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RESEARCH ARTICLE

Incorporating generalist seagrasses enhances habitat restoration in a changing environment

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Abstract

1. Coastal habitat-forming species provide protection and essential habitat for fisheries but their ability to maintain these services are under threat from novel stressors including rising temperatures. Coastal habitat restoration is a powerful tool to help mitigate the loss of habitat-forming species, however, many efforts focus on reintroducing a single, imperilled species instead of incorporating alternatives that are more conducive to current and future conditions. Seagrass restoration has seen mixed success in halting local meadow declines but could begin to specifically utilize generalist seagrasses with climate change-tolerant and opportunistic life history traits including high reproduction rates and rapid growth.
2. Here, we built on decades of successful eelgrass (*Zostera marina*) restoration in the Chesapeake Bay by experimentally testing seed-based restoration potential of widgeongrass (*Ruppia maritima*)—a globally distributed seagrass that can withstand wide ranges of salinities and temperatures. Using field experiments, we evaluated which seeding methods yielded highest widgeongrass survival and growth, tested if seeding widgeongrass adjacent to eelgrass can increase restoration success, and quantified how either seagrass species changes restored bed structure, invertebrate communities, and nitrogen cycling.
3. We found that widgeongrass can be restored via direct seeding in the fall, and that seeding both species maximized total viable restored area. Our pilot restoration area increased by 98% because we seeded widgeongrass in shallow, high temperature waters that are currently unsuitable for eelgrass survival and thus, would remain unseeded via only eelgrass restoration efforts. Restored widgeongrass had higher faunal diversity and double animal abundance per plant biomass than restored eelgrass, whereas restored eelgrass produced three times greater plant biomass per unit area and higher nitrogen recycling in the sediment.
4. *Synthesis and applications*. Overall, we provide evidence that supplementing opportunistic, generalist species into habitat restoration is a proactive approach to combat climate change impacts. Specifically, these species can increase trait diversity which, for our study, increased total habitat area restored—a key factor

to promote seagrass beds' facilitation cascades, stability, and grass persistence through changing environments. Now, we call for tests to determine if the benefits of restoration with generalist species alone or in conjunction with historically dominant taxa are broadly transferrable to restoration in other marine and terrestrial habitats.

KEYWORDS
broadcast seagrass seeding, climate change, eelgrass, marine heatwaves, seagrass restoration, widgeongrass

1 | INTRODUCTION

Reversing the decline of coastal ecosystems through habitat restoration can be a powerful technique to mitigate the loss of shoreline protection, nutrient cycling, and habitat for many ecologically and economically important species (Halpern et al., 2008; Lotze et al., 2006). Yet, there is a global need for more replicable and effective coastal habitat restoration practices as initial success rates vary widely and long-term persistence is rare (Suding, 2011; van Katwijk et al., 2016). More so, while coastal zones are inherently stressful systems, they are experiencing unprecedented stress levels from human-driven eutrophication, shifting temperature trends, and increases in extreme disturbance events (Halpern et al., 2008). We suggest that low restoration success in areas undergoing both novel human and climate disturbances may be from efforts solely using the declining habitat-forming species, rather than incorporating alternative, climate-tolerant species that are better adapted for current and future conditions.

Seagrasses are a valuable habitat undergoing rapid global decline that need novel mitigation approaches to conserve critically valued ecosystem services (Gattuso et al., 2018; Orth et al., 2020). We now know restoration efforts result in enhanced plant survival and persistence when carefully selected sites meet minimum viable thresholds for the species of interest and when plantings are done in high densities (seeds or transplants) at large enough spatial scales to enable positive feedback mechanisms (van Katwijk et al., 2016). However, in areas undergoing long-term or irreversible environmental shifts from global environmental change, local sites that meet the minimum conditions for viable restoration may no longer exist for dominant seagrass species (Kilminster et al., 2015; Turschwell et al., 2021). In these situations, when the goal is to restore lost ecosystem functions, opportunistic, generalist species that can thrive and persist in the altered environment may offer a solution. Such non-target species may not only provide short term restoration success, but through their ecosystem engineering capabilities, may also increase restoration longevity of the target species. For example, the accidental introduction of the rapidly expanding macrophyte *Hydrilla verticillata* to the Potomac River, Virginia, re-vegetated large bare areas and facilitated the recovery of many native plant and faunal species to create stable, high diversity meadows (De Mutsert et al., 2017; Patrick et al., 2018). Use of non-native species in restoration is generally not advisable, but native species with related qualities to successful invaders may provide similar benefits. We identify widgeongrass, *Ruppia maritima*, as a potentially ideal species for restoration in these situations throughout many regions worldwide.

Widgeongrass is a generalist species that is distributed across broad latitudinal ranges in both hemispheres and tolerates a wide range of salinities and temperatures (Short et al., 2007; Unsworth et al., 2022). It is a highly resilient plant and has demonstrated the ability to both rapidly recover and expand its coverage where formerly dominant species like eelgrass, *Zostera marina*, have declined (Cho & May, 2008; Hensel et al., 2023; Richardson et al., 2018). Widgeongrass can be manually seeded or planted, but its establishment under realistic environmental conditions is uncertain as well as its ability to be effectively used for large-scale restoration efforts (Ailstock et al., 2010; Cho et al., 2009; Luckenbach et al., 2011; Strazisar et al., 2013). Furthermore, we lack a clear understanding of how seagrass bed structure and function may be altered when planting widgeongrass in areas where it hasn't been historically dominant.

