CONTEXTUALIZING ENGINEERING:

THE EFFECTS OF BASELINE STRUCTURE, LEGACY ENGINEERING, AND CO-DOMINANT ENGINEERING ON ENGINEERING OUTCOME

by

ROBERT DANIEL HARRIS

(Under the Direction of James E. Byers)

ABSTRACT

Ecosystem engineers have a central role in modifying key attributes of the environment that affect species throughout their community. The outcome of their environmental modification, however, depends on the degree of modification to the existing physical conditions. That is, the magnitude and sometimes direction of engineering outcome often depends on the environmental context in which it occurs. Environmental context can vary spatially often due to gradients in energy flow or baseline structure. Thus, quantifying the strength and sensitivity of ecosystem engineering to spatially variable physical factors like energy or structure can inform their system wide effects, as well as their responses to environmental change. Context is not the only factor controlling influences of ecosystem engineers. Importantly, engineering effects are not limited to the presence of the living engineer, because ecosystem engineering can also affect change through legacy effects, which persist after the engineer's death. Additionally, multiple ecosystem engineers may coexist, and because of their dominant influence, their interactions can affect the entire system.

In the southeastern US, the eastern oyster, *Crassostrea virginica* (Gmelin) and smooth cordgrass, *Spartina alterniflora* (Loisel) are two prominent ecosystem engineers that affect estuarine ecosystem functioning. Here, I examine how environmental context affects the degree to which oysters engineer the environment and their resultant influence on cordgrass habitat. I find that reef building by oysters increases intertidal bank slope, which increases habitat for neighboring cordgrass, but that the magnitude of the engineering effect is highly dependent on unengineered slope, or environmental context. Second, I examine the effect of wave energy on the effects of oyster live and legacy engineering of cordgrass habitat. Results suggest that live engineering effects of reefs formed by oysters primarily buffer erosional forces and increase habitat availability for cordgrass. In contrast, the legacy effect of oysters has the opposite effect. The negative effects of oyster legacy engineering dampen the positive effects of live oyster engineering in high wave energy areas. Increasing wave energy ultimately reverses the net effect of oyster presence on cordgrass from positive to negative. Finally, I quantify how both species reciprocally engineer the habitat of the other. Altogether, this emphasizes the importance of quantifying underlying environmental context, for both live and legacy engineering.

INDEX WORDS: Ecosystem engineers, facilitation, oyster, cordgrass, context dependency, legacy engineering.

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DEDICATION

I dedicate my Ph.D. dissertation to my wife, Laura Hollander. Without her steadfast patience and encouragement, I would never have completed this degree.

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CHAPTER 1

INTRODUCTION

Ecosystem engineers create structural change in ecosystems by either creating, modifying, or removing structure. Structural change through ecosystem engineering (ecosystem engineer structure hereafter), can in turn greatly affect the ecosystem. Ecosystem engineer structure can modify abiotic and biotic systems within an ecosystem. For example, ecosystem engineer structure can modify species assemblages by habitat provisioning. Engineered structure can change nutrient cycling and energy flow, ultimately affecting ecosystem functioning. Structure, abiotic and biotic change can also have feedback effects on the engineer. Collectively, all ecosystem-wide changes that are driven by engineered structure are known as ecosystem engineer outcome.

There are two types of ecosystem engineers, allogenic and autogenic ecosystem engineers. Autogenic ecosystem engineers modify structure by growing body mass. For example, trees grow above- and belowgound body mass. Tree belowground body mass, such as roots, change the soil structure and stabilize the soil. Tree aboveground body mass (trunk, branches, and leaves) is vertical structure that provides habitat for birds and animals and functions as a wind break.

Ecosystem engineering structure and outcome can be affected by environmental context. Context may affect the ecosystem engineer structure, for example, by high winds causing stunted and asymmetrical tree growth. Likewise, in the tree example, changes to engineering structure would be minimal in areas with low wind conditions, whereas the potential for large engineering outcome effects increases as wind energy increases. This increased engineering outcome as a function of physical energy is a common pattern in nature. Context can affect not only the magnitude but also the direction, or sign, of ecosystem engineering outcome. Environmental context often changes along gradients where it might also be possible to observe concomitant changes in engineering strength.

Ecosystem engineer structural change and outcome are not limited to when the engineer is living or actively maintaining structural modification. Engineering can continue to affect ecosystems long after the engineer has died or has stopped modifying structure, known as legacy engineering. Legacy engineering often has similar engineering outcomes to live engineering. In the case of beavers, beaver dams continue to increase aquatic habitat upstream after the beaver has died or has moved. However, legacy effects can also be qualitatively different to that of live engineering. Live tree branch and leaf structure reduces understory light, however, when the tree dies and falls over, the tree structure can knock over other trees, removing canopy cover and creating an opening that allows direct light to reach the understory. Engineering time scales between live and legacy engineering can also be quite different, where legacy engineering effects can be orders of magnitude longer than live effects.

Ecosystem engineers can exist in close proximity to other engineers. Many studies show that some ecosystem engineers, known as foundation species or primary engineers, can create an environment that is suitable for other secondary ecosystem engineers, where the secondary engineers are dependent on the primary engineers. For example, trees provide structure in which woodpeckers excavate holes for nests, adding another element of habitat heterogeneity to the original trunk provided by the tree. Relatedly, multiple ecosystem engineers can interact through facilitation cascades, where engineers are reliant on other engineers in a facilitation chain.

However, as explained earlier, not all engineering is positive, and some engineers may have negative impacts on other engineers.

In the following chapters, I investigate the interactive effects of two ecosystem engineers (Chapter 2), how live and legacy engineering are affected by an environmental gradient (Chapter 3), and how environmental context affects ecosystem structure and outcome (Chapter 4). I conducted this research in an estuary in coastal Georgia, within the South Atlantic bight on the U.S. east coast. This was a particularly good place to conduct this research for several reasons. (1) Estuaries are ecosystems with large environmental gradients over relatively short distances, making them ideal to study the effect of environmental context on ecosystem engineering. (2) Georgia saltmarshes are home to *Crassostrea virginica* (eastern oyster) and *Spartina alterniflora* (smooth cordgrass). Both species are dominant ecosystem engineers that are not reliant on the other. The species are adjacent to one another but segregate slightly in space. Cordgrass is found in the mid intertidal zone, whereas oysters are found in the lower intertidal, with a narrow band of habitat overlap around mean sea level. Given this narrow habitat overlap, this is a great system to examine interactive effects of two engineers at the edge of their habitat limits. (3) Lower intertidal banks in Georgia estuaries are typically either mud flat or oyster reef habitat. There is a stark structural contrast between the two habitat types, where oyster reefs are structurally complex and mud flats are relatively devoid of aboveground structure. Mud flat bank slope fluctuates as a function of wave energy, and oyster reefs modify bank slope through reef building. Additionally, oyster reef structure is known to stabilize sediments and reduce the erosive effects of wave energy. Consequently, this system presents a fitting setting to investigate the effects of structural context on engineered structure and outcome.

CHAPTER 2[1]

FACILITATION BETWEEN TWO DOMINANT ECOSYSTEM ENGINEERS EXTENDS THEIR FOOTPRINTS AND DEGREE OF OVERLAP

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[1] Harris, RD, JA Blaze, and JE Byers. 2023. Facilitation between two dominant ecosystem engineers extends their footprints and degree of overlap. *Journal of Experimental Marine Biology and Ecology*, *568*, 151944.
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Abstract

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 5.25m 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.

Introduction

Ecosystem engineers play important roles within ecosystems by modifying the environment (Jones et al., 2010, 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, 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, Skilleter et al., 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 and Grabowski, 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 Kennedy, 2000). By reducing current speed, cordgrass also facilitates the settlement of suspended particulate matter, thus increasing marsh accretion (Angelini and Silliman, 2012, Byers and Grabowski, 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 out-competed 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 (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 500m 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.

Methods

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 ~ 300m 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 1km 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 (1m radius/1.57m^2) at the waterward edge of the cordgrass zone abutting the oyster reef (Fig. 1). Plots were separated by at least 5 meters and the center of all plots had an average elevation of 0.09m above mean sea level (0.02m above NAVD88). The elevation difference across plots was <0.47m, 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 $1m^2$ plot and added PVC poles to each plot corner and center. PVC poles were used to support a $1m^2$ piece of construction tarp, 1 meter off the ground. The tarp was perforated with a grid of 121, 0.03m diameter holes, which was designed to let through the same amount of light as neighboring cordgrass stands (as measured with a light meter), while minimizing effects on water movement. For the structure mimic treatment, we created a grid of bamboo sticks (0.6m tall, approximately 8mm 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 0.5m central structural support PVC pole, at the top of which were attached three 15cm 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).

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

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, 2021). 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).

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 ~ 100km^2, 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 meters 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, 2021: 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).

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, 2021: 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).

Results

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 3.3mm 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.

Effect of oyster reefs on extension of cordgrass edge

Across sites, cordgrass stands adjacent to bare mud banks on average were set back 5.25m 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.

Oyster and cordgrass habitat overlap

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

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 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 2m, 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 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 5.25m more on bare banks compared to adjacent banks laden with oysters. Our paired bare and oyster reef banks were only 20m 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 1.75m 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 toward 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 6.88m), 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 faciliatory 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 & 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.

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Figures

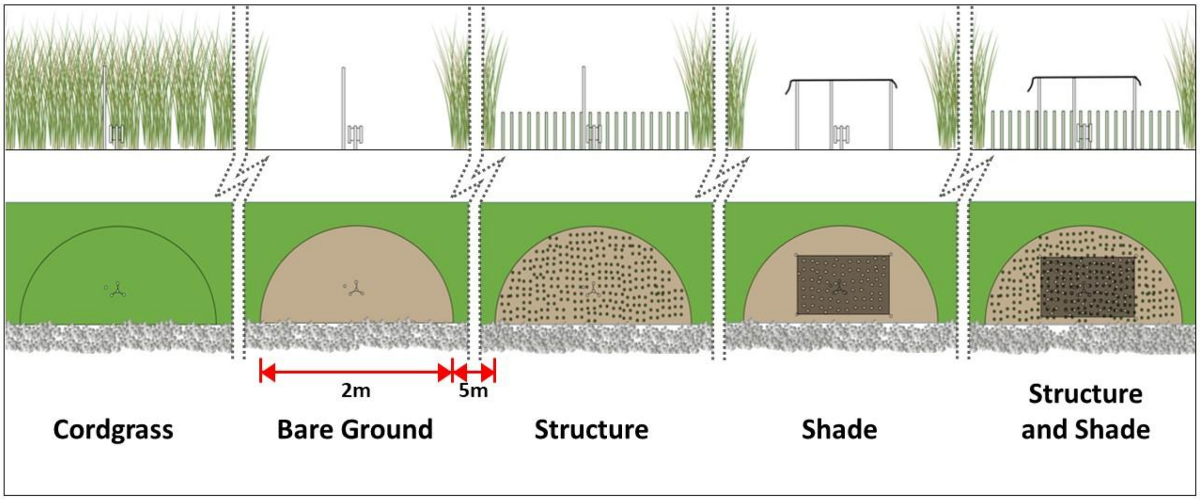

Figure 2.1: Manipulative field experiment design. Top row shows side view of each manipulation, bottom row shows bird's eye view of the corresponding manipulation (note: lightning bolts indicate that separation between plots are not drawn to scale). There were five cordgrass treatments. Cordgrass was 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 2m and were separated by at least 5m.

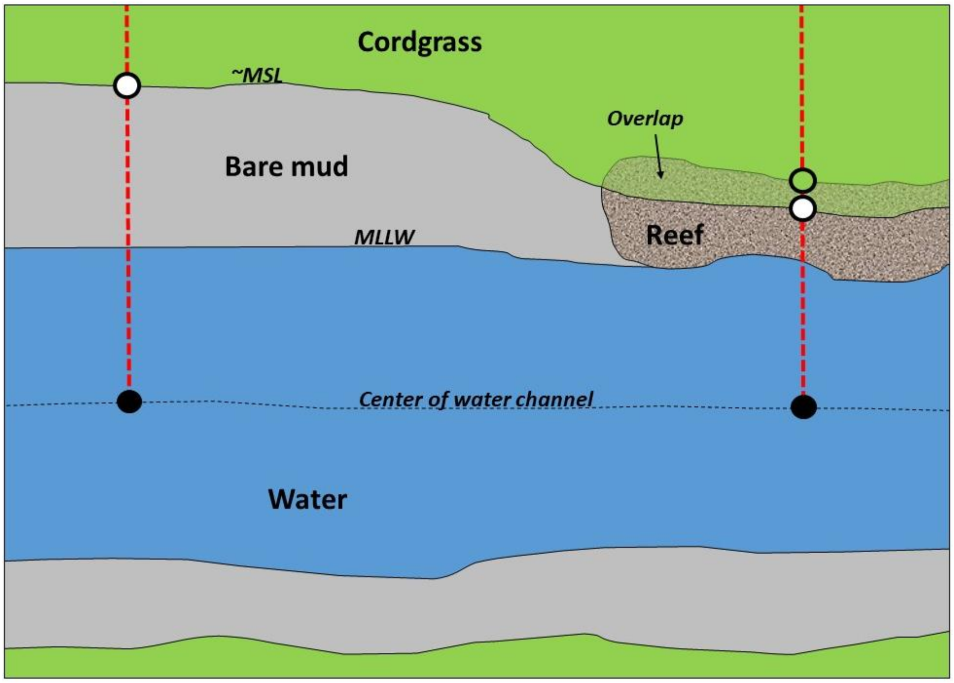

Figure 2.2: Overhead view of field survey design. After establishing a baseline in the exact center of each water channel, we recorded latitude, longitude, and elevation at the waterward cordgrass edge (white dots) along two paired transects (red dashed lines). Upper reef limit (green dot) was also recorded (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.

