting algal mats in Finland, burial of plots in the sheltered Estonian sites; pers. obs.), exposure strongly influences initial survival in small eelgrass restoration plots. In addition, mussel loss—also due to currents and waves—made it difficult to evaluate whether they could actually facilitate eelgrass restoration.

The use of BESEs in the second experiment resolved some of the problems from the first experiment. In particular, by simulating the belowground rhizome structure of established eelgrass meadows (Temmink et al. 2020) they reduced sediment instability that limits seagrass survival and spread (Moksnes et al. 2018), and facilitated the survival of small-scale eelgrass plots. They also reduced loss of adult mussels and provided substrate for juvenile recruits, indicating their potential for mussel restoration in sites where mussels have disappeared, or to bolster declining populations by increasing available substrate, though more research is needed to optimize their use. In Denmark, crab predation on mussels that were attached to BESEs led to very high mortality, so additional measures such as cages may be necessary in areas of high predator abundance, until the mussels are large, or abundant, enough to escape predation (Schotanus et al. 2020a). In addition, as evidenced by the complete loss of mussels at one of the most exposed sites, BESEs alone cannot ensure the survival of translocated mussels in highly exposed areas, and additional nets or fences might be necessary (de Paoli et al. 2015; Schotanus et al. 2020b).

The BESEs showed the importance of incorporating facilitative interactions into small-scale eelgrass restoration plots, and also allowed us to properly evaluate the feasibility of eelgrass-mussel co-restoration. However, contrary to expectations, eelgrass only survived in BESE plots without mussels. The mechanisms behind this are unclear, but could involve physical damage to leaves caused by mussels, or physiological stress due to increased sulfide concentrations during a heat wave in summer 2018, during which water temperatures were 5–8 °C higher than normal (pers. obs; Paalme et al. 2020). Though the literature suggests that mussels usually facilitate eelgrass (Gagnon et al. 2020), they can cause eelgrass mortality by increasing sediment sulfide concentrations (Holmer & Bondgaard 2001; Vinther et al. 2008, 2012; Vinther & Holmer 2008). Sulfide intrusion caused by mussel biodeposition is more likely in high-organic, muddy sediments (Holmer et al. 2006) than in sandy sites like ours, and thus we had not considered or measured sulfide, but the additional stress from the heat wave can increase sulfide stress (García et al. 2013). It is clear that, as heat waves become more frequent, incorporating resilience to heat stress in restoration efforts will be increasingly important. Whatever the mechanisms, our results show that co-restoration does not seem effective at small spatial scales in temperate eelgrass meadows, though it may hold promise at larger scales (Sharma et al. 2016),

Large-scale planting enhances seagrass restoration success (van Katwijk et al. 2016; Paulo et al. 2019), particularly in exposed sites where positive feedbacks between shoots increases survival by stabilizing the sediment (van der Heide et al. 2011). However, due to the large number of shoots required, large-scale restoration can also increase stress on donor meadows. Here, we show that the use of BESEs, which mimic the stabilization effect of eelgrass rhizomes (Temmink et al. 2020) and the hard substrate of a natural bivalve reef, allowed small plots (<0.1 m^2) of both eelgrass shoots and

mussels to survive in conditions in which they otherwise would not, opening up further possibilities for small-scale restoration.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Statistical results of generalized linear mixed models of the Aquarium Experiment.
Table S2. Statistical results (Wald tests of generalized linear mixed models) of Field experiment I.
Table S3. Statistical results (Wald tests of generalized linear mixed models) of Field experiment II.
Figure S1. Sediment organic content (% LOI; mean ± SE) in different treatments.

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