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Matching planting methods to species and site conditions is key in seed-based intertidal seagrass restoration

Lucy Coals [a,b,c,*], Benjamin L.H. Jones [b,c,d], Ally J. Evans [b,c], Richard K.F. Unsworth [b,c], Laney Callahan [a], Rhys A. Coleman [e], Laura L. Govers [f,g], Max L.E. Gräfnings [f,h], Emma L. Jackson [i], Craig D.H. Sherman [a]

[a] School of Life and Environmental Sciences, Deakin University, Geelong, Victoria, Australia
[b] Project Seagrass, Unit 1 Garth Drive, Brackla Industrial Estate, Bridgend CF31 2AQ, UK
[c] Seagrass Ecosystem Research Group, Department of Biosciences, Swansea University, Swansea SA2 8PP, UK
[d] Department of Earth and Environment, Institute of Environment, Florida International University, Miami, Florida, USA
[e] Melbourne Water, Research and Modelling, Docklands, Victoria, Australia
[f] Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences, University of Groningen, 9700, CC, Groningen, the Netherlands
[g] Department Coastal Systems, Royal Netherlands Institute of Sea Research, Utrecht University, 1790, AB, Den Burg, the Netherlands
[h] Tvärminne Zoological Station, Faculty of Biological and Environmental Sciences, University of Helsinki, Hanko, Finland
[i] Coastal Marine Ecosystems Research Centre, Central Queensland University, Gladstone, Queensland, Australia

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ABSTRACT

Seagrass meadows continue to be lost and degraded globally. Restoration is one promising and emerging conservation strategy to combat such losses and place seagrass on a pathway to net gain. However, successful restoration methods remain limited to a few species, and geographically constrained, with few experimental trials comparing planting methods across species and seagrass bioregions. This study trialled three seed-based seagrass restoration planting methods in two seagrass bioregions (the temperate north Atlantic and temperate southern oceans). Using two seagrass species *Zostera marina* and *Zostera muelleri* this research investigated seed-based planting methods and their influence on the likelihood of seedling emergence, shoot emergence, and seedling growth (i.e. leaf length). Seagrass emergence was observed at 50 % of the experimental sites, with the likelihood of seagrass emergence largely influenced by local site conditions. Each planting method performed variably in relation to species and environmental conditions. Dispenser injection seeding resulted in the highest shoot emergence efficiency of the three methods for *Z. marina* while biodegradable planting pots and hessian bags were the more favourable methods for use with *Z. muelleri* seeds. Despite all chosen sites deemed suitable for restoration from habitat suitability models, low seedling emergence suggests that site conditions including wind fetch, redox boundary depth and mud- dominant sediments present specific bottlenecks to seed germination and retention. This work demonstrates the importance of matching seed planting methods to site conditions and species life history traits and highlights the need for greater understanding of mechanisms to overcome germination and emergence bottlenecks in seed-based restoration.

1. Introduction

Humans have become the largest driver of earth system change, so much so that we have transgressed six of the nine planetary boundaries beyond which environmental changes can occur, with serious consequences for our existence (Richardson et al., 2023). The need to reverse degradation of the world's natural resources and restore biosphere integrity has never been more urgent. Although protecting existing ecosystems is paramount, ecological restoration will also be necessary to achieve conservation goals (Gann et al., 2019; Hemraj et al., 2024). Ecological restoration publications across terrestrial, freshwater and marine disciplines have increased 1100-fold in 30 years, a necessary growth to underpin and inform restoration practice (Shen et al., 2023). The increase in restoration research and implementation has also fostered increasing acknowledgement and inclusion of social and economic dimensions of restoration practice (Fernández-Manjarrés et al.,

* Corresponding author at: School of Life and Environmental Sciences, Deakin University, Geelong, Victoria, Australia.
E-mail address: l.coals@deakin.edu.au (L. Coals).

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2018).

Amidst myriad marine and coastal ecosystems undergoing restoration efforts, seagrass systems have received increasing attention from the media, public, researchers and other societal sectors as their importance as an ecosystem engineer becomes increasingly evident (Unsworth et al., 2022b). Seagrass meadows form part of a coupled social-ecological system that provides food security, well-being and recreation to local people, supports biodiversity, serves as a substantial carbon sink, and provides coastal defence (Cullen-Unsworth et al., 2014). However, seagrass meadows remain in decline at an annual rate of 1–2 % (Dunic et al., 2021), largely due to poor water quality, land reclamation, and direct destruction (Turschwell et al., 2021). Elimination of such threats forms the basis of successful conservation and restoration to promote natural recovery. Examples where improved watershed management has reduced nutrient loads illustrate how responsible management and 'passive' restoration can facilitate recovery of seagrass and other subaquatic vegetation (Tanner et al., 2014; Lefcheck et al., 2018; Krause-Jensen et al., 2021).

'Active' seagrass restoration broadly refers to planting shoots (transplanted from elsewhere) or seeds (van Katwijk et al., 2016). Transplanting has been applied widely across temperate and tropical systems (Paling et al., 2009). However, moving mature plant material, either with or without sediment, is time consuming, labour intensive and requires the removal of plant material from a donor meadow which may not be sustainable long term (Tan et al., 2020). Seed-based approaches are increasingly being adopted in seagrass restoration practice and research (Orth et al., 2006a; Unsworth et al., 2019; Tan et al., 2020; Sinclair et al., 2021; Govers et al., 2022). The use of seeds, including for the propagation of seedlings, predominantly involve genera and species that produce high quantities of seeds (e.g., *Zostera* spp.) (Sherman et al., 2018; van Katwijk et al., 2021). When the genera allows, seed-based restoration may provide benefits that outweigh shoot-based approaches, including a lower impact on donor meadows, greater scalability and increased genetic diversity (Orth et al., 2006b; Tanner and Parham, 2010; Orth et al., 2012; Kettenring and Tarsa, 2020).

Crucial to the success of seed-based restoration is determining the deployment method most appropriate for conditions and interacting feedbacks at a site (Tan et al., 2020; Unsworth et al., 2023). Methods range from simple approaches such as hand broadcasting seeds (Orth et al., 2020) or Buoy-Deployed Seeding (BuDS) (Pickerell et al., 2005), to more targeted approaches such as seed injection methods (Seed sleds and Dispenser Injection Seeding (DIS)), or planting seeds within structures such as biodegradable bags or pots that protect them from predation or disturbance (Harwell and Orth, 1999; Unsworth et al., 2019; Govers et al., 2022; Gräfnings et al., 2023b; Tan et al., 2023; Unsworth et al., 2024). Mechanised methods that facilitate upscaling restoration have also been trialled, but knowledge about their efficacy remains limited (Paling et al., 2001; Orth et al., 2009). Despite the development of several seed-based restoration methods, there is no systematic framework for identifying which approach is the most appropriate for a particular species or site. In particular, a mechanistic understanding of seagrass restoration successes and failures are limited in peer-reviewed literature, with particularly few publications reporting failed attempts (Gräfnings et al., 2023a).

Other seed-associated restoration methods exist that aim to facilitate natural recruitment rather than directly planting seeds. For example, in Australia, hessian sand-bags (without seeds inside them) have been used to take advantage of seed traits, notably a distinctive 'grappling hook' in the genus *Amphibolis* which anchors to hessian bags (Irving et al., 2010) and Statton et al. (2017) have identified *Posidonia australis* recruitment bottlenecks, including faunal grazing and bioturbation disturbance, which limit seed and seedling establishment. Establishment bottlenecks are closely linked to seed and seedling life-stages which innovation can align with, such as faunal exclusion cages to restrict seedling grazing. Finally, there is increasing interest in germinating and growing seedlings in land-based nurseries to provide a reliable and sustainable source of material for restoration which can help navigate some of the early-life stage bottlenecks to seed establishment, e.g. seed predation (van Katwijk et al., 2021; Unsworth et al., 2023).

This study draws on two temperate seagrass restoration programmes aiming to restore seagrass meadows at scale to support ecosystem service provisioning. Due to variable local legislation, access to potential restoration sites (e.g. through private land), and supply of donor material, seed- based restoration methods are favoured in these programmes. While multiple methods for seed planting exist, decision-making to identify the most appropriate method is constrained by a lack of direct practical comparisons between planting methods and growth strategies within a single system (Cronau et al., 2023), which, if available, could provide information about the efficacy of different seed planting methods.

