Assessing the recovery of benthic macrofauna communities in restored eelgrass transplantations in the western Gulf of Finland

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Tiivistelmä - Referat - Abstract

Meriruohoniityt ovat tärkeitä rannikkoekosysteemeitä, joita uhkaavat monet häiriö- ja stressitekijät, mikä korostaa ennallistamisprojektien tärkeyttä paikallisen monimuotoisuuden parantamiseksi. Meriruohoniityt luovat otolliset elinolosuhteet monille lajeille parantaen ympäristön rakenteellista ja toiminnallista monimuotoisuutta ja täten ylläpitäen ekosysteemin toimintoja ja palveluita. Meriruohoniittyjen pohjaeläinyhteisöillä on avainrooli merenpohjan ravinne- ja hiilenkierron säätelyssä. On kuitenkin vain vähän tutkimusta meriruohoniittyjen ennallistamisen vaikutuksesta pohjaeläinyhteisöjen palautumiseen pohjoisella Itämerellä.

Tässä tutkielmassa tutkittiin pohjaeläinyhteisöjen rakennetta ja koostumusta ennallistetuilla meriajokkaan siirtoistutuksilla, ja tarkasteltiin niiden palautumista vertaamalla niitä paljaan sedimentin ja luonnollisten meriajokasniittyjen pohjaeläinyhteisöihin. Lisäksi sedimentin ominaisuuksien eroavaisuuksia tutkittiin. Pohjaeläin- ja sedimenttinäytteitä kerättiin syyskuussa 2024 sukeltamalla kahdelta kohteelta läntisellä Suomenlahdella, joissa meriajokkaan siirtoistutuksia oli tehty kesällä 2023. Näytteistä määritettiin pohjaeläinyhteisöjen lajikoostumus ja rakenne (yksilömäärä, biomassa, lajimäärä, monimuotoisuus), sekä sedimentin ominaisuuksia (raekoko, orgaanisen aineksen määrä, hiili- ja typpipitoisuus).

Tämän tutkimuksen tulokset näyttivät, että pohjaeläinyhteisöt ja sedimentin ominaisuudet erosivat merkittävästi tutkimuskohteiden välillä, mikä korostaa paikallisten olosuhteiden ja kontekstin merkitystä. Korkeampia yksilömääriä havaittiin *Z. marina* elinympäristöissä verrattuna paljaaseen sedimenttiin, mikä puolestaan vahvistaa meriruohoniittyjen merkitystä niillä elävien lajien lisäämiseksi. Merkittäviä eroavaisuuksia löydettiin pohjaeläinyhteisöissä paljaan sedimentin ja luonnollisen *Z. marina* niittyjen välillä, kun taas ennallistettujen meriajokkaan siirtoistutusten pohjaeläinyhteisöt eivät olleet palautuneet vielä sille tasolle, jota voi odottaa näillä kohteilla, kun niitä verrataan ympäröiviin luonnollisiin meriajokasniittyihin. Saadut tulokset kuitenkin viittaavat siihen, että pohjaeläinyhteisöt osoittavat vahvoja merkkejä palautumisesta, joka on vielä käynnissä näillä kohteilla. Tutkimukseni osaltaan syventää ymmärrystä pohjaeläinyhteisöjen ja meriajokasniittyjen biodiversiteetin palautumiskehityksestä ennallistamistoimien seurauksena.

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pohjaeläinyhteisöt, meriruohoekosysteemit, ennallistaminen, biodiversiteetti, Itämeri

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Tiivistelmä - Referat - Abstract

Seagrass meadows are critical coastal ecosystems that are globally threatened by various anthropogenic and environmental pressures, stressing the need of restoration projects aimed at enhancing local biodiversity. Seagrass meadows are known to host a variety of associated species enhancing both the structural and functional diversity, and thus sustain ecosystem functioning and services. Benthic infauna assemblages associated with seagrass habitats have a key role in seafloor nutrient and carbon cycling, however there is limited research on the effects of seagrass restoration on faunal recolonisation and recovery in the northern Baltic Sea.

This master's thesis project investigated the structure and composition of infaunal communities in restored *Zostera marina* plots and compared them to those in bare sediment and ambient *Z. marina* meadows to assess the recovery process of associated biodiversity. In addition, the variability in sediment properties was explored. In September 2024, benthic infauna and sediment samples were collected by scuba diving at two different sites in the western Gulf of Finland where eelgrass restoration was conducted by shoot transplantation in summer 2023. The species composition and structure (abundance, biomass, richness, diversity) of infauna communities were measured along with investigating their link to sediment properties (grain size, organic matter, carbon and nitrogen content).

The results from this study showed that infauna communities and sediment properties differed significantly between sites, reflecting the role of local conditions and context. Higher species densities were found in *Z. marina* habitats compared to bare sediment, highlighting the role of seagrass habitats in enhancing associated biodiversity. Furthermore, significant differences were observed in infauna communities between bare sediment and ambient *Z. marina* meadows, while faunal communities in restored plots had not yet fully recovered to the state that may be expected when compared to ambient eelgrass meadows at these study sites. Still, my findings indicate that the communities show strong signs of recovery and that this is likely still an ongoing process at these sites. Thus, my study is contributing to the understanding of recovery trajectories of seagrass-associated biodiversity as a result of restoration efforts.

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Abbreviations

AFDW	Ash-free dry weight
ANOVA	Analysis of variance
C	Carbon
DO	Dissolved oxygen
DW	Dry weight
HDS	Honestly significant difference
LOI	Loss on ignition
N	Nitrogen
NMDS	Non-metric multidimensional scaling
OM	Organic matter
SE	Standard error
TC	Total carbon
TN	Total nitrogen
WWF	World Wildlife Fund

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1 Introduction

1.1 Biodiversity and ecosystem restoration

Ecosystems around the world are facing rapid degradation, and coastal ecosystems are threatened by climate change and anthropogenic stressors, such as commercial fishing practices, pollution and coastal development (He & Silliman, 2019). Related biodiversity loss is also threatening the provisioning of valuable ecosystem functions by these important habitats (Worm et al., 2006). A variety of goods and services provided by marine ecosystems that are critical to human needs and wellbeing, are maintained and promoted by biological diversity (Palumbi et al., 2009). Higher diversity has been shown to promote greater stability of the ecosystem and greater resistance to some disturbances and stressors (Balvanera et al., 2006). Loss of marine biodiversity is accelerating on a global scale, and the consequences are still largely unknown, however, existing data implies that this trend can still be shifted (Worm et al., 2006). Along with environmental protection, restoration of ecosystems has the potential to enhance and increase biodiversity, and it is increasingly implemented as a key conservation strategy (Possingham et al., 2015; Silliman et al., 2015). Ecosystem restoration is also listed as one of the 10 Ocean Decade Challenges that encompass the most immediate priorities for the United Nations Decade of Ocean Science for Sustainable Development (Ocean Decade, 2025). Furthermore, coastal ecosystem restoration of vegetated habitats (e.g. mangrove ecosystems and seagrass meadows) can help mitigate climate change by supporting these important carbon sinks (Duarte et al., 2013). However, the need for developing effective tools for restoration of coastal marine ecosystems has been recognised and is emphasised by an increasing rate of degradation of marine environments (Abelson et al., 2020; Benayas et al., 2009). Challenges concerning coastal restoration include the lack of effective restoration practices, site selection issues, and social-ecological integration of restoration priorities (Abelson et al., 2020). Moreover, clearly defined restoration success criteria and assessment of indicators that reflect the ecological recovery of the ecosystem are urgently needed, in order to close the knowledge gaps regarding feasibility of restoration efforts (Bayrakatarov et al., 2015; Wortley et al., 2013). It is therefore essential to monitor associated biodiversity and ecosystem functions to evaluate the overall success of a restoration project.

1.2 Seagrass ecosystems

Seagrass meadows are some of the most productive ecosystems worldwide (Duarte & Chiscano, 1999), occurring from tropical to temperate regions around the globe (McKenzie et al., 2020). They are critical coastal marine ecosystems that support high biodiversity and ecosystem functioning, and they play an important role in combating climate change with some estimates suggesting that restored seagrass meadows contribute to greenhouse gas offsetting at a rate of 0.42 tCO_2e ha^{-1} annually (Nordlund et al., 2016; Oreska et al., 2020). However, seagrass ecosystems are threatened both locally and globally, by various impacts from anthropogenic and environmental pressures, such as global warming, eutrophication and benthic habitat destruction (Orth et al., 2006). Seagrasses have earlier been reported to be disappearing at a rate of 110 km^2 yr^{-1} since 1980 with accelerating rates of decline (Waycott et al., 2009), while Dunic et al. (2021) recently reported a global net loss of 5602 km^2 of seagrass meadows occurring since 1880, with variable trajectories across bioregions. Loss of seagrasses at this alarming rate demonstrates the critical state of seagrass meadows as some of the most threatened ecosystems in the world.

Common eelgrass (*Zostera marina*) is a vascular plant, and the only seagrass species found in the northern Baltic Sea. It is an important keystone species that forms meadows on sandy seafloor, and creates favourable habitats for many species, such as fish, crustaceans and molluscs, by providing food and shelter (Boström et al., 2006a). *Z. marina* is a near-threatened species in Finland, whereas the conservation status of benthic habitats characterised by *Z. marina* as a habitat type is classified as vulnerable in the Finnish Red list of habitats (Hyvärinen et al., 2019; Kontula & Raunio, 2018). In Finnish coastal areas *Z. marina* habitats are threatened by eutrophication, reduced water clarity, and increased abundance of filamentous algae (Kontula & Raunio, 2018). Reported declines of eelgrass habitats in the Baltic Sea have highlighted the need of urgent management actions through monitoring, protection, and restoration (Baden et al., 2003; Boström et al., 2014). Although successful large-scale seagrass restoration projects have been reported around the world (Orth et al., 2020), examples of large-scale restoration efforts in the Nordics are still widely lacking, as most restoration projects have been small-scale experimental restoration projects with limited success (Boström et al., 2014; Gagnon et al., 2021; Infantes et al., 2016; Pajusalu et al., 2023). However, the restoration of seagrass meadows is a crucial step towards restoring the ecosystem as a whole, as these biodiversity hotspots host a variety of associated species enhancing both the structural and functional diversity, and thus sustain ecosystem functioning and services (Gagnon et al., 2023).

