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RESEARCH ARTICLE

Rapid faunal colonization and recovery of biodiversity and functional diversity following eelgrass restoration

Karine Gagnon[1,2,3], Enora-Hawa Bocoum[1,4], Chiau Yu Chen[5,6], Susanne Pihl Baden[7], Per-Olav Moksnes[5], Eduardo Infantes[5,7]

Seagrass meadows and their associated biodiverse assemblages have declined globally due to environmental and anthropogenic stressors. Restoration of these critical habitats has the potential to reverse coastal biodiversity loss. Here, we tested the role of patch size (which can affect recruitment, food availability, and/or predation) in driving faunal colonization in an eelgrass (*Zostera marina*) restoration trial in Sweden. Eelgrass shoots were transplanted in plots with different configurations (continuous vs. checkerboard patterns with three patch sizes), and we followed invertebrate colonization (biodiversity and functional diversity) during the first two growing seasons. We found rapid faunal colonization following the transplantation of eelgrass shoots in all plots with invertebrate densities reaching 50–80% of the reference meadow after only one growing season (3 months). After two growing seasons (15 months), the faunal density, biodiversity, and functional diversity were similar to the reference meadow, despite eelgrass density and biomass still being lower than the reference meadow. Biodiversity, functional diversity, and community structure were similar among the different planted plots, that is, there was no indication that patch size influenced faunal colonization. We therefore consider that smaller patches embedded within larger restoration plots can be as effective for promoting biodiversity as continuous patches, with reduced costs and fewer shoots required. We also noted high natural variability between years both in the reference meadow and planted plots, showing the dynamic nature of seagrass ecosystems, and the importance of a well-planned monitoring scheme that considers the reference area and restored area within the same temporal scale.

Key words: diversity, epifauna, functional traits, infauna, seagrass, spatial scale

Implications for practice

- Rapid faunal colonization after eelgrass transplantation (within 3 months, i.e. one growing season). We can consider the faunal community in the planted plots to be "restored" after 15 months (two growing seasons), based on faunal density, biodiversity, and functional traits.
- Smaller plots planted in a checkerboard pattern supported as high faunal abundance and diversity as continuously planted shoots and natural eelgrass meadows, indicating that this method has no negative effects for the faunal communities.
- High natural yearly variability shows the importance of comparing restored plots to a reference meadow over time.

Introduction

Biodiversity loss due to a wide array of anthropogenic stressors threatens the stability and ecosystem provisioning capacity of ecosystems worldwide (Cardinale et al. 2012; Gamfeldt et al. 2015). In coastal marine ecosystems, habitat-forming ecosystem engineers (seagrasses, macroalgae, reef-forming organisms, etc.) are critical for sustaining biodiversity and ecosystem functioning (Barbier et al. 2011). The rapid loss of these coastal habitats, and their often-slow recovery times, has led to increasing efforts in restoring them in order to facilitate the recovery of biodiversity and associated ecosystem functions (Halpern et al. 2007; Bayraktarov et al. 2020). Seagrass ecosystems support high associated biodiversity and trophic networks, as well as a wide range of ecosystem services to human societies (Costanza et al. 2014; Nordlund et al. 2016). Though seagrass populations have declined in many parts of the world (Dunic

Author contributions: KG, POM, EI conceptualized the study; KG, POM, EI carried out fieldwork; KG, EHB, CYC, SPB carried out laboratory work; KG, EHB ran the functional and statistical analyses; KG wrote the first draft of the manuscript; all authors contributed to subsequent drafts and approved submission of the manuscript.

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et al. 2021), concerted restoration efforts can lead to the rapid recovery of coastal biodiversity and other ecosystem services (Lefcheck et al. 2017; Orth et al. 2020; Beheshti et al. 2022).

Northern European populations of the widespread seagrass *Zostera marina* (eelgrass) declined heavily in the 1930s, due to a major outbreak in eelgrass wasting disease (*Labyrinthula zosterae*; Den Hartog 1987; Short et al. 1988; Muehlstein 1989). Though many populations recovered to some extent, anthropogenic pressures in the second half of the 20th century have led to continued losses in some areas (Dunic et al. 2021; Turschwell et al. 2021). Along the Swedish West Coast (Skagerrak), over 60% of eelgrass area has been lost since the 1980s (Baden et al. 2003; Nyqvist et al. 2009) due to the combined effects of nutrient enrichment and overfishing favoring fast-growing