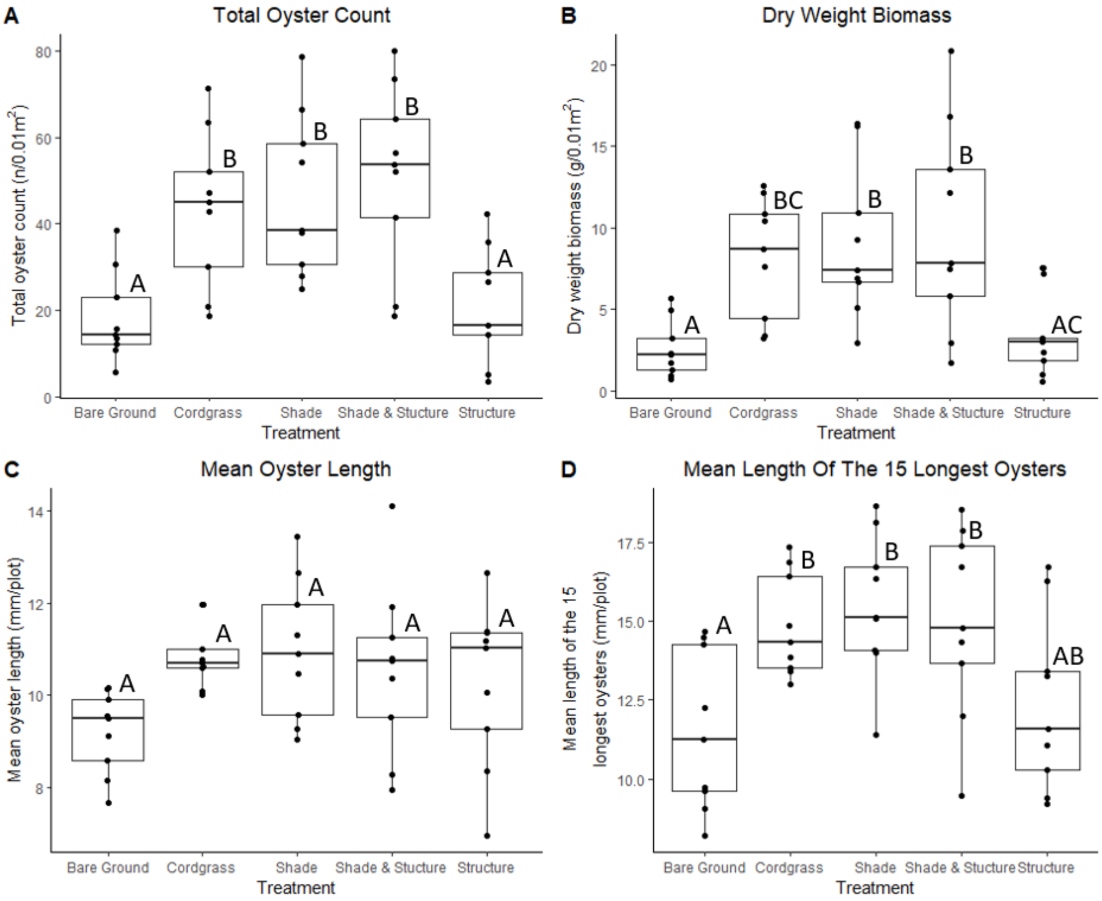

Figure 2.3: Treatment effects on: (A) Oyster count per 0.01m^2 at end of four-month deployment, (B) biomass per 0.01m^2 plot, (C) mean oyster length per plot, and (D) mean length of the 15 longest oysters per plot. Letters indicate significant treatment differences obtained from Tukey tests. Medians are depicted by the horizontal lines, plot-level data are depicted by the black dots, and the whiskers represent 1.5*(inter quartile range).

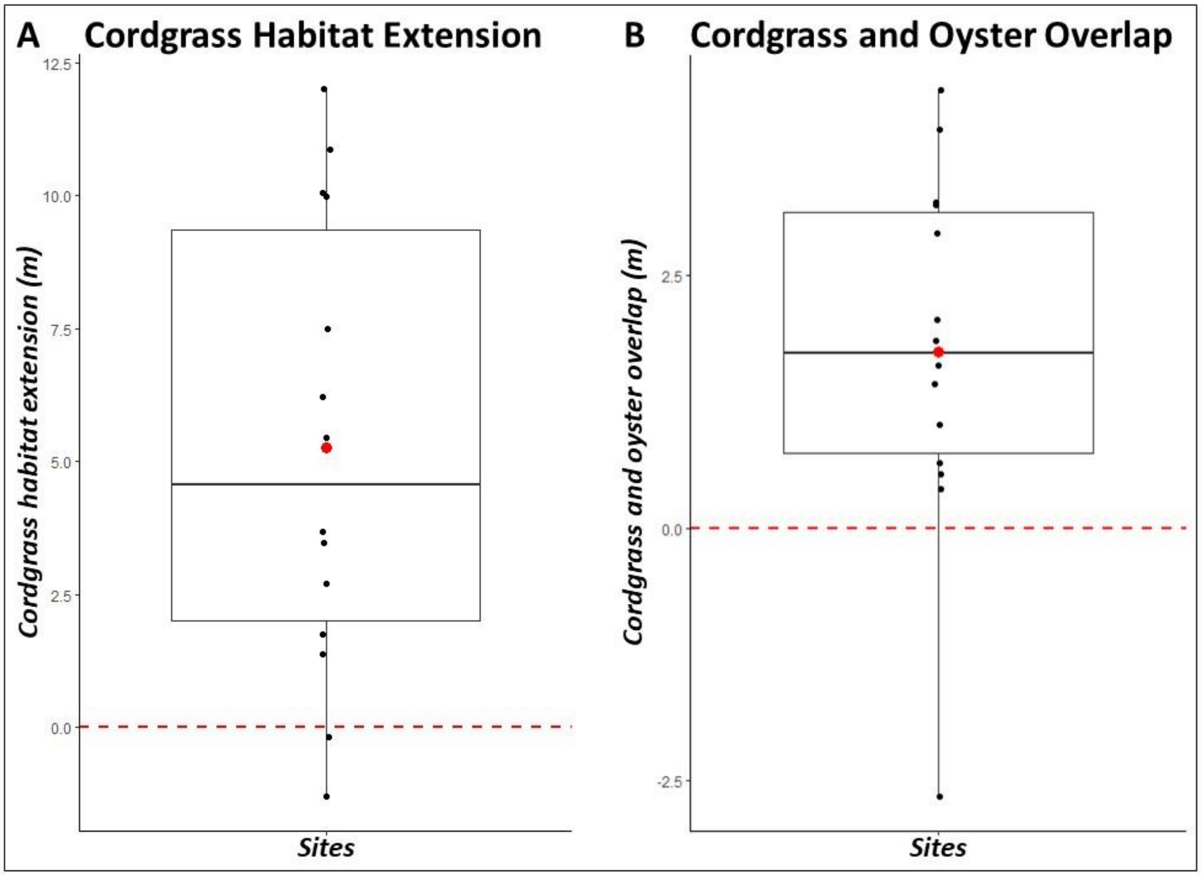

Figure 2.4: (A) Cordgrass habitat extension when fringed by an oyster reef: cordgrass stands adjacent to oyster-laden banks on average extend (positive values) an extra 5.25m towards the center of the creek, relative to stands adjacent to bare mud banks [t(13) = 4.57, *p* = 0.0005]. (B) Cordgrass and oyster habitat overlap: when both species are adjacent, they overlap (positive values) on average by 1.75m. Patch overlap was significantly different than 0 [t(13) = 3.65, *p* = 0.002]. Red dashed line indicates the value of no habitat extension (A) or no overlap (B). Medians are depicted by horizontal lines, means are depicted by red dots, site-level data are depicted by black dots, and the whiskers represent 1.5*(inter quartile range).

CHAPTER 3[2]

LEGACY AND LIVE EFFECTS OF ECOSYSTEM ENGINEER DIFFER ACROSS ENERGY GRADIENT, REVERSING NET ENGINEERING OUTCOME

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[2] Harris, RD, and JE Byers. Submitted to *Ecology*.

Abstract

Ecosystem engineers influence abiotic and biotic properties of communities. However, environmental factors like stress or energy gradients could modify their influence. Furthermore, engineering effects include legacies that persist after the engineer's death that may interact with gradients differently than the live engineer. Here, we show that live and legacy effects of the oyster *Crassostrea virginica*, a reef-building ecosystem engineer, act in opposing directions across an energy gradient, reversing oysters' net engineering effect. When energy is low, live oysters primarily buffer erosional forces and increase habitat availability for cordgrass (*Spartina alterniflora)*. When energy is high, legacy effects of oysters on cordgrass are negative, because high energy piles dead oyster shells onto cordgrass and smothers it. Thus, with increasing energy, net effects of engineering shift from positive live effects to negative legacy effects. Live and legacy engineering can have disparate, context-dependent effects; combined, they determine the overall effects of engineers on communities.

Introduction

Biological systems are heavily influenced by physical abiotic processes. Although all species interact with physical variables, ecosystem engineers (hereafter: "engineers"; Jones et al., 1994, 1997) are particularly adept at modifying the physical processes in their environments, which in turn influence them and other resident species. By altering their physical environment, through structural change, engineers influence co-resident species (Byers et al., 2006). For example, beavers (*Castor canadensis*), construct dams that restrict water flow, and ultimately create a wetland upstream with all of its attendant physiochemical differences, such as biogeochemistry and the rate of water flow (Wright et al., 2002). The physicochemical changes then drive changes in the community that inhabits that locality. Engineering can have both positive and negative effects on other species; however, the magnitude of these effects is typically a function of the physical intensity of the abiotic environment, since it is that intensity that will determine the scope for abiotic modification that can occur (Byers, 2024). For example, in systems with low physical input, engineers have low engineering potential to modulate the physical environment; whereas, in systems with high input, engineering potential is greater (Jones et al., 2010, Crain & Bertness, 2006).

Complementarity in species reactions to the environmental modulation of the engineer can mean an engineer affects one species positively while affecting another negatively. Further variation in effects caused by engineers can stem from differing degrees of environmental modification by engineers across a physical gradient (Jones et al., 2010). For example, the effect a beaver dam has on aquatic habitat characteristics is a function of water flow and channel slope (Byers 2024). The efficacy of the engineering and its impact vary with the amount of physical modulation being performed (Crain and Bertness 2006). In cases of strong environmental gradients, the influence of engineering on a given species could theoretically switch between positive and negative from one end of the gradient to the other.

Engineers affect their communities when they are alive, but they can also affect them after death. The latter are referred to as legacy effects (Jones, 2010, Smith et al., 2018). For example, beaver dams persist many years after the beaver dies or abandons the dam, termite mounds persist for decades after the mound is no longer used (Hastings et al., 2007)). Through live and legacy effects, an engineering species can simultaneously have different interactions within a community. Furthermore, the time scales of live and legacy engineering effects can be different, given that legacy structural changes generally persist longer than the life span of the engineer (Hastings et al., 2007).

