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RESEARCH ARTICLE

Overcoming ecological feedbacks in seagrass restoration

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Overcoming ecological feedbacks is a major limiting factor reducing the success of many seagrass restoration projects. Negative feedbacks occur when biotic or abiotic conditions of a site are changed sufficiently after the loss of seagrass to prevent its recovery, even after the original stressors are remediated. While negative feedbacks in seagrass restoration are common, there remain limited studies of ways to reduce them and kick-start the necessary positive feedbacks to promote recovery. We used field and laboratory experiments to investigate key ecological feedbacks in seagrass (*Zostera marina*) restoration by testing the role of hessian bags and seed burial in reducing seed predation and promoting plant development. We used a double-hurdle model approach to predict "seagrass emergence success" and "seagrass growth success" across planted field plots. We found that planting seeds in hessian bags and burying them in the sediment improved the likelihood of seeds developing into mature plants. We recorded an average 13-fold increase in shoot density for seeds planted in buried bags relative to raked furrows. This could be the combined result of reduced predation as well as bags mimicking emergent traits of mature seagrass to withstand physical impacts. We supplement these findings with laboratory evidence that hessian bags provide protection from predation by green shore crabs. Overall, we found a low and variable success rate for seed-based restoration and indicate other feedbacks in the system beyond those we controlled. However, we show that small methodological changes can help overcome some key feedbacks and improve restoration success.

Key words: crabs, ecological feedbacks, eelgrass, emergent traits, hessian bags, hurdle model, seed predation, Zostera

Implications for Practice

- Ecological feedbacks limit recovery and restoration of seagrass following loss.
- Seed-based restoration in the United Kingdom has a low success rate but can be improved with site-appropriate methodological changes.
- Planting seeds in hessian (jute/burlap) bags and burying them can help overcome feedbacks related to seed predation and physical disturbances, and improve restoration success.
- Unattached macroalgae can be problematic for seed-based seagrass restoration.
- Further studies are needed to optimize planting media and techniques for using hessian bags as a seagrass restoration tool in different environmental contexts.

Introduction

There is growing interest in seagrass restoration as a nature-based solution to manage some of the environmental and societal challenges that we face (Macreadie et al. 2021). Seagrass restoration can deliver a range of benefits to people and biodiversity (Orth et al. 2020), but of paramount importance is its potential to halt or reverse the decline in the carbon sink capacity of the biosphere (Greiner et al. 2013). Although interest is high, there remain limited examples of seagrass restoration at scales large enough to realistically affect this capacity (van Katwijk et al. 2016). Where large-scale restoration has been possible, the methods used have been simplistic and low-cost (Orth et al. 2020). However, they are not necessarily transferable to other species, locations, or environmental contexts. We need to further our understanding of suitable methods for upscaling restoration in different scenarios, along with their relative costs and benefits. Equally, we need to understand what *does not* work in different scenarios, particularly in the context of factors that can become bottlenecks to successful restoration, such as ecological feedbacks (Maxwell et al. 2017; Pausas & Bond 2022).

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Overcoming ecological feedbacks in seagrass systems, which can exacerbate seagrass losses and reduce the success potential of many restoration projects, is a major challenge. Positive feedbacks can be triggered in response to environmental stressors and change seagrass systems into alternative stable states (i.e. the alternative biome state theory described by Pausas & Bond 2022). Negative feedbacks then typically occur when the biotic or abiotic conditions of the site are changed sufficiently after the loss of seagrass to prevent its recovery, even after conditions from the original stressor have been remediated. For example, where poor water quality (e.g. elevated nutrients) has led to seagrass loss, sediments previously trapped by the seagrass become remobilized (Unsworth et al. 2015), impeding recovery as they suffocate seedlings and fail to provide sufficient stability against physical disturbances for new shoots to take anchor. Similarly, herbivory and disturbance by abundant fauna that have proliferated at the site in response to a stressor can suppress seed germination and prevent young plants maturing. For example, large and small crustaceans and polychaete worms are some of the most commonly described predators of seagrass seeds and seedlings in temperate systems (Wigand & Coolidge Churchill 1988; Nakaoka 2002; Infantes et al. 2016*a*). Other problematic ecological feedbacks in seagrass seedling growth are algal dominance and sedimentary hydrogen sulfide toxicity (de Boer 2007), among other less understood sediment properties (e.g. oxygenation and microbiome conditions) that are undoubtedly modified and maintained by established meadows (Piñeiro-Juncal et al. 2022).

The impacts of these feedbacks on seagrass recovery and restoration are often difficult to separate from other overarching drivers of seed production and germination, and of seedling emergence, survival, and growth. Studies on seagrass germination and emergence are characterized by high levels of inter-study variability, with factors such as sulfide and anoxia, scarification, and salinity shown to be key triggers (Probert & Brenchley 1999; Orth et al. 2000). There is also good evidence that factors such as seed planting depth (Cumming et al. 2017) and nutrient availability can affect emergence (Unsworth et al. 2022).