1.3 Seagrass habitats and benthic macrofauna communities in the Baltic Sea

Seagrass act as important ecosystem engineers (Bos et al., 2007), and they have been shown to support higher densities of organisms than nearby unvegetated bare sediments (Fredriksen et al., 2010). Due to steep environmental gradients, salinity in particular, faunal communities in the northern Baltic Sea are often characterized as low in species and functional diversity (Bonsdorff, 2006; Bonsdorff, & Pearson, 1999; Gogina et al., 2016). One organism group associated with seagrass meadows is benthic infauna, which primarily live in the bottom sediment (Boström & Bonsdorff, 1997). Infauna community has an important role in the seafloor nutrient and carbon cycling and energy transfer to higher trophic levels (Baldrighi et al., 2017; Ehrnsten et al., 2022). Despite being comparatively low in diversity, these communities support many vital ecosystem functions and processes (Norling et al., 2007; Rodil & Lastra, 2022). The Baltic Sea infaunal communities show high regional variability, and an extensive inventory of the benthic macrofaunal communities has demonstrated that the communities also vary based on their abundance and biomass composition (Gogina et al., 2016). The large-scale inventory revealed that in terms of species abundance, dominating species in the northern parts of the Baltic Sea include for instance the invasive polychaete *Marenzelleria* spp., that has been reported to show a preference for shallow sandy bottoms, and the bivalve *Macoma balthica* that occurs from muddy to sandy habitats (Gogina et al., 2010; Gogina et al., 2016; Kauppi et al., 2015). Moreover, shallow sandy sediments in the Gulf of Finland are characterized by the bivalve *Cerastoderma glaucum,* the polychaete species *Pygospio elegans,* and gastropods in the Hydrobiidae family. Additionally, other species dominating community biomass in sandy sediments include the polychaete worm *Hediste diversicolor*, and the bivalve species *Mya arenaria* (Gagnon et al., 2016). Furthermore, seagrass beds shape the distribution of many species by providing habitats and sediment stability, and modifying the hydrodynamic environment (Widdows et al., 2008). Species associated with *Z. marina* beds and their spatial distribution have been assessed in the northern Baltic Sea, and the most abundant taxa have been reported to be Hydrobiidae and Oligochaeta (Boström & Bonsdorff, 1997). Other prevalent species in *Z. marina* beds include oligochaetes, nematods, chironomids, and several polychaete and bivalve species. As a result of seagrass restoration, the recovery of benthic macrofauna community may support the overall recovery and functionality of the ecosystem, due to their contribution to ecosystem functioning (Norling et al., 2007). However, the impacts of seagrass restoration efforts on the associated organisms and diversity have been studied little in the Baltic Sea, where the high spatial variability of benthic communities highlights the need to quantify these communities in order to assess the impacts on ecosystem functions.

Facilitation of faunal communities in eelgrass patches is influenced by variable interacting mechanisms and is often context- and species-dependent (Meysick et al., 2019). Dispersal through active and passive mechanisms, including active swimming, resuspension, pelagic settlement and transport via drift algae, vary between species and is influenced by hydrodynamic conditions and eelgrass habitat structure and complexity (Boström & Bonsdorff, 2000; Valanko et al., 2010). Eelgrass shoot density also influences sediment characteristics through particle trapping and sediment deposition and binding, and it has been shown to have strong effects on faunal recruitment (Boström & Bonsdorff, 2000; Hendriks et al., 2008). In addition to reduction of water flow by plants, particle sedimentation is promoted by direct trapping by seagrass canopies through physical collision between the particles and the leaves (Hansen & Reidenbach, 2012; Hendriks et al., 2008). Additionally, increased sediment stability, and thus reduced resuspension by seagrass beds result in finer sediments and organic matter (OM) accumulating in denser seagrass beds (Bos et al., 2007; van Katwijk et al., 2010). In addition to larval recruitment, post-settlement processes and dispersal play an important role in faunal recruitment and colonization (Boström & Bonsdorff, 2000; Valanko et al., 2010). Variable results have been demonstrated regarding the faunal assemblages being influenced by patch size of restored eelgrass shoots and the linked edge effect (higher faunal densities observed closer to habitat edges) (Bologna & Heck, 2012; Boström et al., 2006b; Meysick et al., 2019). A recent study detected rapid colonization and recovery of the faunal communities in restored eelgrass plots in the Skagerrak region after two growing seasons, however, they found no indication that patch size was driving the faunal colonization (Gagnon et al., 2023). Moreover, recolonization rates are mediated by physical, chemical and biological factors and they are dependent on the local hydrodynamic regime (Dernie et al., 2003). Monitoring benthic macrofauna communities after a restoration event is thus important to assess the success of the restoration effort and understand the potential recovery of biodiversity. In addition, comparing the community to a natural reference meadow is necessary to be able to investigate whether the community has recovered to the expected state, and measuring environmental characteristics will help to understand the environmental context.

1.4 Research questions

The main aim of this thesis was to study how eelgrass restoration influences benthic infauna communities and sediment properties by measuring the infauna community composition in restored and ambient *Z. marina* meadows and bare sediments in the western Gulf of Finland. In addition, variability in sediment and *Z. marina* properties was investigated and measured. Results from this thesis will help to assess the recovery of the ecosystem and the overall restoration success and add to the knowledge about the feasibility of restoration efforts, as there is an evident lack of research focusing on quantifying eelgrass associated fauna and their recovery. Specifically, the following three research questions were explored:

1) Do sediment grain size, organic matter content, total carbon and nitrogen (TC and TN), and *Z. marina* shoot density vary between recently restored *Z. marina* meadows, compared to ambient reference meadow and bare sediment at two sites?
2) How do the infaunal communities differ in terms of abundance, biomass, species richness, diversity (*H*) and bivalve size structure between recently restored *Z. marina* meadows, natural reference meadows and bare sediments, and what species contribute to those differences?
3) Do the restored plots show signs of recovery when compared to ambient eelgrass meadows?

I hypothesise that sediment characteristics differ between sites and treatment categories, reflecting the role of local hydrodynamic regime and recovery process of sediment properties. My hypothesis is that finer sediment and higher organic matter content are found in *Z. marina* meadows compared to bare sediments. I hypothesise that higher faunal community metrics are observed in *Z. marina* vegetation compared to bare sediments, and that the infaunal communities in restored eelgrass meadows are more similar to communities in natural eelgrass meadows than to those in bare sediments, reflecting the recovery process of the communities. I also hypothesise that communities vary between study sites reflecting the role of local context.

2 Materials and methods

2.1 Study sites

To study whether benthic infaunal communities show signs of recovery in restored eelgrass meadows, I collected samples in Inkoo archipelago in the western Gulf of Finland in the northern Baltic Sea. This study was conducted in collaboration with World Wildlife Fund (WWF) Finland, who carried out pilot restoration experiments of *Z. marina* at these sites in May and June of 2023 (Tolonen et al., 2023). I collected samples at two sites, off the shore of south of Granö island and west of Stora Fagerö island (Fig. 1), where restoration experiments have been conducted and where *Z. marina* also grows naturally. A preliminary visit to the sites was done in June 2024 to confirm the suitability and exact location of the sites. Actual sampling was conducted during 5th and 6th of September 2024, thus after two growing seasons. Principles of research ethics were considered and followed in the research planning process as the study involved faunal sampling, and an appropriate sampling permit was acquired from the Centre for Economic Development, Transport and the Environment to sample benthic invertebrates in the private nature conservation area of the marine area of Stora Fagerö island.

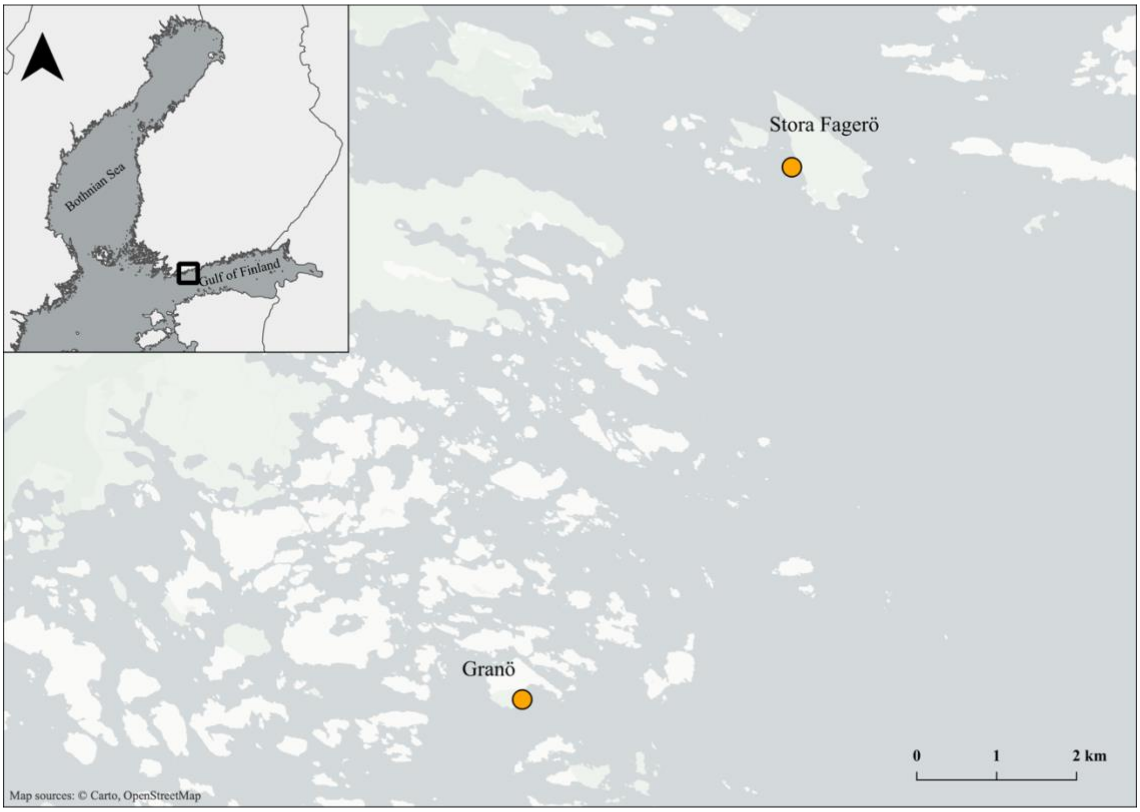

Figure 1. The location of the sampling sites, Stora Fagerö and Granö, in the Inkoo archipelago, western Gulf of Finland, marked with orange points.

2.2 Restoration configuration

Initial eelgrass restoration at both sites took place in May 2023 by WWF (Tolonen et al., 2023). Three restored *Z. marina* plots at each site were transplanted in a checkerboard pattern in 5 m x 5 m patches (Fig. 2A). The transplanted eelgrass shoots were collected from Kolaviken, Hanko and were planted in the four squares adjacent to the middle square of each plot, with 25 shoots planted in each square. Since the initial transplantation, both sites have shown variable progress in *Z. marina* shoot survival and dispersal. Tolonen et al. (2023) reported that after the first growing season the number of shoots per transplanted plot had increased, on average, in Granö (+7.2, SD=8.7), while in Stora Fagerö it had decreased (-3.2, SD=11.6). However, after the second growing season in autumn 2024, close to the time of infauna sampling, both sites showed remarkable decrease in shoot density, with an average reduction of 24.2 (SD=9.4) per transplantation plot in Granö, and 14.3 (SD=11.1) in Stora Fagerö (Tolonen et al., 2024). Bottom water temperature was monitored at both sites between 17th June and 8th October in 2023 and 16th May and 24th October in 2024.

