

Comparison of in- and epifauna communities two years after the seagrass transplantation in Maasholm

Was the seagrass restoration successful?

Bachelor's Thesis Jana Schuster September 1, 2023 Comparison of in- and epifauna communities two years after the seagrass transplantation in Maasholm

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Abstract

Seagrass meadows provide important ecosystem services and are known to be an essential habitat for many species. They mainly grow in coastal areas worldwide with *Zostera marina* being the primary seagrass species found from the temperate zones to the arctic circle. Seagrass species show relatively little biodiversity and populations have declined severely over the last decade. In order to prevent the marine flowering plant from declining further and species getting critically endangered, restoration trials were conducted in many countries. In Germany, the SeaStore project was the first seagrass transplanting attempt. In 2021, Seagrass shoots were planted at two sites in which seagrass vanished either in a high amount or entirely. Furthermore, many studies from participating institutions were conducted, surveying different parameters of the restored site, such as carbon content and biodiversity. This Bachelor's Thesis is researching the faunal biodiversity of the restored *Zostera marina* meadow in Maasholm and comparing it to a natural seagrass bed in Kiel. Samples of the below and above ground biomass were taken in order to investigate the diversity of epi- and infauna species. The infauna diversity was additionally surveyed on bare sediment near the restored site. The statistical analysis was then carried out with different indices measuring the biodiversity, species abundance and community compositions of all treatments. The results confirmed a rapid recovery process for both habitat types with almost all measurements of the infauna community showcasing visible differences from the species found at bare sediment. Due to the discovered high abundances of some species, it can be assumed that the epifauna community is recovering faster. This Thesis represents an inventory of one time point showing a positive recovering process of the faunal communities in the seagrass meadow in Maasholm.

1 Introduction

1.1 Seagrass evolution

The first angiosperms started colonizing marine habitats over a 100 million years ago (Den Hartog, 1970). Nowadays, a small number of 30 seed plants can be found in marine coastal areas, with seagrass being the most common species (Van der Hage, 1996) Seagrass is part of the group of marine flowering plants, which comprises fewer than two percent of the entire clade Angiospermae (Hemminga & Duarte 2000). It adapted to the marine environment in many ways, such as above ground biomass adaptions to high energy habitats and its below ground biomass receiving the required oxygen amount from relatively anoxic sediments (Hemminga & Duarte 2000). Furthermore, the asexual reproduction of seagrass is carried out with dispersing water pollination, revealing a distinguishingly different morphology from terrestrial flora (McConchie & Knox 1989). It has been suggested that the evolution of seagrass species diversity was restricted due to the limitations in dispersal of hydrophilous pollination (van der Hage, 1996), although some species show the ability for wider seed dispersal (Waycott et al. 2006), and the lack of allopatric speciation in coastal areas (Ackermann 1998). Around 50 species are allocated to the 12 genera, with most species found within Zostera, Posidonia and Halophila (Hemminga, & Duarte 2000). At first, all genera were separated into two families (Ascherson and Gräbner 1968), whereas modern approaches divided seagrass into six families, Zannichelliaceae, Zosteraceae, Cymodoceaceae, Ruppiaceae, Posidoniaceae, Hydrocharitaceae. However, the classification of seagrass is still in a variable process (Waycott et al. 2006). The eelgrass *Zostera marina* (L.) forms wide ranging meadows and shows rapid growth rates in short periods of higher sea temperature levels without directly depending on the sediment composition. Its main morphological features are the maximum shoot length of 1.50m, the obtuse leaf tips and the wide leaf widths (den Hartog, 1970).

1.2 Appearance of seagrass

Seagrass meadows are ecosystems that can be found at a depth ranging from 0-30m in coastal water across the globe, excluding antarctica (den Hartog, 1970). Out of all 12 genera, 7 occurred along the shores of tropical regions. The other 5 inhabit temperate oceans with *Zostera* and *Posidonia* demonstrating a bipolar distribution along the north and south of the tropical oceans. The eelgrass species *Zostera marina* (L.) dominates all seas within the northern temperate zone, along with the Baltic Sea, and can uniquely colonize areas that extend the arctic circle (den Hartog, 1970). Today, the maximum growth depth is 8m along the German coastline of the Baltic Sea and the eelgrass covers around 36% of the total area within the depth zone 0-8m (Schubert et al. 2015).

The Baltic Sea, which expands from 54° to almost 66°, consists of brackish water ranging from 2psu in the north of the Gulf of Bothnia to 20psu underneath the deepwater halocline (Elmgren 2001). The low salinity results in a lower biodiversity, including freshwater species as well as specialists for brackish water, leading to a higher susceptibility to ecosystem changes (Elmgren et al. 1984).

Zostera marina covers an area of 140,5km² along the western shores and therefore represents a total of 11.5% of all the acknowledged seagrass meadows in the Baltic Sea (Schubert et. al 2015).

1.3 Importance of seagrass

Seagrass forms key habitats by providing many important functions for faunal communities as well as ecosystem services (Hemminga & Duarte 2000; Short et al. 2000). Their value, in combination with algae beds, was estimated to be US\$3.8 trillion per year making seagrass beds one of the most valuable marine ecosystems existing (Costanza et al. 1997). Due to slow decomposition rates, as well as low nutrient and oxygen concentrations, seagrass sediments are able to store high amounts of carbon (Duarte et al. 2013). Carbon comes mainly from metabolism processes like photosynthesis carried out by seagrass itself and epiphyte algae, which is a vital component of the ecosystem (McRoy & McMillan 1977). In Germany alone, seagrass meadows are withholding 8.14Mt of prospective $CO₂$ emissions (Stevenson et al. 2022). The higher the seagrass density the higher its function to attenuate wave actions, which is an important attribute for coastal protection (Koch et al. 2009) and a habitat with decreased water movement (Kikuchi & Pérès 1977). The below ground biomass of seagrass meadows give shelter to infauna species whereas the above ground biomass provides protection against predators for epifauna species (Klumpp et al. 1989). In this study, seagrass roots and rhizomes form the below ground biomass while the above ground biomass consists of shoots and leaves. The infauna community includes all slow-moving species living within or directly on the sediment while all the motile species, that mainly live within the above ground biomass, are part of the epifauna community. Angiosperms are generally abundant with a high diversity whereas the productivity increases with salinity (Boström et al. 2014). Common species inhabiting *Zostera marina* habitats are marine insect larvae and oligochaetes with many species appearing in areas with higher salinity while seagrass meadows reveal a poor species diversity in lower salinity areas (Kikuchi & Pérès 1977). Nevertheless, seagrass meadows show comparatively high levels of primary production (Hillmann et al. 1989), and therefore function as an important food source building food webs

and reveal a huge variety of trophic interactions between different species (Klumpp et al. 1989). Primary consumers are grazers like amphipods as well as gastropods, bivalves and polychaetes while secondary consumers are species like shrimp and crabs while fish species are on top of the food chain (Klumpp et al. 1989). Some taxa, like the fish species, are highly economically important as well. Therefore, a disappearance of the habitat results in a decrease in species abundance, mainly because they rely on seagrass meadows as their nursery (den Hartog 1977).