Here, we leveraged a planned restoration project in the lower Chesapeake Bay, United States by conducting a manipulative field experiment with widgeongrass and eelgrass and then operationalized our experimental findings during the multi-acre pilot restoration. Specifically we ask: (1) what seeding technique promoted the highest survival and growth for widgeongrass, (2) how does seagrass species identity affect seagrass bed structure and function, including microbial nitrogen cycling processes, (3) do experimental findings from small plots scale up at effective restoration spatial scales, and lastly, (4) what are the implications of our findings for the broader use of widgeongrass and other generalist species in seagrass restoration? This effort is the first large-scale attempt to plant widgeongrass in the lower Chesapeake Bay for seagrass restoration or habitat enhancement. The lower Chesapeake Bay provides an ideal place to evaluate the use of widgeongrass in seagrass restoration as it is naturally present and environmental managers are actively seeking ways to mitigate climate change impacts on local eelgrass populations that are currently threatened from rising temperatures (Orth et al., 2017). Overall, to aid long-term restoration success in the face of climate change, we test the use of a generalist seagrass as an insurance for restored seagrass habitat persistence via expanding planted seagrass coverage and maintaining ecosystem function if and when dominant seagrasses experience die-off from abrupt environmental changes.

2 | MATERIALS AND METHODS

2.1 | Experimental evaluation of widgeongrass restoration techniques

Our study was conducted in Broad Bay in the Lynnhaven River system in Virginia Beach, VA, USA (36.90418 latitude, −76.03084 longitude)—a heavily human-influenced system (Sisson et al., 2010) where practitioners are actively managing the area to improve water and habitat quality through restoration of multiple habitats including seagrass. Our site was chosen based on a combination of available leasing space and environmental conditions including sediment characteristics adhering to Chesapeake Bay's long-term, successful eelgrass restoration protocols (Marion & Orth, 2010a, 2010b; Moore et al., 2014). Additionally, Lynnhaven River shorelines were historically vegetated with widgeongrass and eelgrass, but meadows experienced declines in the early 2000s and the last observation of seagrass was an eelgrass bed in 2012 (https://www.vims.edu/research/units/programs/sav/access/maps/). However, in May 2020, small patches of natural widgeongrass were observed in Broad Bay indicating an improvement in water quality conditions just 2.5 km away from our study site (Patrick et al., 2021). As a reference site, we simultaneously conducted additional plots of each of our experimental treatments (described below) along the southern shoreline of the Goodwin Islands (37.22104 latitude, −76.38951 longitude), part of the Chesapeake Bay National Estuarine Research Reserve (CBNERR-VA) where both widgeongrass and eelgrass are currently established (Moore et al., 2001). This location was selected because it has similar site characteristics to the main study site, and it is known to be viable seagrass habitat. Thus, failure to establish widgeongrass in bare sediment at this reference site would indicate a methodological issue with the seeding technique rather than an environmental issue. The overall study occurred from October 2020—through April 2022. The experiment occurred from October 2020 to August 2021 and was followed by the Lynnhaven River pilot restoration planted in October 2021 with data collected up until April 2022 (Figure 1; Table S1). This work was conducted by employees at the Virginia Institute of Marine Science which has statutory authority under §28.2-1101.B of the Code of Virginia for its officers, agents, and employees to collect marine organisms such as seagrass whole shoots and seeds for scientific purposes including everything conducted for this study; additionally we communicated with Virginia Marine Resource Commission on the final restoration designation in the Lynnhaven River.

Widgeongrass and eelgrass seeds were collected and stored using similar procedures described in Orth et al. (2003), Ailstock et al. (2010), and Orth et al. (1994) and specific modifications for our study are in Appendix S1. At each site, we established 25, 4 m^2 experimental plots at least 5 m apart from one another in October 2020 and assigned one of five treatments with five replicates each: control (no seeds), eelgrass seeded in fall, widgeongrass seeded in fall, widgeongrass seeded in spring, or widgeongrass seeds that were given a 48-h freshwater shock prior to seeding in spring (Figure 1). The 48-h freshwater shock mimics spring freshets which are a natural cue for widgeongrass germination (Ailstock et al., 2010). Fall treatment plots were seeded in October 2020 and spring treatment plots were seeded in March 2021 for both our experimental and reference site. Our two seeding times coincide with lower Chesapeake Bay eelgrass seeding (fall) and upper Chesapeake Bay widgeongrass seeding or planting efforts (spring) (Chesapeake Bay SAV Restoration Methods: Literature review: PDF link).

For each experimental plot minus controls which were left as bare sediment, we broadcast seeded approximately 500 seeds within the 1 m^2 centre, that is hand sprinkled seeds in the water column just above the sediment, allowing a 1 m buffer area to measure grass established from our seeds (Figure 1d). To determine the best seeding technique for widgeongrass, we compared multiple seagrass establishment indicators, that is initial seedling estimates (April 2021): plot percentage survival through the end of the first growing season (June and July 2021 for eelgrass and widgeongrass, respectively), total plot areal cover, and shoot density. Importantly, widgeongrass' initial seedlings or shoots are delicate to hand manipulation which hindered our ability to verify visually if singular, isolated shoots in April 2021 were one seedling or two seedlings directly adjacent to one another; to not overestimate, isolated shoots were considered one initial seedling for widgeongrass. Lastly, at Broad Bay, Lynnhaven River in October 2020, we also transplanted wild widgeongrass and eelgrass shoots in five, 1 m^2 plots per species to aid in identifying site suitability, that is transplant survival during the entirety of our study, because there were no natural occurring beds of these species within 1 km. The transplanted shoots were collected from the same donor beds for our seed collection.

Ambient environmental conditions were monitored using an YSI EXO2 multi-parameter water quality sonde station within 50–130 m from our experimental plots collecting water temperature (°C), turbidity (NTU), salinity, and depth (m) from July 2020 to December 2021 except December 2020 to March 2021 (CBNERR-VA VIMS, 2022). In Broad Bay, water temperature data loggers (Onset® HOBO®) were stationed along the border of potential suitable restoration area and along three mean low tide depth values (0.5, 1 and 1.5 m) to help determine environmental barriers or lethal stressors for grass establishment (Figure 1e). We used 25°C and 30°C as our upper water temperature limits for eelgrass as these water temperatures have been shown to be stressful and lethal, respectively, for eelgrass in the lower Chesapeake Bay (Sheilds et al., 2019). We also monitored water clarity using Secchi discs as a potential environmental stressor for widgeongrass with no set threshold as widgeongrass is known to need high light availability (Batuik et al., 2000; Moore et al., 2014).