2.3 Field sampling

To investigate the effects of *Z. marina* restoration on infauna community composition, I sampled benthic infauna and bottom sediment by SCUBA diving from restored *Z. marina* plots, ambient *Z. marina* meadow, and bare sediment at both sites. Coordinates of the restored plots were received from WWF and the locations of naturally growing ambient *Z. marina* meadows were obtained from observation points from the open Velmu map service (SYKE, 2024). All three transplantation plots were first visually inspected, two of which were then chosen for sampling based on higher restoration success and less patchy growth patterns. The samples from the two transplantation plots were collected from each square where *Z. marina* was originally transplanted (Fig. 2A), and the samples from bare sediment around the transplantation plots, and ambient *Z. marina* meadow were collected randomly. In total, eight benthic infauna samples and four separate sediment samples were collected from each treatment category (bare sediment, restored plots, ambient vegetation) at both sites. In the restored and ambient vegetation, a 27 cm x 27 cm quadrat was first placed at the seafloor and *Z. marina* shoots were counted inside the frame. The growth of *Z. marina* was extremely patchy, especially in restored plots, thus the shoot count was later not converted to density per m^2, as the conversions would not provide realistic estimates. A sediment core (diameter 9 cm) was then placed inside the frame (Fig. 2B, C) and a syringe (diameter 2 cm) was used to take the separate sediment sample next to the core for analysing sediment organic matter content, grain size, and sediment carbon (C) and nitrogen (N) content. At last, to minimise disturbance, I collected the benthic infauna sample, with a sediment core taken to a sediment depth of approximately 15 cm. In addition, temperature, salinity, and oxygen concentration were measured from the water column near the bottom with a YSI ProSolo at both sampling sites.

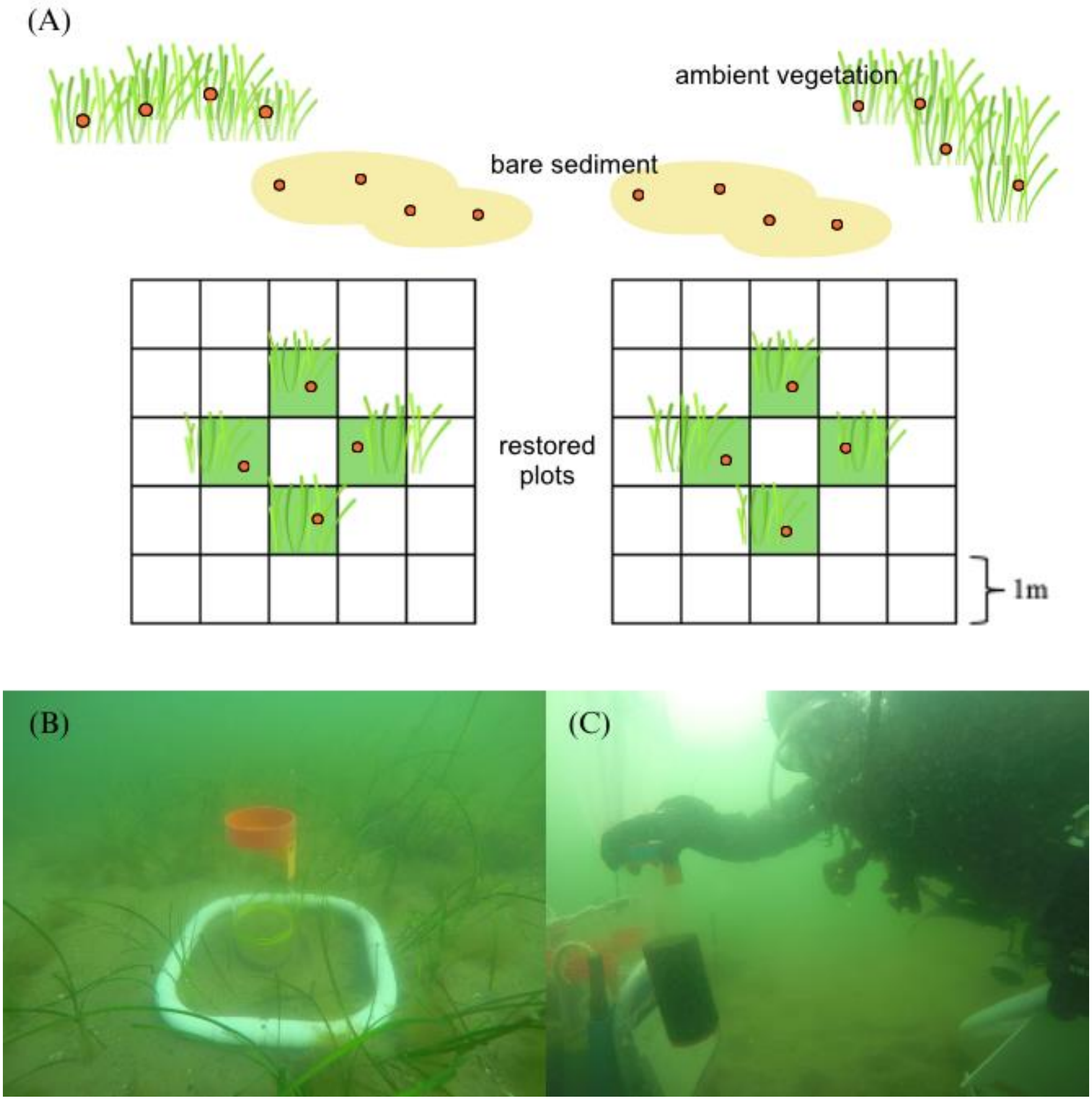

Figure 2. (A) Sampling design used at both sites with orange points representing all replicate samples. Two restored *Z. marina* plots, originally planted in a checkerboard pattern in 5 m x 5 m patches, were sampled at each site, Granö and Stora Fagerö. Samples were collected from the squares marked with green colour, where *Z. marina* shoots were originally planted in. In addition, samples were collected from bare sediment, and nearby ambient *Z. marina* meadow. (B) A quadrat and a sediment core placed on the sea floor. *Z. marina* shoot density was counted inside the quadrat and a sediment core and a sediment syringe were take inside the quadrat. (C) A diver holding a sediment core and a quadrat.

2.4 Sample processing and laboratory analyses

After sampling, benthic infauna cores were stored in seawater in a climate-controlled room set to 10 °C for up to three days. They were sieved (mesh size 0.5 mm) as soon as possible and then preserved in 70 % ethanol. The sediment samples were stored in a freezer. Four infauna replicate samples from each treatment category from both sites were processed and analysed for this master’s thesis. The analysed samples from restored plots in Stora Fagerö were all from the same restored plot, whereas the analysed samples from

Granö included samples from both sampled plots due to loss of some of the samples. For each sample, all benthic infauna individuals were counted and identified to the lowest possible taxonomic level under a light microscope and the blotted wet weight of each taxonomic group was measured. Due to a high abundance of Oligochaeta and Hydrobiidae, an average weight based on 80 individuals was calculated for each group at both sites. Hydrobiidae were further separated into small (< 2 mm) and large (> 2 mm) individuals to obtain a more accurate weight estimation. Additionally, the length of bivalve shells was measured from *Macoma balthica, Mya arenaria* and *Cerastoderma glaucum*. Benthic infauna samples having a considerable amount of sandy sediment were first elutriated using the methodology described by Norkko et al. (2010), with a difference of using a 500 µm sieve. This process was repeated until no animals were found in the supernatant under the microscope. The rest of the sediment was thoroughly examined on a white tray under a bright light for any remaining individuals.

The surface sediment samples (0-1 cm) were homogenised and analysed for organic matter content (%) as loss on ignition (LOI). The sediment was dried (60°C, 48h) and weighed, and then burned (500°C, 3h) and weighed to calculate the organic matter content as LOI with the following formula:

$$LOI = \left(\frac{\left(DW\ (g) - AFDW\ (g)\right)}{DW\ (g)} \right) * 100$$

where DW is the dry weight and AFDW is the ash-free dry weight. All samples were cooled down before weighing.

To determine sediment grain size, large shell fragments and plant material were removed from the sediment samples and the samples were treated with hydrogen peroxide (H_2O_2, 6%) to dissolve remaining organic matter. The samples were then dried (60°C, 72h) and sieved (mesh size 2 mm) to separate and weigh the sediment fraction of > 2 mm. The fraction that was < 2 mm was also weighed and analysed with a particle size analyser (Microtrac SYNC) to obtain the proportions of different particle size classes. Ultrasonic was used for each analysis and an average of three runs with a flow rate of 60% was used as the result from the analysis. The Gradistat program (version 8) was used to determine the median grain size (D50) for each sample (Blott & Pye, 2001). Sediment C and N content were analysed after drying the samples (60°C, 72h) and homogenising and packing a pre-determined amount (approximately 3 mg) of sediment in tin cups to be analysed with Europa Scientific ANCA-MS 20-20 mass spectrometer with a Sercon GSL sample preparation system in the laboratory.

2.5 Statistical analyses

All statistical analyses were conducted in RStudio (version 4.0.3). Water temperature monitoring data from the study sites for summer 2024 was obtained from Alleco Oy, and maximum daily water temperatures were extracted and plotted to provide temporal context of environmental variables. To investigate differences in sediment characteristics across three treatment categories (bare sediment, restored *Z. marina* plots, ambient *Z. marina* vegetation) at the two study sites, I used two-way analysis of variance (ANOVA) in R package "car", (Fox & Weisberg, 2011). Subsequent post hoc tests were conducted using Tukey honestly significant difference (HSD) test. Prior to analysis, data was checked to meet the assumptions of parametric tests. To explore differences in infaunal community metrics, benthic infaunal community abundance and biomass were first converted to densities per m^2. Species richness was determined for each sample, and Shannon diversity index (ln, base *e*) was calculated using R package "vegan" (Oksanen et al., 2020) to describe taxonomic diversity. To test for differences in macrofaunal community metrics (total abundance, total biomass, species richness, Shannon diversity index) between treatment categories and sites, I used permutational multivariate analysis of variance (PERMANOVA; 999 permutations, R package: "vegan") based on Euclidean distances (Anderson et al., 2008). Prior to performing PERMANOVA tests, permutational analysis of multivariate dispersion (PERMDISP; R package: ”vegan") was used to test for homogeneity of dispersion among groups. Subsequent pairwise comparisons between groups were conducted with pairwise PERMANOVA tests (R package: "pairwiseAdonis") (Martín-Fernández & Hidalgo, 2020), and corrections for multiple comparison were done using Holm-Bonferroni method. Relative abundances and biomasses of all found species were determined for each treatment category at both sites to characterise species contributions to community composition. Additionally, I used non-metric multidimensional scaling (NMDS, R package "vegan") based on Bray-Curtis dissimilarity to describe differences in infaunal community composition (abundance, biomass $\log_{10}(x + 1)$ transformed) between sites and treatment categories. The differences were statistically tested with PERMANOVA and pairwise PERMANOVA tests (999 permutations, R package: “pairwiseAdonis”). Furthermore, I used similarity percentage analysis (SIMPER) to determine similarities within and dissimilarities between treatment categories at each study site, and for identifying the species that contributed to those (dis)similarities. Pairwise Kolmogorov-Smirnov tests were used to investigate whether there were differences in the bivalve size frequency distributions between treatments and sites.