1.4 Threats to seagrass meadows

The last chapter clearly shows that seagrass meadows are a highly important ecosystem, and it is therefore even more concerning that the habitat disappeared in the past. There are no recordings of the initial seagrass population of the Baltic Sea prior to massive declines (Schubert et al. 2015). But for instance, a study examined a global area of 29293 km^2 seagrass meadow and revealed a loss of 6156 km 2 from 1880-2016 (Dunic et al. 2021). Another study found large scale declines of 24 seagrass species that occurred at 40 locations globally in the 2000s (Hemminga & Duarte 2000). There are natural causes of seagrass declination like the wasting disease, an epidemic outbreak in seagrass meadows that is caused by the pathogen *Labyrinthula Zosterae sp.* (Mühlenstein et al. 1991). It can reduce the efficiency of photosynthesis of *Zostera marina* by almost 50% (Ralph & Short 2002). Other biological interactions, as well as meteorological and geological events, resulted in declines of natural seagrass meadows (Hemminga & Duarte 2000). While natural threats might play a role in the decline of seagrass, around 70% of declination events were caused by anthropogenic influences (Short & Wyllie-Echeverria 1996, Hemminga & Duarte 2000). Particularly, 54% of the seagrass loss took place due to a decrease in the water quality, while coastal constructions accounted for 15% and 8% were ascribed to mechanical habitat destruction (Van Katwijk et al. 2016). Epiphyte populations are increasing with nutrient availability, which causes problems such as light limitation for seagrass meadows (Wear et al. 1999). This is why eutrophication is the major cause of deteriorating water quality and is therefore responsible for a decrease in the abundance of the seagrass communities (Lapointe et al. 1994). The Schlei Fjord, for instance, lost a minimum of 30 km^2 , which nearly resulted in the entire absence of seagrass meadows (Schubert et al. 2015). Additionally, in the Baltic Sea slow water exchange and eutrophication create wide anoxic zones threatening flora and fauna populations (Cederwall, & Elmgren 1990). Climate change is a threat that becomes more apparent. It alternates sea temperatures, level and salinity as well as UV radiation and atmospheric $CO₂$, and therefore creates changes in the environment that also lead to declines in the seagrass meadows (Short & Neckles 1999). Considering a minimum of

0.3-0.4°C rise in the surface layer of the Baltic Sea (Stockmayer & Lehmann 2023), temperature rise is a critical danger to the seagrass vegetation.

1.5 Seagrass restoration

Restoration efforts are being conducted across the globe in order to prevent seagrass meadows from declining further and to reconstruct areas in which seagrass vanished entirely (Calumpong & Fonseca 2001). When attention is given to specific criteria, mainly concerning location, seagrass restoration can be successful (Race & Fonseca 1996; Short et al. 2000). Furthermore, large-scale transplantation and high plant density lead to a higher survival rate of the restored seagrass meadow (Van Katwijk et al. 2016). Ranging from 1880-2016, a total gain of 554 km² within a total area of 29.293 km² was globally determined with restoration being a main driver (Dunic et al. 2021). Since 1970 around 450 new trials of seagrass restoration were conducted per decade (Van Katwijk et al. 2016). However, seagrass meadows along the German coast of the Baltic Sea were not restored until the SeaStore Project was established in 2020 and 12.288 single shoots were transplanted across two trial plots (Ó Corcora et al. 2021). Single shoots with rhizomes were transplanted into the sediment following the method of Orth et al. (1999).

Successful seagrass restoration cannot only be ascribed to the growth of vegetation, the return of species that use seagrass meadows as a habitat is just as important (Fonseca et al. 1998). This Bachelor's Thesis studied the in- and epifaunal communities living within a restored site of the SeaStore Project, two years after the transplantation and compared them to a natural meadow. Particularly, three hypotheses were established and examined:

1) Due to a rapid recovery process, the restored seagrass meadow reveals significant differences within its biodiversity compared to bare sediment.

2) The restored seagrass meadow is within a transitioning state that gets obvious by exceedingly high faunal abundances of first colonizer species.

3) The epifauna community is recovering faster than the infauna community, following the fast recovery process of above ground vegetation.

2 Methodology

2.1 Sampling site

Sampling occurred in seagrass meadows located along the German shoreline in the southwest of the Baltic Sea. While the maximum depth of the Baltic Sea in this area is 40m, eelgrass meadows cannot be found deeper than 8m (Schubert et al. 2015). The depths of the sampling sites of this Thesis ranged between 1,50m and 4m. The seagrass restoration took place near Maasholm. The donor site is a healthy seagrass meadow next to the boardwalk in Kiel. The data collection for this Thesis took place at donor site in Kiel and the restoration site in Maasholm (Fig. 2).

Figure 2a-c: a) Location of the donor and restoration site b) Restoration site Maasholm c) Donor site Kiel, © Google Earth (Version 7.3.6.9345)

2.1.1 Reference site (Kiel)

The reference site 54° 20' 54.96" (N) 10° 8' 0.1788" (E) is an intact, healthy seagrass meadow in the Kiel Fjord within a marine habitat area that is protected by law (Landeshauptstadt Kiel, 2013). It is affected by the substantial ship traffic and the proximity to urbanity (Stevenson et. al 2022). The total area of the reference site had been mapped

with Google Earth and is approximately $13.890m^2$ (Google Earth, Version 7.3.6.9345). The eelgrass meadow grows on sandy sediment with 20-50% silt at a maximum depth of 1.68m. The salinity is around 18psu (Ricklefs 2013). Notably, all shoots for the restoration work, carried out in Maasholm (2021), were collected at this site.