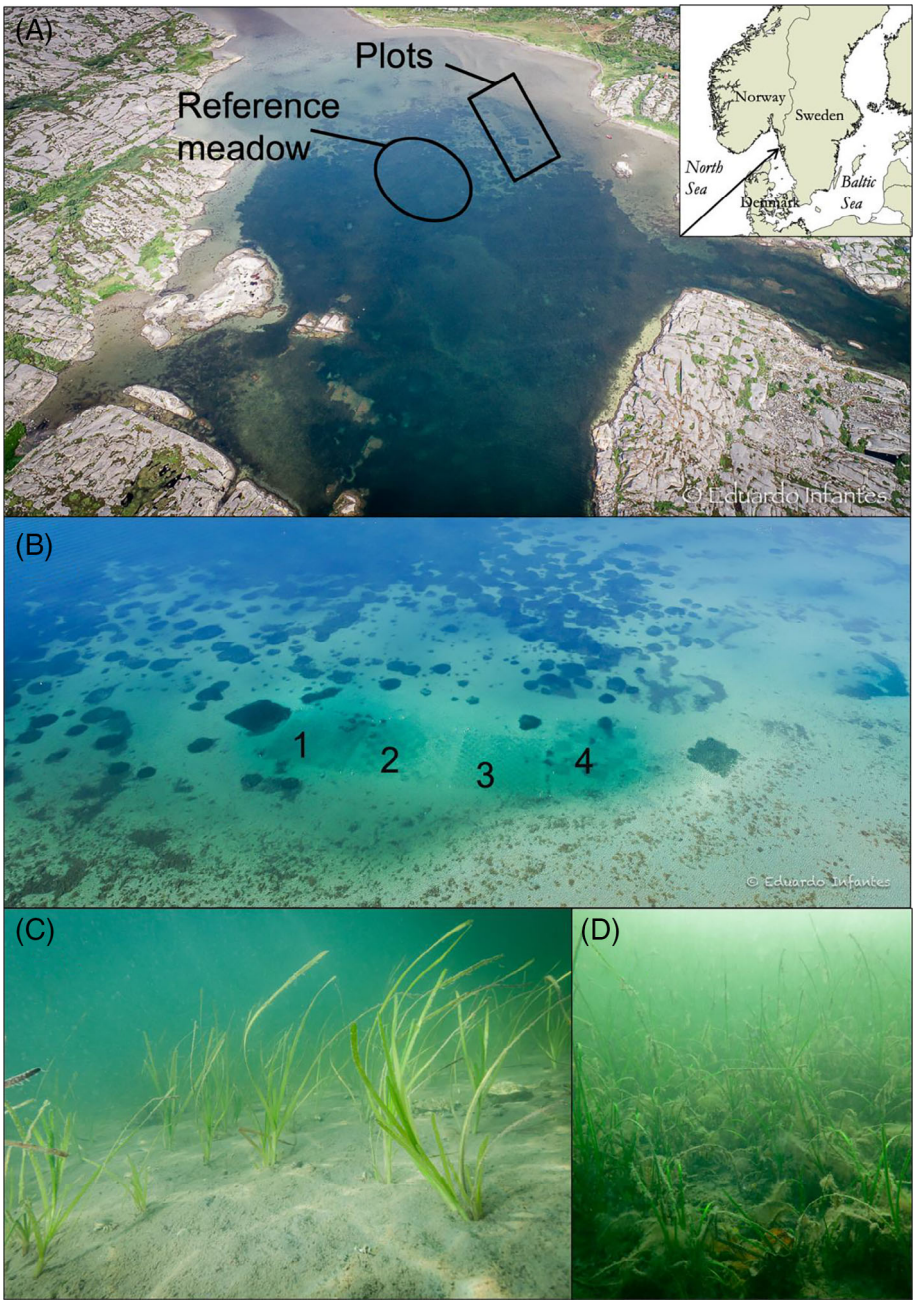

Figure 1. (A) Overview of the study site (Gåsö, 58.233 N, 11.400 E) with reference eelgrass meadow (the area where samples were taken is indicated by a circle) and planted plots (located in the box in upper right corner). (B) Detail of planted plots in July 2019 (∼1 month after transplantation): 1 = continuous, 2 = medium patches, 3 = small patches, 4 = large patches. The two dark plots on either both sides of the transplanted plots are eelgrass plots which were transplanted in 2015 as a pilot experiment to test the feasibility of the site and transplantation method. There is a slight depth gradient: the meadow extends from 2 to 5 m depth, while plots 1–3 are at ∼2 m depth, and plot 4 is slightly shallower (1.5–2 m). (C) Eelgrass shoots in a planted plot shortly after transplantation (July 2019). (D) Eelgrass in a planted plot after two growing seasons (September 2021) showing expansion and spread. Photographs by Eduardo Infantes.

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ephemeral macroalgae over eelgrass (Moksnes et al. 2008; Baden et al. 2010, 2012). Though overall water quality in the area has improved following reductions in nutrient input, eelgrass populations have not recovered due to feedbacks preventing natural recovery (Nyqvist et al. 2009; Moksnes et al. 2018). Initial attempts at small-scale restoration using seeds or shoots in Nordic eelgrass meadows have shown only limited success (Eriander 2016; Infantes et al. 2016*a*; Infantes & Moksnes 2018; Gagnon et al. 2021*a*, 2021*b*). Globally, large-scale restoration of seagrass meadows is associated with positive outcomes (Tanner et al. 2008; van Katwijk et al. 2016; Paulo et al. 2019; Lange et al. 2022), as it allows for the development of facilitative mechanisms between shoots that increase sediment stability, limit resuspension, and promote growth and survival of shoots (van der Heide et al. 2011; Maxwell et al. 2017). Large-scale restoration can be achieved through either seed or shoot transplantation. However, previous studies in the area have shown lower success using seeds than shoots due to the low number of seeds produced in the meadows (Infantes & Moksnes 2018), and the high presence of eelgrass seed predators such as *Carcinus maenas* (Infantes et al. 2016*b*) such, large-scale restoration using shoot transplantation has been recommended in the national guidelines for eelgrass restoration in Sweden (Moksnes et al. 2016). Due to the high number of shoots required for large-scale restoration using the shoot transplantation method, developing strategies to reduce the operational costs of planting and minimize effects on donor meadows is critical. As eelgrass can spread laterally, planting in an alternating checkerboard pattern of vegetated and non-vegetated patches could reduce the number of transplanted shoots needed while still maintaining facilitation between shoots that allows for high growth, spread, and the recovery of associated fauna.

The faunal colonization of restored seagrass ecosystems is an essential step toward the recovery of the ecosystem as whole, as the functional traits of associated fauna drive ecosystem and trophic functioning (Carlucci et al. 2020). Indeed, along with biodiversity, functional diversity should be considered a critical measure of ecosystem recovery (Cadotte et al. 2011). However, despite a growing number of eelgrass restoration projects around the world, only a few large-scale trials have focused on the recovery of associated biodiversity (generally noting rapid faunal colonization; Orth et al. 2020; Steinfurth et al. 2022), and none have considered functional diversity. Structural complexity (shoot density, patch size, patch shape) is a major driver of faunal composition and associated functional traits in seagrass meadows (Moore & Hovel 2010 and references therein; Yeager et al. 2019) and is thus likely to shape the trajectory of faunal communities following restoration. In particular, patch size can affect invertebrate faunal colonization through multiple mechanisms, especially through edge effects. Particle trapping by eelgrass blades at patch edges may reduce food availability at the center of larger patches (Irlandi et al. 1999; Reusch & Williams 1999), while promoting higher settlement of planktonic larvae at edges (Orth 1992; Carroll et al. 2012), leading to overall higher densities in smaller patches with larger edge proportions. On the other hand, predation may also be higher in smaller patches, due to predators often preferring edges (Irlandi 1997; Bell et al. 2001). Due to the interacting nature of these mechanisms, reviews have shown that the effects of patch size and shape on different faunal groups are overall highly variable, species- and context-dependent, and difficult to predict (Boström et al. 2006; Yarnall et al. 2022 and references therein).

Table 1. Functional traits and modalities used in the functional analyses.