Legacy effects can also differ qualitatively from those that arise when the organism is alive. *Sabellaria alveolata* is a colonial polychaete tube worm that builds reefs in shallow coastal systems of western Europe. When alive, *S. alveolata* actively prevents epifauna and infauna recruitment to the reefs. When *S. alveolata* dies, reef biodiversity dramatically increases as local invertebrates colonize the now-unprotected reef structure (Firth et al., 2021). Differences between live and legacy effects can also occur when live and legacy structures interact differently with abiotic processes (Smith et al., 2018). For example, the extensive stationary vegetative stands often formed by estuarine marsh grasses attenuate waves and water currents, promoting marsh accretion. After the grass dies, however, the remnant floating rafts of dead grass are mobile and can smother live marsh plants (Smith et al., 2018). Such observed differences between live and legacy effects are not surprising, given that live engineers can dynamically respond to physical forces (e.g., by continuing to grow or maintain structure), while legacy engineering is inert (e.g., without active maintenance and subject to decay).

Estuarine saltmarshes present ideal conditions to investigate multifaceted ecosystem engineer- community interactions. These systems exhibit strong physical gradients in flow, temperature, inundation time, and salinity, and as a result, set the stage for potentially large variation in engineering responses to changes along these physical gradients. Many marshes in the US Atlantic and Gulf coasts include two key species: *Crassostrea virginica* (hereafter: oysters), an ecosystem engineer and *Spartina alterniflora* (hereafter: cordgrass). Live oyster reefs have been shown, on the one hand, to stabilize sediments and reduce shoreline erosion through wave and current (energy) dissipation (Bahr, 1981; J. H. Grabowski et al., 2012, Meyer et al., 1997), leading to protection and expansion of the footprint of the cordgrass (Harris et al. 2023). However, after oysters die, their shells can persist in the system many years (Thompson et al., 2020), and when transported by currents, over time can accumulate into large rakes (deposited intertidal mounds of shell). Shell rakes are most common on estuarine banks exposed to high wave energy. These rakes engineer the environment as well, but their effects likely differ from those caused by living reefs because of their ability to be transported by energy. For example, shell can be deposited on top of cordgrass stands, and over time, the rake blocks light and water flow, increasing mortality of the cordgrass (Crawford, 2018), and a reduction of cordgrass footprint.

In this study we quantify the magnitude and net outcome of the coupled live and legacy effects of oysters on cordgrass habitat across a hydrological energy gradient. Previous studies have suggested that cordgrass benefits more from protection provided by the oysters in high energy environments (Harris et al., 2023; Meyer et al., 1997; Piazza et al., 2005; Walles et al., 2015); however, shell rakes that accumulate primarily in high energy areas can smother and kill cordgrass (Bahr, 1981). Therefore, we hypothesize that, across the increasing estuarine energy gradient, (a) the beneficial effect of live oysters on cordgrass increases, while (b) the negative effect of legacy oyster shell will increase as the dead shell is aggregated in the marsh in greater quantity, and (c) these two opposing effects (of live and legacy oysters) will partly offset one another. Therefore, we predict that the net effect on cordgrass will depend on the quantitative influence of these two distinct engineering aspects of oysters as a function of the environmental energy gradient.

Methods

To examine how the effect of oysters on cordgrass changes along a wave energy gradient, we utilized a suite of field surveys, remote sensing, and GIS analytic tools. We conducted this study in Liberty County, Georgia, west of St Catherines Island, between St Catherines Sound to the north and Sapelo Sound to the south (hereafter: St Catherines Estuary; 64km^2 study domain; 31.660° N; 81.235° W). The study domain transitions from sounds on the Atlantic Ocean side, to brackish tidal creeks and tidal fresh rivers on the mainland side. This domain was chosen due to the existence of a near-complete inventory of oyster reefs in the domain, which was conducted in 2010 by the University of Georgia Marine Extension Service (MAREX, N=802, Corley & Harris, 2011; Power et al., 2010). The inventory mapped (via handheld GPS units) the perimeter of all live oyster reefs 1m^2 or bigger, provided that the site was accessible by boat at low tides (water channels > 13 m in width). Reefs separated by 1m, or more, were classified as separate reefs.

The study is divided into two sections. The first looks the mechanisms behind oyster engineering effect on cordgrass habitat width (i.e., perpendicular to the shore). A small-scale study conducted by Harris et al. (2023), found that oyster engineering increases cordgrass habitat width by about 5 meters in intermediate estuarine creeks in Georgia. Here we look at this relationship as a function of wave energy across the entire estuary. Additionally, we account for the fact that while oyster engineering may affect cordgrass habitat directly behind the oyster reef patch (see Harris et al., 2023), engineering effects may also occur on either side of the reef, beyond the reef patch. The second section builds off section one, by calculating at larger scale the total area of cordgrass habitat affected by live oyster reefs, dead oyster shell rakes, and the net effect of both for 1km sections of coastline across an estuarine hydraulic energy gradient.

The effect of live oysters on cordgrass habitat width as a function of wave energy

Live oyster reefs often extend farther out into the intertidal mudflats and tidal channels than do the surrounding bare banks (Harris et al., 2023, fig. 1). The space immediately behind oyster reefs at higher elevation is usually filled with cordgrass (Bahr, 1981; Harris et al., 2023). We sought to measure this effect of oysters on cordgrass habitat width both behind and adjacent to reefs and quantify how it varied as a function of wave energy. We used six interconnected steps to investigate this relationship:

Wave energy: As a proxy for wave energy, we quantified fetch for all water in our study domain. First, we obtained 10 years (2006 - 2015) of daily wind data from a local weather station (St Simons airport, Weatherunderground.com). Second, we created a water surface dataset for the study area from a digital elevation model (Alexander & Hladik, 2015; 2m pixel resolution). Lastly, we created a fetch dataset by quantifying weighted fetch (F, hereafter: fetch; Rohweder et al., 2012), for all water surface pixels as

$$F = \sum_{i=1}^{16} w_i \times t_i \tag{1}$$

where w_i is the length of water over which wind can blow without obstruction from the i^{th} direction, t_i is the fraction of the time that wind blows from the i^{th} direction (hereafter: wind direction time), and i refers to one of 16 cardinal wind directions (i=0, 22.5, 45, … 337.5).

Site selection: We selected 30 sites to establish the relationship between fetch and oyster engineering effect on cordgrass habitat. To do this we first extracted fetch data from our fetch dataset for the mid-point of all live oyster reefs in the dataset that were within our study domain (N=802) using ArcGIS. Across all reefs, fetch ranged from 4m to 1986m. To select sites evenly across the fetch gradient, and thus yield a balanced (evenly weighted) analysis with a well-spaced independent variable, we subdivided this range into 30 bins (each with a fetch range of 66m, and randomly selected one reef from each bin for a total of 30 sites.

Coastline classification at each site: Adjacent to each of our 30 reef sites we drew a 100-meter buffer around each reef (50m on each side of each reef). Within this buffer, all coastline was either classified as un-engineered (50m to 20m from reef edge), flank engineered (20m to 0m from reef edge) or leeward engineered (length of the reef itself, Fig. 1). Cordgrass habitat edge is protected on the leeward (relative to hydraulic energy) side of oyster reefs (hereafter: leeward engineering; Harris et al., 2023). However, hardened structure, like oyster reefs, can create localized erosive eddies on the flanking ends of structures (hereafter: flank engineering). To take this into account we classified engineered shorelines as either flank or leeward engineered (Fig. 1). The 20m distance used to designate flank shoreline was defined by measuring flank engineering from aerial photography (NOAA, 2013) at 22 reefs (independent of our study sites) where we established that flank engineering within our study region does not extend beyond 20m from reef edges (Appendix A.B.1). For the majority of sites that have flanking effects substantially less than 20m, our methodologies described in the following steps take this into account and do not over inflate these effects.

Bank width: We elected to measure the average bank width of non-cordgrass habitat (an inverse metric for cordgrass width) for each coastline subsection, because oyster and mud habitat are complementary (mutually exclusive) of cordgrass. Yet oyster and mud habitat are much easier to delineate because there is no need to precisely define a depth dimension to the area behind each segment as there would be if measuring cordgrass directly (Fig. 1). To measure non-cordgrass bank width for each classified coastline subsection at each site we used 4 steps in

ArcGIS. (1) We digitized the bank region between the water's edge and cordgrass edge within each site's 100m coastline buffer using aerial photography taken at low tide (NOAA, 2013, Fig. 1). (2) We subdivided each site's bank region into horizontal segments according to the three engineering classifications: un-engineered, leeward engineered, flank engineered (Fig. 1). (3) We calculated the shoreline length (L) and area (A) for each site subsection. (4) We divided the area of each subsection by its coastline length (A/L) to calculate the mean bank width ($\overline{W}$) for each subsection in meters. It is important to note that the NOAA (2013) imagery dataset is a mosaic of pictures taken as close to low tide as possible. Given that all subsequent GIS steps were relative measurements within sites, any differences in tidal exposure between sites were not a concern.

Coastline reference assumption: To be able to compare differences in cordgrass habitat in areas under the influence of oyster engineering against an un-engineered baseline, we chose distant sites from reefs to use as un-engineered reference. Given that bank width at un-engineered shorelines in our study system is highly correlated with hydrologic energy ($p <$ 0.0001, $R^2 = 0.56$), this baseline seems logical in that these areas are out of the sphere of influence of oyster reefs.

Oyster reef width of influence: To quantify the effects of leeward and flank engineering by oysters on cordgrass at each site, we estimated the change in cordgrass habitat width due to the presence of oyster reefs, or mean Width Of Influence ($\overline{WOI}$). $\overline{WOI}$ for leeward and flank cordgrass habitat was calculated by subtracting the mean leeward and flank bank widths from un-engineered bank width, using equation 2 and 3, respectively,

$$\overline{WOI}_l \textit{ (in meters)} = \overline{W}_u - \overline{W}_l \tag{2}$$

$$\overline{WOI}_f \textit{ (in meters)} = \overline{W}_u - \overline{W}_f \tag{3}$$

where $\overline{W}$ is average bank width, and subscripts u, f, and l are engineering classifications (un-engineered, flank engineered, and leeward engineered, respectively, Fig. 1). Recognizing that bank width is the inverse of cordgrass width, positive $\overline{WOI}$ values indicate gains in cordgrass habitat and negative values indicate cordgrass habitat loss.

Analysis: To test if flank or leeward reef engineering was correlated to wave energy, we tested the effect of fetch on flank ($\overline{WOI}_f$), and leeward ($\overline{WOI}_l$) reef engineering using linear regression. The initial models were not significant due to high variability in cordgrass habitat change at sites with high fetch (>1000m, Appendix A.B.2). Thus, we re-ran the models using sites with fetch values < 1000m that are far more abundant in the estuary. All analysis was conducted in R (R core team, 2021; code/data: Harris, 2024).

The net effect of live oysters and shell rakes on cordgrass habitat area

Oyster reef and shell rake patch size and location, their engineering effects, and coastline fetch magnitude are not evenly distributed across the estuary. Thus, to quantify the net effect of oyster engineering on cordgrass habitat across an energy gradient, we calculated the live and legacy engineering effects of all oyster reefs and shell rakes across the entire study domain.

Live engineering effects: Given our large study domain and oyster reef dataset (N=802) it was time prohibitive to directly measure the oyster engineering effects on cordgrass at each reef site. Instead, we used a two-pronged approach: (1) we estimated oyster engineering effects ($\overline{WOI}_f$ and $\overline{WOI}_l$) for all 467 sites with fetch values less than 1000m using the flank ($\overline{WOI}_f$) and leeward ($\overline{WOI}_l$) regression models developed in the previous section (which had good model fit with low variability). Fetch data for the midpoint of each reef (calculated in the previous section) was used to parameterize the regression models. The estimated $\overline{WOI}_l$ engineering effects (in m) from the regression for each reef was then multiplied by the reef's length (parallel to the shore) to estimate the area of leeward engineering effect (m^2). The estimated $\overline{WOI}_f$ engineering effects (in m) from the regression for each reef was multiplied by 40m (20m on each flank end of a reef) to estimate the area of flank engineering effect (m^2). (2) Because the regression models performed poorly for reefs with fetch > 1000m, for the remaining 335 sites with fetch values over 1000, we used aerial photography (NOAA, 2013) to directly measure the area of oyster flank and leeward engineering effects (m^2) on cordgrass.

Legacy engineering effects: Given that cordgrass typically grows in monocultures of 100% cover, particularly near the lower elevational range of its habitat, here we assume that in the absence of a shell rake, we would find 100% cordgrass cover. Therefore, we assume that shell rake patch size area is equal to its engineering effect on cordgrass. To measure shell rake patch size, we used four band aerial photography (red, green, blue, and near infrared; NOAA, 2013) to remotely map shell rakes. Due to the bleached white nature of dead shell (Fig. 2), we automated shell rake mapping by selecting "white" pixels (all pixels with a summed 4 band value > 800) between mean higher high water and mean sea level (typical cordgrass habitat elevation). For quality control, NOAA aerial photography was subsequently scanned manually for rakes and we detected there were no false negatives or positives in the automated process. Mapped shell rake edges were cleaned using ArcGIS tools (shrink-expand-shrink).

