



# Evaluating Habitat Provisioning and Restoration Potential of a Subtropical Seagrass Species in a Temperate Estuary

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## Abstract

Accelerating human-induced losses of biogenic coastal ecosystems has prompted restoration of these critical habitats. In North Carolina, seagrass restoration has predominantly focused on *Zostera marina*, a temperate species, despite the potential for anthropogenic climate change to cause environmental shifts that favor *Halodule wrightii*, a tropical/subtropical species. We investigated how water depth and seasonality influenced *H. wrightii* distribution, restoration potential, and associated faunal community by (i) surveying North Carolina seagrass meadows to characterize their spatiotemporal distribution and morphology and (ii) conducting a restoration experiment testing the effect of transplantation depth (intertidal vs. subtidal) on *H. wrightii* restoration success and associated faunal communities. Surveyed meadows were increasingly dominated by *H. wrightii* from April to September. Seagrass within-species morphology differed across months, but only *H. wrightii* morphology and canopy height differed across depths, with canopy height increasing with bed depth. Intertidal *H. wrightii* transplants persisted > 18 months post-restoration, whereas nearly all subtidal transplants were lost within 6 months. We found no difference in faunal community abundance or structure between transplanted and control plots across depths. However, communities in the restored bed were less abundant and less species rich than those of a nearby reference bed. Although *H. wrightii* is widely distributed in estuarine waters of North Carolina, our results suggest small-scale transplantation does not lead to successful restoration or host communities equivalent to natural beds. Greater understanding of the role of *H. wrightii* as faunal habitat and identification of best restoration practices are critical to sustain and enhance ecosystem functioning in changing estuaries.

**Keywords** Seagrass transplantation · Coastal restoration · Faunal communities · Mixed-composition beds · Nekton · Water depth

## Introduction

Structurally complex coastal habitats formed by foundation species, such as salt marshes, coral reefs, and seagrass meadows, provide multiple ecosystem services including shoreline protection, nutrient cycling, carbon

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sequestration, and habitat for a wide variety of organisms (Barbier et al., 2011; Beaumont et al., 2007; Beck et al., 2001; Dennis, 1992; Lefcheck et al., 2019; Minello et al., 2003; Sheaves et al., 2013; Sheridan & Hays, 2003; Waycott et al., 2009). In particular, seagrass meadows serve as nursery areas for large and diverse faunal communities, enabling juvenile nekton to mature through high-mortality life stages quicker than they would in other habitats (Heck & Thoman, 1984; Beck et al., 2001; Heck et al., 2003; Lefcheck et al., 2019). Additionally, despite covering less than 0.2% of the world's oceans, seagrasses provide nursery habitat to 21.5% of the species on the FAO's "top 25 most landed species" list (FAO, 2016).

Despite their recognized importance for ecosystem services and function (Duarte, 2002), global seagrass extent has declined by roughly 15–30% relative to coverage records from 1879 (Dunic et al., 2021; Waycott et al., 2009), with declines continuing in recent decades (Green et al., 2021; Turschwell et al., 2021; Unsworth et al., 2018). Current calculations estimate an average annual loss of 2–5% per year globally, with rates possibly as high as 7% per year and increasing (Waycott et al., 2009). Therefore, in recent decades, restoration efforts have increased to combat these losses and preserve ecosystem functioning (Zhang et al., 2018). While some projects have seen high success rates (> 85% survival of transplants; Bastyan & Cambridge, 2008; Balestri & Lardicci, 2012), seagrass restoration can be extremely costly, and survival outcomes are highly variable (Bayraktarov et al., 2016). This is due in part to a lack of information about environmental conditions that would promote growth and establishment of restored seagrasses (van Katwijk et al., 2009). Important factors to consider prior to implementing seagrass restoration projects include proper siting (e.g., energy regime and depth) and restoration strategy (e.g., seed planting and adult transplantation; Fonseca et al., 1998; van Katwijk et al., 2009; Bayraktarov et al., 2016).

Water depth (subsequently, "depth") is an important and potentially "goldilocks" environmental variable in predicting seagrass survival and restoration success (Aoki et al., 2020; Sheridan et al., 1998). Light required for photosynthesis declines with depth, while deeper waters provide protection from desiccation and UV/thermal stress (Duarte, 1991; Duarte et al., 2007; Fonseca & Bell, 1998). Water depth can also influence seagrass morphology, with decreased blade widths, increased leaf area, decreased leaf biomass, and decreased leaf production rates in deeper waters due to decreased light availability (Lee & Dunton, 1997; Olesen et al., 2002; Thayer et al., 1984). Depth may also play a role in the habitat functioning of seagrass beds, with faunal communities varying across depths (Heithaus 2004, Micheli et al., 2008, Hutchinson et al., 2014) and

some fish species showing preferences for deeper seagrasses over shallower beds (Smith et al., 2012). Further, intertidal seagrass beds can be exposed at low tides, limiting the type and abundance of organisms that can remain in these habitats. Thus, the depth at which seagrasses are restored will likely influence overall productivity, seagrass composition and morphology, and habitat provisioning for motile fauna.

The Outer Banks of North Carolina (NC) are a valuable study system to investigate factors affecting seagrass composition and restoration success. In NC, seagrasses face a multitude of threats including thermal stress from climate change, nutrient loading from runoff, and increased storminess (NC Department of Environmental Quality, 2021). These stressors have led to declines of > 10% of high salinity submerged aquatic vegetation in southern areas of the state (south of Barden Inlet at Cape Lookout) from 2006/2007 to 2013, with no clear signs of recovery (Field et al., 2021; NC Department of Environmental Quality, 2021). Therefore, there is a strong need to develop restoration techniques to proactively increase seagrass extent. Additionally, much of the suitable habitat for seagrass in NC is intertidal, with semi-diurnal tides resulting in repeated, daily exposure to desiccation stress (Fonseca et al., 1998; Suykerbuyk et al., 2016).

North Carolina is at the transition zone of temperate and subtropical ecosystems, impacting the composition of seagrass species within meadows (Field et al., 2021; NC Department of Environmental Quality, 2021). Coastal meadows of NC can occur in both monospecific and mixed species assemblages of *Halodule wrightii*, *Ruppia maritima*, and *Zostera marina*. In contrast to *Z. marina*, the efficacy of restoration practices for *H. wrightii* is much less studied, including within NC (Fonseca et al., 1990; Kenworthy et al., 1980; Zhang et al., 2021). However, *H. wrightii* may be a better long-term candidate species for restoration in NC due to its higher temperature tolerance and increasing abundance, particularly in the warmer summer months (Bartenfelder et al., 2022; Wilson & Lotze, 2019). Seagrass composition and seasonal trends have shifted over time within this transition zone due to warming temperatures as well as changes in water clarity (Bartenfelder et al., 2022; Micheli et al., 2008; NC Department of Environmental Quality, 2021). Compared to the temperate *Z. marina*, subtropical *H. wrightii* is likely to become increasingly dominant in coastal NC with climate change (Bartenfelder et al., 2022; Micheli et al., 2008; Wilson & Lotze, 2019). *Halodule wrightii* can also rapidly expand into recently disturbed areas within a seagrass meadow at the start of its growing season in the late spring/early summer and has the potential to become as dense as the surrounding seagrass bed within 1 year after disturbance (Donaher et al., 2021). Given its higher thermal tolerance

and ability to recover from disturbance, it has become increasingly pertinent to decipher best practices for restoring *H. wrightii* should environmental conditions lead to the extirpation of *Z. marina* in this region.

Best practices for enhancing restoration success depend on identifying factors that affect seagrass distribution and seagrass bed composition (Pazzaglia et al., 2021; Tan et al., 2020). Rapid changes in seagrass distribution and composition in NC (Bartenfelder et al., 2022; Micheli et al., 2008; NC Department of Environmental Quality, 2021) require up-to-date assessments of environmental and biotic conditions found in productive, natural seagrass beds prior to informing restoration activities.

To address knowledge gaps in seagrass distribution and restoration practices, we combined field surveys and experimental seagrass transplantation to address the following questions: (1) how do abiotic (i.e., depth) and temporal factors (i.e., seasonality) influence the distribution and morphology of *H. wrightii* and (2) how does depth (intertidal vs. subtidal) impact the restoration success of *H. wrightii* and its associated motile fauna? We hypothesized that at shallow depths, *H. wrightii* would naturally co-occur with *R. maritima* and morphologically display greater leaf numbers per shoot and leaf widths. Whereas, at deeper depths, *H. wrightii* would more likely co-occur with *Z. marina* and exhibit longer shoot lengths. Across all depths, *H. wrightii* would be seasonally dominant in the mid- to late-summer. We further hypothesized that the restoration potential (in terms of survival and persistence over time) of *H. wrightii* would be equivalent across subtidal and intertidal depths (both within the natural depth range of *H. wrightii*). However, motile faunal use of restored (transplanted) *H. wrightii* would increase with depth and seagrass cover. Altogether, our study provides valuable data on the population demographics and community composition of seagrass beds in this unique location along the Atlantic coast where temperate and tropical seagrasses overlap, allowing us to make inferences in seagrass restoration design as climate warms and species distributions shift.