2.1.2 Restoration site (Maasholm)

The restored site (54° 41' 17" (N) 10° 00' 19" (E)) near Maasholm is located adjacent to a nature reserve, which was established for the protection of seabirds and is currently visited by about 12000 tourists per year (Gemeinde Maasholm, 2011). The site is located on the estuary of the Schlei Fjord. The Fjord has a length of 43 kilometers, with the only connection being a 100m-wide channel (Gocke et. al 2003). Shallow depths and the narrow mouth of the Fjord are the cause of limited water exchange with the Baltic Sea (Schwarzer et al. 2019), which leads to a salinity of 13-19psu at the outer part of the Fjord (Landesamt für Natur und Umwelt des Landes Schleswig-Holstein, 2001). Due to eutrophication, the majority of the macroalgae and seagrass species disappeared in most areas of the Fjord (Gocke et. al 2003). This is the reason why the seagrass restoration occurred in Maasholm.

The restoration site contains of 4 squares (Q1, Q2, Q3, Q4), each measuring 16x16m and spaced 2m apart from each other (Fig. 3). The squares were placed parallel to the shore. The eelgrass was planted within these squares in plots of 1 m^2 in 2021 and so this study examines changes in biodiversity two years post restoration. An unvegetated zone of $1m^2$ was left out between each plot to separate them, creating a checkerboard pattern. Control sites consisting of bare sediment are situated 10m away from the planting to the left side of square 1 and to the right side of square 4. A total of 3072 shoots were planted, 16 in each plot of square 1 and 3 and 8 in square 2 and 4.

Figure 3: Theoretical layout of the restoration site

2.2 Sampling

This section covers the entire process from sampling at the study sites to the procedure in the laboratory and statistical analysis. The infauna and epifauna samples were handled differently throughout the sampling and laboratory analysis. The field work was entirely conducted by scuba – diving.

2.2.1 Infauna samples

2.2.1.1 Infauna: field work

The sediment samples were taken using a core with a diameter of 10cm. The core was placed over a spot with a dense eelgrass cover in the restoration, donor treatment and on bare sediment in the control site. It was pushed approximately 15cm into the sediment, depending on silt portion. In order to create a hypotension to keep the sample in place ,while removing the core, a lid was placed on top of it. The final step, prior to ascending, was to place the sample into a plastic bag. The core as well as extensive water was removed above water. Finally, the samples were frozen at -30°C (Fig. 4).

A total of 18 samples were collected, 3 from the donor site, 12 from the restored site, and 3 from the control site.

Figure 4: Methodology of infauna sampling

2.2.1.2 Infauna: sample analysis

The bag containing the sediment sample was defrosted in warm water for approximately one hour and weighed. Next, the sample was sieved through a 1.0 x 1.0 mm mesh sieve (210.2g), until all finer material was removed. This technique was used following a standardized method for surveying Baltic macrofauna communities (Rumohr 2009; Eleftheriou 2013). The sample remaining in the sieve was then weighed again. That is why it is of high importance to know the weight of the sieve in order to subtract the amount and receive the exact weight of the sample. For the examination of the different components of the sample, it was placed in a petri dish or any familiar container suitable for the work with a microscope later on. An estimation of the percentage of organic matter vs. inorganic matter, living organic matter (LOM) vs. dead organic matter (DOM), and flora vs. fauna was carried out. If the sample contained seagrass, it was separated carefully without removing any organisms. A distinction was then made between the shoots/ leaves growing above ground and the roots/ rhizomes below ground. Both biomasses were weighed, and the sample was placed into a dry oven for at least 48 hours before determining the dry weight (Fig. 5).

In a final step, the samples were examined with a microscope in order to count and identify the different organisms at their species level (see supplementary Table 1).

Figure 5: Methodology of laboratory Analysis of infauna samples

2.2.2 Epifauna samples

2.2.2.1 Epifauna: field work

For the collection of epifauna samples a sample device was used, consisting of a 30cm long sampling quadrat, 1mm mesh net, and a jar that could be screwed on top of the net, a side opening to operate inside of the net and a closure frame for closing the net with a bottom plate (fig.6). The jar was screwed on top of the net before going into the water. While diving, the device was positioned over the seagrass meadow. Shoots were pulled out as a whole in order to collect part of the roots as well. This ensured that all organisms living in the seagrass were collected and it was accomplished by putting the hand through the side opening without needing to detach the net from the seabed. After the seagrass collection was finished, the side opening was closed, and the bottom plate attached. The net was turned around before ascending. By doing so, the sample was captured on the inside of the jar while lifting the device. Back on the surface, the sample was removed from the jar and put into a plastic bag, before putting it into the freezer at -30° C.

A total of 15 samples, 3 from the donor and 12 from the restored site, were collected. No sampling occurred at the control site in Maasholm because of the absence of above ground biomass.

Figure 6: Methodology of epifauna sampling

2.2.2.2 Epifauna: sample analysis

Epifauna samples were defrosted within their bags for approximately 20 minutes. To investigate the seagrass shoots separately from the species, they were divided in two different containers. All seagrass shoots were counted and, in exception to the flowering shoots, were laid out for further measurements. Five shoots of the restoration site and all of the shoots from the donor site, that could be determined in the sample, were surveyed. Three of the 5 shoots were picked randomly whereas the two remaining shoots consisted of the smallest and the largest one of the samples. Parameters used were: Number of shoots per plant, number of leaves, leaf length and width. These parameters serve as an indicator of the health and the complexity of the seagrass meadow. Flowering shoots, as well as loose seagrass leaves, root fragments and the shoots which had already been investigated, were separated into above and below ground biomass. First, the wet weights were determined before all biomasses went into the dry oven for a minimum 48 hours in order to measure the dry weights (Fig. 7).

The remaining sample was investigated using the microscope to determine all species up to the researched taxon level (see supplementary Table 1.).

