Role of seagrass physical structure in macrofaunal biodiversity–ecosystem functioning relationships

T. J. Colvin[1,*], P. V. R. Snelgrove[1,2]

[1]Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador A1C 5S7, Canada
[2]Department of Ocean Sciences, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador A1C 5S7, Canada

ABSTRACT: Seagrass above-ground shoot canopies and below-ground rhizome networks provide structurally complex habitat that supports diverse macrofaunal communities. Seagrasses also support biodiversity through their biological activity by influencing food availability. While numerous studies have demonstrated that seagrass physical and biological habitat elements influence macrofaunal diversity and community structure, we lack an understanding of how these elements potentially interact with sedimentary macrofaunal communities to influence ecosystem processes. To understand how physical seagrass structure affects macrofaunal biodiversity and the processes of carbon and nutrient cycling, we deployed artificial seagrass patches that mimicked canopies and surface rhizomes, in tandem with parallel observations of natural seagrass *Zostera marina*, unvegetated habitat, seagrass patch edge, and canopy control treatments. After 3 mo, we recorded rates of oxygen and nutrient flux from sediment cores and assessed macrofaunal biodiversity and environmental variables to relate them to benthic flux patterns. We found significantly higher macrofaunal abundance and diversity in natural seagrass treatments compared to unvegetated, patch edge, canopy control, and artificial seagrass treatments. However, we found no difference in benthic fluxes across all treatments, suggesting a lesser role for macrofaunal bioturbation in nutrient regeneration in these nearshore sediments. Our results also suggest lesser importance for the structural benefits of seagrasses than their biological contributions for supporting macrofaunal biodiversity. Negative edge effects on macrofaunal abundance and diversity suggest potential consequences for macrofaunal communities of fragmented seagrass habitats associated with anthropogenic disturbance.

KEY WORDS: Biodiversity—ecosystem functioning · Eelgrass · Infauna · Habitat structure · Artificial seagrass

1. INTRODUCTION

Researchers have long recognized the essential role of physical habitat structure in assembling ecological communities and supporting diverse ecosystems (MacArthur & MacArthur 1961, Kovalenko et al. 2012). High structural heterogeneity (the number of different structural components) and complexity (the amount of a given structural component) can promote biodiversity by providing increased niche space and greater habitable surface area (Heck & Wetstone 1977, McCoy & Bell 1991, Attrill et al. 2000). However, biogenic habitats formed by living organisms interact with the environment through their physical structure and their biological activity (Edgar 1999).

Seagrasses form highly productive biogenic habitats that support abundant and diverse ecological communities, often attributed to the structural complexity they provide to otherwise bare sediments (Orth et al. 1984). Seagrasses often grow into dense, above-ground canopies that form critical habitat for many fish (Laurel et al. 2003, Murphy et al. 2021) and epifaunal macroinvertebrate (Heck & Orth 1980) species, with abundances often varying with shoot density (Reiss et al. 2019) and above-ground biomass (Heck & Wetstone 1977). Seagrass canopies also modify the

sedimentary environment; consequently, infaunal abundance and diversity also often vary with above-ground complexity (Homziak et al. 1982). Seagrass canopies attenuate waves and currents (Fonseca et al. 1982, Marin-Diaz et al. 2020), and the decreased water flow increases sedimentation of drifting organic matter (Fonseca & Fisher 1986) and dispersing pelagic larvae (Eckman 1983), while simultaneously decreasing particle resuspension (Kennedy et al. 2010) and stabilizing the sediment (Orth 1977).

Seagrasses grow from dense rhizome networks that form complex below-ground habitats and protect infauna from surface predators (Reise 1978, Blundon & Kennedy 1982, Orth et al. 1984). Their tight network of rhizomes can inhibit large burrowers and bioturbators (Brenchley 1982, Githaiga et al. 2019), often favouring small-bodied infaunal communities. Seagrasses also affect the environment through their biological activity, primarily by affecting food availability. Seagrass shoots influence epiphytic algal biomass and community structure (Pinckney & Micheli 1998, Trevizan Segovia et al. 2021), which provide an important food source for macrofauna (Bologna & Heck 1999). Direct inputs of decaying shoot and rhizome material, along with root oxygen and nutrient exudates (Marbà et al. 2007), support diverse sedimentary microbial communities that deposit feeders utilize for food (Levinton 1979, Tarquinio et al. 2019).

Through these physical and biological attributes, seagrasses also greatly influence the ecosystem processes of carbon and nutrient cycling. Highly productive seagrass beds input organic matter in the form of seagrass detritus, epiphytic algae, and accumulated suspended organic matter that all promote microbial carbon mineralization (Mateo et al. 2007). These beds act as carbon sinks (Duarte & Chiscano 1999, Fourqurean et al. 2012) with significant carbon sequestration capacity (Duarte et al. 2010, Fourqurean et al. 2012, Röhr et al. 2018), following export of much of their fixed carbon or burial in anoxic sediments (Duarte & Krause-Jensen 2017). Increased organic matter sedimentation and rhizome oxygen and nutrient exudates also promote microbial decomposition and nutrient regeneration (Marbà et al. 2007), whereas the unique microbial communities harboured in the seagrass rhizosphere influence nitrogen cycling through nitrogen fixation, nitrification, and denitrification processes (McGlathery et al. 1998, Risgaard-Petersen et al. 1998, Welsh 2000).

Alongside the influence of seagrasses on ecosystem functioning, the diverse macrofaunal communities they support closely link with carbon and nutrient cycling (Snelgrove 1997, Biles et al. 2002, Stief 2013).

Infaunal movement and feeding behaviours in the sedimentary matrix alter redox states and organic matter distributions through bioturbation and bioirrigation (Aller 1994, Lohrer et al. 2004), promoting microbial decomposition and nutrient regeneration (Aller & Aller 1998, Welsh 2000, Glud 2008). Furthermore, these processes closely tie to macrofaunal community structure and species-specific functional characteristics (Snelgrove 1997, Ieno et al. 2006). Consequently, studies increasingly address relationships between macrofaunal diversity and ecosystem functioning processes (Snelgrove et al. 2014), with functional diversity metrics often explaining greater variation in functioning than traditional taxonomic diversity (Emmerson & Raffaelli 2000, Waldbusser et al. 2004, Danovaro et al. 2008).

The current global decline in seagrass habitat increases the relevance of understanding relationships between seagrasses and ecosystem functioning (Orth et al. 2006, Waycott et al. 2009, Unsworth et al. 2019). Seagrasses are particularly vulnerable to anthropogenic disturbances because their habitat requirements restrict them to shallow coastal waters; threats include sediment loading, eutrophication, shoreline development, invasive species, and rising ocean temperatures (Orth et al. 2006). These disturbances can fragment seagrass beds, which drastically affects seagrass bed structure by increasing relative proportions of edge habitat (Yarnall et al. 2022). Reduced structural complexity, seagrass biomass, and shoot densities characterize seagrass patch edges compared to patch interiors (Moore & Hovel 2010). The loss and fragmentation of seagrass beds emphasize the need to understand how seagrass habitat interacts with macrofaunal biodiversity in regulating ecosystem functioning processes.