Coastline segmentation: Live engineering and legacy engineering sites do not occur at the same coastline elevations and are not evenly distributed across the study domain. To contrast the two forms of oyster engineering, we subdivided the coastline of the entire estuarine domain into 277 1km segments. Within all segments we calculated the sum of all live, all legacy, and net

(Σ(live) – Σ(legacy)) engineering effects (in m^2). Fetch was sampled continuously (every 50m) across each segment and the median fetch value for each 1km coastline segment was recorded.

Analysis

To examine how live oyster reefs and shell rakes were distributed across the wave energy gradient, we modeled the probability of a 1km coastline segment having oysters (presence/absence of oyster reefs and/or rakes) as a function of fetch with two GLM models (one each for live reefs and shell rakes) with binomial distributions. To build these models, we used all 277 segments, including segments without any form of engineering. McFadden pseudo R^2 values were calculated for both models.

Next, to test how the effect of oyster engineering on cordgrass (i.e., area of cordgrass added or lost per 1km coastline) changed across the wave energy gradient, we modeled the effect of fetch (F) on the area of cordgrass habitat partitioned into the effect of (1) live oyster reef ($Area_{live} \sim F$), and (2) legacy shell rakes ($Area_{legacy} \sim F$). We also looked at the total net effect by summing those components ($Area_{live+legacy} \sim F$). We fit both linear and quadratic models to these three relationships with fetch. Thus, for all analyses we ran a second order polynomial and tested for fit and significance of the full model; if the polynomial term was not significant, it was dropped from the model and only the linear model was fit. Lastly, to summarize the collective amount of oyster engineering of cordgrass habitat that occurs across the entire estuary, we binned all 1km coastline segments into three fetch categories (0 – 667m, 667 – 1333m, 1,334 – 2,000m). We used ANOVA to test if there were differences in net engineering between the three fetch categories. Pairwise treatment comparisons were tested using a Tukey post hoc test. All analysis was conducted in R (R core team, 2021; code/data: Harris, 2024).

Results

The effect of live oysters on cordgrass habitat width as a function of wave energy

Fetch did not significantly affect the flanking effects of oyster reefs on cordgrass habitat ($F_{1,28} = 0.56$, $p < 0.46$, $R^2 = -0.01$, Appendix A.B.2-A), or the leeward effects of oyster reefs on cordgrass habitat ($F_{1,28} = 0.17$, $p < 0.69$, $R^2 = -0.03$, Appendix A.B.2-B). Although these models were not significant, we did see a positive trend in both flanking and leeward effects for fetch values < 1000m. When the models were rerun using sites with fetch values less than 1000m, the fit improved. Fetch (<1000m) significantly affected oyster flank engineering ($F_{1,10} = 8.06$, $p < 0.02$, $R^2 = 0.39$, fig. 3A), and leeward engineering ($F_{1,10} = 5.28$, $p < 0.04$, $R^2 = 0.28$, fig. 3B), of cordgrass edge habitat. With increasing fetch up to 1000m, the effects of both flank and leeward oyster engineering on cordgrass habitat were positive, reaching a maximum $\overline{WOI}$ around 10m (Fig. 3).

The net effect of live oysters and shell rakes on cordgrass habitat area

Across all 277 1km shoreline segments, we enumerated 802 reefs and 182 rakes. Of all these 277 segments, 148 (53%) had live oyster reefs, 38 (14%) had oyster rakes, and 33 (12%) had both. Fetch had a significant positive effect on the probability of the occurrence of oyster reefs ($P < 0.0001$, McFadden pseudo $R^2 = 0.18$, Fig. 4A) and the probability of occurrence of rakes ($P < 0.0001$, McFadden pseudo $R^2 = 0.39$, Fig. 4A).

Both the linear and quadratic terms in the live reef, shell rake and net engineering models were significant. Fetch (F) significantly affected the effects of oyster reefs on cordgrass habitat ($F_{2,274} = 22.66$, $p < 0.0001$, $R^2 = 0.14$, effect of live oyster engineering on cordgrass area= $6344F$

$- 12384F^2 + 578$, Fig. 4B red). Fetch significantly affected the effects of legacy shell rakes on cordgrass habitat ($F_{2,274} = 375.4$, $p < 0.0001$, $R^2 = 0.73$, effect of shell rake engineering on cordgrass area= $21975F + 14521F^2 + 362$, Fig. 4B blue). Fetch also significantly affected the net effect of oyster engineering of cordgrass habitat ($F_{2,274} = 89.7$, $p < 0.0001$, $R^2 = 0.39$, Net oyster engineering effect on cordgrass area= $-15631F - 26905F^2 + 217$, Fig. 4B black). As fetch increased, net engineering switched from positive to negative at ~1000m.

When summed over the whole study area (277km of shoreline within a 64km^2 study area), oysters facilitated the development of 59993m^2 of cordgrass habitat (0.22m^2 net effect for every 1m of shoreline), although the roles of the living and legacy effects were in opposite directions. Legacy effects (via shell rakes) removed 100,250m^2 of cordgrass habitat, while living reefs had a net effect of creating 160,243m^2 of cordgrass habitat. The majority of this positive engineering of cordgrass habitat arose in segments of the estuary with relatively low fetch (<1000), which were the most common (Fig. 4). Although the magnitude of engineering in any of these segments is small (Fig. 4), the large number of them boosts their collective engineering total. Areas with large fetch (>1000m) are not common, but where they occur, net engineering decreases and changes sign, indicating a net loss of cordgrass habitat in those areas (Fig. 5).

Discussion

In our survey of all the oyster reefs and rakes within a 64km^2 study region we found a positive cumulative net effect of both live and legacy engineering on cordgrass habitat (a net increase of 59,993m^2), with 28% of 1km coastal segments demonstrating beneficial effects of oysters on cordgrass. Thus, the balance of oyster reefs and rakes had an overall positive impact upon the cordgrass footprint in the study area. At the same time, live and legacy engineering from reefs and rakes had different quantitative effects on cordgrass. Live engineering had a positive effect that initially increased as physical energy increased, but this positive effect decreased in magnitude at sites with high fetch (>1000m). Because fetches < 1000m predominate in the estuary, net positive effects of oysters on cordgrass are most common. Thus, overall, live reefs primarily affected cordgrass footprint positively, while legacy effects of shell rakes affected it negatively. In the few coastal segments with high wave energy, live effects of oyster reefs on cordgrass became negative, and the magnitude of negative legacy engineering from shell rakes was high, changing the net oyster engineering effects on cordgrass habitat to be substantially negative (Fig. 4B).

Oysters, as autogenic ecosystem engineers, create structural habitat change through the very nature of their footprint (for example, by affecting the habitats of oyster-associated organisms like crabs and mussels), and through the extended engineering effect that that footprint exerts on other habitat nearby (for example, by expanding cordgrass habitat in the marsh). A previous study (Harris et al., 2023), found that oyster reefs in intermediate estuarine channels were associated with slightly wider cordgrass habitat. In this study we have strengthened and quantified that association, finding that positive effects between oysters and cordgrass increase with increasing physical energy up to a point where fetch is ~1000m. We also found that oyster reef effects became negative for coastlines with high fetch (> 1,600m). We believe this tipping point may be due to a qualitative change in the oyster response to the magnitude of physical energy in the system. Specifically, at low to moderate levels of energy (*F*), the positive relationship of oyster reef effects with fetch is congruent with ecosystem engineer theory, whereby the influence of engineering increases in more physically energetic environments, because there is more scope for the engineer to alter or ameliorate increasing physical stress (Crain & Bertness, 2006, Byers 2024). However, this amelioration can be dampened or overpowered in high energy environments, where strong physical conditions may limit the engineers' buffering capacity or even the engineers themselves.

Shell rakes, on the other hand, smother cordgrass, resulting in a decrease in cordgrass habitat equal to the patch size of the shell rake. We found a strong positive relationship between shell rake size and wave energy ($R^2 = 0.73$). As hydraulic energy in the form of fetch increased, so did the size of shell rakes, because dead shell is mobile and increasingly likely to be deposited as large rakes in cordgrass habitat with high wave energy. Although the shell rake footprint smothers cordgrass, it is still possible that shell rakes might benefit cordgrass outside the footprint of the rake by dissipating wave energy. Although this consideration lies beyond the scope of our present study, we would suggest that such beneficial effect is likely to be minimal, given that the rakes normally occur at high tidal elevations where water volume and flow is normally low.

Engineering magnitude – that is, the degree to which oyster reefs and rakes influence cordgrass habitat—is also affected by the interaction between spatial scale and wave energy distribution within the system. We have shown that at the estuary scale there is a net positive effect of oyster engineering. This comes in spite of the fact that at the 1km scale (Fig. 4), net engineering as a function of fetch is unimodal, with negative engineering values at high fetch values. This difference is explained by the fact that most estuarine 1km segments have low to intermediate fetch (Fig. 5), and thus why the positive effects of engineering dominate at the landscape scale.

Our study demonstrates that live and legacy effects, of oyster reefs and rakes upon cordgrass, are not necessarily the same in degree or location. The contrast in effects of live and legacy engineering may stem from the fact that the oyster is an autogenic ecosystem engineer, meaning that when alive, its own body provides the physical structure that engineers the environment. Upon death, its dead body parts take on new properties such as orientation and position within the environment, setting up the possibility for new engineering effects. Most autogenic engineers are sessile for the duration of their life cycle, but their structures often become more mobile after death (Smith et al., 2018, 2021). As a case in point, oyster shell rake material is the result of estuary-wide accumulation of legacy shell over the course of millennia (Thompson et al., 2020), whose placement and effect upon cordgrass habitat is not necessarily related to the present-day location of live reefs. As another example, aquatic vegetation is sessile and grows upright, but falls over after death or becomes detached from the substrate and is mobilized through water and wind. Sessile upright structures will likely interact with the physical environment differently than structures that are more mobile and horizontal. For comparison, because allogenic engineers modify or create structure external to their own bodies, the live and legacy engineering are typically one and the same, the only difference being that legacy engineered structures are no longer maintained. For example, beaver dams and termite mounds are structures that can persist with their form largely intact for many years after the engineer is extirpated.

Given these considerations, we propose that observed differences between live and legacy engineering effects of autogenic engineers are likely to be most pronounced when the legacy effect is mobile, long lasting, and in a different micro-orientation from the live engineer. Reef-forming bivalves often exhibit these traits (Gutiérrez et al., 2003). As a result, we found different positioning and quantitative effects of live and legacy oyster engineering as a function of fetch. The positioning is such a large part of the engineering influence. Namely, live reefs would smother cordgrass if reefs were positioned higher in the marsh, and shell rakes would likely protect cordgrass edges if they remained in the lower intertidal zone armoring the intertidal bank from erosion. These opposite positionings do not occur because the oyster engineer in its live and dead stages interacts with the physics of the environment in different and specific ways.

Live and legacy engineering effects on species and communities may differ. In the oyster-cordgrass system when wave energy is low, live effects are positive, while legacy effects are negative and low in magnitude. However, when wave energy is highest, legacy effects are highly negative, and live effects become negative. Thus, the quantitative differences in the relationships of live and legacy effects with energy are highly influential, and result in net engineering effects that switch sign across the energy gradient. We propose that trait differences between the live and dead engineer may help predict when their engineering effects will differ in important ways.

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Author contributions

Harris and Byers conceived the ideas and designed methodology; Harris collected the data; Harris and Byers analyzed the data; Harris led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Conflict of interest statement

The authors declare no conflicts of interest and confirm this manuscript is being submitted exclusively to Ecology. We are not aware of any other manuscripts or publications with similar information or content as the enclosed manuscript.