Figure 7: Methodology of laboratory analysis of epifauna samples

3 Results

3.1 Statistical analysis

Statistical analysis of infauna and epifauna samples followed the same procedures. The tables were created in Excel (Version 2307). The statistical analysis and the plotting were conducted with Rstudio, Version 4.3.0 (28.07.2023). The most relevant package for result retention of the infauna community was the Community Ecology Package Vegan, Version 2.6-2. To examine all the different components of infauna samples, boxplots were created for: Core weights, sample weights after sieving, dry weight, wet weight and the LOM vs DOM ratio. The infauna abundance of all species and their richness were illustrated. Additionally, to specify results as much as possible, the species abundance for every treatment had been exemplified. The species diversity had been calculated with the Shannon-Wiener Index. The Pilou Evenness formula was applied to receive the related evenness values. To investigate whether the community metrics of all treatments vary from each other one-way ANOVA and additional Post-hoc Tukey Test were carried out. To test for any aberrations within the community composition of the different sites, a Non-Metrical Multidimensional Scaling (NMDS) model was applied. After illustrating a species distribution with the Wisconsin Standardization, the NMDS model was created using the Bray-Curtis similarity Index. The result showed a two-dimensional visual representation of the community compositions per treatment. The stress plot of the model for the infauna community resulted in a value of 0.141 and for the epifauna community in a value of 0.1263363 (see supplementary Fig. 6 & 12). Both were designating weak ties but were still laying below 0.2 and can therefore be validly interpreted (Zuur, A. et. al, 2007). While this model can be used to visually explain differences in the communities, there is no prove of significance. Hence the NMDS1 scores, which represent the first axis of the NMDS model were tested with a one-way ANOVA and the Post-hoc Tukey Test.

The wet and dry weights of the seagrass sample with a weight lower than 0.005g were counted as 0g.

The in- and epifauna abundances were both standardized to one square meter in order to compare the results.

 $A[m^2] =$ $A[\emptyset = 0.1m] * 10000$ $\pi * 5^2$ Infauna Abundance (A):

 $A[m^2] =$ $A[0.3x0.3m^2]$ 0.09 Epifauna Abundance (A):

3.2 Results infauna

One part of the sample analysis consisted of the measurement of weights and the estimation of compositions. Parameters of these analyses were: Core weight, weight of the samples after sieving, dry and wet weights, living organic matter (LOM) and dead organic matter (DOM) coverage. Organic vs. inorganic matter and flora vs fauna were omitted since the unsubstantial result did not reveal any significant differences. The results represent a comparison of the different treatments: Control (C), Donor (D) and Restoration (R). While the results of the total weight of the sample after sieving (Fig. 8) and the dry weight (Fig. 9) were taken into account for giving valuable information about the community composition of the samples, the other components of the infauna samples can be viewed in the appendix (supplementary Fig. 1-3). The infauna abundance was investigated to receive the total amount of species at all treatments (Fig. 10), the species abundance per treatment (Fig. 12) and the comparison of all treatments for species who revealed significant information on the biodiversity of the different sites (Fig. 13). All the other species abundances for all treatments are illustrated in the appendix (supplementary Fig.5). Parameters disclosing results of the infauna community composition and biodiversity at all treatments are illustrated in Figure 14-21.

3.2.1 Components of infauna samples

The total sample weights after sieving showed significant differences (Fig. 8). Although some samples taken in Maasholm weighed less than the ones taken in Kiel, both sites demonstrated similar means (D=66.73g, R=55.02g). The samples taken at the control site displayed a mean value of 86.9g and were therefore heavier.

The highest values of below ground biomass were found at the donor site (Fig. 9). Means of the below ground biomass were: $C = 0g$, $D = 3.3g$, $Q1 = 2.07g$, $Q2 = 0.27g$, $Q3 = 1.4g$ and Q4 = 1.23g. The restoration site displayed the highest weight values for above ground biomasses. Both weights were lowest at the control site.

3.2.2 Species abundance in infauna samples

Figure 10: Total species abundances in infauna samples per treatment

The abundance of all infauna individuals, found in the samples, is illustrated in Figure 10. The donor site revealed the highest number of individuals per $m²$ (mean = 960 individuals/m²) with the lowest number found at the control site (mean = 250 individuals/m²). In the restoration site, Q1 showcased the highest number of individuals (mean =24 individuals/m²), and the lowest value for abundance was found at Q4 (mean = 458 individuals/m²). Square 1 and 3 displayed higher values in their abundance than square 2 and 4. Their abundances differ visibly from those taken in the control and the donor site. In regard to the results of the Post-hoc Tukey Test (p-value <0.05) (Fig. 11) D vs C, Q1 vs C and all of the squares vs the donor site showed a significant difference. This means, that the species abundance of the whole restoration site is more distinguishable from the donor site than from the control site. Q1 was the only square that displayed a significant difference within its species abundance to the control and the donor site. However, while the numbers of individuals found at Q2, Q3 and Q4 were more similar to the resulting values of C than D, the difference in the abundances of Q3 vs C were more noticeable than Q2/Q4 vs C.

Figure 12a)-f): Species abundance in infauna samples for a) Q1, b) Q2, c) Q3, d) Q4, e) Donor and f) Control treatment

All abundances of the species found in the infauna samples are illustrated in Figure 12 and are divided by their treatment. The species that were present at all treatments are: *Pygospio elegans, Polychaeta sp.* and *Hydrobia.* The polychaetes showed a high number of individuals at all treatments. *Littorina littorea* was only found at the donor site while *Idotea baltica* was individually present at Q1. The number of individuals of *Amphipoda sp.* was high at all treatments except for the control site. *Cerastoderma* was abundant at D, C, Q1 and Q3.

Pygospio elegans was mainly found at the restored site (Fig. 13a). While the abundance of the other polychaetes was comparatively high for all treatments (Fig. 12) the number of individuals of *P. elegans* was more than four times greater for Q1 and Q2 than D and C.

The abundance of *Mytilus edulis* (Fig. 13b) showcased a similar result as all of the other bivalves that were found within the infauna samples (Fig. 12). Their abundance was either low or at zero for the restoration and control site, while they were found in high numbers at the control site.

All of the gastropods were mainly abundant at the donor site (Fig. 12). Not only was the amount of *Hydrobia* exceedingly higher at D than at all other treatments, it also appeared to be more abundant at Q1/Q3 than Q2/Q4 (Fig. 13c).