In this study, we investigate the role of seagrass physical structure in supporting macrofaunal biodiversity and the relationships among seagrasses, macrofauna, and ecosystem functioning. To determine the contribution of the physical habitat provided by seagrasses to macrofaunal biodiversity and carbon and nutrient cycling, we deployed artificial seagrass units (ASUs) for 3 mo to replicate the structural benefits provided by seagrass beds to unvegetated sediments. We then examined associated macrofaunal diversity and community structure and measured oxygen and nutrient fluxes across the sediment–water interface to assess carbon and nutrient cycling rates. We compared our ASU macrofaunal communities and benthic fluxes to natural seagrass (eelgrass *Zostera marina*), unvegetated, and ASU treatments lacking a canopy to isolate the structural contrib-

utions from the biological contributions of seagrasses to biodiversity and ecosystem functioning. We also examined seagrass patch edge sediments to assess potential edge effects on macrofaunal biodiversity and benthic flux. We hypothesized that our ASU treatments would support higher macrofaunal biodiversity and abundance than unvegetated sediments, resulting in higher carbon and nutrient fluxes. Furthermore, we hypothesized that the greater the importance of seagrass physical structure for macrofauna, the closer our ASU macrofaunal communities would resemble those from natural seagrass. We also hypothesized that seagrass patch edges would support reduced macrofaunal diversity and abundance compared to natural seagrass treatments but at higher values than those in unvegetated sediments. Our study builds on previous seagrass colonization studies by combining macroinfaunal quantification with benthic flux measurements to relate physical seagrass structure to biodiversity and ecosystem functioning.

2. MATERIALS AND METHODS

2.1. Study design and sampling

We conducted our study in Newman Sound, Newfoundland, Canada (Fig. 1), at 2 sites with clear boundaries between seagrass patches and unvegetated sediments: Buckley's Cove and Salton's Bay. At these sites, seagrass grows in discrete patches sur-
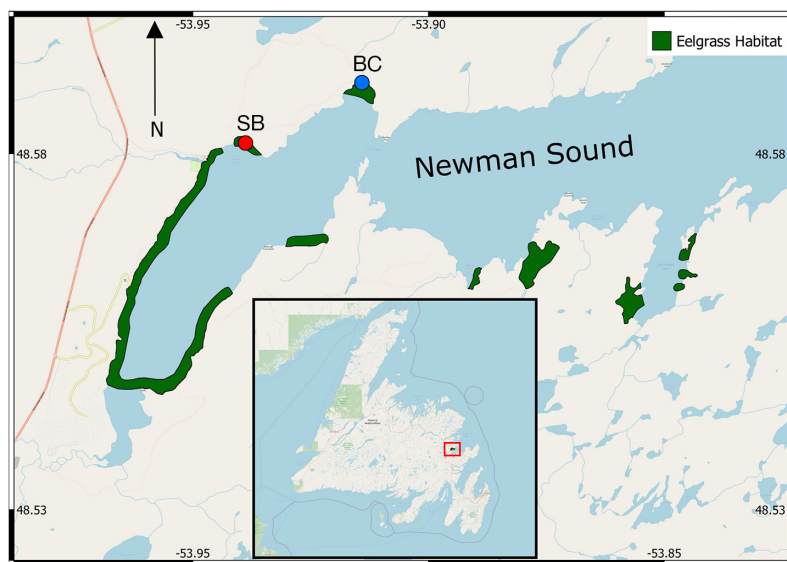

Fig. 1. Sites (SB: Salton's Bay; BC: Buckley's Cove) and eelgrass presence within Newman Sound. Inset shows the location of Newman Sound on the island of Newfoundland. Eelgrass range adapted from Warren et al. (2010)

rounded by barren sand. We collected sediment push cores (diameter: 6.7 cm; length: 35.6 cm) at each site by hand from water depths of ~1 m from patch interior natural seagrass habitat, adjacent unvegetated habitat, and seagrass 'edge habitat' taken from the seagrass patch but within 0.5 m of the seagrass boundary, characterized by lower shoot densities than the interior. We also collected sediment cores from ASUs described in detail below (1 m^2 quadrats with attached plastic blades to emulate seagrasses) as well as canopy control plots (similar quadrats but with the emergent blades removed); we deployed both experimental treatments on unvegetated sediments. Natural treatments, ASUs, and canopy control plots were set up on 4—12 August 2020 and left anchored to the sediment until sampling on 28 October—3 November 2020. At each site, we collected 6 replicate cores of each treatment for incubation and an additional core from each treatment to analyze sedimentary environmental variables. Cores contained 10—15 cm of sediment and 15—20 cm of overlying water.

2.2. Artificial seagrass units

We created ASUs to assess the physical contributions of seagrass habitat for structuring macrofaunal communities. We attached plastic chicken wire (0.25 inch; ~6 mm) to square 1 m^2 PVC pipe frames and tied on strips of green plastic ribbon (75 cm long) to mimic natural eelgrass densities found in Newman Sound (600 shoots m^{-2}; Laurel et al. 2003). We constructed canopy control treatments using chicken wire and PVC frames without ribbon. We cut round holes into the chicken wire of both treatments and covered them with wire trapdoors to create a continuous layer of wire and ribbon canopy that we could open to take the sediment cores during sampling. We deployed bare 1 m^2 PVC frames for each natural treatment (seagrass, unvegetated, seagrass patch edge) and anchored all treatment frames to the sediment using rebar hooks (30 cm long). When anchored flat to the sediment, the chicken wire protected infauna from surface predators much like seagrass rhizomes (Orth 1977), whereas the simulated canopy helped to buffer water flow (Fonseca et al. 1982) and thus potentially collect drift-

ing organic matter (Fonseca & Fisher 1986) and suspended larvae (Eckman 1983).

2.3. Incubations

We lost 1 ASU and 1 unvegetated replicate from Buckley's Cove to a fall storm. Following collection, we acclimated the sediment cores for 12–18 h to allow suspended sediment to settle, while gently aerating the water using aquarium pumps to avoid anoxic conditions prior to incubation. We then incubated the cores for 24 h at *in situ* temperatures and in complete darkness within refrigerators, fully sealing the cores using caps with airtight water sampling ports and magnetic stir bars. To assess nutrient fluxes, we collected 2 water samples of 50 ml from each core at the beginning, midpoint (12 h), and end of each incubation (24 h), replacing samples with the equivalent volume of water taken directly from each site. Water samples were frozen at −20°C before analysis of ammonium (NH_4^+), nitrate (NO_3^-), phosphate, and silicate ($Si(OH)_4$) concentrations using a Seal Analytical AAIII Segmented Flow Analyzer. We measured oxygen concentrations every 4 h using a PreSens Fibox 4 optical oxygen meter with oxygen optode patches attached to the inside of each core. We determined nutrient and oxygen fluxes from linear regressions of their concentrations over time, correcting for the concentrations in the replacement water following nutrient sampling. We refer to both oxygen and nutrient fluxes as benthic fluxes.