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Figures

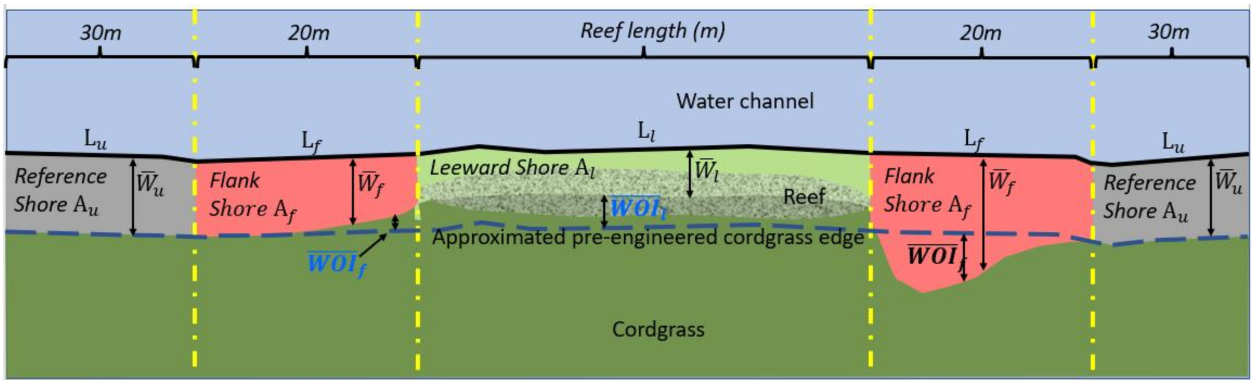

Figure 3.1. Aerial diagram of oyster engineering effects on cordgrass habitat. Areas (A) of non cordgrass intertidal habitats (i.e., oyster reefs and bare mud flats) are shown for un-engineered reference shore (grey, 50 to 20m from reef edge, A_u), flank shore (pink, 20 to 0m from reef edge, A_f) and leeward shore (light green, reef length, A_l), with the shore subsections separated by yellow dashed lines. Cordgrass (green), oyster reef (mottled grey), cordgrass/oyster overlap (mottled green), and water habitat (blue) are shown. Water's edge at low tide (black line, L) is segmented according to the shore subsection it fronts: un-engineered, flank, and leeward (subscripts u, f, l respectively). The average bank width ($\overline{W}$) for each subsection was calculated by dividing subsection area (A) by its length (L). The approximated location of the pre-engineered cordgrass habitat edge (blue dashed line) is shown. Mean leeward width of influence ($\overline{WOI}_l$) is typically positive (blue); mean flank width of influence ($\overline{WOI}_f$) can be positive (blue) or negative (black).

Figure 3.2. Side view (parallel to the waterline) of legacy oyster engineering. Dead oyster shell (rake) accumulates in deep deposits over thousands of years, and can be moved by hydraulic energy. When deposited over cordgrass habitat, live cordgrass patches are smothered and die.

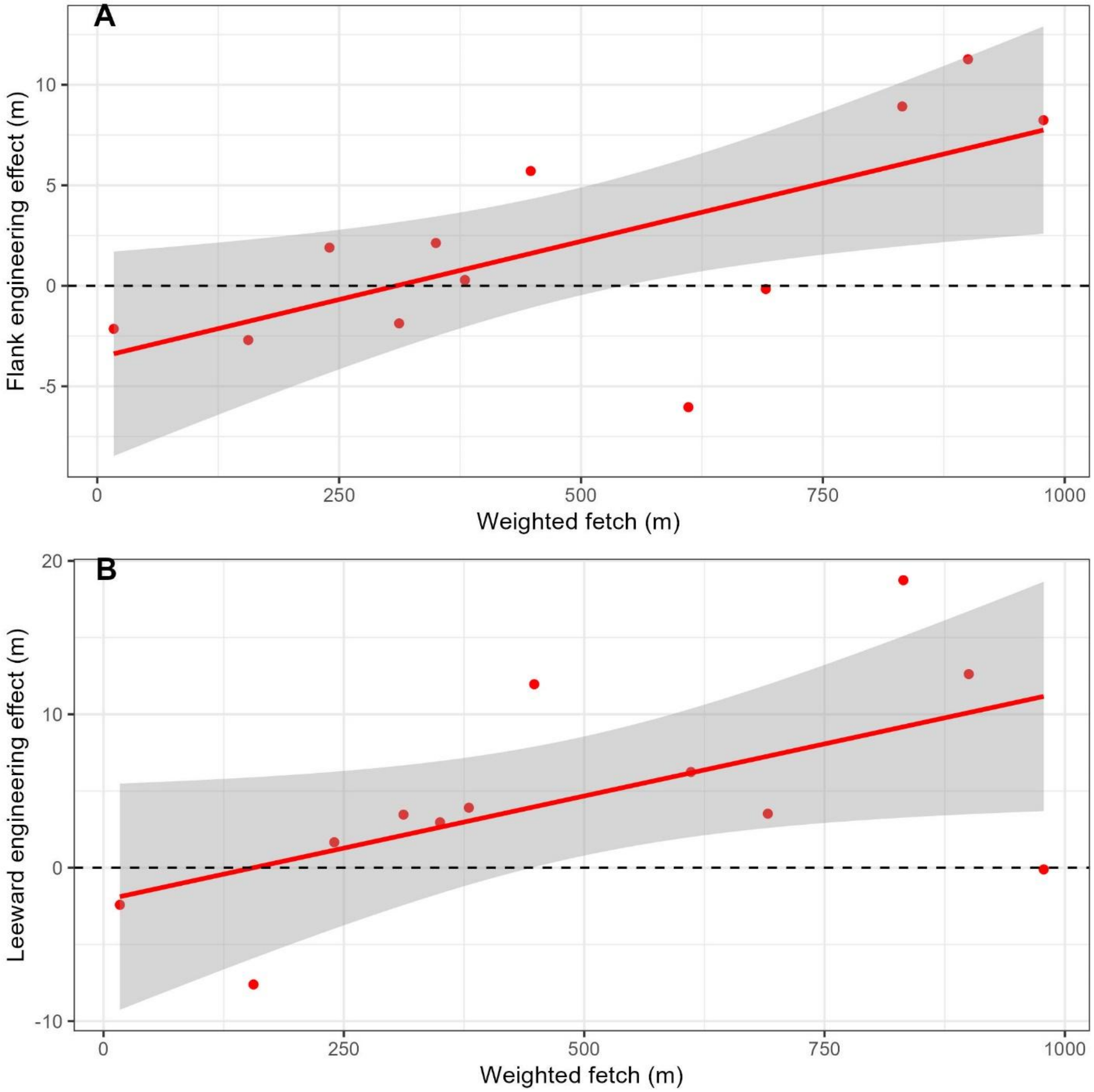

Figure 3.3. Effect of weighted fetch on oyster engineering of cordgrass habitat (WOI). A) Flank (WOI_f) and B) leeward (WOI_l) engineering for sites with fetch values less than 1000. Model regression lines (red), data points (red), and 95% confidence intervals (grey shading) are shown.

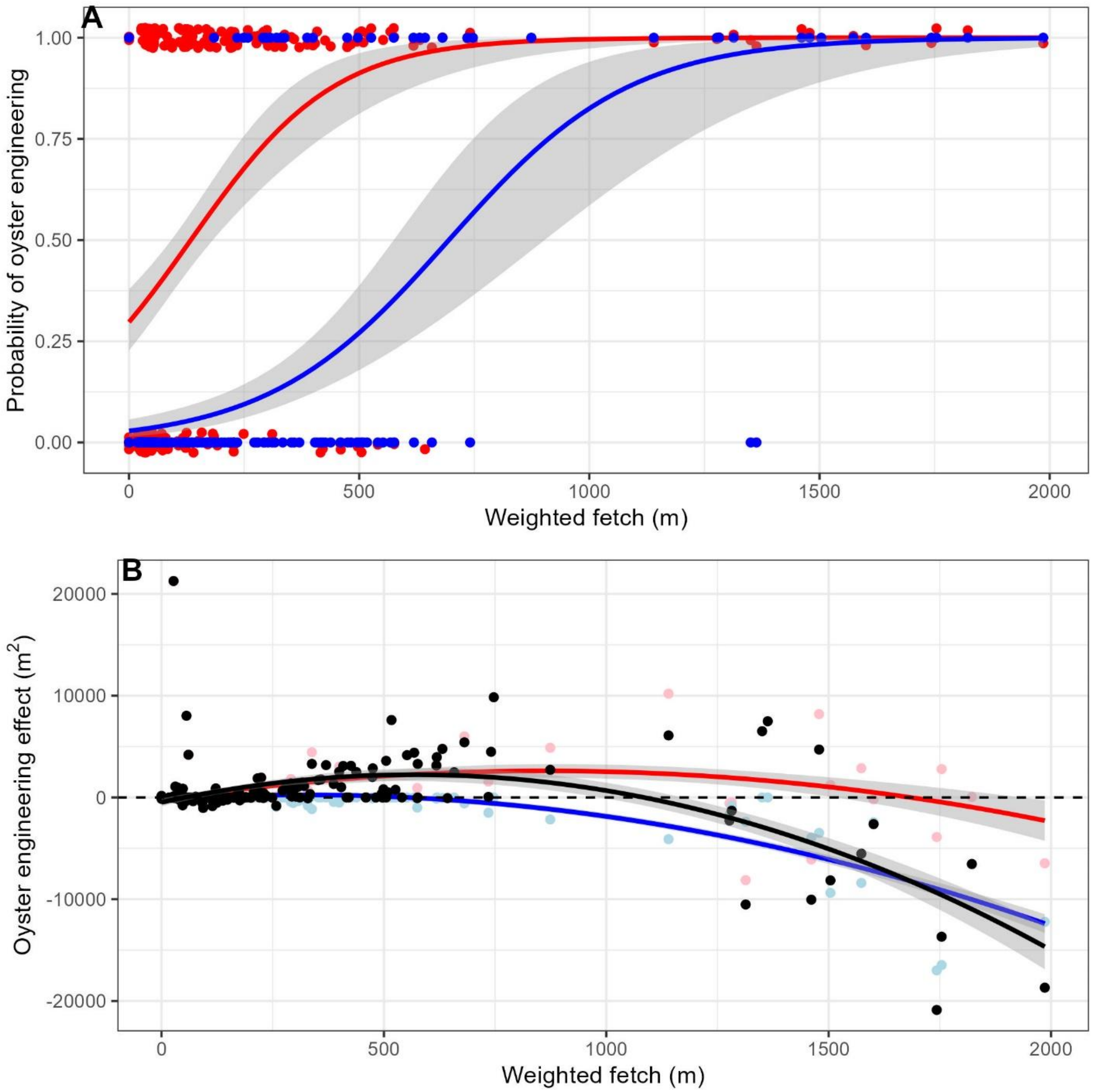

Figure 3.4. A) Probability of cordgrass habitat engineered by live oyster reef (red) and legacy dead shell rakes (blue) as a function of fetch. Data points represent engineering presence/absence per 1km segment of coastline. Model regression lines are shown in corresponding colors. B) Magnitude of live (red regression lines and points), legacy (blue regression lines and points), and the net engineering effect on cordgrass area (black regression lines and black points) as a

function of weighted fetch. Data points represent the summed area (m^2) of live, legacy, and net (live + legacy) engineering of cordgrass area per 1km segment of coastline.

