RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

TAILORED RESTORATION RESPONSE: PREDICTIONS AND GUIDELINES FOR WETLAND RENEWAL

RESEARCH ARTICLE

Understanding the seagrass-sediment-light feedback to guide restoration planning: a case study using *Zostera muelleri*

Oliver Dalby[1], Rhys A. Coleman[2], Yi Mei Tan[1], Geordie Jennings[1], Perran L. M. Cook[3], Emma L. Jackson[4], Peter I. Macreadie[5], Craig D. H. Sherman[1,2]

Seagrass ecosystems are ecologically important but are declining worldwide, prompting restoration efforts. However, restoration success is partially reliant on ensuring that donor material and planting methods are suitable under the environmental conditions expected within restoration sites. This may require planting at critical densities needed to initiate favorable environmental feedbacks, ensuring plants are pre-adapted to local conditions, and setting realistic restoration goals. An understanding of the relationship between local environmental conditions (e.g. the local light environment and seagrass structural complexity) can be particularly important in guiding restoration decision-making. Here, we investigate how sediment-light conditions interact with seagrass structural complexity (density and above-ground morphology) to guide restoration planting approaches for the intertidal seagrass *Zostera muelleri*. Using generalized additive models and empirical data, we identified significant relationships between the local sediment-light environment and the structural complexity of *Z. muelleri* meadows present in Western Port, Victoria, southeast Australia. We found a decrease in shoot density and leaf length with decreasing light availability, potentially reflective of an adaptive change in the species morphology in response to low-light environments. We also found a decrease in sediment sorting and increased fine particles with increasing meadow structural complexity, suggesting that seagrass structural complexity increases sediment stability, and accretion, and may contribute to local water clarity via ecological feedbacks. These findings suggest that understanding both environmental drivers and the potential for ecological feedbacks to occur is needed before large-scale planting begins and that restoration targets should reflect the meadow form most likely to occur under the environmental conditions present.

Key words: light environment, sediment resuspension, target setting, turbidity, turbulence

Implications for Practice

- Developing an understanding of environmental controls on seagrass meadow density, morphology, and spatial extent is critical to guide restoration efforts.
- Interactions between local environmental conditions and seagrass morphology should be considered during restoration planning.
- Restoration target setting should reflect the forms likely supported by environmental conditions within a prospective restoration site. For example, in a turbid environment, reduced density and lessened above-ground biomass may be expected in the short term and should be reflected in initial target setting. However, more structurally complex meadow forms may be established under sustained restoration efforts if adequate density and spatial extent are established to stabilize local sediments.

Author contributions: OD, RAC, ELJ, PIM, PLMC, CDHS conceptualized the paper and designed the research; OD, YMT, GJ conducted fieldwork with help from volunteers; OD conducted analyses; OD wrote initial drafts; all other authors contributed to revisions of the manuscript and gave final approval for publication.

[1]School of Life and Environmental Sciences, Deakin University Geelong Campus, Geelong, Victoria, Australia
[2]Address correspondence to C. D. H. Sherman, email craig.sherman@deakin.edu.au
[3]Melbourne Water, Research and Modelling, Docklands, Victoria, Australia
[4]School of Chemistry, Monash University, Clayton, Victoria, Australia
[5]Coastal Marine Ecosystems Research Centre, Central Queensland University, Gladstone, Queensland, Australia
[6]School of Life and Environmental Sciences, Deakin University, Burwood Campus, Victoria, Australia

doi: 10.1111/rec.14044
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.14044/suppinfo

Introduction

Seagrasses are ecologically important ecosystem engineers that provide a wide range of ecosystem services such as sediment stabilization, fisheries support, and blue carbon sequestration (Nordlund et al. 2016). However, seagrasses are declining worldwide as a result of anthropogenic activities influencing local environmental conditions and wider climate change impacts (Waycott et al. 2009; Dunic et al. 2021). Losses have led to significant investment in developing restoration methods for many species, but results are highly variable (Tan et al. 2020), potentially as a result of mismatches between the environmental needs of the plant and environmental conditions within restoration sites, or the scale and density at which seagrass is planted (Fonseca 2011).

Like other plants, the presence and persistence of seagrasses is closely linked to local environmental conditions. Concordantly, the identification of environmentally suitable restoration sites is a key step in restoration decision-making (Campbell 2002; Short et al. 2002; Gamble et al. 2021). Recently, site selection has increasingly been addressed via suitability modeling for seagrass restoration as a method to identify environmentally suitable restoration sites (Bittner et al. 2020). However, these models operate at large spatial scales and are often driven by modeled (nonempirical) predictor data. As such, finer-scale in situ assessments may be required to confirm environmental suitability. Conversely, traditional in situ assessments of environmental conditions present within seagrass meadows can provide nuanced, site-specific information useful for guiding restoration site selection (Campbell 2002; Jackson et al. 2021) but are often limited by the spatial scale at which data can be collected.

An understanding of local environmental conditions present within prospective restoration sites is also important as seagrasses undergo morphological adaptations to maintain beneficial carbon balances (Ralph et al. 2007). Similarly, meadow spatial arrangement, density, and morphology can be considered as consequences of the environmental conditions present (Kilminster et al. 2015; Enríquez et al. 2019). For example, where conditions are optimal (adequate light availability, depth, stable sediment for anchoring, limited hydrodynamic forces) and such conditions are homogeneous across space and time, seagrasses are more likely to form dense meadows with greater structural complexity (the combination of meadow density and leaf morphology) (Ralph et al. 2007). In contrast, in sites that are only marginally suitable (e.g. sites with increased wave force, temperature, and desiccation), seagrasses may be present but may occur at reduced densities and may exhibit differing morphology (Manassa et al. 2017). However, seagrasses also exhibit a degree of control over local environmental conditions via a suite of ecological feedbacks (Maxwell et al. 2017), most of which exhibit a positive density dependence (Valdez et al. 2020). Previous flume studies have quantified the causative role of increased seagrass structural complexity in stabilizing local sediments, increasing local accretion rates, and improving light availability (Fonseca 1989; Lefebvre et al. 2010; Ganthy et al. 2015). When taken together, these studies summarize the seagrass-sediment-light (SSL) feedback, which encapsulates the role of dense and structurally complex meadows in contributing to a favorable light environment (Adams et al. 2016).

Although seagrass meadows can self-facilitate and affect local environmental conditions, these positive feedbacks can breakdown as seagrass density decreases. If seagrass density and/or structural complexity is reduced past an ecological tipping point (the limit at which a given stable state cannot be sustained), local environmental conditions may deteriorate such that the ecosystem can shift to an alternative stable state (e.g. from seagrass to bare sediment) (Moksnes et al. 2018). Changes can be sudden, and once changed, the alternative stable state may support drastically different environmental conditions, and returning to the original stable state is often difficult (Moksnes et al. 2018).

Given the close and complex linkages between seagrass meadow structural form and local environmental conditions, it is critical that restoration practitioners have information about these relationships at proposed restoration sites before undertaking large-scale restoration efforts. In situ data collection outlining environmental conditions and associated variation in meadow density and morphology can be used to guide the design and implementation of on-ground restoration activities. Existing guidance suggests that it is important to (1) ensure donor sites are environmentally comparable with restoration sites and that donor material is favorably adapted to conditions present (van Katwijk et al. 2009), (2) assess whether there is potential to establish positive ecological feedbacks to increase restoration success (van der Heide et al. 2007), and (3) verify that natural meadows chosen as reference sites reflect environmental conditions present in restoration sites to ensure that targets are ecologically sensible (Gann et al. 2019). Without such context, restoration projects run the risk of selecting unsuitable donor material, planting in inadequate densities to establish favorable feedbacks, and may set unrealistic restoration targets, which may lead to project failure due to an inadequate understanding of the study system. Within this study, we use the term *donor sites* to describe areas where restoration material is sourced, *restoration sites* to describe areas where donor material is planted into, and *reference sites* to describe naturally occurring meadows that can be compared with restored plots to assess restoration success.

In this study, we use empirical data from natural seagrass meadows to understand the relationships between seagrass structural complexity and the surrounding sediment-light environment using *Zostera muelleri* as a focal species. These relationships are then used to (1) suggest whether the SSL feedback can be leveraged to increase restoration success by highlighting variation in densities and surrounding sediment-light conditions and (2) provide context to donor selection and restoration target setting for intertidal seagrass restoration efforts.

Methods

Site Introduction

Western Port is a large coastal embayment southeast of Melbourne, Victoria, Australia (Fig. 1A) and is a Ramsar wetland of international importance and a UNESCO Biosphere Reserve.