Trait	*Modalities*
Maximum size	<1, 1–5, and 5–10 mm, 1–5 and >5 cm
Environmental position	Infaunal, epibenthic
Longevity	<1, 1–2, 2–5, and >5 yr
Reproduction type	Sexual, asexual
Reproductive strategy	Semelparous, iteroparous
Reproductive mode	Broadcast spawner, egg layer, egg brooder
Pelagic stage	No, yes
Mobility	Sessile, semi-mobile, mobile
Movement/ attachment type	Swimmer, crawler, attached (e.g. byssus), tube builder, burrower
Feeding mode	Suspension feeder, surface feeder, subsurface feeder, grazer, predator (including one parasite species)
Diet	Detritivore, herbivore, carnivore

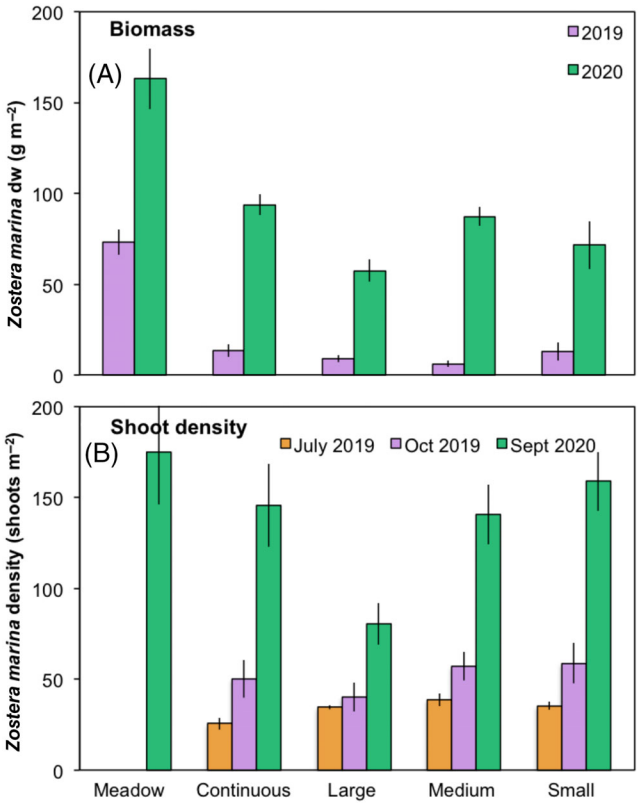

Figure 2. Eelgrass biomass and shoot density (mean ± SE) in the meadow and planted plots in 2019 (orange = after 1 month, purple = after one growing season) and 2020 (green = after two growing seasons).

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Thus, it is difficult to predict how planting configuration and patch size could affect the faunal colonization following seagrass restoration.

In this study, we investigated the role of planting configuration, scale, and temporal variability in determining invertebrate biodiversity, functional diversity, and community structure in restored eelgrass. We followed invertebrate (infauna and epifauna) colonization, and their associated functional traits, during the first two growing seasons of an eelgrass restoration trial in the Skagerrak, Swedish west coast. We focused on small meio- and macro-faunal assemblages (0.2–20 mm), which are likely to reflect potential differences in edge effects (e.g. recruitment, food availability, predation pressure) between patch sizes.

Methods

Study Area

The field experiment was set up in June 2019 in a semi-sheltered bay near the island of Gåsö (58.233 N, 11.400 E; Fig. 1) on the Swedish west coast (Skagerrak). Until the 1980s, the bay was almost entirely covered by eelgrass, but the shallow areas have since retracted (Baden et al. 2003). Currently, the site has a dense eelgrass meadow at 2–5 m depth, which was used as the reference meadow (hereafter referred to simply as "the meadow"; Fig. 1). The eelgrass growing season in the area is from May–October, with maximum biomass in August (Baden & Pihl 1984). Two eelgrass transplantation plots (10 × 10 m) were set up in 2015 and have survived and since expanded (Fig. 1), showing the suitability of the area for further restoration. In 2019, four 20 × 20 m plots were set up on unvegetated soft sediment (1.5–2.5 m depth) between the two previous successful 2015 trials. These consisted of four different treatments (Fig. 1): one treatment was planted at the same density throughout ("continuous") and the other three in a checkerboard pattern of alternating planted and non-planted patches of different sizes ("large": 4 × 4 m patches, "medium": 2 × 2 m patches, "small": 1 × 1 m patches; Fig. 1). Eelgrass shoots were collected from the reference meadow and planted by hand the same day (using scuba diving) at a density of 16 shoots m^{-2} (25 cm apart from each other), for a total of ~6,400 shoots in the continuous plot and ~3,200 in the large, medium, and small plots. Each single shoot planted had a ~10-cm rhizome fragment with at least two to five internodes and was gently pushed into the sediment (Orth et al. 1999).This planting method using shoot transplantation is the recommended practice for eelgrass restoration in Sweden, to minimize shoot loss with relatively low time and costs (as described in Eriander et al. 2016; Moksnes et al. 2016).

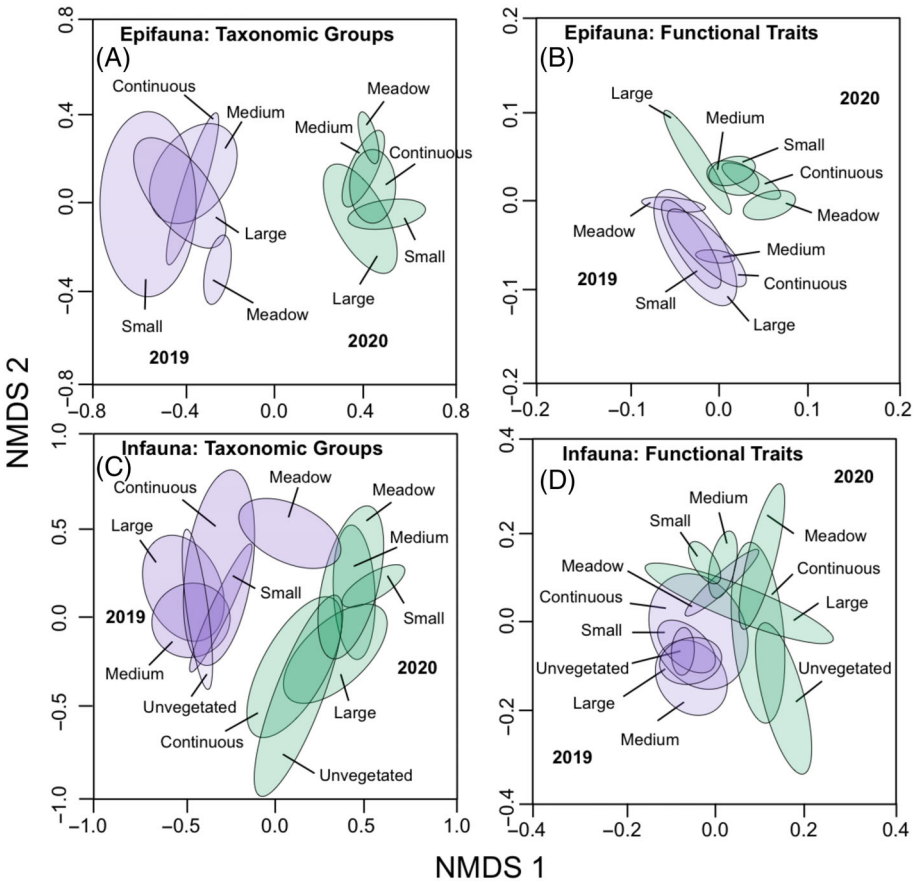

Figure 3. NMDS ordination plots of epifaunal and infaunal communities, based on taxonomy and functional traits. Ellipses are ellipsoid hulls that enclose all points in the group. Purple = 2019, green = 2020.