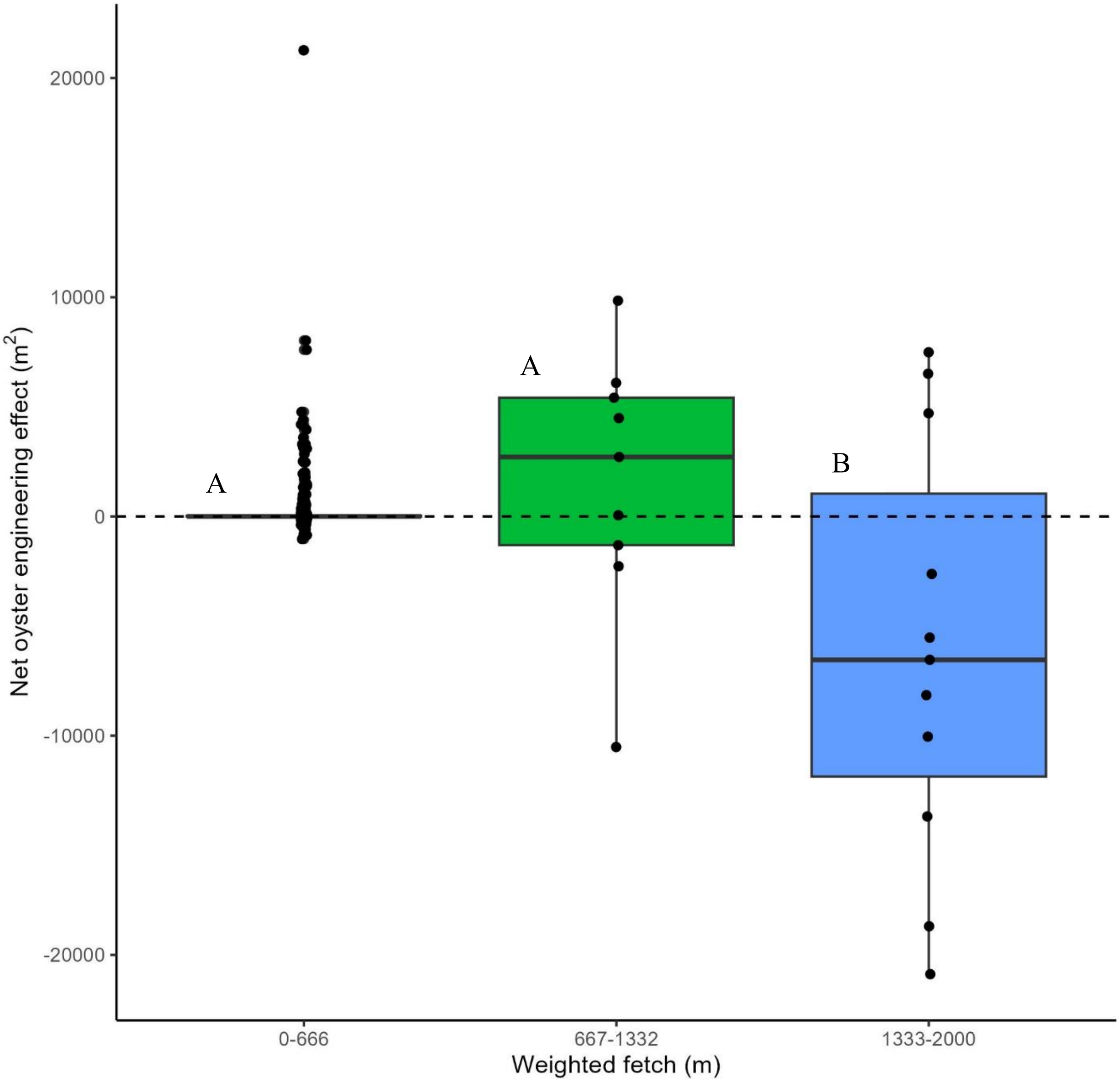

Figure 3.5. Net oyster engineering of cordgrass habitat at low (0-666m, N = 257), mid (667-1332m, N = 9), and high (1333-2000m, N = 11) fetch shorelines. Letters indicate significant treatment differences obtained from Tukey post hoc tests. Medians are depicted by the horizontal lines, plot-level data are depicted by the black dots, and the whiskers represent 1.5 x (interquartile range).

CHAPTER 4[3]

TOPOGRAPHIC CONTEXT LIMITS THE SCOPE OF INFLUENCE OF AN ECOSYSTEM ENGINEER

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[3] Harris, RD, and JE Byers. Submitted to *Ecology Letters*.

Abstract

Ecosystem engineers modify key attributes of the environment that in turn affect species throughout their community. The outcome of their environmental modification, however, depends on the ecosystem engineering performed, as well as the existing environmental context in which it occurs. Here, we explore the deterministic components of the environmental context where ecosystem engineering takes place. In our system, we find that engineering outcome is governed more by the structural or topographic context rather than the magnitude of the engineered structural change. Specifically, we show that reef building by the oyster *Crassostrea virginica* accretes sediment and increases intertidal bank slope, which increases habitat for the neighboring cordgrass, *Spartina alterniflora*. However, we find that the pre-engineered bank slope (i.e., topographic context) greatly determines how much oyster engineering of additional bank slope affects *S. alterniflora* habitat. In fact, 38% of the variability in *S. alterniflora* habitat change after engineering by oysters can be attributed to pre-engineered bank slope. Using a model representing the basic geometric relationships between bank slope, both before and after engineering, and how they affect *S. alterniflora* habitat, we demonstrate why the outcome of oyster structural engineering on *S. alterniflora* habitat is highly context dependent on pre-engineered bank slope. When pre-engineered bank slopes are <5°, the environmental context is most conducive to large engineering effects and even small changes in slope resulting from *C. virginica* engineering dramatically affect *S. alterniflora* habitat. In contrast, when pre-engineered bank slopes are >10°, the scope for influence by oyster engineering on *S. alterniflora* habitat is minimal. Our results emphasize the importance of quantifying underlying structural context (e.g., slope, grain size, rugosity) where engineering takes place to understand the scope for change, and thus accurately predict ecosystem engineering outcome.

Keywords

Crassostrea virginica, ecosystem engineering, environmental modification, estuaries, soft sediment, *Spartina alterniflora*, structural context.

Introduction

Ecosystem engineers modify environments through structural change (Jones et al., 1994 and 1997), which in turn affect abiotic and biotic systems. The overall outcome of their activities depends on both the pre-engineering environmental context and the magnitude of the structural change created by the ecosystem engineer (hereafter: engineered structure) (Crain & Bertness, 2006; Wright & Jones, 2006; Byers, 2024). The biotic and abiotic environmental conditions set an overall context that can modulate the direction (positive, negative, or neutral) and magnitude of the ecosystem engineer's effect on the environment (Jones et al., 2010). For example, it is well established that environmental stress (i.e., context) increases the potential for ecosystem engineers to affect their communities via stress reduction (Crain & Bertness, 2006; Johnson et al. 2016; Umanzor et al. 2017; Byers, 2024). This can take the form of reduced biological stress, such as a structurally formed predator refuge, or through reduced physical stress in the form of structurally reduced energy (e.g., trees as wind breaks) (Jones et al., 1997; Crain & Bertness, 2006). Although an understanding of the biotic and abiotic context can help predict the outcome of engineered structure and its resultant community effects, not surprisingly, these contextual data can be complicated and difficult to study (Byers et al. 2010).

For any given ecological interaction, a better understanding of the context is likely to inform how the interaction will affect the community. Understanding context may be particularly important because ecosystem engineers are a prominent structural building component of most ecological systems (e.g., forests, coral reefs, and beaver habitats) (Jones et al., 1994; Jones et al., 1997, Hastings et al. 2007). Engineered structure can have considerable effects within ecological communities (Byers et al. 2006). Given that context can modulate the magnitude and even the sign of ecosystem engineering outcome, understanding how context modifies engineering outcome may prove highly informative. Such understanding might be especially important if deterministic relationships can be explicated that predict the interrelationships between context, engineering structure, and overall engineering outcome.

Given that engineers by definition create structural change (Jones et al., 1994), it may be insightful to examine the preexisting structural context (i.e., slope, grain size, rugosity in the absence of the engineer) to quantify a baseline for how engineered structure will affect a system with added structure. In many cases, the structural change from engineering may be a simple change in the topography or geometry of the landscape. For example, the engineered structure provided by tree roots slows the processes of erosion by stabilizing soil (Jones et al., 1997), but the magnitude of engineering outcome is influenced by the context of sediment type and ground slope. In this example, if the slope is shallow, tree roots may be of little added utility to slow horizontal water flow and reduce soil loss; whereas on a steep slope the roots have a large engineering influence by slowing and reducing the faster flow of runoff that would occur as a result of the steeper slope. In this example, we see that while ecosystem engineer structure (i.e., presence of tree roots) is important, it is the structural context (i.e., slope) that forms a fundamentally important backdrop, governing the roots' ultimate engineering effects on the community. To investigate the role of structural context on engineering outcome, here we quantify how structural ecosystem engineering by intertidal oysters alters the extent of marsh grass habitat, and how that alteration is influenced by context (topographic slope).

In most estuarine saltmarsh habitats within the U.S. Atlantic and Gulf coasts, *Crassostrea virginica* (hereafter: oyster) and *Spartina alterniflora* (hereafter: cordgrass) occur as two abundant ecosystem engineers (Bahr, 1981; Morris & Haskin, 1990; Beck et al., 2011). In the South Atlantic bight along the coasts of Florida, Georgia, and the Carolinas, where this study was conducted, both species are dominant engineers. Cordgrass forms near monocultures over extensive saltmarsh plains within the upper half of the intertidal zone (approximately between Mean Higher High Water (MHHW) and Mean Sea Lever (MSL)) (Morris & Haskin, 1990). Oysters form dense reefs in the lower intertidal zone (approximately between MSL and Mean Lower Low Water (MLLW)) and create structure in otherwise structure-limited mud flats (Bahr, 1981; Byers et al., 2015; Ridge et al., 2015). As a result, these species abut one-another (and often overlap) around MSL (Harris et al., 2023). Both are keystone species due to the extensive ecosystem functioning and services that they provide, such as providing connectivity between suspended organic matter and the benthos, attenuating erosive wave energy, accreting sediment, and provisioning habitat (Morris & Haskin, 1990; Grabowski & Peterson, 2007; Beck et al., 2011; Zu Ermgassen et al., 2012). Oysters have been shown to positively and facultatively affect cordgrass edge habitat by attenuating waves and stabilizing sediment (Meyer et al., 1997; Harris et al., 2023), while cordgrass positively affects upper-reef oysters by reducing heat stress through shading (Harris et al., 2023).

By building structure that subsequently accretes sediment, oysters, through construction of their reefs, can change the slope of the creek bank, as well as how far the cordgrass habitat extends towards the water channel (Fig. 1). These structural changes can affect the community, principally by increasing cordgrass edge habitat; however, this engineering outcome is likely to be context dependent. Here we examine how the topographical context of pre-engineered intertidal bank slope and the stress context of wave energy jointly affect the ability of oysters to engineer reef structure, as well as the subsequent outcome of their structure on provisioning cordgrass habitat. Our study approach is three-pronged: (1) we quantify the effect of context (both pre-engineered intertidal bank slope and wave energy) on the engineered structure created by oysters building reefs. (2) We examine whether context or oyster-engineered structure is a better predictor of engineering outcome on the community (i.e., the linear change in cordgrass habitat edge relative to the channel, Fig. 1). And (3) We construct a theoretical approach to understand the mechanism driving our results that parses the engineering outcome into its constituent parts of context and engineering structural change as functions of their influences on the geometry of the intertidal bank slope.

Methods

Overview

In this study, we measured the relationship between (1) environmental context, which includes both wave energy (environmental stress) and pre-engineered intertidal bank slope (topographic context); (2) engineered structure, which is oyster-engineered intertidal bank slope change through reef building; and (3) engineer outcome, which is cordgrass habitat change. We measure these relationships using both field and GIS methods. We approximated wave energy, by measuring fetch (*F*). To quantify pre-engineered intertidal bank slope, we measured bank slope at subsites with no oysters (hereafter, bare bank slope) that were immediately adjacent to subsites with oysters (hereafter, reef bank slope) as a proxy for pre-engineered bank slope. To measure oyster-engineered slope change, we measured bank slope change (θ_{Δ}) as the difference between reef bank slope (θ_2) and adjacent bare bank slope (θ_1, Fig. 1). Finally, to measure changes in cordgrass habitat (C_{Δ}), we calculated the linear change in the distance of cordgrass waterward edge (relative to the center of the water channel) between bare (C_1) and reef subsites (C_2, Fig. 1).

Field methods

We chose 30 sites from over a 100km^2 area of saltmarsh across St. Catherines estuary, Georgia (31.66, -81.21), between St. Catherines and Sapelo sounds. Sites were haphazardly chosen to span a large fetch gradient within navigable saltwater creeks and sounds (13m to >3800m wide). Each site consisted of paired subsites: reef bank and adjacent bare bank subsites (Fig. 1). The two paired bank types within each site were separated by at least 20m to minimize effects of the oyster reef on the bare bank (Harris et al., 2023). To calculate both bank slope and engineered cordgrass habitat, we collected Real Time Kinematic GPS (RTK, latitude/longitude/elevation) survey points at the waterward edge of cordgrass stands and at the location of MLLW for both banks at each site (Fig. 1).

GIS methods

We modeled fetch as weighted fetch in meters (*F*, hereafter: fetch; Rohweder et al., 2012), for each site as:

$$F = \sum_{i=1}^{16} w_i \times t_i \qquad (1)$$

where w_i is the length of water over which wind can blow without obstruction from the i^{th} direction, t_i is the fraction of the time that wind blows from the i^{th} direction (hereafter: wind direction time), and i refers to one of 16 cardinal wind directions (i=0, 22.5, 45, … 337.5). Wind direction time was obtained from 10 years (2006 - 2015) of daily wind data from a local weather station (St Simons Airport, Georgia; Weatherunderground.com). We calculated bank slopes (θ_1 and θ_2) in R by measuring the horizontal (package/function: geosphere/distHaversine) and vertical distances between the waterward cordgrass edge and low bank RTK survey points (Fig. 1, white and grey dots) for each bank. We calculated change in slope, (θ_Δ) by subtracting the value of bare bank slope (θ_1) from the reef bank slope (θ_2) at each site. To measure the linear dimension of the change in cordgrass habitat (C_Δ) behind each reef bank subsite (relative to the bare bank subsite), we measured the euclidean distance between cordgrass waterward edge and the center of the adjacent waterbody in ArcGIS (tool: spatial analyst/near) and calculated the difference between distance to center for bare (C_1) and reef banks (C_2, Fig. 1).