2.4. Macrofaunal identification and diversity indices

Following the incubations, we sectioned the sediment cores into 0–2, 2–5, and 5–10 cm depth layers and fixed each section in 10% buffered formalin. We then processed the sections over a 300 µm sieve and transferred sieved samples to 70% ethanol for storage and identification. We identified all macrofauna under a dissecting scope to the lowest taxonomic level possible and used the 'vegan' package v. 2.6-6.1 within R (R Core Team 2021) to calculate diversity indices, including species richness, Simpson's diversity index, Shannon diversity index, and Pielou's evenness. To examine functional trait diversity, we assigned different biological traits to each species using fuzzy coding; i.e. assigning values between 0 and 1 based on the tendency for the organism to express each particular trait level (Table 1), utilizing trait data from the literature

Table 1. Biological traits and their levels used to calculate functional diversity indices. Reworking modes and movements from Queirós et al. (2013)

Biological trait	Level
Feeding mode	Carnivore
	Detritus feeder
	Suspension feeder
	Funnel feeder
	Grazer
	Omnivore
	Parasite
	Scavenger
	Surface deposit feeder
	Sub-surface deposit feeder
Reworking mode	None/epifauna
	Surficial modifier
	Up/down conveyor
	Biodiffusor
Movement	None/fixed
	Limited movement
	Slow movement through sediment
	Free movement in burrows
Habitat	Infauna
	Epifauna
	Pelagic
Adult size	Small (<1 cm)
	Medium (1–5 cm)
	Large (>5 cm)

(Naylor & Haahtela 1966, Pavia et al. 1999, MarLIN 2006, Macdonald et al. 2010, Queirós et al. 2013, Jumars et al. 2015, Degen & Faulwetter 2019, Antczak-Orlewska et al. 2021). We then calculated functional diversity indices using the 'FD' package v. 1.0-12.3 in R (R Core Team 2021). These indices include functional richness, functional evenness, functional divergence, functional dispersion, Rao's quadratic entropy (Villéger et al. 2008, Laliberté & Legendre 2010), and the community-weighted mean values for each trait level (Lavorel et al. 2008). Two canopy control replicates that contained fewer than 3 species precluded calculation of functional richness, evenness, and divergence.

2.5. Environmental variables

To investigate how natural seagrass and our ASUs modified the sedimentary environment, we measured several environmental variables from the extra core taken from each treatment. We initially homogenized the core's 0–2 cm layer and took sub-samples for separate analysis of grain size, carbon and nitrogen content, and phytopigment ratios. We used overall mean grain size (phi), mean of the sortable silt fraction (phi), and percentages of gravel, sand, and mud frac-

tions (%) to assess the effects of seagrass habitat structure on physical sedimentary dynamics. We treated grain size samples with 35% hydrogen peroxide to break down organic material and freeze-dried them prior to analysis. We sieved and weighed the gravel fraction (>2 mm) at ¼ phi intervals to determine the % gravel. We analyzed the remaining sediment (<2 mm) using a Beckman Coulter LS13-320 laser diffraction analyzer to determine the % sand (2 mm−62.5 µm) and mud (<62.5 µm). We then determined the overall mean grain size using all size fractions and calculated the mean sortable silt size (>10 to <62.5 µm).

Total organic carbon (TOC; mg g^{-1}) and total nitrogen (TN; mg g^{-1}) allowed us to assess long-term organic matter freshness and accumulation, whereas chlorophyll a (chl a) concentrations (µg g^{-1}), phaeo-pigment concentrations (µg g^{-1}), and chl a:phaeopigment ratios enabled assessment of freshness over the short term. To assess TOC and TN content, we dried the sediment samples at 60°C for 24 h, followed by treatment with HCl fumes for 24 h to remove inorganic carbon. We then re-dried the samples at 60°C for 24 h, transferred a 2 mg subsample to a tin capsule, and analyzed TOC and TN using a Perkin-Elmer 2400 Series II CHN analyzer. We could not calculate carbon:nitrogen ratios because some TN values fell below our equipment's detection limits. Sediment phytopigment concentrations were determined via a spectrophotometric assay (Danovaro 2009). We added 90% acetone to sediment sub-samples and kept them in darkness for 24 h at 4°C to extract the pigments. We then centrifuged the samples (800 × g, 10 min) and measured the supernatant absorbance to determine chl a concentrations followed by acidification using 0.1 N HCl and reanalysis to assess phaeopigment concentrations.

2.6. Statistical analyses

We compared variation in the macrofaunal community, nutrient fluxes, and biodiversity indices among treatments and sites using three 2-way permutational multivariate analyses of variance (PERMANOVA, 9999 permutations), using the 'adonis2' function in R. Bray-Curtis distances enabled comparisons of community composition, while Euclidean distances were used for comparisons of standardized nutrient fluxes and biodiversity indices. We found similar results in our community and diversity analyses with rare species included and removed; therefore, we report the analysis with rare species removed and note any differences between the 2 analyses. Following PERM-

ANOVA, we verified the homogeneity of multivariate dispersions using the function 'betadisper' in 'vegan'. We used nonmetric multidimensional scaling (NMDS) plots to visualize multivariate differences among treatments. SIMPER analysis on untransformed species abundances determined drivers of community differences among treatments.

To determine how total macrofaunal abundance, diversity indices, and oxygen and nutrient fluxes differed among treatments and sites following demonstration of significance in PERMANOVA, we ran 2-way ANOVAs with 'treatment' and 'site' as fixed factors, noting that we collected and analyzed independent cores from each treatment and during each time period, using a type II ANOVA to handle the unbalanced data. We assessed the assumptions of normality and homogeneous variance using $Q-Q$ plots, plots of residuals, and Levene's tests. Given the indication of non-normality in the residuals, we applied a Kruskal-Wallis test to functional dispersion and functional divergence comparisons. Application of a natural logarithmic transformation to total macrofaunal abundances reduced the elevated variance at higher values.

Two separate redundancy analyses (RDAs) determined the proportion of variation in benthic fluxes explained by biodiversity indices and environmental variables along with the most parsimonious set of explanatory variables that contributed to that variation. Variance inflation factor (VIF) tests removed variables with VIF > 5, followed by a stepwise selection process using permutation tests with a significance level of p < 0.05 to determine the variables explaining the most variation. We used single-variable RDAs to determine the contributions of each variable to the overall model. Finally, a variation partitioning analysis using both sets of explanatory variables determined the relative amount of variation in benthic fluxes explained by biodiversity indices and environmental variables alone as well as the overlap in explained variation by both sets together (Legendre & Legendre 2012). We completed RDAs and variation partitioning analyses in R using functions in the 'vegan' package (R Core Team 2021).