Although negative ecological feedbacks in seagrass restoration are common, there remain limited experimental studies of ways to reduce and eliminate them, while kick-starting the positive feedbacks necessary to promote recovery. Biodegradable matting that mimics the stabilizing effect of established seagrass rhizomes has been recorded to improve restoration success in some environmental contexts by mimicking community-level emergent properties (Temmink et al. 2020). There have also been successful trials using sand capping to control organic-enriched estuarine sediments (Oncken et al. 2022). Control of these feedbacks is thought to ultimately amplify restoration success (Temmink et al. 2020, 2023; van der Heide et al. 2021). Meanwhile studies in the United States have found that planting seeds in hessian (burlap/jute) bags has reduced seed predation (Harwell & Orth 1999), and that burial of seeds may also be beneficial (Marion & Orth 2012). Planting seagrass seeds in hessian bags has since become an increasingly common restoration method. Although some studies have shown success (Harwell & Orth 1999; Unsworth et al. 2019), we know little about best practices for the deployment of hessian bags to maximize their success, especially in the context of ecological feedbacks in the system. With the use of seed-based restoration growing in popularity within some geographies, different methods are also being trialed that place seeds directly into sediments using varied media (Govers et al. 2022), and initial results indicate potential successes in intertidal projects. This is in contrast to studies in some locations that have recorded high levels of seed predation by green shore crabs (*Carcinus maenas*) (Infantes et al. 2016*a*) and consequently an abandonment of seed-based restoration.

In this study, we sought to further our understanding of ecological feedbacks in seagrass restoration through complementary field and laboratory experiments. We planted 162,000 seeds of the seagrass *Zostera marina* at a restoration site in Wales, United Kingdom, using three different planting methods, to test the role of hessian bags and seed burial in reducing seed predation and promoting plant development. We supplemented this study with a laboratory experiment explicitly testing the potential for hessian bags to reduce seed consumption by green shore crabs (*C. maenas*). The combined findings will improve our ability to scale up seagrass restoration projects in wider environmental contexts.

Methods

Field Experiment

A field experiment was initiated at Dale, Wales, United Kingdom, in November 2020 (Fig. 1). Dale is a sheltered bay in the Milford Haven waterway with a sandy/muddy seabed and a large tidal range (7.9 m mean spring range). The waterway is a busy industrial port and recreation area with some areas of elevated nutrients and freshwater influence (Jones & Unsworth 2016). There are other seagrass areas in the waterway (Bertelli et al. 2018), including small patches within the bay at Dale, approximately 400 m from our experimental site (Bertelli et al. 2021). Dale was selected for this experiment based on an initial habitat suitability model and previous small-scale experiments showing successful emergence and growth (Unsworth et al. 2022).

Seagrass seeds of the species *Zostera marina* were hand-collected from a seagrass meadow at Porthdinllaen, Wales, United Kingdom (Fig. 1), under permission during August 2020. The meadow is one of the largest and densest in Wales and is well-studied as a feature of the Pen Llŷn a'r Sarnau Special Area of Conservation (SAC). It has been the key donor site for restoration projects in Wales for several years. Collected seeds were held at approximately 14°C in a recirculating untreated seawater system at Swansea University. They were then planted in subtidal experimental plots (approximately 1.5 m below chart datum) in Dale by SCUBA divers using three different planting methods. Seeds were either planted directly into furrows raked in the sediment ("furrows" treatment) or they were planted in hessian bags, which were either buried flush with the sediment ("buried bags") or placed on the sediment surface ("surface bags"). For the furrows treatment, seeds were

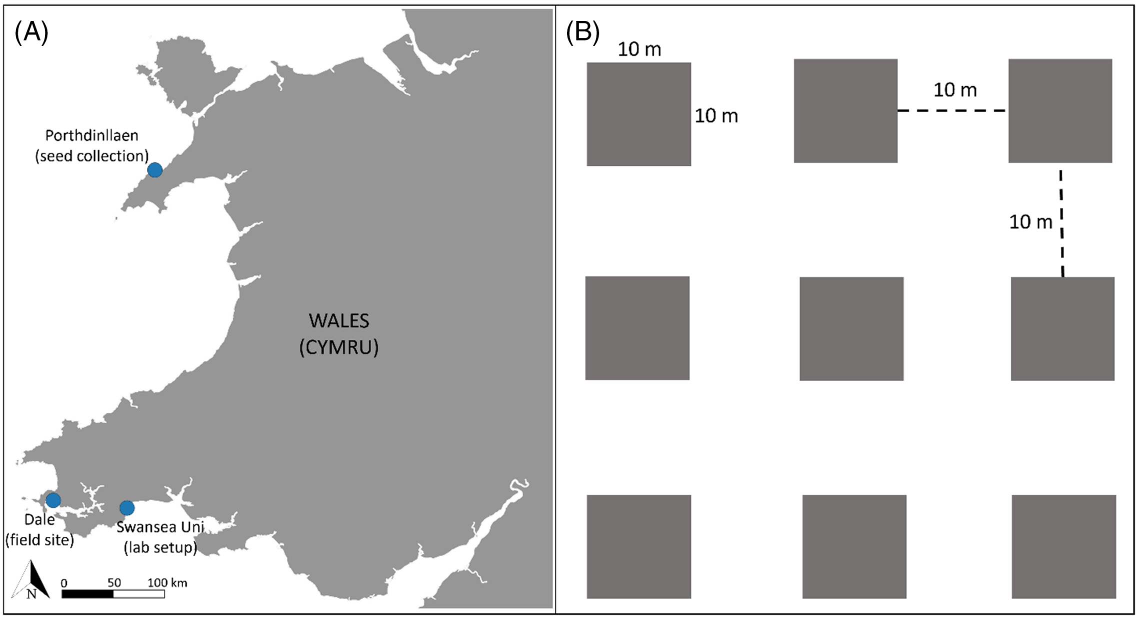

Figure 1. (A) Location of field experiment at Dale in Wales (Cymru), United Kingdom, along with locations of seagrass seed collection at Porthdinllaen and the laboratory experiment at Swansea University. (B) Field experiment setup showing the three-by-three grid of nine 10 × 10 m planting plots, each separated by 10 m (total area covered by the experiment was 0.25 ha).

