



Benthic fauna dynamics following large-scale seagrass restoration in an exposed environment

Theodor Kindeberg, Per Carlsson, Johan Hollander

► To cite this version:

Theodor Kindeberg, Per Carlsson, Johan Hollander. Benthic fauna dynamics following large-scale seagrass restoration in an exposed environment. *Restoration Ecology*, 2025, 34 (3), pp.e70248. <10.1111/rec.70248>. <hal-05608591>

HAL Id: hal-05608591

<https://hal.science/hal-05608591v1>

Submitted on 30 Apr 2026

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons CC BY 4.0 - Attribution - International License

RESEARCH ARTICLE

Benthic fauna dynamics following large-scale seagrass restoration in an exposed environment

Theodor Kindeberg^{1,2,3} , Per Carlsson¹, Johan Hollander⁴

Seagrass meadows are vital habitats, modifying hydrodynamic energy flows and sustaining biodiversity in the benthic environment. As such, there is a growing interest in using seagrass as a nature-based solution for coastal adaptation. However, planting seagrass in hydrodynamically exposed environments is challenging, and the trajectories and timescales of biodiversity recovery are not well studied in such environments. In this case study, we present early-stage findings from a large-scale eelgrass (*Zostera marina*) restoration project in Southern Sweden, with a focus on recovery dynamics of the benthic fauna. We observed variable eelgrass establishing rates, ranging from 0 to 200% depending on the timing of restoration, mainly in relation to storm events. In plots with high eelgrass survival, benthic fauna reached taxonomic and functional diversity comparable to adjacent reference plots in natural eelgrass within 4 months. These findings show that single-shoot eelgrass transplantation without any anchoring technique can be feasible in hydrodynamically exposed areas, but timing is key for success. The rapid effects on benthic fauna diversity indicate how ecological integrity can be restored within a growing season. These observations corroborate the importance of seagrass for benthic diversity and are useful for coastal managers considering eelgrass restoration in exposed environments.

Key words: colonization, eelgrass, functional diversity, succession, transplant

Implications for Practice

- Planting eelgrass at wave-exposed sites is a high-risk endeavor, vulnerable to stochastic events.
- Plan for failure and prepare for multiple restoration attempts in exposed areas.
- When successful, benthic fauna communities can recover within one season, displaying biodiversity values on par with reference sites.
- High annual and seasonal variability of fauna community structure needs to be accounted for in monitoring programs.

Introduction

Coastlines are facing pressures due to anthropogenic effects that range from sea-level rise to overexploitation, all leading to coastal squeeze (Dolan & Walker 2006). This amplifies the negative effects of coastal erosion dynamics on many sandy coastlines and different forms of coastal protection measures are required (Temmerman et al. 2013; Chávez et al. 2021). Over the past decades, there has been a growing consensus that applying such measures in a nature-based approach leads to more resilient and multifunctional coastal defenses that can simultaneously support coastal biodiversity (Hanley et al. 2019; Kindeberg et al. 2023).

Out of the many ecosystem services seagrass meadows sustain (e.g. Nordlund et al. 2016), their capacity to attenuate wave energy has led to seagrass restoration being proposed as a nature-based solution (NbS) for climate change adaptation, that can constitute a multifunctional coastal protection measure that

can increase biodiversity values and augment the coastal sink of atmospheric CO₂ (Paul 2018). However, areas needing coastal protection are often exposed and characterized by high wave energy, which introduces additional stressors to newly planted seagrass shoots that lack sufficient root- and rhizome structures to withstand wave and current energy. Consequently, it is difficult to restore seagrass in exposed areas (van Katwijk & Hermus 2000; Paling et al. 2003). However, there are a few examples of successful restoration in areas with high wave energy regimes, for example, in Australia (Paling et al. 2003; Wear et al. 2010), Portugal (Paulo et al. 2019), United Kingdom (Unsworth et al. 2019) and Tanzania (Wegoro et al. 2022). These studies all used anchoring techniques or plugs to enhance shoot survival. Yet, such methods imply higher costs compared to single-shoot planting, which illustrates potential trade-offs in terms of how many shoots can be planted (Moksnes et al. 2021). Due to density-dependent facilitation of shoots through positive

Author contributions: TK, JH, PC conceived the study; TK, PC carried out fieldwork; TK analyzed data and drafted the manuscript; JH, PC commented on the draft.

¹Department of Biology, Lund University, Sölvegatan 37, 223 62, Lund, Sweden

²Address correspondence to T. Kindeberg, email theo.kindeberg@gmail.com

³Present address: Laboratoire d'Océanographie de Villefranche, Sorbonne Université-CNRS, Villefranche-sur-Mer, 06230, France

⁴Ocean Sustainability, Governance & Management Unit, World Maritime University, Malmö, Sweden

© 2025 The Author(s). Restoration Ecology published by Wiley Periodicals LLC on behalf of Society for Ecological Restoration.

This is an open access article under the terms of the [Creative Commons Attribution License](#), which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

doi: 10.1111/rec.70248

Supporting information at:

<http://onlinelibrary.wiley.com/doi/10.1111/rec.70248/supinfo>

feedbacks on hydrodynamic exposure and light availability, there may exist a lower threshold of planting density. Indeed, the initial number of shoots planted is positively related to survival rate but success ultimately relies on the planting method (van Katwijk et al. 2016).

Seagrass meadows facilitate biodiversity as a foundation species, providing habitat for a wealth of organisms that range from microalgae to fish (Boström et al. 2006; Duffy 2006; Unsworth et al. 2018). They comprise communities of infaunal and epifaunal macroinvertebrates which are important for ecosystem functioning, and re-planting seagrass is an important conservation measure to improve coastal biodiversity (Orth et al. 2020). While studies have shown that restored seagrass meadows can reach the same level of associated species (e.g. Reynolds et al. 2016; Lefcheck et al. 2017), at least in sheltered environments, the timescales of recovery can differ vastly between systems (Benayas et al. 2009). Without information on the timescales of recovery, it is difficult to evaluate if the intended goals of improving biodiversity are met.

An inherent assumption of a NbS is that it has a net positive—or at the very least not a detrimental—effect on biodiversity and nature values, broadly construed (Temmerman et al. 2013; Morris et al. 2018; IUCN 2023). This assumption therefore needs to be carefully monitored following restoration and is an integral component of evaluating the efficacy of the NbS. Ultimately, obtaining evidence that the assumptions of the NbS are fulfilled is critical to positively affect public perception and ensure the legitimacy of NbS projects. In addition, it is important to understand the spatio-temporal dynamics of benthic fauna community structures in seagrass meadows to be able to design monitoring programs and obtain accurate cost–benefit analyses on eelgrass restoration.

Recent studies from Scandinavia have shown fauna recovery within a year following eelgrass (*Zostera marina*) restoration (Steinfurth et al. 2022; Gagnon et al. 2023). However, these studies investigated restored plots in sheltered environments (i.e. semi-enclosed bays or fjords with low wave energy) and with a large natural eelgrass meadow in direct proximity to the restored plots. Moreover, the above studies concern eelgrass restoration projects commenced specifically to restore a lost habitat, rather than to create a multifunctional NbS for coastal protection and biodiversity.

The aim of this study was to (1) assess the feasibility of large-scale eelgrass planting in an exposed environment using the single-shoot method; (2) evaluate the biodiversity effects of restoration, focusing on the dynamics of benthic fauna and their functional traits; and (3) understand how the timing and planting density affect the traits composition and recovery trajectory of benthic fauna when planting eelgrass in an exposed environment.

We transplanted over 30,000 shoots of eelgrass in a wave-exposed area in Southern Sweden and monitored benthic fauna communities over three consecutive years. We evaluated both taxonomic and functional diversity by assessing short-term effects on species and functional traits composition. Concomitant monitoring of adjacent natural reference plots and a continuous meadow further away allowed for assessment of the natural spatial and temporal variability of intact fauna communities.

Methods

Study Area

The west coast of Southern Sweden is characterized by sandy beaches ranging from dissipative beaches with fine sediments and gentle slopes in the southern parts toward progressively more exposed areas toward the north. The area is microtidal (amplitude of approximately 30 cm) and water levels mainly fluctuate due to meteorological conditions including wind and air pressure (Lumborg 2005). The restoration site in Båstad (56.4359°, 12.8516°) is located within the Laholm Bay which is a relatively large (310 km²) and shallow (mean depth 15 m) bay in the southeastern part of Kattegat. Seawater salinity varies on short timescales, with a mean salinity ranging from 18 to 23 during winter and from 11 to 19 during summer months (Wennberg 1992).

The coastline in Båstad is characterized by active sediment transport, with alternating erosion and accumulation. However, due to the high erodibility, the coastline is anticipated to experience coastal erosion with future sea-level rise (Persson et al. 2017). The area is considered moderately exposed to exposure with a fetch length of over 300 km, rendering the site vulnerable to storms from the northwest. The site exhibits a generally mild to moderate wave climate (Wijkmark & Isæus 2010; SGI 2023). Waves are predominantly from the northwest and north, and can reach an estimated maximum significant wave height between 1.0 and 2.7 m based on wave model data (Adell et al. 2023). The mean wave period at the restoration site in Båstad between the years 1979–2019 was 3.4 ± 1.9 seconds but reached up to 10.2 seconds (Adell et al. 2023; SGI 2023). Sediment properties provide further information on the hydrodynamic exposure, and are often used as a proxy for the hydrodynamic regime (Fonseca et al. 1983). Sediment grain size of unvegetated sediments at 2–3 m depth is on average 338 ± 50 µm, moderately sorted and coarse skewed with a silt and clay content below 1% which further implies its exposure to hydrodynamic energy.

Furthermore, information on the historic distribution of eelgrass at this site is sparse and inconclusive, with only anecdotal observations. Other macrophytes including brown macroalgae *Fucus* spp. diminished in the 1980s related to eutrophication-driven expansion of filamentous algae such as *Cladophora* spp. (Wennberg 1987). It is possible that eelgrass in the area was also adversely affected and has not recovered since. Today, only very sparse patches of eelgrass (often ≤ 1 m²) exist, with a maximum observed depth limit at 4.8 m (Emanuelsson et al. 2019).

