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MARINE
HABITAT

Restoration of eelgrass (*Zostera marina*) in Estonian coastal waters, Baltic Sea

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Abstract. Seagrass meadows are facing structural degradation worldwide, losing both area and biodiversity. Habitat restoration could reverse this degradation, but so far, the success rate of seagrass restoration has been low. Incorporating facilitative interactions between plants and mussels into habitat restoration projects could potentially improve restoration success by increasing eelgrass survival and growth. In this study, we tested whether co-restoring two ecosystem engineers, namely eelgrass *Zostera marina* and blue mussels *Mytilus edulis/trossulus* would increase eelgrass restoration success in different sites. We also tested the rope method of eelgrass transplantation in sites where eelgrass was known to have previously existed. These small-scale field experiments were conducted in 2017–2019, in the northeastern Baltic Sea where the eelgrass reproduces only vegetatively. We found that co-restoration of eelgrass and mussels did not work at small scales because mussels were washed away within the first growing season. However, the shoot density of eelgrass increased over time, especially over the second growing season in the sheltered site, indicating that restoration is possible in these areas. Similarly, the restoration was most successful with the rope method in the sheltered site, suggesting that this method also has potential at larger spatial scales. Our results suggest that in such dynamic ecosystems abiotic factors, particularly exposure, play a larger role compared to biotic interactions, and thus the success of habitat restoration largely depends on local environmental conditions.

Keywords: habitat restoration, co-restoration, ecosystem engineers, eelgrass, facilitative interactions, mussels.

INTRODUCTION

Seagrass meadows are essential components of soft-bottom coastal ecosystems worldwide. Seagrasses are important primary producers (Larkum et al. 2006) and their meadows contribute to coastline protection (Ondiviela et al. 2014), sediment stabilization (Newell and Koch 2004), the cycling of nutrients (McGlathery et al. 2007) and carbon sequestration (Mazarrasa et al. 2015). Moreover, they provide habitat and shelter for numerous marine species and thereby are known as important hotspots of biodiversity (Hyman et al. 2019). Due to their large global coverage, seagrass habitats play an important role in commercial fisheries production through the provision of nursery habitats, trophic subsidies, and fishing activity (Unsworth et al. 2019). Seagrass meadows are nowadays acknowledged to have an important role in mitigating the effects of climate change and ocean acidification through the uptake and storage of carbon (Pendleton et al. 2012; Duarte et al. 2013; Koch et al. 2013).

The rapid expansion of global human population has intensified and diversified the pressure applied on the marine environment. Different uses of the marine environment by humans, such as fishing, trawling, anchoring, and

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fish farming, together with land-based activities, such as agriculture and industrial pollution, combine, and affect seagrass meadows in multiple detrimental ways (Boudouresque et al. 2009). In addition, extreme climatic and oceanic events such as marine heat waves (Arias-Ortiz et al. 2018; Duarte et al. 2018) and storms (Gera et al. 2014) have a strong negative effect on these habitats. As a consequence of the cumulative effects of these factors, seagrass meadows are facing remarkable degradation of structure and biodiversity and areal loss worldwide (Waycott et al. 2009; Short et al. 2011; Dunic et al. 2021).

Many marine ecosystems are not able to recover without human intervention. As such, direct restorative actions represent an important component in marine conservation and the preservation of key habitats (Jones et al. 2018). The success rate of seagrass habitat restoration has been reported to be as low as 37% (van Katwijk et al. 2016), pointing to the need to develop new approaches and methods promoting successful restoration. Recently, new approaches have been developed that involve co-restoring ecosystem engineers to take advantage of facilitative interactions (e.g. Silliman et al. 2015; Reeves et al. 2020; Valdez et al. 2020). Gagnon et al. (2020) showed that the co-restoration of plants and bivalves through promoting their positive interactions could improve restoration success by increasing survival, growth, and resilience of foundation species. For instance, mussels can facilitate eelgrass productivity through their suspension-feeding activities by filtering the seawater and consequently increasing the light availability (Wall et al. 2008). Furthermore, the increase in sediment nutrient concentrations through mussels' biodeposition may increase the growth rate of eelgrass (Reusch et al. 1994; Worm and Reusch 2000). In addition, to increase the success rate of seagrass restoration it is beneficial to incorporate artificial structures that can limit sediment resuspension (e.g. hessian bags, etc.) (van Katwijk et al. 2016).

It is expected that abiotic environmental variables may modulate the strength of facilitative interactions between plants and suspension-feeding bivalves. Namely, exposure to waves is particularly important as it defines the feeding condition of suspension-feeders. Moreover, exposure regime defines benthic stability and hence, contributes to the success of seagrass restoration (van Katwijk et al. 2009). Additionally, Gagnon et al. (2020) showed that water temperature played an important role in regulating positive and negative interactions between plants and bivalves. It is important to incorporate local abiotic environmental variables into seagrass restoration actions because they may affect the success of restoration through modulating the strength of facilitative interactions.

This study focuses on eelgrass *Zostera marina* which inhabits temperate coastal waters throughout the Northern Hemisphere (Moore and Short 2006). In the brackish Baltic Sea, *Z. marina* grows mainly on sandy sediments in shallow (2–5 m depth) subtidal ecosystems where it stabilizes sediment and hosts diverse invertebrate communities (Boström et al. 2014; Möller 2017). In such habitats, the species grows in its lowest observed salinity levels (salinity 5–7 PSU). Due to low salinity levels, *Z. marina* reproduces vegetatively in this region, with flowering being a rare event, and thus seed restoration is not an option (e.g. Marion and Orth 2010). Numerous studies have shown a decline in the distribution of *Z. marina* within different regions of the Baltic Sea, mainly due to coastal eutrophication (Boström et al. 2014 and references therein). Moreover, the future consequences of climate change for eelgrass meadows are difficult to predict: seawater warming and reduced ice cover may have positive effects on growth, but increased hydrodynamics and reduced salinity are likely to have particularly strong negative effects on eelgrass meadows in these marginal habitats (Möller 2017).