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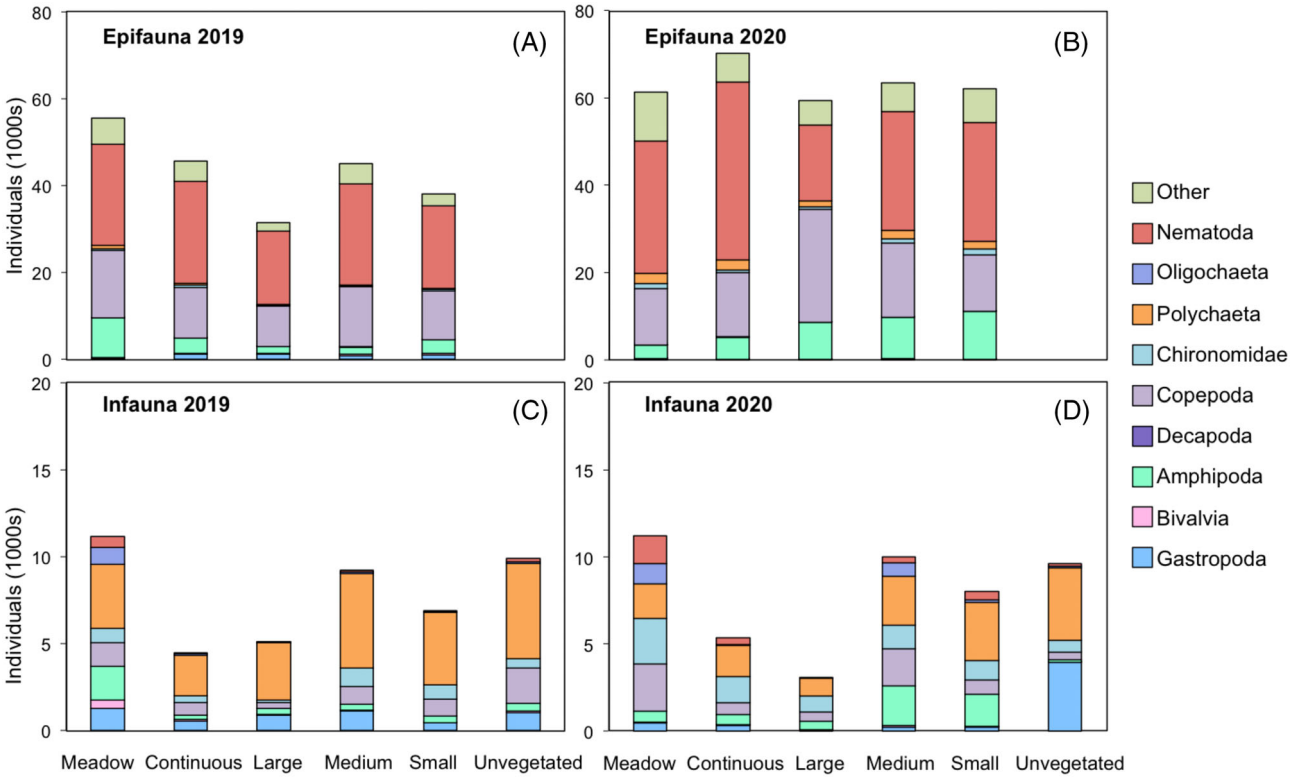

Figure 4. Faunal taxonomic composition and overall abundance of Zostera epifauna and infauna in September 2019 and 2020. "Other" includes Ostracoda, Halacaridae, Nemertea, Platyhelminthes, Foraminifera, Cnidaria, Porifera. See Figures 5 and S3 for detailed breakdown by group, and Table S1 for full statistical results.

Sampling and Processing

Eelgrass. We measured shoot densities in July 2019 (1 month after transplantation), October 2019 (after one growing season), and September 2020 (after two growing seasons). In 2019, only the planted plots were measured, while in 2020, the reference meadow was also sampled (within the meadow at least 10 m from the edge; Fig. 1). Shoot densities were measured by counting the number of shoots in 8–10 random 50 × 50 cm quadrats in each planted plot, and six random quadrats in the meadow. We also measured eelgrass aboveground biomass during the epifaunal sampling: after separating the shoots from the fauna, we dried them at 60°C for 72 hours, then calculated eelgrass dry weight m^{-2} for each sample.

Fauna. We sampled epifauna and infauna in September 2019 (after one growing season) and September 2020 (after two growing seasons). Five epifauna and infauna samples were randomly taken from the meadow and from each transplanted plot. All samples were at least 2 m away from each other, and at least 0.5 m from the patch edge to limit edge effects. We took an additional five infauna samples from the unvegetated sediment to represent the ambient infauna community which would have been already present in the area prior to establishing the transplanted plots. Epifauna samples were collected by placing a 35 × 35 cm mesh bag (mesh size 0.2 mm) over the eelgrass shoots, closing the bag, and cutting the shoots at the sediment surface. Infauna samples were collected using a 10.5 cm diameter core to a sediment depth of 10 cm. All samples were transported to the laboratory in seawater. For logistical reasons (space and time limitations, and COVID-19 restrictions), samples were processed in slightly different ways. In both 2019 and 2020, infauna samples were immediately sieved at 0.5 mm, then preserved in ethanol with Rose Bengal staining. Epifauna samples in 2019 were stored in mesh bags in flow-through aquaria for 1–2 days so they could be processed and counted while fresh, while in 2020 they were immediately frozen in bags with seawater then processed several months later. In both cases, eelgrass shoots were first separated from the epifauna, counted, and dried (60°C for 48 hours) to obtain eelgrass biomass (see above) in each sample. The epifauna were then sieved at 0.2 and 1.0 mm to obtain two size fractions ("meiofauna" and "macrofauna," respectively), and preserved in ethanol with Rose Bengal staining.

In the laboratory, we counted and identified all organisms to the lowest practical taxonomic level. For the infauna and epifauna "macrofauna" fraction, we counted all organisms in the sample, while for the epifauna "meiofauna" fraction, we counted organisms in three subsamples (~0.5 g wet weight each) and then calculated the total abundance based on the total weight of the sample. We then combined the "meiofauna" and "macrofauna" to obtain the total abundance of epifauna in each sample.

