Facilitation between two dominant ecosystem engineers extends their footprints and degree of overlap

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A B S T R A C T

Ecosystem engineers influence the habitat, diversity, and productivity of ecosystems. However, multiple ecosystem engineers may coexist, and because of their dominant influence, how they interact can affect the entire system. In the southeastern US, the eastern oyster, *Crassostrea virginica* (Gmelin) and coarse cordgrass, *Spartina alterniflora* (Loisel) are two prominent ecosystem engineers that affect estuarine ecosystem functioning. Despite both species' importance and their proximity to one-another, few studies have focused on bidirectional interactions between these two species. First, we assessed the potential effect of fringing oyster reefs on adjacent cordgrass stands. We found that when tidal creek banks are occupied by oysters, cordgrass horizontally extends towards the water 5.25 m more (often overlapping with the oysters) than adjacent bank areas that were lacking oysters. Ostensibly, the positive effect of oysters to increase cordgrass occupancy is due to known abilities of oysters to stabilize shoreline, baffle hydrodynamic energy, and accrete sediment. Second, we experimentally examined the effects of cordgrass on oysters using the presence and absence of cordgrass and cordgrass-mimic treatments to parse the mechanistic effects of structure and shade provided by cordgrass. We found that oysters recruited 2.4 times more and increased biomass 3.2 times more underneath natural cordgrass and shade mimics compared to plots with cordgrass removal and structure-only mimics. Thus, cordgrass shade is an important mechanism of facilitation, especially on small recruiting oysters that are vulnerable to desiccation. Collectively, the mutualism between these two engineers expands their footprints and amount of overlap, strengthening their presence and thus their ecosystem services to the estuary.

1. Introduction

Ecosystem engineers play important roles within ecosystems by modifying the environment (Jones et al., 2010; Jones et al., 1994) and shaping ecosystem functions (Byers et al., 2006; Crain and Bertness, 2006). Autogenic ecosystem engineers, such as trees and coral reefs, affect ecosystems by growing biomass and creating structure (Hedin et al., 1988; Jones et al., 1994; Wild et al., 2011). This autogenic structure can influence species assemblages, potentially enhancing community diversity and productivity (Naiman, 1988, Jones et al., 1994, Bertness, 1984). As a result, particularly in areas that otherwise lack much structure, the presence of ecosystem engineers can substantially influence ecosystem functioning by affecting processes such as energy flow and nutrient cycling (Bruno and Bertness, 2001; Gutiérrez et al., 2011; Hastings et al., 2007).

If systems include more than one ecosystem engineer, their effects may combine additively or synergistically, or they may negate one another's effects. For example, ecosystem engineers can form hierarchies whereby the effects of secondary engineers are dependent on the presence of the first (Bishop et al., 2012). These are known as facilitation cascades, where multiple engineers interact hierarchically, affecting system diversity and ecosystem functioning (Altieri et al., 2010). But it is equally possible that ecosystem engineers, which are often the primary space occupiers, would compete. For example, black mangroves, which are an important ecosystem engineer, are expanding northward in Florida USA invading salt marshes and displacing the existing ecosystem engineer *Spartina alterniflora* (Chen et al., 2020; Smith et al., 2021; Smith et al., 2018). Thus, understanding the net interaction between engineers and the mechanisms governing their interactions may help to better quantify and understand their net effects on a system. Synergistic linkages between adjacent intertidal habitats are well understood (Skilleter et al., 2005, 2017; Irlandi and Crawford, 1997; Bertness, 1984), however, given the complexity of interacting structural, abiotic, and biotic feedbacks among engineers, small perturbations in abiotic stress (e.g.,

temperature) that affect engineers could have broad scale ecological implications (Jones et al., 2010).

Here we quantify how two dominant, adjacent ecosystem engineers affect one another. The eastern oyster, *Crassostrea virginica* (Gmelin, hereafter: oyster) and coarse cordgrass, *Spartina alterniflora* (Loisel, hereafter: cordgrass) are autogenic ecosystem engineers native to US East and Gulf Coasts. Both species create structural complexity, often in areas that would otherwise be devoid of structure. Cordgrass thrives in a polyhaline environment that few marsh plants can tolerate, and oyster reefs create structure both in the intertidal and subtidal zones, often on mud substrate with little to no existing aboveground structure (Byers et al., 2015; Coen et al., 1999; Grabowski et al., 2012; Zu Ermgassen et al., 2012a). Both oysters and cordgrass attenuate wave and current energy, helping to stabilize creek banks (Coen et al., 1999, Grabowski et al., 2012, Bruno and Bertness, 2001). By reducing current speed, cordgrass also facilitates the settlement of suspended particulate matter, thus increasing marsh accretion (Angelini and Silliman, 2012; Byers et al., 2015). Both species also create habitat for many species, and are of particular interest economically, as they provide nursery habitat for commercially important fish and shellfish (Grabowski et al., 2012; Irlandi and Crawford, 1997). Both species are carbon sinks (Davis et al., 2015; Fodrie et al., 2017; Grabowski et al., 2012), via the below-ground storage of cordgrass biomass and via the production of oyster shell material (which can last for thousands of years).