Similar to *Z. marina,* the blue mussel complex, *Mytilus* spp., has a broad distribution in coastal regions of the Northern Hemisphere where the species are important ecosystem engineers in intertidal and subtidal hard- and soft-bottom communities (Wenne et al. 2020). Virtually over the whole range of the Baltic Sea, such mussel beds are highly productive and provide food and refuge for numerous organisms (e.g. Kotta et al. 2015; Lauringson and Kotta 2016). Dense populations of suspension-feeding mussels have been shown to facilitate macrophytes, including seagrasses, especially in the context of mussel farms and harvesting (Valentine and Heck 1993; Crawford et al. 2003; Airoldi et al. 2005), but moderately dispersed mussel populations may also foster the diversity of macrophyte assemblages and associated invertebrates through a moderate fertilizing effect (Bracken and Nielsen 2004; Kotta et al. 2009). Contrary to eelgrass, elevated eutrophication does not pose a serious threat to the populations of *M. edulis/trossulus* in the Baltic Sea region (Kotta et al. 2015). Evidence suggests that detrimental changes in *Z. marina* and *M. edulis/trossulus* communities may have a strong impact on local communities, resulting in the collapse of important underwater habitats, changes in benthic-pelagic nutrient coupling, and loss of related ecosystem services (Almqvist et al. 2010; Kotta et al. 2018).

During extreme eutrophication events in the 1980s *Z. marina* disappeared from extensive areas in the Estonian coastal waters of the Baltic Sea (Databases of the Estonian Marine Institute, University of Tartu). So far, no restoration activity of *Z. marina* has been conducted there. The main aim of this study was to develop new restoration techniques and approaches for eelgrass *Z. marina* in such a marginal brackish water environment. Furthermore, there is a large degree of seasonal and interannual variation in environmental factors (e.g. nutrients, light, and water temperature) in the northeastern Baltic Sea (Feistel et al. 2008) which makes the success of restoration trials highly unpredictable. This study consisted of two experiments. The aim of Experiment 1 was to determine whether co-restoring the eelgrass *Z. marina* with the blue mussels *M. edulis/trossulus* would increase the success of eelgrass restoration in different sites. The main difference between the experimental sites was the level of exposure, thus we named the sites 'sheltered' and 'exposed' for this research. This study is a follow-up to Gagnon et al. (2021) which focuses on eelgrass restoration experiments in multiple Northern European countries. Our hypotheses were that mussels would increase eelgrass growth and survival, while eelgrass would facilitate mussel retention in the restoration plots, with the response being dependent upon the site effect. The aim of Experiment 2 was to develop and apply a restoration technique, using rope to transplant eelgrass shoots (e.g. Fonseca et al. 1998) in those sites where eelgrass was known to have previously existed. The rope provides substrate and stabilisation for the eelgrass shoots, and in addition, this is a low-cost and low-effort method.

MATERIALS AND METHODS

Experiment 1. Co-restoration of eelgrass and mussels

The transplantation experiments were set up in two different sites in Tagalaht Bay (sheltered site) and in the Soela Strait (exposed site) in the Estonian coastal waters, northeastern Baltic Sea in May 2017 (Table 1; Fig. 1). However, the first attempt of the transplant experiment failed in Tagalaht Bay, and a replacement experimental site was set up in Kihelkonna Bay (sheltered site) in June 2017 (Table 1; Fig. 1). The experimental sites were chosen next to existing eelgrass meadows to ensure suitable environmental conditions (Table 1).

This study focuses in detail on the Estonian component of a larger-scale experiment set up in multiple Northern European countries (see Gagnon et al. 2021 for a detailed description of the experimental design). Eelgrass and mussels were collected from nearby donor sites (see Table 1), rinsed, and stored in flow-through aquaria until needed. In each site, 30 experimental plots were set up 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 with mussels (Z + M). The location of each plot on the experimental site was randomized. The control plots were only bare sand, while the procedural control plots included a buried plastic mesh (25 × 25 cm, mesh size 5 cm) which

Table 1. Coordinates and characteristics of the experimental sites in Experiment 1 (see Gagnon et al. 2021 for details)

Site name	Coordinates	Site class	Wave exposure (m^2 s)	Mean fetch (km)	Max fetch (km)	Sediment	Eelgrass at sites	Donor site for eelgrass	Donor site for mussels
Tagalaht Bay*	58.41981 N, 22.09293 E	Sheltered	38 884	7	~175	Fine sand 100%	Small patches	Küdema Bay, 58.5330 N, 22.2380 E	Küdema Bay, 58.5578 N, 22.2789 E
Soela Strait	58.64202 N, 22.60303 E	Exposed	152 767	14	~200	Fine sand 100%	Large patchy meadow	Küdema Bay, 58.5330 N, 22.2380 E	Küdema Bay, 58.5578 N, 22.2789 E
Kihelkonna Bay	58.37997 N, 21.96010 E	Sheltered	104 622	2.5	~200	Dominant sediment is medium sand	Large patchy meadow	Kihelkonna Bay (same site)	Küdema Bay, 58.5578 N, 22.2789 E

* Note that the plots at Tagalaht were buried within one month of planting, and the experiment was restarted at Kihelkonna Bay