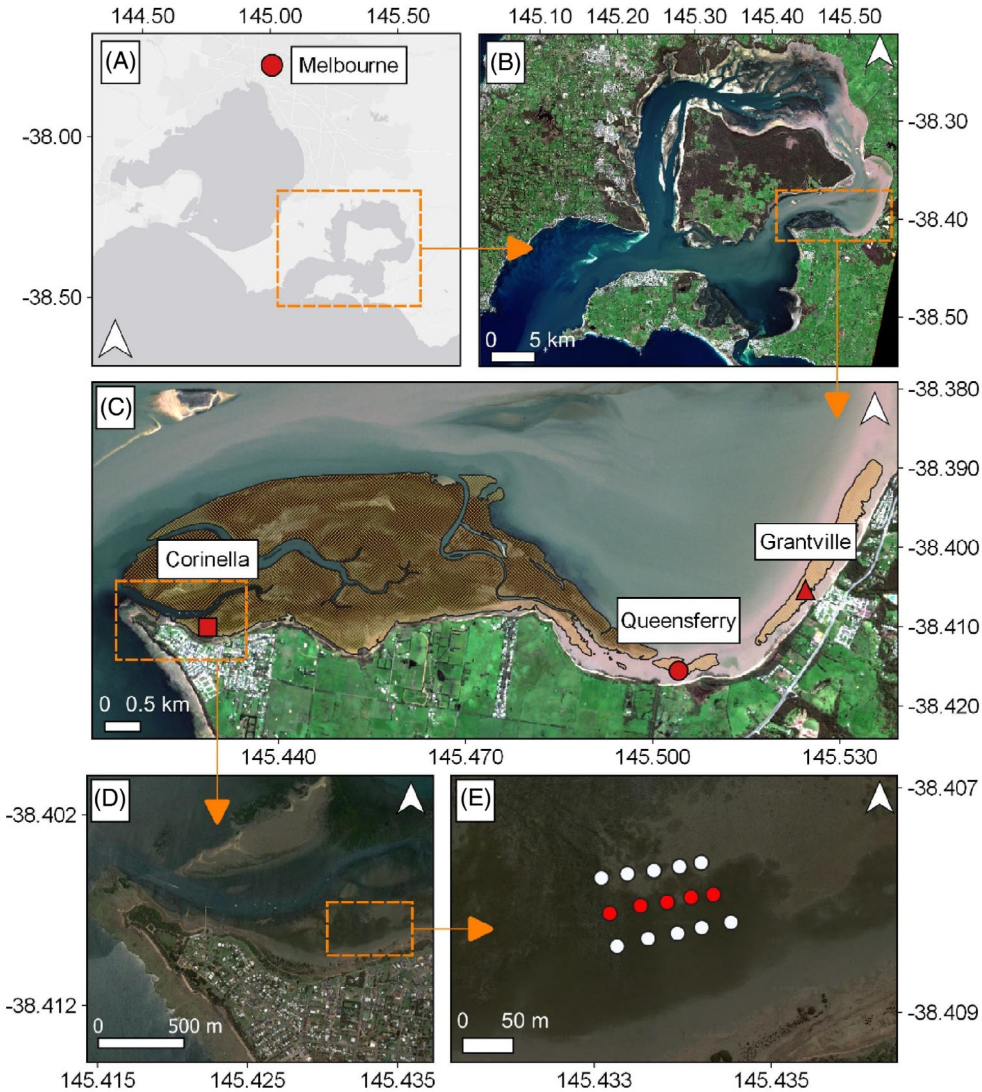

Figure 1. Locations sampled showing (A) location of Western Port relative to Melbourne, (B) region of interest for field sampling (inset box), (C) focal locations sampled throughout this study (labeled points) and estimated seagrass spatial extent (hashed polygons), (D) enlarged view of sampling area at Corinella for context, and (E) sampling stations at Corinella demonstrating sampling stations (red points) and additional locations where seagrass samples were collected (collected at both red and white points). Imagery: (A) ESRI Basemap, (B, C) Sentinel 2 image collected 13 September 2019, and (D, E) Google Satellite Image.

Western Port has historically contained extensive seagrass meadows (251 km^2 in 1973–1974; Bulthuis 1981), which are predominantly formed of *Zostera nigricaulis* (Kuo 2005) Jacobs and Les (2009) (Syn. *Heterozostera nigricaulis*, Kuo (2005)) and *Zostera muelleri* Irmisch ex Ascherson (1867) (Blake & Ball 2001). However, significant declines (up to 70%) occurred in the 1970s and early 1980s (Keough et al. 2011) as a result of increased sediment loads and associated reductions in light penetration due to changes in catchment activities, including urban development, vegetation clearing, and the draining of large (approximately 400 km^2) areas of local swampland for farming (Keough et al. 2011). Recent mapping work suggests that seagrasses within Western Port have recovered naturally (approximately 222 km^2 in 2019; Dalby et al. 2023), perhaps due to improved land and catchment management practices in the last 30 years and natural flushing of suspended sediments (Wallbrink et al. 2003). As such, environmental conditions within areas of Western Port are now considered suitable for assisted recovery. Although seagrasses within Western Port appear to have undergone natural recovery, many areas are still thought to be light-limited (Keough et al. 2011). As such, there is a need to identify seagrass structural complexity and associated environmental conditions to guide planting methods and inform site selection and target setting.

Study Locales and Spatiotemporal Considerations. To assess relationships between seagrass structural complexity and the light environment, three study locations were chosen within the east (termed the Corinella Segment) of Western Port, where seagrass meadows of varying densities occur (Fig. 1). Locations included Corinella, which supports a large and dense meadow (approximately 10 km^2), Grantville, which supports a more heterogeneous distribution of medium-sized (patch diameter of tens to hundreds of metres) patches (total area approximately 0.7 km^2), and Queensferry which supports small, low-density patches (diameter on the scale of metres to tens of metres, total area approximately 0.1 km^2) (Fig. 1B & 1C). Locations are geographically close and experience similar environmental conditions (similar proximity to riverine inputs and associated sediment loads [Wilkinson et al. 2016], benthic particle sizes, salinity, and prevailing current and wave forces [Keough et al. 2011]). Furthermore, locations sampled were present at comparable depths (depth compared to mean sea level [mean $\pm$ standard deviation], Corinella: -0.81 ± 0.05 m, Grantville: -0.60 ± 0.02 m, Queensferry: -0.46 ± 0.10 m). As such, chosen locations are ideal for identifying linkages between light availability, sedimentary characteristics, meadow density, and morphology in the field. Within each location, five stations were placed in the intertidal along a uniform tidal height (Fig. 1E). Environmental and ecological data (see below) were collected over 3 weeks in the Austral summers of 2019–2020 and 2020–2021, respectively. Throughout each period, study locations were visited twice over a 6-day interval.

Available Light

Available light was determined using an Odyssey photosynthetically active radiation (PAR) logger deployed at the center of each station at each of the three locations ($n = 15$ per year) for a period of approximately 20 days during each summer sampling deployment. PAR loggers were calibrated using a Licor Li-1400 before being deployed at seagrass canopy height (approximately 30 cm above the benthos) and detected light hitting the sensor at 15-minute intervals as photosynthetic photon flux density (PPFD). Loggers were wiped clean of any accumulated sediment during field visits to increase the accuracy of the light data collected. Light data were extracted where the timepoint of collection fell within (1) daylight hours (sunrise to sunset) and (2) 1 hour on either side of high tide to identify trends in light availability associated with water column conditions. Sunrise varied from 06:11 to 07:24 and sunset varied from 19:24 to 20:43 across sampling years. High tide occurred between 06:23 and 20:27 across the sampling years and locations. Focussing on high tide timepoints was required as this study assessed components of the SSL feedback, and periods of aerial exposure are not likely to limit available light via the SSL feedback but via reduced photosynthetic efficiency and self-shading when leaves lay atop one another (Clavier et al. 2011). The median light availability per 15-minute interval was then calculated for each logger, each day, and each high tide period. The mean daily light integral (mol photons m^{-2} day^{-1}) was also calculated for each location to provide a general estimate of light availability irrespective of tidal state.

Sediment Accretion Rates

Sediment accretion rates were investigated using cylindrical sediment traps (PVC tubes 300 mm in length, 38 mm internal diameter [Hargrave & Burns 1979]). Duplicate traps were deployed at seagrass canopy height at each sampling station. Furthermore, duplicate disc traps (diameter 12.5 cm) were deployed level with surrounding sediment at each station to provide data on accretion rates that allow current and wave-induced resuspension to occur. Both tube and disc traps were deployed over two 3-day intervals (once per field visit per year) and accumulated sediments were collected for analysis at the end of each 3-day interval ($n = 60$ per year). Accumulated sediments were sieved using a 1,000 μm sieve to remove large materials (glass, rocks, etc.) before drying at 60°C until a constant mass was achieved (Erftemeijer & Koch 2001). The mass exchange was then calculated as g m^{-2} day^{-1}. Dried sediment samples were subsampled and burnt at 450°C for 4 hours to assess the proportion of organic and inorganic material present (Erftemeijer & Koch 2001).

Turbidity and Suspended Solids

Each year, we visited each location twice at high tide to collect data on turbidity and suspended sediment concentrations at seagrass canopy height. Sampling events corresponded with the deployment and collection of sediment traps. Turbidity data (NTU) were collected in triplicate at each sampling station using a calibrated YSI EXO2 multiparameter sonde 1 hour on either side of high tide to standardize tidal forces between sampling days ($n = 90$ per year). Suspended sediment samples were collected using a horizontal water sampler (31 cm length, 9 cm diameter, volume approximately 1.97 L) deployed once at each station and coincided with turbidity data collections ($n = 30$ per year). Once collected, a 500 mL subsample was extracted, filtered through a 1.2 μm glass microfiber filter, dried, weighed, burnt at 450°C for 4 hours, and weighed again to assess the proportion of organic and inorganic material present (Erftemeijer & Koch 2001).

Current Speed

Within each location, duplicate Lowell TCM1 tilt current loggers were deployed. Current loggers sampled the speed and direction of currents using a 15 Hz burst every second and were deployed for 3-day periods twice per year (coinciding with deployment windows of sediment traps and water sampling). Current speed and direction were then extracted 1 hour on either side of high tide to remove data collected where the depth of water was below the logger minimum operating depth (76 cm) before being summarized as rose plots using the openair package (version 2.8-3).

Benthic and Suspended Sediment Particle Sizes

To assess sediment particle size, five sediment samples were collected once per year from the top 2 cm of the benthos at each location ($n = 15$ per year). A second 500 mL subsample was extracted from water samples collected twice per year at each sampling station ($n = 30$ per year). Sediment particle size samples were analyzed using a Beckman Coulter LS 13 320 laser particle sizer. For sediment, analyses were run on an Aqueous liquid module, and for water, on a micro liquid module. Sediment greater than 1.7 mm was analyzed by weight using standard sieves. Once particle size distributions were calculated, the modal particle size and degree of sorting present in benthic samples were calculated using GRADISTAT V.8.0. The degree of sorting was calculated using a geographic method of moments approach (Blott & Pye 2001). Both variables are presented on the μm scale. The degree of sorting represents the standard deviation of sediment particle sizes in the sample. High values indicate a poorly sorted sample and a low value indicates strong sorting (Blott & Pye 2001).

Seagrass Characteristics

To assess seagrass density and morphology, three replicate quadrats (0.5×0.5 m) were sampled at each station per year ($n = 45$ per year). A digital image of each quadrat was taken and the percentage cover of seagrass was quantified visually. All biomass within quadrats was removed and transported back to the laboratory, where the following morphological traits were assessed: shoot density, leaf density, leaf length, leaf width, internode length, and rhizome thickness. The latter four variables were assessed from 10 randomly chosen individuals taken from each quadrat. Rhizome thickness was measured manually using a Vernier caliper, whilst leaf length, leaf width, and internode length were determined using still images and ImageJ software (V1.50e). All leaves and shoots were counted individually for samples collected from Queensferry. Samples from Corinella and Grantville were subsampled due to large quantities of biomass present and density estimates scaled up. Above- and below-ground biomass was quantified by splitting extracted and cleaned biomass into above and below-ground material and drying at 60°C until a constant mass was achieved (Erftemeijer & Koch 2001).