By working across hemispheres, with one programme in Wales (United Kingdom) and another in Victoria (Australia), this study capitalises on the histories of these restoration programmes. In doing so, we conduct a series of trials exploring intertidal seed-based planting approaches to identify commonalities across and between similar species and temperate restoration locations. We believe that information and lessons learned from the well-studied *Zostera marina (Linnaeus,* Sp. *Pl: 968 (1753))* can be used to inform restoration of a less understood intertidal species, *Z. muelleri,* Irmisch ex Ascherson (1867). For both programmes, seed-based restoration locations have been guided by the development of local habitat suitability models (HSMs). To date, intertidal seed-based trials in the UK and Australia have been conducted using seeds, primarily planted in hessian bags (Unsworth et al., 2019; Tan et al., 2023). The DIS method has been employed at sites across Europe and presents a potential new method for effective upscaling of restoration efforts. Each method has met with varying degrees of success and failure, but there are currently no studies which directly compare planting methods in-situ between *Z. marina* and *Z. muelleri*.

In the context of the multiple methods being used for seed-based seagrass restoration globally, this research aimed to trial the effectiveness of three of these seeding techniques (DIS, biodegradable pots and hessian bags), for two seagrass species: *Z. marina* and *Z. muelleri*. By planting at locally selected and deemed suitable intertidal restoration locations, this study represents a comparison of planting methods in *real world* restoration sites. In doing so, this study had three aims. First, to investigate the likelihood of seagrass emerging at sites, given use of different planting methods and influencing environmental conditions. Second, to investigate the efficiency of each planting method at promoting seedling emergence (e.g. shoot number), and third, to investigate the growth of seedling from each planting method (e.g., leaf length). Broadly, these aims relate to key questions asked by restoration practitioners; 1) can we plant at a site, 2) what methods should we use to plant at a site, and 3) which methods will out plants grow best with at a site?

2. Methods

2.1. Study areas and sites

Zosteraceae seeds were used in experimental planting trials in two seagrass bioregions (Short et al., 2007), the Temperate North Atlantic & Temperate Southern Ocean, where seagrass meadows often comprise just one or two species from the Zosteraceae family. Trials were conducted in Wales, UK (Temperate North Atlantic) and Bunurong Country, Victoria, Australia (Temperate Southern Ocean).

Since the 1920s, the UK has suffered declines of up to 92 % in seagrass extent (Hiscock et al., 2005; Green et al., 2021), largely because of poor water quality and coastal development. Detailed long-term data on their extent remain spatially limited but the Welsh coastline supports a scattered distribution of *Zostera marina* and *Nanozostera noltei* meadows across estuarine environments, intertidal zones, inland seas and coastal waters (Jones and Unsworth, 2016; Bertelli et al., 2018).

Bunurong Country of the Kulin Nation in the Australian state of Victoria encompasses Western Port. Western Port is listed as a UNESCO Biosphere Reserve and Ramsar Wetland of International Importance. Seagrass meadows across Western Port have suffered substantial declines since the 1970s (Keough and Quinn, 2011), though some intertidal areas show signs of natural recovery (Dalby et al., 2023b). Western Port comprises fragmented mixed species meadows of *Z. nigricaulis* (Kuo, 2005), Jacobs and Les (2009), (Syn. *Heterozostera nigricaulis;* (Kuo, 2005)), *Halophila australis* (Doty and Stone, 1966) and *Amphibolis antarctica* (Labill.), Sonder and Ascherson ex (Ascherson, 1868), with the fast-growing *Z. muelleri* now dominating soft-sediment intertidal zones.

Seagrass planting trials using *Z. marina* seeds were undertaken at six sites across the Llŷn Peninsula (Penrhyn Llŷn in Welsh) and the Isle of Anglesey (Ynys Môn) in Wales: Abersoch, Llanbedrog and Penychain, and Traeth Bychan, Traeth Lligwy and Porth y Môr, respectively (Fig. S1A). Four *Z. muelleri* trial sites were chosen in Western Port: Grantville, Pioneer Bay, Coronet Bay, and Jacks Beach (Fig. S1B; Table S1). Sites in each region were chosen using locally developed habitat suitability models which highlighted favourable areas for restoration (Bertelli et al., 2023; Dalby et al., 2024).

In Wales, particularly on the Isle of Anglesey, there was limited historical information on the presence and distribution of seagrass for two of the three chosen sites (Traeth Bychan, Traeth Lligwy) and anecdotal evidence of seagrass at one (Porth y Môr) – though at these sites, extensive human impacts (e.g., mining effluents and military activity) have previously influenced the seabed. Sites across the Llŷn Peninsula include those where seagrass currently exists (Pen- Y-Chain) and anecdotal observations suggesting seagrass used to exist (Abersoch, Llanbedrog). In Australia, however, recent remote sensing and in-situ mapping provide broad-scale evidence of persistent and ephemeral seagrass patches in Western Port (Dalby et al., 2023b).

2.2. Seed collection and processing

In each bioregion, seagrass seeds were collected from a donor meadow within 2–52 km of the planting trial sites. In Wales, *Z. marina* seeds were collected in August 2021 by walking the intertidal zone and SCUBA diving shallow subtidal areas and picking reproductive spathes by hand at Porthdinllaen (N52.943246, E-4.566664). Following collection and storage (SI, appendix 1), seeds underwent viability drop testing before planting the seeds deemed viable in February 2022 (Marion and Orth, 2010). In Australia, *Z. muelleri* seeds were collected by walking the intertidal zone and picking reproductive spathes by hand at Woolley's Beach (N-38.351786, E145.218486) in February 2022. Following collection and storage (SI, appendix 1), all seeds underwent a density drop test for viability prior to planting in September 2022.

2.3. Planting methods and experimental design

In this trial, a total of 28,800 *Z. marina* seeds were planted across the six UK sites and 19,200 *Z. muelleri seeds* across the four Western Port sites (Table S2).

At each site, four circular split plots (⌀ 4 m, area 12.6 m^2, 4 m apart) were marked out in a row running parallel to the shore, as close as possible to the mean spring low water mark (MLWS) given conditions on the day (no plots were > 0.6 m above MLWS). We used a nested design to trial planting methods by site, plot and sector. We planted four plots at each site using three seed planting methods; hessian bags (Harwell and Orth, 1999; Unsworth et al., 2019), Dispenser Injection Seeding (DIS) (Govers et al., 2022) or biodegradable pots (Orth et al., 2006a).

Each plot was split into three equal 'pie-shaped' sectors of ~4 m^2. Within each plot, each sector was randomly assigned to one of the three planting methods, so that all plots contained a sector planted using DIS, one with biodegradable pots and another with hessian bags. We planted a total of 400 seeds per sector, equating to each plot containing 8 hessian bags, 16 pots or 80 DIS injections. Seeds were distributed evenly within a sector using the assigned planting methods (Fig. 1). Circular plots were used to minimise the effects of fine-scale site heterogeneity, and to mimic the growth shape of natural seagrass patches.

Hessian bags (5 × 13 cm) of uncoated hessian with 1 mm weave were each filled with 80 ml of sterile sand with 50 seeds mixed evenly into it. Commercially available play-sand or local sand, sieved to 2000 μm (with D50 = 292 μm) and heated to 160 °C for 2 h, was used in hessian bags to represent commonly used methods in restoration practice. Each plot was planted with eight bags (100 seeds/m^2), and each bag was buried horizontally flush with the surface of the sediment and secured using a biodegradable stake (Unsworth et al., 2024). Biodegradable pots (4 × 4 cm) (coir and recycled paper) were each filled with 40 ml sterile sand and 25 seeds planted at 1.5 cm depth within the pot. Pots were then buried flush with the sediment with 16 pots planted per plot (100 seeds/m^2). DIS used a caulking gun filled with a mix of thickened intertidal mud and seeds from the donor meadow to inject the mix directly into the sediment. A hole positioned 2 cm from the end of the caulking nozzle was used to deliver the seeds at a depth of ~1–2 cm into the sediment for both *Z. marina* and *Z. muelleri* with 80 injects per 4 m^2 (~5 seeds per inject, 100 seeds m^2).

2.4. Monitoring

In-situ monitoring was conducted during low tide over six months following planting to record seagrass emergence and morphometric data within each split-plot sector. We recorded the presence or absence of seedling emergence (/sector), shoot number (/sector), and average leaf length (mm). Monitoring was conducted approximately monthly from April – July 2022 in the UK (at 35, 70, 100, 130 and 160 days post-planting) and October 2022 – March 2023 in Australia (at 30, 65, 110, 140 and 180 days post-planting). By July 2022 in the UK and March 2023 in Australia, almost all seagrass had disappeared from plots, so the experiments were ended after 160 and 180 days, respectively.