The reference meadow and the donor meadow (see below) are located in Råå (55.9949°, 12.7373°) and Rydebäck (55.9844°, 12.7572°), respectively, which is approximately 60 km from the restoration site (Fig. 1). These sites are in the Öresund strait between Sweden and Denmark, which is less exposed, ranging from sheltered to moderately exposed based on fetch (Wijkmark & Isæus 2010). As such, the wave climate is mild (38% of waves 0–1 m height), with waves predominantly from the west (Adell et al. 2023; SGI 2023). The area is dominated by a vast continuous eelgrass meadow growing from about

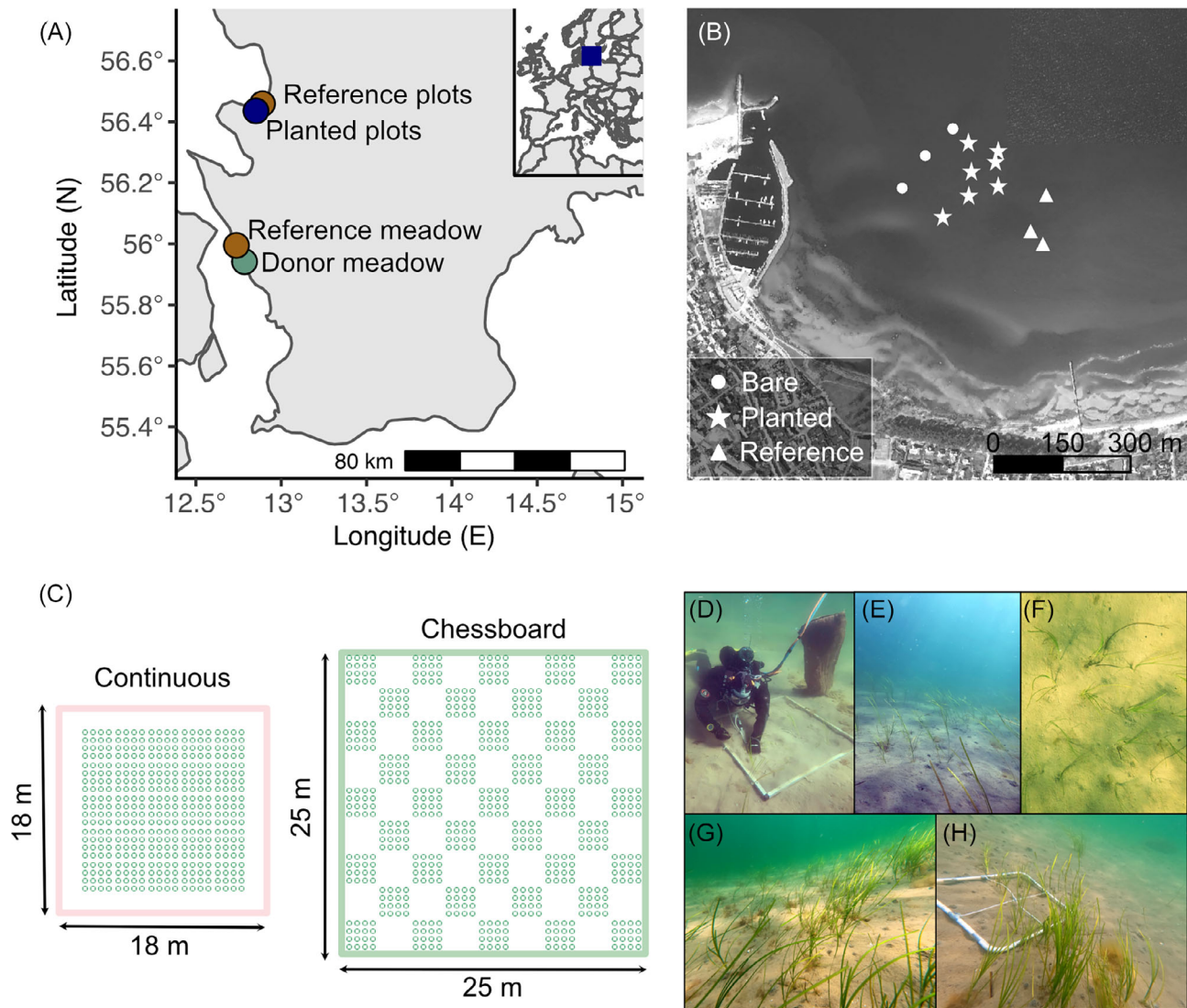


Figure 1. (A) Map of planted plots and reference plots in Båstad and the reference meadow in Råå, with the inset indicating the location of the study; (B) shows the location of bare plots, planted plots and reference plots in Båstad, outlined on orthophoto ©Lantmäteriet; (C) shows schematic of the two planting patterns, (D) shows planting by diver during 2022 and (E) and (F) depicts the newly planted eelgrass; (G) shows one of the continuous plots (BP5) during revisit summer 2023, and (H) illustrates an example of a small eelgrass reference plot in Båstad, the white frame of 0.5×0.5 m is included for scale.

2–7 m depth and extending several kilometers alongshore (County Administrative Board Skåne 2016). Besides transient large abundances of ephemeral algae, eelgrass is the dominant macrophyte (Emanuelsson et al. 2019; Kindeberg et al. 2022). Shoot density (mean $\pm$ SE) at 2–2.5 m depth ranges between 133 ± 30 and 167 ± 20 shoots/m² in June. Mean grain size in bare and vegetated sediments ranges between 280 ± 31 and 235 ± 11 μ m, respectively, further suggesting a milder hydrodynamic regime compared to Båstad.

Eelgrass Restoration

Eelgrass restoration was part of a regional project testing several different nature-based methods to decrease the negative effects of coastal erosion (www.lifecoastadaptenglish.se). The goal

was to evaluate the possibility of planting eelgrass in areas prone to coastal erosion to reduce wave energy during storms. Following test planting in six locations testing multiple planting and anchoring methods, survival, labor cost and feasibility were evaluated for each method and site (see Test planting section in Supplement S1). Based on this evaluation, Båstad (Fig. 1) was selected for large-scale restoration using single-shoot transplantation (Moksnes et al. 2021). Transplantation of 32,384 eelgrass shoots was conducted in 2021 (“Trial 1”) and 2022 (“Trial 2”), totaling a net area (A_n) planted of 2002 m² over a total gross area (A_g) of 3434 m² (Table S1). The area and number of shoots were deemed sufficient to spread risks and induce self-facilitating mechanisms that would respectively increase the chance of restoration success (van Katwijk et al. 2016). During Trial 1 in 2021, the single-shoot method with 16 shoots/m²

was applied in three 25×25 m plots distributed along a depth gradient ranging from 2 to 3 m (Table S1). Plots in Trial 1 were assigned BP1 for the plot at shallow depth (approximately 2 m), BP2 for the intermediate depth plot (approximately 2.5 m) and BP3 for the deepest plot (approximately 3 m; Table S1). Each plot was planted in a chessboard pattern with every other square meter left unplanted (Fig. 1).

The chessboard pattern has been shown to be a cost-effective method, based on the expectation that the planted patches will eventually coalesce into a continuous meadow (Orth et al. 1999; Lange et al. 2022). This planting pattern substantially decreases labor intensity and the number of shoots required while at the same time increases the gross surface area planted. Due to large mortality rates especially in the shallowest plots during Trial 1, additional planting in 2022 was concentrated to a depth between 2.7 and 3.3 m. During Trial 2, two 25×25 plots with chessboard pattern (BP4 and BP7) were planted together with two 18×18 m plots (BP5 and BP6) in which shoots were planted continuously with a shoot density of 16 shoots/m^2 . These plots were included to assess whether the denser pattern would increase self-sustaining feedbacks and thus overall survival (Fig. 1).

Due to the lack of self-sustaining eelgrass meadows outside nature reserves in the restoration area, shoots were harvested from a meadow approximately 60 km away from the restoration site (56.9689° , 12.7517°). Shoots were harvested by SCUBA at a depth between 3.8 and 4.8 m in 2021 and between 3.2 and 3.7 m in 2022. Harvested shoots were transported moist to the restoration site, where they were stored submerged in hessian bags in situ until planting within the recommended 72 hours (Davis & Short 1997).

We evaluated restoration outcomes based on shoot density and areal coverage measurements from two revisits per trial. Trial 1 was revisited in October 2021 and May 2022 whereas Trial 2 was revisited in October 2022 and June 2023. During revisits, we assessed the change in shoot density in each planted plot (BP1–BP7) by counting the shoots in 10 randomly placed 1 m^2 frames per planted plot. In addition, underwater video surveys were carried out along a diagonal transect in each plot. No shoot counting was performed during the June 2023 revisit.

We monitored in situ seawater temperature, irradiance and dissolved oxygen (DO) at the restoration site in Båstad and reference meadow in Råå during the first 3 months of Trial 1. Two Hobo loggers (Onset) recording light (lux) and temperature ($^\circ\text{C}$) every 10 minutes were mounted on a frame at two different depths. From this data we calculated the light-extinction coefficient (Kd) using Lambert-Beer's law as:

$$\text{Kd} = \frac{-\ln(I_{\text{deep}}/I_{\text{shallow}})}{D}$$

where I_{deep} and I_{shallow} are the irradiance in lux at 34 and 100 cm above the bottom, respectively. D is the difference between the two sensors in meters (i.e. 0.66 m). A DO logger (miniDOT, PME Inc., Vista, CA, USA) was mounted next to the deep Hobo logger. The miniDOT recorded DO (mg/L) and temperature

($^\circ\text{C}$) every 10 minutes. Regrettably, the miniDOT and one Hobo logger was lost in Råå resulting in no Kd or DO data from this site. Because of this and due to a temporal mismatch in the deployment of sensors, comparison of light conditions between the sites was not straightforward.

We obtained wind data recorded at a nearby weather station at Hallands Väderö (56.4496° , 12.5453°) from the Swedish Meteorological and Hydrological Institute (SMHI). We extracted maximum mean wind per day for winds coming from 270° to 360° , representing westerly to northerly winds which correspond to the major fetch length direction. We gathered simulated wave data including significant wave height (m), peak wave period (s) and wave direction ($^\circ$) from a wave node located within the restoration site (node 268; 56.43506 , 12.84907 ; Adell et al. 2023; SGI 2023).