## Methods

### Study Sites

This study was conducted in Back Sound within the Albemarle-Pamlico estuarine system in Carteret County, NC (Fig. 1). Back Sound is a shallow, well-mixed estuarine system characterized by high salinity and semidiurnal tides due to its proximity to the Beaufort and Barden inlets. The transplantation experiment was conducted in Back Sound adjacent to Harker's Island in Carteret County, NC (34° 43' 25.07" N, 76° 34' 47.04" W). This site is characterized by

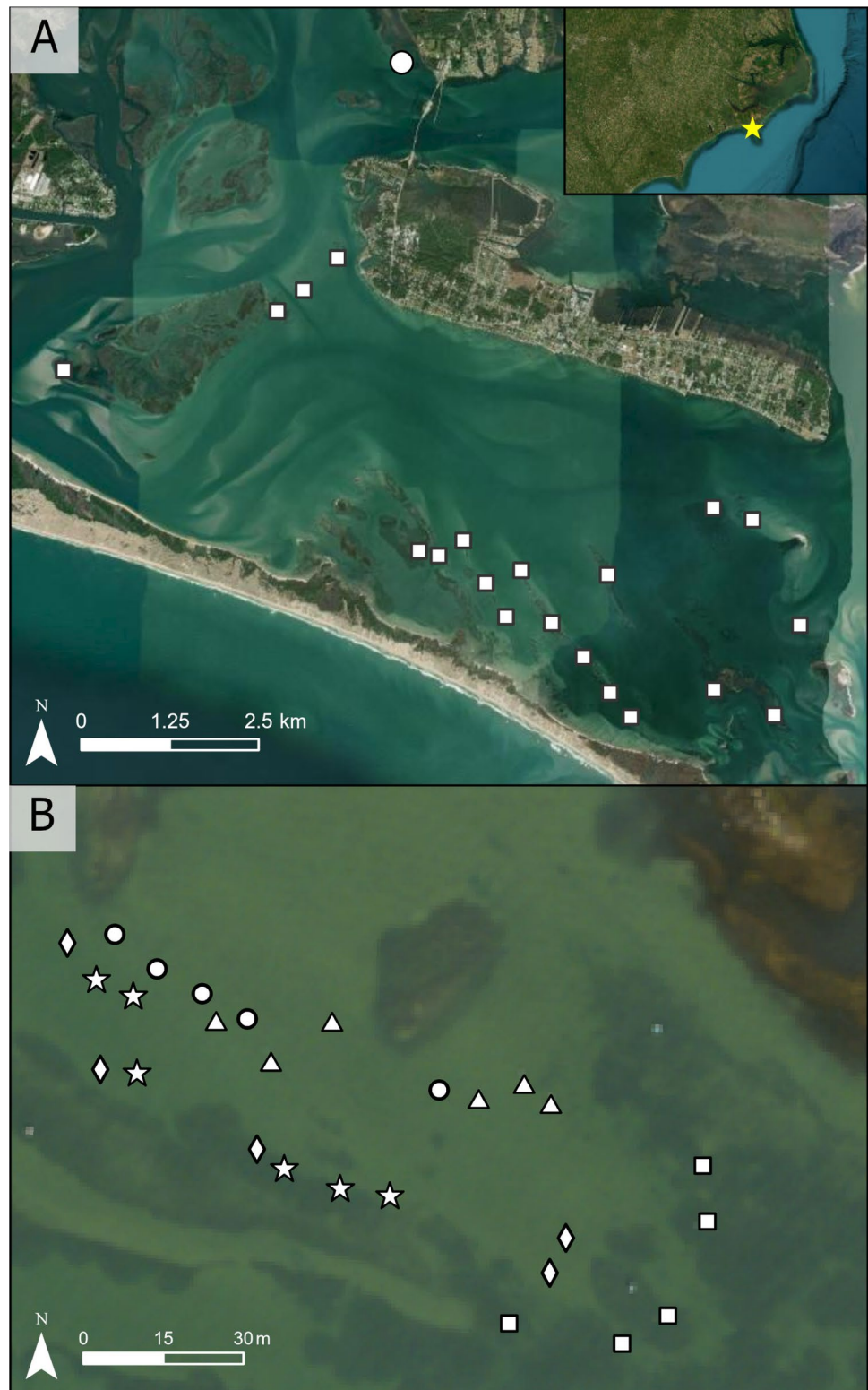
a large, continuous seagrass bed surrounded by a matrix of salt marsh, oyster reefs, and sandy habitats (Fig. 1). The natural (control comparator), continuous seagrass bed at the restoration site is dominated by *H. wrightii*, interspersed with *R. maritima* and *Z. marina*, with the presence of *Z. marina* declining in the mid to late summer after a spring and early summer peak (*personal observation*, Field et al., 2021, NC Department of Environmental Quality, 2021).

### Seagrass Survey Design

To determine how *H. wrightii* co-occurrence and morphology shift spatiotemporally, we conducted 2 years (2019 and 2020) of seagrass surveys. Specifically, monthly surveys conducted in April–September of 2019 assessed trends in seasonality; whereas surveys conducted in June and July 2020 examined gradients in depth. In 2019, each month from April to September, we randomly selected six beds from a pool of 20 seagrass beds across the entirety of Back Sound to sample (Zhang et al., 2021; Fig. 1). At each site, we delineated three, 50-m transects across the seagrass bed to quantify seagrass species composition and morphological metrics. Where possible, transects were placed parallel to each other within the meadow. In smaller, more patchy beds, transects were placed end to end or perpendicularly (though not overlapping) to minimize sampling of bare sand across the transect. Percent cover of *Z. marina* and *H. wrightii*/*R. maritima* and canopy height was measured within 0.0625-m<sup>2</sup> quadrats every 5 m along the transect. We combined *H. wrightii* and *R. maritima* for percent cover measurements, as it is difficult to visually distinguish between the two species in the field. We estimated percent cover according to the North Carolina Vegetation Survey Index (NCVI), which maximizes the ability to distinguish differences between areas of low cover (e.g., 1% and 2% cover) more easily than high cover (e.g., 74% and 75% cover; Peet et al., 1998). Canopy height was quantified as the mean of the 5 tallest seagrass shoots within the quadrat, regardless of species. A single core was taken along each transect at the first sampling location to surpass 50% cover or where seagrass cover was the highest if no quadrat had over 50% cover.

Core samples were taken with a 10-cm diameter metal corer pushed into the sediment to a depth of 15 cm and sieved in the field to remove sediment and shells. Core samples were frozen until processing at which point they were thawed and quantified (Donaher et al., 2021) for shoot density and morphological metrics for each seagrass species (with separate counts of *R. maritima* and *H. wrightii*). Specifically, we haphazardly selected five shoots of each species within each core and measured shoot

**Fig. 1** **A** Map of seagrass bed and experiment locations in Back Sound, North Carolina. Squares denote individual seagrass beds sampled in 2019 and 2020. Circle denotes location of seagrass transplantation experiment. **B** Map of transplantation experiment site. Shape denotes plot type. Circles represent intertidal transplanted ( $N=5$ ), stars represent subtidal transplanted ( $N=6$ ), triangles represent intertidal sand flat ( $N=6$ ), diamonds represent subtidal sand flat ( $N=5$ ), and squares represent continuous seagrass control plots ( $N=5$ ). Imagery from USDA and acquired through NOAA Data Access Viewer



length, leaf width, number of leaves per shoot, and number of branches (*R. maritima* and reproductive shoots of *Z. marina* only; Figure S1) per shoot. For *H. wrightii* and vegetative *Z. marina* shoots that do not display branching,

branch number was recorded as one. The aboveground biomass from the five selected shoots to be measured (leaves and shoots) was dried at 60 °C and massed separately from the rest of the core following measurement as described

above. The remaining shoots in the core were identified to species, enumerated, separated into above- and below-ground biomass, dried, and massed as described above (Donaher et al., 2021).

To quantify seagrass composition during peak productivity and to assess how meadow composition and seagrass morphology varied across depths, we sampled 18 seagrass beds in June and July 2020, which coincided with the highest seagrass canopy heights observed in 2019 sampling. This time frame also coincides with when *H. wrightii*, *R. maritima*, and *Z. marina* are all present in NC seagrass beds (Bartenfelder et al., 2022; Fig. 2). Seagrass bed composition was measured in five haphazardly placed 0.0625-m<sup>2</sup> quadrats throughout the meadow. Percent cover and canopy height were measured in each quadrat identically to the 2019 sampling design. Additionally, the elevation of the seagrass bed relative to the North American Vertical Datum of 1988 (NAVD88) was taken at the location of each quadrat using a Trimble R10 Real-Time Kinematic (RTK) GPS (0.5–1.0 cm horizontal and 1.0–4.0 cm vertical resolution) as a proxy for bed inundation. A seagrass core was taken from the center of each quadrat at each site, and cores were processed as described above for 2019 sampling.