3. RESULTS

3.1. Multivariate community comparisons

The macrofaunal community differed significantly across both treatments (Fig. 2; PERMANOVA: $F_{4,48}$ = 2.1, p < 0.01) and sites ($F_{1,48}$ = 3.5, p < 0.01), with no sig-
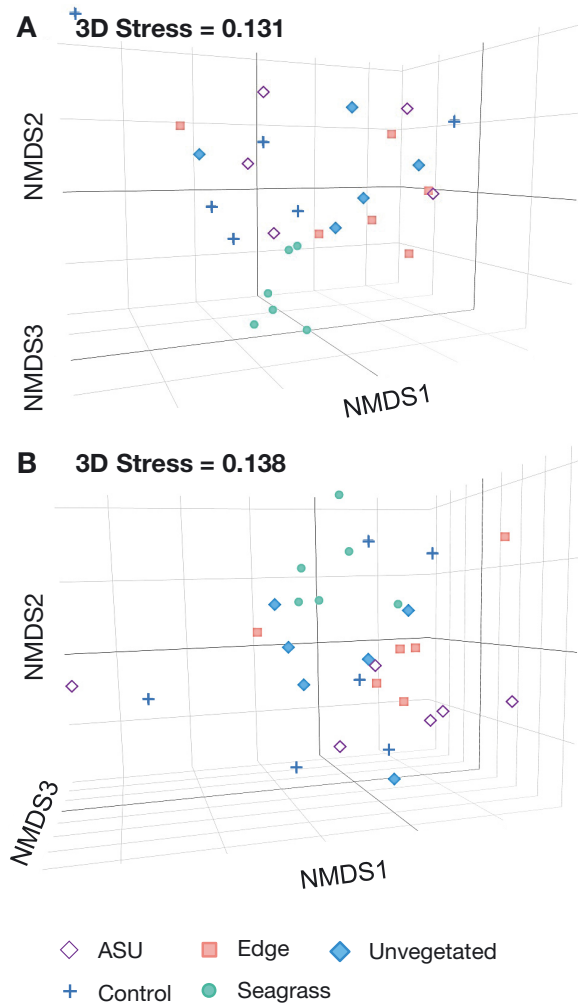
Fig. 2. Three-dimensional nonmetric multidimensional scaling (NMDS) plot of macrofaunal communities among the treatments (artificial seagrass unit [ASU], control, edge, seagrass, unvegetated), based on Bray-Curtis dissimilarities. (A) Buckley's Cove, (B) Salton's Bay

and unvegetated sediments (overall dissimilarity: 60%), in contrast to the most dissimilar communities in control and eelgrass sediments (overall dissimilarity: 83%). Similarly, SIMPER on Bray-Curtis dissimilarities at Salton's Bay identified *Microphthalmus* sp. and *P. elegans* as the dominant contributors to treatment community differences (19.4–58.8% contribution). Edge and eelgrass sediments were the least dissimilar (45.9%), whereas ASU and control treatments were the most dissimilar (78.5%).

3.2. Multivariate patterns in biodiversity and benthic fluxes

Multivariate standardized biodiversity indices differed significantly across both treatments (Fig. 3A; PERMANOVA: $F_{4,46} = 1.9$, $p < 0.01$) and sites ($F_{1,46} = 3.9$, $p < 0.01$) with no significant interaction ($F_{4,46} = 1.1$, $p = 0.28$), noting homogeneous multivariate dispersions across both factors. We also found no significant differences in multivariate benthic fluxes across either treatment or site when analyzed together, although we note significant differences in multivariate dispersions between sites (Fig. 3B; $F_{1,55} = 6.91$, $p < 0.05$).

3.3. Univariate infaunal abundance and biodiversity comparisons

Macrofaunal abundances differed significantly among treatments (Fig. 4; 2-way ANOVA: $F_{4,48} = 6.2$, $p < 0.001$), but not between sites ($F_{1,48} = 3.7$, $p > 0.05$) and with no significant interaction ($F_{4,48} = 2.1$, $p > 0.05$). Tukey's tests indicated significantly higher macrofaunal abundances in seagrass treatments compared to all other treatments ($p < 0.05$).

We also observed significant differences in species and functional richness across treatments (Figs. 5A & 6A; 2-way ANOVA: species richness: $F_{4,48} = 8.9$, $p < 0.001$; functional richness: $F_{4,46} = 3.8$, $p < 0.01$) but not sites, with no significant interaction. We found higher species richness in seagrass treatments than in all other treatments and higher functional richness in seagrass treatments compared to all treatments except the canopy control treatment. We also observed significant differences in Simpson's diversity, Shannon diversity, Pielou's evenness, functional dispersion, and functional divergence between sites (2-way ANOVA: Simpson's diversity: $F_{1,48} = 8.4$, $p < 0.01$; Shannon diversity: $F_{1,48} = 4.9$, $p < 0.05$; Pielou's evenness: $F_{1,48} = 9.4$, $p < 0.01$; Kruskal-Wallis: functional

nificant interaction between the two ($F_{4,48} = 1.3$, $p = 0.13$). However, multivariate dispersions differed significantly among treatments (permutation test: $F_{4,53} = 5.4$, $p < 0.01$). Noting the sensitivity of PERMANOVA to unbalanced datasets (Anderson & Walsh 2013), we interpreted the treatment differences with caution.

SIMPER analysis on Bray-Curtis dissimilarities at Buckley's Cove identified the abundant polychaetes *Microphthalmus* sp. and *Pygospio elegans* as primary drivers of differences among all treatments, accounting for 21–48% of the differences. Other significant contributors included *Mytilus edulis*, *Monocorophium* sp., Bivalvia indet. 1, and *Spiophanes bombyx*. Examining overall dissimilarity, we observed the least dissimilar communities when comparing edge
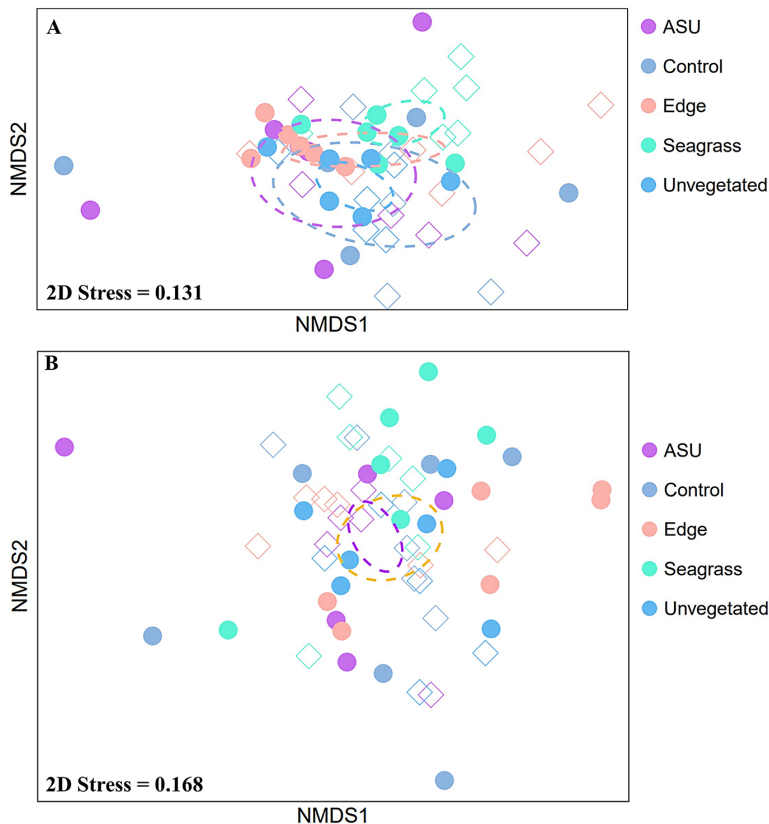
Fig. 3. Nonmetric multidimensional scaling (NMDS) plots of (A) multivariate biodiversity metrics and (B) multivariate benthic fluxes among treatments (artificial seagrass unit [ASU], control, edge, seagrass, unvegetated) and between sites (Buckley's Cove [diamonds], Salton's Bay [circles]), based on Euclidean distances between standardized variables. Dashed ellipses show (A) treatment 95% confidence intervals and (B) site 95% confidence intervals (Buckley's Cove [purple ellipse], Salton's Bay [yellow ellipse])
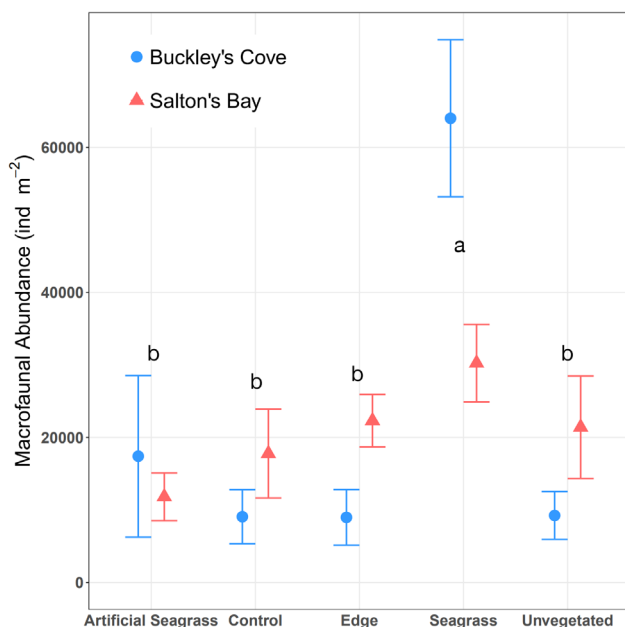
dispersion: $\chi^2_1 = 8.1$, $p < 0.01$; functional divergence: $\chi^2_1 = 5.1$, $p < 0.05$) with higher diversity in Buckley's Cove, and no significant differences among treatments and no interaction (Figs. 5 & 6). Rao's Q also differed significantly across both treatments (Fig. 6E; $F_{4,48} = 2.7$, $p < 0.05$) and sites ($F_{1,48} = 10.9$, $p < 0.01$) with no significant interaction, with Tukey's tests discerning higher Rao's Q in seagrass than ASU treatments and in Buckley's Cove compared to Salton's Bay.