Benthic Fauna Surveys

We carried out surveys of benthic fauna following a predefined monitoring scheme sampling planted plots and adjacent natural eelgrass ("Reference plots") 0–1, 3–4, and 12–15 months after restoration (Table 1; Fig. 1). Reference plots were located circa 100–200 m away from restored plots and consisted of multiple small patches (approximately 1 m^2) which varied in their distribution and exact location between years. In addition, bare sediments adjacent to planted plots were sampled during Trial 1 to assess the benthic fauna communities associated with this habitat. Due to high eelgrass mortality rates in the first planting trial, sampling efforts were concentrated on plots with surviving eelgrass and with the addition of four planted plots in 2022 together with the nearby reference plots, it was not feasible to maintain the same sampling regime for bare plots. Consequently, there are no continuous time series of benthic surveys at the restoration site covering the entire restoration period (2021–2023) and benthic fauna data from bare plots are only available from Trial 1 (Table 1).

To census natural temporal variability of intact seagrass communities, we conducted concurrent surveys in the reference meadow in Råå (Table 1; Fig. 1). Together with additional data from the same site from a previous study (Kindeberg et al. 2022), we obtained a biannual time series ranging from 2019 to 2023 capturing seasonal dynamics. No sampling was, however, carried out in 2020 (Table 1).

To sample benthic fauna, we collected 10 cm sediment cores using polyvinyl chloride (PVC) core liners (inner diameter = 7.4 cm; length = 30 cm; $n = 134$). At each survey, a 0.5 m^2 frame was haphazardly thrown three times in each sampling point and a core was collected within the frame via free diving, yielding three cores per point per survey (Table 1). We stored core samples frozen (-20°C) in mesh bags until subsequent analysis. After thawing, we sieved samples through a 0.5 mm sieve, sorted and stored fauna in 70% ethanol. We counted and identified fauna to the lowest taxonomic level possible using a stereomicroscope. Species names were aligned to accepted nomenclature according to the World Register of Marine Species (WORMS; www.marinespecies.org). Using sediment cores predominantly targets bottom-dwelling, sessile

Table 1. Location, number and depth of benthic surveys. Point is the sampling point, Type is either donor meadow, reference meadow, bare sediment, reference plot, or planted plot. Surveys refer to the date (mm/yy) of each survey. Depth is water depth in meters.

Site	Point	Type	Latitude (°N)	Longitude (°N)	Surveys	Depth
Råå	R-Don-1	Donor	55.98437	12.74715	06/21	3.2
	R-Don-2	Donor	55.98347	12.74783	06/21	2.7
	R-Don-3	Donor	55.98275	12.74812	06/21	3
	R-Ref-1	Ref. meadow	55.99485	12.73757	08/19	2.4
					06/21, 09/21	
					06/22, 09/22	
					06/23	
	R-Ref-2	Ref. meadow	55.99485	12.73728	08/19	2.9
					06/21, 09/21	
					06/22, 09/22	
Båstad	R-Ref-3	Ref. meadow	55.99482	12.73762	06/23	2.4
					08/19	
					06/21, 09/21	
					06/22, 09/22	
					06/23	
	B-Bare-1	Bare sed.	56.43568	12.84924	06/21, 09/21	2.0
	B-Bare-2	Bare sed.	56.43502	12.84846	06/21, 09/21	2.5
	B-Bare-3	Bare sed.	56.43622	12.85019	06/21, 09/21	3.0
	B-Ref-1	Ref. plot	56.43398	12.85354	06/21, 09/21	2.0
	B-Ref-2	Ref. plot	56.43494	12.85360	06/21, 09/21	2.7
					09/22	
	B-Ref-3	Ref. plot	56.43423	12.85308	06/21, 09/21	2.2
					06/23	
	B-Plant-1	Planted	56.43447	12.84993	06/21, 09/21	2.2
	B-Plant-2	Planted	56.43491	12.85084	06/21, 09/21	2.4
	B-Plant-3	Planted	56.43573	12.85179	06/21, 09/21	2.8
					09/22	
					06/23	
	B-Plant-4	Planted	56.43595	12.85077	09/22	3.0
					06/23	
	B-Plant-5	Planted	56.43539	12.85090	09/22	2.8
					06/23	
	B-Plant-6	Planted	56.43555	12.85177	09/22	3.0
					06/23	
	B-Plant-7	Planted	56.43513	12.85191	09/22	2.8
					06/23	

and slow-moving macroinvertebrates (referred to as benthic fauna hereafter).

We collected separate cores (ID: 7.4 cm; depth 5 cm; $n = 29$) for sediment grain size and organic matter (OM) analyses. For detailed information on sample analyses, refer to Kindeberg et al. (2022). Due to logistical constraints, data on grain size distribution and OM are only available for 2021–2022 (Table S2).

Data Analyses

The effects of seagrass restoration on benthic fauna communities were assessed using both univariate and multivariate measures. We estimated the abundance (number of individuals per square meter), species richness and univariate and multivariate diversity indices of taxonomic and functional diversity using the *vegan* and *FD* packages in R, respectively. These included the effective number of Shannon diversity index ($H_{\text{eff}} = \exp. [H']$) and the effective number of Rao's quadratic entropy (FD_{eff}) following Jost (2006), functional richness (FRic),

functional evenness (FEve) and functional dispersion (FDis). Functional metrics were based on functional traits, serving as proxies for dispersal potential and ecological interactions. These traits described mobility, feeding, bioturbation, morphology, living habit and reproduction of each species (Table S3). Because several species exhibit plasticity in their modalities due to environmental conditions or life history strategies, we applied fuzzy coding (Chevenet et al. 1994), whereby each modality was assigned a score from 0 to 3 based on affinity to a modality with the sum of each trait always being 3. From this, we constructed a trait-by-species matrix encompassing a total of eight traits distributed across 32 modalities. Lastly, to be able to compare individual traits to each other, we standardized trait modalities by dividing each score by the total number of modalities of each trait.

To investigate the difference between treatments and seasons during each trial, we employed a repeated measures approach using linear mixed effects models with treatment (Planted/Reference) and season (June/September) as fixed factors and

individual plot ID as a random factor. The function `lmer` from the R package *lme4* (Bates et al. 2015) was used and Akaike Information Criterion (AIC) was evaluated to select the best models. Including water depth as a covariate in models did not improve AIC, and was not included in further analyses. Since the sampling effort was not balanced between years (e.g. only one sampling occasion in 2023) and finished in different months, we also ran individual models for each year. We tested fixed factors using type III Analysis of Variance (ANOVA) with $\alpha = 0.05$ set as the level of significance. We complemented `lmer` models with simple linear models (`lm`), testing the differences between planted and reference plots for each sampling event. Individual comparisons were obtained by Tukey's Honest Significant Difference post hoc test. Where necessary, dependent factors were log or sqrt-transformed to fulfill model assumptions.

Changes in community and functional trait composition were assessed using multivariate ordinations of species abundances and trait values, respectively. Trait values were assessed by computing community-weighted means of trait values (CWM) for each sample. We employed non-metric multidimensional scaling (NMDS) to visualize overall patterns in community structure across the Båstad dataset. In contrast, detrended correspondence analysis (DCA) was applied to Trial 2 data to assess spatiotemporal variation in community composition, as its gradient lengths provide an interpretable measure of species turnover and the assumptions of unimodal species responses were met in this subset. Finally, permutational analysis of variance (PERMANOVA) was run with community composition (i.e. species matrices) as the dependent variable and treatment and season and their interaction as predictor variables. Separate analyses were run for Trial 1 (including bare, planted and reference plots) and Trial 2 (including planted and reference plots). Similar to linear mixed effects models above, we included plot as a covariate (strata) to apply a repeated measures design. Multivariate homogeneity of group dispersions was controlled using the function `betadisper` in the *vegan* package. All distance matrices used Bray Curtis distances and all analyses were carried out using R version 4.2.3 (R Core Team 2023).

Results

Eelgrass Restoration

The first large-scale trial (Trial 1) in 2021 exhibited high mortality rates where only the deepest plot (BP3) had any surviving shoots (12.5% , 2 ± 2 shoots/ m^2) upon revisiting the same year. Consequently, BP1 and BP2 were excluded from further restoration and sampling efforts and additional transplantation was concentrated in the deeper area around 3 m depth (Table S1). Evaluation of the 2022 trial (Trial 2) revealed a survival rate of nearly 100% in chessboard plots, with 15.4 ± 2.1 and 12.1 ± 1.8 shoots/ m^2 remaining in BP4 and BP7, respectively. In the continuous plots, up to a doubling in shoot density was observed with 37.1 ± 10.9 and 25.3 ± 3.9 shoots/ m^2 in BP5 and BP6, respectively (Fig. 2). Importantly, note that chessboard plots BP4 and BP7 were planted up to 2 months later than continuous plots (Table S1).

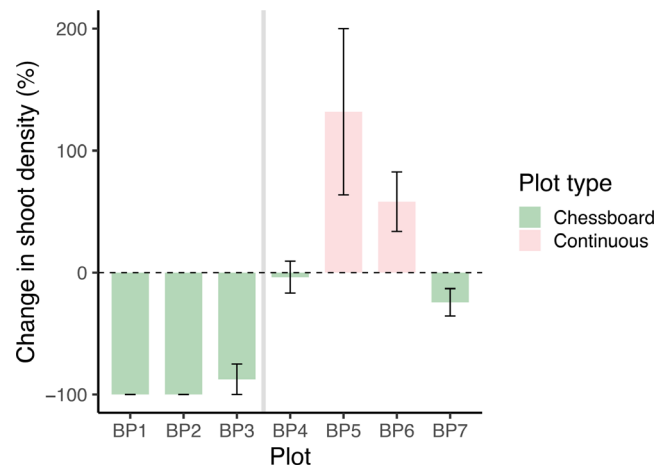


Figure 2. The change in shoot density (mean $\pm$ standard deviation) between planting during summer and revisits of the planted plots in October 2021 (BP1–BP3) and 2022 (BP4–BP7). Dashed horizontal line equals 100% survival, that is, no change in shoot density.

Underwater video surveys the following year (early June 2023) indicated a maintained total areal cover, albeit with an estimated lower shoot density across all plots. This was to some extent expected considering the earlier season, being months prior to the expected peak shoot density and biomass in late summer (Eriander et al. 2016).