3 Results

3.1 Environmental parameters

The sampling depth varied from 4.0 m at Granö to 3.3 m at Stora Fagerö. At the time of sampling the bottom water temperatures were 16.9 °C and 17.5 °C, and the measured salinities were 6.29 ppt and 6.37 ppt at Granö and Stora Fagerö, respectively. High dissolved oxygen concentrations were measured at both sites (Table 1).

Table 1. Environmental variables (temperature, salinity, dissolved oxygen) measured at the study sites during sampling.

Site	**Sampling date**	**Depth (m)**	**Temperature (°C)**	**Salinity (ppt)**	**DO (%)**	**DO (mg/L)**
Granö	5.9.2024	4.0	16.9	6.3	114.0	10.7
Stora Fagerö	6.9.2024	3.3	17.5	6.4	119.3	11.0

Maximum daily bottom water temperature ranged from 8.66 °C to 22.61 °C at Granö, and 7.55 °C to 22.48 °C at Stora Fagerö during the growing season in 2024 (Fig. 3). The number of days when the water temperature exceeded 20 °C during the monitoring season in 2024 (16.5.2024-24.10.2024) was 21 at Granö and 18 at Stora Fagerö (Tolonen et al., 2024) (Table 2). In contrast, the number of days when the water temperature exceeded 20 °C during the first growing season in 2023 was one and three days at Granö and Stora Fagerö, respectively (Tolonen et al., 2023).

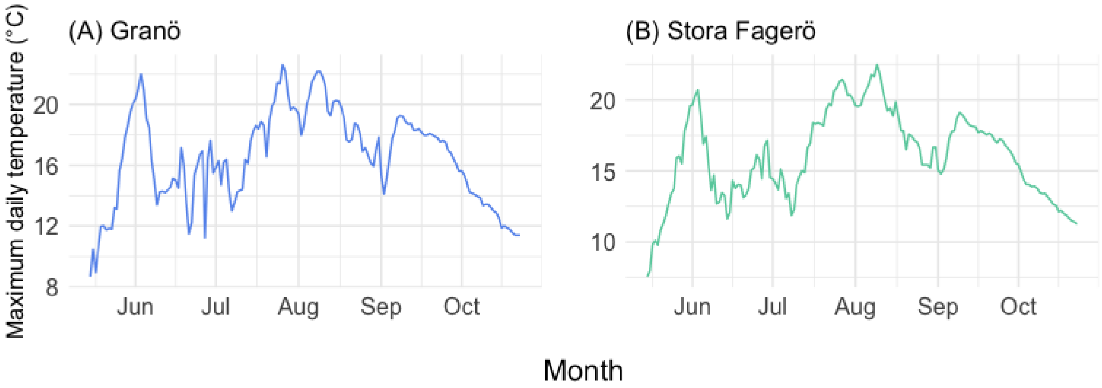

Figure 3. Daily maximum bottom water temperature measurements from a temperature logger from growing season 2024 between 16.5.2024 and 24.10.2024 (Tolonen et al., 2024).

Table 2. Number of days when the water temperature exceeded 20 °C at the study sites (Tolonen et al., 2024).

Site	**No. of days when water temp. exceeded +20 °C in**	
	2023	**2024**
Granö	1	21
Stora Fagerö	3	18

3.2 Sediment characteristics and *Z. marina* properties

Sediment grain size ranged between 189.0 µm and 260.0 µm at Granö and was characterised as fine sand in ambient vegetation, and as medium sand in bare sediment and in the restored plots (Wentworth, 1922). At Stora Fagerö sediment grain size ranged between 402.2 µm and 430.0 µm and was classified as medium sand in all treatment categories (Table 3). Sediment organic matter content varied between 0.86 % measured in bare sediment and 0.95 % measured in ambient vegetation at Granö, and 0.65 % in bare sediment and 0.76 % in restored plots at Stora Fagerö. Sediment carbon content ranged from 0.30 % in ambient vegetation to 0.40 % in bare sediment at Granö, and from 0.26 % in ambient vegetation to 0.30 % in restored plots at Stora Fagerö. Only one reliable result was obtained for carbon content analysis from restored plots at Stora Fagerö (Table 3). No reliable results were obtained from nitrogen analysis, as nitrogen content was below detection limits (<5 µg) for all samples. Overall, *Z. marina* shoot count differed significantly between treatment categories (two-way ANOVA: df=1, F=27.62, p<0.001), with ambient vegetation having significantly higher number of shoots compared to restored plots. At Granö *Z. marina* shoot count inside the 27 cm x 27 cm frame was on average 3.6 and 8.4 in restored plots and ambient vegetation, respectively (Table 3). In addition, some shoots of macrophyte species *Ruppia* sp. and *Stuckenia pectinata* were detected in some of the quadrats in restored plots. At Stora Fagerö*, Z. marina* shoot count was on average 4.6 and 9.6 in restored plots and ambient vegetation, respectively (Table 3). Additionally, between three and ten shoots of macrophyte species *Zannichellia major* and *Ruppia* sp. were observed in two of the quadrats in ambient vegetation.

Table 3. Sediment characteristics and *Z. marina* shoot count across three treatment categories (bare sediment, restored plots, ambient vegetation) from two study sites sampled in September 2024. Mean (±SE) sediment grain size (µm), organic matter content (%), *Z. marina* shoot count (n=4), and carbon content (%) (n=2).

Site & treatment category		**OM (%)**	**Grain size D50 (µm)**	**C content (%)**	**Shoot count**
Granö	bare sediment	0.86 ± 0.06	260.0 ± 30.4	0.40 ± 0.09	
	restored plots	0.88 ± 0.03	258.4 ± 15.6	0.37 ± 0.02	3.6 ± 0.5
	ambient veg.	0.95 ± 0.02	189.0 ± 17.2	0.30 ± 0.02	8.4 ± 0.8
Stora Fagerö	bare sediment	0.65 ± 0.03	430.0 ± 28.6	0.28 ± 0.06	
	restored plots	0.76 ± 0.03	402.2 ± 49.1	0.30	4.6 ± 0.5
	ambient veg.	0.68 ± 0.02	426.6 ± 44.1	0.26 ± 0.02	9.6 ± 0.7

Sediment grain size was significantly different between the two study sites (two-way ANOVA: df=1, F= 25.50, p<0.001). Grain size was significantly larger at Stora Fagerö in comparison to Granö (Tukey-test: p<0.001) (Fig. 4A). No significant interaction or significant effect of treatment category was detected. There was also a significant difference in sediment organic matter content between the study sites (two-way ANOVA: df=1, F= 29.42, p>0.001). Organic matter content was significantly higher at Granö (Tukey-test: p<0.001) (Fig. 4B).

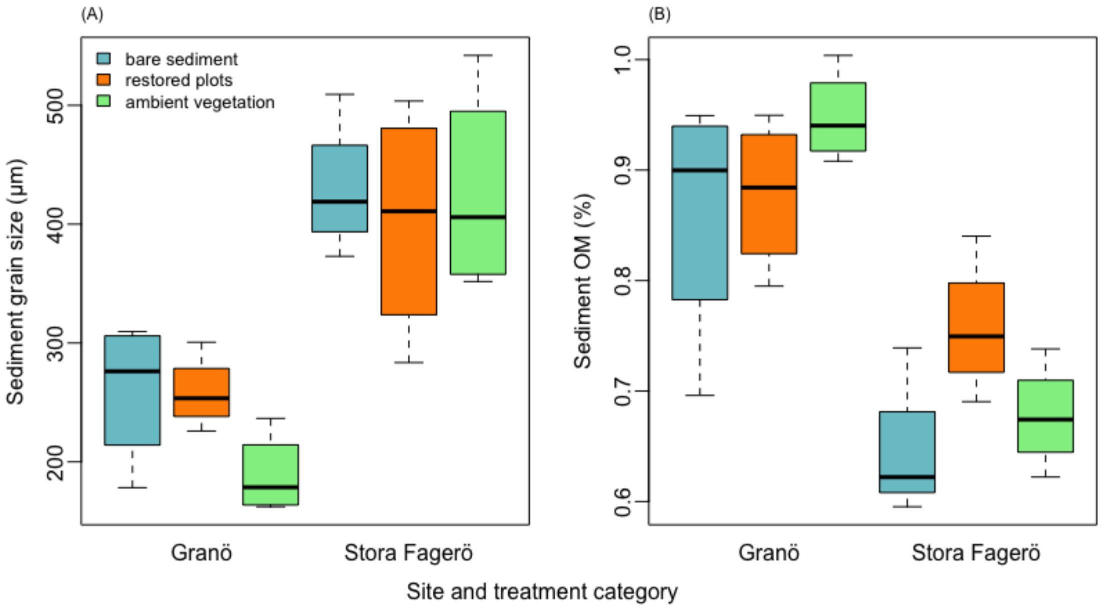

Figure 4. (A) Boxplot showing the distribution of sediment grain size (µm) and (B) sediment organic matter content (%) across the three different treatment categories at two sites, Granö and Stora Fagerö (n=4). The lower edge of each box indicates the first quartile, the top edge shows the third quartile, and the black line inside the box represents the median. The whiskers represent the minimum and maximum values.