Oyster and cordgrass distributions at estuarine scales are often governed by tidal elevational gradients (Morris et al., 2002). Specifically, tides govern exposure to wave and current energy, soil hypoxia, competition with other species, heat stress, inundation time, and exposure to predators. For instance, oysters experience greater predation pressure from aquatic species than terrestrial species, and as a result, predation pressure increases at lower elevations due to increased inundation duration and exposure to aquatic predators (Fodrie et al., 2014). This gradient in predation intensity in many areas sets the lower distributional limit of oysters (at approximately mean lower low water, MLLW: Ridge et al., 2015). At higher tidal elevations, physiological stress associated with emersion increases (Ridge et al., 2017; Bahr, 1976) and sets the upper distributional limit of oysters (at approximately mean sea level, MSL: Ridge et al., 2015). Cordgrass at its upper tidal elevation limit (approximately mean higher high water) is outcompeted by less salt-tolerant species that are physiologically restricted to the upland-marsh boundary. The cordgrass lower limit (approximately MSL) is a result of increasingly hypoxic soils (Morris et al., 2002) and habitat loss from sediment erosion (Meyer et al., 1997). Thus, although oysters and cordgrass segregate along the elevational gradient, they have a small range of overlap near MSL. This habitat edge results from the physiological constraints that govern their distributions. Moving down in elevation, the relatively flat saltmarsh dominated by cordgrass ends and is replaced by steep mud banks that are often dominated by intertidal oyster reefs, with relatively sharp edges between both habitats (Bahr, 1981). In estuaries with tidal creeks, most oyster reefs occupy mid- to low-intertidal banks that are steeply sloped and typically adjoin cordgrass stands at MSL. In these habitats, given the close proximity of both engineers, and their dominance on the landscape, it is likely that they influence one-another's distributions.

Oyster reefs create structure that baffles and absorbs water energy (Coen et al., 2007; Grabowski et al., 2012; Zu Ermgassen et al., 2012b). Although oyster reefs likely protect the waterward edge of cordgrass marsh stands (Bahr, 1981; Ridge et al., 2017; Chowdhury et al., 2019), few empirical studies have quantified this relationship. Piazza et al. (2005) found that intertidal restored oyster reefs created a wave energy shadow between the reef and the marsh, facilitating cordgrass waterward expansion in low energy environments, whereas Meyer et al. (1997) found a similar pattern, but only at some restored reefs. Scyphers et al. (2011) found experimental subtidal oyster sills or breakwaters reduced marsh edge erosion by 40% at one site, but in general were not effective at erosion control. All of these studies were done with restored

reefs, and are not necessarily directly comparable to more established natural reefs. Walles et al., 2015 found the non-native, but established Pacific oyster (*Crassostrea gigas*) in the Netherlands increased mudflat elevation on the leeward side of naturally occurring oyster reefs. However, the study sites in the Netherlands lack fringing cordgrass (oysters and cordgrass are over 500 m apart). Thus, to our knowledge no studies have directly measured to what degree natural fringing oyster reefs affect the horizontal extent of cordgrass.

Here we quantify the bi-directional engineering effects of (1) cordgrass on oyster vital rates and performance and (2) natural fringing oyster reefs on cordgrass distribution. We hypothesize that contiguous cordgrass benefits oyster recruitment and growth at the upper, vertical end of oyster reefs by reducing heat stress and providing enhanced structure for retention of recruits and attenuation of hydrologic energy. We hypothesize that sediment accretion, wave attenuation and bank stabilization by oysters increase cordgrass habitat. Finally, we predict that, because of these facilitative interactions between the two species (present especially when intertidal creek banks are steep sloped), their footprint at the adjoining edge expands relative to areas where they exist alone, resulting in increased spatial overlap between them.

2. Materials & methods

2.1. Effect of cordgrass on upper-reef oysters

To examine the mechanisms driving the effect of *Spartina alterniflora* (hereafter: cordgrass) on *Crassostrea virginica* (hereafter: oyster), we manipulated patch overlap between oysters and cordgrass through a cordgrass removal experiment. The experiment was conducted on ~300 m wide Walburg Creek, St. Catherines Island, Ga (31.67603° N, 81.16085° W), with a mean tide range of 2.108 m (data from Fort Pulaski, Ga). A 1 km long site was chosen for its consistent bank orientation (east-facing), bank slope (~18°), sheltered (back island) location, consistent oyster and cordgrass presence, and focal species overlap. Our treatments consisted of (i) cordgrass control, (ii) bare ground, (iii) structure mimic, (iv) shade mimic, and (v) shade and structure mimic (Fig. 1). These five treatments were devised to discover (A) if cordgrass affects oysters by comparing the control to the bare ground treatment, and (B) if there was a response, what was the driving mechanism, by comparing the bare ground and cordgrass control treatments to each of the mimic treatments. The mimic treatments use purely physical means (i.e., divorced of biology) to parse the influence of two likely mechanisms of cordgrass effect on oysters—structure and shade provisioning. Each treatment plot was a semicircle (1 m radius/1.57m²) at the waterward edge of the cordgrass zone abutting the oyster reef (Fig. 1). Plots were separated by at least 5 m and the center of all plots had an average elevation of 0.09 m above mean sea level (0.02 m above NAVD88). The elevation difference across plots was <0.47 m, or between 42% and 58% time exposed to air. To ensure adequate interspersion of replicate plots of each treatment along the experimental domain, we used a randomized complete block design, dividing the bank into 9 adjacent blocks, with each block containing one replicate of 5 treatments, the position of which was randomly assigned within each block. Thus, there were a total of 45 plots, with each treatment replicated 9 times.