The contrasting results between the first and second trials can be due to several factors. A gale from the northwest occurred within a week after planting plots BP1, BP2 and 40% of BP3 (Fig. S1) and may have caused high mortality of the newly established shoots. The gale lasted 3 days with wind gusts up to 18.3 m/s, potentially sufficient to exfoliate newly planted shoots and/or perturb light conditions. The winter 2021–2022 had several storm events culminating with the storm Malik in January 2022, with wind gusts exceeding 32 m/s (Fig. S1). The winter 2022–2023 following Trial 2 had no such severe storm events, and this could have been a factor in the lower mortality rates observed relative to Trial 1. We found no evidence of deterioration in light conditions, ambient oxygen concentrations or elevated temperatures that could explain the early eelgrass mortality (Fig. S2). Yet, mean and cumulative monthly irradiance were 35 and 34% lower, respectively, in the restoration site relative to the reference meadow in Råå. These values are, however, difficult to evaluate since measurements were not performed simultaneously in the sites and differences could therefore be due to differing weather. Importantly, mean light attenuation (K_d) was 0.44 ± 0.30 at the restoration site during June 2021 which most likely represents sufficient light availability, despite not being directly transferrable to a photosynthetic proton density flux (Thom et al. 2008; Moksnes et al. 2021).

Benthic Fauna

We collected a total of 9303 individuals distributed across 53 taxa. Predominant groups were bivalves (36.7%), gastropods (33.2%), polychaetes (23.0%) and crustaceans (5.7%). We

observed the highest abundance of benthic fauna ($53,900 \pm 16,500$ individuals/m²) in Båstad reference plots during the September 2022 sampling event and the lowest (2790 ± 355) in bare sediments during June 2021. Fluctuations in abundance were to a large extent driven by a few species that occurred in vast numbers such as mud snails (*Hydrobiidae*), the polychaete *Pygospio elegans* and the Blue mussel (*Mytilus edulis*).

Fauna Dynamics in Planted Eelgrass

Differences in benthic fauna diversity metrics between restored and reference plots in Båstad were a function of eelgrass survival and time period. Most taxonomic and functional parameters were higher in reference plots relative to planted plots during Trial 1 when restoration largely failed. During Trial 2, however, no taxonomic diversity variable was significantly different between restored and reference eelgrass, but the

magnitude varied between seasons. As such, time period and treatment generally displayed a significant interaction. Notably, functional richness ($F_{[1,13]} = 5.83$; $p = 0.03$) was significantly higher in planted plots compared to reference during the last sampling event in June 2023, and despite not being significantly different, there was a trend toward higher mean values of abundance, species richness and H_{eff} (Fig. 3) in planted plots compared to reference plots in 2023. Less than 2 months after planting, neither abundance, species richness, taxonomic diversity (H_{eff}) nor functional diversity (FD_{eff}) differed between planted and reference plots (Fig. 3).

Community structure showed a similar pattern where multivariate ordination of community composition completely overlapped between the two treatments. During the first trial, benthic communities in planted plots resembled bare sediments whereas in Trial 2 where planting was successful, no significant difference could be detected between planted plots or reference plots (PERMANOVA: pseudo- $F_{[1,15]} = 0.40$; $p = 1$; Fig. 4).

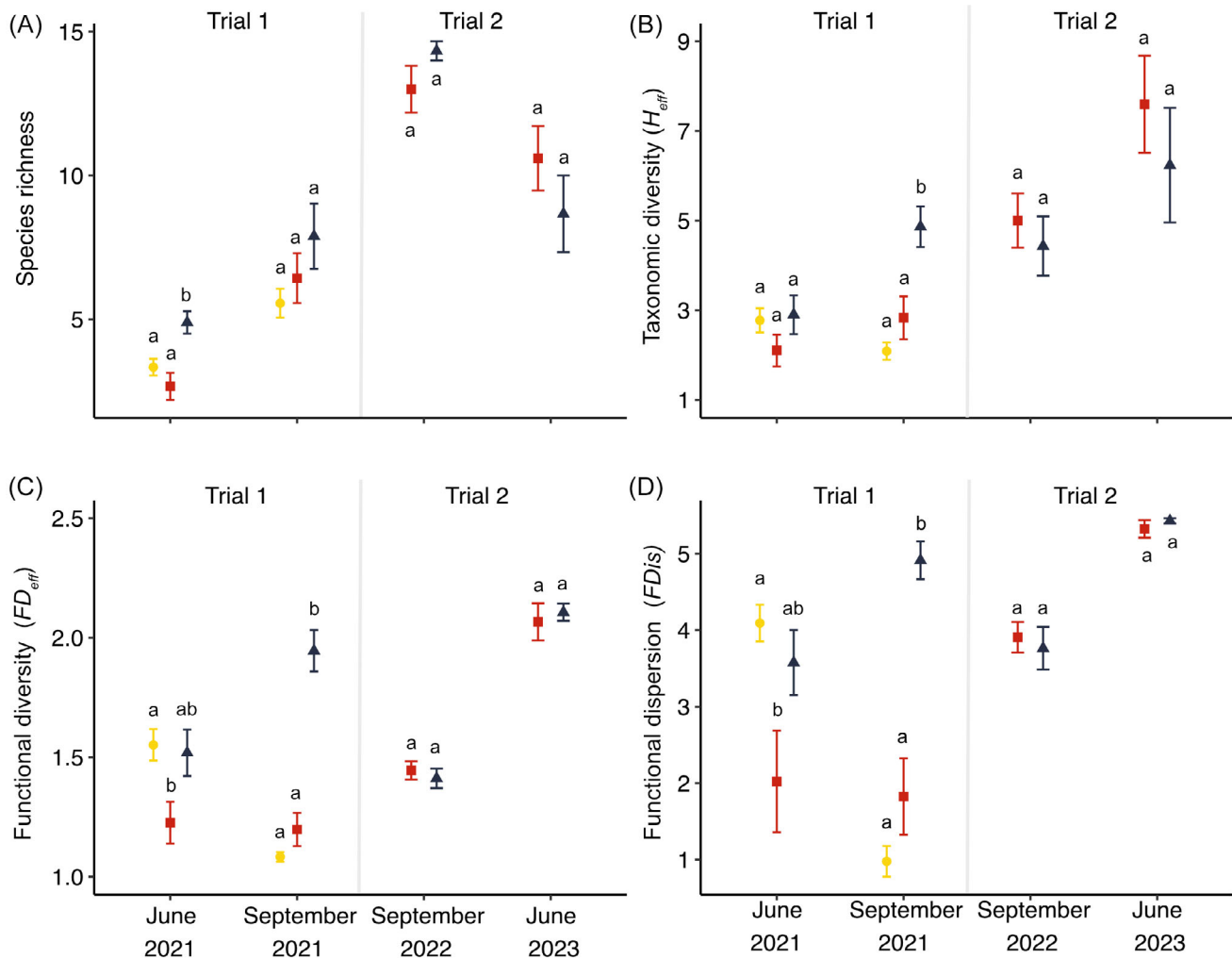


Figure 3. Species richness (A), taxonomic diversity (B), functional diversity (C) and functional dispersion (D) (mean $\pm$ SE) in bare, planted and reference plots in Båstad. Trial 1 refers to plots planted in 2021 and Trial 2 to plots planted in 2022. Yellow circles are bare plots; red squares are planted plots and blue triangles are reference plots. Letters indicate post hoc significant difference ($p < 0.05$) between treatments at each sampling event.

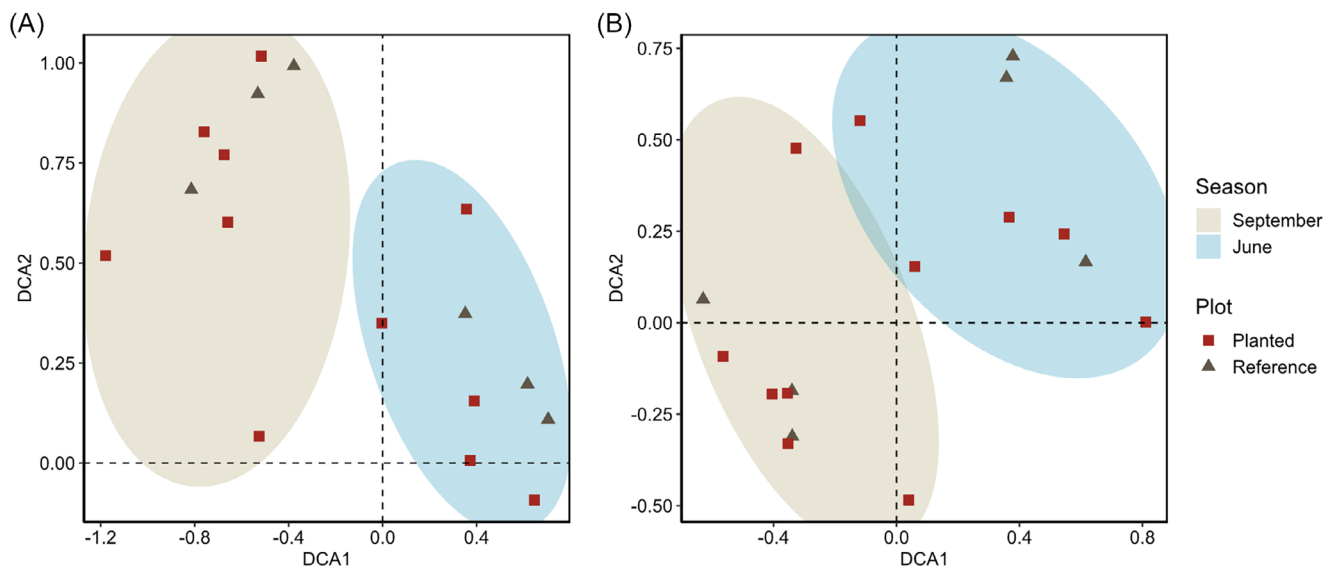


Figure 4. Detrended correspondence analysis (DCA) of (A) fauna community composition and (B) composition of traits as community-weighted means (CWM) in planted plots and reference plots in Båstad during restoration Trial 2 in 2022–2023. Shaded areas show ellipses based on season.

Notably, the multivariate dispersion was larger in 2021 as indicated by the marked separation between shallow planted plots (2–2.4 m) and deeper plots (Fig. S3). Shallow plots BP1 and BP2 resembled bare sediments whereas deep plots in BP3 had a community structure similar to reference plots. At the revisit in September 2021 when almost all eelgrass had been lost, all planted plots clustered closely with bare plots (Fig. S3). Contrastingly, the samples from the revisit in September 2022 displayed a high similarity with reference plots (Figs. 4 & S3).