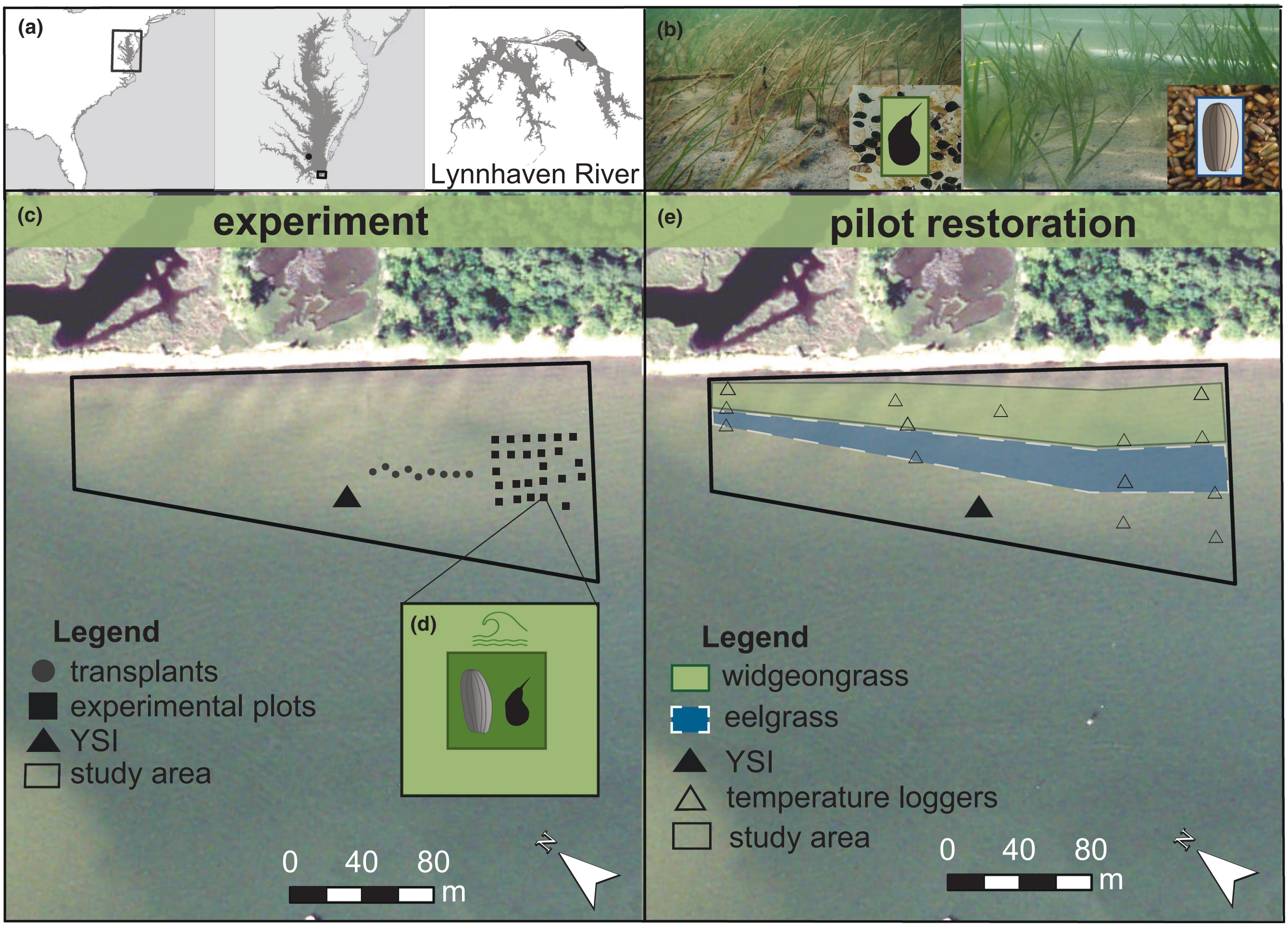

FIGURE 1 (a) Location of main experimental and pilot restoration site along the shoreline of Broad Bay within the Lynnhaven River System of the Chesapeake Bay in Virginia. Goodwin Island, VA, our reference site is indicated with a black point on the middle onset showing the Chesapeake Bay. (b) Images of widgeongrass (left) and eelgrass (right) grass and seed morphology. (c) Experimental setup from October 2020 to July 2021 where black squares represent 4 m^2 experimental seeding plots (d) that are a minimum 5 m apart from one another with either widgeongrass or eelgrass treatments had seeds broadcasted into the center 1 m^2 to allow a 1 m buffer perimeter to measure any effects from seeds that dispersed from wave action. Grey points are transplant plots planted to verify site viability for grass survivorship. (e) Same image as (c) with the seeding seagrass pilot restoration area layer that was seeded in October 2021 with data collected until April 2022 for this study. Aerial imagery of site is provided by SAV VIMS Monitoring Program. Total study area parameter is outlined in solid black. YSI stands for YSI EXO2 multi-parameter water quality sonde station and temperature loggers were Onset® HOBO®.

2.2 | Comparing restored seagrass bed structure, associated invertebrate community and ecosystem function

Seagrass bed structural differences between our experimental treatments was determined by differences in grass areal coverage, shoot density and canopy height. Measurements were collected monthly starting March 2021 until our final data collection at time of peak biomass—late June 2021 for eelgrass and late July 2021 for widgeongrass. Because we seeded our spring treatments prior to lower Chesapeake Bay's spring seedling emergence, all treatments had an equal growing season duration, and we did not need to account for any experimental seeding time difference between our fall and spring treatments. We measured the 4 m^2 area surrounding our 1m^2 plot (Figure 1) by subdividing it into 16, 0.25 m^2 subplots. For each subplot, we recorded shoot density using a haphazardly placed 0.01 m^2 quadrat and measured five randomized shoot heights to the nearest centimetre. Because we seeded the center 1 m^2 of the 4 m^2 plot but collected data over a 4 m^2 area to observe growth from seeds that were locally dispersed by wave action before settling into the sediment, our final seagrass plot area coverage (m) was calculated as the total number of subplots with at least 5% seagrass cover at peak growth season, multiplied by 0.25 m^2. To measure mean shoot density and canopy height where most seeds settled, we took the mean of the four subplots (1 m^2) that had the highest seagrass percent cover.