Several environmental parameters recorded at each site were used to make inferences about site and method interactions and monitor changes in conditions across the experimental period. At each site, irradiance (lux) was recorded with a single HOBO Pendant light logger (MX2000), captured at 30-min intervals. We calculated daily means over the duration of the experiments from measurements recorded between sunrise and sunset (Fig. S2). These were then used to calculate an overall mean daily lux for each site. During the planting phase, sediment characteristics at each site were classified using a 4-point scale from mud - sand (mud, sandy mud, muddy sand, sand), modified from Folk (1954). Although we used a 4-point scale, sites fell into sand or mud categorisation. Sediment redox boundary depth (cm) was also recorded by measuring the redox line from a 20 cm core. Deposition rates of suspended sediments (kg/m^2/day) were measured using 45 cm PVC pipes (⌀ 5 cm, $n = 3$ per site approx. 10 m apart) embedded in the sediment for 1 month in spring during the season of planting and growth. We estimated wave exposure at each site using the proxy metric of wind fetch (Burrows, 2012), the distance over which wind can travel across open water (km). This simple fetch metric is useful for predicting distribution of intertidal organisms, including seagrass (Downie et al., 2013; Callaghan et al., 2015), and wave exposure models that have integrated simple fetch metrics have been shown to produce near identical results to more complex models (Sundblad et al., 2014). In the absence of detailed exposure and bathymetry data at a scale that was comparable across the two bioregions, we used the *windfetch* package for R to calculate the fetch distance for 36 wind directions (0–360°) across each site. To account for variation in dominant wind patterns, we then averaged fetch across all directions to calculate effective fetch at each site.

2.5. Data analysis

All statistical analyses were conducted using R version 4.3 (R Core

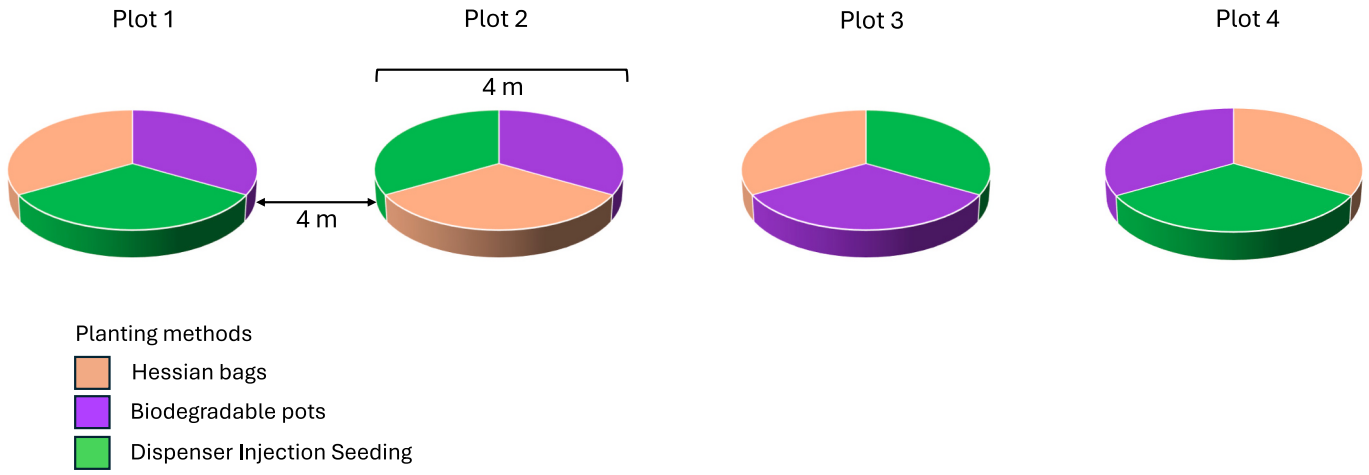

Fig. 1. Experimental design of four split plots planted at 6 restoration sites in the UK and 4 restoration sites in Australia. Each plot is planted using DIS (green) hessian bags (purple) and biodegradable pots (orange), which were randomly assigned to each of the plot sectors. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Team, 2023). Our analysis focuses on assessing three main aims: 1) the likelihood of seagrass emergence 2) shoot emergence, and 3) temporal variation in shoot number and leaf length.

Summary data are presented as shoot emergence efficiency which we calculated a percentage of the total number of emergent shoots from the total number of seeds planted for each method across the entire experiment for each bioregion. This was reported for each planting method at each monitoring time point, pooled per site. For the emergence efficiency of the two sites with the most records of emergence (Abersoch, UK and Coronet Bay, Australia) percentages were calculated using the number of shoots emerged per planting method from the number of seeds planted per method at that site. In this experiment we define success as the emergence of seagrass, where emergence is measured as the observation of a shoot or cotyledon.

2.5.1. Likelihood of emergence

For both species, we used generalised linear mixed-effects models (GLMMs) (Zuur et al., 2009) to evaluate the influence of Planting Method (3 levels: bags, pots and DIS) on the likelihood of seagrass emergence, while accounting for environmental variables (Fetch, Redox Boundary Depth, Average Daily LUX, Sediment Deposition and Sediment Type), the nesting of site, plot, sector, and time since planting. To do this, we used a binary GLMM to understand what factors influenced the emergence of seagrass, or not. We based this on the presence of seagrass in a sector at any defined time point, irrespective of number of shoots present. For example, sectors where seagrass did emerge received a 1, and sectors where it did not, received a 0.

Binary GLMM's were constructed to retain all variables (e.g. to reduce Type I errors), and were assessed for multicollinearity using variance inflation factors (VIF).We ensured all VIF values were < 3 (Zuur et al., 2010; Matuschek et al., 2017). Average Daily LUX and Sediment Deposition were removed from models because they were highly correlated with Fetch, and with each other (Fig. S3). Their data was also patchy due to burial of sediment pipes and light logger units and Fetch appeared to better incorporate both variables.

Binary GLMM's were fit separately for each species. For the *Z. marina* model, we excluded Sediment Type as a predictor, given that all sites were classified as sand. This left the remaining environmental variables of Fetch and Redox Boundary Depth. For *Z. muelleri,* we excluded Redox Boundary Depth as its inclusion resulted in complete separation, whereby one or more covariates perfectly predicted the dependent variable, plus it was weakly correlated with Sediment Type. The remaining model contained Sediment Type and Fetch. Sediment Type was a categorical predictor, while other environmental variables were continuous. For both species models we included two random functions: the nesting of sector within plot within sites, and days (since planting) as a continuous variable. Models were fitted with the glmer() function in the *lme4* package for R (Bates et al., 2015). Finally, we predicted the likelihood of emergence for all planting methods across sites for visualisations. Importantly, site characteristics (e.g. Fetch) were not used to determine the drivers of seedling emergence but are to acknowledge the interaction of the environment with each of these planting methods and to provide some broad-scale inferences about site indicators that may link to seedling emergence.

2.5.2. Seagrass emergence

We calculated "seagrass emergence" as the measure of the number of shoots present in each sector at any time point. All sites were included in the analysis of "seagrass emergence", regardless of the presence or absence of seagrass, because this study aims to understand which planting methods are effective across potential restoration sites. These analyses included all the 0 data points in order to provide an understanding of how each method performed. We used a GLMM with Poisson distribution to evaluate the influence of planting method on the emergence of seagrass, and like the likelihood of emergence analysis, constructed separate models for each species. The conditions of each model were the same as detailed for "likelihood of emergence" but instead used the number of shoots per sector as the response variable. For both species models, we included two random functions: the nesting of sector within plot within sites, and days (since planting) as a continuous variable.