poured evenly into 20 mm deep raked furrows (length: 500 mm; width: 20 mm), with 50 seeds per furrow. The raked sediment was then carefully replaced over the furrows by hand. For the bag treatments, seeds were packed into bags (130 × 70 mm) along with 100 mL clean sand, with 50 seeds per bag. Buried bags were hand-buried horizontally flush with the seabed (bottom of the bag approximately 40–50 mm depth; seeds presumed to be approximately 20 mm depth), whereas surface bags were placed horizontally flat on the surface of the seabed. A 200 mm long wooden stake was used to help secure each buried and surface bag to the sediment.

The three planting treatments (furrows, buried bags, and surface bags) were randomly assigned to nine 10 × 10 m plots, each separated by 10 m in a three-by-three grid pattern, with three plots per treatment (Fig. 1). To facilitate consistent planting densities and patterns within plots in low visibility, the plots were divided into quarters, with a surface buoy and weighted line deployed at the center of each quarter, down which a diver descended. Within each quarter, a 0.5 × 0.5 m quadrat was placed at the center and at each of the eight points of the compass. Within each quadrat, 500 seeds were planted: either 10 seed bags (buried or surface) haphazardly spread; or 10 furrows evenly spaced to fill the quadrat area. Thus, each plot contained 18,000 seeds, regularly spaced, regardless of the planting treatment.

After 10 months, the nine experimental plots were surveyed by divers during September 2021. Due to challenging conditions with poor visibility and dense mats of drifting maroalgae in some plots, it was unfortunately not possible to reliably relocate and survey the exact planted quadrats. Furthermore, some bags were seen to have been displaced from their original position by waves/currents as the small stakes proved not to be very effective in anchoring them in the long term. Therefore, the plots were sampled in a stratified way using 0.5 × 0.5 m quadrats, with $n = 20$ quadrats per plot (five quadrats haphazardly placed within each quarter plot). Seagrass shoot density, seagrass canopy height, and macroalgal cover were recorded in each quadrat. Shoot density was recorded by counting the number of shoots within the quadrat, then scaling up to shoots per meter square. Canopy height was estimated by measuring the length of the longest leaf within the quadrat (mm) (Duarte & Kirkman 2001). Macroalgal cover was visually estimated as percentage cover within the quadrat (%) following Seagrass-Watch methodologies (McKenzie et al. 2001). Macroalgal cover was recorded as it can potentially inhibit seagrass growth (Han & Liu 2014) and so may influence outcomes across the experiment. Importantly, the macroalgae recorded in this study were almost exclusively unattached drift algae and it was not possible to know how long they remained in their observed positions.

Laboratory Experiment

A laboratory trial was conducted under ethics permission SU-Ethics-Staff-110322/448 at Swansea University, Wales, United Kingdom, to test whether hessian bags protected seeds from predation by green shore crabs (*Carcinus maenas*) under controlled conditions. Five mesocosm tanks (L 500 × W 400 × H 250 mm) were set up within a flow through enclosed aquaria system containing untreated seawater and sand from Swansea Bay. Each tank held 40 L water and 20 L sand, creating a water depth of 100 mm above an even sandy bottom of depth 100 mm (Fig. 2). The sand was collected from the

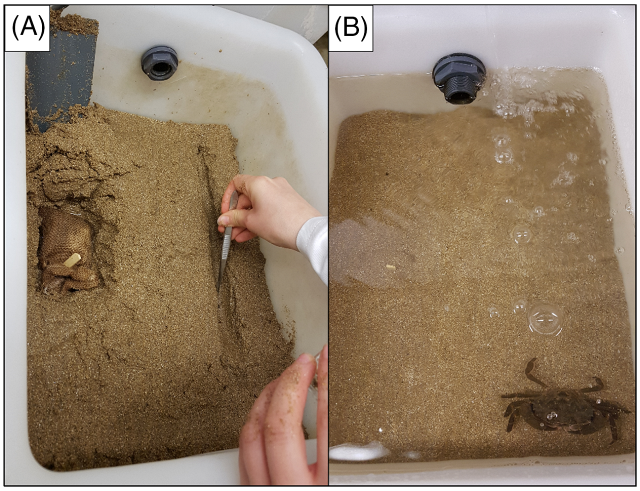

Figure 2. Laboratory experiment testing whether hessian bags protect *Zostera marina* seagrass seeds from predation by green shore crabs (*Carcinus maenas*). Each of five replicate tanks contained one hessian bag containing sand and 50 seeds and one 20 mm deep furrow with 50 seeds deposited evenly-spaced using a pipette (A). The bag and furrow were covered over with sediment and a single male crab was introduced with recirculating seawater for 7 days (B).