In all treatments other than the cordgrass control, we clipped and removed all aboveground cordgrass by hand and kept the plots free of aboveground vegetation by weekly clipping throughout the duration of the experiment. Cordgrass control plots were not manipulated. For the bare ground treatment, other than cordgrass removal, no further alterations were made. For the shade treatment, we measured out a central 1m² plot and added PVC poles to each plot corner and center. PVC poles were used to support a 1m² piece of construction tarp, 1 m off the ground. The tarp was perforated with a grid of 121, 0.03 m diameter holes, which was designed to let through the same amount of light as neighboring cordgrass stands (as measured with a light meter), while
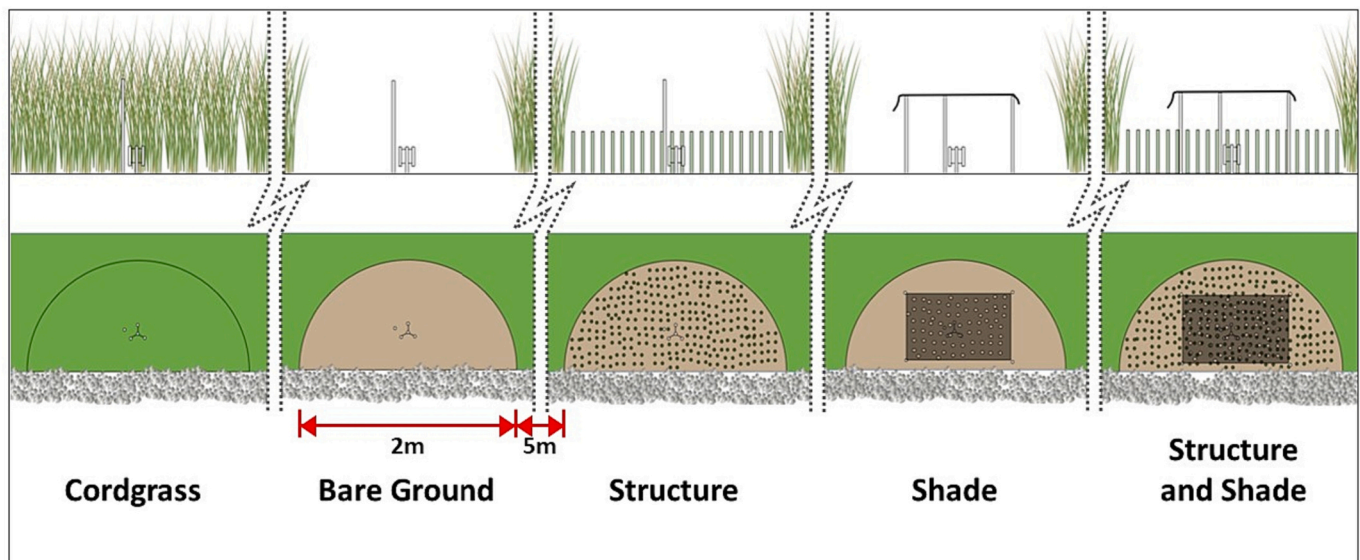
Fig. 1. Manipulative field experiment design. Top row shows side view of each manipulation, bottom row shows bird's eye view of the corresponding manipulation (note: lightning bolts indicate that separation between plots are not drawn to scale). There were five cordgrass treatments. Cordgrass was removed from all treatments, with the exception of the Cordgrass plot (left) which was unaltered as a control. Remaining treatments from left to right include: Bare ground – no artificial cordgrass addition. Structure – bamboo sticks added to simulate cordgrass structure. Shade – a tarp added to simulate cordgrass shade. Shade and Structure – a tarp and bamboo sticks added to simulate cordgrass shade and structure. All plots had a diameter of 2 m and were separated by at least 5 m.

minimizing effects on water movement. For the structure mimic treatment, we created a grid of bamboo sticks (0.6 m tall, approximately 8 mm in diameter, with a density of $160/m^2$) to fill the plot to simulate natural cordgrass density, to baffle water currents while minimizing shading. Finally, for the shade and structure treatment, we added both the tarp and the bamboo sticks as described above (Fig. 1). The experiment ran from June through October 2016.

To measure differences in oyster recruitment and growth between treatments we deployed one spat-collecting trident in the center of each treatment (spat are newly recruited oysters). Spat tridents were constructed from a 0.5 m central structural support PVC pole, at the top of which were attached three 15 cm vertically oriented spat sticks (PVC pipe infused with corrugated cement, 15 cm length, 2 cm diameter, 94 cm^2). Collective spat stick total surface area was $0.028m^2$ on each spat trident. Each spat trident was deployed for the duration of the 4-month experiment to quantify oyster post-recruitment abundance, biomass, and growth. As a result of sizable oyster clusters growing over the 4-month deployment, it was impossible to count every oyster by eye. We therefore disassembled spat tridents to photograph all three spat sticks from each trident. One side of each stick was haphazardly chosen and photographed ($0.014m^2$ per plot). The length of each oyster was measured using ImageJ (Schneider et al., 2012). Spat recruitment was estimated by counting the number of oysters (per $0.014m^2$). Average spat growth was estimated by calculating the mean oyster length per plot. Biomass was estimated by using the length to mass ratio from Grabowski et al. (2020).