2.5.3. Seagrass growth

Restoration is not solely related to emergence, but also the subsequent production and survival of numerous and healthy seagrass shoots over time. Therefore, we also used generalised linear spline models to assess the temporal trends in shoot number and leaf length between different planting methods. Given that seagrass did not emerge at all sites, and to test the relative importance of planting method on shoot number and leaf growth, these analyses included only sites where emergence was recorded across multiple plots with all three methods (Abersoch, UK, and Coronet Bay, Australia). The model structure included Days as a continuous variable to allow for the sequential comparison of shoot number and leaf length across monitoring points. Splines (points where directional slope can change) were set at each time point where seagrass was observed (i.e. excluding the first and last monitoring points). Then linear spline models were parameterized as a marginal test to detect changes in slope from the preceding time point,

so consecutive model coefficients correspond to the change in slope as compared to the previous time point. We included an interaction between Days and Planting Method, because we wanted to understand how seagrass growth was affected by each method across time. As we had previously tested for broad scale environmental variables, and how these relate to shoot number, we instead used Plot as a fixed factor. Linear spline models were performed with the *lspline* package for R (Bojanowski, 2017).

2.5.4. Site and method differences

Lastly, given the low levels of seagrass emergence observed at many of the experimental sites, we also wanted to identify if this broadly related to the site itself or associated environmental factors. A simplistic branched tree model was used to explore factors influencing shoot number by recursively splitting data to produce a 'tree' of sub-populations and their associated 'risk factors' (Quinn and Keough, 2002). The resultant model visually resembles a tree where the first node represents the tree's root. We used a Conditional Inference Tree (CIT) framework (Hothorn et al., 2006), which uses a statistically-determined stopping criterion, an a priori P value (0.05), to determine where splitting is no longer valid. For both experiments (UK and Australia), we used a model structure where shoot number was predicted by Site, Planting Method, Fetch, Sediment Type, Redox Boundary Depth and Days.

3. Results

Seagrass emerged at 50 % of: 2 of 6 sites in the UK (Abersoch and Pen-y-chain) and 3 of 4 sites in Australia (Coronet Bay, Grantville and Pioneer Bay). However, only one site in the UK (Abersoch) and one site in Australia (Coronet Bay) had emergence from all planting methods and across numerous plots. After 160 days in the UK and 180 days in Australia, 95.8 % and 93.2 % of seedlings had disappeared respectively so experiments were terminated at those respective times.

The emergence efficiency of seeds was variable across species, planting method, and site. When summarised across all experimental plots and sites for each species, emergence efficiency was consistently very low with <1 % of seeds emerging from each planting method (Table S3). Broadly, planting using DIS was most favourable for *Zostera marina* seeds. However, at one site in the UK, Pen-y-chain, emergence was only observed from a bag sector and these seedlings had the longest leaves of all plots. Bags and pots appeared the more favourable planting methods relative to DIS for *Zostera muelleri*.

For the two sites where emergence was observed from all planting methods and across numerous plots (Abersoch, UK, and Coronet Bay, Australia) we found the shoot emergence efficiency to be highly variable between plots and treatments, yet comparatively 4 % higher for *Z. marina* than for *Z. muelleri*.

Sectors planted with *Z. marina* seeds using DIS were we found to have a shoot emergence efficiency ranging from 0 %- 8.75 % (Table S4). Emergence peaked at 110 days with 8–9 % of planted seeds having emerged in two of the four DIS sectors. However, the remaining two DIS plots demonstrated extremely low emergence efficiency, ranging between 0 % - 2.5 % of seeds planted. Emergence from pots was consistent in three of the four plots, with an emergence efficiency of 2–4 % in each. However, by day 180 only 1 shoot was present. Bags were found to have the lowest emergence efficiency of the three methods, with observations of shoots at only two plots with a 0.5 % of seeds emerging.

Total emergence was lower for *Z. muelleri* than *Z. marina*. Bags were found to have the highest shoot emergence efficiency of the three methods, with 4.5 % emergence 2-months post planting. Both bags and pots were found to emerge from each of the experimental plots 2-months post planting. DIS emergence efficiency was <1 % of seeds planted (Table S5).

3.1. Likelihood of seedling emergence

We found no significant effects of Planting method on the likelihood of *Z. marina* emergence at sites in the UK (e.g. the probability of seagrass emerging, irrespective of shoot numbers, at any point in the experiment). While no significant effects were observed, the effects of Dispenser Injection Seeding (DIS) and pots were positive when compared with hessian bags, and the likelihood of seagrass emerging was 75 % higher and 67 % higher if planted using DIS and pots than hessian bags, respectively (Fig. 2, panel B). Fetch was found to be inversely proportional to the likelihood of emergence and a deeper redox boundary was also associated with reduced likelihood of emergence ($p < 0.05$) (Fig. 2, panel D & Table S6).

Fetch was positively correlated with Sediment Deposition ($r = 0.64$, $p < 0.001$) and Average Daily LUX ($r = -0.42$, $p < 0.001$) (Fig. S3), suggesting that low emergence may have been influenced by a combination of high wind- and wave-driven disturbance, sediment movement and consequential low light availability, though data were patchy for a number of the sites.

The likelihood of emergence of *Z. muelleri* at Australian sites was comparable between bags and pots. The likelihood of emergence was predicted to be 117 % higher for bags than DIS. We found that Sediment Type had a significant effect on the likelihood of *Z. muelleri* emergence ($p < 0.05$). In Australia, wind fetch was shown to have a positive effect on the likelihood of seagrass emergence, where the greater the fetch the higher the likelihood of emergence. Wind fetch was on average 4-fold higher at UK sites than Australian sites, and it is unclear at what level of fetch the likelihood of emergence would start to decline for *Z. muelleri*. Finally, *Z. muelleri* seeds planted in sites comprised of sand dominant sediments were over nine times more likely to emerge than seeds planted in sites comprised of mud dominant sediments (Fig. 2, panel E, H.

3.2. Shoot emergence

Investigating effects of Planting Method on the number of emerged shoots from all sites throughout the experiment revealed contrasting findings between *Z. marina* and *Z. muelleri*. Planting Method was shown to have a significant effect on the number of *Z. marina* shoots which emerged in experimental plots. DIS ($p < 0.05$), had significantly more shoots than bags over the course of the experiment (Fig. 3, panel A, B). Low shoot density was observed across each planting method. We again found that fetch had a weak negative effect on shoot emergence, where the site with the least exposure produced comparatively more shoots than sites with higher exposure (where no shoots emerged). There was a significant effect of Redox Boundary Depth on shoot number, where the deeper the boundary the fewer the shoots particularly when compared to a shallow boundary depth ($p < 0.05$) (Table S7).

For all locations where *Z. muelleri* emergence was observed fewer shoots emerged from DIS plots than from pots or bags. Compared with DIS, 5.8 times more shoots were found in pots, and 4.7 times more shoots from bags. The local fetch range was positively related with shoot emergence, where more exposed sites were found to have more emerged shoots than extremely sheltered sites. Significant and positive effects of sandy sediments ($p < 0.05$) suggest that low shoot number was likely to be influenced by, or associated with, the planting medium (e.g., mud) (Fig. 3, panel E, H; Table S7).

3.3. Temporal variation in shoot number and leaf length

At the two sites where emergence was observed across methods and plots, linear spline models showed distinct temporal patterns in shoot number and leaf length across species and planting methods. For *Z. marina*, spline models explained 94%and 90 % of the variance in shoot density and leaf length respectively. For *Z. muelleri*, models explained 84 % and 97 % of the variance in shoot number and leaf length