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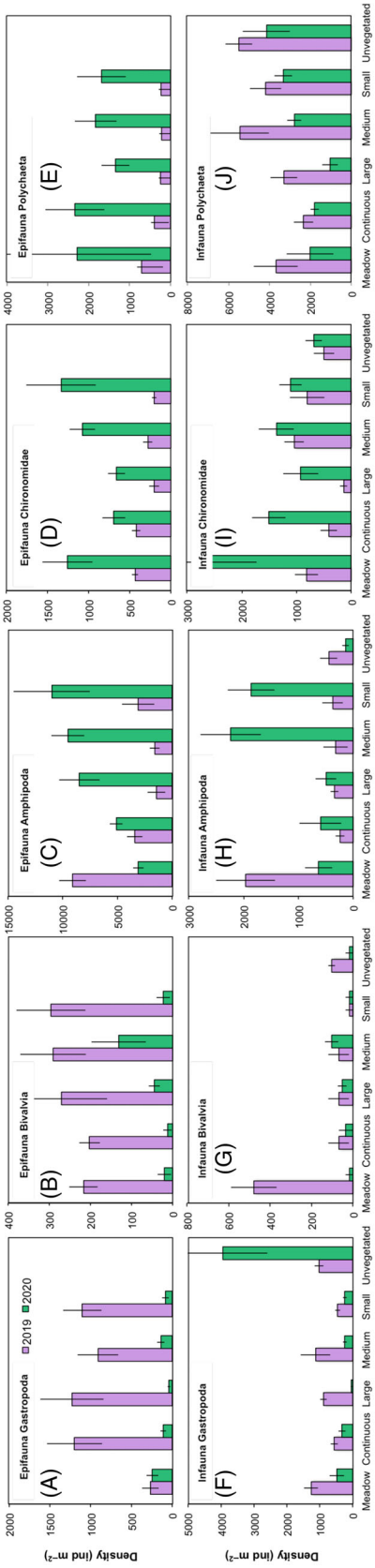

Figure 5. Density (mean ± SE) of selected taxonomic groups in different treatments in 2019 (purple) and 2020 (green). See Figure S3 for additional groups and Table S1 for full statistical results.

All infauna and epifauna values were then converted to density (individuals m^{-2}).

Functional Traits

For each taxon, we created a functional trait matrix, which included 11 traits linked to life history, dispersal, mobility, and feeding (adapted from Törnroos & Bonsdorff 2012; Table 1). For each sample, we calculated three taxonomic diversity metrics (species richness, Shannon diversity, evenness) and four functional diversity metrics (functional diversity, functional evenness, functional dispersion, functional divergence). We also calculated the community weighted mean (CWM) of each trait for each sample. Diversity and functional metrics were calculated using the *FD* (Laliberté & Legendre 2010; Laliberté et al. 2014) and *vegan* (Oksanen 2013) packages, respectively, in R version 3.6.2.

Statistical Analysis

We used generalized linear mixed models (GLMMs) with Poisson distribution to determine differences between treatments and time for eelgrass biomass and shoot density. For the fauna analyses, we first used multivariate approaches (non-metric multidimensional scaling [NMDS] and permutaional multivariate analysis of variance [PERMANOVA]) to determine differences in communities based on both taxonomy and functional traits (based on the CWM), then similarity percetange analysis (SIMPER) to run pairwise comparisons and determine which species and traits contributed to differences between years, planted plots and the meadow within each year, and planted plots and the unvegetated sediment within each year. As SIMPER will usually return the most abundant species rather than the species that differ the most, we also calculated pairwise ratios of the density of species or traits in 2019 versus 2020, planted plots vs. meadow within each year, and planted plots vs. unvegetated within each year, and determined the species which varied the most. All multivariate analyses were run using the *vegan* package in R version 3.6.2. We then used GLMMs (with normal distribution for diversity and functional metrics, negative binomial distribution for most invertebrate densities; see Tables S3 and S4 for all distributions) to determine if there were differences between treatments and years for total epifauna and infauna density, selected taxonomic groups (Bivalvia, Gastropoda, Amphipoda, Copepoda, Decapoda [epifauna only], Ostracoda [epifauna only], Chironomidae, Halacaridae [epifauna only], Polychaeta, Oligochaeta [infauna only], Nematoda, diversity and functional metrics).

Results

There was a significant interaction of Year × Treatment on eelgrass metrics (Table S1): overall, eelgrass biomass and shoot densities were lower in the planted plots than in the reference meadow in both years, but were higher in all treatments in 2020 than 2019 (Fig. 2). Transplanted eelgrass shoots grew laterally in all directions, resulting in higher densities within the planted plots, as well as extension outside the plots with time (Fig. 1).

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The epifauna and infauna taxonomic and functional traits varied significantly by year and treatment (PERMANOVA $p < 0.001$ for all; Table S2). Epifauna communities were taxonomically and functionally different in 2019 and 2020, though in both years there was high overlap between planted plots, but less overlap with the meadow (Fig. 3A & 3B). Infaunal communities differed taxonomically between years, but there was some overlap in functional traits (Fig. 3C & 3D). Epifauna species and functional richness were higher in 2019 than 2020, but other biodiversity and functional diversity indices were similar across treatments and years (Figs. S1 & S2).

Total epifauna abundance in 2019 was higher in the meadow, followed by the continuous and medium plots, then the small plot and large plot, while in 2020 abundance was highest in the continuous plot while the others were similar (Fig. 4A & 4B). Total infauna abundance was highest in the meadow, followed by the unvegetated sediment, medium, and small plots, and this pattern was similar in both years (Fig. 4C & 4D). Taxa which were most abundant also had the highest contribution to dissimilarity (i.e. Nematodes, Copepods, Capitellids, Hydrobids, Chironomids; Tables S3 & S4), but these were not necessarily the species which differed the most between treatments and years (Table S5). Among the most notable differences were the almost complete disappearance of gastropod and bivalve species in 2020 in all treatments except unvegetated sediment where *Retusa trunculata* was very abundant (Table S5; Fig. 5).