The initial planting density (i.e. chessboard or continuous) did not appear to have a large influence on community composition, despite a tendency toward an overall higher abundance and diversity in continuous relative to chessboard plots (Fig. 5). The relative and absolute abundance of amphipods was consistently higher in continuous relative to chessboard plots (Fig. S4).

Temporal Variability in Community Composition

The temporal component of community structure was much stronger than the spatial, as indicated by the clear separation between seasons and high similarity between treatments (Figs. 4 & S3). September 2022 displayed a spike in abundance in both planted ($34,600 \pm 7920 \text{ m}^{-2}$) and reference plots ($53,900 \pm 16,500 \text{ m}^{-2}$) in Båstad. This was largely driven by high densities of *Mya truncata* dominating the samples. Correspondingly, the lowest taxonomic and functional evenness was observed during this sampling event in both treatments. Similarly, a surplus of hydrobiid snails in June 2021 made gastropods the dominating class across all sites (Fig. S5). The large temporal variability in community structure was further supported by the dataset from the reference meadow in Råå, which displayed a pronounced seasonal and annual variation in diversity parameters and community composition and traits (Fig. 6). Averaged across all years (mean $\pm$ standard deviation), this meadow had an abundance of

$22,600 \pm 11,800 \text{ ind/m}^2$, a species richness of 7.7 ± 2.4 , H_{eff} of 4.08 ± 1.31 and FD_{eff} of 2.03 ± 0.38 .

Species and Traits Driving Colonization and Variability

Looking broadly at species classes, it was evident that the relative proportion of different classes differed markedly over both seasonal and annual timescales (Fig. S5). Some years were dominated by gastropods (e.g. hydrobiids in 2019) whereas the relative abundance of polychaetes or malacostraca exceeded 50% of the total abundance for the remaining years in Råå. The class composition in reference and planted plots was similar during Trial 2, albeit with a higher abundance of malacostracans in continuous plots relative to chessboard plots.

Opportunistic gastropods displayed a higher relative abundance in planted plots compared to reference plots within 4 months post-restoration. For instance, *Rissoa sarsii* and *R. membranacea* were three- and two-fold more abundant, respectively, in planted plots relative to reference plots. Additionally, the opportunistic polychaete *Capitella capitata* was on average ($\pm$ SE) more abundant in planted plots ($651 \pm 205 \text{ m}^{-2}$) relative to reference plots ($388 \pm 229 \text{ m}^{-2}$) 12 months post-restoration, albeit with large within-site variability.

From a functional trait perspective, CWM trait values were largely similar between planted and reference plots (Figs. 7 & S6). Mobile modalities (i.e. swimmer, drifter, crawler, or burrower) displayed a tendency toward higher values in planted plots (0.59 ± 0.01) compared to reference plots (0.52 ± 0.10). Similarly, planted plots exhibited nearly twice as high CWM for the living habit “Free” compared to reference plots, in summer 2023 (Fig. S6). Conversely, during this time, reference plots hosted 13% sessile organisms, and planted plots only consisted of 1% sessile with the majority exhibiting a mobile movement

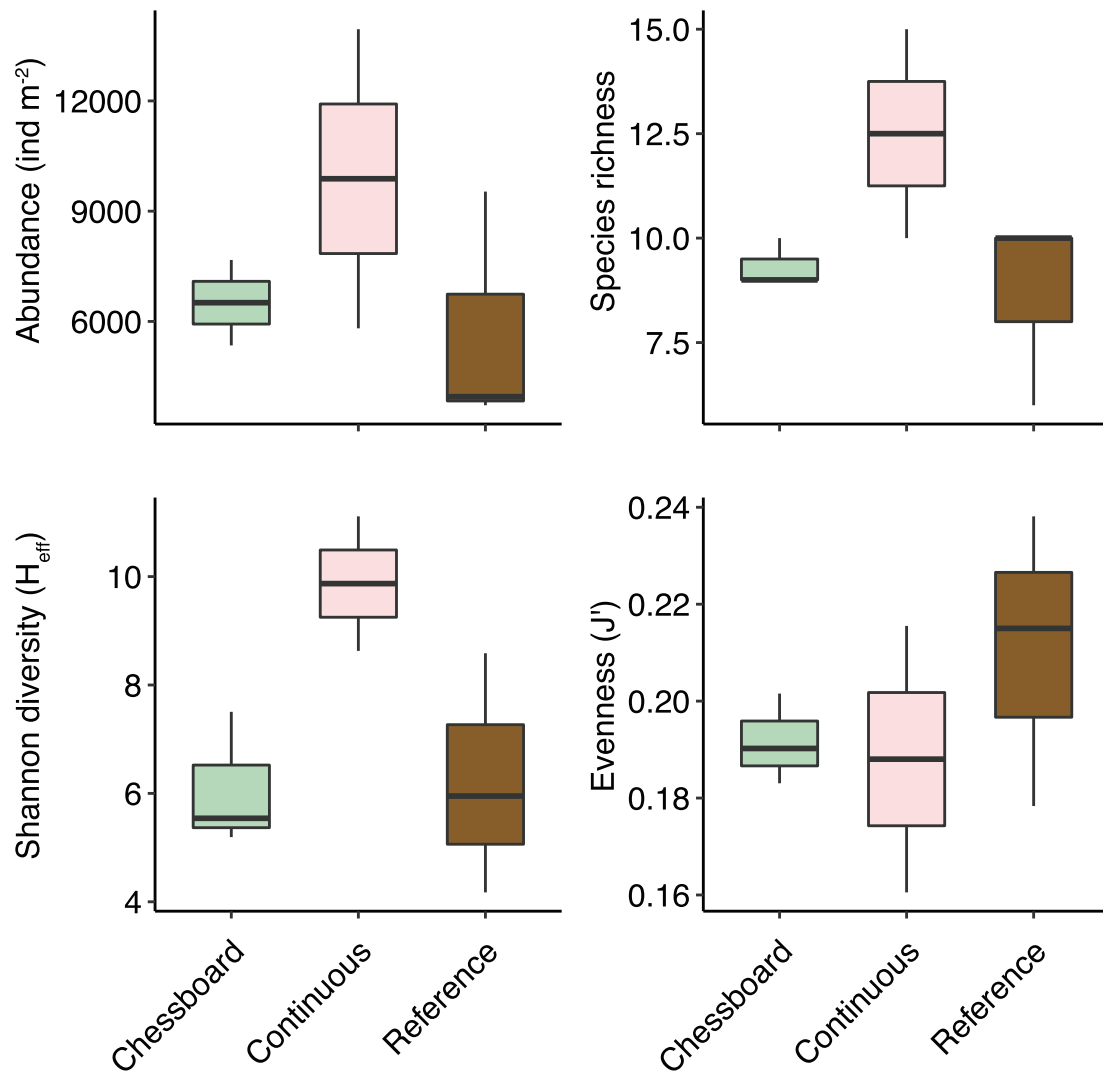


Figure 5. Diversity metrics of benthic fauna in different plot types in Båstad during the last sampling event in June 2023. Chessboard indicates plots (25 m × 25 m) planted in a chessboard pattern with every other square meter left empty; Continuous indicates plots (18 m × 18 m) planted continuously and Reference indicates reference plots of in natural eelgrass patches in Båstad.

modality. Traits related to reproduction displayed highly variable results. In September 2022, brooders were more common in planted plots compared to reference plots, whereas broadcast spawners were relatively more abundant in planted plots in summer 2023 (Fig. 7). Direct larval development was more than twice as common a modality in planted plots during September 2022, but these differences were absent in 2023 (Fig. S6).

Sediment Composition

Mean sediment grain size was significantly lower in reference plots ($223 \pm 39 \mu\text{m}$) compared to newly planted eelgrass plots ($307 \pm 78 \mu\text{m}$) and bare sediment ($322 \pm 47 \mu\text{m}$; $F_{[2,17]} = 9.97$; $p = 0.001$). However, the sediment grain size in eelgrass plots planted in 2022 decreased within 4 months after planting

to $235 \pm 25 \mu\text{m}$ and obtained a mean grain size comparable to reference plots (Table S2). During Trial 1, the median sediment grain size (D_{50}) was lowest in reference plots ($165 \pm 8 \mu\text{m}$) compared to planted ($259 \pm 69 \mu\text{m}$) and bare ($272 \pm 61 \mu\text{m}$) plots. During the revisit of Trial 2, planted plots had attained a D_{50} similar to reference plots ($176 \pm 1 \mu\text{m}$) and a four-fold higher silt content compared to the planted plots a year earlier, suggesting that trapping of fine particles had occurred (Bos et al. 2007).

Discussion

Lessons Learned From Planting in a Challenging Environment

Evaluation of the restoration outcomes within this study tells two different stories. The first trial in 2021 was a failure,