Figure 13a)-c): Infauna samples: Total species of a) *Pygospio elegans*, b) *Mytilus edulis*, c) *Hydrobia* abundance per $m²$ at all treatments

3.2.3 Biodiversity measurements of infauna samples

diversity per treatment

Figure 14: Infauna samples, Shannon Index: species Figure 15: Infauna samples, corresponding evenness

Figure 16: Post-hoc Tukey Test plot for infauna species diversity and the affiliated evenness

The biodiversity (Fig. 14) and evenness (Fig. 15) of all infauna species at each treatment had been measured with the Shannon Wiener Index (H) and its corresponding evenness (H'). The control site held the lowest biodiversity and also showed the most uneven distribution of its community. In contrast, the highest biodiversity was determined at the donor site, which also represents the most even community distribution of all sites (mean value= 0.662). In regard to the restoration site, a visible difference between Q1/Q3 and Q2/Q4 in both their biodiversity and evenness was found. The highest values of the restoration site for species diversity and evenness were reached in Quadrat 3. In order to see, whether the values are significant the Post-hoc Tukey Test (p-value < 0.05) was conducted. It presented the same results for biodiversity and evenness (Fig. 16). The differences between all sampling sites and the control site proved to be significant. Apart from that, the model showed insignificant differences at all other sites. Nevertheless Q2/Q4 showed a greater difference in their biodiversity and evenness to the donor site than Q1/Q3 did.

richness

The species richness is illustrated in Figure 17. The highest number of species was determined at the donor site (mean = 7). The lowest value of species richness was discovered at the control site (mean = 2.667). In addition, treatments of the restoration site also showed a difference in species richness. While Q1 and Q3 displayed the same values for species richness (mean = 5.667), Q2 showed the lowest number of species (mean = 4) with Q4 showcasing a species amount that is just slightly higher (mean = 4.333).

While the differences between the treatments are obvious, their significances were examined with the Post-hoc Tukey Test (p-value < 0.05) (Fig. 18). The test determined a significant difference between D vs C. The species richness of Q2/Q4 vs. the D was not significant but nevertheless, the differences proved to be higher compared to Q1/Q3 vs D. A corresponding result occurred in comparison of Q1/Q3 and the control site. While the difference was not significant it resulted in a higher difference than Q2/Q4 vs C.

3.2.4 Community compositions in infauna samples

Figure 19: NMDS model for infauna community composition per treatments

Figure 20: NMDS1-scores of infauna communities per treatment Figure 21: Infauna species distribution in NMDS model

The NMDS model of the infauna community composition for every treatment is illustrated in Figure 19. The results from the restoration site reflect similar composition for all communities of each square. Apart from that, both the donor and control site revealed a difference in their communities. Especially Q1 and Q3 displayed a trend of a slight approach towards the community structure of the donor site.

Figure 21 is an approximation of which species mainly had been discovered at the different treatments. No species had been primarily identified at the control site. Both, *Littorina littorea* and *Mytilus edulis,* were discovered mainly at the donor site. The squares of the restoration site were characterized by their abundances of *Bittium reticulatum, Amphipoda sp.* and *Pygospio elegans. Polychaeta sp.* was mainly found at the control site, Q2, Q3 and Q4. *Hydrobia sp.* was noticeably occurring at Q1, Q3 and the donor site.

The NMDS1- Scores (Fig. 20) reveal that both the control and donor site certainly obtained a different community composition than the squares of the restoration site. The pvalues resulting from the Post-hoc Tukey Test (p-value < 0.05) confirmed that the differences of donor vs control ($p \approx 0.00014$), Q1 vs control ($p \approx 0.0039$) and Q2 vs donor (p ≈ 0.0044) are significant. All other results from the Tukey Test did not prove a significant difference. The most insignificant p-values were detected for Q2 vs Q4 ($p \approx 0.994$) and Q1 vs. Q3 ($p \approx 0.8$).

3.3 Results epifauna

Before analyzing the epifauna species, different parameters of the seagrass within a sample had been recorded. Parameters were: Plant coverage (including the total number of plants and of the flowering shoots), Seagrass growth (measured with the number of shoots and leaves per plant), Leaf measurement (the leaf width and length), wet and dry weights. The plant coverage (Fig. 22) and dry weights (Fig. 23) of epifauna samples function as valuable indicators of the conditions for the surveyed habitat and are therefore taken into account. All of the other seagrass measurements are illustrated in the appendix (see supplementary Fig. 7-9). The epifauna species abundance had been investigated for all treatments (Fig. 24), all species for each treatment (Fig. 26) and for the abundance of unique species comparing all treatments (Fig. 27). The results of the biodiversity and community composition studies, measured for the epifauna samples at each treatment, are displayed in Figure 28-35.

3.3.1 Seagrass measurements

Figure 23: Above ground & below ground biomasses measured with dry weight of epifauna samples Figure 22: Total plant coverage discovered in epifauna samples

The restoration site showcased a higher number of plants in total (Fig. 22). Remarkably more flowering shoots were found within each epifauna sample (30 x 30cm²) at the restored site (mean: 13,08) than at the donor site (mean: 0,75). It becomes evident that although the total number of plants was higher at the restored site, their number was lower when the flowering shoots weren't included. Meanwhile, the total number of plants didn't abundantly differ from the number excluding all flowering shoots at the Donor Site.

The dry weights (Fig. 23) indicate that the amount of eelgrass growing above ground was higher at the restored site which is coherent to the number of flowering shoots. The results of below ground biomass at the donor site clearly appeared to be higher than at the restored site.

3.3.2 Species abundance in epifauna samples

The total species abundance of epifauna per treatment is illustrated in Figure 24. The highest number of individuals was found at the donor site (mean = 2126 individuals/m²). The highest abundances of all infauna species from the restoration site were discovered at Q3 (mean= 2011 individuals/m²), while the lowest abundance was found at Q1 (mean=1485 individuals/m²). The number of individuals of the two squares Q2 and Q4 demonstrated a similar result which can also be observed within the illustration of the Post-hoc Tukey Test ($p < 0.05$) (Fig. 25). The p-value is almost at 1.0 ($p = 0.9999955$), which indicates that Q2 vs Q4 showed almost no differences in their abundances of epifauna species. However, no treatment comparison of abundances displayed a significant difference. Visibly, the abundances discovered at Q1 vs D differed most from each other ($p ≈ 0.74$).