intertidal foreshore at Mumbles pier, near the university (Fig. 1) and flushed through a 0.5 mm sieve with freshwater to remove macrofauna and large detritus that could provide a food source for crabs. On one side of each tank, one hessian bag packed with clean sand and 50 seagrass seeds was buried flush with the sand and held in place with a wooden stake (as per the "buried bag" treatment in the field experiment described above). On the other side of the tank, 50 seeds were planted evenly spaced along a single 20 mm deep furrow and lightly covered with sand (as per the "furrows" treatment in the field experiment). Five small adult male crabs with 43–56 mm carapace width were hand-collected from the rocky shore at Mumbles pier and transferred to separate holding tanks with 40 L seawater for 24 hours. They were then transferred individually to the five experimental tanks and left for 7 days before being returned to the holding tanks. The experimental tanks were drained and the hessian bags carefully removed to individual sorting trays and inspected for damage. On finding all bags intact, the remaining tank sand and the sand from within bags was sieved through a 0.5 mm mesh to isolate and count the seeds remaining in each treatment.

Data Analysis

All statistical analyses were conducted using R v. 4.1.3 (R Core Team 2021).

Due to low seagrass emergence across our field experiment, shoot density and canopy height data were semi-continuous with a mixture of zeros (quadrats where seagrass had not emerged) and continuously distributed positive values (quadrats where seagrass had emerged). When summarizing data at the quadrat level ($n = 60$ replicate quadrats per treatment), the zero-inflated distribution of the data concealed potential patterns of interest (Fig. S1). Therefore, we aggregated summary data at the more ecologically meaningful plot level ($n = 3$ replicate plots per treatment). We present mean scores per plot along with overall means and standard deviations and correlate seagrass density with macroalgal cover.

For statistical analyses testing the effects of planting treatment on seagrass response metrics, we took a conservative approach and considered zeros to be true zeros (i.e. not false or structural zeros), and therefore used a hurdle model approach that accounts for and includes these excess zeros (Cragg 1971). Such an approach is widely used for ecological count data that has excess zeros, including for terrestrial forest restoration (Rehm et al. 2023) and bird observations (Balderama et al. 2016).

We used a double-hurdle model approach to predict "seagrass emergence success" across plots, as two sequential hurdles must be surpassed for a treatment to be "successful." Firstly, for a treatment to produce shoots (i.e. shoot density $\neq 0$), seagrass must have emerged from the sediment (hurdle one). Secondly, when seagrass has emerged, "success" also depends on *how many* shoots have been produced (hurdle two). The latter is conditional on the first hurdle, and the double-hurdle model allows for the possibility that the probability of initial seagrass emergence and its subsequent density have independent variables with different effects. Combining these two hurdles gives us a truer representation of overall emergence success that accounts for the likelihood of seagrass emergence, and for differences in shoot density across treatments. For simplicity, we refer to these two models as the "presence model" (hurdle one) and the "shoot density model" (hurdle two).

For the presence model (hurdle one), we fitted a generalized linear mixed effects model (GLMM) with binomial distribution to analyze the singular fixed effects of planting treatment ("furrows," "buried bags," and "surface bags") and macroalgal cover on the probability that shoot density was greater than zero. The model included a random "plot" effect to account for potential between-plot variability. We initially included an interactive effect of planting_treatment*macroalgal_cover, as hypothetically treatment success may depend on algal cover. However, based on Akaike's information criterion (AIC) score (Akaike 1974), removing this interaction improved the fit of the model. For the shoot density model (hurdle two), we fitted a GLMM with Poisson distribution to analyze the effects of planting treatment and macroalgal cover on shoot density, but excluded quadrats where seagrass had not emerged (i.e. shoot density $= 0$). We again included "plot" as a random effect. This time, AIC scores indicated inclusion of the planting_treatment*macroalgal_cover interaction. Model predictions were then multiplied so that overall seagrass emergence success was a product of both likelihood of emergence (hurdle one) and shoot density (hurdle two).

We followed the same approach to predict "seagrass growth success," combining the same "presence model" (hurdle one) with a "canopy height model" (hurdle two) using maximum leaf length data and a Gaussian distribution.

Seed count data from the laboratory experiment were simply converted to percentage of seeds consumed by crabs for each of the planting treatments: "furrows" and "buried bags."

Results

Field Experiment

After 10 months, seagrass emergence was low. Out of 180 quadrats sampled across the nine experimental plots, only 33 contained seagrass. The overall mean shoot density was 4 shoots/m^2, ranging from zero shoots in two of the plots (one furrows plot and one surface bags plot) to a maximum plot mean of 10 shoots/m^2 (surface bags plot) (Fig. 3A). On average, density was 7 shoots/m^2 in buried bags, 4/m^2 in surface bags and less than 1/m^2 in furrows. While surface bags plots were variable, the density in buried bags plots was consistently higher (on average 13-fold higher) than in furrows plots (Fig. 3A). These shoot densities equate to low seed emergence and survival relative to the number of seeds planted (i.e. 18,000/plot = 180/m^2), ranging from 4% in the buried bags, 2% in the surface bags, and less than 1% in the furrows.

Canopy height data reflected the same pattern as shoot density, with an overall mean maximum leaf length of 59 mm, ranging from zero in plots with no shoots to a maximum plot mean of 171 mm in a surface bags plot (Fig. 3B). Macroalgal cover ranged from 6 to 50% at the plot level (although some quadrats had 100% cover; Fig. S1) with an overall mean of 24% (Fig. 3C). This was again variable in the surface bags plots but otherwise showed an inverse pattern to the seagrass metrics, being consistently lower in buried bags plots than furrows (Fig. 3C).