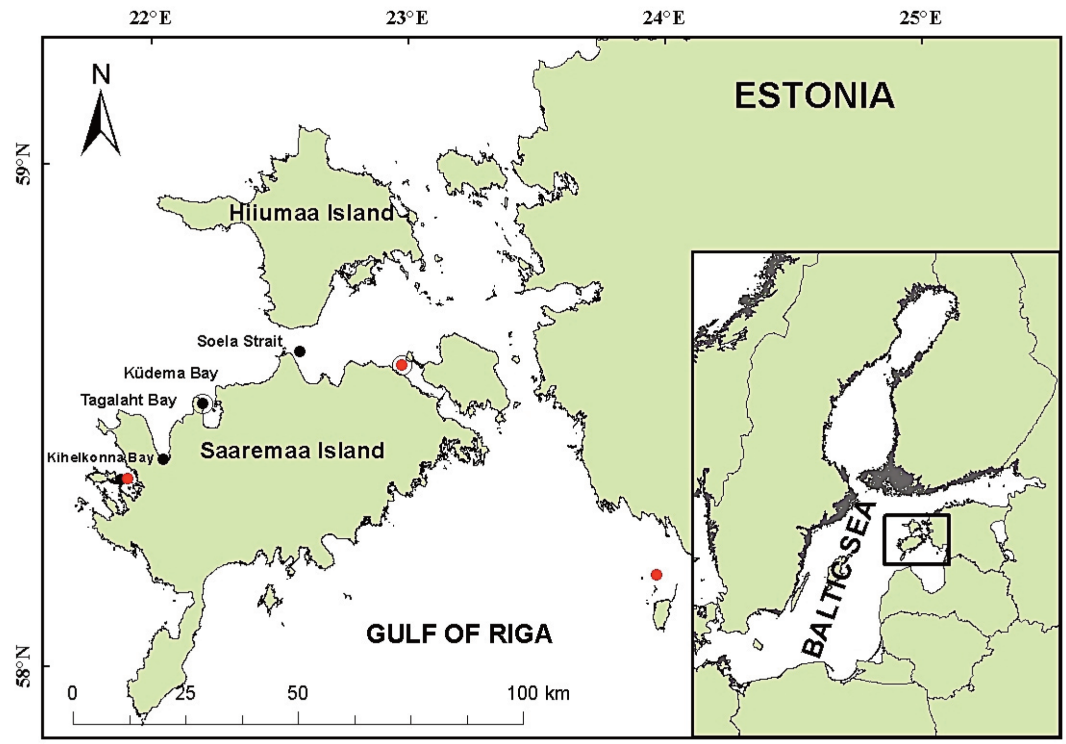

Fig. 1. Location of the study area. Black dots indicate the experimental sites of co-restoration of eelgrass *Zostera marina* with blue mussels *Mytilus edulis/trossulus*. Red dots show the eelgrass transplantation sites with the rope method. Circles mark the locations of donor areas.

was also used for the mussel and eelgrass plots. The mussel plots included the same mesh with approximately one litre of mussels (wet weight ~300 g, mussel length: 1–2 cm), and the eelgrass plots included the mesh with 16 shoots of eelgrass attached using cable ties (approximate shoot length 20 cm, rhizome length 5–10 cm). Combined plots of eelgrass and mussels included 16 shoots of eelgrass with one litre of mussels added between the shoots. The meshes were buried under ~1 cm of sediment at a depth of 3.0 m and fixed to the bottom with two metal pins.

Prior to transplantation, we measured the initial condition index (flesh dry weight/shell dry weight; Davenport and Chen 1987) and shell length of 10–12 mussels. The initial shoot length of 12 eelgrass shoots as well as aboveground (dry weight of the leaves) and belowground (dry weight of rhizome and roots) biomasses were also measured (Short and Duarte 2001). Eelgrass was transplanted in spring-summer to observe responses over the growing season, and resampled to determine survival after a winter season: Soela Strait was visited in September 2017 and May 2018, while Kihelkonna Bay was visited in September 2017, May 2018, and September 2018. On each visit, we counted shoots and measured mussel percent cover in plots. During the first sampling (September 2017), we also took a sediment core from the centre of each plot to determine organic content (loss on ignition, LOI) and measured the mussel condition index in all sites. At the same time, we also measured eelgrass growth (by puncturing and marking six shoots per treatment two weeks prior to the sampling; Short and Duarte 2001), longest shoot length, and aboveground biomass. Some plots could not be found due to lost markers, floating macroalgal mats or sand mobility (seven plots in 2017 in the exposed site and three plots in 2018 in the sheltered site).

In all experimental sites, water temperature and light intensity (lux) were measured continuously using the HOBO Pendant Temperature/Light Data Logger (model: UA-002-64). Measurements were recorded during the full experimental period in 2017–2018 with the interval of 30 minutes. As algae quickly covered the HOBO loggers, we did not use the data from the full experimental period to compare the general light intensity between the sites. Mean fetch was measured at each site from eight directions. Wave exposure values are based on the simplified wave exposure model (Isæus and Rygg 2005; Nikolopoulos and Isæus 2008; see Table 1, 2).