3.3 Macrofaunal communities

In total, 13 different species or taxonomic groups were observed in the benthic fauna samples from the two study sites. All 13 species or taxonomic groups were found at Stora Fagerö, and 12 of these species were found at Granö (see Appendix 1). On average, species richness varied from 8.3 to 8.8 in different treatment categories at Granö, and from 9.5 to 9.8 at Stora Fagerö (Table 4). Total infauna abundance at Granö was the highest in restored plots with a density of 24 404 ind. m^{-2}, followed by ambient vegetation with 22 753 ind. m^{-2}, and bare sediment with 17 252 ind. m^{-2}. At Stora Fagerö, the highest total abundance was observed in ambient vegetation with 40 476 ind. m^{-2}, followed by restored plots with 28 727 ind. m^{-2}, and the lowest abundance was observed in bare sediment with 23 893 ind. m^{-2} (Table 4, Fig. 5). Mean total biomass was generally lower at Granö in comparison to Stora Fagerö and ranged, on average, from 89.68 g m^{-2} in bare sediment to 318.81 g m^{-2} in ambient vegetation at Granö. In contrast, densities from 358.75 g m^{-2} in ambient vegetation to 535.55 g m^{-2} in restored plots were noted at Stora Fagerö (Table 4, Fig. 5). Shannon diversity index ($H'_{\ln}$) of macrofauna communities ranged from 0.95 in restored plots to 1.22 in bare sediment, and from 1.31 in ambient vegetation to 1.45 in bare sediment, at Granö and Stora Fagerö, respectively. It is also worthwhile to mention that one individual of the invasive Harris mud crab

Rhithropanopeus harrisii was observed while sampling in one of the restored plots at Stora Fagerö, but it was not recorded in any of the samples.

Table 4. Mean (±SE) species richness (n), total abundance (ind. m^{-2}), total biomass wwt (g m^{-2}), and Shannon diversity index of macrofauna communities across three different treatment categories (bare sediment, restored plots, ambient vegetation) at two sites, Granö and Stora Fagerö (n=4).

Site & treatment category		**Richness (n)**	**Abundance (ind. m^{-2})**	**Biomass wwt (g m^{-2})**	**Shannon diversity index**
Granö	bare sediment	8.8 ± 0.8	17 252 ± 2 467	89.68 ± 14.13	1.22 ± 0.15
	restored plots	8.3 ± 0.5	24 404 ± 3 786	152.17 ± 28.60	0.95 ± 0.09
	ambient veg.	8.5 ± 0.3	22 753 ± 2 265	318.81 ± 118.27	1.19 ± 0.18
Stora Fagerö	bare sediment	9.8 ± 0.4	23 893 ± 4 338	370.24 ± 106.64	1.45 ± 0.06
	restored plots	9.8 ± 0.9	28 727 ± 1 567	535.55 ± 213.31	1.42 ± 0.14
	ambient veg.	9.5 ± 0.9	40 476 ± 4 521	358.75 ± 67.88	1.31 ± 0.10

Benthic infauna communities differed significantly between sites in terms of abundance, biomass, and Shannon diversity index (PERMANOVA, abundance: df=1, F=12.24, p=0.004; biomass: df=1, F=6.48, p=0.017; Shannon diversity index: df=1, F= 6.86, p=0.024). Total abundance, total biomass, and Shannon diversity index were all found to be significantly higher at Stora Fagerö than in Granö (Fig. 5B, C, D). Moreover, a significant difference was detected in benthic infauna abundance between treatment categories (PERMANOVA, df=2, F=5.45, p=0.019). Abundance was significantly higher in ambient vegetation compared to bare sediment (PERMANOVA: df=1, F=5.17, p=0.033). Species richness was generally slightly higher at Stora Fagerö than Granö, however no statistically significant difference was observed in species richness neither between sites nor treatment categories (Fig. 5A, see Appendices 2 & 3). No significant interaction of treatment category and site was detected for any of the measured community metrics.

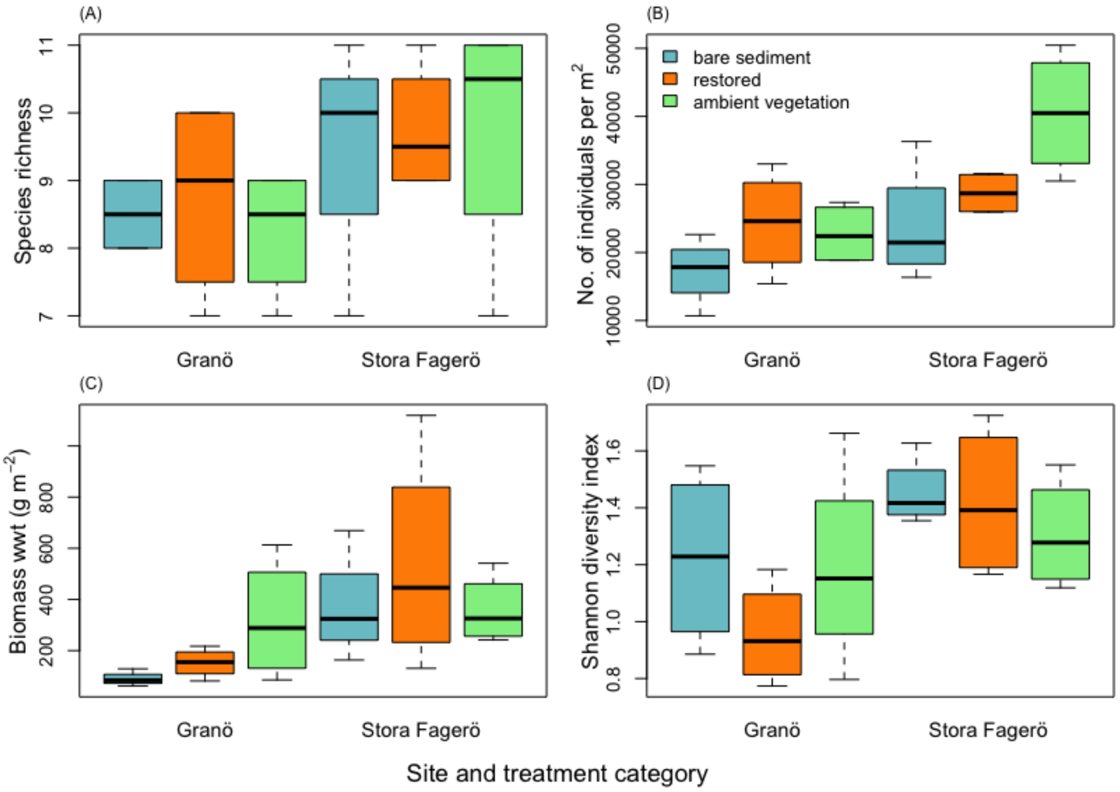

Figure 5. Boxplot showing the distribution of (A) species richness, (B) abundance (ind. m^{-2}), (C) biomass wwt (g m^{-2}), and (D) Shannon diversity index values across three different treatment categories at two sites, Granö and Stora Fagerö (n=4). The lower edge of each box indicates the first quartile, the top edge shows the third quartile and the black line inside the box represents the median. The whiskers represent the minimum and maximum values.

In terms of abundance, Hydrobiidae was the most dominant taxonomic group contributing with at least 49 % to the total abundance in the macrofauna communities in all treatment categories at both sites (Fig. 6A, B). At Stora Fagerö, Oligochaeta was the second most dominant taxonomic group in all treatment categories representing between 16.67 % and 25.24 % of the macrofaunal community, whereas at Granö, its relative abundance was notably lower (between 2.31 % and 5.33 %). *M. balthica* was the most abundant bivalve species in all treatment categories across both sites, representing between 6.98 % (ambient vegetation at Stora Fagerö) and 13.24 % (bare sediment at Granö) of the total abundance of the macrofaunal community.

Macrofauna community biomass was dominated by *M. balthica* in all treatment categories at both sites (representing on average over 43 % of the community biomass) (Fig. 6C, D). At Granö, other taxonomic groups, each representing over 5 % of the community biomass included Hydrobiidae (13.09-18.54 %) and *Marenzelleria* spp. (6.16-10.11 %) in all treatment categories, and *C. glaucum* (28.52 %) and *H. diversicolor*

(10.29 %) in ambient vegetation, and *M. arenaria* (7.35 %) in the bare sediment. At Stora Fagerö, other dominant taxonomic groups included *M. arenaria* (15.98-32.71 %) and Hydrobiidae (10.72-14.74 %) in all treatment categories, *C. glaucum* (6.63-7.51 %) in bare sediment and restored plots, and *H. diversicolor* (5.86 %) in ambient vegetation.

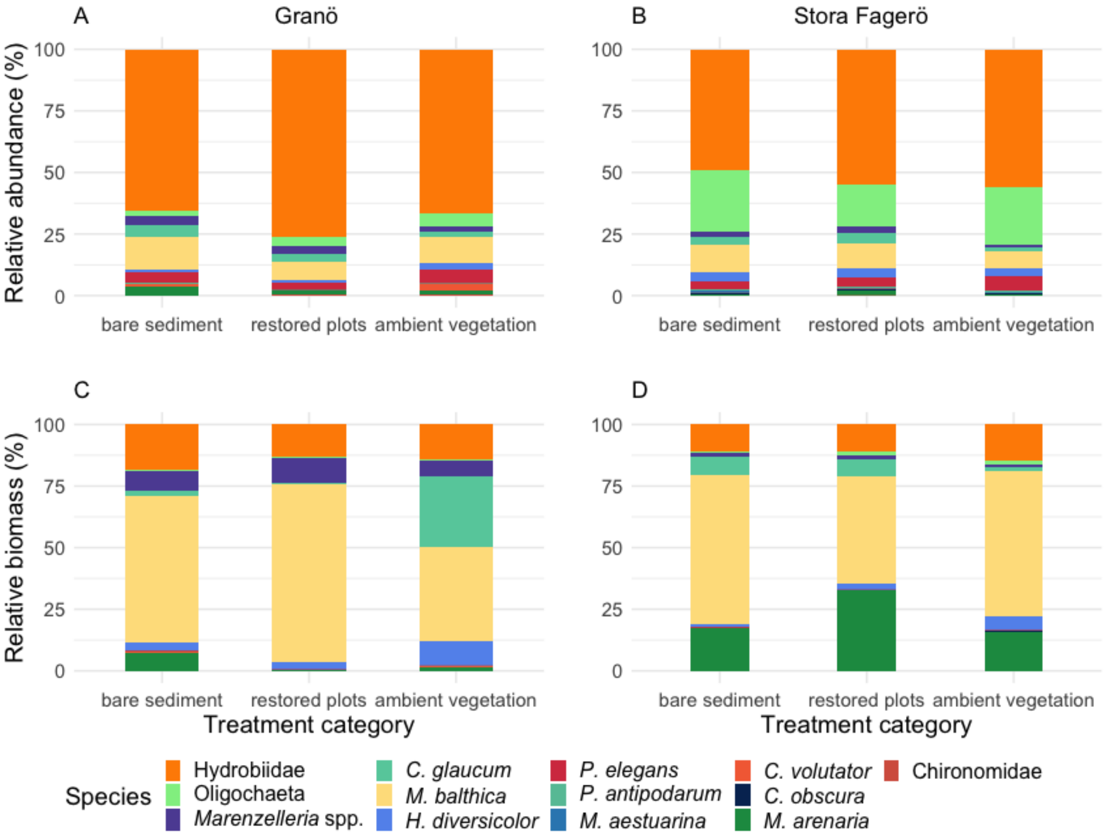

Figure 6. Relative abundances (A, B) and biomasses (C, D) of recorded species at Granö (left panel) and Stora Fagerö (right panel). Bars show the averaged proportion of each species from samples in three treatment categories across the two sites and add up to 100 %.