Biomass (g) = 0.0008 x Oyster length (mm)$^{2.2224}$

All lengths from a spat trident were input and then summed to compute biomass per $0.014m^2$. Finally, we estimated maximum oyster size by calculating the mean of the largest 15 oyster lengths per plot (5 oysters from each spat stick). Lastly, to help facilitate the ease of comparison with other studies, we standardized the recruitment and biomass data from per $0.014m^2$ to $0.01m^2$.

Analyses were conducted in R version 4.1.2 (R Core Team, R, 2013). We used four separate ANOVAs to evaluate the effects of block and treatment on spat recruitment, biomass, average growth, and maximum size. If not significant, block was removed from the model. The data

were tested for, and met assumptions of normality and homogeneity of variance (analyzed using Shapiro-Wilk's and Bartlett's tests, respectively). We used Tukey's HSD to assess which pairwise comparisons contributed to significant overall effects. All graphics were created in R using the ggplot2 package version 3.3.5 (Wickham, 2016).

2.2. Effect of oyster reefs on extension of cordgrass edge

To measure the effect of oysters on cordgrass extension from the marsh, we compared the horizontal distance from cordgrass' waterward edge to the center of the adjacent water channel, between intertidal banks with fringing oyster reefs and adjacent banks with no oysters that were bare mud (Fig. 2). We chose 14 sites from the back-barrier island marsh between St. Catherines Island, GA and the mainland (a total sampling area of ~100km², centered on 31.665° N, 81.211° W). Sites were randomly chosen from large creeks (150–820 m wide, (NOAA Office of Coast Survey, 2011) in order to be comparable to our manipulative field experiment. Sites were surveyed at low tide during a spring tide series in September 2019. We set two transects at each site perpendicular to the shore, with one transect spanning the bank with oyster reef and the other spanning adjacent bare bank (Fig. 2). The neighboring edge of the oyster reef and bare bank transect at a site were separated by ~20 m to avoid reef edge effects. Survey points were recorded on transects at the lower elevational limit of cordgrass (both transects) and the upper oyster limit (reef transect only). Horizontal and vertical position was obtained with a Real Time Kinematic (RTK, Trimble R6) GPS at <2 cm accuracy. The center of the adjacent water body channel (hereafter: channel) was calculated in ArcGIS (ESRI, 2011, see methods in Keisling et al., 2020). Euclidean distances between cordgrass edge (RTK data) and channel center (GIS data) were calculated in ArcGIS (ArcGIS: near tool) for both bare mud and reef banks at each site (Fig. 2). A paired *t*-test was conducted in R (R Core Team, R, 2013: version 4.1.2) to compare the within-site differences in cordgrass edge to channel center when the cordgrass was over reef versus over bare bank. Positive values reflect sites where the cordgrass edge is closer to the water channel center when over the oyster reef bank compared to the adjacent paired bare bank. The data was tested for, and met assumptions of normality (analyzed using Shapiro-Wilk's test).
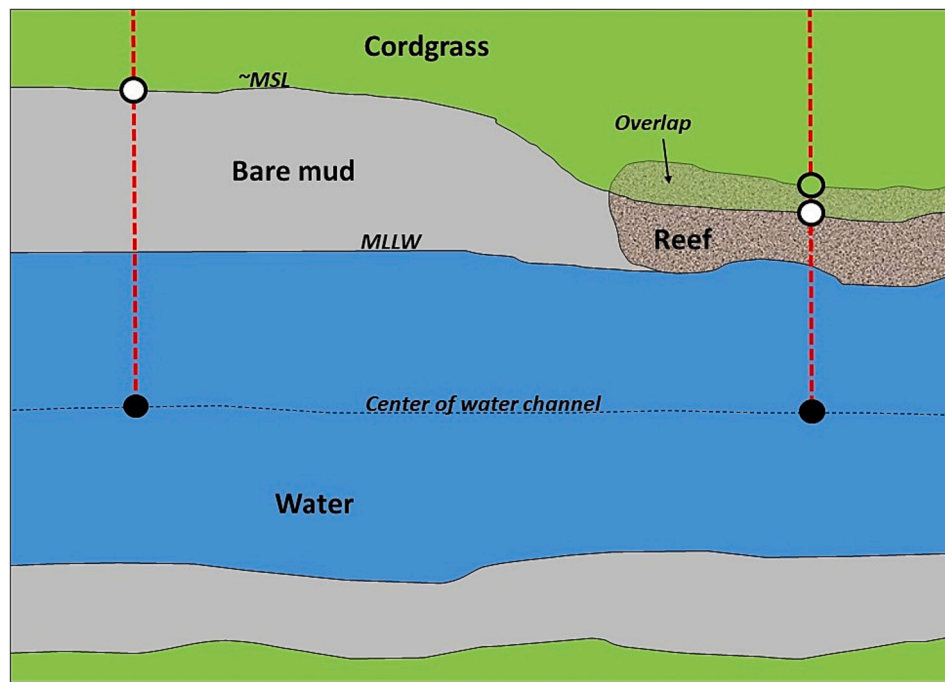
Fig. 2. Overhead view of field survey design. After establishing a baseline in the exact center of each water channel, we recorded latitude, longitude, and elevation at the waterward cordgrass edge (white dots) along two paired transects (thick dashed lines). Upper reef limit (grey dot) was also recorded (only on the reef-bank transect, right) to quantify overlap of reef and cordgrass. Approximate Mean Sea Level (~MSL) and Mean Lower Low Water (MLLW) are marked.