The epifauna abundance, specified by the different species abundance for all treatments, is illustrated in Figure 26 a)-e). The species *Polychaeta sp., Mytilus edulis, Littorina littorea, Idotea baltica, Hydrobia* and *Amphipoda sp.* were discovered at all treatments. Furthermore, a few individuals of some species were found occasionally: *Syngnathus typhle* at Q1/Q3, *Pandalus sp.* at Q1/Q2, *Cerastoderma* at D, *Asteria sp.* at D/Q3 and *Carcinus maenas* at Q1.

By examining the results of the species *Amphipoda sp.* (Fig. 27a) it becomes evident that the number of individuals, found at the restoration site, exceeded those of the donor site. In general, the amount of their individuals was the highest by far.

Idotea baltica was another species whose abundance at the restored site was numerously higher than at the donor site (Fig. 27b). Furthermore, the number of individuals found at Q1 and Q3 was greater than the discovered abundance at Q2 and Q4.

All the abundances of the bivalves (*Mya, Cerastoderma, Mytilus edulis*), found in the epifauna samples (Fig. 26), were ubiquitously higher at the donor site. Those differences can be mainly observed for the abundance of *Mytilus edulis* (Fig. 27c).

The results of the gastropods (*Littorina littorea, Hydrobia, Bittium reticulatum*), discovered in the epifauna samples (Fig. 26), displayed the same trend than the bivalves. Not only was the abundance of *Littorina littorea* (Fig. 27) highest at D, it also was visibly higher at Q1/Q3 than Q2/Q4.

Figure 27: a)-d).: Total epifauna abundances per m² for: a) Amphipoda sp, b) *Idotea baltica,* c) *Mytilus edulis*, d) Bittium *reticulatum*

3.3.3 Biodiversity measurements of epifauna samples

Figure 28: Epifauna samples, Shannon Index: species Figure 29: Epifauna samples, corresponding evenness diversity per treatment

Figure 30: Post-hoc Tukey Test plot for epifauna species diversity and the affiliated evenness

The biodiversity (H) of epifauna species per treatment is illustrated in Figure 28. The donor site appeared to be the most diverse site (mean = 1.431) while Q4 showed the lowest value for its epifauna biodiversity. In regard to the restoration site, the highest biodiversity value was measured at Q1 (mean = 0.682) although Q3 (mean = 0.641) displayed a similar result. All of the species found at D were most evenly distributed over the site in comparison to the restored site. Generally, in regard to the low evenness values (Fig. 29), the epifauna species are clearly unevenly distributed over all of the squares of the restoration site. Following the results of the species diversity, Q1 (mean = 0.662) showed the highest evenness values and is similar to the values of Q3 (mean = 0.237) while Q4 (mean = 0.152) displayed the lowest result. In order to prove whether the differences of biodiversity and evenness, when comparing two treatments are significant, the Post-hoc Tukey Test (p-value < 0.05) had been conducted (Fig. 30). All four squares of the restoration site presented a significant difference in their biodiversity and evenness compared to the donor site.

richness

Figure 31 illustrates the species richness of the epifauna from the different treatments. The donor site showcased the highest number of species (mean = 9) of all sites. Q3 (mean = 7.667) was the species richest site in comparison to all 4 squares of the restoration site. Meanwhile, Q4 (mean = 4.667) presented the lowest number of species compared to D and Q3 and additionally revealed a significant difference, which was examined with the Post-hoc Tukey Test (p-value < 0.05) (Fig. 32). The only other significant difference had been determined between Q1 and the donor site while all other dissimilarities could not be proved to be significant.

3.3.4 Community compositions in epifauna samples

Figure 33: NMDS model for community compositions of epifauna samples per treatment

Figure 34: NMDS1-scores of epifauna communities per
Figure 35: Epifauna species distribution in NMDS Model treatment

The NMDS model of the epifauna community compositions for every treatment is illustrated in Figure 33. While all of the epifauna communities found at the 4 squares of the restoration site were showing a similar structure, the donor site clearly appeared to have a different community composition.

When looking at the appearance of the different epifauna species in the communities (Fig. 35), especially *Idotea baltica, Amphipoda sp.* and *Polychaeta sp.* were identified with the restoration site. *Mytilus edulis, Asterias sp., Cerastoderma* and *Bittium reticulatum* were mainly found at the donor site.

The NMDS1-scores (Fig. 34) proved that the donor site obtained a different community composition. This was confirmed by the results of the Post-hoc Tukey Test (p-value < 0.05), where all of the NMDS1-scores of the squares compared to the donor site revealed a significant difference. Q1 vs D displayed the lowest p value ($p \approx 0.00015$) while Q3 vs Q4 almost revealed the same community composition ($p \approx 0.9994$).

4 Discussion

4.1 Rapid recovery process of the restoration site in Maasholm

Two years after the restoration progress the epi- and infauna communities of the seagrass meadow in Maasholm showcased similarities to the donor site in Kiel. Several studies indicate, that the faunal communities of restored seagrass meadows adapt to communities of healthy, natural seagrass beds within a few years (Tanner et al. 2021; McSkimming et al. 2016; Lefcheck et al. 2017). This is a remarkably fast adaptation process, compared to restoration efforts in other marine ecosystems, in which the time span until full recovery was reached has been estimated to 10-42 years without regarding consecutively slow recoveries (Lotze et al. 2011).

Natural seagrass meadows provide habitats to a greater faunal biodiversity than bare sediment does (Orth et al. 1984). It can therefore be assumed that having a significantly higher number of infauna individuals at the restored site than at bare sediment is yet another indicator showing that the seagrass bed in Maasholm is recovering. A rapid recovery can not only be defined as a positive growth rate of seagrass, the colonization of fauna in high abundances compared to non-vegetated habitats is just as important (Fonseca et al 1998). Since this can be observed when comparing infauna abundances of the control site to the restored site (Fig. 10) it can also be held as proof, that the recovery of the restored meadow in Maasholm can so far be regarded as successful.