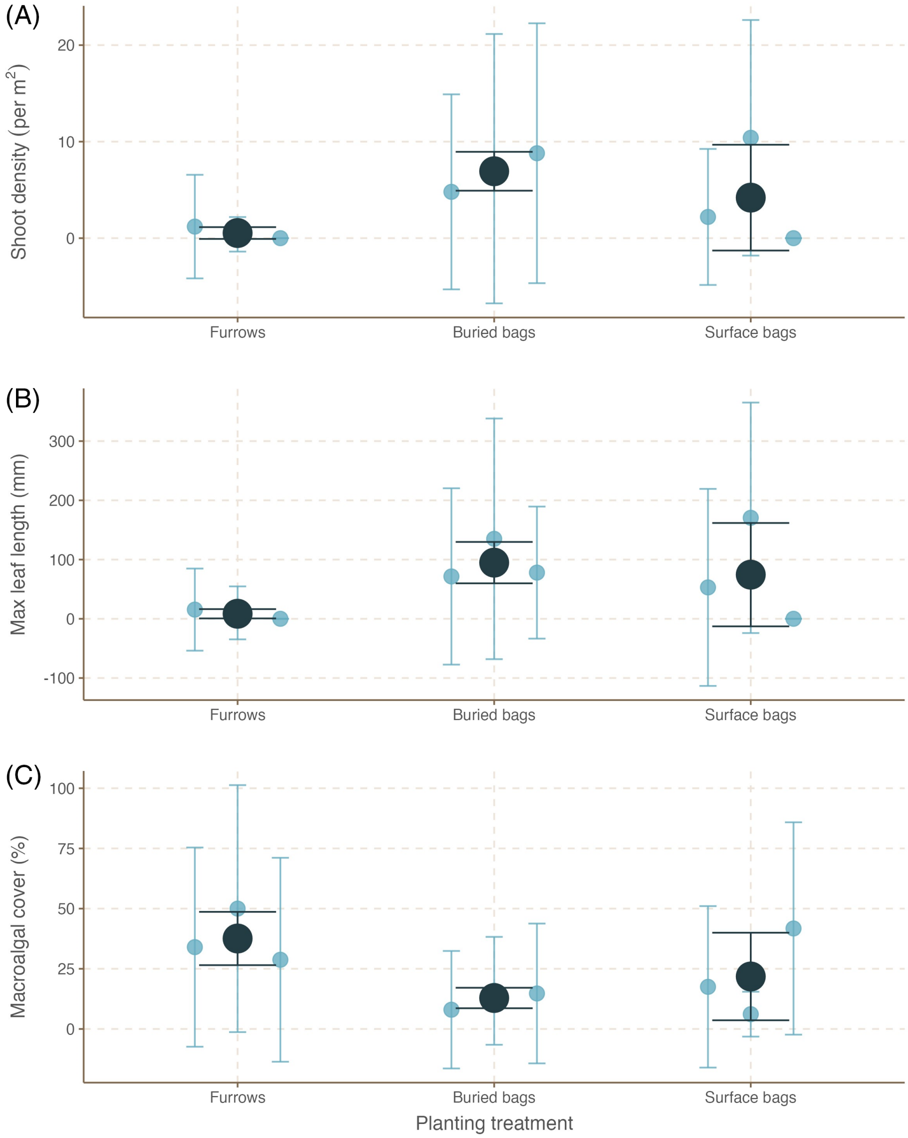

Figure 3. (A) Seagrass shoot density (per m^2), (B) maximum leaf length (mm) and (C) macroalgal cover (%) recorded in nine 10 × 10 m experimental plots subject to three different planting treatments (furrows, buried bags, and surface bags), with $n = 3$ plots per treatment. Plots were sampled haphazardly using 20 quadrats (0.5 × 0.5 m) per plot; data were averaged over plots because of zero-inflation in the data (Fig. S1). Small points represent plot means ± 1 SD; large points represent overall treatment means ±1 SD.

Pearson's test confirmed that there was a significant negative correlation ($r = -0.8$; $p < 0.05$) between seagrass shoot density and macroalgal cover, explaining 64% of the variability in the data (Fig. S2). The lowest seagrass densities were recorded in plots where macroalgal cover was greater than 20% (Fig. S2).

A double-hurdle GLMM to investigate the drivers of emergence success first modeled the drivers influencing the probability that shoots would emerge ($r^2 = 0.40$) (Table S1A), and second the drivers of actual shoot density above zero ($r^2 = 0.57$) (Table S1B). The predicted mean likelihood of