Data Analyses

Transformations. Before analyses, outliers were removed from environmental data. Outliers originated from logging equipment making contact with the benthos during high tide sampling and produced notable spikes in turbidity. Seagrass and environmental data were then assessed for normality and homogeneity of variances using Shapiro–Wilk and Fligner tests, respectively. If a variable was deemed to be non-normal or contained unequal variances, it was transformed using a power (ranging from -1.875 to 4.25) or log transformation. Optimal transformations were determined using Tukey's Power Ladder in rcompanion (version 2.4.1).

Testing Effects of Location. Despite transformations, some variables did not have a normal distribution or equal variances. As such, Kruskal–Wallis tests were used to assess whether untransformed seagrass and environmental variables showed significant differences based on location (a separate test was used for each year). A post hoc Dunn's test using a Bonferroni correction was applied to identify significant pairwise comparisons.

Data Aggregation, PCAs, PERMANOVA, and PERMDISP. Environmental data representing the sediment-light environment (PPFD, turbidity, total suspended particulates, total suspended sediments, plate trap accretion, tube trap accretion, modal benthic particle size, degree of benthic sediment sorting, and modal suspended particle size) and seagrass above-ground structural complexity (percentage cover, shoot density, leaf density, above-ground biomass, leaf length, and leaf width) were used to construct two scaled and centered principal component analyses (PCAs) using the median value of each variable between stations, deployment years, and locations ($n = 30$). One PCA was generated for environmental variables and one for seagrass structural complexity variables. The first two principal components of each PCA were then plotted and the contribution and direction of the first two principal components were assessed (principal components 3 and onwards accounted for <10% of data variation in either analysis).

PCA coordinates were converted to Euclidean similarity matrices and passed to permutational multivariate analysis of variance (PERMANOVA) and permutational analysis of multivariate dispersions (PERMDISP) tests (Anderson 2001) to identify significant effects of location, deployment year, and the interaction of these two factors using the Vegan package (version 2.5-7). PERMANOVA and PERMDISP tests contained 999 iterations. Once overall PERMANOVAs were completed, pairwise PERMANOVAs were completed using the pairwiseAdonis package (version 0.4) to identify significant pairwise trends. PERMDISP tests identified homogeneous cluster dispersals in all PERMANOVAs, indicating that cluster dispersals were equal between groups. Once testing and plotting of PCA coordinates were completed, the first principal component of the seagrass structural complexity and environmental PCAs were extracted and used as unidimensional proxies in subsequent analyses. Both first principal components were correlated using a Pearson's correlation to identify correlative relationships between each unidimensional measure.

Generalized Additive Models. Generalized additive models (GAMs) were used to identify multivariate relationships between seagrass structural complexity (predictor variables) and environmental variables (response variables). GAMs were chosen as they are simple to fit and interpret, but can model complex nonlinear relationships (Wood 2017); which was important as ecological feedbacks and thresholds often form nonlinear relationships. Environmental data (the first principal component of the environmental PCA, PPFD, turbidity, total suspended particulates, total suspended sediments, plate trap accretion, tube trap accretion, modal benthic particle size, and degree of benthic sediment sorting) were modeled as multivariate GAMs using untransformed shoot density, leaf length, and leaf width as predictor variables in mgcv (version 1.8-31). GAMs were preferentially fitted with untransformed predictor and response data to allow for increased interpretability. However, where heteroscedasticity was prominent, transformed response variables were implemented using transformations outlined prior. Predictor variables were checked for collinearity before modeling and no combination exceeded a Pearson's r of 0.7 or produced a variance inflation factor of ≥2 (Zuur et al. 2010). GAMs were fitted using a Gaussian distribution, using thin plate splines, and a maximum basis complexity (K) of 5. Each predictor was modeled as a separate smooth using the restricted maximum likelihood estimate to select the smoothness parameter due to improved numerical stability versus other methods (Wood 2011). Multivariate models were chosen as they explained more deviance and residuals were better distributed in diagnostic plots compared to univariate models using shoot density as the predictor. Once fitted, model quality was assessed using gratia (version 0.6.0) and DHARMa (version 0.4.4).

Once a final GAM was derived for each variable, areas containing a significant change in the seagrass shoot density trend line were identified using a finite differences approach. For a given GAM, 100 finite points along the x-axis were calculated, and the first derivative and 95% confidence intervals of the GAM trend line were extracted. Where extracted confidence intervals did not contain 0, the first derivative was deemed significantly different from 0 and was retained as an area of significant change. The minimum and maximum shoot densities associated with this area of significant change were then extracted, back-transformed if required, and used to predict thresholds for the model response variable. Finite difference methods were only completed on shoot density as this variable is readily controllable during restoration, whilst leaf length and width are dependent on donor population morphologies.

Results

Environmental Variation

Comparisons of environmental data between locations and years showed that Grantville and Queensferry had similar environmental conditions but were different from Corinella (Table S1; Fig. 2). Corinella experienced significantly greater PPFD, higher current speeds, lower turbidity, lower total suspended particulates and sediments, greater plate trap accretion, and lower tube trap accretion compared to either Grantville or Queensferry (Table S1; Fig. 2). Although not compared statistically between locations, the mean daily light integral (mol photons m^{-2} day^{-1}) was highest at Corinella compared to Grantville and Queensferry (Corinella = 14.0 ± 6.6 SD, Grantville daily light integral = 11.7 ± 6.4 SD, Queensferry = 12.9 ± 6.3 SD). Sediment collected on plate traps in Corinella had a significantly higher percentage of organic content compared to Queensferry in 2020, but comparisons with Grantville were insignificant; as were comparisons between locations in 2019 (Table S1; Fig. 2). Benthic particle sizes increased in a stepwise manner from Corinella to Grantville and Queensferry. However, only comparisons between Corinella and Queensferry in 2019 were significant. Benthic sediments were primarily comprised of sandy muds and muddy sands and could be considered poorly or very poorly sorted based on thresholds present in Folk and Ward (1957) (sorting ranged between approximately 3–8 μm) (Fig. 2). Sediments present at Corinella were significantly less sorted than those present at Grantville across both years of sampling whilst sediments at Queensferry were not significantly different from either Corinella or Grantville (Table S1). There was no difference in suspended particle size between any location. Current speeds differed between all locations, with pairwise comparisons of Grantville and Queensferry showing significantly lower current speeds compared to those at Grantville. The direction of water movement was comparable between Corinella and Queensferry (primarily moving southwest), whilst current directions at Grantville were more variable (Fig. S1).

A PCA showed that 76% of the variation in environmental data was accounted for in the first two principal components (Fig. 3). PERMANOVAs showed that location, deployment year, and the interaction of the two factors had significant effects on clustering present ($p < 0.05$ throughout) (Fig. 3). Environmental conditions at Corinella were different compared to Queensferry and Grantville with little overlap between clusters present (pairwise PERMANOVA, Corinella-Grantville, $F_{1,15} = 79.96$, $p = 0.001$, Corinella-Queensferry, $F_{1,14} = 82.10$, $p = 0.001$). Nevertheless, although clusters overlapped more, Grantville and Queensferry could still be considered significantly different when testing the influence of location (pairwise PERMANOVA, $F_{1,15} = 20.36$, $p = 0.001$) (Fig. 3). Separation of clusters was primarily driven by PPFD, total suspended particulates, total suspended sediments, and turbidity, with secondary influences of tube and plate trap accretion, measures of particle sizes, and degree of sorting. The effect of deployment year was significant when comparing Corinella to Grantville ($F_{1,15} = 4.07$, $p = 0.046$) or when comparing Grantville to Queensferry ($F_{1,14} = 24.16$, $p = 0.001$, all other comparisons $p > 0.05$). The effect of the interaction of location and deployment year was significant when comparing Corinella to either Grantville or Queensferry (Corinella-Grantville, $F_{1,15} = 7.63$, $p = 0.013$; Corinella-Queensferry, $F_{1,15} = 5.97$, $p = 0.023$). Generally, measures associated with the optical clarity of the water column (PPFD, total suspended sediments, total suspended particulates, and turbidity) were strongly associated with the first principal component of the environmental PCA (hereafter $PC1_{Env}$) (Fig. 3). Whereas the second principal component was primarily associated with the size of suspended and benthic sediment particles and the degree of sorting present. Overall, an increasingly negative $PC1_{Env}$ value indicated an improved light environment (increased PPFD, less turbidity, total suspended sediment and particulates, and higher accretion in tube traps).

Seagrass Density and Morphology

Comparisons of above-ground and below-ground seagrass traits showed that seagrass at Corinella differed significantly from Queensferry and Grantville (Table S2; Fig. 4). Overall, Corinella showed significantly higher shoot density, leaf density,