2.3. Oyster and cordgrass habitat overlap

We used the same survey data to quantify the degree to which oyster and cordgrass patches overlap in large estuarine creeks (Fig. 2). The horizontal distance of the lower cordgrass limit was subtracted from the upper limit of the oyster reef to calculate the distance of overlap using ArcGIS (ArcGIS: near tool). Negative values for overlap reflect reef-bank sites where cordgrass and oysters did not overlap (i.e., cordgrass was set back from oysters). A t-test was conducted in R (R Core Team, R, 2013: version 4.1.2) to test if species patch overlap was significantly different than 0. The data was tested for, and met assumptions of normality (analyzed using Shapiro-Wilk's test).

3. Results

3.1. Effect of cordgrass on upper-reef oysters

In the manipulative field experiment, treatment significantly affected *Crassostrea virginica* (hereafter: oyster) recruitment over four months ($F_{4,32} = 9.4$, $p < 0.001$, Fig. 3A, Appendix Table 1). On average, there were 2.4 times more oyster recruits to the *Spartina alterniflora* (hereafter: cordgrass) treatment compared to the bare treatment. All treatments containing shade (whether natural or mimic) had significantly higher oyster recruitment than bare and structure-only treatments (Fig. 3A): bare vs shade ($p = 0.003$); bare vs shade and structure ($p < 0.001$); bare vs cordgrass ($p = 0.01$); while bare and structure-only were not significantly different ($p = 0.1$). Block had a modestly significant effect ($F_{8,32} = 2.25$, $p = 0.05$, Appendix Table 1).

Treatment also significantly affected oyster biomass over four months and yielded a similar pattern to that of oyster recruitment ($F_{4,40} = 6.1$, $p < 0.001$, Fig. 3B, Appendix Table 2). On average, oyster biomass in the cordgrass treatment was 3.2 times greater, compared to the bare treatment. The bare treatment was significantly different from all treatments containing shade, whether natural or mimic [bare vs. shade ($p = 0.01$); bare vs. shade and structure ($p = 0.004$); bare vs. cordgrass ($p = 0.048$)]. Structure was not significantly different from both

cordgrass and bare.

Treatment did not affect mean size over four months ($F_{4,40} = 2.2$, $p = 0.09$, Fig. 3C, Appendix Table 3), and there were no pairwise differences between treatments. Finally, treatment had a significant effect for the 15 longest oysters per plot ($F_{4,40} = 4.7$, $p = 0.003$, Fig. 3D, Appendix Table 4). Specifically, the maximum sized oysters were longest in all treatments with natural or mimic shade compared to the bare treatment: bare vs shade ($p = 0.01$); bare vs shade + structure ($p = 0.038$); bare vs cordgrass ($p = 0.049$). On average the largest oysters were 3.3 mm larger in the cordgrass treatment compared to the bare treatment. The largest oysters in the structure-only treatment were not significantly different than any other treatment.

*3.2. Effect of oyster reefs on extension of cordgrass edge*

Across sites, cordgrass stands adjacent to bare mud banks on average were set back 5.25 m more (± 4.30, SD), relative to the channel, than cordgrass adjacent to oyster-laden banks ($t(13) = 4.57$, $p = 0.0005$, Fig. 4A). Out of the 14 sites surveyed, 12 oyster-fringed cordgrass sub-sites extended waterward relative to their non-oyster laden sub-site pairs.

3.3. Oyster and cordgrass habitat overlap

On average cordgrass and oyster distributions overlapped by 1.75 m (± 3.85 SD, $t(13) = 3.65$, $p = 0.002$, Fig. 4B). Oyster and cordgrass patches overlapped at 13 out of 14 sites surveyed.