To measure differences in habitat provision between widgeongrass and eelgrass, epi-benthic and -phytic invertebrate fauna were collected from our fall widgeongrass and eelgrass treatments and control to measure differences in community composition, that is effective Shannon guild diversity, abundance, and biomass. This sampling was conducted after all habitat characteristic data was collected in June 2021. For each plot, we placed a mesh bag 20 cm in diameter over the seagrass to the benthos and collected the top benthic surface (<2 cm into the sediment) and aboveground plant material and froze each sample until later processed in the laboratory. All invertebrates were counted and identified to one of the following groups or guilds based on taxonomy as well as specific habitat and/or niche use: sponge (Porifera), free squirt tunicate (Tunicata), mud snail (*Ilyanassa obsolete*), *Bittium* spp. snail, mobile amphipod (Amphipoda), sessile amphipod (Caprellidae), worms (Annelida), shrimp (non-Brachyura Decapoda) and blue crabs (*Callinectes sapidus*). Faunal and plant materials were dried for 4 days at 60°C and weighed to the nearest 0.1 mg. Faunal community composition metrics were expressed on a per sample basis and calculated as a ratio to the aboveground plant biomass.

To compare differences in primary production between seagrass species, we collected one biomass core from each plot during their respective peak growth seasons. Cores were 20 cm in diameter and went 10 cm into sediment or where no more roots and rhizomes were observed. Core location was representative of the four subplots with the highest seagrass cover. In the laboratory, plant material was separated into above- and belowground biomass with epiphytic algae scraped off the blades. Seagrass material was dried for 4 days at 60°C and weighed to the nearest 0.1 mg.

To measure selected microbial nitrogen cycling processes, sediment cores were collected in triplicate from our fall widgeongrass and eelgrass treatments and control in fall October 2020, spring April 2021, and peak growth season which was June 2021 for eelgrass and July 2021 for widgeongrass. At each of the plots, cores were collected within one of the four subplots that had the highest seagrass percent cover. Core collection tubes were fashioned from plastic 50 mL falcon tubes to collect the top 5 cm of sediment and placed on ice until returned to the lab and homogenized. To measure the rates of denitrification (DNF; nitrogen removal) and dissimilatory nitrate reduction to ammonia (DNRA; nitrogen recycling), sediment slurry incubation experiments were conducted as described by Song and Tobias (2011) and Fortin et al. (2021); details are reported in Appendix S1.

2.3 | Seagrass restoration pilot

For our large-scale restoration pilot at Broad Bay, Lynnhaven River, suitable habitat to grow seagrass was constricted by various environmental characteristics observed during the experiment including water temperature, clarity, depth, and physical disturbances within available space for restoration. Overall, our pilot restoration area totaled 7761 m^2 with grass species seeded into two monocultures directly adjacent to one another (Figure 1e). In October 2021, we dispersed 90 widgeongrass seeds per m^2 over a total area of 3837 m^2 close to the shoreline with a mean low tide depth from 30 to 50 cm and 50 eelgrass seeds per m^2 over a total area of 3924 m^2 in areas with a mean low tide depth from 50 to 150 cm. The shallower zone where we seeded widgeongrass, temperatures above 25°C were observed for 133 days and reached 30°C for total of 40 days whereas our area selected to grow eelgrass encountered above 25°C for 119 days and reached 30°C for total of 30 days.

To compare and test the scalability of our experimental outcomes to the larger spatial scale of our restoration efforts, in April 2022 we collected initial seedling percentages, that is the proportion of seedlings to seeds dispersed, a seagrass establishment indicator to compare our pilot restoration to 69 restorations throughout the Chesapeake Bay from 2015 to 2020 (Orth et al., 2020). Because the restoration pilot overlapped with our experimental area, we excluded our experimental and transplant plots to avoid overestimation of April 2022 initial seedling percentages.

2.4 | Statistical analyses

Data were analysed with R version 4.2.1 (RStudio Team, 2022). To describe the effect of our experimental restoration technique treatments on bed structure measurements we fit three linear models allowing treatment to predict final bed area, shoot density and canopy height. We did not include data from our Goodwin Island site into our analyses because wild widgeongrass and eelgrass runners from adjacent meadows colonized our plots, confounding our experimental treatments. To quantify seagrass species effects on fauna, we fit three linear models allowing treatment to predict effective Shannon guild diversity using the hillR R package (Chao et al., 2014), abundance, and biomass. To understand changes in primary production and nitrogen cycling, we fit three linear models allowing species identity to predict final total plant biomass as well as sediment nitrogen recycling (DNRA) and removal (DNF). One-way ANOVAs were conducted to assess main effects and Tukey's test were used for post-hoc multiple comparisons. Normality of the residuals and heterogeneity of variances were checked prior to data analyses using Kolmogorov–Smirnov normality test as well as the Performance R package (Lüdecke et al., 2021).

3 | RESULTS

3.1 | Widgeongrass seeding techniques

Widgeongrass plots seeded in the fall with no pre-seed treatment had the highest mean plot survival, areal cover, and shoot density within the first growing season (Table 1; Figure 2). Transplant shoots of widgeongrass and eelgrass all survived during the duration of our experiment providing evidence our Broad Bay site is conducive for widgeongrass and eelgrass to grow and survive. These results show that any environmental differences between the study and reference (Goodwin Islands) site did not influence our response variables; temperature and water clarity during the study are shown in Figure S1. For our reference site, we only measured seeding technique responses from plots not confounded by natural colonization.

TABLE 1 To help determine which widgeongrass seeding technique had the most optimal outcome from our experiment, we compared mean treatment plots percent survival, areal cover (m^2), and shoot density (per 0.01 m^2) in July 2021 ($n=5$ per treatment).