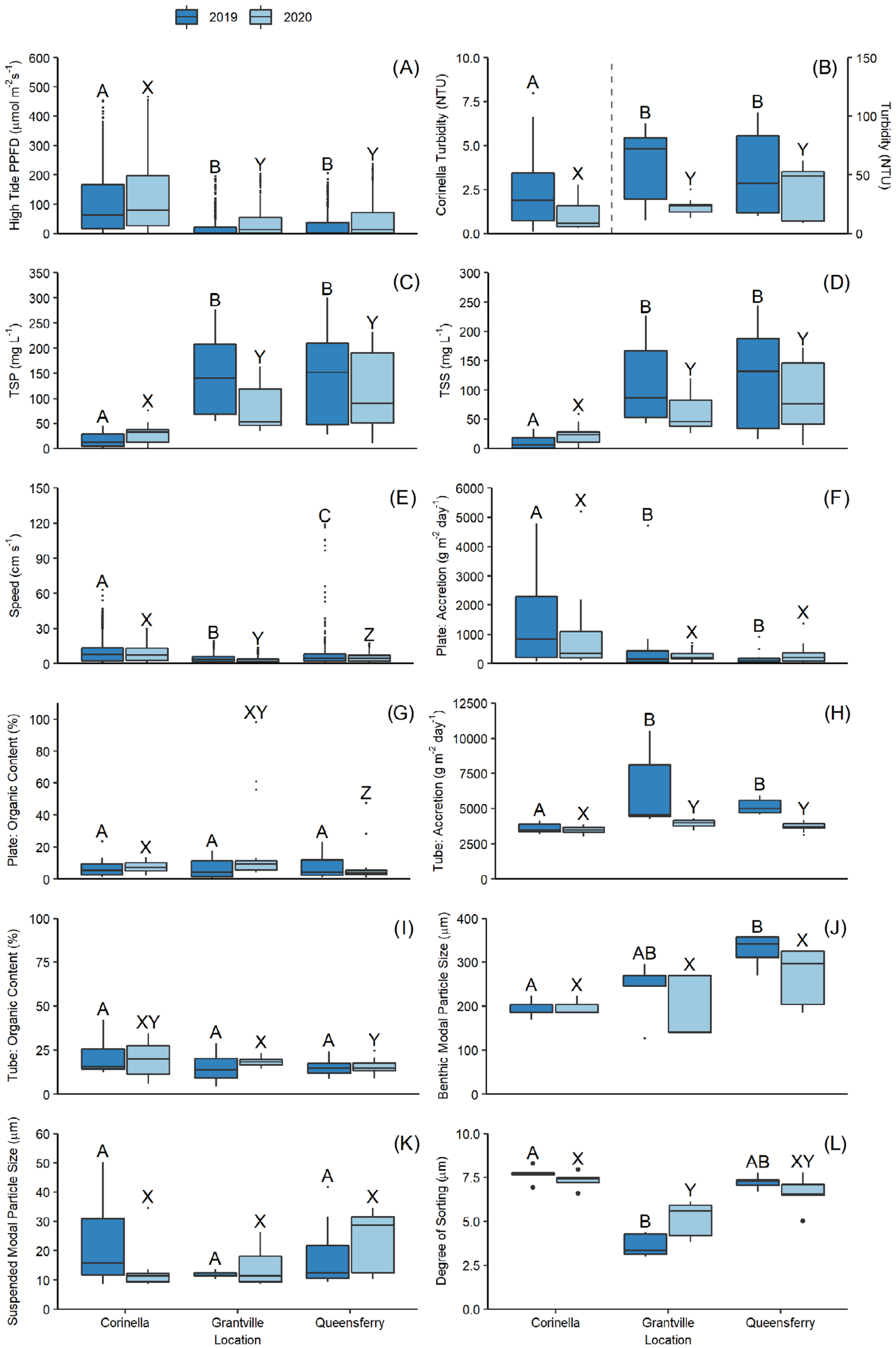

Figure 2. Variation in untransformed environmental variables measured between locations (*x*-axis) and deployment years (dark blue = 2019, light blue = 2020). Letters indicate the significance of pairwise tests (A–C for 2019 tests and X–Z for 2020 tests). Comparisons between years were not undertaken. Note the multiple axes scales present for turbidity (panel B), Corinella data (left of the dashed line) use a different scale to the other locations (right of the dashed line). PPFD, photosynthetic photon flux density.

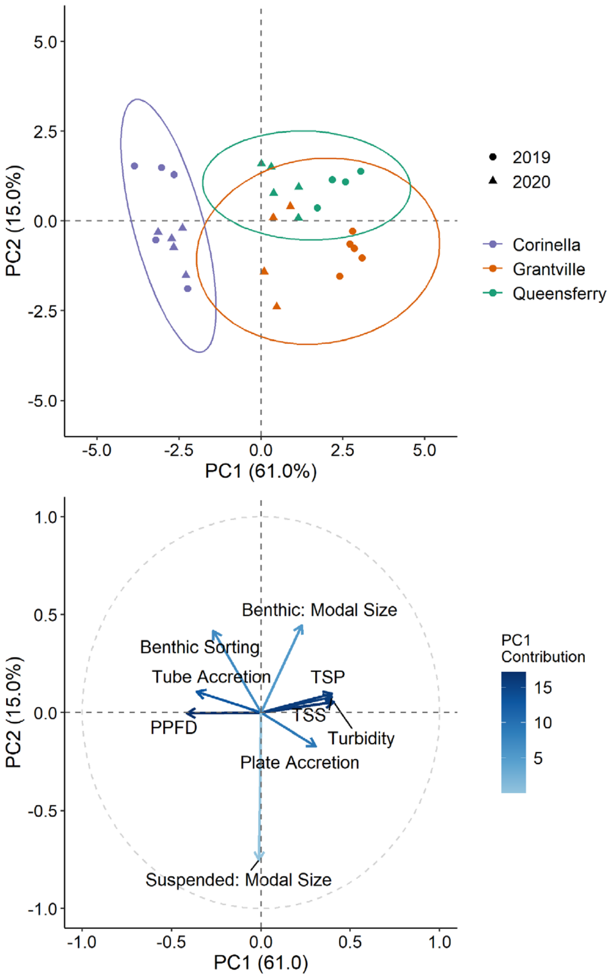

Figure 3. Environmental principal component analysis is presented as a score plot (left) showing distinct clusters and a loadings plot (right) showing directionality and strength of loadings. TSP, total suspended particulates; TSS, total suspended solids; PPFD, photosynthetic photon flux density.

above-ground biomass, below-ground biomass, and leaf length compared with Grantville or Queensferry (Table S2; Fig. 4). Corinella was also shown to have a significantly higher percentage cover than Queensferry across both years sampled but had a comparable cover to Grantville in both years. Leaf width and internode length did not show consistent pairwise trends for comparisons containing Corinella, with the significance and direction of the trend changing between years sampled (Table S2; Fig. 4). Rhizome thickness was significantly higher in Corinella compared to Grantville or Queensferry in 2020 only. Seagrass density, biomass, and morphological variables could largely be considered comparable between Grantville and Queensferry. A single significant trend was detected within both sampling years; leaf length was significantly longer at Grantville compared to Queensferry. Leaf width and internode length were significantly higher at Grantville in 2019, although this trend was not consistent between sampling years.

PCAs of seagrass data showed the first two components accounted for 91% of the variation in the dataset (Fig. 5). PERMANOVAs indicated significant effects of location and deployment year (location, $F_{2,21} = 16.3$, $p = 0.001$; deployment year, $F_{1,21} = 9.0$, $p = 0.004$), but the interaction of the two factors was not significant ($p > 0.05$). Although the overlap between clusters was present, seagrass density and morphology at Corinella could be considered different from Grantville or Queensferry when the effect of location was assessed (pairwise PERMANOVA, Corinella-Grantville, $F_{1,16} = 20.0$, $p = 0.001$, Corinella-Queensferry, $F_{1,13} = 26.9$, $p = 0.001$). Seagrass density and morphology could be considered comparable between Grantville and Queensferry ($p > 0.05$). Deployment year was shown to have a significant effect when comparing any two locations in pairwise PERMANOVAs (Corinella-Grantville, $F_{1,16} = 8.46$, $p = 0.005$; Corinella-Queensferry, $F_{1,13} = 5.65$, $p = 0.023$; Grantville-Queensferry, $F_{1,13} = 6.09$, $p = 0.01$) whilst the interaction of location and deployment year was only significant when comparing Corinella to Grantville ($F_{1,16}$, $p = 0.041$). Clustering present was primarily driven by measures of density or biomass (density of shoots and leaves present, percentage cover, and above-ground biomass) and secondarily by morphological measures (leaf width and length). Overall, an increasingly negative value of the first principal component of the seagrass PCA (hereafter $PC1_{Sg}$) was indicative of an increased above-ground structural complexity (increased density of leaves and shoots, above-ground biomass, percentage cover, and leaf length).

Relationship between Seagrass and Environmental Conditions

A comparison between seagrass complexity ($PC1_{Sg}$) and local light-sediment conditions ($PC1_{Env}$) found a strong correlation between the two variables, highlighting linkages present between seagrass structural complexity present at a location and the quality of the surrounding light environment (Fig. 6).

Overall, seven of the nine GAMs fitted identified significant relationships between a component of seagrass structural complexity and the surrounding environmental conditions (Fig. 7). GAMs predicted that an increased shoot density was associated with greater water clarity and light penetration (more negative $PC1_{Env}$, higher high tide PPFD, lessened suspended sediments, particulates, and turbidity), greater sediment accretion in tube traps, and less well-sorted sediments (a higher degree of sorting value) (Fig. 7). Seagrass structural complexity was a better predictor of water clarity ($PC1_{Env}$, turbidity, total suspended sediments, total suspended particulates, PPFD) (79.2–95% deviance explained) compared to measures of sediment accretion and modal sedimentary characteristics (28.4–58.4% deviance explained) (Fig. 7). Leaf length and width were less commonly identified as significant predictors within models fitted. Three GAMs identified significant effects of leaf length; namely, increased light availability at high tide (PPFD), a decrease in turbidity, and an increase in tube accretion with increasing leaf length (Fig. 7). Leaf width was only identified as a significant predictor of the degree of sorting present. No significant predictors of benthic modal particle size or the mass of sediment accreted on plate traps were identified (Fig. 7).

Density thresholds for significant environmental change varied substantially across variables modeled (Fig. 7).