We measured epibiont load to better understand how bed depth and seagrass morphology may influence abundances of seagrass-associated epifauna, which are a food source for many nekton (Bologna & Heck, 1999; Hall & Bell, 1988). Five haphazardly selected shoots of each species from each seagrass core in 2020 were scraped with a glass microscope slide to release epibionts from the blade, and length and width of the scraped blades were recorded; then, blades were dried and massed as described above. Scraped epibionts were dried and massed as described above. Epibiont load was standardized by blade weight to account for sample variation in blade size and surface area available for colonization.

## Seagrass Transplantation Experimental Design

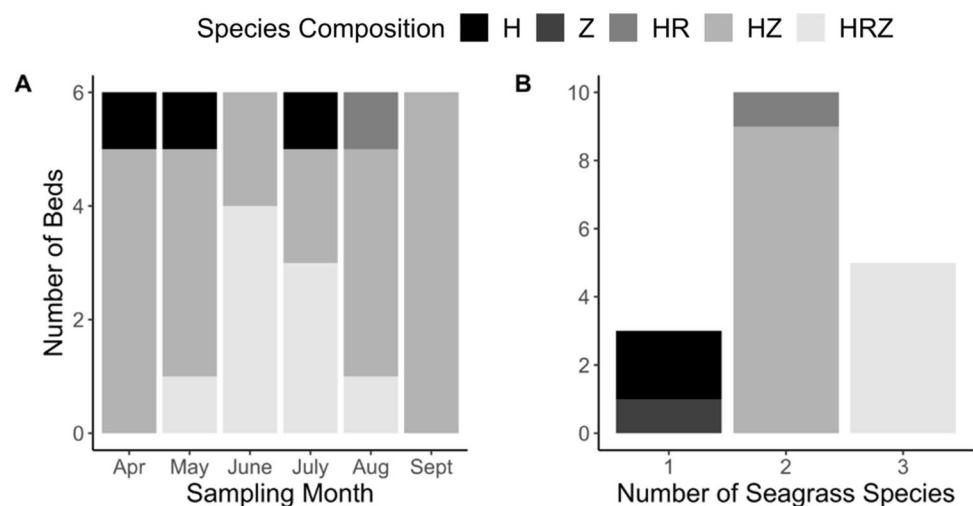
To test how depth influenced restoration success and faunal community composition, we conducted a transplantation experiment informed by our seagrass surveys. We delineated 27 2-m by 2-m plots for our experiment with the following treatments: intertidal transplanted ( $N=5$ ), subtidal transplanted ( $N=6$ ), intertidal sand flat ( $N=6$ ), subtidal sand flat ( $N=5$ ), and continuous seagrass ( $>75\%$  cover of *H. wrightii*,  $N=5$ ). All continuous seagrass plots, which served as experimental controls, were at the intertidal depth range, as none of the nearby ( $<100$  m) continuous *H. wrightii* seagrass beds existed at the subtidal depth range.

In April 2021, we identified sites at two elevation categories informed by prior-described surveys: intertidal ( $-0.4$  m –  $-0.55$  m NAVD88) and subtidal ( $-0.6$  m –  $-0.8$  m NAVD88). These elevation categories correlated to a depth of 0.3–0.45 m below local mean sea level (LMSL) for intertidal and 0.5–0.6 m below LMSL for subtidal plots (Gittman et al., 2018). Intertidal plots were selected such that they would be exposed at spring tides but remain submerged during neap tides.

Because *H. wrightii* predominantly exhibits clonal growth in NC, we opted to transplant *H. wrightii* shoots rather than attempting to collect and sow seeds (Digiantonio et al., 2020; Ferguson et al., 1993; Fonseca & Bell, 1998; Fonseca et al., 1998). Transplanting also allowed standardization for shoot density, clump size, initial canopy height, and percent cover across plots and depths.

On April 26–28, 2021, we transplanted 23 clumps comprised of 15 shoots of *H. wrightii* each from a nearby ( $<400$  m) seagrass bed into 2 m by 2 m plots in a grid arrangement (Figure S2B). We followed the staple method as described by Fonseca et al., (1998; Figure S2B). Care was taken while transplanting to ensure intact roots and rhizomes were included within each clump rather than individual,

**Fig. 2** The species composition of each surveyed bed **A** across months ( $N=6$  per month) in 2019 and **B** across the number of beds comprised of 1, 2, and 3 seagrass species in 2020 ( $N=18$ ). Shading denotes the makeup of the beds by seagrass presence. H, *H. wrightii*; R, *R. maritima*; Z, *Z. marina*



unconnected shoots of *H. wrightii*. Clumps were anchored to the sediment with lawn staples to minimize transplant loss until their root system became established in the transplant location (Figure S2). High winds during initial planting efforts and stingray activity within a transplanted plot resulted in significant transplant loss within the first week. Therefore, we conducted a supplemental transplant on May 25, 2021, to replace all lost clumps for 23 total clumps per plot.

To assess initial conditions and variability across treatments, we measured the biomass of eight randomly selected clumps (including all roots and rhizomes) collected for planting ( $\bar{x} = 0.605 \pm 0.058$  g dry weight) and quantified shoot lengths from ten random clumps, five assigned “subtidal” and five assigned “intertidal.” We further measured the biomass of an additional eight clumps from the supplemental planting to ensure minimal differences in clump size between April and May ( $\bar{x} = 0.639 \pm 0.1$  g dry weight). Every 2 weeks from June through October 2021 and 2022, we counted the number of remaining clumps transplanted in each plot out of the original 23.

### Faunal Monitoring

To assess faunal communities associated with transplanted seagrass relative to continuous seagrass and sand flat sites, we employed three separate approaches: minnow traps and standardized monitoring units for the recruitment of fish (SMURFs; Ammann, 2004) for fishes and macroinvertebrates, and squid pops as a proxy for consumption (Duffy et al., 2015). Baited minnow traps (with 2 pieces of dried kibble) were deployed every other week in all 27 transplanted, sand flat, and continuous seagrass plots (Yarnall & Fodrie, 2020). Each minnow trap was placed in the plot center while avoiding direct contact with transplanted grasses. Traps were deployed within 2 h of low tide during a neap tide for 24 h, and all fish and crustaceans within recovered traps were identified to the lowest taxonomic level possible, enumerated, wet-weighed then released (Table S1; IACUC AUP #371; SEAP Collection Permit #706,671, #706,481). Minnow trap catches were standardized to 24-h deployments to account for any trap that may have been retrieved slightly early or late of the 24-h mark to calculate catch per unit effort (CPUE).

Concurrently with minnow trap deployments, we conducted 24-h squid-pop consumption assays, which give a measure of relative feeding intensity, and thus a proxy of predation pressure, of the consumers of small motile organisms (Duffy et al., 2015). Measures of consumption and predation pressure can then be used to identify areas that may act as a refuge for small and juvenile fauna (Lefcheck et al., 2021). Squid-pops were comprised of a 1.3-cm-diameter circular piece of dried squid attached to a garden stake with

a 5-cm-long piece of monofilament line (Duffy et al., 2015; Lefcheck et al., 2021). A single squid-pop was deployed in the center of each plot 1 h prior to low tide such that the dried squid was 20 cm above the substrate. Consumption was checked 1-, 2-, and 24-h post-deployment and marked as consumed, partially consumed, or intact. Any active predation was noted as partially consumed and, when identifiable, the species preying upon the squid-pop was recorded. The proportion consumed in each plot across all sampling dates was averaged, and average plot consumption was included in the model (see statistical analyses below).

Finally, we conducted 2-week deployments of SMURFs each month to capture larval and juvenile fish and crustaceans entering the site (Figure S3; Ammann, 2004; Yarnall, 2021). SMURFs were deployed between plots in subtidal and intertidal sand flat and within intertidal seagrass reference plots. SMURFs could not be placed within transplanted plots, as the large size and method of anchoring (sand screws) would negatively impact transplanted plots. All organisms within SMURFs were flushed, collected, and preserved in labeled jars with 70% ethanol for later identification. Organisms were identified to the species level and enumerated, and the first 10 individuals of each species haphazardly selected from each SMURF were measured to the nearest mm (total length for fishes and shrimp; carapace width for crabs; Tables S2, S3).

## Statistical Analyses

### Seagrass Surveys

Linear mixed models (LMMs) and generalized linear mixed models (GLMMs) were used to determine the relationship between the fixed effect of 2019 sampling month and the random effect of site on seagrass composition and morphology metrics (Table S4). Additionally, a LMM was used to determine the fixed effect of *H. wrightii* and *R. maritima* percent dominance (analyzed as a proportion) by biomass and the random effect of site on the canopy height of the bed. We delineated beds as “low” versus “high” cover following sampling and prior to percent cover analysis of *H. wrightii* and *Z. marina* to understand how overall seagrass cover may be impacted by month and depth. For analyses, we gave cover of 0–50% a score of 0 and cover from 50 to 100% a score of 1. We conducted one-way analysis of variance’s (ANOVA’s) to test if there were differences across seagrass species in their (1) average shoot length, (2) leaf width, (3) leaf number per shoot, (4) branch number per shoot, and (5) shoot count per bed. For all significant results from the above tests, we conducted Tukey’s post hoc tests to assess pairwise differences. Analyses were conducted separately for seagrass metrics measured in 2019 and 2020.