Treatment per site	Plot survival %	Areal cover	Shoot density
Eelgrass			
Broad Bay	100	3.10 ± 0.34	11.55 ± 0.64
Goodwin Island	100	2.75 ± 0.16	3.75 ± 0.54
Widgeongrass (fall)			
Broad Bay	75	2.05 ± 0.68	6.95 ± 2.26
Goodwin Island	100	2.50 ± 0.73	1.70 ± 0.97
Widgeongrass (spring)			
Broad Bay	100	0.25 ± 0.18	3.00 ± 2.76
Goodwin Island	80	1.17 ± 0.30	1.45 ± 0.35
Widgeongrass (spring) 48-hour freshwater shock			
Broad Bay	25	0.15 ± 0.10	0.15 ± 0.15
Goodwin Island	80	1.30 ± 0.51	0.85 ± 0.26
Control			
Broad Bay	–	–	–
Goodwin Island	–	1.42 ± 0.48	–

Note: Values after means are stand errors. The symbol '–' is used below if there was no data to collect or collected.

3.2 | Structure and ecosystem function comparison between widgeongrass and eelgrass

Restoration seagrass seeding technique affected seagrass total area cover ($F_{(3,15)}=12.14$, $p<0.01$), shoot density ($F_{(3,15)}=9.0$, $p<0.001$), and canopy height ($F_{(3,9)}=83.0$, $p<0.001$; Figure 2). Specifically, fall-seeded widgeongrass with no pre-seed treatment and fall-seeded eelgrass had the largest areal growth while both spring widgeongrass plots produced negligible or highly variable coverage. Fall widgeongrass and eelgrass also had the highest shoot density (Figure 2). Lastly, eelgrass had a significantly higher canopy height than any widgeongrass plot (Figure 2). No grass was found in unseeded control plots at Broad Bay.

Fall widgeongrass had higher faunal guild diversity ($F_{(1,8)}=55.0$, $p<0.001$) and abundance ($F_{(1,8)}=14.7$, $p<0.001$) than fall eelgrass per plant biomass (g) (Figure 3). We found no differences between seagrass species for total faunal biomass (g) per plant biomass (g) (mean 0.36 ± 0.22 fall widgeongrass, mean 0.62 ± 0.37 eelgrass; $F_{(1,8)}=0.37$, $p=0.56$) as well as mean individual biomass of each organism (g) per plant biomass (g) ($F_{(1,8)}=1.9$, $p=0.2$; Figure 3). No fauna were observed in bare sediment control plots.

For plant biomass, all widgeongrass treatments produced less than 25% biomass compared to eelgrass ($F_{(1,6)}=10.71$, $p=0.02$; Figure 4). For sediment microbial nitrogen cycling activities, we conducted analyses on samples from our final data collection. Nitrogen recycling (DNRA) was enhanced by eelgrass and reduced by widgeongrass compared to bare sediment control ($F_{(2,10)}=4.33$, R^2-adj $=0.36$, $p=0.04$; Figure 4). Nitrogen removal (DNF) from the sediment microbial community was not affected by either grass species ($F_{(2,10)}=2.31$, $p=0.15$; Figure 4).

3.3 | Pilot restoration and comparisons to other chesapeake bay eelgrass restorations

In Spring 2022, we successfully restored 0.38 ha of widgeongrass and 0.39 ha of eelgrass. Our initial seedling percentages for the pilot restoration, a main seagrass establishment indicator used in the lower Chesapeake Bay, paralleled our experimental findings (Figure 5). While widgeongrass seedling percentages (initial establishment indicator) were lower than our study's eelgrass estimates, they were within range of previous eelgrass restoration efforts (Figure 5).

4 | DISCUSSION

We show that incorporating a generalist, heat-tolerant seagrass can enhance habitat restoration in a changing environment by expanding total habitat area restored and increasing biodiversity. In our seagrass system, we found widgeongrass can be grown from broadcast, hand seeding at both experimental and restoration spatial scales and these methods were as effective when compared to past seeding efforts of eelgrass in our study area. Seed timing was important for widgeongrass restoration, with fall seeding being the optimal period (Figure 2). Our experimental results demonstrate that, while both species cover similar bottom area within their first growing season, there were structural and functional differences primarily observed through habitat provision for invertebrate fauna and primary production. For the restoration pilot, initial seedling percentages for both species mirrored experimental observations, suggesting our techniques and experimental findings scale up to effective restoration size. Furthermore, total area seeded, or suitable restoration