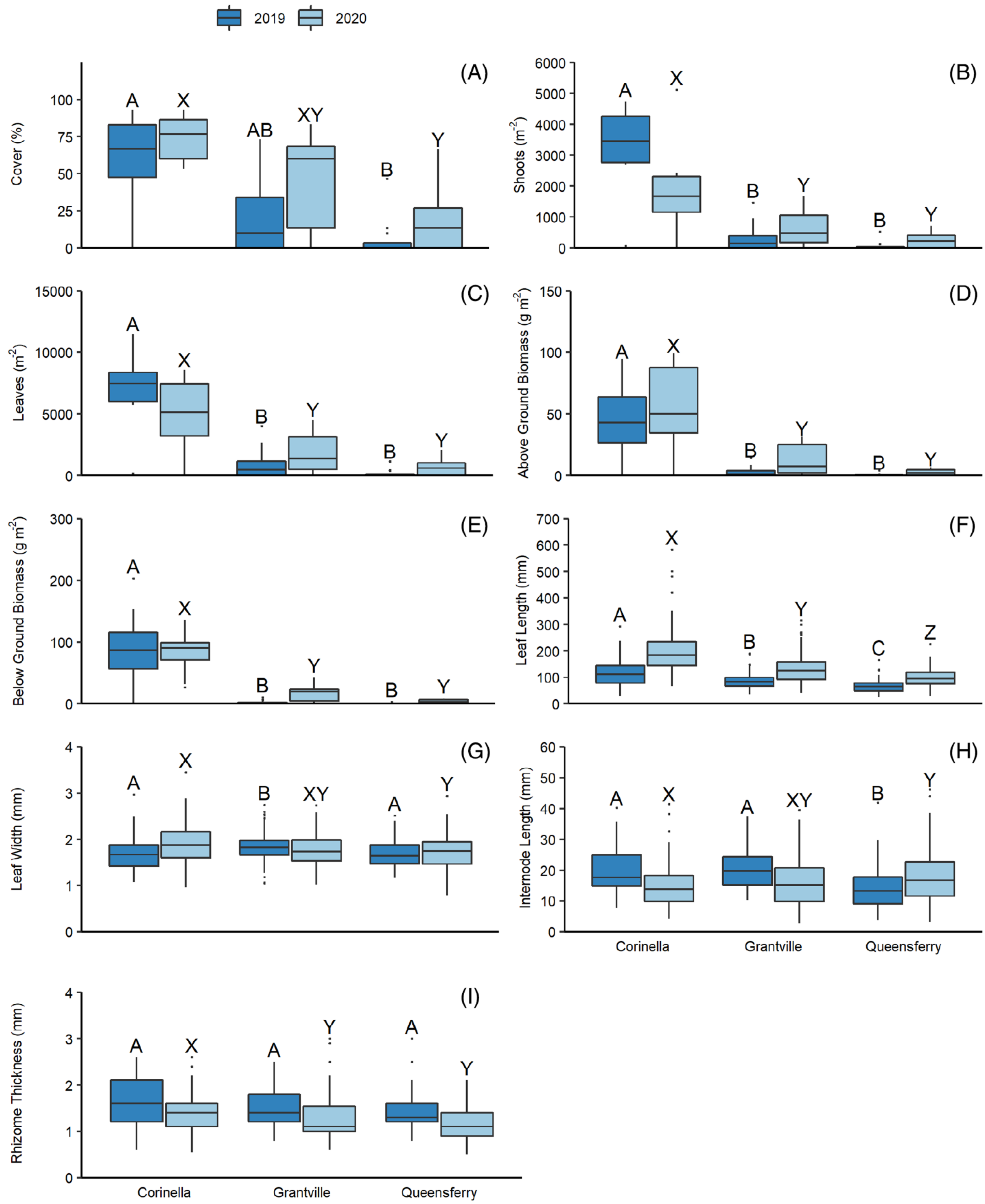

Figure 4. Variation in untransformed seagrass variables measured between locations (x-axis) and deployment years (dark blue = 2019, light blue = 2020). Sites with no seagrass present are included in medians here. Letters indicate the significance of pairwise tests (A–C for 2019 tests and X–Z for 2020 tests). Comparisons between years were not undertaken.

GAMs predicting $PC1_{Env}$, light availability, concentrations of suspended particulates and sediments, and turbidity identified areas of statistically significant change with increasing seagrass shoot density, highlighting fitted trend lines with an initially steep, but gradually lessening gradient (Fig. 7). These models predicted that areas of significant change occurred between the

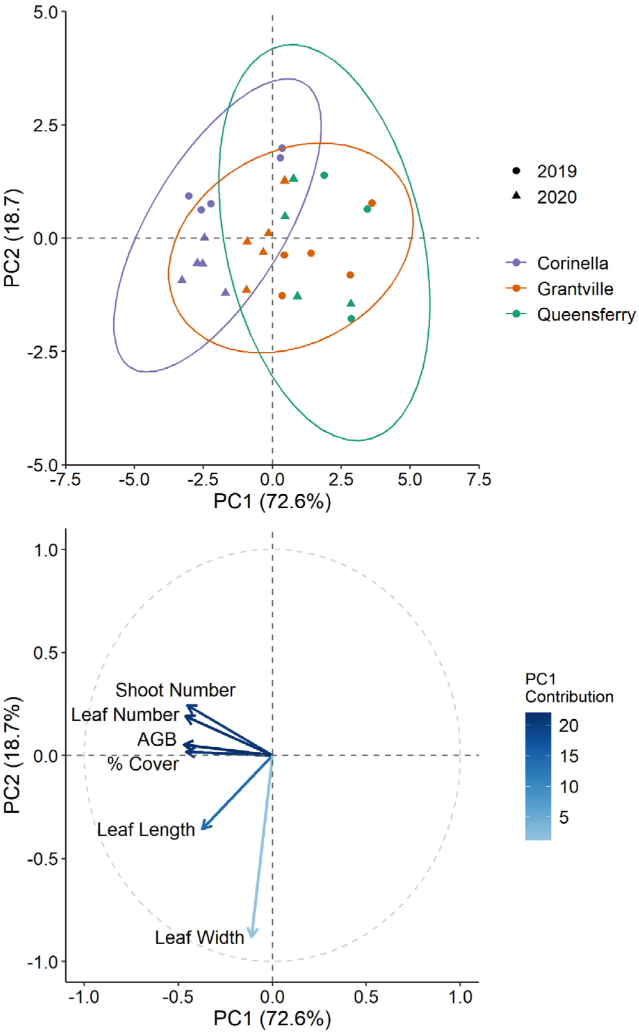

Figure 5. Seagrass above-ground structural complexity principal component analysis is presented as a score plot (left) showing distinct clusters and a loadings plot (right) showing directionality and strength of loadings.

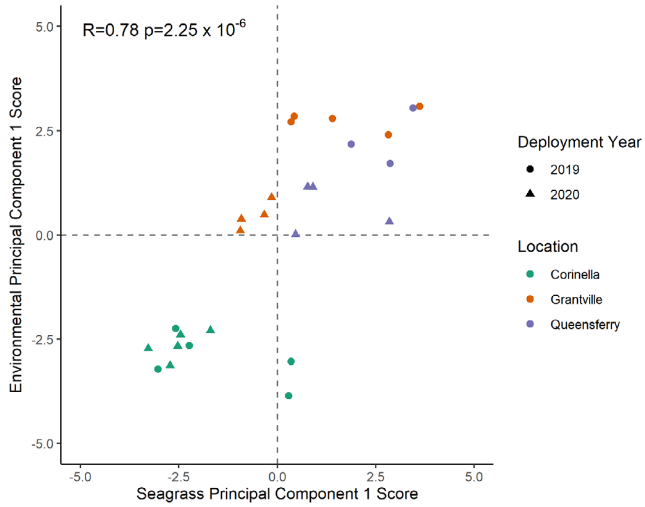

Figure 6. Pearson correlation between the first principal components of seagrass above-ground complexity (*x*-axis) (increasingly negative value indicates increasing structural complexity) and environmental principal component analyses (*y*-axis) (increasingly negative value indicates greater water clarity).

smallest nonzero density used in finite difference analyses (45 shoots/m^2) and 1,771–2,952 shoots/m^2 (beyond which little change was detected). However, given that 100 finite differences were calculated across a maximum density of approximately 4,500 shoots/m^2, minimum density thresholds identified in these models are likely an artifact of the discretisation used. The GAM predicting sediment accretion on tube traps identified a very small area of significant change (Fig. 7), although insufficient data was present to draw conclusions. The entire trend line of the GAM predicting the degree of sorting present was identified as an area of significant change (spanning the smallest nonzero density to 4,451 shoot/m^2), likely because a linear relationship with a steep gradient was predicted. Under this scenario, each incremental change in the trend line was uniform and identified as significantly different from zero. No thresholds were derived from GAMs predicting modal benthic particle size or accretion on plate traps.

Discussion

Local sediment-light environments and the density and structural complexity of seagrass meadows are intrinsically linked (Ralph et al. 2007; Adams et al. 2016). To improve the success of restoration efforts, site- and species-specific information on three components is required: (1) the potential for favorable ecological feedbacks to take place (van der Heide et al. 2007), (2) the likelihood that donor material is favorably adapted to environmental conditions within the restoration site (van Katwijk et al. 2009), and (3) suitable reference sites for restoration target setting (Prach et al. 2019). This study explored the relationships between seagrass structural complexity and local sediment-light conditions in intertidal *Zostera muelleri* meadows in temperate south-eastern Australia to guide restoration planning for this species. Overall, significant relationships between seagrass structural complexity and local environmental conditions were identified, highlighting positive relationships between water clarity and light availability and the structural complexity of seagrass meadows present. However, some relationships supported the inverse directionality; highlighting the complex nature of the feedback present. Taken together, the findings of this study highlight the close association between local environmental conditions and the density and morphology of seagrasses. Results also highlight the importance of developing a thorough understanding of these aspects before undertaking restoration, as restoration success likely hinges on the alignment of environmental conditions present, densities planted, donor morphology, and spatial extent; although the latter is not assessed here.

Environmental Trends and Potential Drivers

The results of this study highlight the close associations between seagrass structural complexity and the surrounding light and sediment environments. However, a lack of data from manipulative (e.g. manually changing densities in the field) or temporal experiments (e.g. logging changes in environmental conditions as the meadow grows and becomes denser) prevent this study from attributing causative relationships to observed trends. Nevertheless, we posit that in a highly turbid and environmentally variable system such as Western Port, both environmental conditions and local ecological feedback likely act simultaneously to determine environmental suitability for seagrass within sites.