Analytical Methods

All analyses were done in R version 4.1.2 (R Core Team, 2013). At the estuarine scale (~ 100km^2) we selected 30 replicate survey sites (banks), each with two subsites (Table 1).

How do fetch and initial bare intertidal slope influence oyster-engineered slope change?

To quantify the association between oyster-engineered slope change (θ_Δ) and engineering context (fetch and bare bank slope), we analyzed oyster-engineered slope change (θ_Δ) as a function of bare bank slope (θ_1), fetch (F), and both (with and without interactions). Models were analyzed using linear regression, where bare bank slope and fetch were $\log_{10}$ transformed to meet analysis assumptions. Additionally, we investigated if the two types of engineering context considered in this study, namely bare bank slope (θ_1) and fetch(F), were correlated using linear regression on the log-transformed variables.

How do context and oyster-engineered slope change correlate to cordgrass habitat change?

To assess which are the most important mechanisms driving oyster-engineered cordgrass habitat, we modeled cordgrass habitat change (C_Δ) as a function of the two context variables—bare bank slope (θ_1) and fetch (F)—and oyster-engineered bank slope change (θ_Δ).

To select the best model for cordgrass habitat change, we (1) $\log_{10}$ transformed bare bank slope and fetch to meet analysis assumptions, and (2) established a global general linear model: cordgrass habitat change (C_Δ) as a function of bare slope (θ_1), fetch (F), oyster slope change (θ_Δ) and their interactions (Fig. 2). (3) We subjected the global model to forward and backward stepwise model selection using AICc as the selection criteria (r package: AICcmodavg). (4) We used linear regression to model the top-performing models based on their AICc scores.

Why does bare bank slope affect oyster-engineered cordgrass habitat?

To assess the mechanisms behind engineered cordgrass habitat change (C_Δ) identified in the previous section, we distilled our system of study into simplified two-dimensional component geometry within a theoretical model (Fig. 2, Equation 2). We mathematically modeled cordgrass habitat change as a function of bare bank slope and oyster-engineered slope change in Equation 2.

$$Equation\ 2 \qquad C_\Delta = \frac{v}{Tan\theta_1} - \frac{v}{Tan(\theta_1 + \theta_\Delta)}$$

Where C_{Δ} is cordgrass habitat change, θ_1 is bare slope, θ_{Δ} is slope change engineered by oysters, and v is the tidal range over which oysters grow in Georgia. This simplified component geometry makes three assumptions: (1) cordgrass habitat is on a uniform horizontal plane at MSL, (2) bare bank and reef bank slopes are uniform planes (no rugosity), and (3) oyster habitat is between MSL and MLLW.

To determine the sensitivity of cordgrass habitat change to pre-engineered bare bank slope, we parameterized our model with some empirical data measured in the previous sections. We approximated v as the elevational difference between MSL and MLLW, or 1.16m as measured at nearby Fort Pulaski tide station: 8670870. We analyzed the cordgrass habitat change (C_{Δ}) within our simplified model, as a function of bare bank slope for three values of oyster-engineered slope change (θ_{Δ}). The three values we used (19°, 5.9°, and 0.09°) bounded the maximum, mean, and minimum values of θ_{Δ}, respectively, measured across our 30 field sites.

Results

How do fetch and initial bare intertidal slope influence oyster-engineered slope change?

Oyster-engineered slope change (θ_{Δ}) as a function of both bare bank slope (θ_1) and fetch (F) was not significant (with interaction: $F_{3,26} = 2.419$, $p = 0.09$, $R^2 = 0.13$; or with no interaction: $F_{2,27} = 1.788$, $p = 0.19$, $R^2 = 0.05$). We found that oyster slope change (θ_{Δ}) was not correlated with either variable singly: bare bank slope (topographical context: θ_1, $F_{1,28} = 3.544$, $p = 0.07$, $R^2 = 0.08$) or fetch (stress context: F, $F_{1,28} = 3.067$, $p = 0.09$, $R^2 = -0.07$). Finally, fetch explained 67% of the variability in initial bare bank slope, with larger fetch associated with smaller slopes ($F_{1,28} = 58.6$, $p < 0.0001$, $R^2 = 0.67$, $\theta_1 = 1.89 - 0.48(\log_{10} Fetch)$, Fig. 3).

How do context and oyster-engineered slope change correlate to cordgrass habitat change?

The best fit model to explain the change in cordgrass habitat (with 59% of the weight of all models) included only one parameter: bare bank slope (Table 2). The second-best model, with 25% of the model AICc weight and ΔAICc =1.73, included bare slope and oyster-engineered slope change (θ_{Δ}) with no interaction. Both models were assessed for significance and fit using linear regression. Change in cordgrass (C_{Δ}) as a function of bare slope was significant, explaining 38% of the variability ($F_{1,28} = 18.8$, $p = 0.0002$, $R^2 = 0.38$, Fig. 4). Change in cordgrass as a function of bare slope and oyster-engineered slope change was also significant, explaining 38% of the variability ($F_{2,27} = 9.79$, $p = 0.0006$, $R^2 = 0.38$), where bare bank slope was the only significant variable in the model ($p = 0.0008$). Other models including those with interactions and fetch (F) did not fit as well. AICc model selection placed the global model last (0.01 AICc weight; global model: cordgrass habitat change (C_{Δ}) as a function of bare slope (θ_1), fetch (F), slope change (θ_{Δ}) and their interactions, Table 2).

Why does bare bank slope affect oyster-engineered cordgrass habitat?

Using our 2-dimensional geometric model, we found the smallest bare bank slopes (θ_1) result in the highest maximum cordgrass habitat expansion (C_{Δ}), and this potential for expansion drops exponentially with increases in pre-engineered bare bank slope (Fig 5). Specifically, when bare bank slopes are small ($\theta_1 < 5°$), cordgrass habitat is highly sensitive to any oyster-engineered slope change (θ_{Δ}), (Fig. 5). However, when bare bank slopes are large ($\theta_1 > 10°$), the effects of even large oyster-engineered slope change on cordgrass habitat were infinitesimally small (Fig. 5). When oyster-engineered bank changes are small (0.09°), bare bank slopes even as small as 1° show almost no habitat change. Empirically, half (50%) of our sites had bare bank slopes less than 5° with an average slope of 6.7° (Fig. 6).

Discussion

Here we have demonstrated strong effects of context on the effects of engineering outcomes. We expected the biggest oyster engineering benefits on cordgrass habitat to be in high wave energy areas. We did indeed find that wave energy (approximated with weighted fetch) is correlated with the magnitude of oyster engineering effect on cordgrass habitat (engineering outcome). However, we show in this case that effects on cordgrass habitat are not due to direct stress relief or protection, but because of simple geometry of shallower bank slopes associated with higher fetch (Fig. 3) (Komar 1998). Bank slopes abutting areas with a large fetch were shallower, and this set a very important context on which oyster engineering then took place. Namely, areas with high fetch and thus low initial bank slope (θ_1) have a higher sensitivity to, and higher scope for influence by, ecosystem engineering (Figs. 4 and 5).

We decomposed our system into a simple geometric model to expose the mechanisms responsible for change. Our model shows that although the magnitude of structural change engineered by oyster reefs (θ_Δ) has some bearing on engineering outcomes, the main driver is context (θ_1). Specifically, even large amounts of engineered structural change will have minimal effects on cordgrass habitat when pre-engineered bank slope is high (Fig. 5). Whereas, when pre-engineered bank slope is low (< 5°), modest amounts of engineered structure can have large effects on cordgrass habitat.

In this study, we have isolated slope as our structural unit for both context and engineered structure. However, oysters engineer in many other ways (e.g., by affecting rugosity, grain size, substrate hardness). This multidimensional engineering may be important for other species (e.g., rugosity provides an important refuge from predation). Modeling of multidimensional engineering outcomes is likely to be challenging. Because of this, future studies may find structural context to be a highly predictive tool when investigating the effects of multidimensional engineering on ecosystems.

Coupled biological and physical interactions are complex and hard to model (e.g., Werner et al., 2007). However, when considered on its own, the context is relatively deterministic; as a result, it is considerably easier to model. Given this, knowledge of the context may prove fruitful when modeling ecosystem engineering. We propose that future research should consider whether physical processes (waves, wind, etc.) or the resulting structure (slope, grain size, etc.) have more utility for predicting ecosystem engineer outcome. We define this context as the shape, slope, size, and any other structural metric of the physical environment. We hypothesize that, as we have shown here, the magnitude of engineering outcome may often be more a function of the structural context (the baseline condition that the engineer changes) than of the magnitude of engineered structural change itself.

As an example, consider the engineering function of trees and how their root structures stabilize soils (Jones et al., 1997). In doing so, this stabilizing process brings about resistance to erosive forces such as gravity and water runoff. The amplitude of this engineering process is dependent on several physical factors such as soil depth, grain size, bedrock cracks etc., but the effect of the engineering is largely driven by the slope of the landscape. Therefore, the effect of engineering will be much larger on steep slopes where erosive forces are greater, rather than on flat ground. It is worth noting that Jones et al., (1994 and 1997) clearly defines ecosystem engineering to include the abiotic physical context; however, to the best of our knowledge most studies looking at engineering have considered context in terms of stress gradients instead of the structural or topographical context.

These results are likely to be applicable to oysters in other regions, and to other structure-forming intertidal engineers that are physically constrained between an upper and lower elevation. However, the magnitude of the engineering will also be highly dependent on the tidal range because reductions in v will reduce the scope for engineering change (Equation 2). Our results are for an intertidal zone that has an average tidal amplitude of 2 meters and an oyster range of approximately 1m (see Ridge et al., 2015 for relationship between tides and oyster habitat). Our geometric model predicts that for oyster-cordgrass interactions in areas with a lower tidal range the general pattern will remain the same but will be reduced in magnitude. For example, in our system a 1-degree oyster-engineered slope change (θ_{Δ}) on a bank with a bare slope (θ_1) of 2 degrees translates to an 8-meter increase in cordgrass habitat. The same scenario in a region with a 1-meter tidal range (v= 0.5m) would translate to 4 meters of cordgrass habitat (Fig. 7).

This research has the potential to be useful for intertidal oyster and cordgrass restoration projects. By linking how pre-restoration bank slope and tidal range are correlated to enhanced cordgrass habitat after oyster restoration, resource managers will be better positioned to make predictions on restoration outcomes. Restoration projects are expensive (Power et al., 2010; Beck et al., 2011), and this research will help maximize results and beneficial outcomes. For example, if resource managers are interested in restoring the most cordgrass habitat with the smallest restored reef footprint, our results would advise projects at sites with shallow slopes.

Crain and Bertness (2006), and Jones (2010) suggested environmental stress affects the strength of ecosystem engineering because in harsh environments engineering has more scope to alleviate stress. For example, energetic processes such as wave energy can magnify the buffering effects of engineers on a community. Here we add pre-engineered structure (such as topography) as another important consideration that can control the scope for engineering influence and thus its outcome on a community (Byers, 2024). In this study we demonstrate, using simple geometry, how engineering outcome is context dependent, as well as how structural context (not just stress) can be more important than the magnitude of engineered structure when determining engineering outcome. We also show that the structural context (slope) is correlated to stress context (wave energy). These findings suggest that in many instances topographic or structural context may be a better, or easier-to-use predictor of engineering outcome than stress context. We also draw attention to the utility of thinking about engineering context (θ_1) in terms of both engineering process (θ_Δ) and engineering outcome (C_Δ), demonstrating that context may have different effects on each.