The benthic infauna community composition was different between the study sites and between treatment categories based on species abundances (PERMANOVA, sites: df=1, F= 8.38, p= 0.001, Fig. 7A; treatment categories: df=1, F= 2.54, p= 0.044, Fig. 7B). Although infaunal communities in different treatment categories across the study sites showed a high overlap, post hoc pairwise comparison revealed a significant difference in infauna community composition between bare sediment and ambient vegetation (PERMANOVA, df=1, F= 3.45, p= 0.03). No significant interaction effect of site and treatment category was observed (see Appendix 4 & 5). Moreover, the infaunal community composition based on abundance data overlapped across treatment categories at both sites (Fig. 7C, D). Infaunal taxonomic community composition also differed significantly between the two study sites based on species biomass (PERMANOVA, df=1, F= 6.91, p=0.002). Overall, treatment category did not have a significant effect on species biomass composition, and no significant interaction of treatment category and site was detected. There was relatively high overlap in infauna communities based on species biomass across treatment categories at both sites (Appendix 6).

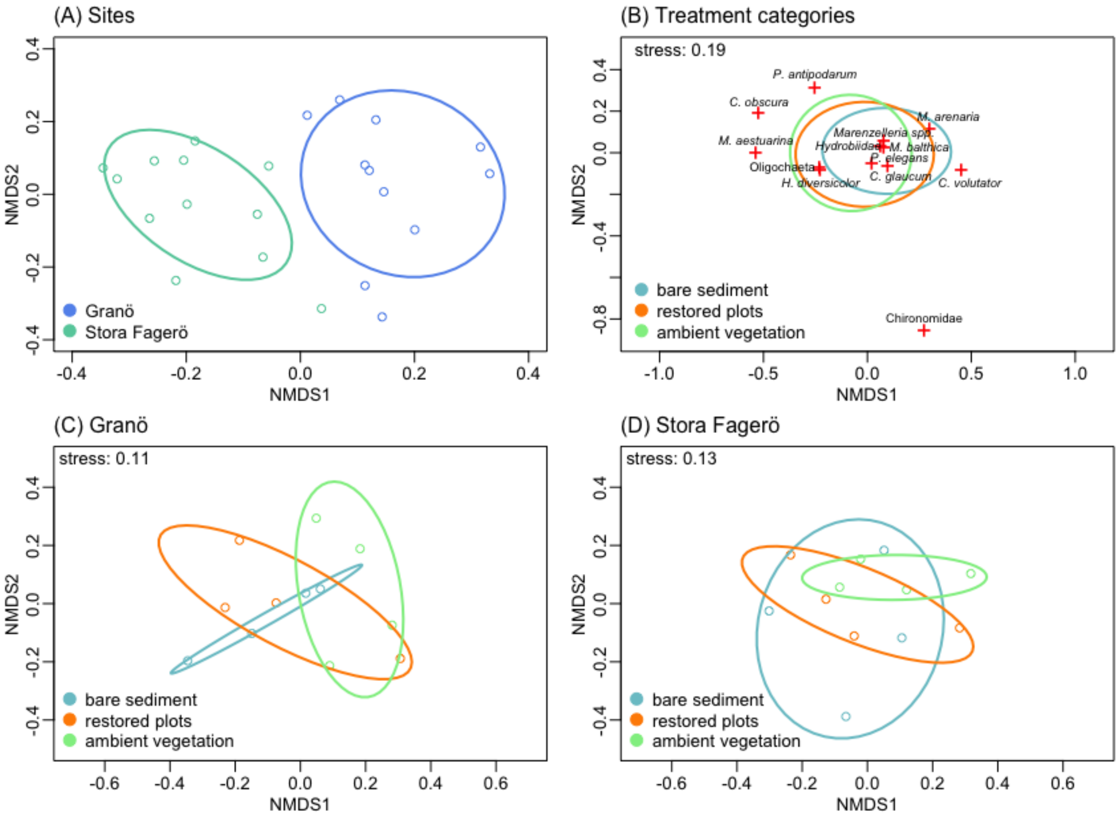

Figure 7. NMDS of the community composition based on species abundance for (A) samples at different sites (B) different treatment categories, the community composition in different treatment categories in (C) Granö and (D) Stora Fagerö. Infaunal species are represented by red crosses, and coloured points represent collected samples, and the corresponding coloured ellipses indicate the ordination confidence interval (60 %) and represent the sampling sites (A) and treatment categories (B, C, D).

Benthic infauna communities showed slightly variable similarities within treatment categories, and dissimilarities between treatment categories (Table 5). At Granö, infaunal communities in restored plots showed the highest similarities based on abundance, followed by the communities in bare sediment and ambient vegetation, with very little differences observed in these values. Based on biomass, the similarities within groups were relatively similar in bare sediment and restored plots, whereas in ambient vegetation it was notably lower. The highest dissimilarities between treatment categories at Granö was observed between bare sediment and restored plots (27.67 %), and bare sediment and ambient vegetation (58.33 %), based on abundance and biomass, respectively. However, the dissimilarity between bare sediment and ambient vegetation was almost the same as between bare sediment and restored plots, based on abundance. Based on abundance, Hydrobiidae contributed the most to the dissimilarities between all groups, with other important species contributors including *M. balthica*, Oligochaeta, and *P. elegans*. In comparison, three most contributing species or taxonomic groups to dissimilarities between ambient vegetation and bare sediment, as well as ambient vegetation and restored plots based on biomass were *C. glaucum, M. balthica, H. diversicolor*, while *M. balthica, M. arenaria, Marenzelleria* spp. contributed the most to the dissimilarities between bare sediment and restored plots.

Infaunal communities at Stora Fagerö showed relatively consistent similarities within groups based on abundance, with the highest similarity observed in ambient vegetation, followed by restored plots and bare sediment. Lower similarities were observed within groups based on biomass, with bare sediment showing the highest similarity, followed by ambient vegetation and restored plots. Dissimilarities between groups were higher based on biomass than based on abundance. At Stora Fagerö, bare sediment and ambient vegetation showed the highest dissimilarity between each other based on abundance (33.41 %), while the least similar treatment categories based on biomass were restored plots and ambient vegetation (48.80 %). The most important taxonomic group contributing to the dissimilarities between all treatment categories based on abundance was Hydrobiidae, followed by Oligochaeta, whereas the three most important species contributing to the dissimilarities between all treatment categories based on biomass were *M. arenaria, M. balthica* and *C. glaucum.*

Table 5. Summary of SIMPER analysis comparing the percentage similarity within infauna communities in different treatment category groups, and dissimilarity between communities in different groups, as well as three species that contribute the most to the differences between groups based on abundance and biomass.

Site/Treatment category	**Abundance**	**Biomass**
Granö	**Similarity %**	
bare sediment	73.06	73.51
restored plots	75.25	71.29
ambient vegetation	71.48	41.21
	Dissimilarity %	
bare sediment - restored plots	27.67	36.00
bare sediment - ambient vegetation	27.64	58.33
restored plots - ambient vegetation	24.63	49.34
	Species contributing to dissimilarities	
bare sediment - restored plots	Hydrobiidae, *M. balthica*, Oligochaeta	*M. balthica, M. arenaria, Marenzelleria* spp.
bare sediment - ambient vegetation	Hydrobiidae, *P. elegans,* Oligochaeta	*C. glaucum, M. balthica, H. diversicolor*
restored plots - ambient vegetation	Hydrobiidae, Oligochaeta, *P. elegans*	*C. glaucum, M. balthica, H. diversicolor*
Stora Fagerö	**Similarity %**	
bare sediment	73.33	62.08
restored plots	75.18	36.83
ambient vegetation	77.93	58.05
	Dissimilarity %	
bare sediment - restored plots	25.33	48.10
bare sediment - ambient vegetation	33.41	37.12
restored plots - ambient vegetation	26.16	48.80
	Species contributing to dissimilarities	
bare sediment - restored plots	Hydrobiidae, Oligochaeta, *M. balthica*	*M. arenaria, M. balthica, C. glaucum*
bare sediment - ambient vegetation	Hydrobiidae, Oligochaeta, *P. elegans*	*M. arenaria, M. balthica, C. glaucum*
restored plots - ambient vegetation	Hydrobiidae, Oligochaeta, *M. balthica*	*M. arenaria, M. balthica, C. glaucum*

3.4 Bivalve size structure

Overall bivalve size distribution did not differ significantly (bare sediment vs. restored plots: D = 0.12, p-value = 0.130; bare sediment vs. ambient meadow: D = 0.09, p-value = 0.376; restored plots vs. ambient meadow: D = 0.10, p-value = 0.270) between treatment categories across sites. Significant differences were however, detected in bivalve size frequency distributions between treatment categories at Stora Fagerö. Bivalve size structure in bare sediment differed significantly from restored plots (Kolmogorov-Smirnov: D= 0.224, p-value = 0.014) and from ambient vegetation (Kolmogorov-Smirnov: D= 0.210, p-value = 0.046). The proportion of juveniles (< 5mm) at Stora Fagerö were 65.6 %, 81.9 % and 68.8 % in bare sediment, restored plots and ambient vegetation, respectively. No differences in bivalve size frequency distributions were observed between treatment categories at Granö, however the proportion of juvenile *versus* adult bivalves in all treatment categories was at least 82 % (Fig. 8).