Linear models (LMs) and generalized linear models (GLMs) were used to determine the fixed effect of seagrass bed elevation, hereafter referred to as depth relative to LMSL, on the 2020 measurements of seagrass composition and morphology metrics (Table S5). Additionally, a LM was used to determine the fixed effect of *H. wrightii* and *R. maritima* percent dominance by biomass on the average canopy height of the bed. We scored percent cover of *H. wrightii* and *Z. marina* as either 0 or 1 as described above and ran a binomial GLM to test for effects of depth on the percent cover of *H. wrightii* and *Z. marina*. No models were run on seagrass morphological metrics that had no variance across samples (e.g., leaf width of *H. wrightii* and *R. maritima*, Table 1).

### Seagrass Transplantation Experiment

Differences in depth relative to LMSL between the “subtidal” and “intertidal” plots were assessed using ANOVA. To ensure that depths were similar (1) across transplanted, sand flat, and continuous seagrass plots in the intertidal depth category and (2) between transplanted and sand flat plots in the subtidal depth category, we conducted an ANOVA with the fixed effect of transplantation category (transplanted vs. sand flat vs. continuous seagrass (intertidal only)) on the measured depth relative to LMSL of the plots. Finally, we compared the lengths of shoots planted across treatment plots using an ANOVA with the fixed effect of depth category (intertidal, subtidal) on the average shoot length of clumps to be planted.

We used a LMM to analyze the fixed effect of depth (subtidal vs. intertidal), date, and their interaction on the number of clumps remaining during 2021 and included plot number as a random effect. We also used a LMM to analyze the fixed effect of date on the number of clumps remaining in intertidal plots in 2022 and included plot number as a random effect. We conducted a one-way ANOVA to determine differences in minnow trap CPUE across the continuous seagrass, intertidal and subtidal transplanted, and sand flat plots. We then used Tukey’s post hoc test to assess pairwise differences for statistically significant ANOVA results. A quasi-Poisson GLM was used to analyze the fixed effects of depth treatment, the number of clumps remaining in transplanted seagrass, and their interaction on minnow trap CPUE. We did not include any plots where all transplanted clumps had been lost at the time of sampling as these could no longer be considered “transplanted.”

We used multivariate analyses to determine if minnow trap or SMURF community composition differed across plot types. Prior to all analyses, we removed samples with zero catch (no community data), as well as rare species, defined as species that were caught only once across all samples for each gear type. For all multivariate analyses (unless otherwise noted), catch data were log ( $x + 1$ ) transformed (due to right-skew, zero-inflated data and to down-weight the value of low counts across sites) and then, following transformation, a Bray–Curtis similarity matrix was created.

Due to a lack of subtidal continuous seagrass plots in our experiment, we first compared minnow trap communities across only intertidal plots comparing continuous

**Table 1** Mean (standard error) of seagrass composition and morphology metrics for 2019 and 2020 across the bed, *H. wrightii*, *R. maritima*, and *Z. marina*. Any metric not measured for the specific species or bed is left blank

|                                                            | Year | Bed            | <i>H. wrightii</i> | <i>R. maritima</i> | <i>Z. marina</i> |
|------------------------------------------------------------|------|----------------|--------------------|--------------------|------------------|
| Canopy height (mm)                                         | 2019 | 184.26 (12.04) | -                  | -                  | -                |
|                                                            | 2020 | 173 (12.15)    | -                  | -                  | -                |
| Average shoot length (mm)                                  | 2019 | -              | 125.84 (5.25)      | 88.08 (7.44)       | 105.46 (6.7)     |
|                                                            | 2020 | -              | 92.81 (2.76)       | 93.01 (9.73)       | 111.69 (8.87)    |
| Aboveground biomass per core (g)                           | 2019 | 0.92 (0.07)    | 0.72 (0.05)        | 0.05 (0.02)        | 0.15 (0.03)      |
|                                                            | 2020 | 0.76 (0.06)    | 0.49 (0.04)        | 0.04 (0.02)        | 0.23 (0.06)      |
| Leaf width (mm)                                            | 2019 | -              | 1 (0)              | 1 (0)              | 2.11 (0.1)       |
|                                                            | 2020 | -              | 1 (0)              | 1 (0)              | 2.21 (0.05)      |
| Leaf number per shoot                                      | 2019 | -              | 2.78 (0.05)        | 4.94 (0.38)        | 3.81 (0.14)      |
|                                                            | 2020 | -              | 2.88 (0.04)        | 3.67 (0.28)        | 3.28 (0.12)      |
| Shoot count per core                                       | 2019 | 63.84 (3.13)   | 56.32 (2.84)       | 3.82 (1.42)        | 3.69 (0.80)      |
|                                                            | 2020 | 71.12 (4.43)   | 59.55 (4.49)       | 5.97 (2.95)        | 5.6 (1.07)       |
| Branch number per shoot                                    | 2019 | -              | 1 (0)              | 3.26 (0.35)        | 1.06 (0.04)      |
|                                                            | 2020 | -              | 1 (0)              | 2.07 (0.25)        | 1 (0)            |
| <i>H. wrightii</i> + <i>R. maritima</i> percent by biomass | 2019 | 85.54 (2.61)   | -                  | -                  | -                |
|                                                            | 2020 | 73.59 (6.14)   | -                  | -                  | -                |
| Epibiont load (grams/gram of seagrass)                     | 2020 | 0.64 (0.09)    | -                  | -                  | -                |

seagrass, transplanted seagrass, and sand flat. We conducted a permutational multivariate analysis of variance (PERMANOVA) with the fixed effects of date and plot treatment, their interaction, and the random effect of plot number nested within category to account for repeated sampling. We then conducted a pairwise PERMANOVA for pairs of the factor plot category within each date. Permutational multivariate analysis of dispersion (PERMDISP) was conducted for plot category and date, and finally, we conducted a similarity percentages breakdown (SIMPER) analysis to determine species driving differences across plot types. Second, to compare communities across transplanted and sand flat plots in the intertidal and subtidal, we conducted PERMANOVAs with the fixed effects of transplantation category, depth category, and their interaction. Due to small sample size across dates and treatments, we summed samples across dates for each plot and analyzed the total community caught in each plot across the sampling period. We visually represented the communities through non-metric multidimensional scaling (NMDS) conducted PERMDISPs on the transplantation and depth categories to ensure homogeneity of dispersion.

Because SMURFS could not be placed inside transplanted plots, we compared communities sampled between (1) intertidal plots (continuous seagrass and intertidal sand flat) and (2) depths (subtidal and intertidal sand flat). We conducted PERMANOVAs with the fixed effects of date, plot category (continuous seagrass vs. intertidal sand flat and intertidal sand flat vs. subtidal sand flat), their interaction, and the random effect of plot number nested within plot category to account for repeated sampling of the plots. We next ran PERMDISP on the plot category and date for each analysis to ensure homogeneity of dispersion. Finally, we ran a SIMPER analysis on the shallow plots only between continuous seagrass and intertidal sand flat plots.

To compare how consumption varied across treatments, we analyzed squid pop consumption at 1- and 2-h intervals using quasibinomial GLMs testing the (1) fixed effects of restoration transplantation category (transplanted vs. sand flat control) and depth treatment (intertidal vs. subtidal) and (2) the fixed effect of habitat type (continuous seagrass, sand flat, and transplanted seagrass). Tukey's post hoc tests were used to assess pairwise differences for any significant treatment or interaction effects from the models. For all plots, all squid pops were consumed after 24 h.

All LMs, LMMs, GLMs, and GLMMs for both the observational seagrass surveys and manipulative field experiment were conducted in R statistical software using the package lme4 (Bates et al., 2015). All community analyses for the manipulative field experiment were conducted in Primer7 software (Anderson et al., 2008).