4. Discussion

Spartina alterniflora (hereafter: cordgrass) facilitates upper intertidal *Crassostrea virginica* (hereafter: oyster) by enhancing recruitment over the course of the recruitment season. We found that when present, cordgrass can increase upper reef oyster recruitment 2.4 times that of areas with cordgrass removed. We found no difference in average oyster size between treatments, but we did find that cordgrass treatments had
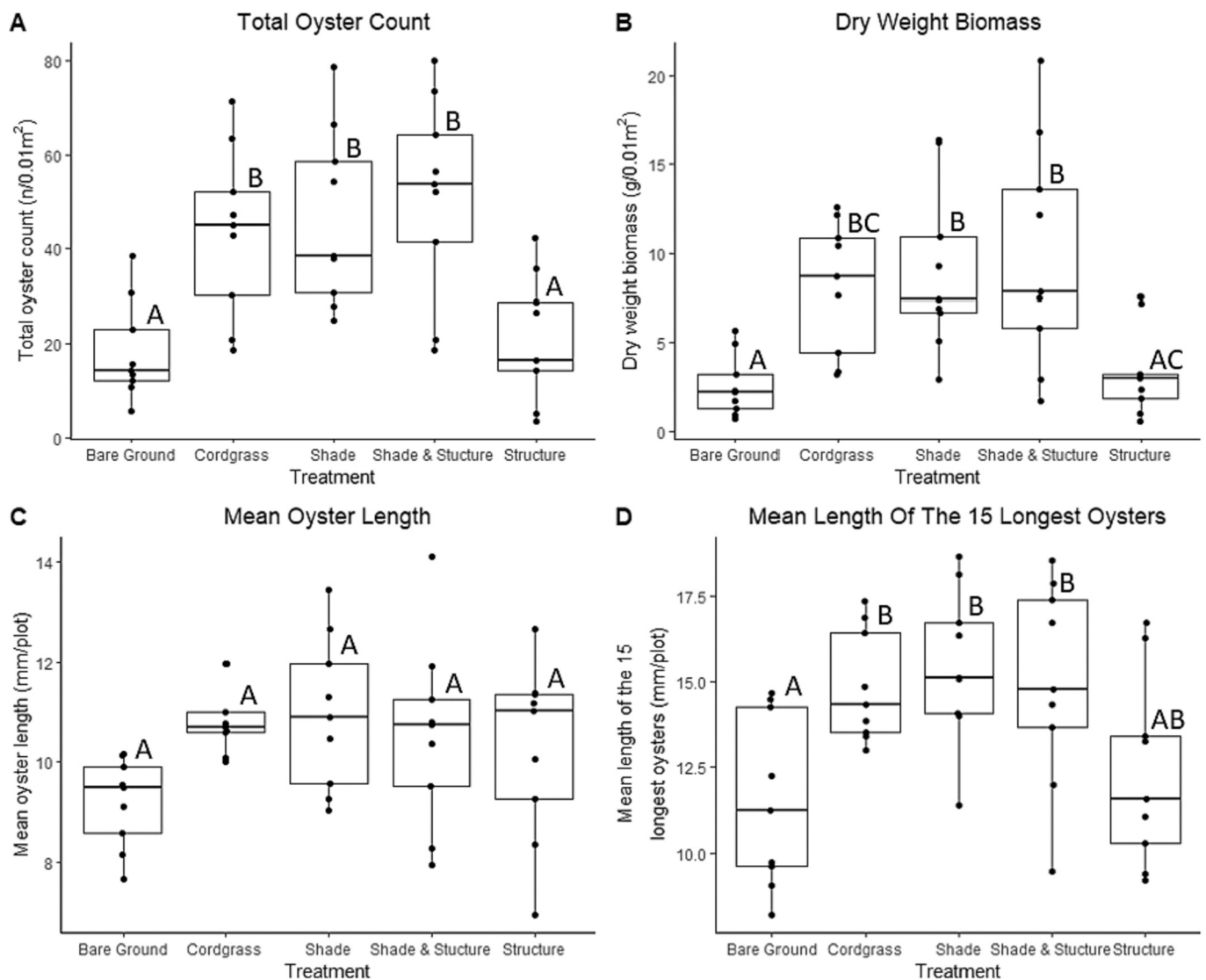
Fig. 3. Treatment effects on: (A) Oyster count per 0.01m² at end of four-month deployment, (B) biomass per 0.01m² plot, (C) mean oyster length per plot, and (D) mean length of the 15 longest oysters per plot. Letters indicate significant treatment differences obtained from Tukey tests. Medians are depicted by the horizontal lines, plot-level data are depicted by the black dots, and the whiskers represent 1.5*(inter quartile range).

3.2 times the biomass compared to treatments with removed cordgrass. This suggests that biomass was driven primarily by enhanced recruitment rather than oyster growth. However, we did find that the very largest oysters were significantly larger with cordgrass present relative to when cordgrass was removed. Because the mean sizes were similar across treatments (Fig. 3C), we acknowledge that this larger size is not a plot-wide effect, but rather relegated just to the upper end of performance. However, having even a few oysters reach these larger sizes after only four months could positively affect population-level fecundity. Furthermore, the first month or two after settlement are particularly important for oysters because, due to their small size, they are highly susceptible to predation, smothering, and desiccation. Accelerated growth can dramatically increase survival by reducing time spent in small vulnerable size classes. Finally, it is also worth noting that higher oyster abundances in the cordgrass and shaded treatments through density-dependent mechanisms like crowding may have reduced some of the growth advantages that oysters might otherwise have had in those treatments.

Shade appears to be the primary mechanism driving improved oyster success, as we found that in all significant tests, all treatments with shade (namely, cordgrass, shade, and shade and structure) responded

similarly and had greater oyster recruitment, biomass, and largest maximum size. Contrastingly, Fivash et al. (2021) found that cordgrass can have positive effects on oysters through a reduction in hydrodynamic disturbance. However, our results are similar to other cordgrass-bivalve systems, namely with mussels (Bertness, 1984). Of all oysters on a reef, those at the upper intertidal edge have the longest exposure time to air, and therefore the highest heat exposure and desiccation stress. Their upper limit is likely partly influenced by this heat-threshold. Adult oysters are very temperature tolerant (Malek and Byers, 2018), but the juveniles can be highly thermally sensitive (Crosby et al., 1991; Roegner and Mann, 1995). By mitigating heat stress by shading, cordgrass can have dramatic effects on oyster survival. Given that cordgrass plants at bank edges typically grow to about 2 m, cordgrass shading effects do not extend far outside its patch. Consequently, engineering effects of cordgrass on oyster reefs will be primarily concentrated where these two organisms overlap.