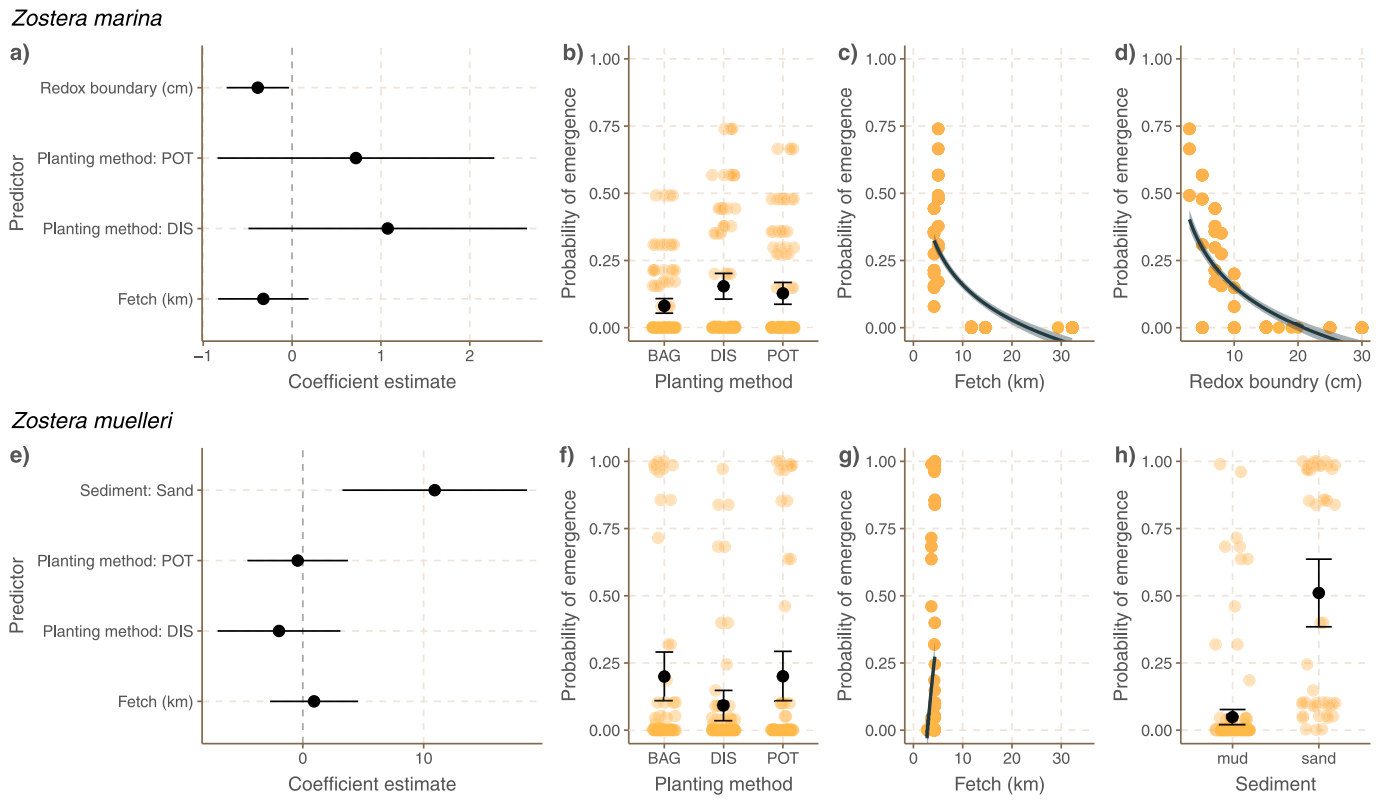

Fig. 2. Predicted effects of planting method and environmental variables on the likelihood of seagrass emergence for *Zostera marina* at all experimental sites in the UK (top row: panels a-d) and *Zostera muelleri* in all Australian sites (bottom row: panels e-h). Panels a and e show predictor coefficients, where values over 0 represent a prediction of an increase in the likelihood of emergence, (dotted line) while a value <0 indicates a prediction of a decrease in the likelihood of emergence (points) with standard error and 95 % confidence intervals (thick lines). Estimates for biodegradable pots (POTS) and dispenser injection seeding (DIS) are relative to hessian bags (BAGS). Panels b-d and f-h show model predictions for each explanatory variable. Panels show the mean fitted effect (black lines and points) and 95 % confidence intervals (shaded bands and error bars). Orange points show predictions for each sector and site at each time point generated from a binomial GLMM.

respectively.

Only one location where shoot emergence was observed across planting methods and plots (Abersoch) was used for *Z. marina.* Here, only marginal increases in shoot number were recorded by the end of the experiment (day 160). Despite increases in shoot number recorded for DIS and pots, very few shoots persisted by the end of the experiment.

Leaf lengths for *Z. marina* showed significant increases (day 100; $p <$ 0.05 and day 130; $p < 0.05$). Despite early increases in growth and consistent growth throughout the experiment for DIS and pots, leaf length decreased from day 100. Leaf length was significantly longer at day 130 in bags than seedlings from DIS and pots. However, at the final monitoring point shoots from bags were no longer present in the experiment at this site (Fig. 4).

For *Z. muelleri* at Coronet Bay, where shoot emergence was observed across planting methods and plots, we also observed marginal increases in shoot number by the end of the experiment (day 180). We observed subtle increases in shoot number early in the experiment (day 65), but these increases were offset by significant declines from day 65 to day 110 ($p < 0.05$). Late germination and emergence (by day 140) meant shoot number increased again, but all methods were characterised by relatively weak persistence. We observed no significant effects of method across time points.

Leaf length in *Z. muelleri* followed a similar trend to *Z. marina*, and significant but weak increases in length were observed across all methods from day 0–65 ($p < 0.001$), day 65–110 ($p < 0.05$) and day 110–140 ($p < 0.05$). Emergence from pots and bags was greater than from DIS plots, despite this, plants from DIS plots had the longest leaves, and relative to bags had the most significant increase in leaf length between day 65 and 130 ($p < 0.05$).

3.4. Site and planting method differences across species

For *Z. marina* in the UK, the conditional inference tree retained Site ($p < 0.001$) and Planting Method ($p < 0.05$) as significant predictors of shoot number across experimental trials (Fig. 5). The estimated regression relationship between factors found that *Z. marina* shoot number in UK trials were primarily separated by site, with planting method nested within site. The primary site categorisation represents a single site where significant seedling emergence was observed from each planting method, and all other sites supported either no, or very limited, emergence. In the single site where emergence occurred across methods, DIS shoot number was shown to be significantly different to bag and pots. For Australia, the conditional inference tree retained sediment type as the only dividing factor influencing shoot density across experimental trials ($p < 0.001$). The effect of sediment type outweighed any individual effects of planting method, or other environmental factors (Fig. 6).

4. Discussion

This study sought to explore differences in the influence of seed planting method on seedling emergence in intertidal seagrass systems across species and locations. It demonstrates that there is no "one-size-fits-all" approach to selecting seed planting methods and that it is important to consider site suitability and conditions in tandem with planting method when developing seagrass restoration programs. Dispenser Injection Seeding (DIS) promoted seedling emergence in, *Zostera marina*, in the UK, while pots and hessian bags were most effective for use with *Zostera muelleri* seeds in Australia. However, emergence rates across all sites and planting methods were extremely