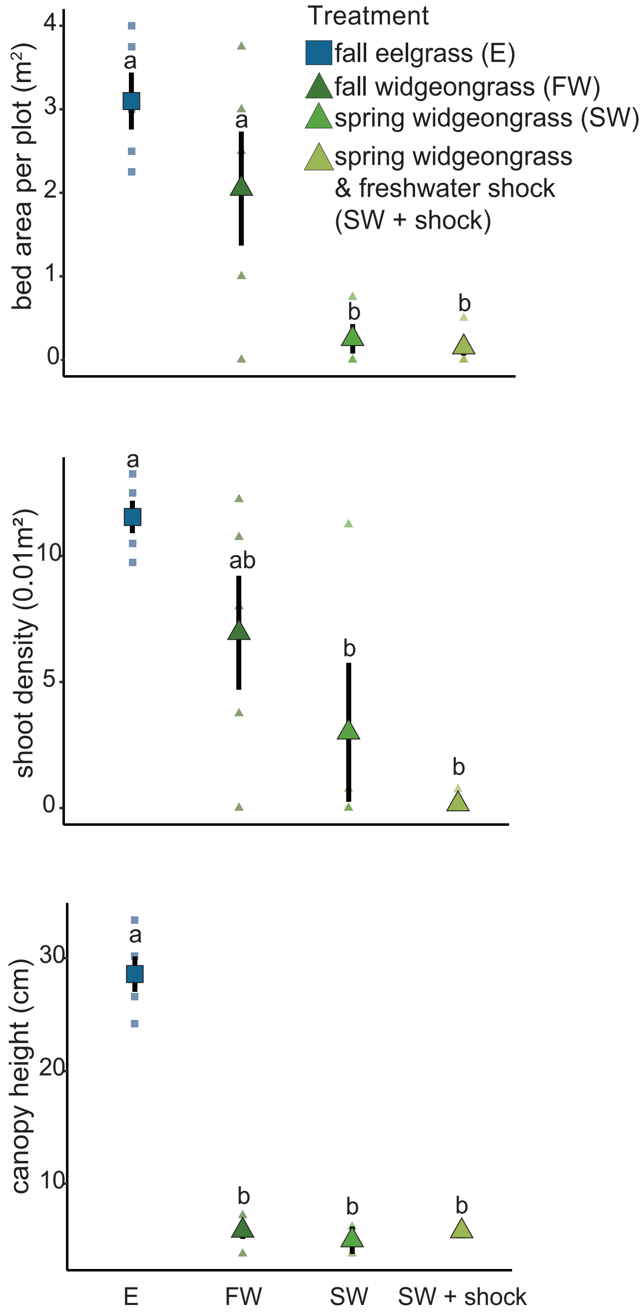

FIGURE 2 Total bed area cover is altered by planting season ($F_{(3,15)} = 12.14$, $p < 0.01$). Shoot density is altered by both planting season and seeding method ($F_{(3,15)} = 9.0$, $p < 0.001$). Canopy height is altered by seagrass species ($F_{(3,9)} = 83.0$, $p < 0.001$). The letters above the standard error bars represent statistically similar groups according to Tukey's HSD at $\alpha = 0.05$. Means are calculated from the five replicate plots per treatment for each grass species' respective peak growth season, that is June 2021 for eelgrass and July 2021 for widgeongrass; individual replicates are shown as transparent points.

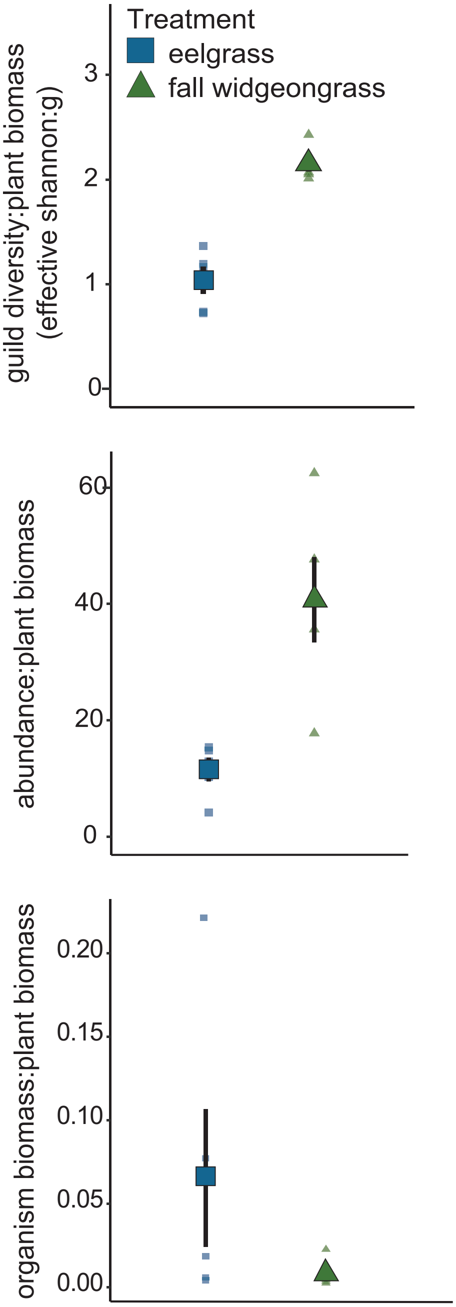

FIGURE 3 Invertebrate guild diversity to plant biomass ratio ($F_{(1,8)} = 55$, $p < 0.001$) and invertebrate abundance per plant biomass were higher in widgeongrass restoration plots than eelgrass ($F_{(1,8)} = 14.7$, $p < 0.001$) in late June 2021. Biomass of individual organisms to plant biomass ratio was not altered by seagrass species ($F_{(1,8)} = 1.9$, $p = 0.2$). Mean and standard error are calculated from the five replicate plots per treatment; individual replicates are shown as transparent points.

habitat, increased 98% by seeding widgeongrass in shallow areas where persistent high-water temperatures would likely be unsuitable for eelgrass. The combination of finding widgeongrass can establish at an effective restoration scale as well as widgeongrass' global distribution and tolerance to wide ranges in environmental conditions, support widgeongrass in being a promising candidate species for seagrass conservation in the face of climate change. Broadly, we show that using opportunistic, generalist species in habitat restoration is an effective approach to increase foundation species diversity and restored habitat area, which can then promote facilitation cascades (Valdez et al., 2020), stability (Lefcheck et al., 2017), and overall habitat persistence through changing environments.