## Results

### Seagrass Surveys

For seagrass bed surveys conducted in both 2019 and 2020, meadow composition varied between one and three seagrass species, with percent cover ranging from 0 to 75% per bed for both *H. wrightii* and *Z. marina* (Tables S6, S7). In 2019, the highest seagrass diversity (i.e., the most beds with 3 co-occurring species) was observed in June (67%) and July (50%; Fig. 2). The majority of the beds surveyed in 2020 (June and July) were a mix of *H. wrightii* and *Z. marina* with just over a quarter of the beds comprised of all three species (Fig. 2). Seasonal composition shifts were evident in all seagrass bed-level metrics aside from *H. wrightii* shoot count ( $p=0.3523$ ; Figures S4; Table S7) and *Z. marina* percent cover, which was low ( $<50\%$ ) across all months surveyed ( $p=0.3011$ ; Figures S4–11; Table S7). *Halodule wrightii* and *R. maritima* contribution to percent cover increased from April through September ( $p=0.0020$ ; Figure S5; Tables S8, S9). Percent cover of *H. wrightii* + *R. maritima* also shifted seasonally with increased cover of *H. wrightii* + *R. maritima* during June–July compared to April–May ( $p=0.0045$ ; Tables S7, S9). June and July were additionally characterized by the highest aboveground biomass for *H. wrightii*. June specifically was characterized by the highest *R. maritima* aboveground biomass, shoot count, and highest overall shoot counts of the beds ( $p<0.05$ , Figures S4, S6, Tables S7–9). In May, *Z. marina* biomass and shoot counts peaked ( $p<0.05$ ; Figures S4, S6; Tables S7–9). September was characterized by the lowest *Z. marina*, *R. maritima* (with April), and overall shoot counts ( $p<0.05$ ; Figure S4, Tables S7, S9). *Ruppia maritima* was not present in the seagrass beds in April and September (Figure S4).

Field measures of seagrass canopy height varied across months and were lowest in April and May compared to all other months ( $p<0.05$ ; Figure S7; Tables S8, S9). Canopy height did not, however, vary based on the dominance of *H. wrightii* + *R. maritima* by biomass over *Z. marina* ( $p=0.2408$ ; Figure S12; Table S8). Additionally, there were structural differences in all three seagrass species temporally from April to September (Figures S8–11; Tables S7–9). Of note, *Z. marina* had narrower leaf widths and lower leaf numbers per shoot in July and August as compared to April–June, yet exhibited the highest branching of leaves per shoot (indicative of reproductive shoots) in April, with no variation across other months ( $p<0.05$ ; Figures S8–10; Tables S8, S9). *Ruppia maritima* had fewer branches in August than in June and July and longest shoots in June ( $p<0.05$ ; Figure S10, S11; Tables S7, S9), while the number of leaves per shoot for *R. maritima* did

not differ across months ( $p=0.5195$ ; Figure S9; Table S8). *Halodule wrightii* and *R. maritima* demonstrated no macroscale variation in leaf width across samples (Table 1). However, the length of *H. wrightii* shoots increased from April through July and then decreased in August and September, while the number of leaves per shoot of *H. wrightii* increased monthly from April through September, except for June when leaf number peaked ( $p < 0.05$ ; Figures S9, S11; Tables S7, S9).

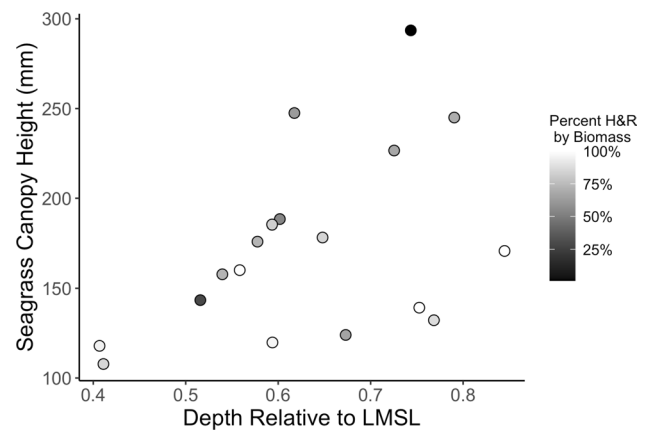
The three species of seagrass differed in morphology in both 2019 and 2020. On average, *R. maritima* had the highest number of leaves per shoot, while *H. wrightii* had the highest shoot count and *Z. marina* had the widest leaves ( $p < 0.05$ ; Figure S15; Tables 1, S10, S11). In 2019 surveys, *H. wrightii* had the longest shoots ( $p < 0.05$ ; Figure S15, Tables S10, S11), whereas in 2020, *Z. marina* shoots were marginally longer than both *H. wrightii* and *R. maritima* ( $p = 0.0865$ ; Figures S13, S14; Table S10).

The average depth of the shallowest measured seagrass bed was  $0.41 \pm 0.01$  m below LMSL, while the average depth of the deepest measured seagrass bed was  $0.84 \pm 0.06$  m below LMSL. The overall deepest depth measured was 1.01 m below LMSL, and the shallowest measured depth was 0.32 m below LMSL. While the metrics of seagrass presence and productivity (cover, dominance, biomass) differed across months, none of these metrics differed across bed depth when sampled in June and July 2020 ( $p > 0.05$ ; Figure S15, S16; Tables S12–14). In contrast, some metrics of seagrass morphology varied with depth of the seagrass bed. Specifically, deeper beds were characterized by fewer and longer shoots of *H. wrightii* than shallower beds ( $p < 0.05$ ; Figures S17, S18; Tables S12, S13). Similarly, deeper beds had marginally taller canopy heights than shallower beds ( $p = 0.0529$ ; Fig. 3, Table S12). All other measures of seagrass morphology, including epibiont load, did not differ across depths ( $p > 0.05$ , Figures S18–22; Table S12).

### Seagrass Transplantation Experiment

In the *H. wrightii* transplantation experiment, intertidal plots had a mean depth of  $0.40 \pm 0.01$  m (mean  $\pm$  standard error) below LMSL, and subtidal plots had a mean depth of  $0.58 \pm 0.02$  m below LMSL ( $p < 0.001$ ; Figure S23; Table S15). There was no difference in depth below LMSL within the intertidal ( $p = 0.610$ ) or subtidal elevation categories ( $p = 0.763$ ; Figure S23; Table S16, S17). The initial mean shoot length of *H. wrightii* clumps transplanted did not differ between subtidal ( $76 \pm 3$  mm) and intertidal plots ( $81 \pm 3$  mm;  $p = 0.2745$ ; Table S18).

The average number of transplanted *H. wrightii* clumps per treatment declined over time from 23 clumps per plot on May 25, 2021, to  $8.4 \pm 2.8$  clumps in intertidal plots and  $1.3 \pm 0.8$  clumps in subtidal plots on October 5, 2021

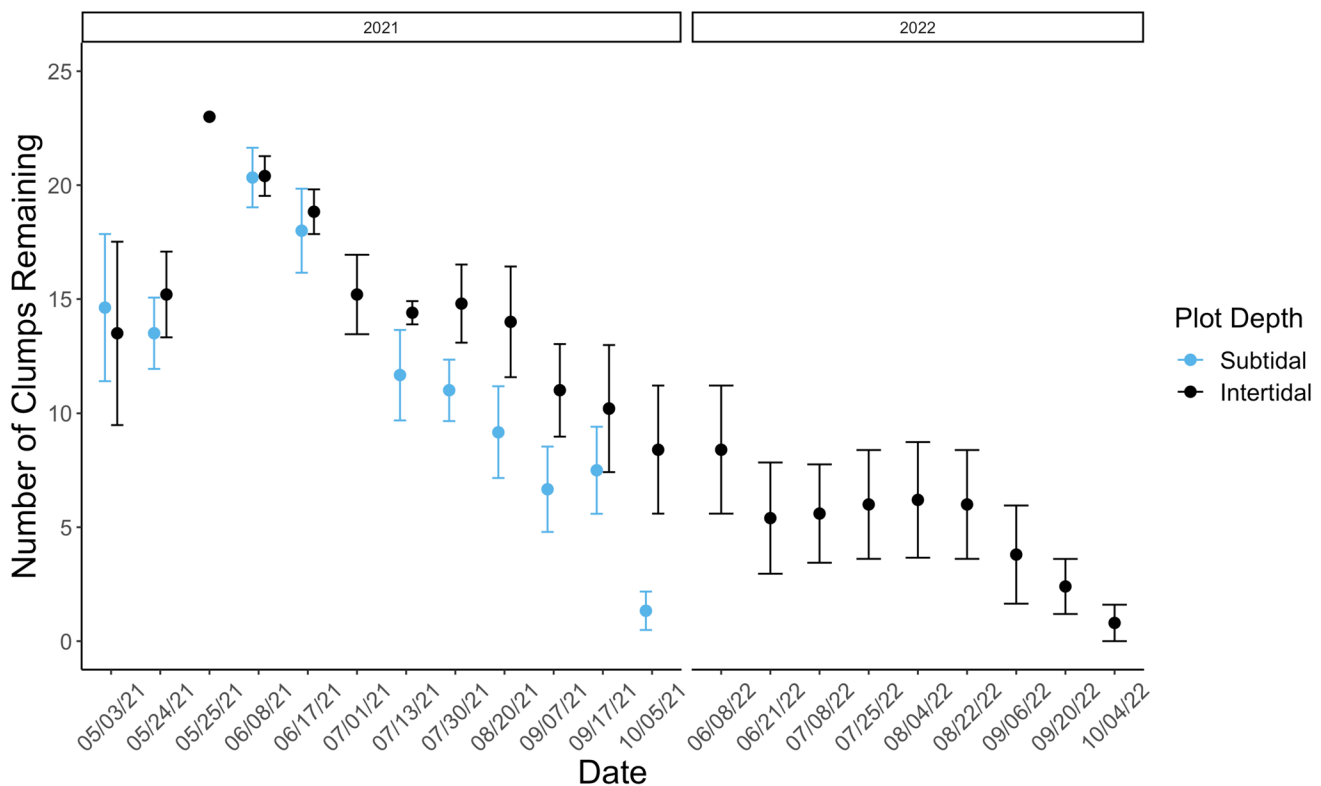


**Fig. 3** Canopy height and depth relative to local mean sea level (LMSL) of each seagrass bed sampled in 2020. Point shading indicates dominance of the seagrass bed by biomass with white indicating a higher percentage (dominance) of *H. wrightii* and *R. maritima* combined and black indicating dominance of *Z. marina*