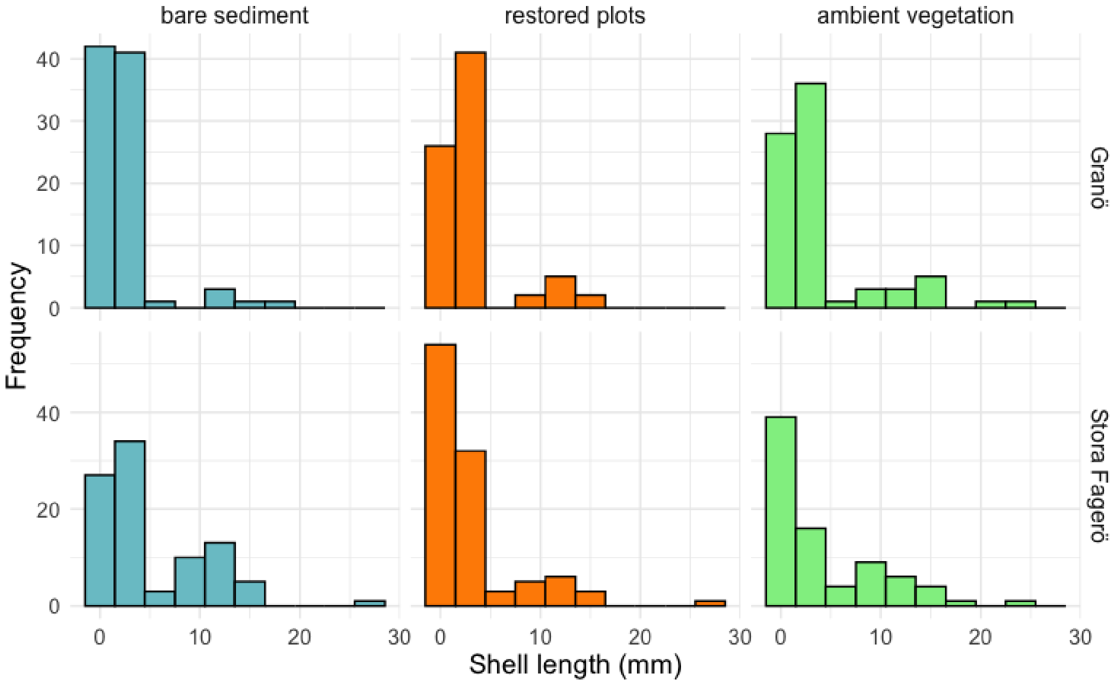

Figure 8. Bivalve (*M. balthica, M. arenaria* and *C. glaucum*) length (mm) distribution histograms for different treatment categories across two study sites, Granö (top panel) and Stora Fagerö (bottom panel). Lengths over 30 mm were treated as outliers and were excluded from this figure for better readability of the figure.

4 Discussion

In seagrass restoration projects it is essential to monitor the recovery of associated fauna and ecosystem functionality to determine the success and feasibility of a restoration project. This master's thesis project investigated the structure of infaunal communities in restored *Z. marina* plots and compared it to those in bare sediment and ambient *Z. marina* meadows to assess the recovery process of associated biodiversity. In addition, the variability in sediment properties was explored. Differences were observed in infaunal assemblages and community metrics, as well as sediment characteristics, between sites and treatment categories, thus these results provide insights into the recovery process of seagrass ecosystems.

4.1 Eelgrass survival

The number of *Z. marina* shoots was significantly lower in restored plots in comparison to reference *Z. marina* meadows, indicating that eelgrass has not yet recovered to levels that may be expected at both sites. Moreover, monitoring of eelgrass from the restored plots has revealed that despite showing signs of establishment after the first growing season, both sites showed remarkable declines in eelgrass survival after the second growing season (Tolonen et al., 2024). The importance of eelgrass shoot density on faunal recruitment has been demonstrated before (Boström & Bonsdorff, 2000), thus the weak recovery of eelgrass is likely reflected in the recovery of faunal assemblages. Gagnon et al. (2023) observed an increase in eelgrass shoot density and biomass in restored eelgrass plots after two growing seasons. However, they also reported a twofold difference in eelgrass biomass within the reference eelgrass meadow between two study years, which reflects the influence of environmental conditions, such as light availability or temperature on seagrass growth, and highlights the natural variability of seagrass ecosystems. A previous study has also suggested that in areas where eelgrass meadows have disappeared and have no longer stabilised sediments, wind-driven resuspension of sediments has resulted in deteriorated light conditions. Together with disturbance from drifting algal mats, this prevents both the natural recovery and restoration of eelgrass (Moksnes et al., 2018). Water turbidity and increase in filamentous algae have been reported to be major threats for eelgrass meadows in Finnish coastal areas (Gustafsson & Boström, 2014; Kontula & Raunio, 2018), and some filamentous algae was also noted among eelgrass at both sites while sampling in this study. The water temperatures at the study sites were notably higher in the second growing season than in the first growing season at both sites (Table 2), which demonstrates the high temporal variability of environmental conditions. The number of days when the water temperature exceeded 20 °C during the monitoring period in 2023 was 1 and 3 in Granö and Stora Fagerö, respectively, while in 2024 they were 21 and 18, respectively (Tolonen et al., 2024). Furthermore, temperatures above this value have been reported to be unfavourable for eelgrass growth and survival (Nejrup & Pedresen, 2008). However, Tolonen et al. (2024)

suggest that the higher water temperatures in 2024 in contrast to 2023 do not alone explain the observed declines in eelgrass survival, as declines had already been observed to some extent in spring 2024.

4.2 Sediment characteristics

Significant differences were observed in sediment properties between the two study sites, as hypothesised, with significantly smaller grain size and higher organic matter content found in Granö. While local circumstances, such as hydrodynamic conditions (e.g wave exposure) and sediment composition, influence the belowground structure of these habitats, eelgrass beds are known to modify bottom sediment through direct particle trapping and reduced wave attenuation (Reidenbach & Thomas, 2018; Widdows et al., 2008). van Katwijk et al. (2010) found that dense seagrass meadows accumulate more fine sediments and organic matter than sparse vegetation or adjacent bare sediments, which supports some of the findings of this study. While the differences in sediment grain size between treatment categories were less pronounced in Stora Fagerö, notably finer sediment size was observed in ambient vegetation compared to restored plots and bare sediment in Granö. Furthermore, sediment organic matter content in Granö was higher in ambient *Z. marina* meadow than in bare sediment and restored plots. These results were consistent with a previous study by Greiner et al. 2013, where higher organic matter content was observed in 10-year seagrass meadows relative to 4-year meadows and bare sediment. Sediment OM content has also been documented to recover already after one or two years post-restoration (McGlathery et al., 2012). In contrast, sediment carbon content in Granö was the highest in bare sediment, followed by restored plots and ambient meadow, which are contrary to the results documented by Tanner et al. (2021). The results from this study showed that in Granö, the sediment properties in restored eelgrass plots are more similar to those in bare sediment than ambient eelgrass meadow after two growing seasons, reflecting the potentially longer recovery time of sediment properties. Furthermore, the overall differences in sediment properties were not statistically significant between any treatment categories, suggesting that the effect of *Z. marina* vegetation on sediment is less pronounced at these study sites. Recovery of some faunal metrics and sediment properties, such as grain size, in a restored seagrass meadow have been reported to take 4-6 years (Tanner et al., 2021). Although the sediment analyses were conducted from the top 1 cm sediment layer, it was observed that deeper sediment layers at Granö were dense clay. Pajusalu et al., (2023) also point out, that prevailing sediment type and its mobility in the area are key factors influencing the success of eelgrass restoration. Furthermore, benthic fauna habitat preferences have been shown to be strongly affected by sediment type (Rousi et al., 2011), thus the differences in faunal metrics and communities between the two study sites in this study could partly be explained by this.

4.3 Macrofaunal communities and their recovery

The benthic fauna communities differed significantly between sites and between some treatment categories, as was hypothesised. Generally, higher species richness and significantly higher abundance, biomass and diversity were observed at Stora Fagerö, indicating that local conditions there could be more favourable for faunal establishment and recovery. Furthermore, lower community metrics observed at Granö, where organic matter content was higher and sediment grain size smaller, emphasizes the role of sediment composition in shaping benthic community structure. In addition, eelgrass shoot count was slightly higher in restored eelgrass plots and in the ambient eelgrass meadow at Stora Fagerö compared to Granö. At both sites, total faunal abundance was higher in restored *Z. marina* plots and natural meadows than in bare sediment, supporting my hypothesis and adding to increasing knowledge about the critical role of seagrass habitats in enhancing associated biodiversity specifically in the northern Baltic Sea (Boström & Bonsdorff, 1997; Fredriksen et al., 2010; Rodil et al., 2021; York et al., 2018).

Overall, a significantly higher abundance was observed in ambient *Z. marina* meadows than in bare sediment, although at Granö, the total abundance in restored plots was higher than in ambient meadow. The abundances observed in ambient meadows were similar to the values observed by Boström & Bonsdorff (1997), but slightly higher abundances were observed in bare sediment compared to their results. However, the faunal communities showed less variation in total abundance across different treatment categories at Granö (17 252-24 404 ind. m^{-2}) than at Stora Fagerö (23 893-40 476 ind. m^{-2}). The ambient meadow at Granö was located closer to the restored plots than at Stora Fagerö, potentially allowing faster colonization of fauna from the ambient meadow that could have acted as a source population for some species. In terms of abundance, faunal communities were dominated by gastropods from the family Hydrobiidae in all treatment categories at both sites, which is consistent with findings from Boström & Bonsdorff (1997), who found that Hydrobiidae was the most abundant taxon in *Z. marina* beds and bare sand. In addition to this, the second most abundant taxonomic group found in their study was Oligochaeta, which was also the case at Stora Fagerö, but not at Granö. These species also contributed the most to the dissimilarities in community composition between treatment categories based on abundance.

The opportunistic nature of these species has been highlighted in previous studies and is considered central in the facilitation of the early stages in recovery and succession of soft sediment habitats (Maximov & Berezina, 2023; Norkko et al., 2000; Norkko et al., 2006). Furthermore, recovery of soft sediment habitats in the Baltic Sea has been shown to follow a more deterministic pattern, with biological traits of individual species acting as important predictors of recovery potential (Gladstone-Gallagher, 2021). Infaunal density in restored eelgrass plots has been shown to be similar to natural reference meadows after two growing seasons (15 months), despite eelgrass density and biomass not having reached reference meadow conditions yet (Gagnon et al., 2023). Moreover, Tanner et al. (2021) documented a rapid faunal colonization with infaunal abundance reaching similar values to natural seagrass meadows after two years. They also found that habitat type did not affect species richness, which is consistent with results in this study, as no differences were observed in species richness between treatment categories at either of the study sites. While infaunal abundance was different between bare sediment and ambient meadows, total abundance in restored plots was not significantly different neither from ambient eelgrass meadows, nor bare sediment suggesting that the restored plots are showing strong signs of faunal recovery, but it is still ongoing. This is seen in the community metrics (abundance and biomass) that were higher than in bare sediment, but still lower than in ambient meadows. In contrast, diversity index values were the highest in bare sediment at both sites, while Boström & Bonsdorff (1997) recorded higher Shannon diversity in *Z. marina* associated infauna than in bare sand. However, the difference that they noted was not statistically significant, which is similar to the findings in this study.