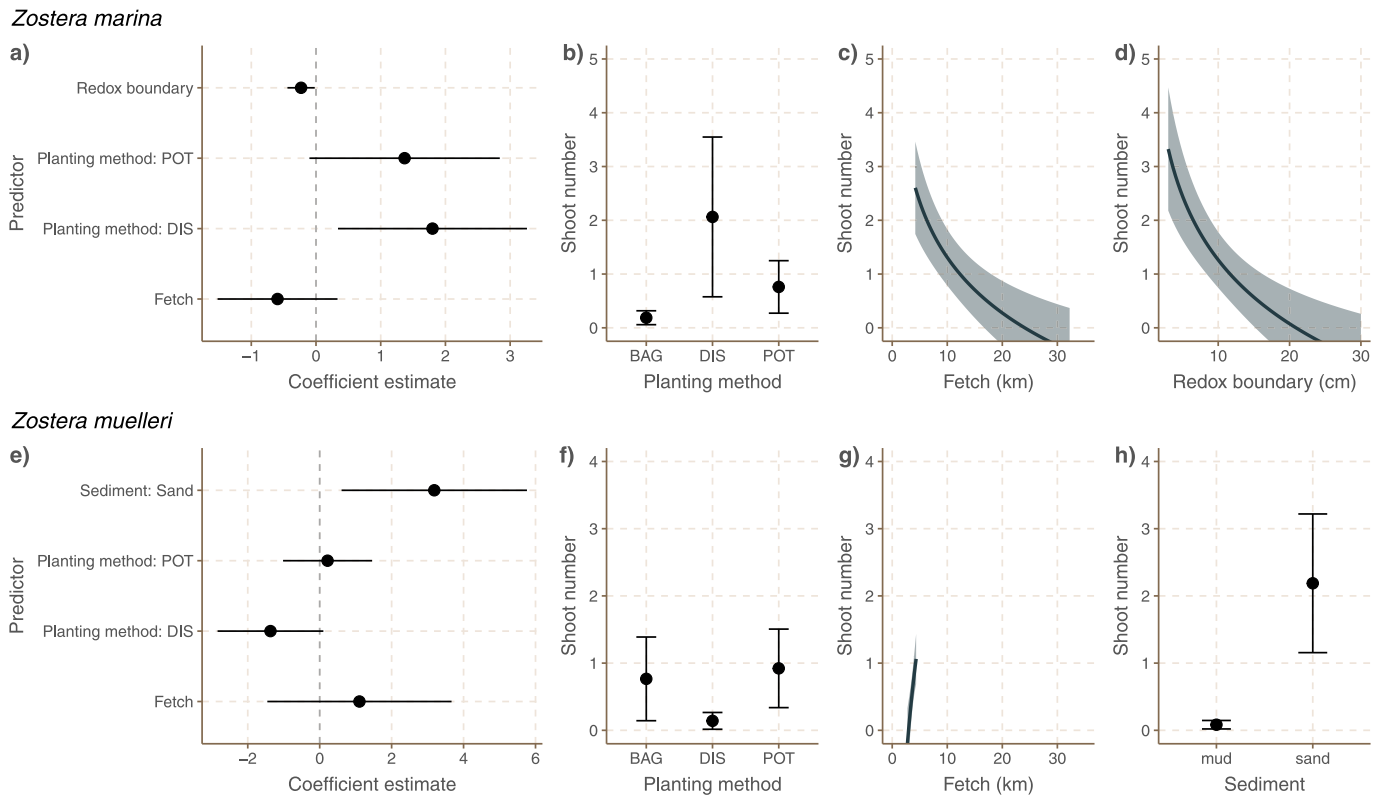

Fig. 3. Method and environmental predictors of shoot emergence from all experimental sites of *Zostera marina* (top row: panels a-d) and *Zostera muelleri* (bottom: panels e-h). Panels a and e show effect size estimates of predictor coefficients (points) with standard error (thick line) and 95 % confidence intervals (thin line); positive coefficient estimates predict high emergence and negative coefficient estimates predict low of emergence, where values over 0 represent an increase in the shoot emergence and below 0 represents a decrease in shoot emergence (dotted line). Estimates for biodegradable pots (POTS) and dispenser injection seeding (DIS) are relative to hessian bags (BAGS). Panels b-d and f-h show model predictions for explanatory variables. Panels show the mean fitted effect (lines and points) and 95 % confidence intervals (shaded bands and error bars).

low. Fetch, redox boundary depth and sediment type were all shown to have varying degrees of influence on seedling emergence and growth across both species and locations. Despite there being limited published literature that trials a variety of planting techniques at the same restoration sites or within the same system (Cronau et al., 2023), this research appears consistent with other temperate and tropical seagrass restoration studies and shows that there is a need to trial a variety of shoot and seed-based methods in tandem for Zosteraceae intertidal restoration. Emergence aligns to the environmental characteristics of the site, so trialling multiple methods while considering species life-history traits which match site conditions are key requirements for understanding the relationship between site suitability and seed or shoot based planting methods at new restoration sites.

We observed emergence at 50 % of experimental sites and recorded average emergence efficiency of <1 % of planted seeds. Although seagrass emergence from each planting method differed between species (and therefore biospheres), our findings align with the notion that seed planting method is not the only factor limiting restoration planting potential, and that site selection is a vital driver of effective restoration (Fraschetti et al., 2021; Mokumo et al., 2023; Unsworth et al., 2023). The scale of this experiment targeted the nuance of different planting methods, though increased experimental scale and seed input would likely facilitate increased fitness and survival (van Katwijk et al., 2016; Gräfnings et al., 2023b). Undertaking trials at this scale provide opportunities to scrutinise the planting method and not the interaction of the surrounding biomass or any newly grown biomass on facilitating more stable meadow conditions which promote further growth.

Shoots failed to emerge at 4 of the 6 sites using *Z.marina* seeds and only one site supported emergence across multiple methods and plots. Dispenser Injection Seeding (DIS) and pots were found to be more favourable than bags for promoting seedling emergence. Biodegradable planting pots are well established methods for protecting and maintaining seeds in-situ while providing aeration to plant roots and safely degrading, yet few in-situ experiments use them with seagrass seeds (Tomadoni et al., 2020; Cherian et al., 2022). DIS has been trialled across Europe using *Z. marina* seeds, with increasing refinement of the method for this species, resulting in increased seedling emergence in intertidal regions (Govers et al., 2022; Gräfnings et al., 2023b) but this study serves as one of the first to trial DIS with *Z. muelleri* seeds. Deliverance of seeds to a suitable burial depth for germination and seedling growth is important in each planting method, where seeds should be buried no deeper than 6 cm and 2 cm for *Z. marina* and *Z. muelleri*, respectively (Jørgensen et al., 2019; Tan, 2022; Gräfnings et al., 2023b). If DIS will be trialled again with *Z. muelleri* seeds, we recommend a deeper injection depth than used here (1–2 cm), because seeds injected this close to the sediment surface have high chance to be washed away. In the UK, where emergence was observed, our results suggest that disruption to seed burial depth was minimal as seeds directly injected into the sediment emerged without the structural support of a bag or pot. Bags and pots typically deliver and anchor seeds to a more predictable depth in sediments than DIS. However, the structure of hessian bags can serve as a holdfast for macroalgae which typically outcompete *Zostera* spp. Also, possible accumulation of sulphide within bags as a result of poor water flow (van der Heide et al., 2021) may surpass tolerable thresholds for *Zostera* spp. which is well documented to stifle seedling growth (Dooley et al., 2013). A shallow sediment redox boundary was associated with increased likelihood of seagrass emergence in the UK. Paradoxically, in small doses, anoxia has been reported to serve as seed germination cue (Van Vierssen, 1982). Deeper redox boundaries and associated rapid sediment draining in

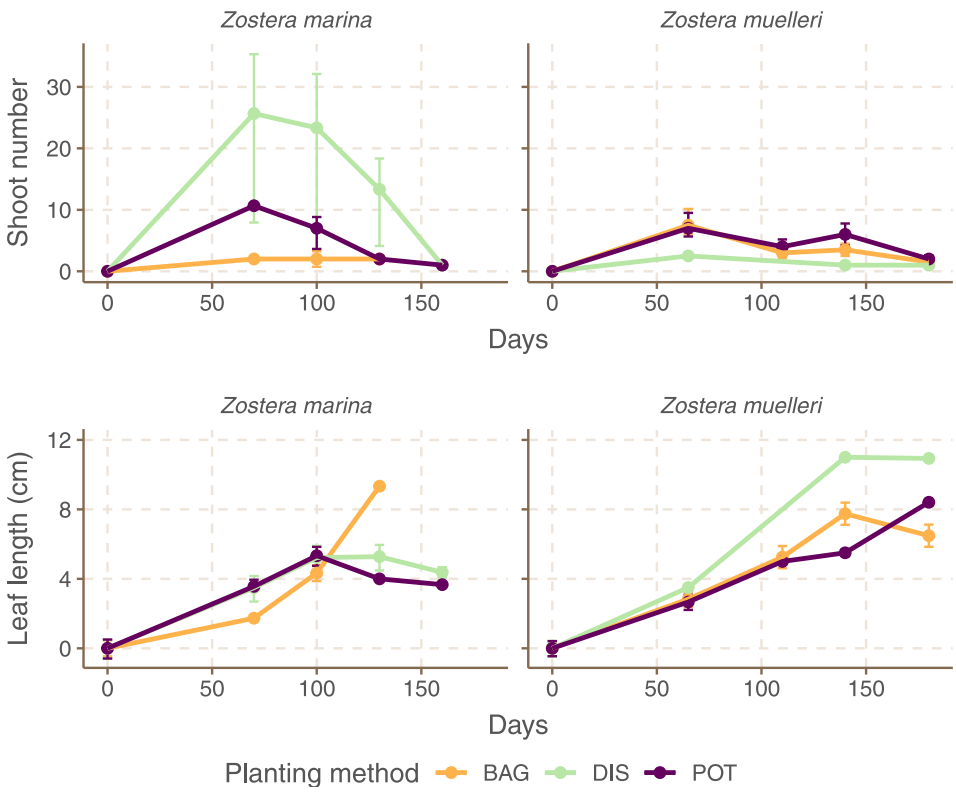

Fig. 4. Temporal variation in shoot number and leaf length of *Zostera marina* (left) and *Zostera muelleri* (right) seedlings predicted from generalised linear spline models. Values are predicated for two sites with the most seagrass emergence; Abersoch (United Kingdon) and Coronet Bay (Australia). Each figure is coloured according to seed planting method where differences in number of emerged shoots between hessian bags (Bags; orange), dispenser injection seeding (DIS; green) and biodegradable pots (Pots; purple) are presented across a each monitoring time point (0 = 0, 1 = 30, 2 = 70, 3 = 100, 4 = 130, 5 = 160 days post planting) for *Zostera marina* and (0 = 0, 1 = 30, 2 = 65, 3 = 110, 4 = 140, 5 = 180 days post planting) for Zostera muelleri. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sandier conditions may be indicative of sediment dynamics likely to disrupt germination and long-term plant survival (R. Unsworth, personal communication, 2023). Anecdotal evidence suggests that seedling survival may also have been influenced by beach usage in Abersoch, a popular local and tourist destination. Despite the low emergence rates from bags in the UK, seedlings grew longer leaves than *Z. marina* shoots from DIS and pots. This may be indicative of temporal factors relating to time taken for seedling emergence to be observed through hessian, or the length of monitoring period not being reflective of time required for hessian to degrade. Despite phenotypic responses to light stress of increased leaf length not being typical in seagrasses, the potentially low light levels within bags may stimulate an increase in leaf length (Longstaff and Dennison, 1999; Ralph et al., 2007).