3.4. Variation in multivariate benthic flux explained by biodiversity and environmental factors

Following the removal of colinear variables or those with VIF > 5, the biodiversity RDA model explained 8.6% of the variation (adjusted $R^2 = 0.086$) and included species richness, Pielou's evenness, functional richness, functional evenness, functional divergence, and community weighted means of carnivores, detritus feeders, funnel feeders, grazers, omnivores, sub-surface deposit feeders, up/down conveyors, limited movement, and medium-sized organisms (1—5 cm). Following stepwise selection, the final model chosen explained 12.6% of the variation (adjusted $R^2 = 0.126$) and included functional divergence, species richness, and community-weighted mean of detritus feeders. The first RDA axis explained 7.9% of the variation in benthic flux and was associated with high species richness, detritus feeders, and oxygen consumption. The second axis explained 7.5% of the variation and was associated with functional divergence and NH_4^+ and $Si(OH)_4$ flux (Fig. 7). When we included rare species in the analysis, functional richness became the best explanatory variable. The initial RDA model using environmental variables explained just 3.5% of the variation (adjusted $R^2 = 0.035$) and included mean grain size, % mud, total carbon, and chl a concentration.
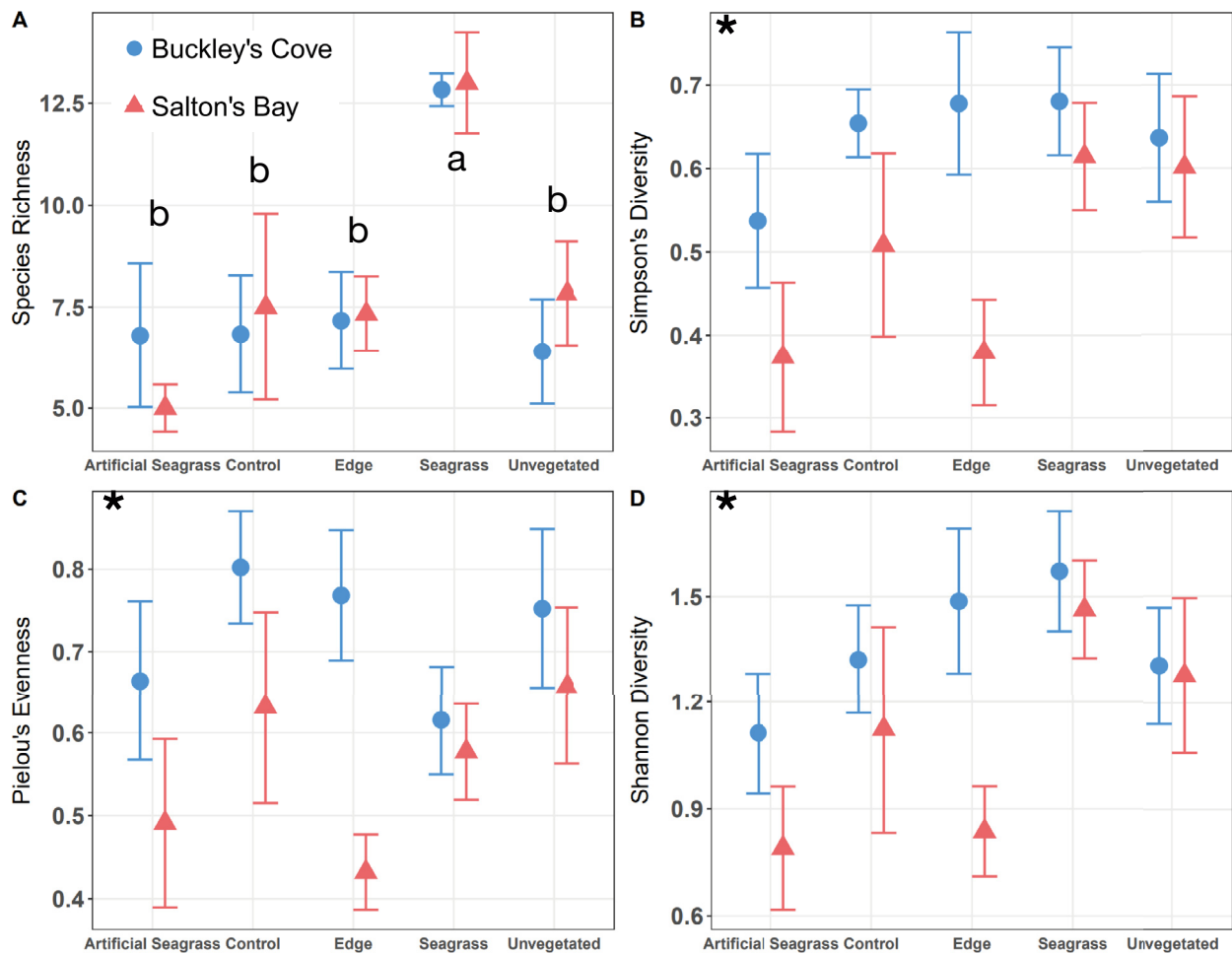

Fig. 4. Mean (±SE) abundances of macrofauna (densities were calculated from sediment cores 0.0035 m^{-2} in area) across treatments between Buckley's Cove and Salton's Bay. Letters denote significant differences between treatments (Tukey's test, $p < 0.05$)

Fig. 5. Mean (±SE) taxonomic diversity indices across treatments between Buckley's Cove and Salton's Bay, showing (A) species richness, (B) Simpson's diversity, (C) Pielou's evenness, and (D) Shannon diversity. Letters denote significant differences between treatments; asterisk denotes significant site differences between Buckley's Cove and Salton's Bay (Tukey's test, p < 0.05)

Following the stepwise selection of variables, the final model included mean grain size, explained just 3.8% of the variation (adjusted R^2 = 0.038), and the single RDA axis was associated with NH_4^+, NO_3^-, and $Si(OH)_4$ flux.