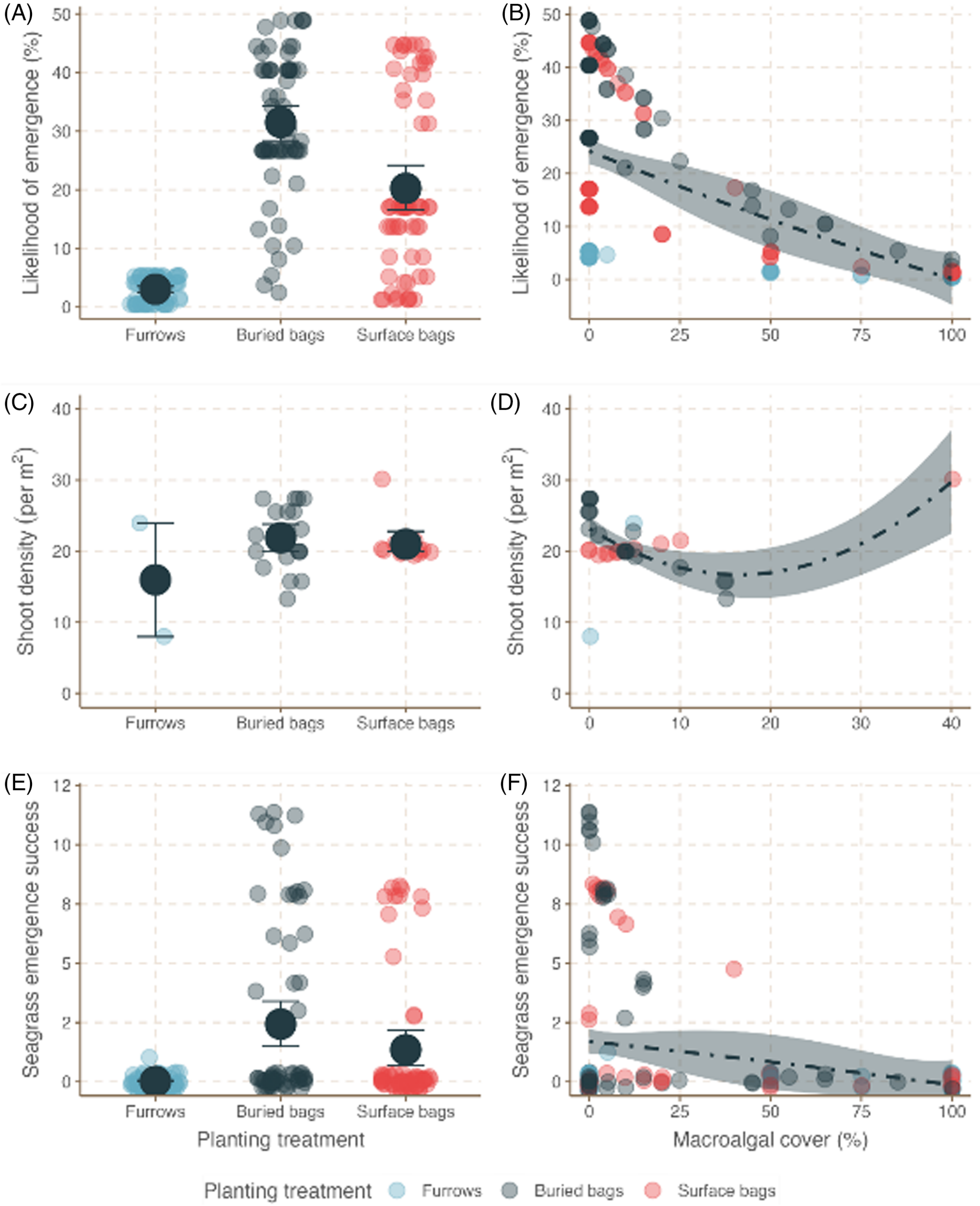

Figure 4. Double-hurdle model of the predicted effects of planting treatment (furrows, buried bags, and surface bags) and macroalgal cover (%) on: (A, B) the likelihood of seagrass emergence (%) (hurdle one); (C, D) shoot density (per m^2) (hurdle two); and (E, F) overall seagrass emergence success (combined model). Small symbols represent predicted values for 0.5 × 0.5 m quadrats sampled within nine 10 × 10 m experimental plots, with $n = 60$ quadrats per planting treatment (20 quadrats per plot, three plots per treatment). The shade of symbols reflects the density of points overlying one another. Large symbols in A, C, and E represent predicted group means with 95% CI. Gray shading in B, D, and F represents 95% CI.

Table 1. Seed consumption by green shore crabs (*Carcinus maenas*) recorded in five experimental tanks over 7 days. Each tank contained one crab and 100 seagrass seeds planted using two planting treatments (furrows and buried bags), with 50 seeds per treatment. *Crab deceased.

Tank	*Maximum carapace width (mm)*	*Bag condition*	*Seeds consumed (%)*	
			Furrows	*Buried bags*
1*	56	Perfect	0	0
2	43.5	Perfect	36	0
3	53.6	Small tear	18	0
4	55.3	Perfect	0	0
5	43	Perfect	62	0
Mean			23.2	0
SE			11.8	0

shoots emerging was higher for seeds planted in bags (buried bags: 32%; surface bags: 20%) than for seeds planted in furrows (3%), but only significantly so for buried bags (Table S1A; Fig. 4A). The likelihood of shoots emerging was significantly negatively influenced by macroalgal cover, although the effect size was relatively small (Table S1A; Fig. 4B). When conditions for the first hurdle had been met (i.e. shoots had emerged), we found that both buried bags (22 shoots/m^2) and surface bags (21/m^2) produced significantly more shoots than furrows (16/m^2), despite high variability in the furrows treatment (Table S1B; Fig. 4C). Macroalgal cover had a significantly positive (but relatively weak) effect on shoot density (Table S1B; Fig. 4D). The interactive effects of planting treatment and macroalgae, however, indicated a negative effect on shoot density for buried and surface bags (Table S1B). This suggests that the overarching positive relationship was predominantly driven by the two furrows quadrats in which shoots were recorded (one with algae having higher shoot density) plus an outlying surface bags quadrat with high shoot density and high algal cover (Fig. 4D).