Emergence results from these experimental sites are synonymous with previous studies that found sites with low fetch ranges promoted seagrass recruitment and emergence (Orth et al., 1994; Carus et al., 2021). We found that increasing fetch had a significant negative effect on *Z. marina* shoot emergence likely due to fetch driving hydrodynamics, aerial exposure, and sediment shifts in dynamic intertidal zones (Paulo et al., 2019). During this trial, Storm Eunice hit the UK in February 2022 with gusts over 81 mph in parts of North Wales (Kendon, 2022). Sediment movement, which presents opportunities for seed disruption, dislodgement or burial likely increased during this time, particularly at more exposed sites. Seed-based planting approaches may well be less resilient to storm effects than shoot or seedling planting strategies as the feedbacks for sediment stabilisation and protection are not yet established (Paling et al., 2003; Paulo et al., 2019; Kamperdicks et al., 2025). Consideration of planting timing to account for seasonality in addition to planting method and site choice is therefore needed in restoration planning.

Emergence efficiency of *Z. muelleri* was low, with a maximum emergence efficiency of 4.5 % (18 shoots) from the most productive plot sectors. We found that hessian bags and pots were the most favourable methods for promoting *Z. muelleri* seed emergence though sediment type significantly influenced emergence. Other studies that have used bags have also shown favourability using *Z. muelleri* seeds (Tan et al., 2023). At the sand dominant site, emergence rates were lower from DIS planted seeds than pots and bags. At the site with most emergence, the deep redox boundary indicates sediment movement and aeration which would impact the seeds directly dispensed into the sediment by DIS when bags and pots would more suitably maintain seeds within the sediment. Sandier sediments showed greater seedling emergence than mud dominant sites. Muddy sediments are typically associated with less exposed sites which encourage seagrass recruitment (Van Katwijk et al., 2009), yet this study proposes that mud dominant sites present a range of life-stage associated bottlenecks to seed germination and retention in seed-based restoration. Examples of inhibitors to seed germination may include infaunal communities with seed-herbivory tendencies, planting structures (hessian bags) which may clog, macroalgae growth, in-sediment sulphide accumulation and associated toxicity, and light limited conditions resulting from no seagrass–sediment stabilisation–-light (SSL) feedbacks (Unsworth et al., 2023; Unsworth et al., 2024). Priming seeds using chemical and natural germination triggers may facilitate overcoming site-based conditions which otherwise inhibit restoration and deem sites as unsuitable (Pieraccini et al., 2024). The interaction of seagrass presence, suspended sediment and benthic light either promotes or inhibits seagrass growth (Adams et al., 2016). Where seagrass is present, sediment stability and accretion increase with seagrass structural complexity suggesting that mature plants foster an ecoengineering ability which favours further seagrass growth (Dalby

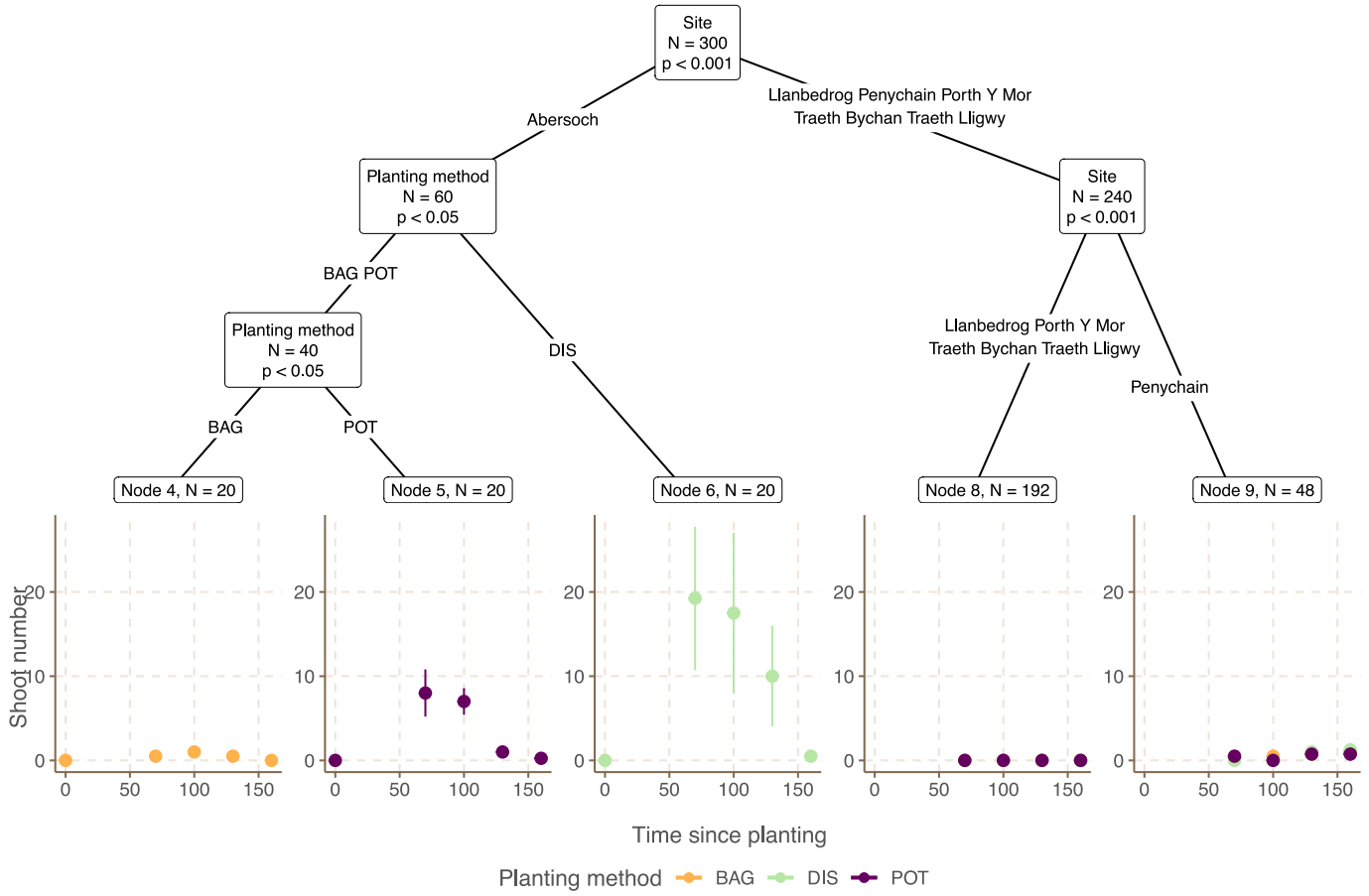

Fig. 5. Conditional inference tree examining differences in *Zostera marina* shoot number across experimental sites in North Wales, UK. Data were best classified into five sub-groups. Nodes 4, 5 and 6 represent a site (Abersoch) where emergence was recorded across all methods, but differences between methods were significant. Node 9 represents a site (Pen-y-Chain) with only limited emergence where differences between methods were not significant. Node 8 represents the remaining sites where no emergence was observed.

et al., 2023a). In mud dominant conditions, the resuspension of fine sediments, which block light and increase the chance of seed/seedling burial, especially where bed shear stress is high, inhibit seed germination and growth. Seed-based restoration, therefore, faces challenges whereby a lack of preexisting seagrass and associated SSL-feedback perpetuates the absence/poor establishment of seedlings. At such sites, hydrodynamic energy and turbidity are required to be at be at lower levels than if seagrass was present to enable seagrass establishment in the absence of the SSL-feedback (van der Heide et al., 2007). In the absence of seagrass in mud dominant locations, sand capping can be used to reduce these seed germination and retention bottlenecks, and feed into sediment-stabilisation light feedback (Infantes et al., 2016; Carus et al., 2021; Zabarte-Maeztu et al., 2021; Flindt et al., 2022).