In terms of total biomass, higher biomass was observed in ambient *Z. marina* meadow and in restored plots compared to bare sediment at Granö. Contradictory results were observed at Stora Fagerö, where the lowest total biomass was observed in ambient meadow, having a similar value as in bare sediment, while the highest total biomass was found in restored plots. All treatment categories at both sites were dominated by *Macoma* *balthica*, which was also the most abundant bivalve. *M. balthica* is an ecologically important species in the Baltic Sea tolerating a wide range of physical conditions with multiple factors influencing its recruitment, establishment and survival success (Bonsdorff et al., 1995). Furthermore, other bivalve species contributed notably to the total biomass, which is consistent from previous literature (Boström et al., 2001). For example, the relative biomass of *M. arenaria* was considerable in all treatment categories, especially in restored plots (>30%), at Stora Fagerö, and *C. glaucum* contributed considerably to the total biomass in ambient eelgrass meadows at Granö, despite their low abundances. This is explained by some large bivalve individuals' comparatively high contribution to the total biomass. Especially *M. arenaria* individuals, can grow relatively large, as was observed in this study, where the largest individual that was found had reached the shell length of 47 cm. Thus, the contribution of these species to community biomass in shallow coastal habitats can be substantial (Kube, 1996). The presence of single larger individuals also explains the high variability in similarities within and consequently high variability in dissimilarities between treatment categories that were obtained from the SIMPER analysis based on community biomass. All found bivalve species (*M. balthica, M. arenaria, C. glaucum*) were among the species that contributed most to those dissimilarities, further underlining this. These large, long-lived species have been present in the area prior to restoration efforts, and the sites have likely varied in the pre-existing faunal communities prior to restoration, which is reflected in the differences in the bare sediment communities at both sites. On the other hand, the bivalve size frequency distribution at Stora Fagerö showed that *Z. marina* vegetation has a significant influence on the size structure of bivalves, with higher proportion of juveniles present in restored plots and ambient meadow in comparison to bare sediment. While this was not observed in Granö, the proportion of juvenile bivalves in all treatment categories was high. Boström & Bonsdorff (1997) noticed no difference in juvenile *M. balthica* recruitment pattern between eelgrass habitats and bare sand. Moreover, Boström et al. (2002) also found that vegetation cover had no effect on juvenile *M. balthica* numbers. They also suggested that the vegetation cover of *Z. marina* reduced the predation effect on infauna, which also implies that larger bivalve individuals are also more protected in vegetated habitats. The differences in species biomass between sites is also seen in the higher contribution of the invasive polychaete *Marenzelleria* spp. to the biomass at Granö compared to Stora Fagerö. Kauppi et al. (2015) found that environment type was an important environmental factor affecting *Marenzelleria* spp. abundance patterns, thus potentially influencing the species biomass too.

These observed differences in infaunal assemblages were further demonstrated in the variation in the community composition between sites and treatment categories based on both, abundance and biomass. Statistically significant differences between treatment categories were observed between ambient eelgrass meadow and bare sediment, supporting the abovementioned conclusions about the state of infaunal recovery in restored plots. SIMPER analysis also revealed that based on abundance, the infaunal communities in restored *Z. marina* plots at Granö are more similar to the communities in ambient *Z. marina* meadows than bare sediment, while at Stora Fagerö, the restored plot communities are only slightly more similar to bare sediment communities than to ambient meadow communities. Benthic community composition in restored seagrass meadows has been shown to resemble natural seagrass meadow community taxonomically and functionally within two years (Gagnon et al., 2023; Gräfnings et al., 2024). Such structural recovery pattern is supported by the results obtained in this study, as my findings indicate that the communities show signs of recovery, potentially reaching similar conditions to ambient eelgrass meadows in the future, as high faunal densities were observed in *Z. marina* habitats, both natural and restored. The potential slower recovery trajectory of infauna communities at these sites could be affected by multiple interacting factors such as eelgrass density and survival, elevated sea temperatures, presence of algal mats or differences in the relative dispersal capability of different life stages of the species involved (Norkko et al., 2000; Whitlatch et al., 1998).

This small-scale project was limited to two sites, but a larger scale study could provide better insights from recovery patterns across spatial scales. Further monitoring of the communities in restored eelgrass plots could provide a better understanding of the recovery trajectory of faunal assemblages followed by eelgrass restoration by shoot transplantation, while also broadening our knowledge of the expected outcomes of such restoration efforts, and their implications for Baltic Sea biodiversity. In addition, epifaunal communities should be considered in future studies to enhance the knowledge of the overall eelgrass associated invertebrate communities. Even if diverse communities are observed in bare sand habitats, the species associated with the aboveground seagrass structure increase the overall diversity in vegetated habitats and have also been shown to recover rapidly (McSkimming et al., 2016). While quantifying taxonomic diversity provides us a better understanding of the communities present in these key habitats, measuring functional diversity would increase our knowledge of the spatial differences in the ecosystem functioning, as differing communities were observed at different sites. In a broader context, these results are also linked to ecosystem functioning and thus, ecosystem services provided by eelgrass ecosystems in the Baltic Sea. These findings show that *Z. marina* habitats, both natural and restored, host high densities of infauna which is also relevant for a seagrass conservation perspective and highlights the need to conserve and protect the existing meadows through decision-making, while implementing effective restoration measures. Moreover, the results from this study could be utilised in future assessments when selecting sites for restoration efforts of eelgrass. Demonstrating the recovery of biodiversity and ecosystem functioning is also essential for maintaining support and funding for future restoration projects, as well as for establishing effective criteria for seagrass restoration.

5 Conclusions

In order to understand the potential for enhancing local biodiversity through seagrass restoration, we need to study and monitor the communities that are associated with the restored habitats. Despite *Z. marina* showing signs of establishment after the first growing season, the remarkable declines in eelgrass survival after the second growing season indicated that eelgrass had not yet successfully recovered at the restored plots at our study sites. However, this study shows that *Z. marina* habitats are important habitats for abundant and diverse benthic infauna communities, with communities in restored plots exhibiting signs of recovery when compared to bare sediment and ambient eelgrass meadows. Sediment properties were not significantly impacted by the presence of eelgrass. However, significant differences observed in sediment characteristics and infauna community structure and composition between the two study sites highlight the importance of local context in shaping the benthic infauna communities associated with eelgrass meadows. These findings contribute to the understanding of the role of restored seagrass habitats in facilitating the recovery trajectories of associated biodiversity and provide an assessment of the restoration success of the restoration plots and infaunal recovery at the studied sites. Further studies are needed to gain a deeper understanding of the context-dependency of faunal recovery following seagrass restoration and to improve our knowledge of the temporal dynamics of such recovery trajectories.

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Appendices

APPENDIX 1

Presence-absence table of the found species across three different treatment categories at the two study sites, Granö and Stora Fagerö.

Species	**Granö**			**Stora Fagerö**		
	bare sediment	restored plots	ambient vegetation	bare sediment	restored plots	ambient vegetation
Cerastoderma glaucum	x	x	x	x	x	x
Chironomidae		x	x	x		
Corophium volutator	x	x	x	x	x	
Cyanophthalma obscura		x		x	x	x
Hediste diversicolor	x	x	x	x	x	x
Hydrobiidae	x	x	x	x	x	x
Macoma balthica	x	x	x	x	x	x
Manayunkia aestuarina				x	x	x
Marenzelleria spp.	x	x	x	x	x	x
Mya arenaria	x	x	x	x	x	x
Oligochaeta	x	x	x	x	x	x
Potamopyrgus antipodarum	x	x	x	x	x	x
Pygospio elegans	x	x	x	x	x	x

APPENDIX 2

Global two-way PERMANOVA test results to investigate differences in benthic macrofauna community metrics between study sites and treatment categories and their interaction. Bolded p-values indicate a significant difference.

Community metrics	**Comparison between sites**			**Comparison between treatment categories**			**Interaction: site * treatment category**		
	df	**F**	**p-value**	**df**	**F**	**p-value**	**df**	**F**	**p-value**
Species richness	1	4.45	0.063	2	0.09	0.912	2	0.09	0.892
Abundance	1	12.24	**0.004**	2	5.45	**0.019**	2	2.29	0.114
Biomass	1	6.48	**0.017**	2	0.65	0.560	2	1.22	0.351
Shannon diversity index	1	6.86	**0.024**	2	0.73	0.475	2	0.98	0.395

APPENDIX 3

Post hoc pairwise PERMANOVA test results to investigate differences in benthic macrofauna community metrics between study sites and treatment categories. Bolded p-values indicate a significant difference in the community metrics between the compared groups after correction with Holm-Bonferroni method.

Community metrics	**comparison**	**df**	**F**	**p-value**
Abundance	restored plots vs. bare sediment	1	3.21	0.088
	restored plots vs. ambient veg.	1	1.22	0.270
	bare sediment vs. ambient veg.	1	5.17	**0.038**
	Granö vs. Stora Fagerö	1	8.04	**0.012**
Biomass	Granö vs. Stora Fagerö	1	6.56	**0.012**
Shannon diversity index	Granö vs. Stora Fagerö	1	7.05	**0.018**

APPENDIX 4

Global PERMANOVA test results to investigate differences in benthic macrofauna community composition based on species abundance and biomass between study sites and treatment categories. Bolded p-values indicate a significant difference.

Community metrics	**Comparison between sites**			**Comparison between treatment categories**			**Interaction: site * treatment category**		
	df	**F**	**p-value**	**df**	**F**	**p-value**	**df**	**F**	**p-value**
Abundance	1	8.38	**0.001**	2	2.54	**0.044**	2	1.15	0.334
Biomass	1	6.91	**0.002**	2	1.16	0.332	2	1.71	0.124

APPENDIX 5

Post hoc pairwise PERMANOVA test results to investigate differences in benthic macrofauna community composition based on species abundance and biomass between study sites and treatment categories. Bolded p-values indicate a significant difference in the community metrics between the compared groups after correction with Holm-Bonferroni method.

Community metrics	**comparison**	**df**	**F**	**p-value**
Abundance	restoration vs. bare sediment	1	1.48	0.246
	restoration vs. ambient	1	0.68	0.573
	bare sediment vs. ambient	1	3.45	**0.03**
	Granö vs. Stora Fagerö	1	7.27	**0.002**
Biomass	Granö vs. Stora Fagerö	1	6.40	**0.002**

APPENDIX 6

NMDS of the community composition based on biomass ($\log_{10}(x + 1)$ transformation) for (A) samples at different sites (B) different treatment categories, the community composition in different treatment categories in (C) Granö and (D) Stora Fagerö. Infaunal species are represented by red crosses, and coloured points represent collected samples, and the corresponding coloured ellipses indicate the ordination confidence interval (60 %) and represent the sampling sites (A) and treatment categories (B, C, D).