The GLMM analyses showed that for most taxonomic groups, the Year × Treatment interaction was significant, with no consistent patterns across groups. In most cases, the magnitude of difference was larger between years than between treatments (Table S1; Figs. 5 & S3). As noted above, we found an almost complete absence of gastropods and bivalves in all treatments in 2020 (Figs. 4 & 5). Decapods (mostly *Palaemon* spp.) were also more abundant in 2019 than 2020 in most treatments (Fig. S3). On the other hand, chironomids, epifaunal polychaetes, and platyhelminthes were much more abundant in

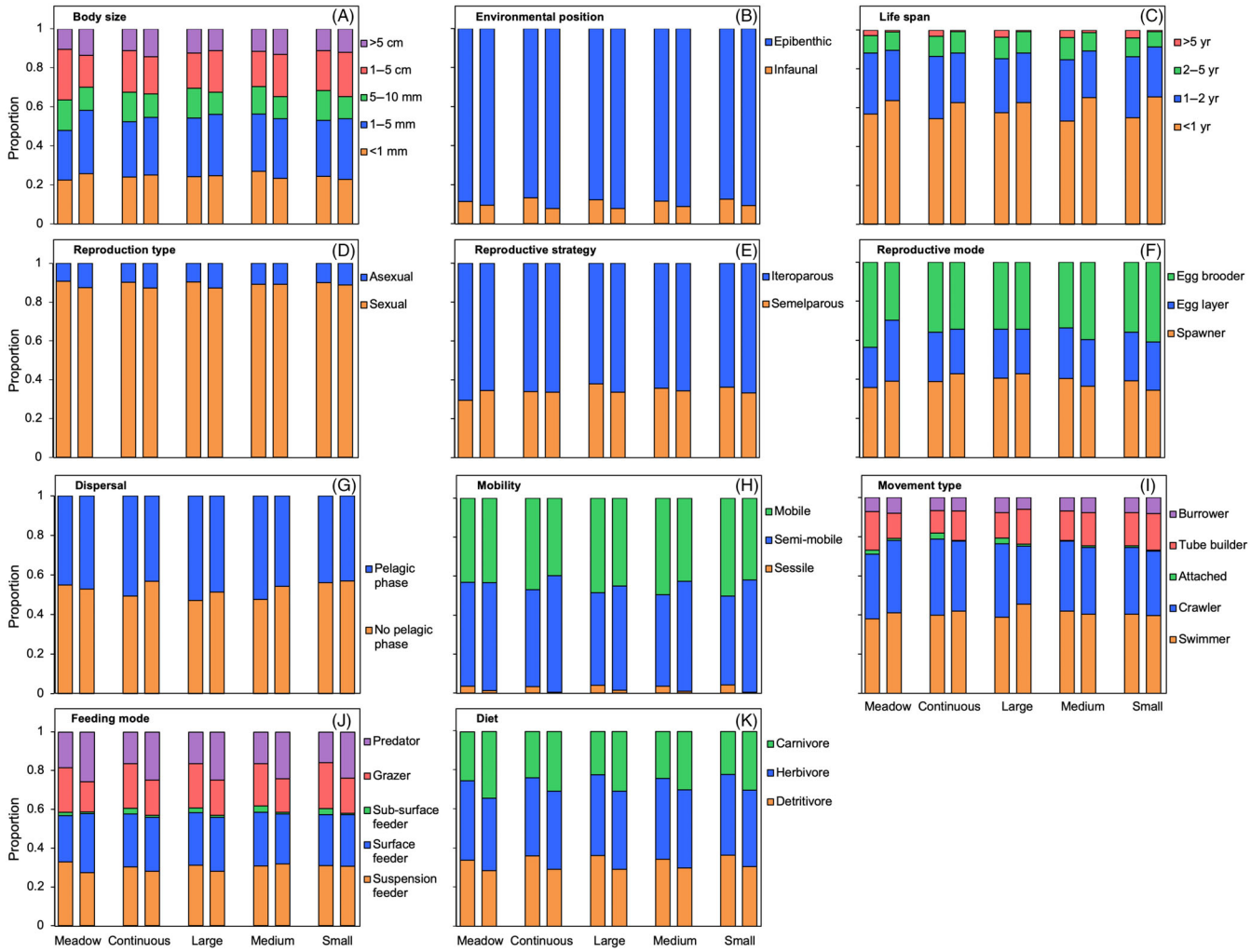

Figure 6. Proportional community weighted mean traits of epifauna in 2019 and 2020,

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2020 than 2019 (Figs. 5 & S3), but this pattern was reversed in 2020, particularly in the medium and small plots (Fig. 5). Amphipods were more abundant in the meadow than the planted plots in 2019, but more abundant in the smaller planted plots than the meadow in 2020 (Fig. 5). Finally, infaunal polychaetes were more common in the unvegetated sediment and in the medium and small planted plots than the meadow and larger plots in both years (Fig. 5).

The relative proportion of most epifauna and infauna functional traits were similar across treatments and years (Figs. 6 & 7). Among the notable differences between years for both epifauna and infauna were shifts in life span (a decrease of long-lived (>5 years) and increase in short-lived (<1 year) organisms), mobility (a decrease in mobile organisms), feeding mode (a decrease of sub-surface feeders and increase in predators), and diet (a decrease of detritivores and increase in carnivores) (Figs. 6 & 7).

Discussion

Eelgrass and Faunal Recovery

Both the shoot density and biomass of eelgrass in the planted plots increased from 2019 to 2020, though they had not yet reached the values observed in the reference meadow. We also noted a twofold difference in eelgrass biomass within the meadow between 2019 and 2020. This may be due to differing environmental conditions such as light or temperature, which could have affected growth over the season or slight differences in the timing of the natural leaf loss in late summer (Baden & Pihl 1984). Despite lower eelgrass density and biomass than in the reference meadow, colonization of the planted eelgrass plots by epifaunal invertebrates was rapid: within one growing season (3 months), epifaunal density was 50–75% that of the meadow, and within the range of previously published data on eelgrass epifauna density in the Skagerrak (Baden 1990; Riera et al.