Seagrass emergence was unsuccessful at 50 % of sites, despite their proposal from habitat suitability models (HSMs). HSMs typically use predictive metrics based on seagrass presence and absence. However, in absence of seagrass, models do not accommodate for a lack of positive feedbacks associated with plant biomass (i.e. the meadows) which makes the site appear favourable (Adams et al., 2016; Maxwell et al., 2017). HSMs need to include new metrics which capture site suitability for planting seeds, instead of whole plants, and need to be modelled in a way which differentiates between subtidal and intertidal meadows. Introduction of seeds into the environment will not immediately add structural complexity or stabilising sediment factors in the same way as whole plants will (Gräfnings et al., 2023a). Consideration of sediment stability and infauna seed grazing which are indicative of sites which are devoid of seagrass is required and, factors such as rate of sediment draining (R. Unsworth, personal communication, 2023) may be important for maintaining seed viability and emergence in restored intertidal systems. Sediment type, wind fetch and redox boundary depth all influenced the emergence of seagrass seeds. The correlation of fetch with light availability and sediment deposition suggests that wind fetch may be a good predictor of sites that are feasible for restoration, particularly when coupled with information on sediments.

Exposure on the extremes of the continuum in restoration sites present polarising bottlenecks for the likelihood of seedling emergence (Statton et al., 2017). Sites on fringing extremes of exposure should consider transplant restoration, or a combination of seeds and whole-plant planting, which have better established methods and parameters for guiding planting sites and method choices Species life histories and the nuances of each planting method should be used to pair site, species and planting method (Cronau et al., 2023; Tan et al., 2023; Watson et al., 2023). Perhaps the seagrass restoration sector needs to embrace synergies between methods, or rather consider that a portfolio of methods may be needed to tackle restoration challenges (Pettorelli and Bullock, 2023).

Factors such as permitting, biosecurity cautions, funding, work capacity and timeframes shape restoration project decision making, feasibility and budgeting (McDonald-Madden et al., 2010; Baker and Eckerberg, 2013; Luz, 2021; Bell-James et al., 2023). In our study, selection of appropriate sediment types was required, where sterile sediment was selected for use in hessian bags and pots to adhere to permitting, biosecurity and logistical requirements (Unsworth et al., 2022a), and intertidal mud was used in DIS canisters to allow cannister functioning (Govers et al., 2022). Consideration of sediment type for each planting method, feasibility of collection, and monitoring

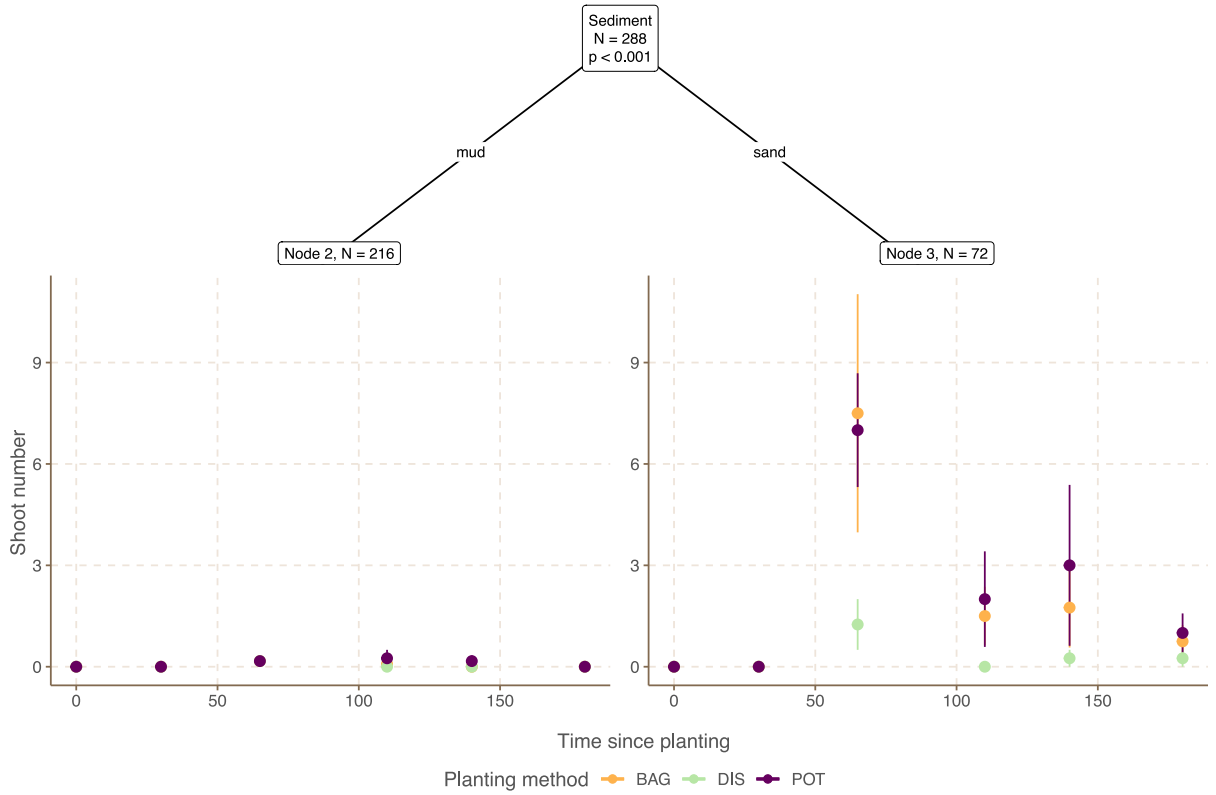

Fig. 6. Conditional inference tree examining differences in *Zostera muelleri* shoot number across experimental sites in Australia. Data were best classified into two sub-groups. Node 2 represents sites where no or limited emergence was recorded across all methods; these sites were typical of mud dominant sediments. Node 3 represents a single sand dominant site where emergence was observed across planting methods.

microbiome profiles is required particularly in light of the upscaling of restoration attempts (Størdal et al., 2023). Despite the acknowledgment of such trade-offs in restoration, the narrative in seagrass restoration literature continues to be of successful attempts with very few studies publishing on failures and learnings, how challenges can be navigated in the future (Catalano et al., 2019; Chambers et al., 2022).

The low shoot emergence and post-emergence survival highlight the challenges that still exist in selecting suitable sites. Results from this study indicate that both ecological and social characteristics of sites are likely to have contributed to unfavourable conditions for seedling persistence. We, therefore, consider the inclusion of both ecological and social dimensions in site selection and restoration practice of upmost importance (Fernández-Manjarrés et al., 2018). We also suggest further species-specific investigations, in particular, optimising maintenance of seed viability, seed priming to overcome germination bottlenecks, and the use of nursery generated seedlings to increase restoration potential. Finally, we suggest holistic approaches to seagrass management and restoration, such as watershed management and protection, and where active restoration is plausible it is crucial to match site suitability to species life histories and planting methods.

CRediT authorship contribution statement

Lucy Coals: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Benjamin L.H. Jones:** Writing – review & editing, Writing – original draft, Formal analysis, Data curation. **Ally J. Evans:** Writing – review & editing, Data curation, Conceptualization. **Richard K.F. Unsworth:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Laney Callahan:** Data curation. **Rhys A. Coleman:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Laura L. Govers:** Writing – review & editing, Methodology. **Max L.E. Gräfnings:** Writing – review & editing, Methodology. **Emma L. Jackson:** Writing – review & editing, Supervision, Conceptualization. **Craig D.H. Sherman:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Richard Unsworth reports financial support was provided by Heritage Lottery Fund. Craig Sherman reports financial support was provided by Melbourne Water. Lucy Coals reports financial support was provided by Holsworth Wildlife Research Endowment. Ally Evans reports financial support was provided by Heritage Lottery Fund. Lucy Coals reports financial support was provided by Melbourne Water. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2025.118123.

Data availability

The datasets presented in this study can be found in online repositories. All data and R code are available from https://doi.org/10.6084/m9.figshare.27237846

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