(Fig. 4). Intertidal plots lost *H. wrightii* clumps at a significantly slower rate than the subtidal plots over the 2021 sampling period ( $p = 0.0009$ ; Fig. 4; Table S19). By April 2022, no subtidal plots contained transplanted clumps. In comparison, the average number of *H. wrightii* clumps in intertidal plots declined from  $8.4 \pm 2.8$  clumps on June 8, 2022, to  $0.8 \pm 0.8$  clumps remaining on October 4, 2022 ( $p < 0.001$ ; Fig. 4; Table S20). No *H. wrightii* clumps remained in intertidal plots by April 2023.

The mean faunal CPUE in minnow traps was highest in intertidal continuous seagrass plots with  $18.1 \pm 0.8$  organisms compared to all other plots types regardless of transplantation status ( $p < 0.0001$ ; Fig. 5; Tables S1, S21, S22). Minnow trap CPUE decreased as number of clumps remaining in transplanted plots decreased ( $p = 0.0029$ , Figure S24, Table S23). However, there was no difference in CPUE between intertidal and subtidal transplanted plots ( $p = 0.874$ ) nor was there a difference in the rate at which CPUE decreased with decreasing clump number between intertidal and subtidal plots ( $p = 0.087$ ; Figure S24; Table S23).

Faunal communities differed across sampling date and plot type ( $p < 0.0001$ ), as well as across plots ( $p = 0.0085$ ; Table S24). Specifically, catches in continuous seagrass plots were dissimilar to catches from both the intertidal transplanted and intertidal sand flat plots (Figure S25). However, some of these differences may be attributed to differences in within group dispersion of plot type with more variation within transplanted seagrass and sand flat communities than continuous seagrass communities ( $p < 0.001$ ; Tables S25, S26). Communities sampled in continuous seagrass using minnow traps differed from both the intertidal transplanted and intertidal sand flat plots ( $p < 0.05$ ) for all dates except the final sampling where continuous seagrass



**Fig. 4** Mean number of transplanted *H. wrightii* clumps remaining in transplanted plots over time in 2021 and 2022. Color denotes plot depth. Error bars indicate standard error

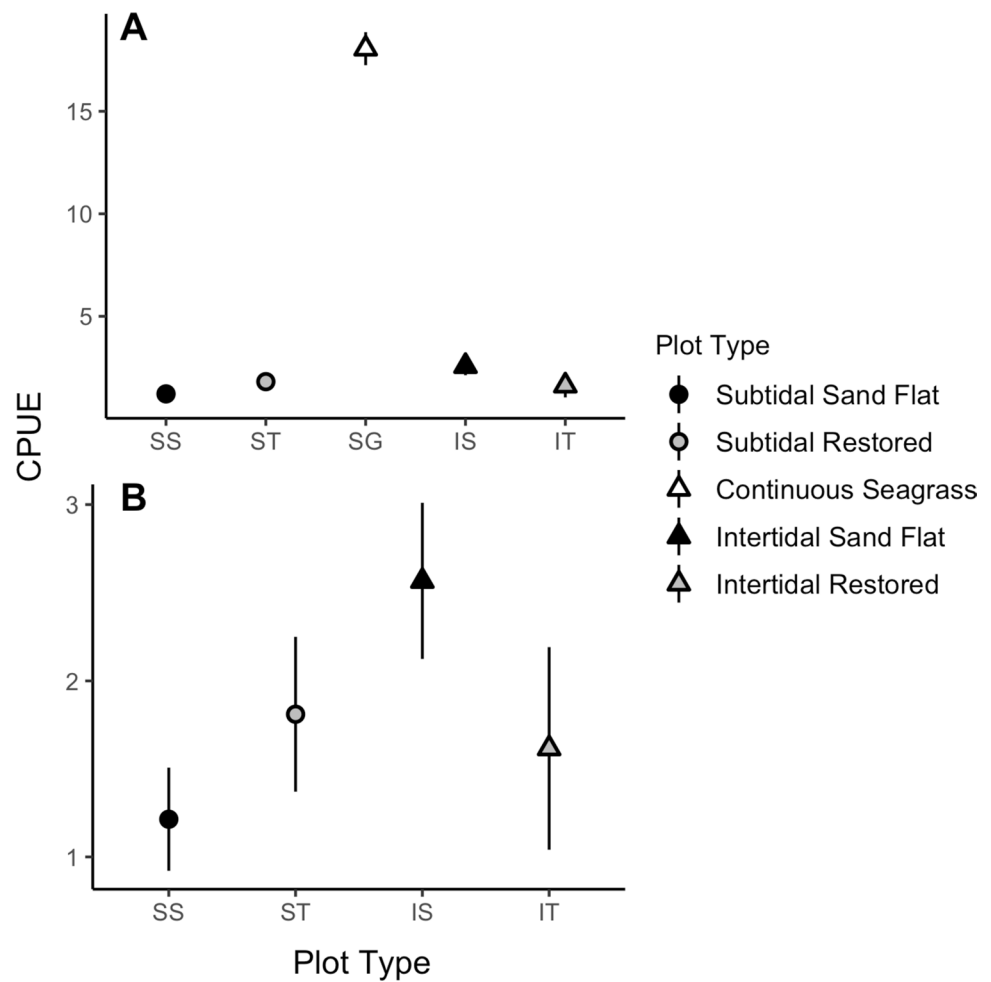
and transplanted communities were only marginally different from each other ( $p=0.0534$ ; Table S27). Communities observed in intertidal transplanted and sand flat plots were similar in composition regardless of sampling date ( $p>0.05$ ; Table S27). Differences between continuous seagrass and intertidal transplanted and sand flat plots were driven by higher abundances of pinfish (*Lagodon rhomboides*), pigfish (*Orthopristis chrysoptera*), blue crabs (*Callinectes sapidus*), and planehead filefish (*Stephanolepis hispidus*) in continuous seagrass plots (Table S28). There were no differences in faunal communities captured in intertidal and subtidal plots regardless of transplantation category or depth ( $p>0.05$ ; Tables S29–S31).

Communities caught in the SMURF sampling across the intertidal plots were similar over time ( $p=0.2068$ ; Table S32). However, communities differed between intertidal continuous seagrass and intertidal sand flat plots ( $p=0.0216$ ) potentially due to greater variance in community assemblages in bare plots compared to continuous seagrass plots ( $p=0.021$ , Tables S32–S34). There were also only slight differences in species abundance across plot types (SIMPER) and a high degree of overlap between communities captured in continuous seagrass and sand flat plots visualized in NMDS plots (Figure S26; Table S35). We found no differences in communities observed within the

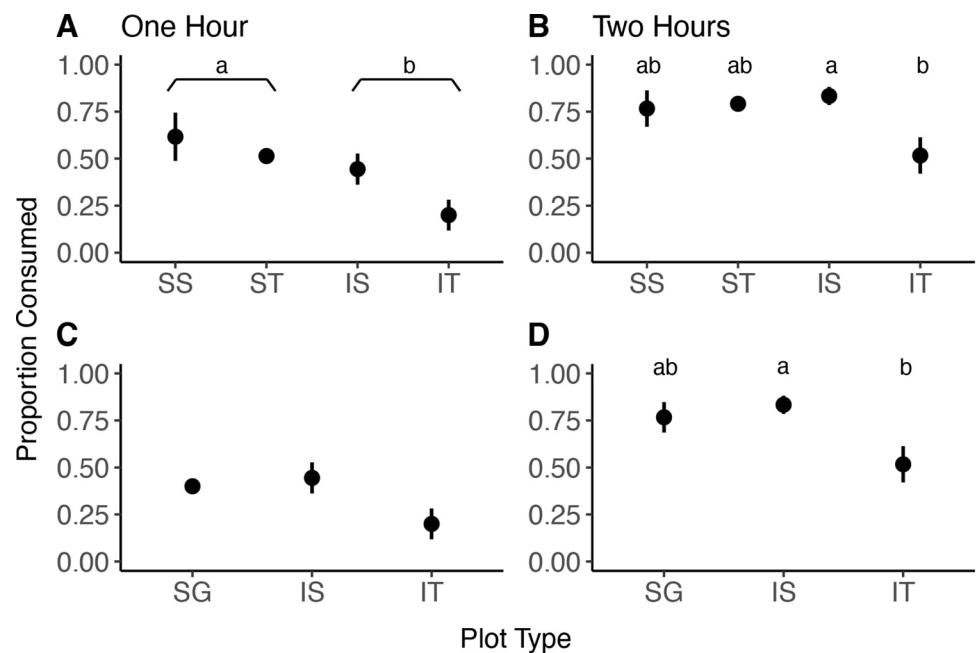
SMURF samples between intertidal and subtidal sand flat plots ( $p=0.7607$ ), across dates ( $p=0.114$ ), or between plot types across dates ( $p=0.7354$ ; Table S36–S38).