The results outlined should be interpreted within the context of local environmental variation. Subtidal areas immediately offshore of Queensferry are a net deposition zone for mobilized

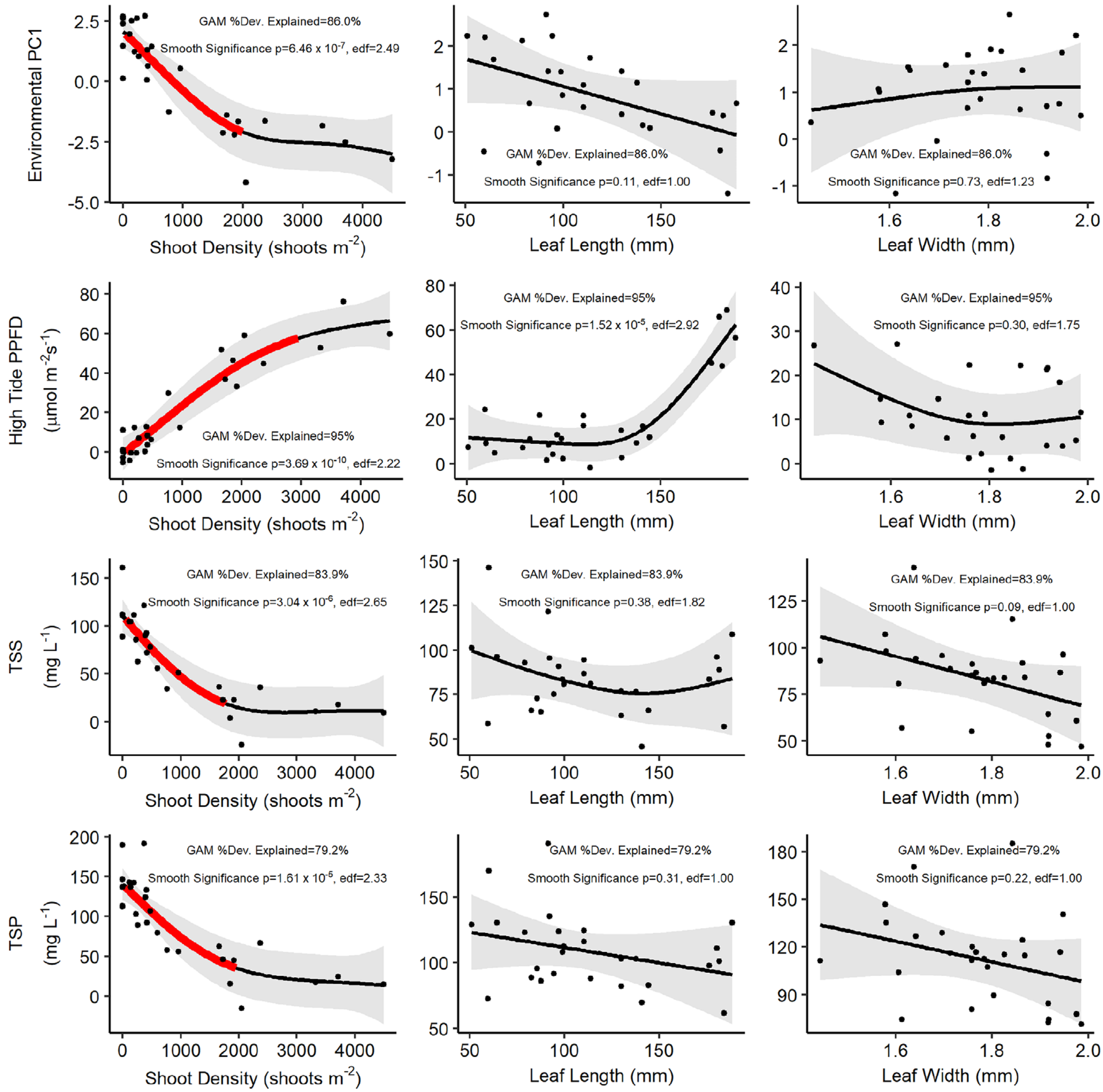

Figure 7. Partial effects multiplot of generalized additive models predicting environmental variables using shoot density (left), leaf length (middle), and leaf width (right). Each row represents a single GAM. %Dev. Explained, percentage deviance explained by full GAM; Smooth Sig., significance of the smooth term within the GAM; edf, effective degrees of freedom of the smooth; PPFD, photosynthetic photon flux density; TSP, total suspended particulates, and TSS, total suspended sediments. Black line represents the fitted trend line, red line represents the area of significant change in the first derivative, and the gray ribbon represents 95% CI. Points shown are partial residuals plotted on the response scale.

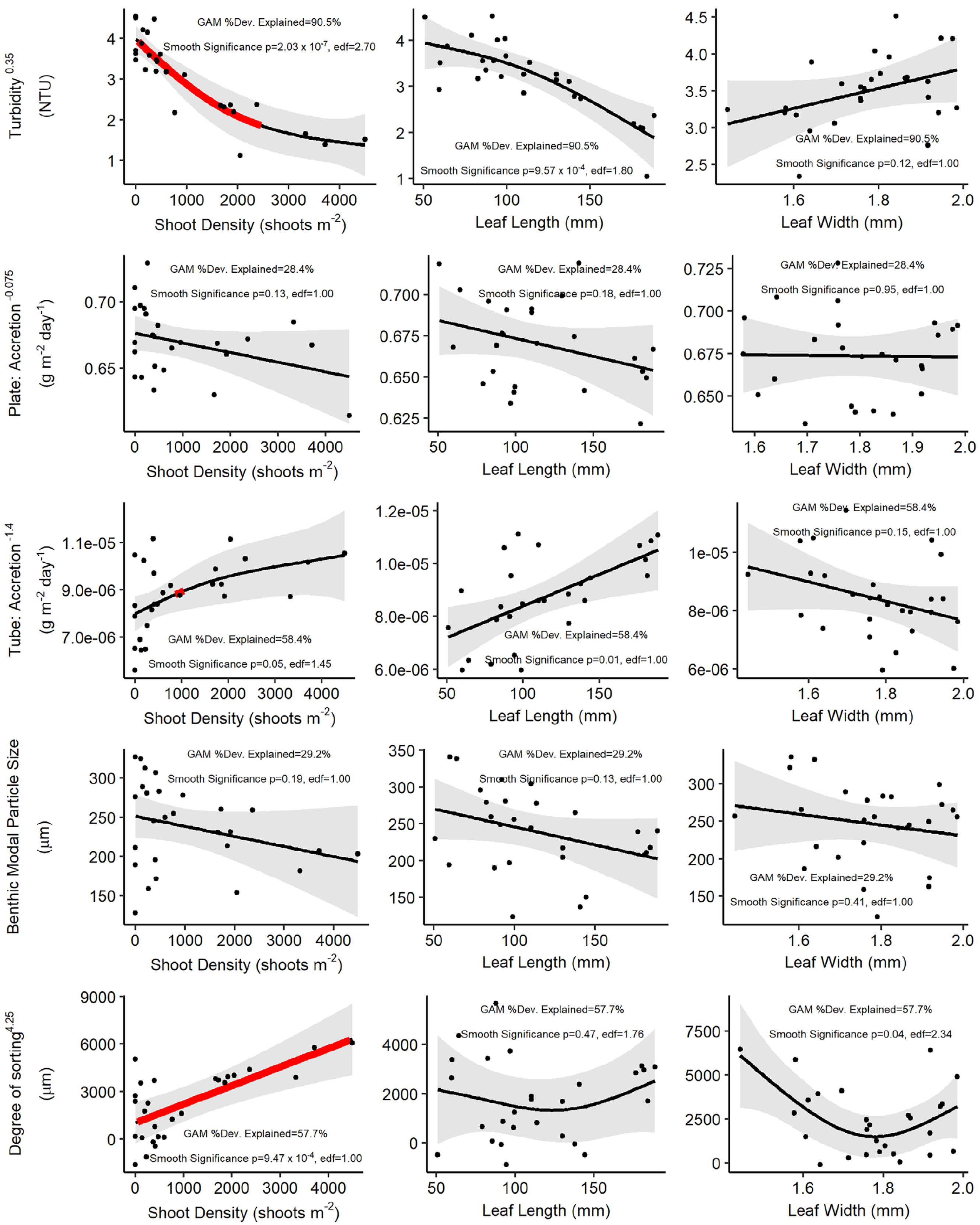

Figure 7 (Continued)

sediments originating from other regions of Western Port (Hancock et al. 2001) and bay-wide environmental models suggest continuous cycles of local resuspension and deposition may be occurring in these areas (Cinque et al. 2018). Furthermore, clay-rich cliffs in the northeast of the bay undergo substantial erosion (Tomkins et al. 2014), forming a plentiful source of suspended particulates in areas assessed in this study. Our analyses identified significant decreases in benthic modal particle sizes when comparing low (Queensferry), medium (Grantville), and high (Corinella) structural complexity meadows, but detected no difference in the particle size of resuspended material between locations. These findings suggest that the bulk of turbidity present may originate externally, may drift to locations sampled during high tide, and may exceed contributions of local resuspension to turbidity present.

Geographically, all locations sampled could be considered broadly equidistant to potential sources of turbidity. Thus, sediment supply is likely comparable between locations sampled; although some variation is expected as local hydrodynamic regimes are complex (Hinwood 1979). Thus, increased light penetration and quantities of fine particulates in the benthos, coupled with decreased turbidity and degree of sediment sorting in more structurally complex meadows, suggests seagrasses exert a stabilizing effect on local sediment dynamics. However, given that stabilization effects enforced by seagrass meadows are a product of structural complexity, extent, and spatial arrangement (Carr et al. 2016), all locations sampled may not have equal stabilization potential. Dense, long-leafed, and spatially large meadows at Corinella are likely to be having a stabilizing effect on benthic sediments. Whilst low density, patchy meadow forms, and short-leafed morphotypes present at Grantville and Queensferry likely have a reduced potential to exert control via the SSL feedback. Environmental data assessed between sites support this narrative, with the light environment at Corinella significantly improved, whilst conditions at Grantville and Queensferry were broadly comparable. As such, meadow forms present at Grantville or Queensferry likely did not have sufficient structural complexity or meadow extent to substantially alter concentrations of suspended solids present during the high-tide window.

Although we suggest that seagrasses present at Corinella may be exerting some degree of control on light availability, water clarity, benthic particle size, and associated sorting, other aspects of the SSL feedback produced less clear associations. No clear trends were detected for current speed or accretion rates; which is of particular interest as the baffling of current speeds is a direct driver of increased sediment stability and reduced resuspension (Adams et al. 2016). A lack of conclusive evidence for increased accretion rates in more structurally complex meadows is also of interest as reductions in turbidity often result from increased particle settlement within meadows as a direct result of reduced kinetic energies present (Lefebvre et al. 2010). Increased accretion was detected in structurally complex meadows during inter-site analyses, suggesting that changes to accretion rates may have been present but were difficult to model. Regardless, given the importance of identifying causal mechanisms concerning the SSL feedback, further work undertaking flume studies or manipulative field experiments is suggested to quantify the role that intertidal *Z. muelleri* plays in stabilizing local sediments and influencing accretion rates.