3.5. Variation partitioning

Variation partitioning analysis of benthic fluxes across biodiversity indices and environmental variables indicated that both sets of explanatory variables together explained 13.4% of the variation (adjusted R^2 = 0.134). Biodiversity indices alone explained 9% of that variation, whereas environmental variables alone accounted for just 1% of the explained variation, with 3% explained by both sets of variables. Our

analyses left 87% of the variation in benthic fluxes unexplained.

4. DISCUSSION

By comparing macrofaunal communities across a seagrass patch boundary, we observed significantly lower macrofaunal abundance and diversity in seagrass patch edges and unvegetated sediments than in seagrass patch interiors, supporting studies that associate seagrass density and complexity with macrofaunal biodiversity (Heck & Wetstone 1977, Webster et al. 1998, Rodil et al. 2021). We then used ASUs to assess the contribution of above-ground seagrass structure in supporting macrofaunal communities and observed similar macrofaunal abundance and
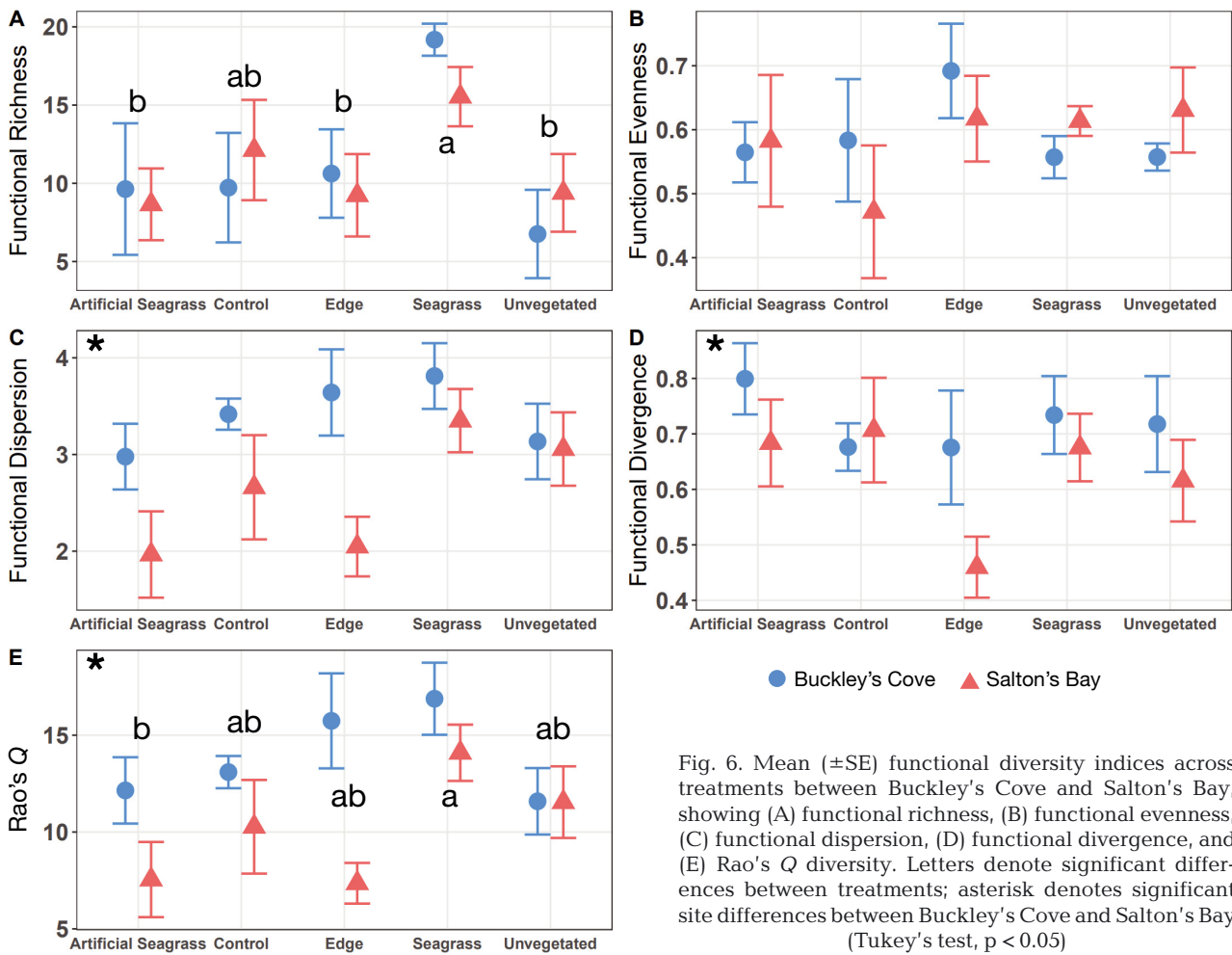
Fig. 6. Mean (±SE) functional diversity indices across treatments between Buckley's Cove and Salton's Bay, showing (A) functional richness, (B) functional evenness, (C) functional dispersion, (D) functional divergence, and (E) Rao's *Q* diversity. Letters denote significant differences between treatments; asterisk denotes significant site differences between Buckley's Cove and Salton's Bay (Tukey's test, p < 0.05)
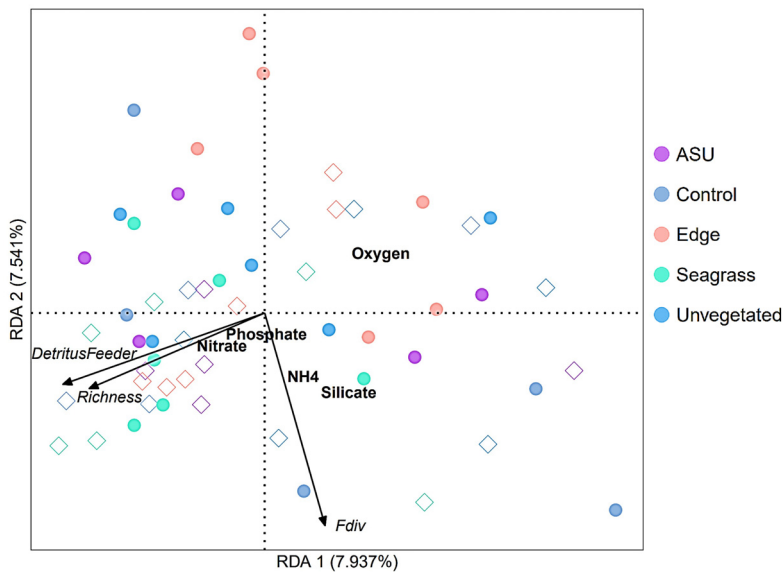