Table 2. Coordinates and characteristics of the experimental sites in Experiment 2. Sediment organic content (LOI, mean ± SE) in different study areas (*n* = 9)

Experimental site	Coordinates	Sediment	Wave exposure (m^2 s)	Eelgrass at sites	Sediment organic content (LOI)
Case study area (Gulf of Riga)	58.20366 N, 23.96813 E	Medium sand	357 673	Small patches	0.89 ± 0.45
Donor area (Kõinastu Islet)	58.61843 N, 22.99244 E	Fine sand and clay	40 695	Large patchy meadow	0.80 ± 0.15
New study area (Kihelkonna Bay)	58.3797 N, 21.9602 E	Medium sand	104 622	Large patchy meadow	0.60 ± 0.11

Experiment 2. Eelgrass transplantation with rope method

A suitable transplantation site was identified in the northeastern region of the Gulf of Riga (area north of Kihnu Island), a location where *Z. marina* is known to have been present previously (Table 2; Fig. 1). A suitable *Z. marina* donor site was identified in the western basin of the West Estonian Archipelago Sea (Table 2; Fig. 1). The donor site was selected because its environmental conditions (e.g. salinity, nutrients level, sediment organic content) are similar to those found at the experimental site. Furthermore, *Z. marina* communities were found to be in good health within this area, providing a good stock for transplanting. Due to high sand accumulation, the first attempt of the transplanting experiment failed after the first growing season. However, we selected a new site to test the success of the rope transplant method in a sheltered area. The new site was chosen in Kihelkonna Bay (Table 2; Fig. 1), using the same donor area.

The first small-scale transplanting experiment plot with an area of 5 m^2 was set up in the Gulf of Riga in July 2017. The second experiment plot with an area of 3 m^2 was then set up in Kihelkonna Bay in June 2018. In the lab, 10 shoots containing long rhizomes (rhizome length: 5–10 cm) were attached to a 1 m cotton rope using cable ties (in the Gulf of Riga) and biodegradable (cotton) thread (in Kihelkonna Bay). Divers using SCUBA buried the ropes containing the attached eelgrass shoots under the sediment. The ropes were held in place by driving attached metal hooks into the sediment at a depth of 3.0 m. A density of 50 shoots per square metre was achieved using this method. The experiment was set up with five replicates in the Gulf of Riga and three replicates in Kihelkonna Bay.

The initial organic content of sediment (%LOI) was determined in all studied sites (*n* = 3 per site). For sampling, the Gulf of Riga site was visited in November 2017 and June 2018, while Kihelkonna Bay was visited in September 2018, May 2019, and September 2019. On each visit, eelgrass shoots on the ropes were counted. In all experimental sites water temperature (Fig. 5), light intensity (lux) (Fig. 6), and wave exposure values were measured as described in detail above (see Table 2).

Statistical analyses

We used a linear mixed model to assess the effects of treatment (levels: eelgrass, mussels, eelgrass + mussels), site (levels: sheltered and exposed) and temporal succession on eelgrass shoot count and mussel percent cover in Experiment 1 and the effect of temporal succession on eelgrass shoot count in Experiment 2. The studied experimental plot treatment was used as a random factor to properly account for the repeated measurements at the sites. Satterthwaite's approximation method was used to correct for the degrees of freedom of F-distribution. Estimated marginal means were used for presentation of modelling results. Distributions of model residuals were inspected visually and as there were deviations of the Gaussianity of model residuals, negative binomial distribution (instead of Gaussian) was used for the conditional distribution of all dependent variables. The model outcomes did not change after applying a different data distribution pattern. For the sediment organic content, the values for different sites were compared using a two-tailed t-test. The analyses were performed in the R environment (version 3.6.1) using the following packages: lme4, lmerTest and emmeans (Bates et al. 2015; Kuznetsova et al. 2017; Lenth et al. 2020).

RESULTS

Experiment 1. Co-restoration of eelgrass and mussels

Eelgrass shoot count significantly differed between sampling times ($p < 0.001$) but not between different treatments and sites (levels: sheltered and exposed) (Fig. 2a; Table 3; $p > 0.05$). However, the interactive effects of Site × Time ($p < 0.001$) and Time × Treatment × Site ($p < 0.05$) were statistically significant (Table 3). The addition of mussels did not increase the survival of eelgrass ($p > 0.05$). In the sheltered site eelgrass shoot counts increased in time but the difference was not significant ($p > 0.05$). In the exposed site, however, eelgrass shoot counts were significantly reduced both in the eelgrass with mussel ($p < 0.001$) as well as in eelgrass only ($p < 0.05$) treatments.

Similarly, mussel density significantly differed between sampling times ($p < 0.001$) but not between different treatments and sites (Table 4; $p > 0.05$). However, the interactive effects of Site × Time were statistically significant ($p < 0.001$). All mussel treatments lost mussels over the course of the experiment. The retention of mussels was higher in the sheltered site compared to the exposed site but only for treatments including eelgrasses ($p < 0.001$) (Fig. 2b). After 15 months almost all mussels had disappeared from both sites with the sheltered site retaining only ~5% of initially seeded mussels (Fig. 2b).

In plots not seeded with mussels, eelgrass growth rate, shoot length, aboveground and belowground biomasses were quantified at two sites in September 2017. Only shoot length differed among the two sites with higher values observed in the exposed site. However, the difference was only nearly significant at $p = 0.07$. Exposure had no significant effect ($p > 0.05$) on eelgrass growth rate, aboveground and belowground biomasses.