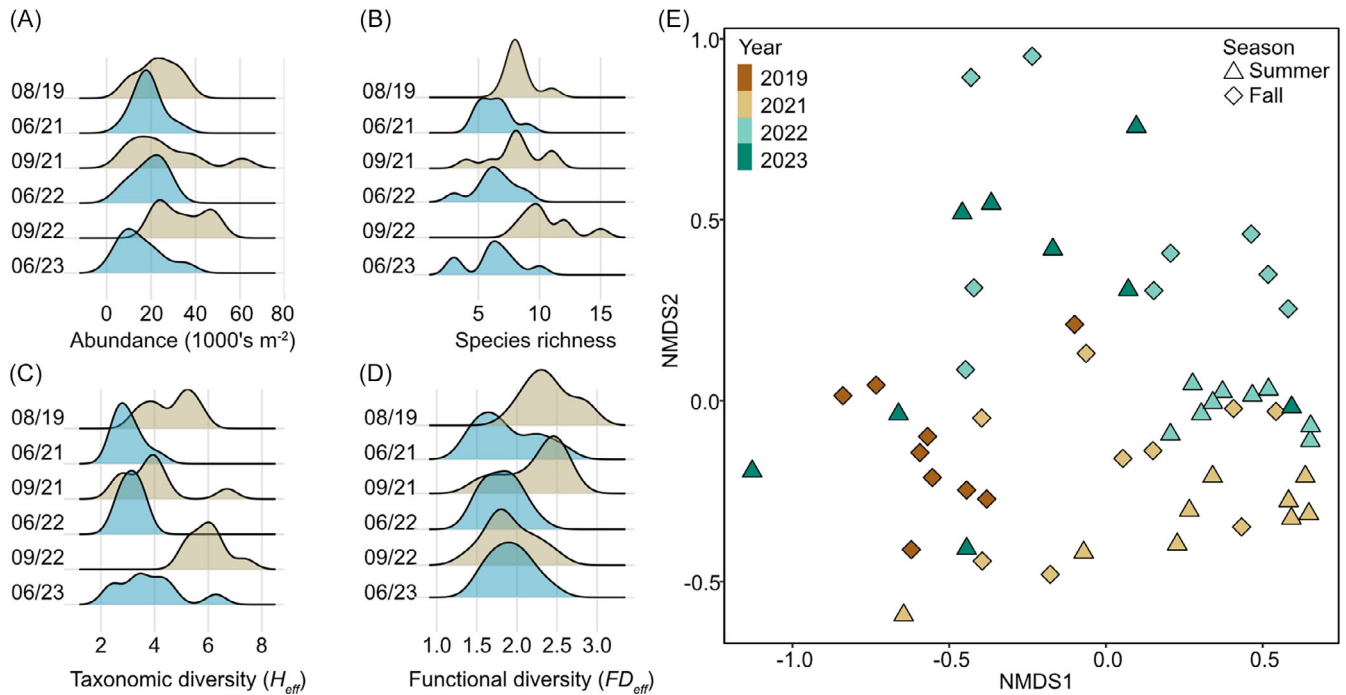


Figure 6. Temporal variation in the reference meadow in Råå. Ridge plot showing variation of benthic fauna abundance (A), species richness (B) taxonomic diversity (C) and functional diversity (D), as illustrated by density distributions of samples across periods. Rows indicate different sampling periods (format mm/yy). Tan color represents fall and blue color represents summer. (E) shows non-metric multidimensional scaling of fauna community composition in the reference meadow in Råå. Color indicates year and shape indicates season. Two K stress: 0.12.

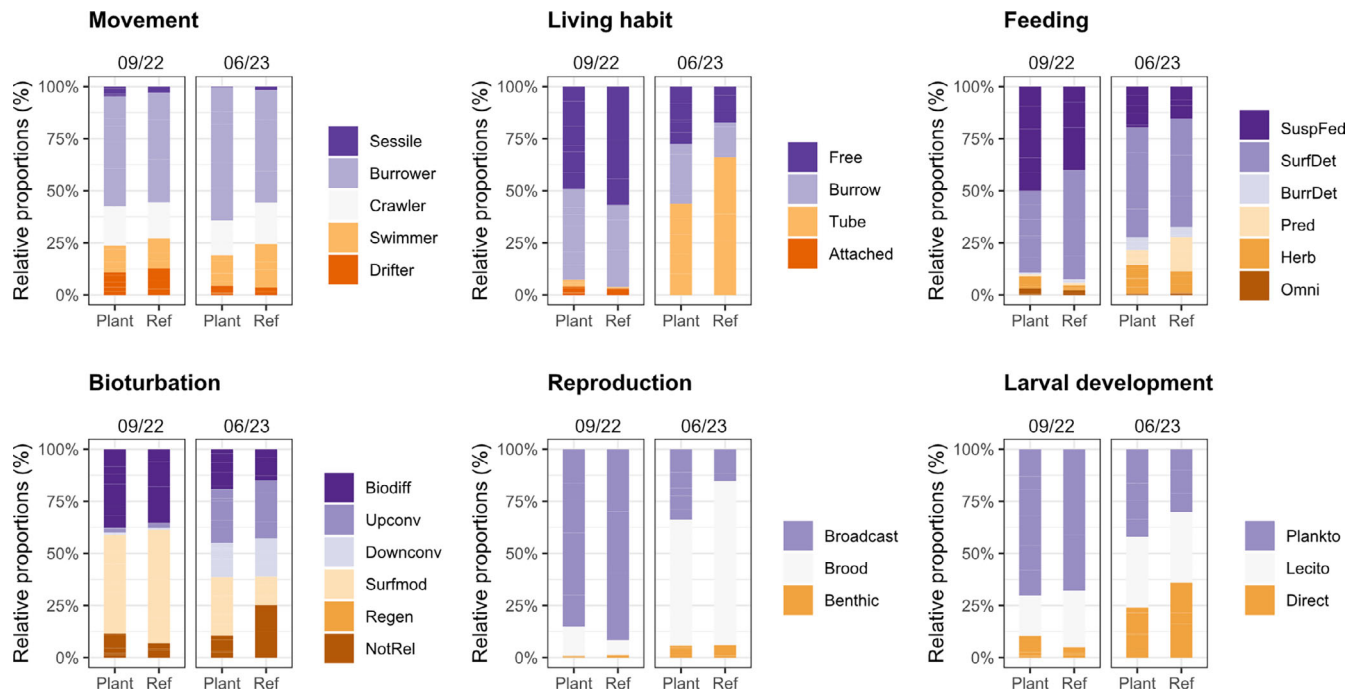


Figure 7. Relative proportions of community-weighted mean trait values (CWM) during September and June in planted plots (Plant) and reference plots (Ref) in Båstad for the traits Movement mode, Living habit, Feeding mode, Bioturbation mode, Reproductive strategy, and Larval development. Biodiff, Biodiffusor; Broadcast, Broadcast spawning; Brood, Brooder/egg layer; BurrDet, Burrowing detritivore; Direct, Direct development; Downconv, Downward conveyor; Herb, Herbivore; Lecito, Lecitotrophic; NotRel, Not relevant; Plankto, Planktrophic; Pred, Predator; Regen, Renerator; SurfDet, Surficial detritivore; Surfmod, Surficial modifier; SuspFed, Suspension feeder; Upconv, Upward conveyor.

considering mortality rates of between 87.5 and 100%, much of which likely occurred within the first few weeks after restoration. A gale event with high wind speeds from the NW is hypothesized to have been the main culprit as our monitoring data reveal no apparent signs of temperature stress, light limitation or hypoxic conditions during the first critical weeks post-planting. A further sign of the destructive hydrodynamics is that the two shallower plots had 100% mortality whereas some shoots (12.5%) remained in the deepest plot, despite being planted later and thus would have had even less time to anchor roots and rhizomes. As a result, additional restoration in 2022 was concentrated to a depth around 3 m which turned out well, with nearly zero mortality and up to a doubling in shoot densities within 4 months after planting. The maintained surface cover observed a year after planting suggests the restored plots withstood the storm season, but extended monitoring is needed to confirm long-term results. Nevertheless, the results are promising considering that eelgrass restoration is challenging (Ward & Beheshti 2023), especially in exposed locations (van Katwijk & Hermus 2000; van Katwijk et al. 2009). However, the disparate results between 2021 and 2022 illustrate the high risk of planting in areas susceptible to high wave energy during intermittent and largely unpredictable weather events. Essentially, there is a considerable element of chance associated with the outcomes. The time it took to finish the restoration during 2022 further highlights the difficulties with restoration in exposed areas. Although anchoring was not deemed necessary in this project, further testing with different anchoring methods is recommended. Moreover, planting in a continuous pattern is preferable to a chessboard pattern in wave-swept environments such as Båstad. Importantly, the expected success rate must be thoroughly weighed both against initial costs associated with planting and the uncertainty of stochastic events such as storms during early phases of planting.

Planting eelgrass in exposed areas such as Båstad may increase the risk of not finding self-sustaining donor meadows nearby, and shoots may have to be transported from further away. This increases the risk of poor suitability if eelgrass with gene complexes not locally adapted are transplanted (Hämmerli & Reusch 2002; Sinclair et al. 2013; van Katwijk et al. 2016). Indeed, the distance between donor meadow and transplant site has been found to be negatively related to restoration success (van Katwijk et al. 2016; Gamble et al. 2021), but see Paulo et al. (2019). In fact, van Katwijk et al. (2016) found that restoration success decreased by nearly 75% when donor locations were more than 50 km away from the restoration site. In this project, shoots were harvested from a donor population nearly 80 km away, from a meadow in a different environmental setting and possibly different genetic structure (Martínez-García et al. 2021; Ries et al. 2023). The early signs of high establishment illustrate the ability of eelgrass to acclimatize to a new environment and support the idea that donor and transplant sites may not need to be as similar as previously thought (Eriander et al. 2016). However, an often-overlooked factor is that long distances between donor site and restoration site can significantly increase labor costs. Together with the potential need for planting with a higher density, the costs per shoot can be

substantially higher in these types of projects compared to ecological restoration projects where goals and focus are different. Long-distance transport of eelgrass shoots is feasible due to their high plasticity, but the risk of spreading invasive species must always be considered.

It is acknowledged that restoration success depends on careful site selection with a priori knowledge on environmental conditions such as light- and hydrodynamic regimes (Fonseca et al. 1998; Moksnes et al. 2021). However, using seagrass as an NbS for coastal protection adds another dimension to the site selection process in which sites in need of coastal protection should be weighed against expected restoration success. Areas in need of protection are often characterized by more exposed locations, higher hydrodynamic energy and more mobile sediments, which are counter to generally recommended site properties (Fonseca et al. 1998; van Katwijk et al. 2009, 2016; Moksnes et al. 2021). As such, the conventional preconditions for a successful restoration may unavoidably be given less priority, which further increases the risk of restoration failure. The massive losses of planted eelgrass experienced in this project question the feasibility of using seagrass restoration as an NbS for coastal protection.

Variability in Benthic Diversity

Despite the challenges above, our findings suggest that restoration, when successful, rapidly results in benthic biodiversity values similar to reference eelgrass in the area. The restored eelgrass enhanced both taxonomic and functional diversity to levels comparable to the naturally occurring eelgrass plots, and on par with one of the largest natural eelgrass meadows in the region (Kindeberg et al. 2022). This finding corroborates a growing body of evidence from recent studies including a large-scale U.S. restoration effort (Orth et al. 2020) and projects in Scandinavia (Steinfurth et al. 2022; Gagnon et al. 2023) and the Dutch Wadden Sea (Gräfnings et al. 2024).