The infauna abundance was significantly lower at the restored site compared to the donor site enhancing the differences within the community compositions. The donor site revealed exceedingly high amounts of *Mytilus edulis* and *Hydrobia* while the restoration site showed low abundances of all gastropods and bivalves, but high numbers of polychaetes. Similar results were discovered in other studies, like Gagnon et al. (2023). Furthermore, the species found in the donor site were the same species discovered at the restoration site hence the insignificant differences in their biodiversity and evenness. This development of communities in restored seagrass meadows had been discovered in the past. While the species diversity and richness of the restored seagrass beds displayed similar results as natural meadows after a year (McSkimming et. al 2016), it takes the faunal community in restored meadows 3-5 years to recover and fully evolve like natural seagrass habitats (Sheridan 2004).

The epifauna species richness was not significantly different at Q2/Q3 compared to the donor site, indicating that the same species are present within both sites, yet it takes time to obtain a similar community composition. The abundances showed similar results for both sites, mainly because the density of amphipods was exceedingly high at the restored site, equalizing the high abundances of gastropods and bivalves found at the donor site. Amphipods function as a prey for species like the pipefish *Syngnathus typhle.* Furthermore, the fish *Gasterosteus aculeatus* is mainly feeding on copepods and fish eggs (Kennish & Loveland 1984). Both species were found in samples at the restored site implicating that the amphipod abundances had a decisive influence on the biodiversity of the restoration site. The resulting significant differences between restoration and donor site, that were discovered within the epifauna community composition, biodiversity and evenness, are enhancing the theory that the amphipod abundance had a chief impact on the different community composition. However, discovering predators at the restored habitat is yet another indication that the seagrass restoration has led to a successful recovery process of the faunal community (Lefcheck et al. 2017). Similar results, presenting differences within epifaunal composition and biodiversity were determined in a previous study, suggesting that a firmly established meadow can fulfill its ecological role even if the community structure evolved slightly different (Brown-Peterson et al. 1993). Since the high abundance of *Amphipoda sp.* is attracting predators, it could be the case, that the eelgrass meadow in Maasholm will prospectively continue to represent a slightly different community composition. Therefore, it would be interesting to observe the community composition over a longer term and to reevaluate, whether the seagrass meadow can only be regarded as successfully restored when it shows a similar community composition like the donor site in Kiel. The recovery might be just as successful if it had established a habitat in which the community evolved based on the early food web structures.

4.2 High faunal abundances of unique species at the restored site

Polychaete abundances at the restored site were irregularly high within the infauna community while the epifauna community chiefly consisted of amphipods. The isopod *Idotea baltica* had higher numbers within the restoration site as well. (Fig. 27b). Meanwhile gastropod and bivalve species were comparatively low at Maasholm. Restored seagrass meadows can be characterized by getting rapidly colonized by a few species in the first stages of the recovery process while their abundances decrease again until maintaining communities that are similar to natural habitats (Lefcheck et al. 2017).

The reproduction rate as well as the secondary production of fauna like polychaetes were discovered to be higher for planted seagrass meadows, mainly because more individuals were participating, and a newly planted seagrass meadow can present good immigration conditions with high survival rates (Bell et al. 1993). This could be a reason for the exceptionally high numbers of polychaetes and amphipods. Although, it would need to be investigated further through studies that would compare secondary production of natural and restored seagrass meadows as well as the reproduction rate of the species that are inhabiting the recovered meadow with high abundances.

There is a correlation between the grain size of the sediment and deposit feeders with higher abundances found in areas consisting of fine, muddy sediment (Rhoads & Young 1970). Seagrass meadows are known for sedimentation processes which lead to finer sediments at the vegetated areas, than at non-vegetated areas (Van Katwijk et al. 2010). Total weights of the infauna samples (Fig. 8) can be used as an approximate representation of the grain size since finer sediment will get sieved through the mesh, whereas coarse sediment will result in a heavier sample. Further studies on the grain sizes and sediments of the restoration site at Maasholm would provide more advanced information than sample weights and are therefore highly recommended. In regard to the weights, the sediment having the largest grain size was found at the control site. This might be the reason why *Pygospio elegans* was found in such small numbers at the control site. On the other hand, Polychaeta *sp.* showcased the highest abundance within the bare sediment while the number of individuals at the restored meadow was only slightly smaller. Q2/Q4 displayed higher abundances of polychaetes than Q1/Q3 (Fig.12). Similar results were observed within the study of Gagnon et al. (2023). Since the below ground biomass was the highest at the donor site (Fig. 9), it may reflect that species living within the sediments decrease with an increase in the root biomass. A different community living within the sediment of seagrass may be due to the shelter some species find in the root system (Orth et al. 1984). Not only was the density of epifaunal polychaetes expected to increase with nutrient availability (Gagnon et al. 2023), some species became exceedingly high abundant due to eutrophication (Sandonnini et al. 2021). The Schlei Fjord has been showing high levels of organic material, as well as ammonium, nitrate and phosphate, mainly due to anthropogenic eutrophication (Schwarzer et al. 2019). Contrariwise, the Kieler Fjord has currents that can be as fast as 0.5m/s, resulting in an increased water circulation (Ricklefs 2013). This leads to a greater dispersal of the nutrients, prospectively. These differences between the conditions at survey sites might also be an additional reason why *Pygospio elegans* was so abundant within the Schlei Fjord at Maasholm.

Dispersing fauna like Amphipods recolonizing seagrass meadows rapidly in high numbers is a common process (Virnstein & Curran 1986; McSkimming et al. 2016). Moreover, the recolonization rate can be influenced by the proximity of a nearby meadow (Sheridan et al. 2003). Interspecific competition and mating are reasons why motile fauna leave the natural seagrass meadow, although they become more vulnerable to predation (Robertson & Howard 1978). Furthermore, amphipods have a short generation time with some species generating up to 9 generations per year (Fredette & Diaz 1986). The high abundance of amphipods found in this study could therefore be expected and exposes the transitioning state of the epifaunal community of Maasholm. The high abundance of amphipods also explains that the biodiversity (Fig. 28) and evenness (Fig. 29) values of the epifaunal community at the restored site were lower than the values determined at the donor site.