Our surveys demonstrate that oyster reefs are positively correlated with enlarged cordgrass stands. Cordgrass patch edge is vulnerable to erosive wave and current energy. Oyster reef structure helps dissipate this energy (Coen et al., 2007; Grabowski et al., 2012; Zu Ermgassen et al., 2012b) and in doing so can protect nearby cordgrass edge (Meyer
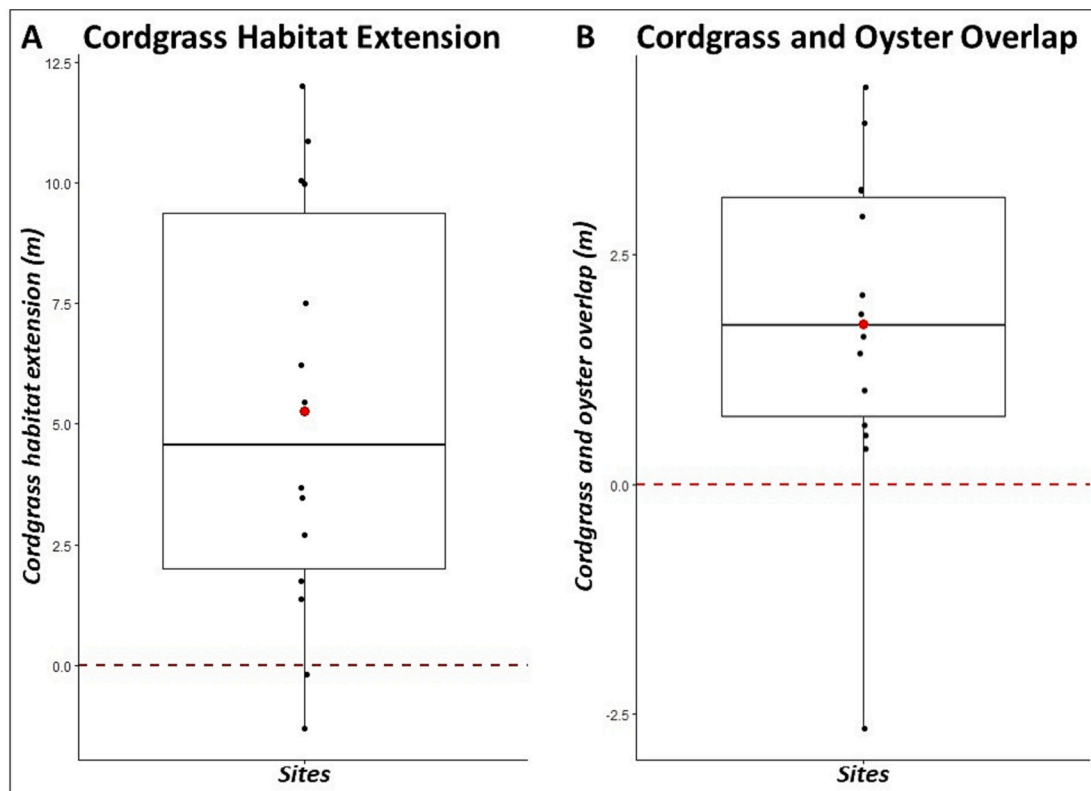
Fig. 4. (A) Cordgrass habitat extension when fringed by an oyster reef: cordgrass stands adjacent to oyster-laden banks on average extend (positive values) an extra 5.25 m towards the center of the creek, relative to stands adjacent to bare mud banks [t(13) = 4.57, p = 0.0005]. (B) Cordgrass and oyster habitat overlap: when both species are adjacent, they overlap (positive values) on average by 1.75 m. Patch overlap was significantly different than 0 [t(13) = 3.65, p = 0.002]. Dashed line indicates the value of no habitat extension (A) or no overlap (B). Medians are depicted by horizontal lines, means are depicted by grey dots, site-level data are depicted by black dots, and the whiskers represent 1.5*(inter quartile range).

et al., 1997; Piazza et al., 2005; Scyphers et al., 2011). To the best of our knowledge this is the first study to quantify effects of natural fringing reefs on cordgrass. It is possible that other mechanisms play a role as these survey data are just a snapshot in time; however, given that other work has shown oyster reefs (albeit restored reefs) affect cordgrass distribution, we believe these data represent the cumulative effects of oyster reef engineering on cordgrass distribution over longer time scales. We found that cordgrass stands were, on average, set back 5.25 m more on bare banks compared to adjacent banks laden with oysters. Our paired bare and oyster reef banks were only 20 m apart to standardize for site level differences such as physical exposure that could affect bank edge variation.

Our survey data of large tidal creeks with steep banks also indicate that oysters and cordgrass overlap 1.75 m on average, supporting our hypothesis that positive effects between oysters and cordgrass facilitate co-occurrence on a small spatial scale. We found that on average oyster presence is correlated with the lateral extension of cordgrass towards the center of the channels, while cordgrass facilitates extension of oysters into the marsh by increasing recruitment by creating shade. In both cases, the mechanism underlying facilitation arises from a reduction of abiotic stress (i.e., shoreline erosion or desiccation). This facilitation manifests itself within a relatively narrow band on intertidal banks (mean horizontal distance between cordgrass edge and mean lower low water in this study was 6.88 m), where both species are surviving at the edges of their fundamental niche. Facilitation among the ecosystem engineers expands each of their niches. Although the absolute amount of expansion for a species edge boundary may at first seem small, it is important to note that environmental gradients are extremely steep (e.g., temperature and inundation) with intertidal elevation. Thus, even though the expanded distance is only a handful of meters, it represents a

lot of environmental mediation. Furthermore, even a small area increase down the width of a tidal creek channel multiplies across expansive distances of tidal creeks into a very large amount of absolute real estate at a regional scale.