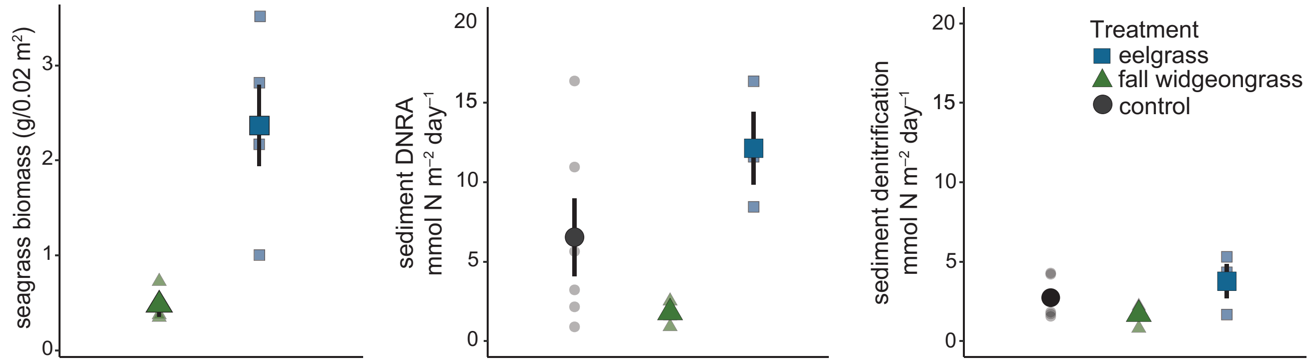

FIGURE 4 Total plant biomass collected at peak growth season (i.e., June for eelgrass and July for widgeongrass) is altered by seagrass species ($F_{(1,6)}=10.71$, $p=0.02$; $n=5$ replicates per treatments). Also during peak growth season, sediment nitrogen recycling (DNRA) was enhanced by eelgrass and reduced by widgeongrass compared to bare sediment control ($F_{(2,10)}=4.33$, R^2-adj$=0.36$, $p=0.04$; $n=3$ replicates per treatment). Nitrogen removal (DNF) from the sediment microbial community was not affected by either grass species ($F_{(2,10)}=2.31$, $p=0.15$; $n=3$ replicates per treatment). Error bars are standard error; individual replicates are shown as transparent points.

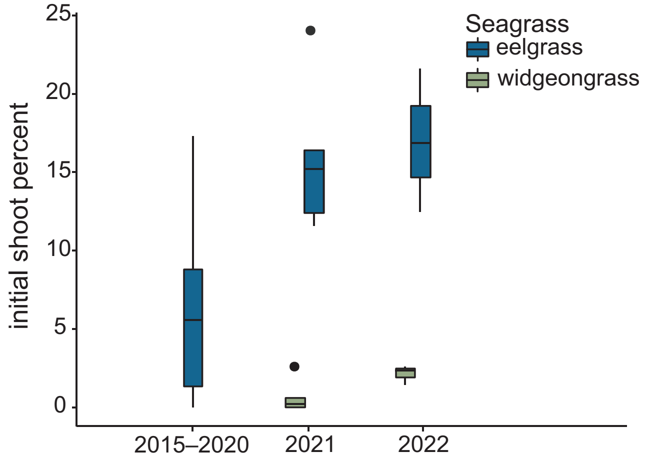

FIGURE 5 Standard boxplots comparing all initial shoot or seedling percentage estimates from identified eelgrass restoration efforts in the lower Chesapeake Bay, USA from 2015 to 2020 ($n=69$) and our study's estimates from our 2021 experimental plots (fall eelgrass and widgeongrass plots only) as well as 2022 pilot restoration. Estimates from eelgrass restoration from 2015 to 2020 varied in restoration spatial scale and seeding density which ranged from 25 to 100 seeds dispersed per m^2. Our experimental plots ($n=5$ per species) seeded in 2021 had 500 seeds per m^2 dispersed, and for our 2022 pilot restoration we seeded 50 eelgrass seeds per m^2 and 90 widgeongrass seeds per m^2. We had three replicate estimates for each species for our 2022 pilot restoration estimates where total seeded area was evenly divided into three areas. Standard boxplots show interquartile range with median represented by a black horizontal line; error bars show minimum and maximum values without boxplot outliers which are shown by points.

4.1 | Seeded widgeongrass can establish at effective restoration spatial scales

We strategically focused on testing the most optimal seed-based restoration approach because we were able to directly compare widgeongrass to decades of eelgrass' broadcast-seeding outcomes and, when available, seed-based habitat restoration is inherently the most cost-effective, large-scale restoration approach (van Katwijk et al., 2016). Seeds can also be easily transported to seagrass depauperate areas for restoration efforts; however, we stress ecological and genetic diversity implications of the (re-)introduced material should first be considered (van Katwijk et al., 2021).

For our investigation on broadcast seeding technique, widgeongrass establishment, growth, and survival over its first growing season was exceedingly higher when seeded in the fall with no pre-seed treatment (Table 1). This is an advantageous finding for restoration practitioners because the most effective method requires the least maintenance and time. The better performance from our fall seeded widgeongrass is likely from a combination of overwintering and retaining a closed, seed shape when seeded, that is the seeds were not germinated with a cracked-open seed shell prior to seeding. By overwintering, seeds had adequate burial time without seed predators present (Fishman & Orth, 1996) and were exposed to a natural winter cycle of temperatures and oxygen conditions for emergence cues (Orth et al., 2000). However, optimal seeding season for widgeongrass restoration has not been extensively explored, and we suggest more research is needed. With the seeds remaining whole, that is seed shells were not cracked open or germinated from a pre-seed freshwater shock treatment, seed loss was minimized. Seeds were heavier and more hydrodynamically shaped to sink and more readily settle and root within the sediment; cracked-open, germinated seeds are more vulnerable to being lifted and dispersed by waves to potentially less ideal environmental conditions for establishment.

By operationalizing our experimental findings into a pilot restoration (~1 ha), we found our experimental results are scalable—showing that seeding widgeongrass is a viable option for seagrass restoration efforts. Widgeongrass performance matched eelgrass, having similar shoot densities and ground cover by its peak growth season even though spring seedling estimates (i.e. a seagrass establishment indicator) were 23 times lower than eelgrass. This vast difference in seedling percentages may simply be from widgeongrass having a later seedling emergence than eelgrass for our study system (Moore et al., 2014). Moreover, our widgeongrass seedling percentages were within median range estimates of Chesapeake Bay eelgrass restoration efforts conducted from 2015 to 2020 (Figure 5). While the pilot's seedling percentages mirrored the experiment, a notable difference was widgeongrass estimates were four times greater at the restoration scale than the experiment within the first 5 months after seeding (Figure 5). We hypothesize that by seeding widgeongrass over a larger area for the pilot restoration, we enabled seagrass positive feedback mechanisms including increases in root stabilization from physical disturbances (e.g. wave action and bioturbators; Carr et al., 2010).