4.3 Epifauna community recovers faster than infauna community

When comparing the below ground biomass (figure 9) to the above ground biomass (figure 23) and the plant coverage (figure 22) at the restored meadow, it is evident that the above ground vegetation already reveals a more complex system. Above ground biomasses of seagrass meadows principally recover faster than below ground biomasses (Di Carlo & Kenworthy 2008). If the habitat of epifauna is recovering faster, it could be assumed that the epifauna population is more advanced in its recovery state than the infauna community. Coherently, the species richness of epifauna (Fig. 31) is higher than the species richness of infauna (Fig. 17). While this can be no more than a reflection of higher species abundances (Fernando et al. 2011), it has already been discussed that the epifauna population started to become more complex due to the arrival of predators. Gastropods and bivalves simply need more time to colonize areas due to their lower mobility (Virnstein & Curran 1986), hence the low abundances of those species within the restored site (Fig. 12). The shoot density is yet another parameter supporting the hypothesis, that epifauna is recovering faster than infauna in restored meadows. Faunal abundances get affected by shoot densities within the early stages of seagrass restoration while they get less important the more advanced the recovery state (Fonseca et al 1996). In order to investigate, how the shoot density affects the abundance, twice as many plants were planted within the squares Q1 and Q3 than Q2 and Q4 (Fig. 3). There was a visible difference within the species abundances for both infauna and epifauna. However, the infauna seems to be more affected by the different shoot densities than the epifauna. *Syngnathus typhle* was the only epifauna species that was exclusively discovered at Q1 and Q3. *Mya, Cerastoderma* and *Mytilus edulis,* that were discovered within the infauna samples (Fig. 12), were singularly found at the higher shoot densities. In regard to those results, the epifaunal community seems to be less dependent on the shoot density and therefore further into the recovery process than the infauna community.

4.4 Methodological challenges

Restored seagrass meadows can be affected by nearby natural meadows (Brown-Peterson et al. 1993), therefore it needs to be considered that this might have happened in Maasholm as well. The entire absence of natural seagrass meadows, that were located around Maasholm, was confirmed in a previous study by Schubert et. al (2015). Nevertheless, a return of small patches of natural seagrass should be considered. Studies show that seagrass meadows can be restored without having the proximity to a natural habitat (Lefcheck et al. 2017), however further mapping should be conducted in order to investigate the influence of vegetated areas. The comparison of the donor site in Kiel and the restored site in Maasholm already led to important and plausible results. However, in regard to potential variations at survey sites (Thayer & Chester 1989), if new mapping validates the return of seagrass meadows, it would be interesting to take the natural seagrass bed in Maasholm as a reference site. This would also have been advantageous in order to compare two treatments having the same conditions like nutrient availability and sediment composition. While it is presumable that the *Pygospio elegans* population got affected by the higher levels of eutrophication in the Schlei Fjord, there are some polychaete species inhabiting seagrass meadows that were determined to be indicators for that issue (Sandonnini et al. 2021). It would therefore have been useful to determine all polychaetes to species level. Likewise, there could have been differences in the community composition of the polychaetes inhabiting the bare sediment, restored site and donor site. It is recommended to examine them in further studies, while a determination of higher taxa levels of amphipods and isopods did not seem to be important, at least for this study. Furthermore, for both sampling methods there was a bycatch of in- and epifaunal species in the opposite sample. While they were willingly taken into account within the statistical analysis, in order to get a picture of what actually lives within the restored meadow, it may be interesting to find a method to investigate the communities entirely separated from each other. Lastly, the study is a representation of no more than three samples per treatment from one time point. In order to observe more significant differences within the community compositions, a further study needs to include sampling over years in different seasonal time points in regard to fluctuations in some species abundances (Fonseca et al. 1996; Stoner 1980).

5 Conclusion

The seagrass restoration in Maasholm, with a focus on the return of species that are using *Zostera marina* as their habitat, can so far be regarded as successful. It is important to note, that the study is a reflection of one time point on the scale of a transitional recovery state. The community compositions of epi- and infauna as well as their biodiversity, abundance and species richness improved, with some values being insignificantly different to a natural meadow. In order to ensure that the seagrass meadow continues to develop its habitat structure and provides the resources and complexity for the faunal community to evolve, the area needs to be surveyed more frequently. This will provide the ability to react to unwanted changes and prevent the restoration attempt from failing. Threats to seagrass, especially the nutrient intake of the Schlei Fjord, need to be investigated further including all the addressed suggestions made within the discussion.

Nevertheless, this study attributed that the restored site in Maasholm is rapidly recovering, showed the expected high abundances of fast colonizers and gave plausible evidence to the hypothesis that epifaunal communities evolve faster than infaunal communities.

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8 Appendix

Supplementary Table 1: Species list of discovered epi- and infauna, not sorted by species discovered within the epi- and infauna samples.

Supplementary Figure 2: Total wet weights of infauna samples

Supplementary Figure 3: LOM and DOM biomass in infauna samples

Supplementary Figure 4: Total species abundance in infauna samples of all treatments

Supplementary Figure 6: Stress plot of NMDS Model for the infauna community composition

Wet weights of Epifauna Samples

Supplementary Figure 8: Leave lengths of shoots discovered in epifauna samples.

Supplementary Figure 10: Total species abundance in epifauna samples of all treatments

Supplementary Figure 11: Species abundance in epifauna samples, a) *Sygnathus typhle,* b) *Pygospio elegans,* c) *Polychaeta sp.,* d) *Pandalus sp.,* e) *Mya,* f) *Hydrobia,* g) *Gasterosteus aculeatus,* h) *Cerastoderma,* i) *Carcinus maenas,* j) *Bittium reticulatum,* k) *Asterias sp.*

Supplementary Figure 12: Stress plot of NMDS Model for the epifauna community composition

9 Declaration (Erklärung)

Hiermit versichere ich and Eides statt, dass diese Arbeit selbstständig verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe. Außerdem versichere ich, dass ich die allgemeinen Prinzipien wissenschaftlicher Arbeit und Veröffentlichung, wie sie in den Leitlinien guter wissenschaftlicher Praxis der Carl von Ossietzky Universität Oldenburg festgelegt sind, befolgt habe.

Zaberfeld, den 01.09.23
Zaberfeld, den 01.09.23