Fig. 7. Redundancy analysis (RDA) of multivariate benthic fluxes as a function of biodiversity, among treatments (artificial seagrass unit [ASU], control, edge, seagrass, unvegetated) and between sites (Buckley's Cove [diamonds], Salton's Bay [circles]). Oxygen and nutrient locations represent associations with higher rates of flux. Vectors represent direction and influence of explanatory biodiversity variables. Richness: species richness; FDiv: functional divergence; DetritusFeeder: community-weighted means of detritus feeders. Some variable names have been offset slightly for clarity of presentation

diversity in ASU treatments and unvegetated treatments, potentially highlighting the importance of below-ground complexity and biological contributions of natural seagrasses we did not replicate. Similar nutrient fluxes across all treatments supported our previous conclusion (Colvin & Snelgrove 2023) that macrofaunal bioturbation might impact ecosystem functioning less in nearshore sandy sediments than in other systems (Santos et al. 2012, Braeckman et al. 2014, Huettel et al. 2014).

4.1. Macrofaunal diversity at patch edges

Seagrass patch interiors had higher macrofaunal abundances and species and functional richness than patch edges and unvegetated sediments, which were similar. Other studies examining seagrass edge effects have yielded conflicting results (Colomer & Serra 2021), with some finding similar macrofaunal densities and species richness between interior and edge habitats (Boström et al. 2006, Lohrer et al. 2016) and many others reporting higher densities of epifauna and infauna closer to patch edges (Bologna & Heck 2002, Tanner 2005, Yarnall et al. 2022) or patch interiors (Vonk et al. 2010, Matias et al. 2013). Positive macrofaunal edge effects may result from the hydrodynamic characteristics of edges, where seagrass canopies reduce current velocities (Fonseca et al. 1982), potentially accumulating suspended pelagic larvae at patch edges (Bologna & Heck 2002). Mobile macrofauna traversing unvegetated sediments may also accumulate in edges as they seek refuge between patches (Bologna & Heck 2002). In contrast, our results align with studies finding strong positive relationships between macrofaunal abundance and diversity with seagrass habitat density and complexity (Heck & Wetstone 1977, Webster et al. 1998, Rodil et al. 2021). Numerous studies have reported higher diversity and macrofaunal abundance in seagrass beds compared to unvegetated habitats (Orth 1977, Heck & Orth 1980, Boström & Bonsdorff 1997) and declining abundances with lower seagrass densities (Heck & Wetstone 1977, Webster et al. 1998). Our results align with these observations because lower seagrass densities in the transition between dense seagrass and unvegetated sediments characterized our edge treatments. The negative edge effects we observed suggest that increased edge area through seagrass bed fragmentation may negatively impact macrofaunal density and biodiversity, contrasting previous research (Yarnall et al. 2022).

The NMDS plot of the communities at the unbalanced Buckley's Cove site separated seagrass from the other treatments, and the significant difference in abundance and richness in the seagrass treatments at Buckley's Cove suggests different communities. High abundances of deposit-feeding polychaetes, juvenile *Mytilus edulis*, and suspension-feeding amphipods characterized interior seagrass treatments; these communities closely resembled the seagrass communities described in a parallel study (Colvin & Snelgrove 2023), which we attributed to fresh organic matter inputs (Boon & Duineveld 1996) and seagrass canopy hydrodynamics (Eckman 1983). In this study, fresh organic matter inputs represented by finer sediments and higher chl *a*:phaeopigment ratios were observed in seagrass treatments only at Salton's Bay (Table A1 in the Appendix). We did not observe high abundances of suspension feeders in Buckley's Cove and Salton's Bay unvegetated communities, as reported in Colvin & Snelgrove (2023). Instead, species present in unvegetated, patch edge, ASU, and canopy-control communities were similar to those in seagrass communities, albeit in different relative abundances.

4.2. Macrofaunal diversity in artificial seagrass

Macrofaunal abundances and species and functional richness in our ASU, unvegetated, and edge treatments were significantly lower than in natural seagrass. The majority of macrofaunal studies using ASUs focus on the role of the canopy in supporting epifauna (Lee et al. 2001, Arponen & Boström 2012, Gartner et al. 2013); fewer studies have used ASUs to examine the roles of seagrass structure on infaunal communities (Eckman 1983, Edgar 1999, Eggleston et al. 1999). Studies that solely replicate the seagrass canopy have generally attributed positive relationships between infaunal abundance and canopy structure to increased larval settlement (Eckman 1983) and protection from disturbance events (Boström & Bonsdorff 2000). Those studies that manipulate the below-ground component have attributed positive relationships between below-ground complexity and infaunal abundance to sediment stabilization and protection from surface predators (González-Ortiz et al. 2016).

Our results using ASUs suggest that we cannot attribute higher abundance and diversity in dense seagrass habitat compared to sparse edge habitat to the hydrodynamic benefits of the canopy. Our ASU canopies were intended to replicate the tendency of natural seagrasses to collect suspended pelagic larvae (Eckman 1983, 1987) and drifting organic matter

utilized by infauna for food (Orth 1977, Fonseca & Fisher 1986). Despite research emphasizing the roles of the seagrass canopy in supporting infaunal communities (Orth et al. 1984), other studies have given little importance to seagrass above-ground structure for infauna. Boström et al. (2006) observed similar macrofaunal abundance and diversity between seagrass patch interiors and edges lacking above-ground structure, in contrast with our results on seagrass edge effects but supporting our conclusion on the relative unimportance of the canopy in supporting macrofaunal biodiversity.

Our deployment from mid-August to early November potentially minimized any effect of ASU canopies on macrofaunal diversity by missing summer reproductive events, noting larval dispersal often plays an essential role in infaunal colonization of seagrass beds (Smith & Brumsickle 1989). Whereas larval settlement following a spring or early summer deployment may have yielded different results, the COVID-19 pandemic forced us into an August deployment, changing the focus from a spring—summer larval-focused study to one addressing fall response dominated by post-larval stages. Additionally, installation of the ASUs may have disturbed the sediments and affected macrofaunal diversity. However, Colvin & Snelgrove (2023) demonstrated the role of post-larval migration in recently disturbed seagrass patches over the same timeframe, suggesting that 3 mo represents a sufficient time interval for macrofauna in adjacent habitats to migrate to our ASUs following a disturbance, provided they offer appropriate habitat. Given that we did not see any significant post-larval migration to our ASUs with replicated above-ground structures, we suggest that the below-ground habitat and biological inputs provided by seagrasses may play a more significant role in structuring infaunal communities at our study locations than the benefits provided by the canopy. Future studies capturing spring and summer reproductive events would likely yield different results; larvae dispersing from adjacent seagrass beds may colonize the ASUs. However, the COVID-19 pandemic lockdown precluded this timing option for our study. Additionally, extending the experiment beyond November would increase the likelihood of loss of treatments because of approaching winter weather and frequent storms.