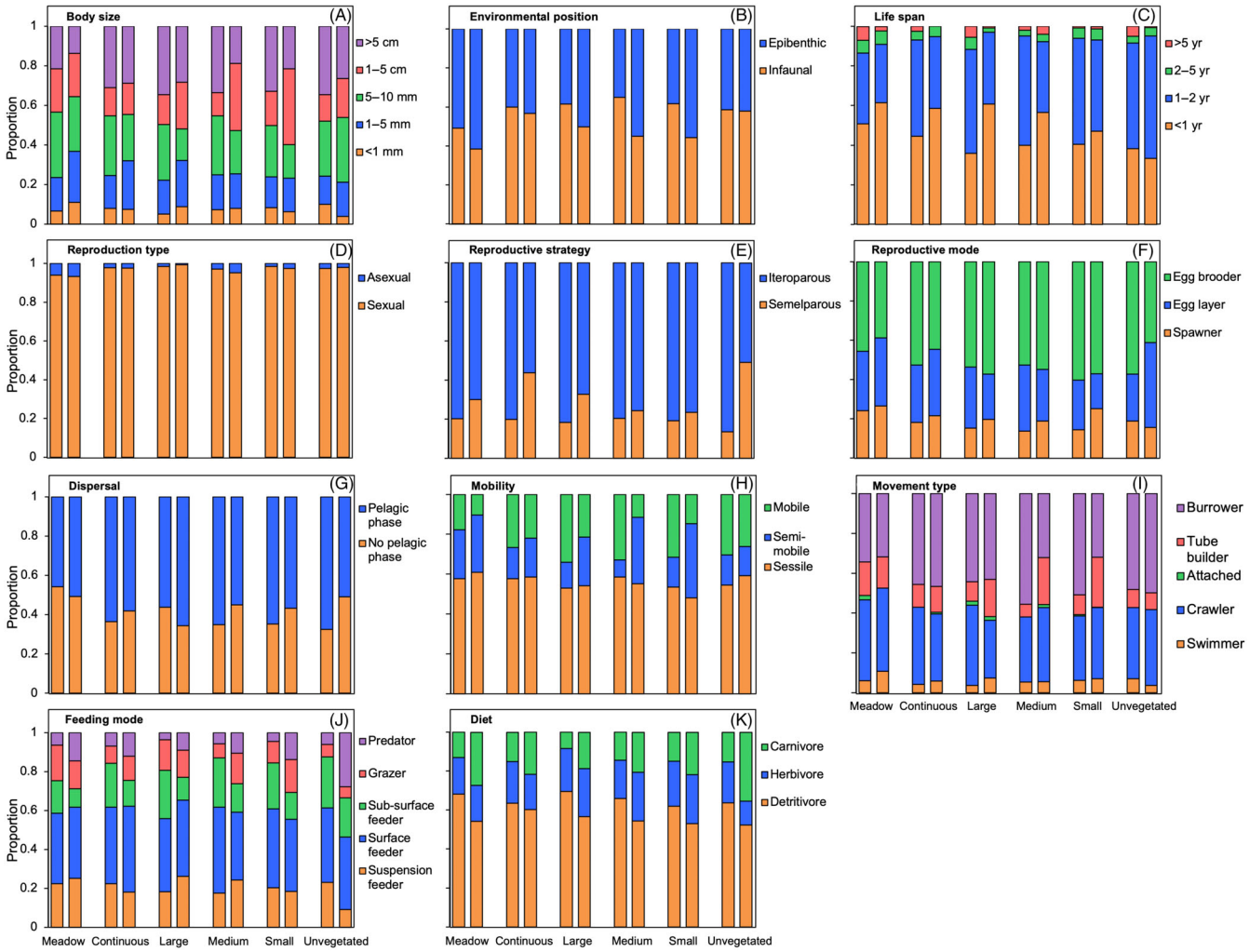

Figure 7. Proportional community weighted mean traits of infauna in 2019 and 2020.

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2020). Riera et al. (2020) also found no correlation between epifauna abundance and eelgrass biomass within a wide range (21–286 g DW m^{-2}) of eelgrass biomass, and here we show that a relatively low threshold of eelgrass biomass (10–20 g DW m^{-2}) was needed to support a large and diverse invertebrate community. After 15 months (two growing seasons), epifauna (including meiofauna) density as well as taxonomic and functional diversity metrics were similar between the meadow and planted plots, indicating a recovered epifaunal invertebrate community. Colonization of infaunal invertebrates was slightly slower: after two growing seasons, density was still lower in the planted plots than the meadow, while diversity metrics were similar to the meadow in only two of the four plots. This may reflect a higher proportion of sessile species in the infauna community, a longer time for colonization due to the presence of an existing infauna communities in the bare sand, or longer recovery times for sediment properties and belowground seagrass biomass. For example, though organic carbon and infauna abundance recovered within 2 years in a restored *Amphibolis antarctica* meadow, it took 4–6 years for faunal richness, belowground biomass, and sediment grain size to become similar to natural seagrass (Tanner et al. 2021).

Patterns in Faunal Composition and Functional Traits

We expected that differences in, for example, differential trapping or predation pressure caused by the different patch sizes might shape the invertebrate communities in the different treatments as previously observed in many studies (Boström et al. 2006; Yarnall et al. 2022 and references therein). However, we did not observe any consistent relationships between patch size and the density of any of the faunal groups, nor were any of the patterns we observed consistent between years. We did note that several measures (eelgrass density, eelgrass biomass, total faunal abundance) indicated that the "Large" treatment was the least effective, but this is likely a reflection of this plot being located slightly shallower than the others, and subject to different environmental conditions (pers. obs.). Nematodes and harpacticoid copepods were the most abundant epifaunal groups, with similar densities in the planted plots and the meadow, as seen in previous studies of seagrass fauna in the area (Baden 1990; Riera et al. 2020) while the infauna was dominated by polychaetes. However, due to different sieve size used (0.2 mm for epifauna vs. 0.5 mm for infauna), the two groups are not directly comparable.

In 2019, epifaunal gastropods (mostly Rissoid species) in the planted plots quickly reached densities higher than the meadow and on par (1–2000 m^{-2}) with previous studies (Baden 1990; Riera et al. 2020). These species are opportunistic, fast colonizers with planktotrophic larvae and play an important role as epiphyte grazers (Jaschinski et al. 2011; Ávila et al. 2012). In the infauna samples, gastropods were represented mostly by epibenthic Hydrobids, and these were present in similar densities in the meadow, planted plots, as well as bare sand plots. Hydrobids are generalist detritus feeders, and not specifically associated with eelgrass. Epifaunal bivalves (dominated by the blue mussel *Mytilus edulis*) also quickly colonized planted eelgrass in the first year and were more abundant in the checkerboard plots than the meadow and continuous plots. This likely represents an edge effect in which the eelgrass blades are trapping bivalve larvae (Carroll et al. 2012). On the other hand, infaunal bivalves (including epibenthic *My. edulis* and infaunal *Macoma balthica*) were much less common in the planted plots than in the meadow. Eelgrass shoots likely represent temporary habitat for juvenile bivalves, which settle on the shoots in early summer, but migrate to become epibenthic in late summer, either within the eelgrass or in rockier habitats (Möller et al. 1985; Baden 1990; Boström & Bonsdorff 1997; Baden et al. 2021). Both mussels and clams may play an important role in fertilizing and stabilizing sediment and thus facilitating restored seagrass (Gagnon et al. 2020; Meysick et al. 2020). In 2020, both gastropods (dominated by Rissoids) and bivalves (dominated by *My. edulis*) had unusually low abundances in all treatments (except for carnivorous *Retusa truncatula* in unvegetated plots), though the reasons for this are unclear. One possible explanation could be much higher densities of the invasive ctenophore *Mnemiopsis leidyi* along the Swedish west coast in 2020 than 2019 (3–5 times higher densities; data from Swedish Meteorological and Hydrological Institute SMHI, https://sharkweb.smhi.se/hamta-data/). *Mnemiopsis leidyi* blooms from August could potentially decimate the planktotrophic larvae of small gastropods settling in eelgrass in late summer (Baden 1990), but further sampling and experimentation would be needed to verify this.