In the sheltered site, eelgrass shoot count significantly differed between sampling times ($p < 0.001$; Fig. 2a) but was not affected by treatment or the interactive effect of

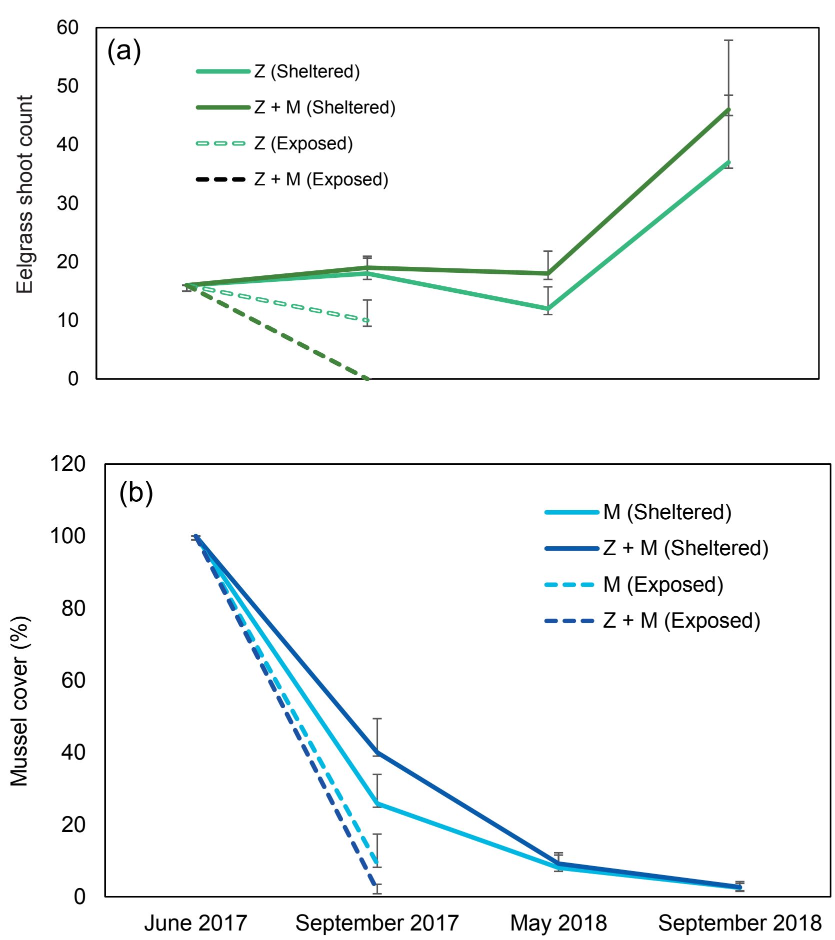

Fig. 2. Eelgrass shoot count (a) and mussel percent cover (b) (mean ± SE) after 3, 12, and 15 months post-transplantation in eelgrass (Z), mussel (M), and eelgrass + mussel (Z + M) plots in sheltered and exposed sites.

Table 3. Results of a linear mixed model analysis with Satterthwaite's method on the separate and interactive effects of time, treatment and site on the shoot count of *Zostera marina*. Significant effects ($p < 0.05$) are indicated in bold

Source	MS	df	F	*p*
Time	234.08	1	13.5814	**0.0014**
Treatment	0	1	0	0.9999
Site	0	1	0	0.9999
Time × Treatment	65.33	1	3.7906	0.0655
Time × Site	507	1	29.416	**<0.001**
Treatment × Site	0	1	0	0.9999
Time × Treatment × Site	90.75	1	5.2653	**0.0325**

Table 4. Results of a linear mixed model analysis with Satterthwaite's method on the separate and interactive effects of time, treatment and site on the percent cover of *Mytilus* spp. Significant effects ($p < 0.05$) are indicated in bold

Source	MS	df	F	*p*
Time	78328	1	495.4452	**<0.001**
Treatment	0	1	0.0003	0.9872
Site	0	1	0.0001	0.9929
Time × Treatment	35	1	0.2215	0.6421
Time × Site	2255	1	14.2637	**<0.001**
Treatment × Site	0	1	0.0001	0.9934
Time × Treatment × Site	347	1	2.1929	0.1515

treatment and sampling time ($p > 0.05$). There was a slight increase in eelgrass shoot count after the first growing season, but the difference was not significant ($p > 0.05$). After the second growing season, however, the shoot count increased significantly compared to all other sampling times ($p < 0.001$).

At the end of the first growing season, the eelgrass growth rate, shoot length and aboveground biomass were higher in plots with mussels compared to plots without mussels in the sheltered site (Fig. 3a–c). However, this difference was statistically significant for shoot length only ($p < 0.05$; Fig. 3b), whereas for eelgrass growth rate and aboveground biomass this difference was only nearly significant ($p = 0.088$ and $p = 0.066$). Treatment had no effect on the belowground biomass.

Sediment organic content was approximately 10% higher in the sheltered site compared to the exposed site. There were no significant differences in sediment organic content between different experimental sites (two-tailed t-test: $t = 0.15$, $p > 0.05$).

Experiment 2. Eelgrass transplantation with rope method

Field trial I

The number of *Z. marina* shoots was significantly (approximately 45%) lower after the first growing season in the NE region of the Gulf of Riga in November 2017 ($p < 0.001$). No live *Z. marina* shoots were detected during the next sampling in June 2018.