Combining the two models to predict overall seagrass emergence success revealed that buried bags were, on average, the most successful planting treatment, and almost three times more successful than furrows (Fig. 4E). The emergence success decreased with increasing macroalgal cover and, although the relationship was relatively weak, predicted success was mostly zero when cover exceeded 20% (Fig. 4F).

When using the same double-hurdle model approach to predict seagrass growth success, we found no significant effects of planting treatment or macroalgal cover on maximum leaf length (hurdle two) (Table S2; Fig. S3).

Laboratory Experiment

After 7 days, one of the crabs was found deceased but it is not clear on which day he died. Three of the remaining four crabs had consumed seeds planted in furrows (18–62% seeds consumed), whereas no seeds had been consumed from within buried bags (Table 1). One of the bags had a small tear which may have been caused by the crab, but this did not penetrate the bag.

Discussion

This study finds that the use of hessian bags as a means of holding seagrass seeds in restoration projects can help overcome some key ecological feedbacks in the system and improve the likelihood of seeds germinating and developing into mature plants. We provide clear laboratory evidence that hessian bags protect *Zostera marina* seagrass seeds from predation by green shore crabs (*Carcinus maenas*), at least in the short term. Our field data then provides evidence that burying bags into the sediment further increases seedling emergence success and survival, perhaps by providing additional protection against predation, but also possibly by helping mimic the emergent traits of mature seagrass to withstand physical impacts (Temmink et al. 2020). We did not find evidence of hessian bags influencing the growth of seagrass once it had emerged, either through the timing of seedling emergence or access to nutrients/light. Growth instead appeared to be driven by ambient conditions at the site (Hemminga & Duarte 2000). Overall, our results reveal a low and variable success rate for seed-based restoration and suggest other feedbacks in the system beyond those we controlled, such as the presence of drift macroalgae, which can also disrupt restoration success.

Green shore crabs have long been established as a key predator of seagrass seeds, resulting in losses during restoration efforts (Infantes et al. 2016*a*), creating a negative feedback upon the process. In our laboratory experiment, no seeds planted in hessian bags were consumed by crabs, whereas a large proportion of unprotected ones were. Our field experiment reflected this with an average 7- to 13-fold increase in shoot density in hessian bags relative to seeds planted unprotected in raked furrows. These figures are comparable to improvements shown in similar trials in the United States where 4- to 10-fold increases were recorded (Harwell & Orth 1999). In our case, we hypothesize that a large proportion of the increased success stems from mechanical protection against predation afforded to seeds by the hessian bags. Our laboratory findings clearly show that green shore crabs have the ability to locate and consume seagrass seeds buried unprotected under 20 mm of sediment (i.e. the depth of furrows in our field experiment). In contrast, there was limited evidence of crabs attempting to access seeds within hessian bags, apart from one small non-penetrating tear in one bag. Of course, this does not mean that crabs cannot and will not access seeds in hessian bags under different conditions or over longer timeframes, but it suggests that when alternative more easily accessible food is available, they made limited attempts to locate seeds in bags. At our experimental field site, anecdotal observations of large groups of children regularly fishing (catch and return) for green shore crabs from the local pontoon indicate a thriving population in the bay. Whether this population would scavenge for seeds in hessian bags remains to be seen, but our laboratory-observed animals collected from a rocky shore did not. There may be other seed predators at the site, such as polychaete worms and gobies, but presumably crabs with their dexterity and sharp claws would be at least as capable of penetrating bags as other species. We would, therefore, expect the same protection to be offered against other predators.

Our field experiment demonstrates that the use of hessian bags contributes to higher abundance of emergent *Z. marina* seedlings compared to seeds sown directly into raked sediment. Predicted emergence success was significantly higher when bags were buried flush in the sediment, but not when placed on the sediment surface. Although we hypothesize predation to be a factor, other influences are likely to have contributed to this. Unbagged seeds could easily have been lost to lateral transport (i.e. washed away) within the dynamic tidal environment of the South Wales coast (≈7.9 m tidal range), particularly as the seeds were planted in November before the characteristic United Kingdom winter storms. Seeds planted directly in the sediment have been washed away in other studies, particularly if the sediment itself was redistributed (Gräfnings et al. 2023). It is similarly possible that surface-planted bags were more easily washed away than those buried into the sediment. There is anecdotal evidence of bags (external to this trial but within the vicinity) being washed away during storm events, with small stakes having minimal anchoring effect. Therefore, we hypothesize that burying bags further reduces the likelihood of their movement, thus enhancing seed germination, at least in the intended restoration area. The propensity for seagrass seedlings to be easily damaged by physical disturbance means that minimizing bag movement post-germination must also surely promote seedling survival. In some successful trial-use of hessian bags, ropes have been used to secure bags to the seabed, reducing their potential to be moved by storm events (Unsworth et al. 2019). Studies in China, where germination rates upwards of 20% have been recorded using hessian bags, used large metal U-shaped pins to secure bags into the sediment (Zhang et al. 2015). We suggest that the evidence points to clear benefits of burying and securing hessian bags into the sediment. Stabilizing seedlings long enough to allow the beginnings of a rhizome network to develop would then kick-start a positive feedback process to further stabilize sediments and promote meadow recovery (Dalby et al. 2023). However, these benefits may not always apply in environments when hydrodynamic influences are reduced (e.g. in lagoons).