Notably, there was a tendency toward higher biodiversity metrics such as abundance, species richness and H_{eff} in the smaller continuous plots relative to the larger chessboard plots, implying that shoot density rather than surface coverage is the important determinant of fauna diversity. Differences between the two planting patterns were largely driven by amphipods, in which the relative and absolute abundance of, e.g. gammarids were consistently higher in continuous relative to chessboard plots. Gagnon et al. (2023) found no difference in fauna communities between continuous and chessboard plots, but there was a large inter-annual variability in community structure and diversity. Importantly, the continuous plots in this study were planted earlier in the season which likely facilitated both a more developed eelgrass meadow and a longer window of colonization. It is therefore not possible to infer causality of the planting density and future restoration projects evaluating different densities must ensure a narrow time window of planting or a completely randomized design with respect to timing.

The plot size and patchiness (i.e. planting pattern) could both influence fauna community properties through different mechanisms. Continuous and chessboard plots differ in the gross area,

with the former (324 m²) being about half the size of the latter (625 m²). Considering that planted plots are within 300 m from existing reference plots it can be argued that these are integrated in a patchy eelgrass landscape, with high connectivity and rapid mobility of species between patches in the landscape. As such, dispersal and colonization mechanisms rest on theory from habitat fragmentation models. Dispersal of typical eelgrass-associated fauna is facilitated both by larval dispersal and by high mobility during adult stages (Boström et al. 2006). For instance, bivalve recruitment is largely a passive process controlled by hydrodynamics by which the eelgrass facilitates sedimentation of larvae (Eckman 1987). Here, the bivalve *Cerastoderma glaucum* was more abundant in planted compared to reference plots. This burrower has a pelagic larval stage, with spawning occurring between May and July. Settling is facilitated by clinging on to drifting filamentous algae (Barnes 1973), which often accumulate in eelgrass. This illustrates how planted plots can indirectly acquire benthic fauna during their pelagic phase (Carroll et al. 2012). Relatedly, Gagnon et al. (2023) found quick colonization of gastropods and bivalves with planktotrophic dispersal modes in restored eelgrass plots, displaying a higher abundance of, e.g. Blue mussels in chessboard compared to continuous plots or the reference meadow. The authors suggested that this could be due to more pronounced edge effects in chessboard plots, where eelgrass leaves trap pelagic larvae.

Our observations from the restoration site and the long-term dataset from the reference meadow in Råå revealed a marked temporal variability in benthic fauna community dynamics. Our results from restoration plots are similar to Gagnon et al. (2023) who found that the difference in taxonomic and functional diversity between years completely overshadowed differences between plots. This large temporal variability has ramifications for the evaluation of biodiversity effects and underscores the importance of comparing reference and planted plots within a narrow time window and preferably across multiple seasons and/or years. At the very least, binary conclusions on success or failure should not be based solely on single sampling events comprising a snapshot of benthic diversity. Moreover, eelgrass fauna communities are naturally heterogeneous over small spatial scales (Boström & Bonsdorff 1997), further underscoring that monitoring programs and post-restoration evaluation of fauna diversity need to consider this spatiotemporal variability, especially when addressing early effects.

In conclusion, we have shown early indications that single-shoot transplanting without any sheltering or anchoring is possible in hydrodynamically challenging environments. Crucially, longer-term monitoring is needed to confirm enduring meadow development and eelgrass persistence. With respect to taxonomic and functional diversity parameters, planted plots are virtually indistinguishable from nearby reference plots within one growing season. Nevertheless, colonization is partly dependent on the functional traits of species where opportunistic species exhibit a combination of traits conducive to early colonization. However, succession patterns are difficult to discern due to large natural temporal variation which confounds spatial differences. Jointly, our observations substantiate the importance of seagrass

for benthic diversity and are useful for coastal managers who consider using eelgrass restoration in exposed environments.

Acknowledgments

All eelgrass planting was carried out by the consultant agency WSP. Financial support was received from the European Commission Life Programme (LifeCoastAdapt, grant no. LIFE/CCA/SE/00048) and the restoration was administered through the organization Skånes kommuner. J.H. would like to acknowledge the generous support by The Nippon Foundation of Japan and FORMAS (grant no. 2018-00640). We thank J. Müller, J. Severinson, J. Hüller, and C. Havsblad for their invaluable assistance in the lab and field. We also thank B. Almström, P. A. Olsson and two anonymous reviewers for comments that improved an earlier version of this manuscript.

LITERATURE CITED

- SGI (Swedish Geotechnical Institute) (2023) Kustdataportal. Swedish Geotechnical Institute, Linköping, Sweden <https://gis.sgi.se/kustdataportal> (Accessed 12 Dec 2023).
- Adell A, Almström B, Kroon A, Larson M, Uvo CB, Hallin C (2023) Spatial and temporal wave climate variability along the south coast of Sweden during 1959–2021. *Regional Studies in Marine Science* 63:103011. <https://doi.org/10.1016/j.rsma.2023.103011>
- Barnes R (1973) The intertidal lamellibranchs of Southampton water, with particular reference to *Cerastoderma edule* and *C. glaucum*. *Journal of Molluscan Studies* 40:413–433. <https://doi.org/10.1093/oxfordjournals.mollus.a065239>
- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48. <https://doi.org/10.18637/jss.v067.i01>
- Benayas JMR, Newton AC, Diaz A, Bullock JM (2009) Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. *Science* 325:1121–1124. <https://doi.org/10.1126/science.1172460>
- Bos AR, Bouma TJ, De Kort GLJ, Van Katwijk MM (2007) Ecosystem engineering by annual intertidal seagrass beds: sediment accretion and modification. *Estuarine, Coastal and Shelf Science* 74:344–348. <https://doi.org/10.1016/j.ecss.2007.04.006>
- Boström C, Bonsdorff E (1997) Community structure and spatial variation of benthic invertebrates associated with *Zostera marina* (L.) beds in the northern Baltic Sea. *Journal of Sea Research* 37:153–166. [https://doi.org/10.1016/S1385-1101\(96\)00007-X](https://doi.org/10.1016/S1385-1101(96)00007-X)
- Boström C, Jackson EL, Simenstad CA (2006) Seagrass landscapes and their effects on associated fauna: a review. *Estuarine, Coastal and Shelf Science* 68:383–403. <https://doi.org/10.1016/j.ecss.2006.01.026>
- Carroll JM, Furman BT, Tettelbach ST, Peterson BJ (2012) Balancing the edge effects budget: bay scallop settlement and loss along a seagrass edge. *Ecology* 93:1637–1647. <https://doi.org/10.1890/11-1904.1>
- Chávez V, Lithgow D, Losada M, Silva-Casarin R (2021) Coastal green infrastructure to mitigate coastal squeeze. *Journal of Infrastructure Preservation and Resilience* 2:7. <https://doi.org/10.1186/s43065-021-00026-1>
- Chevenet F, Dolédec S, Chessel D (1994) A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology* 31:295–309. <https://doi.org/10.1111/j.1365-2427.1994.tb01742.x>
- County Administrative Board Skåne (2016) Ålgräs i Skåne – Fältinventering och satellitbildstolkning [in Swedish]. Report no. 2017:04. County Administrative Board Skåne, Malmö, Sweden.
- Davis RC, Short FT (1997) Restoring eelgrass, *Zostera marina* L., habitat using a new transplanting technique: the horizontal rhizome method. *Aquatic Botany* 59:1–15. [https://doi.org/10.1016/S0304-3770\(97\)00034-X](https://doi.org/10.1016/S0304-3770(97)00034-X)