Field trial II

The number of *Z. marina* shoots differed significantly between sampling times in Kihelkonna Bay ($p < 0.05$). In replicate plots 1 and 2, eelgrass shoot counts were significantly reduced between sampling times ($p < 0.001$; Fig. 4). In replicate plot 3, the eelgrass shoot count on the ropes was not significantly different during sampling times ($p > 0.05$; Fig. 4). However, in this plot the shoot

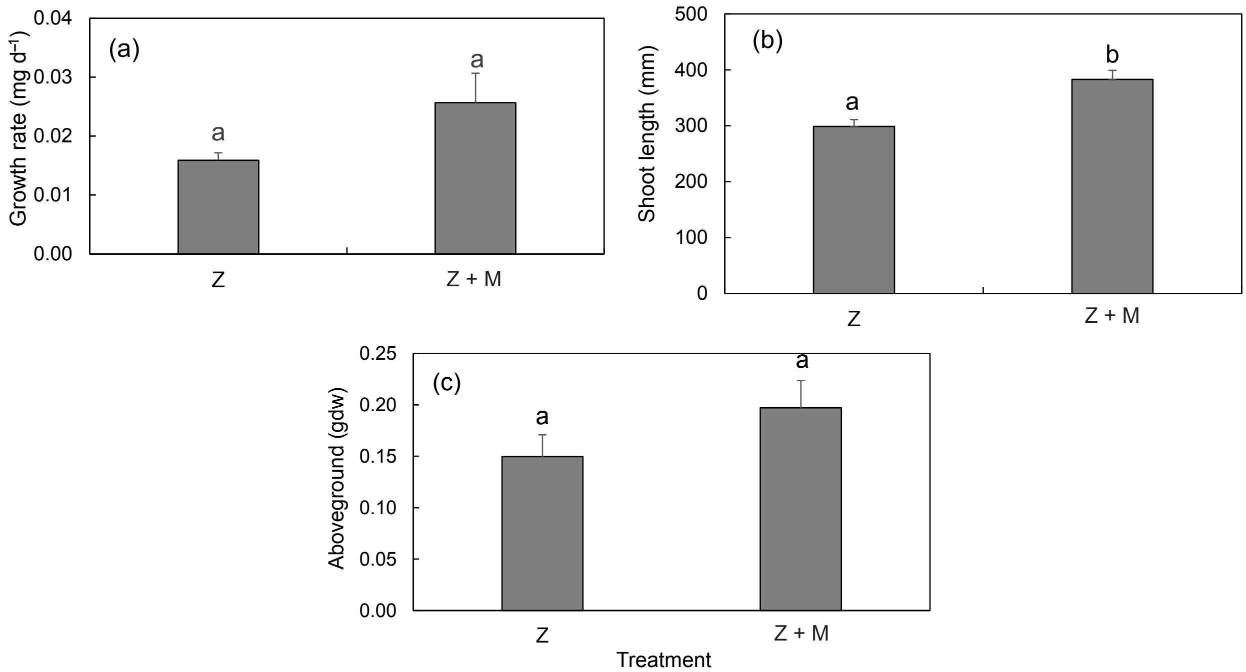

Fig. 3. Eelgrass growth (a), longest shoot length (b) and aboveground biomass (dry weight of the leaves) (c) (mean ± SE) in eelgrass (Z) and eelgrass + mussel (Z + M) plots in the sheltered site after the first growing season. Means were calculated for 6 shoots per treatment. Lowercase letters indicate significant differences ($p < 0.05$).

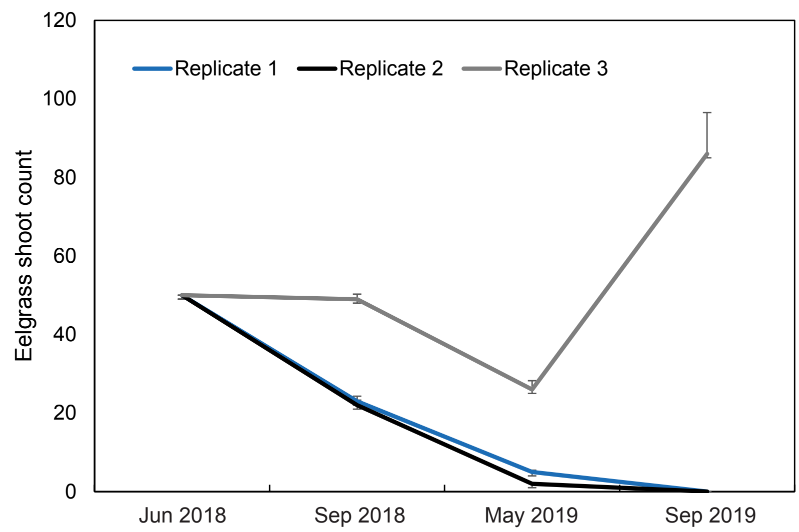

Fig. 4. A density of 50 eelgrass shoots per replicate plot was achieved at the start of the experiment in June 2018. The shoot count (mean ± SE) after 3, 12, and 15 months of transplantation with the rope method in Kihelkonna Bay site (new study site).

count had decreased approximately 50% by May 2019 compared to autumn 2018. After the second growing season (September 2019), the shoot count was approximately three times higher compared to May 2019.

DISCUSSION

In this study co-restoring eelgrass *Z. marina* with blue mussels *M. edulis/trossulus* in different sites did not increase the survival of eelgrass. When considering differences between the sites, a significant impact on eelgrass shoot length and nearly significant impacts on growth rate and aboveground biomass were found in plots with mussels in the sheltered site. Importantly, the experiment showed that the outcome of restoration was highly dependent on the hydrodynamic conditions of the experimental sites.

Demonstrating the importance of physical stressors, the mortality of eelgrass and mussels was very high in the exposed site (Soela Strait), likely due to currents and waves. In contrast, in the sheltered site the number of eelgrass shoots increased over time, especially over the second growing season, though mussels were almost completely lost. Due to high mussel mortality in both experimental sites, it is difficult to evaluate whether an addition of mussels has a long-term effect on eelgrass restoration success. In a controlled aquarium experiment, Gagnon et al. (2021) showed that the growth of eelgrass was nearly twice as high in treatments with mussels compared to treatments without mussels. This suggests that the small-scale facilitative interactions between mussels and seagrasses are possible in systems characterized by the absence of or very low hydrodynamic forcing. However, such conditions are rarely met in the field.