Variation in seagrass above-ground morphology observed was also related to environmental conditions present; especially in Grantville and Queensferry. Reduction of above-ground biomass when faced with reduced light availability is a common response of plants and acts to reduce respiration demand (Ralph et al. 2007) and increase photosynthetic efficiency of remaining above-ground biomass by reducing self-shading (Enríquez et al. 2019). Previous work on *Z. muelleri* by York et al. (2013) highlighted reduced above-ground to below-ground biomass ratios, shoot biomass, and leaf width in plants exposed to shading. As such, reduced density and leaf length at Grantville and Queensferry may be indicative of plants exposed to stress via light limitation.

Comparisons of light availability to literature-derived values also suggest that light environments sampled may be stressful for seagrasses present. On average, light availability at high tide was below thresholds needed to saturate photosynthesis during summer in intertidal *Z. muelleri* meadows in Whangapou Harbor, New Zealand (242 μmol m^{-2} s^{-1} [Schwarz 2004]), suggesting that plants may be light-limited at high tide even in summer months when light availability is greatest. When daily measures of light availability were assessed, daily light integrals (approximately 11–14 mol m^{-2} day^{-1}) were below those needed to induce reductions in effective quantum yield, photosynthetic light harvesting efficiency, and below-ground carbohydrate content identified in previous experiments using Western Port *Z. muelleri* populations (approximately 16 mol m^{-2} day^{-1}) (Dr. Rachel Manassa, 20 May 2022, DELWP, pers. comm.). However, daily light levels were above those associated with morphological impacts on *Z. muelleri* in Chartrand et al. (2016) (4–5 mol photons m^{-2} day^{-1}). Furthermore, excessive light availability, such as that available during low tide, can decrease the efficiency of photosynthesis (Petrou et al. 2013; Manassa et al. 2017). Light availability during both high and low tides may, therefore, be stressful for seagrasses present within locations sampled, although it remains unclear whether light availability is sufficiently poor to drive morphometric changes identified between locations. To better identify the role of light availability in controlling seagrass density and morphology within locations sampled, shading experiments similar to those conducted by Chartrand et al. (2016) are suggested.

Directions for Restoration

Restoration efforts may see increased success by selecting donor material from sites that exhibit comparable environmental conditions to prospective restoration sites (van Katwijk et al. 2009; Jahnke et al. 2015). Using this approach, donor material may be more favorably adapted to environmental conditions genetically (Pazzaglia et al. 2021) and may be more tolerant of future stress events due to stress priming (Nguyen et al. 2020). This study identified variation in meadow morphology and density within a small geographic subset of the focal embayment, highlighting that meadow form can be highly variable even over comparatively small spatial scales. Within the context of Western Port, prospective restoration sites may commonly exhibit fine benthic particle sizes and spatiotemporally variable resuspension rates, turbidity, light availability, and sediment mobility. As such, of the locations sampled here, donors sourced from Grantville or Queensferry may outperform those from Corinella when planted at lower densities as increased leaf length and above-ground biomass may represent detrimental adaptations in restoration sites where light availability is reduced and temperature and desiccation stress are high. However, reduced below-ground biomass in individuals sampled from Grantville and Queensferry may indicate a reduced capacity to adapt to changes in environmental conditions, as carbohydrate stores are often used to enable physiological and morphological change (Teresa et al. 1999). Limited scope for acclimation in low-light adapted individuals here further stresses the importance of ensuring environmental similarity between donor sites and restoration locations, as a close match may limit the need for acclimatization and improve the chance of transplantation success.

It is unclear whether planting densities identified in this study should be used as guidelines for restoration due to technical issues encountered. As such, authors suggest that in situ, manipulative restoration experiments are undertaken to identify the effects of planting density, area planted, and spatial arrangement on restoration success. However, maximal densities associated with areas of significant change may represent thresholds beyond which restoration practitioners would gain little benefit, as environmental conditions showed little improvement when exceeding this density. Manipulative experiments are also needed to confirm any causative effects. Furthermore, planting densities on the scale of thousands of shoots/m^2 are unlikely to be feasible in upscaled restoration efforts as donor supply may be unable to produce such high numbers of propagules without eliciting damage to existing meadows or requiring substantial nursery propagation. Such densities are also orders of magnitude above current planting guidelines. For example, Moksnes et al. (2016) suggest that shoot-based planting of *Zostera marina* be undertaken on the scale of ones to tens of shoots/m^2 and be planted across a spatial area of at least 1,000 m^2. In the interim, we suggest that shoot-based restoration be undertaken under comparable guidelines or, alternatively, seed-based restoration be undertaken following approaches similar to those employed in Govers et al. (2022).

Finally, restoration ecology requires the identification of ecologically relevant reference sites (those with which restored material will be compared to monitor success) and targets (goals practitioners aim to achieve within the restoration site) to ensure that the success of a project can be properly evaluated (Gann et al. 2019). To this end, reference sites chosen should represent meadow forms expected under environmental conditions present at restoration sites. Although existing guidelines recommend restoration projects *seek the highest level of recovery attainable* (Gann et al. 2019), this may not always equate to establishing homogeneous and dense meadows—especially in highly variable and challenging environmental conditions such as those present in turbid and turbulent areas such as Western Port. For example, if scaled-up restoration efforts were implemented at a site environmentally similar to Grantville or Queensferry, reference meadow forms and associated targets should reflect the patchy and sparse meadow forms demonstrated by natural meadows under similar conditions, not those present in areas of greater light availability such as Corinella. However, to achieve any level of success, planting methods will likely still need to introduce material in larger densities to those present in reference meadows, as considerable post-introduction losses are common (Govers et al. 2022). Evidently, considerable monitoring and prior knowledge are required to ensure that meadow forms naturally present can be considered *healthy* and that density or patch size is not currently limited by an unknown stressor that, once removed, may allow greater biomass to persist. Such a consideration reiterates the need to fully understand stressors and controls on seagrass meadow form before investing in upscaled restoration efforts (Campbell 2002; Cunha et al. 2012).

Acknowledgments

We acknowledge and pay our respects to the Bunurong people, the Traditional Owners of the land on which this work was carried out, and we thank our colleagues who assisted in the field. We also thank Professor David Kennedy for facilitating sediment particle size analyses within the University of Melbourne. This work was funded by Melbourne Water, Deakin University, and the Holsworth Wildlife Research Endowment. Open access publishing facilitated by Deakin University, as part of the Wiley - Deakin University agreement via the Council of Australian University Librarians.

LITERATURE CITED

Adams MP, Hovey RK, Hipsey MR, Bruce LC, Ghisalberti M, Lowe RJ, et al. (2016) Feedback between sediment and light for seagrass: where is it important? Limnology and Oceanography 61:1937–1955. https://doi.org/10.1002/lno.10319

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x

Bittner RE, Roesler EL, Barnes MA (2020) Using species distribution models to guide seagrass management. Estuarine, Coastal and Shelf Science 240: 106790. https://doi.org/10.1016/j.ecss.2020.106790

Blake S, Ball D (2001) Victorian Marine Habitat Database: seagrass mapping of Western Port. Marine and Freshwater Resources Institute Report No 29. Marine and Freshwater Research Institute, Queenscliff

Blott SJ, Pye K (2001) GRADISTAT: a grain size distribution and statistics package for the analysis of unconsolidated sediments. Earth Surface Processes and Landforms 26:1237–1248. https://doi.org/10.1002/esp.261

Bulthuis DA (1981) Distribution and summer standing crop of seagrasses and macro-algae in Western Port, Victoria. Proceedings of The Royal Society of Victoria 92:107–112

Campbell ML (2002) Getting the foundation right: a scientifically based management framework to aid in the planning and implementation of seagrass transplantation efforts. Bulletin of Marine Science 71:1405–1414

Carr JA, D'Odorico P, McGlathery KJ, Wiberg PL (2016) Spatially explicit feedbacks between seagrass meadow structure, sediment and light: habitat suitability for seagrass growth. Advances in Water Resources 93:315–325. https://doi.org/10.1016/j.advwatres.2015.09.001

Chartrand KM, Bryant CV, Carter AB, Ralph PJ, Rasheed MA (2016) Light thresholds to prevent dredging impacts on the great barrier reef seagrass, *Zostera muelleri* ssp. *capricorni*. Frontiers in Marine Science 3:106. https://doi.org/10.3389/fmars.2016.00106

Cinque K, Okely P, Yeates P (2018) Hydrodynamic and sediment modelling to forecast seagrass coverage and recovery in Western Port. Pages 30–41. In: Coleman R, Bathgate R, Keough MJK (eds) Understanding the Western Port Environment 2018. Melbourne Water, Docklands

Clavier J, Chauvaud L, Carlier A, Amice E, Van der Geest M, Labrosse P, Diagne A, Hily C (2011) Aerial and underwater carbon metabolism of a *Zostera noltii* seagrass bed in the Banc d'Arguin, Mauritania. Aquatic Botany 95:24–30. https://doi.org/10.1016/j.aquabot.2011.03.005

Cunha AH, Marba NN, van Katwijk MM, Pickerell C, Henriques M, Bernard G, Ferreira MA, Garcia S, Garmendia JM, Manent P (2012) Changing paradigms in seagrass restoration. Restoration Ecology 20:427–430. https://doi.org/10.1111/j.1526-100X.2012.00878.x

Dalby O, Pucino N, Tan YM, Jackson EL, Macreadie PI, Coleman RA, Young MA, Ierodiaconou D, Sherman CDH (2023) Identifying spatio-temporal trends in seagrass meadows to inform future restoration. Restoration Ecology 31:e13787. https://doi.org/10.1111/rec.13787

Dunic JC, Brown CJ, Connolly RM, Turschwell MP, Cote IM (2021) Long-term declines and recovery of meadow area across the world's seagrass bioregions. Global Change Biology 27:4096–4109. https://doi.org/10.1111/gcb.15684

Enríquez S, Olivé I, Cayabyab N, Hedley JD (2019) Structural complexity governs seagrass acclimatization to depth with relevant consequences for meadow production, macrophyte diversity and habitat carbon storage capacity. Scientific Reports 9:14657. https://doi.org/10.1038/s41598-019-51248-z

Erftemeijer PLA, Koch EW (2001) Sediment geology methods for seagrass habitat. Pages 345–367. In: Short FT, Coles RG (eds) Global seagrass research methods. Elsevier, Amsterdam. https://doi.org/10.1016/B978-044450891-1/50019-0

Folk RL, Ward WC (1957) Brazos River bar [Texas]; a study in the significance of grain size parameters. Journal of Sedimentary Research 27:3–26. https://doi.org/10.1306/74D70646-2B21-11D7-8648000102C1865D