After 1 h, the proportion of squid pops consumed was greatest in subtidal sand flat plots ( $0.62 \pm 0.13$ ) and lowest in intertidal transplanted plots ( $0.20 \pm 0.08$ ; Fig. 6). Across subtidal and intertidal sand flat and transplanted seagrass plots, we found higher consumption in subtidal plots as compared to intertidal plots ( $p=0.0132$ ) regardless of transplantation category ( $p>0.05$ ; Fig. 6A; Table S39). However, after 1 h within only intertidal plots, consumption was marginally different across plots with highest consumption in the sand flat and lowest in the transplanted seagrass plots ( $p=0.0865$ ; Fig. 6C; Table S39). After 2 h, consumption across subtidal and intertidal sand flat and transplanted seagrass plots differed by plot type, with consumption significantly higher in intertidal sand flat plots as compared to intertidal transplanted plots ( $p=0.0382$ , Fig. 6B; Tables S39, S40), but neither differed from either subtidal transplanted or subtidal sand flat plots ( $p>0.05$ ; Fig. 6B; Tables S39, S40). Within just the intertidal plots 2 h post-deployment, consumption of squid pops varied ( $p=0.0307$ ), with lower consumption in transplanted plots as compared to sand flat plots ( $p=0.0245$ ; Fig. 6D; Tables S39, S41). However, continuous seagrass plots were only marginally higher than transplanted

**Fig. 5** Motile fauna CPUE as a function of plot type. **A** and **B** show the same data; however, **B** is a closer view of bare sand and transplanted plots to allow better distinguishment between catch rates. Color denotes transplantation category and shape denotes elevation category. Error bars denote standard error



**Fig. 6** Proportion of squid pops consumed as a factor of plot type after one (**A, C**) and two (**B, D**) hours. Comparisons are for bare sand and transplanted plots across intertidal and subtidal areas (**A, B**) and across only intertidal habitats (**C, D**). SS, subtidal sand flat; ST, subtidal transplanted; IS, intertidal sand flat; IT, intertidal transplanted; SG, continuous seagrass. Points are average across plots with error bars denoting standard error. Letters above plots indicate significant ( $p < 0.05$ ) results from ANOVA and Tukey's post hoc tests



( $p=0.0924$ ) and did not differ from consumption in sand flat plots ( $p=0.8017$ ; Fig. 6D; Tables S39, S41).

## Discussion

Accelerating losses of biogenic coastal ecosystems, including seagrasses, has highlighted the increasing need for knowledge about their current ecology and ways to conserve and restore them. Seagrass distribution, morphology, and productivity are influenced by a multitude of factors including the local climate, water depth, and seasonality and are likely changing with global and local effects of climate change (Bartenfelder et al., 2022; Lee & Dunton, 1997; Micheli et al., 2008). The effects of climate change may be most pronounced at biogeographic transition zones which are often characterized by the upper- or lower-most limits of species distributions (Bartenfelder et al., 2022; Mieszowska & Sugden, 2016). Climate change, and subsequently sea level rise, could additionally impact the locations in which the water depth is suitable for seagrass persistence and restoration, particularly at the edges of seagrass depth distributions (Capistrant-Fossa & Dunton, 2024; Davis et al., 2016; Valle et al., 2014). We investigated the distribution, morphology, and seasonal biomass of seagrasses at the transition zone of coastal NC. It is necessary to understand the native seagrass makeup and distribution of natural seagrass ecosystems to inform restoration strategies (Pazzaglia et al., 2021; Tan et al., 2020) along with identifying proper restoration methods (Fonseca et al., 1998; van Katwijk et al., 2016; Zhang et al., 2021) for greatest success. Here, we show that across sampled beds in Back Sound, NC, *H. wrightii* is the dominant seagrass species from April through September, and this dominance did not change with depth relative to LMSL. While the morphology of all three seagrass species changed temporally, morphology varied little with depth regardless of seagrass species.

Restoration of seagrasses through adult transplantation or planting of seeds has been the primary method to combat seagrass loss and restore ecosystem functioning (Fonseca et al., 1998; Reynolds et al., 2016; van Katwijk et al., 2016). Based on our results, *H. wrightii* may have high potential for restoration using adult transplants but potentially only in shallow, intertidal areas, despite naturally occurring in deeper, subtidal beds (Fig. 3). This is in agreement with results from previous efforts to restore *Z. marina* where seedlings were more resilient in depths that excluded the shallowest and deepest portions of the natural range (Aoki et al., 2020). Our results paired with those from previous efforts provide evidence for the existence of a potential “goldilocks zone” for seagrass restoration where restoration efforts have the highest success in only a portion of the natural distribution. Further, our small-scale transplantation of

*H. wrightii* did not host faunal communities as abundant or as rich as the continuous seagrass beds, indicating ecosystem functioning in the form of faunal habitat was not restored to natural levels during our sampling period. Further work is needed to enhance ecosystem functioning following restoration. Our results highlight the need for increased focus on developing methods for restoration of *H. wrightii*, an emerging dominant seagrass species in NC, and a greater understanding of the habitat requirements for estuarine fauna.

## Seagrass Distribution and Morphology Differ Seasonally and With Depth

North Carolina seagrass meadows have long been studied due to their habitat provisioning and the unique co-occurrence, interactions, and physical limitations of three seagrass species: *H. wrightii*, *R. maritima*, and *Z. marina* (Bartenfelder et al., 2022; Field et al., 2021; Micheli et al., 2008). Though beds are often a mix of the three seagrass species, historically, *Z. marina*, a temperate species, is dominant in cooler months (i.e., spring) and found in deeper water than *H. wrightii*, a subtropical/tropical species (Bartenfelder et al., 2022; Field et al., 2021; Micheli et al., 2008; Thayer et al., 1984). Similarly, we observed seagrass beds comprised of a mix of up to three species with metrics of seagrass bed composition (biomass, shoot count, cover, and dominance) changing seasonally from April through September (Bartenfelder et al., 2022; Micheli et al., 2008; Fig. 2). Though seagrass composition changed seasonally, *H. wrightii* was consistently the dominant seagrass compared to *Z. marina* regardless of sampling month with only a single *Z. marina* dominated bed sampled in 2020 (Figs. 2 and 3). Although *H. wrightii* is thought to be temperature-limited in colder months, we found high dominance of *H. wrightii* in the spring (April and May), a period previously characterized by dominance of *Z. marina* rather than *H. wrightii* (Bartenfelder et al., 2022; Micheli et al., 2008). Seagrass distributions are influenced by water depth, particularly in NC where deeper beds are characterized by higher presence and abundance of *Z. marina* (Micheli et al., 2008; Thayer et al., 1984). We observed a more significant shift in the dominance from *Z. marina* to *H. wrightii* than described in previous studies. However, beds sampled in this study were generally shallow (< 1 m) and randomly selected; therefore, we may have missed the deeper, high *Z. marina* cover beds at their peak dominance in early spring.

The distribution (Micheli et al., 2008; Thayer et al., 1984), morphology, and structure of seagrass often changes with depth (Enríquez & Pantoja-Reyes, 2005; Olesen et al., 2002) and light availability (Fitzpatrick & Kirkman, 1995; Longstaff et al., 1999). During periods of light stress, seagrasses have fewer, shorter leaves and lose overall biomass (Biber et al., 2009; Enríquez & Pantoja-Reyes, 2005; Fitzpatrick

& Kirkman, 1995). However, this was not observed in our system as the distribution of *H. wrightii* and *Z. marina*, and most morphological metrics did not differ with depth, potentially indicating a lack of light stress. Interestingly, we found an increase in *H. wrightii* shoot length with increased bed depth, despite the high light requirement of *H. wrightii* (Biber et al., 2009). Surveyed beds in this study were generally shallow (< 1 m relative LMSL) with little variation in depth (0.4 m), so the variation in light availability may not have been great enough to observably impact morphology or seagrass distribution across depths. This possibly indicates that seagrasses in this study were not at the lower limits of their potential depth distributions in NC, and grasses could persist deeper than measured here.