The Tagalaht Bay site had a lower fetch during the experiment compared to the two other experimental sites. Therefore, we assumed that eelgrass restoration was more likely to be successful in this area. However, contrary to our expectations, the *Mytilus–Zostera* transplant experiment was a complete failure after only one month due to high sand accumulation which buried the experimental plots. The prevailing sediment in the study site was fine sand (100%) and despite the lower fetch, during larger storms sediment was easily mobilized and redeposited onto the transplanted eelgrass plots. This suggests that sand mobility is a key element controlling the success of eelgrass restoration in sediment accumulation areas. Thus, exposure levels (measured as fetch) do not necessarily indicate the extent of sand mobility. Seagrass restoration in areas with high sand mobility is known to be difficult (Suykerbuyk et al. 2016; Moksnes et al. 2018), and to improve success rates the restoration actions should incorporate methods that effectively limit sediment resuspension, such as artificial structures (hessian bags, etc.) or large-scale seagrass plots that can bind sediment through their rhizome mat (van Katwijk et al. 2016).

The aim of Experiment 2 was to develop a new restoration technique (the rope method) in the sites where eelgrass was known to have previously existed. This method has several potential advantages: the rope provides a stabilising substrate for the eelgrass shoots without using plastic, and the method is low-cost and low-effort. Although we experienced some success in the transplantation of *Z. marina* in the highly exposed site in the Gulf of Riga during the first growing season, no shoots were found after the first winter and the losses were attributed to the dense drifting mats of macroalgae (thickness ~20–30 cm, personal observations). Due to high nutrient loading into the Baltic Sea region, the excessive growth of opportunistic algae is being observed practically in all of its coastal regions, and as a result these algae detach from their substrate during and after the growing season and form extensive drifting algal mats (Lehvo and Bäck 2001; Berglund et al. 2003; Paalme et al. 2004). The formation of such algal mats has previously been shown to impoverish growth conditions of many habitat-forming benthic macrophytes and invertebrate species (Norkko and Bonsdorff 1996; Gustafsson and Boström 2014) and in the most severe cases can even lead to a complete disappearance of benthic communities (Lyons et al. 2014). In the second transplantation trial in our new study site in Kihelkonna Bay, where the algal cover was intermittent and low, we were more successful. Despite eelgrass being lost from most ropes over the first winter, some ropes were found to have eelgrass expansion after the second growing season, with the number of shoots increasing significantly since the initial establishment, suggesting that this method has potential and should be tested at a larger scale. Due to high mortality during autumn and winter period, the success of eelgrass restoration can only be assessed after the second growing season, suggesting the importance of longer-term sampling/monitoring in restored areas.

Our study demonstrated that the restoration success was highly site-specific. As mentioned above, all mussels in the *Mytilus–Zostera* transplant experiment were lost, but despite that the number of eelgrass shoots increased over time in the sheltered site (Kihelkonna Bay). Furthermore, the eelgrass restoration in this study site was also more successful using the rope method. The dominating sediment type in this study site was medium sand and in addition, this site had a lower fetch than others, and thus the sediment mobility and redeposition onto the transplanted eelgrass plots during storms was also lower. In contrast, in the sites with high wave intensity sediment resuspension increases considerably, reducing the light available for the growth of rooted macrophytes (Madsen

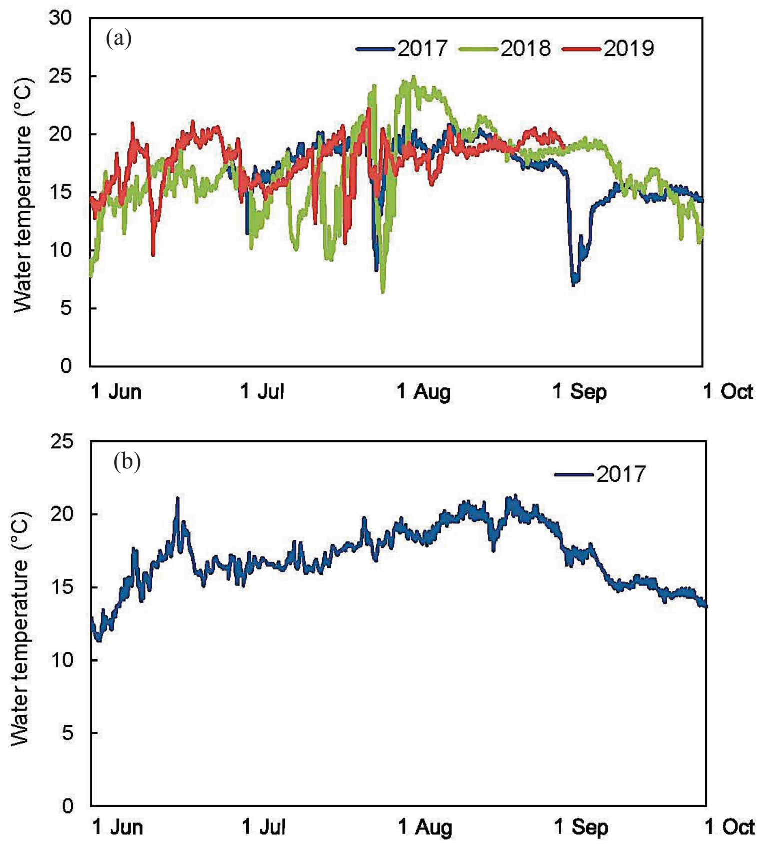

Fig. 5. Water temperature at approximately 3 m depth during the experimental period (a) in Kihelkonna Bay site in 2017–2019 and (b) in the Soela Strait in 2017 (continuous recordings).