Our results suggest that ecosystem engineers can reduce abiotic stressors driving edge habitat limits; however, it is likely that these relationships are context dependent and may change across abiotic gradients, especially hydrologic energy. For example, tidal bank morphology, such as bank slope and sediment type, is often driven by current and wave energy (Karunarathna et al., 2016). Current and wave energy are highly influenced by estuary size and position within the estuary (small channel vs sound). Air temperature and water currents change over regional to global scales. Thus, although we see facilitatory ecosystem engineering in this study, the nature of these interactions may change under different abiotic conditions and at different scales. Given the extensive ecosystem services that both species provide this should be the topic of future research.

Climate change is likely to alter all of the drivers and engineering feedbacks that shape the distribution of these two species, which will likely result in a change in their relationship. These changes are likely to be most pronounced at habitat edges. For example, Rodriguez et al. (2014) found that oysters at central reef elevations (approximately the mid vertical point between mean sea level and mean lower low water) can keep pace with sea level rise, but Ridge et al. (2015) found that increasing rates of sea level rise can outpace lower intertidal oysters, increasing predation risk and effectively reducing intertidal oyster range. Although intertidal oysters have been shown to be adept at dealing with extreme temperatures (Malek and Byers, 2018), our data has revealed that shading can increase recruitment and growth rates (of the 15 largest oysters) for vulnerable upper reef juvenile oysters. This

might be an increasingly beneficial effect as climate warms, because predicted elevated and sustained maximum temperatures (Masson--Delmotte et al., 2021) are likely to have the highest adverse effects on upper intertidal oysters.

Because of their extensive roles in ecosystem functioning, oysters and cordgrass have been the focus of extensive, yet separate research. Both species are targeted for conservation programs such as oyster restoration and living shoreline projects (Beck et al., 2011; Grabowski et al., 2012; Walker et al., 2011). This study highlights the importance of considering both species in tandem when designing conservation projects. For example, our data indicate that conservation projects that pair both oysters and cordgrass are likely to have less cordgrass edge erosion and greater upper reef spat recruitment when oysters and cordgrass overlap than if the species were planted in isolation. Our data suggest that cordgrass facilitation of oysters is dependent on the species being in close proximity to one another, and as such suggests, that restoration projects should consider creating oyster habitat that fringes cordgrass stands.

Intertidal habitats exhibit strong abiotic gradients, where small changes in elevation can have large consequences for the organisms that live there, including imposing strong limits to their distribution over fine spatial scales (Connell, 1961). Ecosystem engineers are known to have the capacity to modify the environment, and often facilitate other species in stressful environments (Crain and Bertness, 2006; Smith et al., 2018; Byers, 2023). Here ecosystem engineers are reciprocally facilitating each other. This allows for the expansion and robustness of their realized niches, stabilizing the distribution of the two dominant habitat-forming species in the estuary. Given the centrality of ecosystem engineers in ecosystem structure and function, interactions between them, including those with no obligate (i.e., hierarchical) association, should be an area of research focus.

Author statement

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Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests.

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Data availability

Do you have any related research objects (data, methods, protocols, software, hardware) that you would like to publish alongside your original research as an additional paper in Research Elements? Research Elements is a suite of Open Access journals, with associated APCs (article processing charges), which make research objects findable, accessible, and reusable. Manuscripts can be prepared by any member of the team who worked on the original research and submitted at any time. No

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Appendix A. Appendix

Table 1
ANOVA table for total oyster recruits.

Predictor	Sum of Squares	df	Mean Square	F	p
Treatment	8498	4	2124.5	9.360	<0.001
Block	4091	8	511.4	2.253	0.0492
Residuals	7264	32	227.0		

Table 2
ANOVA table for oyster dry weight biomass. Block was removed because it was not significant.

Predictor	Sum of Squares	df	Mean Square	F	p
Treatment	420.2	4	105.05	6.132	<0.001
Residuals	685.3	40	17.13		

Table 3
ANOVA table for mean oyster length Block was removed because it was not significant.

Predictor	Sum of Squares	df	Mean Square	F	p
Treatment	18.0	4	4.499	2.184	0.0882
Residuals	82.39	40	2.06		

Table 4
ANOVA table for mean length of the 15 longest oysters. Block was removed because it was not significant.

Predictor	Sum of Squares	df	Mean Square	F	p
Treatment	114.6	4	28.650	4.669	0.0035
Residuals	245.4	40	6.136		

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Glossary

Please supply, as a separate list, the definitions of field-specific terms used in your article.:

Autogenic ecosystem engineers: Autogenic ecosystem engineers change the environment via their own physical structures, i.e., their living and dead bodies.

Ecosystem engineers: Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials.

Ecosystem functioning: Ecosystem functioning reflects the collective life activities of plants, animals, and microbes and the effects these activities (e.g., feeding, growing, moving, excreting waste) have on the physical and chemical conditions of their environment.

Facilitation cascades: Facilitation cascades are chains of positive interactions that occur as frequently as trophic cascades and are equally important drivers of ecosystem function, where they involve the overlap of primary and secondary, or dependent, habitat-forming foundation species

Foundation species: Foundation species *create complex habitats in which associated organisms find refuge from biological and physical stress*

Secondary engineers: Ecosystem engineers that co-occur with, and are reliant on, a dominant ecosystem engineer.