The emergence success of seedlings in our field experiment was found to be influenced by an additional feedback that we did not control, namely macroalgal cover. While the relationship was relatively weak, and we cannot be sure how long drifting macroalgae had remained in their observed positions, predicted emergence success was mostly zero when macroalgal cover exceeded 20%. This agrees with previous studies that have found seedlings to be highly vulnerable to physical impacts from moving algae (Valdemarsen et al. 2010) and confirms the vulnerability of seed-based restoration to small-scale site changes (Hootsmans et al. 1987). Our uncertainty regarding when and for how long floating macroalgae may have been a hindrance on the seeds and/or seedlings reflects the challenges associated with subtidal restoration research necessitating dive teams, where regular monitoring is not always feasible. Experimentation in controlled environments may elucidate this.

Burying seeds in hessian bags may have additional benefits for seeds and seedlings, beyond protection from surface predators and enhanced stability, through presentation of environmental cues for germination and growth. Many laboratory studies find optimum seed germination of *Z. marina* occurs when seeds are buried at less than 20 mm sediment depth (Jørgensen et al. 2019). We now know that crabs can easily access unprotected seeds buried at this depth and that bags can protect them and anchor them in the sediment. Bags furthermore enable the deployment of seeds in a controlled media compared to often unknown or unsuitable chemistry in *in situ* sediments, which can also present negative feedback to recovery and restoration. Although to date there is limited understanding of this, nutrient additions have been shown to provide an improved level of seedling success (Unsworth et al. 2022), while smaller grain sizes have been found to favor germination (Cumming et al. 2017). Further testing to determine and mimic the optimal sediment type, microbiome conditions, and levels of nutrients, anoxia, and sulfide is required to improve planting methods using hessian bags, to kick-start further positive feedbacks necessary to promote a return to a stable seagrass ecosystem state. Future experimentation should attempt to detect and measure—beyond the traditional emergence and growth performance metrics—whether and how planted seagrass modifies its sediment to affect the growth of the next generation (Pausas & Bond 2022).

The overall conversion rate of seeds to mature plants was low in our field study at less than 5%. Although we may have recorded higher emergence with increased sampling effort (5% of plot areas sampled), we suspect this low success rate also reflects other as-yet undetected factors. For example, our anecdotal observations of hessian bags used in a different trial (bag inspections in the lab 12 months after planting) revealed that in some instances seedlings were not able to emerge through the hessian fabric. So although we observed improved shoot emergence in this study, the method performs poorly (in terms of shoot emergency) relative to other seed-based methods being used for seagrass restoration (Orth et al. 2000; Xu et al. 2016). Overall, although the hessian bag method may be quite effective at protecting seeds relative to direct planting in furrows, the design of bags, their contents, and deployment needs to be more rigorously examined to determine the most effective application.

Seagrass restoration at scale remains challenging, and where it has been successful, this has largely been focused on seed-based methods (Orth et al. 2020; Hori & Sato 2021). Here, we record rates of seed success (defined as mature plants) of less than 5%, creating challenging decisions for the effectiveness of these methods. Examination of the literature indicates that low germination (or emergence) rates are common in field-based studies (Valdemarsen et al. 2011; Eriander et al. 2016; Infantes et al. 2016*b*) but also highly variable without obvious explanations for the magnitudes of difference. The costs of seed collection and processing are high when success is relatively low. Greater research effort is required into the exact conditions necessary to be able to place seeds into marine sediments and observe high emergence rates that make such work more viable at large scales (Unsworth et al. 2023). The negative feedback of floating macroalgae observed here (not a eutrophication-type response) also highlights the need to look beyond the immediate in order to examine the unexpected and, with it, be prepared to take potential management strategies to deal with such events.

Although not largely practiced in seagrass restoration projects, algal clearance has been conducted in other ecological restoration (e.g. corals) (Ceccarelli et al. 2018) and may need to be considered when the arrival is not due to an over-riding eutrophication problem but an episodic event.

In conclusion, we present evidence that planting seeds in hessian bags and burying them in the sediment can help to overcome some key negative ecological feedbacks in seagrass restoration and kick-start some positive feedbacks necessary to promote a return to a stable seagrass ecosystem state. We propose that this is principally the result of decreased predation, but also on account of increased stability against physical disturbance. This study also illustrates how other less avoidable factors, like macroalgal cover, can also create negative feedbacks in the system, reducing the success rate of restoration. Seagrass restoration performance remains highly variable across different coastal contexts. However, small, subtle site-appropriate changes to methods are key for overcoming feedbacks and improving the potential of restoration success.

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Supporting Information

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

Figure S1. Quadrat-level (A) seagrass shoot density (per m^2), (B) maximum leaf length (mm), and (C) macroalgal cover (%).
Figure S2. Pearson's correlation between macroalgal cover (%) and seagrass shoot density (per m^2).
Figure S3. Double-hurdle model of the predicted effects of planting treatment and macroalgal cover on seagrass growth success.
Table S1. Double-hurdle model of the effects of planting treatment and macroalgal cover on seagrass emergence and shoot density.
Table S2. Double-hurdle model of the effects of planting treatment and macroalgal cover on seagrass emergence and max. leaf length.

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