Previous studies have reported higher infaunal abundances and richness with denser below-ground seagrass habitat (Orth et al. 1984), independent of above-ground density (González-Ortiz et al. 2016); previous researchers have attributed this difference to the protection from surface and burrowing predators that rhizomes provide (Orth 1977, Reise 1978, Goshima & Peterson 2012). However, we suggest that direct predation by surface predators may not primarily drive these patterns, given that the dense plastic mesh in our ASU and canopy control treatments emulated the protection from predators provided by seagrass rhizomes (Orth et al. 1984, Reynolds et al. 2018). Rather, higher macrofaunal abundances in seagrass habitats may result from habitat selection by motile fauna for complex below-ground habitat, an attribute our design did not emulate. In studying seagrass epifauna, Bell & Westoby (1986) demonstrated habitat selection for dense above-ground seagrass habitat, even when excluding predators. A similar process may operate here, where infauna choose protective habitat based on below-ground complexity, regardless of the presence of actual predation.

Biological modification of the environment by natural seagrasses may also explain the low macrofaunal abundance and diversity in our ASU treatments. Although macrofauna rarely feed on seagrass detritus directly, they consume the abundant epiphytic algae that grow on shoots (Pinckney & Micheli 1998, Bologna & Heck 1999, Trevizan Segovia et al. 2021). Seagrass roots also exude oxygen and nutrients directly into the surrounding sediment (Marbà et al. 2007) and, alongside increased organic matter inputs from seagrass detritus, stimulate microbial decomposition and influence the sedimentary microbial community that deposit-feeding infauna rely upon (Levinton 1979, James et al. 2006, Tarquinio et al. 2019). Given that we attempted to replicate the primary benefits of seagrass physical structure and found no macrofaunal response, our results suggest that these biological contributions from natural seagrass may outweigh the physical structural benefits often ascribed to seagrass beds.

4.3. Benthic fluxes

The lack of difference in nutrient fluxes among treatments contrasts with studies that have shown strong influences of seagrasses on nutrient cycles (Caffrey & Kemp 1990, Jensen et al. 1995, Holmer et al. 2006) related to their role in affecting sedimentary redox states (Aller 1994), organic matter accumulation (Mateo et al. 2007, Kennedy et al. 2010), and microbial activity (Ottosen et al. 1999, Welsh 2000, Jensen et al. 2007). However, these results align with our previous observations (Colvin & Snelgrove 2023), in which we attributed nutrient flux similarities to minimal seagrass activity during incubations in total

darkness. Similarly, we attribute the absence of a link between nutrient cycling and macrofaunal abundance and diversity to a lesser role for macrofaunal bioturbation in nutrient dynamics in coarse nearshore sediments than in other marine systems; previous studies have demonstrated the importance of physical mechanisms of pore water exchange compared to bioturbation in permeable shelf sediments (Santos et al. 2012, Braeckman et al. 2014, Huettel et al. 2014).

4.4. Biodiversity indices and environmental factors influencing benthic flux variation

Noting the minimal variation in benthic flux among treatments and across sites in our study, the low explanatory power of our RDA models comes as no surprise. Functional divergence explained the most variation in benthic flux resulting from significantly lower functional divergence and significantly higher NH_4^+ influx at Salton's Bay. The inclusion of rare species in the analysis elevated functional richness to the best explanatory variable; these findings align with previous studies that have reported a greater influence of functional diversity on benthic processes than taxonomic diversity (Ieno et al. 2006, Danovaro et al. 2008). Species richness and community-weighted means of deposit feeders explained similar amounts of benthic flux variation and were associated with high oxygen consumption. We attribute these patterns to higher species richness and deposit-feeder abundances in seagrass treatments, in which higher oxygen consumption occurs, often a result of seagrass respiration (Duarte et al. 2010). The higher contribution of biodiversity indices than environmental variables to benthic fluxes through variation partitioning contrasts with Colvin & Snelgrove (2023); however, these results align with previous studies that also reported greater biological than environmental contributions to benthic fluxes (Godbold & Solan 2009, Miatta & Snelgrove 2021).

4.5. Conclusions

Interior seagrass habitat supported higher macrofaunal abundance and diversity than the sparse edge and unvegetated habitat, suggesting a positive relationship between seagrass density and macrofaunal abundance and diversity (Heck & Wetstone 1977). These negative edge effects have important consequences for macrofaunal communities in fragmented seagrass beds; the increased proportion of edges in fragmented habitats may significantly negatively impact seagrass macrofaunal biodiversity. However, the results from our ASU treatments suggest that these relationships between seagrass density and macrofaunal diversity do not result from canopy hydrodynamics or protection from predators, the primary physical benefits seagrasses provide. Rather, we suggest that the biological influence of natural seagrasses on food availability and macrofaunal habitat selection for below-ground rhizome density potentially explains the positive relationship often observed between seagrass density and macrofaunal diversity. The absence of a relationship between macrofaunal diversity and nutrient cycling also suggests a lesser role for infaunal bioturbation in nutrient dynamics of nearshore seagrass ecosystems than physical sediment mixing processes. Our results illustrate the value of protecting continuous, natural seagrass beds for providing the greatest benefits for maintaining their diverse macrofaunal communities.

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Appendix.

Table A1. Environmental variables measured from extra sediment cores. MGS: mean grain size; MSS: mean sortable silt (>10 μm, <63 μm) size; TOC: total organic carbon; TN: total nitrogen. % Mud consists of % silt plus the clay fraction

Treatment	MGS (phi)	MSS (phi)	% Gravel	% Sand	% Mud	% Silt	TOC (mg g^{-1})	TN (mg g^{-1})	Chl a (μg g^{-1})	Phaeopigment (μg g^{-1})	Chl a: phaeo ratio
Buckley's Cove											
Artificial seagrass	2.123	4.789	0	98.8	1.2	0.9	11.352	1.342	3.697	28.079	0.132
Control	2.068	4.805	0.4	98.2	1.4	1.1	15.273	1.772	5.568	28.211	0.197
Edge	2.109	4.83	0	98.8	1.2	0.8	8.650	0.758	5.928	27.557	0.215
Seagrass	2.02	4.72	2.9	95.5	1.6	1.2	0.640	0.000	6.319	35.082	0.180
Unvegetated	2.143	4.791	0	98.9	1.1	0.8	0.937	0.174	4.432	27.294	0.162
Salton's Bay											
Artificial seagrass	1.656	4.773	6.3	92.4	1.3	1.1	4.611	0.487	2.589	35.655	0.073
Control	1.671	4.859	5.9	92.8	1.3	0.9	23.297	3.064	0.000	33.180	0.000
Edge	0.568	4.86	35.5	63.5	1.0	0.7	22.932	2.454	1.966	27.351	0.072
Seagrass	1.931	4.832	0	98.8	1.2	0.9	10.865	1.517	4.380	27.395	0.160
Unvegetated	1.871	4.809	1.3	97.7	1.0	0.7	10.970	1.119	3.109	27.221	0.114