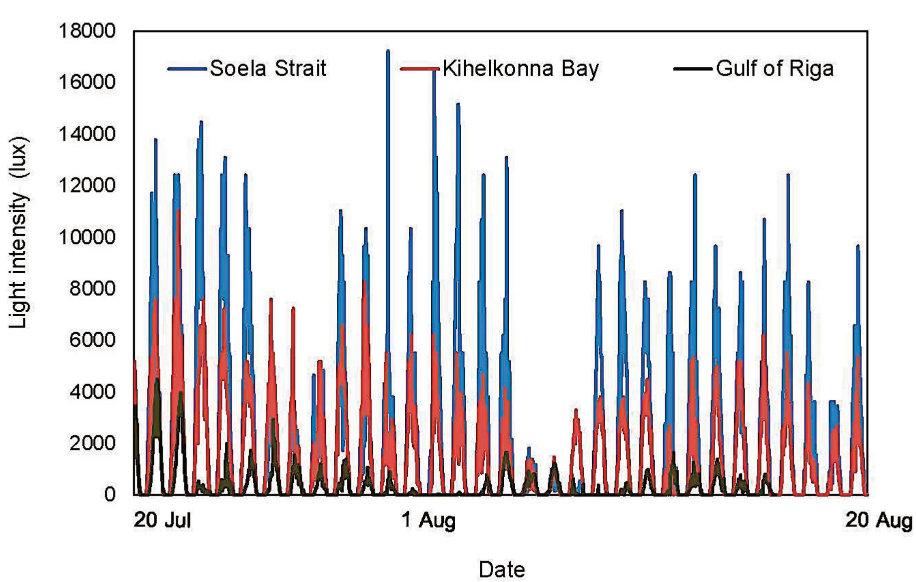

Fig. 6. Light intensity (lux) at approximately 3 m depth over the experimental period of 20 July until 20 August in the Soela Strait, Kihelkonna Bay and the Gulf of Riga in 2017 (continuous recordings).

et al. 2001). Moreover, high wave intensity can also cause the uprooting of seagrasses (Fonseca and Kenworthy 1987). Importantly, moderate wave intensity and less mobile sediment improved the success rate of restoration actions in the Kihelkonna site.

The daily water temperature showed remarkable variation due to frequent upwelling events occurring on occasions with extreme temperature shifts in the Kihelkonna site (Fig. 5; Paalme et al. 2020). As a result, underwater light intensity (Fig. 6) increased, having a positive effect on the growth of eelgrass. We found that both sites (sheltered and exposed) had a good underwater light climate condition, as often water transparency was to the bottom. This finding further supports our notion that the hydrodynamic forces and type of prevailing sediment and its mobility in the area are key elements that control the success of eelgrass restoration.

CONCLUSIONS

Despite major challenges, seagrass restoration actions are becoming an important part of coastal management and conservation with some success stories demonstrated around the world (e.g. Matheson et al. 2017; de los Santos et al. 2019; Paulo et al. 2019). Here, our results highlight the importance of considering and evaluating local environmental conditions (in this case, wave regime, sediment mobility, and algal cover) in potential restoration sites (van Katwijk et al. 2009). In a marginal environment such as the northern Baltic Sea, small-scale eelgrass restoration seems to be possible in sites with appropriate environmental conditions (low sediment mobility and rare events of drifting macroalgae), but larger-scale restoration efforts need to incorporate the self-facilitating mechanisms, for instance using high-density eelgrass shoots (Bos and van Katwijk 2007).

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Meriheina (*Zostera marina*) elupaikade taastamine Läänemere kirdeosas

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Meriheinakooslused on madala mere pehmete põhjade elupaikadest ühed kõige produktiivsemad ja väärtuslikumad. Viimase 50 aasta jooksul on nende levikuala kogu maailmas vähenenud ligikaudu 30%. Samuti on meriheina levik Läänemere rannikumere eri piirkondades ahenenud peamiselt eutrofeerumise tagajärjel. Siiani on meriheinakoosluste taastamise edukus olnud väike, mis on ajendanud otsima uusi lahendusi ja meetodeid. Käesoleva töö üks eesmärk on uurida rannakarpide *Mytilus edulis/trossulus* mõju pika meriheina *Zostera marina* taastamisele. Varasemad uuringud on näidanud, et rannakarbid võivad mõjuda meriheina kasvule soodsalt. Lisaks katsetasime nöörimeetodit meriheina taastamisel nendes kohtades, kus teadaolevalt on ta varem kasvanud. Kuna merihein *Z. marina* paljuneb Läänemeres ainult vegetatiivselt, siis katseid tehti taimi ümber istutades. Veealused istutamise eksperimendid viidi läbi aastatel

2017–2019 Läänemere kirdeosas. Katsealadeks valiti tuultele vähem ja rohkem avatud alad. Uuringu tulemused näitavad, et meriheina ja rannakarpide koos taastamine ei õnnestunud, kuna karpide arvukus vähenes märkimisväärselt juba esimesel kasvuperioodil. Samal ajal aga meriheina taimede arv suurenes aja jooksul, seda eriti teisel kasvuperioodil tuultele ja lainetusele vähem avatud kasvukohas, mis näitab, et nendel aladel on taastamine võimalik. Meriheinakoosluste taastamisel mängivad abiootilised tegurid suuremat rolli kui biootilised interaktsioonid ja seega sõltub taastamise edukus suuresti kohalikest keskkonnatingimustest.