4.2 | Restored widgeongrass and eelgrass differ in structure and function

Habitat structural complexity was altered by seagrass species, which can translate to differences in faunal habitat provisioning. Specifically, our data show widgeongrass plots had higher fauna abundance and diversity than eelgrass, while eelgrass appeared to harbour larger individuals (Figure 3; Hovel et al., 2002). We determined widgeongrass' structural complexity has higher morphological diversity than eelgrass because its branching shoots increase surface area to volume ratio compared to eelgrass' single, ribbon-like blades. Additionally, widgeongrass grew unevenly in patchy distributions, providing three types of unique microhabitats: dense grass, sparse grass, and bare sediment. Eelgrass grew in relatively even, dense monocultures providing one habitat type: dense grass. In nearshore ecosystems, faunal diversity often mirrors its habitat structural diversity as these fauna are dependent on both habitat type and its morphology (Boström & Bonsdorff, 2000). For example, many tropical coral reef fishes have high site fidelity to reefs that have refuge areas matching their body size and shape (Eggleston et al., 1997). For eelgrass habitat provision, our data were highly variable but suggest eelgrass harboured larger individuals than widgeongrass, specifically individual blue crabs (*Callinectes sapidus*). Parallel with previous research, our eelgrass plots likely provided better protection for adult blue crabs to hunt than our widgeongrass plots with their dense, continuous shoots and high canopy (Hovel & Lipcius, 2001).

Structural differences may also explain differences in primary production and microbial nitrogen cycling between seagrass species. Primary production, here estimated as the total biomass produced at each species' peak growth season, was five times less per area for widgeongrass than eelgrass. The difference in biomass is expectedly from widgeongrass having a less extensive root and rhizome system as well as thinner leaf morphology than eelgrass. The former is generally the case when comparing any opportunistic grass species to more stable, dominants as the two life histories have different energy allocation strategies for growth and establishment. While widgeongrass will almost always have less biomass per area than eelgrass, the magnitude of this difference may decrease with bed age. In our study system, for example, wild widgeongrass' shoots grow much taller canopies (*observations in Broad Bay*, ~20–50 cm in length) in their second growing season compared to a widgeongrass bed's first established shoots, which were our final experimental measurements. The observed plant biomass disparity from eelgrass to widgeongrass plots also likely explain why eelgrass plots recycled more nitrogen (DNRA) than widgeongrass within the sediment (Figure 4). Our findings are helpful in the context of seagrass restoration when seeding in a bare bottom area. When eelgrass beds are initially reintroduced, their nitrogen recycling ability that increases available nitrogen is only beneficial under oligotrophic or nutrient poor conditions. In eutrophic or nutrient-rich conditions, like areas that are typically in need of coastal management including planting seagrass, this positive feedback may experience a directional shift by promoting macro- and epi-algal growth, and thus create resource competition between grasses and algae. In the same context, the small reduction in available nitrogen observed in our widgeongrass plots (Figure 4) may be evidence of how the presence of opportunistic grass species can increase the chances for successful establishment and persistence of the targeted, lost species, by directing ambient nutrient conditions more conducive for grass than algal growth within human-influenced or eutrophic areas (Lee et al., 2007).

4.3 | Integrating opportunistic, generalist species for proactive seagrass restoration

By using native, generalist species for seagrass restoration, efforts are able to provide lost functions while maintaining native species assemblages, restore seagrass habitat where conditions are no longer conducive for historically dominant seagrasses, and in some cases, facilitate the recovery of the lost, targeted species via ecosystem engineering (Cho et al., 2009; Derksen-Hooijberg et al., 2018; Lefcheck et al., 2017; van Katwijk et al., 2016). For our pilot restoration, we revegetated 98% more space by seeding widgeongrass in the high temperature shallows adjacent to eelgrass. We also mimicked the natural extant seagrass meadows of the lower Chesapeake Bay as they are undergoing dominant species shifts from eelgrass to widgeongrass (Hensel et al., 2023). The use of opportunistic species in seagrass restoration, particularly widgeongrass, has been controversial among seagrass experts due to their unpredictable, ephemeral nature (Trussell et al., 2006). However, at the most extreme, in areas where the lost species may never be able to reestablish, planting and maintaining opportunistic species through routine restoration management can still provide habitat and other critical seagrass services (Beck et al., 2011; Rinkevich, 2005; Török et al., 2021; Van Kooten et al., 2005). Conservatively, we argue by planting opportunistic species complimentary with the target, dominant species in restoration efforts, restored beds will be more stable by proactively creating seagrass meadows that are resistant to rapid environmental changes like rising temperatures. Specifically, the persistence of grass, regardless of species, is key in seagrass ecosystems as they rely on positive density dependence mechanisms including shoot density thresholds for successful reproduction (Angelini et al., 2011; Van Tussenbroek et al., 2016), density of algal grazers present (Lefcheck et al., 2017), and effective sediment retention and particle capture that decreases water turbidity (Orth et al., 2020). Therefore, as human activity and climate change impacts continue to amplify unconducive conditions for declining seagrasses, using alternative species that can survive rapidly shifting environments will aid in restoration success, maintenance of ecosystem function and desired services, and create conditions conducive for the reintroduction of the lost dominant species.

AUTHOR CONTRIBUTIONS

Enie Hensel, Christopher J. Patrick, and Robert J. Orth conceived the ideas and designed methodology; Bongkeun Song designed methodology for sediment microbial nitrogen activities; Enie Hensel, Stephanie J. Wilson, and William G. Reay collected and analysed the data; Enie Hensel led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. Our study includes authors and partners from a diversity of Chesapeake Bay stakeholders from state, federal, academia and conservation agencies and organizations.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.n5tb2rc3m (Hensel et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Daily mean water quality data (derived from 15 min interval data) during the experimental study from October 2020 to the end of September 2021 (denoted with the vertical grey line).

Table S1: Timeline by year and month for both the 2020–2021 experiment and 2021–2022 pilot restoration study.

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