- Dolan AH, Walker IJ (2006) Understanding vulnerability of coastal communities to climate change related risks. *Journal of Coastal Research* 39:1316–1323. <https://www.jstor.org/stable/25742967>
- Duffy JE (2006) Biodiversity and the functioning of seagrass ecosystems. *Marine Ecology Progress Series* 311:233–250. <https://doi.org/10.3354/meps311233>
- Eckman JE (1987) The role of hydrodynamics in recruitment, growth, and survival of *Argopecten irradians* (L.) and *Anomia simplex* (D'Orbigny) within eelgrass meadows. *Journal of Experimental Marine Biology and Ecology* 106:165–191. [https://doi.org/10.1016/0022-0981\(87\)90154-7](https://doi.org/10.1016/0022-0981(87)90154-7)
- Emanuelsson A, Peterson M, Andersson S (2019) Marinbiologisk kontroll – Älgräsinventering i Skåne 2019 [in Swedish]. Clinton Marine Survey AB, Gothenburg, Sweden.
- Eriander L, Infantes E, Olofsson M, Olsen JL, Moksnes P-O (2016) Assessing methods for restoration of eelgrass (*Zostera marina* L.) in a cold temperate region. *Journal of Experimental Marine Biology and Ecology* 479:76–88. <https://doi.org/10.1016/j.jembe.2016.03.005>
- Fonseca MS, Kenworthy WJ, Thayer GW (1998) Guidelines for the conservation and restoration of seagrasses in the United States and adjacent waters. Pages 222. In: Program NCO. NOAA Coastal Ocean Office, Silver Spring, Maryland
- Fonseca MS, Zieman JC, Thayer GW, Fisher JS (1983) The role of current velocity in structuring eelgrass (*Zostera marina* L.) meadows. *Estuarine, Coastal and Shelf Science* 17:367–380. [https://doi.org/10.1016/0272-7714\(83\)90123-3](https://doi.org/10.1016/0272-7714(83)90123-3)
- Gagnon K, Bocoum E-H, Chen CY, Baden SP, Moksnes P-O, Infantes E (2023) Rapid faunal colonization and recovery of biodiversity and functional diversity following eelgrass restoration. *Restoration Ecology* 31:e13887. <https://doi.org/10.1111/rec.13887>
- Gamble C, Glover A, Debney A, Bertelli C, Green B, Hendy I, Lilley R, Nuuttila H, Potouroglou M, Ragazzola F (2021) Seagrass restoration handbook: UK and Ireland. Zoological Society of London, London, United Kingdom
- Gräfnings ML, Grimm I, Valdez SR, Findji I, Van Der Heide T, Heusinkveld JH, Meijer KJ, Eriksson BK, Smelele Q, Govers LL (2024) Restored intertidal eelgrass (*Z. marina*) supports benthic communities taxonomically and functionally similar to natural seagrasses in the Wadden Sea. *Frontiers in Marine Science* 10:1294845. <https://doi.org/10.3389/fmars.2023.1294845>
- Hämmerli A, Reusch TB (2002) Local adaptation and transplant dominance in genets of the marine clonal plant *Zostera marina*. *Marine Ecology Progress Series* 242:111–118. <https://doi.org/10.3354/meps242111>
- Hanley ME, Bouma TJ, Mossman HL (2019) The gathering storm: optimizing management of coastal ecosystems in the face of a climate-driven threat. *Annals of Botany* 125:197–212. <https://doi.org/10.1093/aob/mcz204>
- IUCN (International Union for Conservation of Nature and Natural Resources) (2023) IUFCONaNR. <https://iucn.org/our-work/nature-based-solutions> (accessed 11 Dec 2023)
- Jost L (2006). Entropy and diversity. *Oikos*, 113(2), 363–375. Portico. <https://doi.org/10.1111/j.2006.0030-1299.14714.x>
- Kindeberg T, Almström B, Skoog M, Olsson PA, Hollander J (2023) Toward a multifunctional nature-based coastal defense: a review of the interaction between beach nourishment and ecological restoration. *Nordic Journal of Botany* 2023:e03751. <https://doi.org/10.1111/njb.03751>
- Kindeberg T, Severinson J, Carlsson P (2022) Eelgrass meadows harbor more macrofaunal species but bare sediments can be as functionally diverse. *Journal of Experimental Marine Biology and Ecology* 554:151777. <https://doi.org/10.1016/j.jembe.2022.151777>
- Lange T, Oncken NS, Svane N, Steinfurth RC, Kristensen E, Flindt MR (2022) Large-scale eelgrass transplantation: a measure for carbon and nutrient sequestration in estuaries. *Marine Ecology Progress Series* 685:97–109. <https://doi.org/10.3354/meps13975>
- Lefcheck JS, Marion SR, Orth RJ (2017) Restored eelgrass (*Zostera marina* L.) as a refuge for epifaunal biodiversity in mid-Western Atlantic coastal bays. *Estuaries and Coasts* 40:200–212. <https://doi.org/10.1007/s12237-016-0141-x>
- Lumborg U (2005) Modelling the deposition, erosion, and flux of cohesive sediment through Öresund. *Journal of Marine Systems* 56:179–193. <https://doi.org/10.1016/j.jmarsys.2004.11.003>
- Martínez-García L, Hansson B, Hollander J (2021) Assessment of local genetic structure and connectivity of the common eelgrass *Zostera marina* for seagrass restoration in northern Europe. *Marine Ecology Progress Series* 664:103–116. <https://doi.org/10.3354/meps13658>
- Moksnes P-O, Gipperth L, Eriander L, Laas K, Cole S, Infantes E (2021) Handbook for restoration of eelgrass in Sweden - national guideline. Report no. 2021:5. Report no. 2021:5 (excluding appendices). Swedish Agency for Marine and Water Management, Göteborg, Sweden.
- Morris RL, Konlechner TM, Ghisalberti M, Swearer S (2018) From grey to green: efficacy of eco-engineering solutions for nature-based coastal defence. *Global Change Biology* 24:1827–1842. <https://doi.org/10.1111/gcb.14063>
- Nordlund LM, Koch EW, Barbier EB, Creed JC (2016). Seagrass Ecosystem Services and Their Variability across Genera and Geographical Regions. *PLOS ONE*, 11(10): e0163091. <https://doi.org/10.1371/journal.pone.0163091>
- Orth RJ, Harwell MC, Fishman JR (1999) A rapid and simple method for transplanting eelgrass using single, unanchored shoots. *Aquatic Botany* 64:77–85. [https://doi.org/10.1016/S0304-3770\(99\)00007-8](https://doi.org/10.1016/S0304-3770(99)00007-8)
- Orth RJ, Lefcheck JS, Mcglathery KS, Aoki L, Luckenbach MW, Moore KA, Oreska MPJ, Snyder R, Wilcox DJ, Lusk B (2020) Restoration of seagrass habitat leads to rapid recovery of coastal ecosystem services. *Science Advances* 6:eabc6434. <https://doi.org/10.1126/sciadv.abc6434>
- Paling EI, Van Keulen M, Wheeler KD, Phillips J, Dyhrberg R (2003) Influence of spacing on mechanically transplanted seagrass survival in a high wave energy regime. *Restoration Ecology* 11:56–61. <https://doi.org/10.1046/j.1526-100X.2003.00072.x>
- Paul M (2018) The protection of sandy shores – can we afford to ignore the contribution of seagrass? *Marine Pollution Bulletin* 134:152–159. <https://doi.org/10.1016/j.marpolbul.2017.08.012>
- Paulo D, Cunha AH, Boavida J, Serrao E, Gonçalves EJ, Fonseca M (2019) Open coast seagrass restoration. Can we do it? Large scale seagrass transplants. *Frontiers in Marine Science* 6:52. <https://doi.org/10.3389/fmars.2019.00052>
- Persson KM, Nyberg J, Ising J, Rodhe L (2017) Skånes känsliga stränder – erosionsförhållanden och geologi för samhällsplanering, SGU-rapport 2016: 17. Sveriges Geologiska Undersökning, Uppsala, Sweden.
- R Core Team (2023) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Reynolds LK, Waycott M, Mcglathery KJ, Orth RJ (2016) Ecosystem services returned through seagrass restoration. *Restoration Ecology* 24:583–588. <https://doi.org/10.1111/rec.12360>
- Ries SR, Faust E, Johannesson K, Jonsson PR, Moksnes P-O, Pereyra RT, Jahnke M (2023) Genetic structure and diversity of the seagrass *Zostera marina* along a steep environmental gradient, with implications for genetic monitoring. *Frontiers in Climate* 5:1303337. <https://doi.org/10.3389/fclim.2023.1303337>
- Sinclair EA, Verduin J, Krauss SL, Hardinge J, Anthony J, Kendrick GA (2013) A genetic assessment of a successful seagrass meadow (*Posidonia australis*) restoration trial. *Ecological Management & Restoration* 14:68–71. <https://doi.org/10.1111/emr.12028>
- Steinfurth RC, Lange T, Oncken NS, Kristensen E, Quintana CO, Flindt MR (2022) Improved benthic fauna community parameters after large-scale eelgrass (*Zostera marina*) restoration in Horsens Fjord, Denmark. *Marine Ecology Progress Series* 687:65–77. <https://doi.org/10.3354/meps14007>
- Temmerman S, Meire P, Bouma TJ, Herman PM, Ysebaert T, De Vriend HJ (2013) Ecosystem-based coastal defence in the face of global change. *Nature* 504:79. <https://doi.org/10.1038/nature12859>
- Thom RM, Southard SL, Borde AB, Stoltz P (2008) Light requirements for growth and survival of eelgrass (*Zostera marina* L.) in Pacific northwest (USA) estuaries. *Estuaries and Coasts* 31:969–980. <https://doi.org/10.1007/s12237-008-9082-3>
- Unsworth RK, Bertelli CM, Cullen-Unsworth LC, Esteban N, Jones BL, Lilley R, Lowe C, Nuuttila HK, Rees SC (2019) Sowing the seeds of seagrass

- recovery using hessian bags. *Frontiers in Ecology and Evolution* 7:1–7. <https://doi.org/10.3389/fevo.2019.00311>
- Unsworth RKF, Nordlund LM, Cullen-Unsworth LC (2018) Seagrass meadows support global fisheries production. *Conservation Letters* 12:e12566. <https://doi.org/10.1111/conl.12566>
- van Katwijk M, Hermus D (2000) Effects of water dynamics on *Zostera marina*: transplantation experiments in the intertidal Dutch Wadden Sea. *Marine Ecology Progress Series* 208:107–118. <https://doi.org/10.3354/meps208107>
- van Katwijk MM, Bos AR, De Jonge VN, Hanssen LSM, Hermus DCR, De Jong DJ (2009) Guidelines for seagrass restoration: importance of habitat selection and donor population, spreading of risks, and ecosystem engineering effects. *Marine Pollution Bulletin* 58:179–188. <https://doi.org/10.1016/j.marpolbul.2008.09.028>
- van Katwijk MM, Thorhaug A, Marbà N, Orth RJ, Duarte CM, Kendrick GA, et al. (2016) Global analysis of seagrass restoration: the importance of large-scale planting. *Journal of Applied Ecology* 53:567–578. <https://doi.org/10.1111/1365-2664.12562>
- Ward M, Beheshti K (2023) Lessons learned from over thirty years of eelgrass restoration on the US west coast. *Ecosphere* 14:e4642. <https://doi.org/10.1002/ecs2.4642>
- Wear RJ, Tanner JE, Hoare SL (2010) Facilitating recruitment of *Amphibolis* as a novel approach to seagrass rehabilitation in hydrodynamically active waters. *Marine and Freshwater Research* 61:1123–1133. <https://doi.org/10.1071/MF09314>
- Wegoro J, Pamba S, George R, Shaghude Y, Hollander J, Lugendo B (2022) Seagrass restoration in a high-energy environment in the Western Indian Ocean. *Estuarine, Coastal and Shelf Science* 278:108119. <https://doi.org/10.1016/j.ecss.2022.108119>
- Wennberg T (1987) Långsiktiga förändringar av makroalgorans sammansättning och utbredning i södra Laholmsbukten sedan 1950-talet: long-term changes in the composition and distribution of the macroalgal vegetation in the southern part of Laholm Bay, south-west Sweden, during the last thirty years. Statens naturvårdsverk, Solna, Sweden
- Wennberg T (1992) Colonization and succession of macroalgae on a breakwater in Laholm Bay, a eutrophicated brackish water area (SW Sweden). *Acta Phytogeographica Suecica* 78:65–77, ISBN: 91-7210-078-8.
- Wijkmark N, Isæus M (2010) Wave exposure calculations for the Baltic Sea. AquaBiota report. AquaBiota Water Research AB, Stockholm, Sweden.

Supporting Information

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

Figure S1. Wind data from Båstad.

Figure S2. Temp, light, DO data from Båstad in 2021.

Figure S3. NMDS of all fauna samples in Båstad.

Figure S4. Taxonomic diversity in different types of plots.

Figure S5. Relative abundance of fauna classes between sites.

Figure S6. Community-weighted means (CWM) of trait values.

Table S1. Planted plots.

Table S2. Sediment properties from 2021 and 2022 in Båstad.

Table S3. Functional traits and their modalities used in functional diversity analyses.

Supplement S1. Supplementary methods.

Coordinating Editor: Gary Kendrick

Received: 20 September, 2024; First decision: 16 October, 2024; Revised: 24 October, 2025; Accepted: 26 October, 2025