Fonseca MS (1989) Sediment stabilization by *Halophila decipiens* in comparison to other seagrasses. Estuarine, Coastal and Shelf Science 29:501–507. https://doi.org/10.1016/0272-7714(89)90083-8

Fonseca M (2011) Addy revisited: what has changed with seagrass restoration in 64 years? Ecological Restoration 29:73–81. https://doi.org/10.3368/er.29.1-2.73

Gamble C, Debney A, Glover A, Bertelli C, Green B, Hendy I, et al. (2021) Seagrass restoration handbook. Zoological Society of London, London, UK

Gann GD, McDonald T, Walder B, Aronson J, Nelson CR, Jonson J, et al. (2019) International principles and standards for the practice of ecological restoration. Second edition. Restoration Ecology 27:S1–S46. https://doi.org/10.1111/rec.13035

Ganthy F, Soissons L, Sauriau PG, Verney R, Sottolichio A (2015) Effects of short flexible seagrass *Zostera noltei* on flow, erosion and deposition processes determined using flume experiments. Sedimentology 62:997–1023. https://doi.org/10.1111/sed.12170

Govers LL, Heusinkveld JHT, Gräfnings MLE, Smeele Q, van der Heide T (2022) Adaptive intertidal seed-based seagrass restoration in the Dutch Wadden Sea. PLoS One 17:e0262845. https://doi.org/10.1371/journal.pone.0262845

Hancock GJ, Olley JM, Wallbrink PJ (2001) Sediment transport and accumulation in Western Port. CSIRO Land and Water technical report 47/01. CSIRO, Canberra, Australia.

Hargrave BT, Burns NM (1979) Assessment of sediment trap collection efficiency. Limnology and Oceanography 24:1124–1136. https://doi.org/10.4319/lo.1979.24.6.1124

Hinwood JB (1979) Hydrodynamic and transport models of Western Port, Victoria. Marine Geology 30:117–130. https://doi.org/10.1016/0025-3227(79)90009-4

Jackson EL, Aiken CM, Mulloy R, Harrison L, McKenzie L (2021) Resilience-based mapping to support seagrass restoration and management in the Whitsundays. Great Barrier Reef Foundation

Jacobs SWL, Les DH (2009) New combinations in Zostera (Zosteraceae). Telopea 12:419–423. https://doi.org/10.7751/telopea20095827

Jahnke M, Serra IA, Bernard G, Procaccini G (2015) The importance of genetic make-up in seagrass restoration: a case study of the seagrass *Zostera noltei*. Marine Ecology Progress Series 532:111–122. https://doi.org/10.3354/meps11355

Keough MJ, Boon PI, Dann P, Dittami S, Jenkins G, Lee R, Quinn G, Ross J, Walker D, Wilson R (2011) Pages 1–226. Understanding the Western Port environment. A summary of current knowledge and priorities for future research. Melbourne Water, Docklands

Kilminster K, McMahon K, Waycott M, Kendrick GA, Scanes P, McKenzie L, et al. (2015) Unravelling complexity in seagrass systems for management: Australia as a microcosm. Science of the Total Environment 534:97–109. https://doi.org/10.1016/j.scitotenv.2015.04.061

Kuo J (2005) A revision of the genus *Heterozostera* (Zosteraceae). Aquatic Botany 81:97–140. https://doi.org/10.1016/j.aquabot.2004.10.005

Lefebvre A, Thompson CEL, Amos CL (2010) Influence of *Zostera marina* canopies on unidirectional flow, hydraulic roughness and sediment movement. Continental Shelf Research 30:1783–1794. https://doi.org/10.1016/j.csr.2010.08.006

Manassa RP, Smith TM, Beardall J, Keough MJ, Cook PLM (2017) Capacity of a temperate intertidal seagrass species to tolerate changing environmental conditions: significance of light and tidal exposure. Ecological Indicators 81:578–586. https://doi.org/10.1016/j.ecolind.2017.04.056

Maxwell PS, Eklöf JS, van Katwijk MM, O'Brien KR, de la Torre-Castro M, Boström C, et al. (2017) The fundamental role of ecological feedback mechanisms for the adaptive management of seagrass ecosystems—a review. Biological Reviews 92:1521–1538. https://doi.org/10.1111/brv.12294

Moksnes PO, Eriander L, Infantes E, Holmer M (2018) Local regime shifts prevent natural recovery and restoration of lost eelgrass beds along the Swedish West Coast. Estuaries and Coasts 41:1712–1731. https://doi.org/10.1007/s12237-018-0382-y

Moksnes PO, Gipperth L, Laas K, Cole S, Infantes E (2016) Pages 1–111. Handbook for restoration of eelgrass in Sweden—National guideline. Report Number 2021:5. Swedish Agency for Marine and Water Management, Gothenburg, Sweden.

Nguyen HM, Kim M, Ralph PJ, Marín-Guirao L, Pernice M, Procaccini G (2020) Stress memory in seagrasses: first insight into the effects of thermal priming and the role of epigenetic modifications. Frontiers in Plant Science 11:494. https://doi.org/10.3389/fpls.2020.00494

Nordlund LM, Koch EW, Barbier EB, Creed JC (2016) Seagrass ecosystem services and their variability across genera and geographical regions. PLoS One 11:e0163091. https://doi.org/10.1371/journal.pone.0163091

Pazzaglia J, Nguyen HM, Santillán-Sarmiento A, Ruocco M, Dattolo E, Marín-Guirao L, Procaccini G (2021) The genetic component of seagrass restoration: what we know and the way forwards. Water 13:829. https://doi.org/10.3390/w13060829

Petrou K, Jimenez-Denness I, Chartrand K, McCormack C, Rasheed M, Ralph PJ (2013) Seasonal heterogeneity in the photophysiological response to air exposure in two tropical intertidal seagrass species. Marine Ecology Progress Series 482:93–106. https://doi.org/10.3354/meps10229

Prach K, Durigan G, Fennessy S, Overbeck GE, Torezan JM, Murphy SD (2019) A primer on choosing goals and indicators to evaluate ecological restoration success. Restoration Ecology 27:917–923. https://doi.org/10.1111/rec.13011

Ralph PJ, Durako MJ, Enríquez S, Collier CJ, Doblin MA (2007) Impact of light limitation on seagrasses. Journal of Experimental Marine Biology and Ecology 350:176–193. https://doi.org/10.1016/j.jembe.2007.06.017

Schwarz AM (2004) Contribution of photosynthetic gains during tidal emersion to production of *Zostera capricorni* in a North Island, New Zealand estuary. New Zealand Journal of Marine and Freshwater Research 38:809–818. https://doi.org/10.1080/00288330.2004.9517280

Short FT, Davis RC, Kopp BS, Short CA, Burdick DM (2002) Site-selection model for optimal transplantation of eelgrass *Zostera marina* in the Northeastern US. Marine Ecology Progress Series 227:253–267. https://doi.org/10.3354/meps227253

Tan YM, Dalby O, Kendrick GA, Statton J, Sinclair EA, Fraser MW, et al. (2020) Seagrass restoration is possible: insights and lessons from Australia and New Zealand. Frontiers in Marine Science 7:617. https://doi.org/10.3389/fmars.2020.00617

Teresa A, Richard CZ, Donald GK, Randall SA (1999) Resource allocation and sucrose mobilization in light-limited eelgrass *Zostera marina*. Marine Ecology Progress Series 187:121–131. https://doi.org/10.3354/meps187121

Tomkins K, McLachlan G, Coleman R (2014) Quantification of coastal bank erosion rates in Western Port. CSIRO water for a healthy country flagship. CSIRO, Australia

Valdez SR, Zhang YS, van der Heide T, Vanderklift MA, Tarquinio F, Orth RJ, Silliman BR (2020) Positive ecological interactions and the success of seagrass restoration. Frontiers in Marine Science 7:91. https://doi.org/10.3389/fmars.2020.00091

van der Heide T, van Nes EH, Geerling GW, Smolders AJP, Bouma TJ, van Katwijk MM (2007) Positive feedbacks in seagrass ecosystems: implications for success in conservation and restoration. Ecosystems 10:1311–1322. https://doi.org/10.1007/s10021-007-9099-7

van Katwijk MM, Bos AR, de Jonge VN, Hanssen LSAM, Hermus DCR, de Jong DJ (2009) Guidelines for seagrass restoration: importance of habitat selection and donor population, spreading of risks, and ecosystem engineering effects. Marine Pollution Bulletin 58:179–188. https://doi.org/10.1016/j.marpolbul.2008.09.028

Wallbrink P, Hancock G, Olley J, Hughes A, Prosser I, Hunt D, Rooney G, Coleman R, Stevenson J (2003) The Western port sediment study. CSIRO Consultancy report

Waycott M, Duarte CM, Carruthers TJ, Orth RJ, Dennison WC, Olyarnik S, et al. (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proceedings of the National Academy of Sciences of the United States of America 106:12377–12381. https://doi.org/10.1073/pnas.0905620106

Wilkinson S, Anstee J, Joehnk K, Karim F, Lorenz Z, Glover M, Coleman R (2016) Western Port sediment supply, seagrass interactions and remote sensing. CSIRO, Australia

Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society: Series B (Statistical Methodology) 73:3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x

Wood SN (2017) Generalized additive models: an introduction with R. 2nd ed. CRC Press LLC, Philadelphia, PA. https://doi.org/10.1201/9781315370279

York PH, Gruber RK, Hill R, Ralph PJ, Booth DJ, Macreadie PI (2013) Physiological and morphological responses of the temperate seagrass *Zostera muelleri* to multiple stressors: investigating the interactive effects of light and temperature. PLoS One 8:e76377. https://doi.org/10.1371/journal.pone.0076377

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

Supporting Information

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

Table S1. Results of Kruskal–Wallis tests and post hoc pairwise Tukey test to identify the influence of sampling location on environmental variables.

Figure S1. Rose plots of benthic current speeds identified during 2019 (bottom) and 2020 (top) sampling periods.

Table S2. Results of Kruskal–Wallis tests and post hoc pairwise Tukey test to identify the influence of sampling location on seagrass variables.

Guest Coordinating Editor: Pawel Waryszak

Received: 29 June, 2022; First decision: 14 September, 2022; Revised: 1 October, 2023; Accepted: 2 October, 2023