### Key Factors for Restoration Success

*Halodule wrightii* is emerging as a dominant seagrass species in NC, and developing effective methods for its restoration are becoming increasingly critical as seagrasses continue to be lost. It is recommended that local seagrass depth distributions should be incorporated into restoration planning to enhance success (Fonseca et al., 1998; van Katwijk et al., 2009). While *H. wrightii* naturally grows across a wide depth range (0.32–1.01 m below LMSL), our transplantation experiments suggest that adult outplants are more likely to persist at intertidal, rather than subtidal, depths. However, much like previous restoration studies, overall mortality of transplants was high (Bayraktarov et al., 2016; van Katwijk et al., 2016). This suggests that while transplanting in intertidal areas rather than subtidal may enhance persistence of transplants, in our study, depth alone did not lead to a successful restoration. Previous exploration of seagrass restoration across depths has also found distinct depth thresholds for where restored grasses cannot persist (e.g., > 1.5 m deep in Virginia; Aoki et al., 2020), which may be different than the observed depths of naturally occurring seagrasses (Fonseca et al., 1998). Further, in other biogenic habitats, such as oyster reefs, processes, such as predation, may create distinct vertical thresholds for successful establishment despite the potential survival of oysters outside of the thresholds (Fodrie et al., 2014; Esquivel-Muelbert et al. 2022). These thresholds can then inform restoration of the biogenic habitats to enhance future restoration success. Our results support the existence of these distinct thresholds, as subtidal transplants sown at  $0.584 \pm 0.018$  m below LMSL did not persist beyond one growing season, despite this depth being well within the natural depths of *H. wrightii* in NC (Biber et al., 2008; Ferguson et al., 1993).

Depth thresholds for persistence and restoration success may not remain static in the face of climate change and sea level rise (Capistrant-Fossa & Dunton, 2024; Davis et al., 2016; Valle et al., 2014). Sea level rise may lead to further

losses of seagrasses, particularly on the deep edge of meadows where interactions between water depth and clarity may exceed physiological tolerance (Saunders et al., 2013). However, sea level rise may also submerge new areas for seagrasses to colonize, particularly what is currently considered very shallow intertidal habitat (Valle et al., 2014). Because depth is a critical component for successful restoration, it will likely become increasingly important to understand how future changes may impact restoration siting. Future work should continue to investigate the restoration depth thresholds of *H. wrightii* in NC and how changes to sea level will impact seagrass persistence and restoration success.

In addition to proper siting, restoration success is also often impacted by planting method and the initial number of seeds or transplants per restoration plot with increased restoration effort (e.g., transplant number and aerial extent) leading to increased survival and mean growth rate of restored seagrasses (van Katwijk et al., 2016; Zhang et al., 2021). Our restoration had a low density of seagrass transplants which may have negatively impacted survival and growth of transplanted grasses. Plantings are likely more stressed than established beds, which may rely on facilitation from adjoining shoots at the deep edge of large beds (Fonseca et al., 1998). Large, dense seagrass beds also reduce scouring and aid in sediment trapping and stabilization, thus improving water quality and resulting in more resilient restoration efforts (Aoki et al., 2020). Survival of transplants may also be enhanced by harnessing both intra- and inter-specific facilitations (Valdez et al., 2020; Zhang et al., 2021). It is possible the mechanism for initial loss of seagrass at the restoration site had lasting impacts that further reduced restoration success, lowering the possibility for facilitations, sediment trapping, and stabilization. Though the mechanism of loss is unknown, we observed extensive stingray activity and associated scouring that may have lowered restoration success. Further, increasing the genetic diversity of seagrass plants included in a restoration project can enhance the survival and growth of restored grasses (Reynolds et al., 2012). Therefore, the presumed low genetic diversity in *H. wrightii* in NC due to almost exclusive clonal reproduction (Digiantonio et al., 2020; Ferguson et al., 1993; Fonseca & Bell, 1998) may have also played a role in our low observed restoration success (Reynolds et al., 2012; van Katwijk et al., 2009; Williams, 2001).

### Habitat Provisioning of Restored Grasses Did Not Match Natural Grasses

Despite differences in short-term restoration success based on depth, there were no differences in faunal community composition and structure between intertidal and subtidal plots. However, we did find more abundant and rich faunal communities in continuous seagrass as compared to sand

flat and transplanted plots, indicating that despite grass persistence, transplanted grasses did not provide faunal habitat equivalent to natural seagrass meadows. Faunal abundances may be increased in the natural, continuous seagrass compared to transplanted plots due to the large difference in cover, biomass, and surface area of the established seagrass bed compared to the newly established transplanted areas which may increase a beds' value as a nursery area (Hovel et al., 2002; McCloskey & Unsworth, 2015; Orth et al., 1984). Further, faunal abundances in restored areas often may not reach levels equivalent to reference areas despite increasing abundance compared to degraded conditions (Benayas et al., 2009). Interestingly, while there were no statistically significant differences in CPUE across treatments, generally, transplants at subtidal depths supported more fishes than subtidal sand flat, whereas the opposite was true at intertidal depths with intertidal sand flats supporting more fishes than intertidal transplants (Fig. 5B). In mangrove habitats, small fish will seek out refuge in shaded areas as water depth increases, while the same fish are found in more open, well-lit foraging grounds in shallow water due to increased predation pressure in deeper water (Ellis & Bell, 2004). Our study supports this finding, where fish may seek refuge, in this case within transplanted seagrass, in deeper waters, whereas it may be unnecessary to seek out the same refuge in shallower areas that likely lack a strong predator presence.

Lower consumption of squid-pops, a proxy for predation, in intertidal compared to subtidal plots after 1 h, but not 2 h, is likely due to a lack of access by consumers to intertidal plots at low tide. Fish may leave shallow areas at low tide to prevent stranding, even when beds are not completely exposed (Sogard et al., 1989), returning to shallow seagrass beds rapidly after low tide (Espadero et al., 2020). Interestingly, consumption was lowest in intertidal, transplanted seagrass plots and highest in intertidal sand flat plots at the 2-h check, indicating a potential role of transplanted seagrass as a refuge from predation. A small increase in seagrass cover from bare sand may provide valuable habitat and refuge from common squid-pop consumers, such as blue crabs (*Callinectes sapidus*; personal observations, Duffy et al., 2015, Rodemann & Brandl, 2017). Previous studies found the presence of artificial vegetation decreased predation of softshell clams (*Mya arenaria*) and juvenile blue crabs by adult blue crabs compared to sand flats, even at low densities of cover (Blundon & Kennedy, 1982; Orth & van Montfrans, 1982). Faunal abundance increased with increasing number of transplanted clumps per plot, further pointing towards the transplanted plots as valuable habitat and a potential refuge for fauna.

## Conclusions

Seagrass species distributions in NC, where *H. wrightii* and *Z. marina* are at their range limits, are shifting with climate change. Our study and others suggest that this may lead to spatiotemporal differences in morphology and seagrass species composition in beds (Bartenfelder et al., 2022; Lee & Dunton, 1997; Micheli et al., 2008). As seagrass losses continue (NC Department of Environmental Quality, 2021; Waycott et al., 2009), it is imperative to understand and document the composition and structure of natural seagrass beds and ascertain the biological and physical factors that influence productivity and support nekton communities in order to develop best practices for restoring these critical habitats. Our results indicate that *H. wrightii* is a common seagrass species and potentially the most prevalent species, in Back Sound, NC during the spring and summer months. However, additional widespread seagrass surveys are needed to confirm the dominance of *H. wrightii* over a larger spatial scale and larger depth range. In our study, seagrass presence and morphology varied temporally, as in previous analyses (Bartenfelder et al., 2022; Micheli et al., 2008), but not spatially with depth. However, *H. wrightii* transplant persistence did vary with depth, with subtidal restoration failing within 6–12 months of transplantation, followed by intertidal transplantation failure at or around 18 months. Previous studies near our restoration site have documented the beneficial impacts of inter- and intraspecific facilitation on restoration of *Z. marina* and mixed assemblages (Zhang et al., 2021), as well as *H. wrightii* disturbance recovery (Donaher et al., 2021). It may therefore be critical to determine if and how facilitation can be harnessed (e.g., bigger clump sizes or restoring with bivalves) to improve the restoration success of *H. wrightii*, particularly as seagrasses continue to be lost (NC Department of Environmental Quality, 2021; Zhang et al., 2021). Further, transplanted beds supported fewer species and abundances of fauna than natural seagrass beds. Restoration of seagrasses is also likely to be increasingly necessary with continued anthropogenic impacts (Capistrant-Fossa & Dunton, 2024; Davis et al., 2016; Valle et al., 2014), and, if restoration does not lead to faunal habitat provisioning, fauna may not have adequate habitat, particularly as juveniles, regardless of restoration effort. Therefore, more work is needed to identify restoration strategies to enhance the habitat provisioning of restored *H. wrightii* rather than merely the persistence of seagrass as the two are likely not equivalent in restoration outcomes. Increased focus on uncovering best practices for restoring *H. wrightii* should continue with focus on how to enhance success of restoring *H. wrightii* across depths within its natural distribution and to restore ecosystem functioning.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s12237-025-01495-3>.

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**Data Availability** Data are available from Zenodo: <https://zenodo.org/records/14885146>.

## Declarations

**Competing Interests** The authors declare no competing interests.

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