Both epifaunal (*Ericthonius* spp., *Microdeutopus gryllotalpa*, *Monocorophium insidiosum*) and infaunal (*Corophium volutator*) amphipods were less abundant in the planted plots than meadow in 2019, indicating slower colonization than mollusks. However, in 2020, this trend was reversed, and they were especially abundant in the smaller plots. As amphipods have non-planktonic reproduction with brood pouches, they may thus have slower colonization of planted plots. However, once established, they may move to the smaller plots due to lower predation from intermediate fish predators which avoid the less dense planted plots and open spaces between (Baden et al. 2012). Though our sampling method was not targeted toward larger invertebrates, we found higher densities of decapods (especially *Palaemon* spp.) in 2019 than 2020. Epifaunal polychaete (mostly *Platynereis dumerilii*) density decreased with plot size but was 3–5 times more abundant in 2020 than 2019. As this species builds tubes on seagrass shoots, this likely represents a response to higher substrate availability. On the other hand, infaunal polychaetes (dominated by *Capitella capitata* and several Nereid species) were more abundant in the medium and small plots, in similar densities to the unvegetated plots, while they were less abundant and more similar to the meadow in the continuous and large plots. This likely reflects a longer transition time from the original infaunal communities to the eelgrass-associated communities in smaller plots. Chironomid larvae were more common in 2020 than 2019, though with no consistent differences between treatments, supporting another recent study showing that they have become an important part of the faunal communities in eelgrass meadows over the last 20 years (Riera et al. 2020). Other faunal groups were highly variable, and overall, there was no clear plot size favored across groups.

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This study is one of the first to explore how functional traits recover in restored eelgrass. In this case, we found that, as species composition was similar between the meadow and the planted plots, the functional trait composition also reflected this similarity. The shift we observed in some functional traits between years also reflects the temporal shift in community composition. Invertebrate communities in both the meadow and planted plots showed a diverse range of functional traits, including multiple sizes, trophic positions, feeding modes, and mobility. Somewhat surprisingly, we found only a slight increase in the proportion of individuals with a pelagic larval phase in the planted plots in the infauna only, and no difference in the epifauna, indicating that invertebrates are not only colonizing through larval dispersal. Other dispersal mechanisms are also at play, with some larger organisms likely colonizing through their own power (especially epifaunal species, which include many species able to swim or crawl such as crustaceans), or through rafting or drifting with tidal currents from the meadow to the planted plots in the shallower part of the bay (Edgar 1992; Orth 1992; Boström & Bonsdorff 2000). Here, the distance between the plots and the meadow was <100 m; pelagic larval dispersal is likely to be more important in the colonization of restored seagrass areas that are further from intact meadows.

The Importance of Patch Size and Temporal Variation

The lack of consistent relationships between patch size and density or invertebrate body size indicates that patch size was not a primary driver of invertebrate colonization, despite a large body of literature indicating the contrary due to differences in, for example, predation pressure or food availability (Irlandi 1997; Bell et al. 2001). However, differences between the planted plots and meadow were noticeable, some of which could potentially be attributed to differing densities of intermediate predators. However, our sampling was aimed at small invertebrates, and though we did capture some larger decapod predators (*Palaemon* spp., *Carcinus maenas*), additional sampling using traps, gill nets, or video monitoring would be needed to explore whether and how mesopredators use the planted plots in comparison to the meadow. Predation, particularly by fish, is known to have a strong influence on eelgrass ecosystems in the North and Baltic Seas, and trophic cascades caused by changes in predator communities have been linked to shifts in eelgrass and associated communities (Baden et al. 2012). Here, we observed a strong shift in community structure (also reflected in the functional traits) between 2019 and 2020, particularly a notable decline in mollusks. Though this may have been due to predation by an invasive ctenophore, as described above, predation/consumption assays combined with stable isotope studies would be needed to unravel trophic dynamics in restored eelgrass meadows (as previously carried out in natural meadows; Jephson et al. 2008; Thormar et al. 2016; Gagnon et al. 2021b). Whatever the cause of these community shifts, our results show the complex, dynamic nature of seagrass meadows and their associated communities.

The high temporal variation and community shift we observed also shows that beyond planting methods and scale, monitoring of reference sites and restoration projects deserve careful consideration. Metrics of restored areas should be compared to metrics of the reference site taken at the same time, rather than comparing different areas across different years. The idea of a "restored state" should not be considered as a static measure, but instead focused on a community that resembles the current reference site both taxonomically and functionally. Given the similarity in communities between the meadow and the planted plots, we assume that the meadow is acting as a source population for most species. In cases where natural seagrass meadows are further away, the choice of a reference site may be more difficult, as restored communities may instead reflect ambient available communities in surrounding habitats, which might be rockweed or filamentous algae. Overall, we show that restored eelgrass habitats rapidly become habitat for an abundant and diverse invertebrate fauna, which over time is likely to lead to increased ecosystem service provisioning and support increased coastal biodiversity. We therefore suggest that planting eelgrass in a checkerboard pattern can be an effective method for large-scale restoration that results in similar outcomes for the epifaunal and infaunal communities while using fewer shoots than planting in a continuous method. We expect that, as the eelgrass continues to grow and fill the bare patches between plots, forming a continuous meadow, the restored habitat will provide similar biodiversity and production to support higher trophic levels as natural meadows do. In a practical sense, as faunal abundance and diversity were similar across plots, the best practice is likely to consider patch sizes that are most efficient to plant in a specific environment. We also note that without replicating this study in a variety of environmental conditions, these results may not hold true in, for example, highly hydrodynamic areas, where less space between plots may be necessary to maintain intraspecific facilitation. Although we show seagrass restoration is an effective method to rapidly enhance coastal biodiversity, we point out the importance of context-dependency and testing methods to ensure their effectiveness in different environmental settings.

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Supporting Information

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

Table S1. Statistical tables for all GLMMs.
Table S2. PERMANOVA results of differences in community structure.
Table S3. Mean densities of epifaunal taxa and contribution to dissimilarity.
Table S4. Mean densities of infaunal taxa and contribution to dissimilarity.
Table S5. Faunal taxa which differed the most between years, planted plots and the meadow, and planted plots and the unvegetated sediment.
Figure S1. Taxonomic diversity metrics of eelgrass epifauna and infauna communities.
Figure S2. Functional diversity metrics of eelgrass epifauna and infauna communities.
Figure S3. Density of additional taxonomic faunal groups in different treatments.

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