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Figures

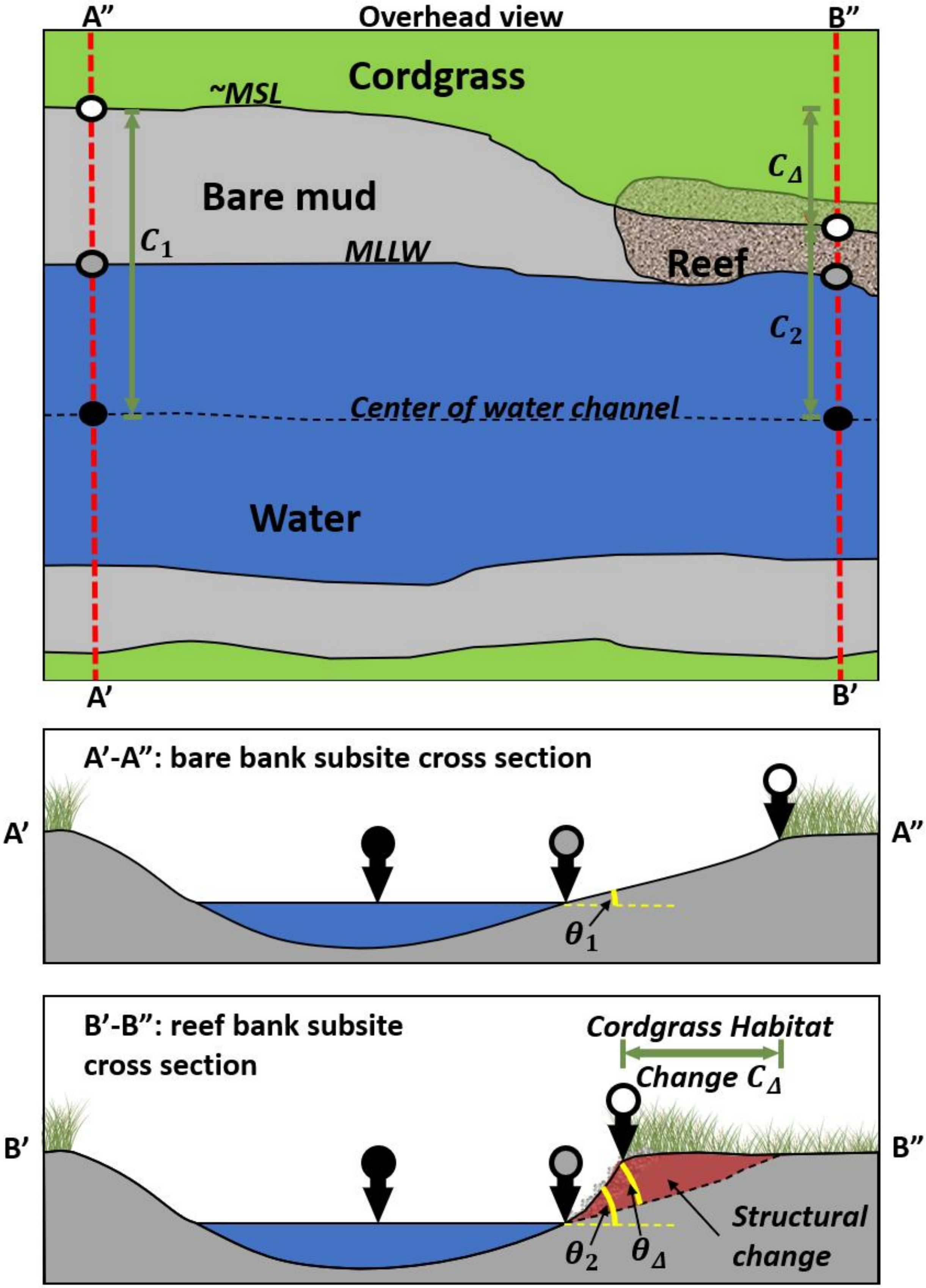
A”
Overhead view
B”
Cordgrass
~MSL
C_Δ
Bare mud
C_1
MLLW
Reef
C_2
Center of water channel
Water
A’
B’
A’-A”: bare bank subsite cross section
A’
A”
θ_1
B’-B”: reef bank subsite cross section
Cordgrass Habitat
Change C_Δ
B’
B”
Structural change
θ_2
θ_Δ

Figure 4.1. Overhead and cross section (bare bank: A’-A”; reef bank: B’-B”) views of field survey design. After establishing a baseline in the center of each water channel, we recorded latitude, longitude, and elevation at the waterward cordgrass edge (white dots) and at MLLW (grey dots) along two paired transects (red dashed lines). Approximate Mean Sea Level (~MSL) and MLLW are marked. Oyster-engineered slope change (θ_{Δ}: difference between the bare bank slope θ_1 and reef bank slope θ_2, red shading) and its effect on cordgrass habitat (C_{Δ}: difference between waterward cordgrass edge to water channel center distance at bare bank subsites C_1 vs reef bank subsites C_2) are marked on the reef bank cross section (B’-B”).

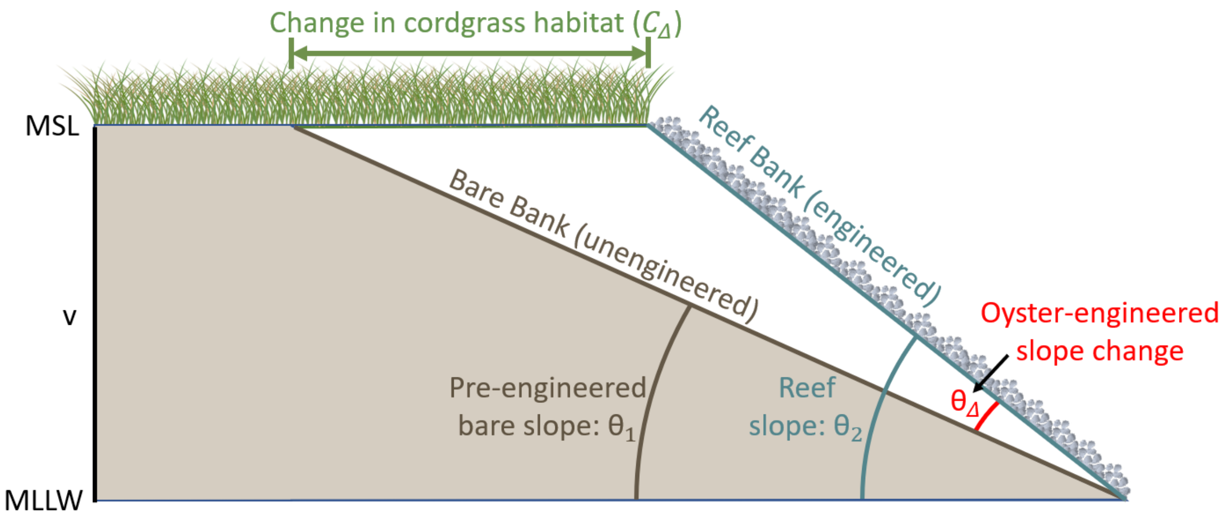

Figure 4.2. Conceptual diagram illustrating the spatial relationship between pre-engineered bare bank slope (θ_1), reef bank slope (θ_2), oyster-engineered slope change (θ_{Δ}), oyster habitat elevation ($v = \mathrm{MSL} - \mathrm{MLLW}$), and cordgrass habitat change (C_{Δ}).

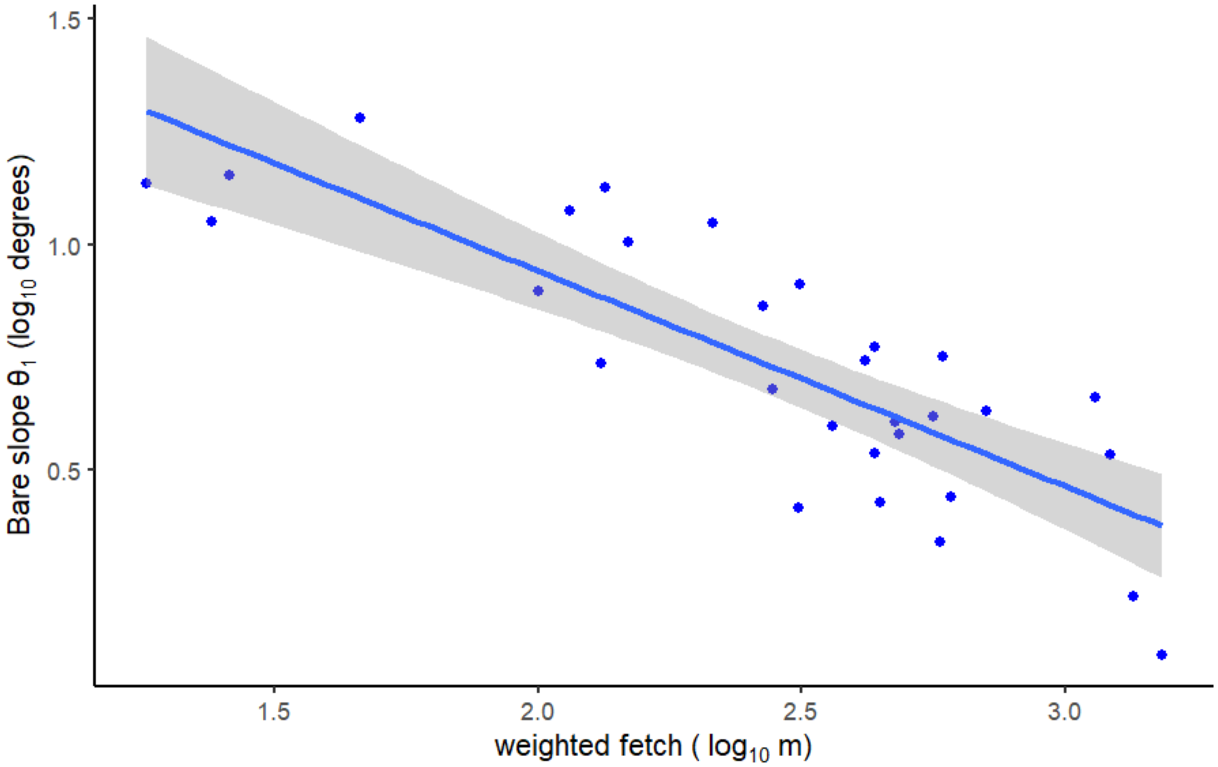

Figure 4.3. Correlation between bare bank slope as a function of weighted fetch (both log-transformed) at 30 sites with regression model output (line) and 95% confidence interval (grey shading).

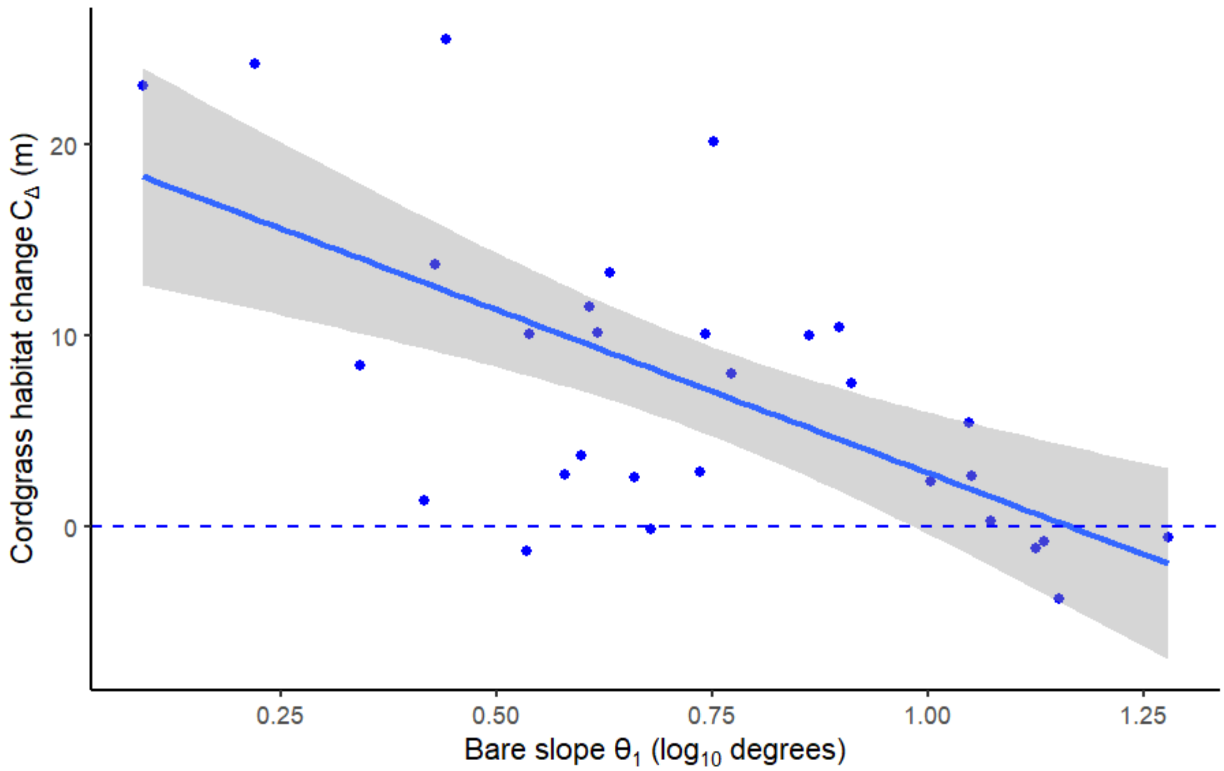

Figure 4.4. Correlation between cordgrass habitat change as a function of bare bank slope ($\log_{10}$-transformed) at 30 sites with regression model output (line) and 95% confidence zone (grey shading).

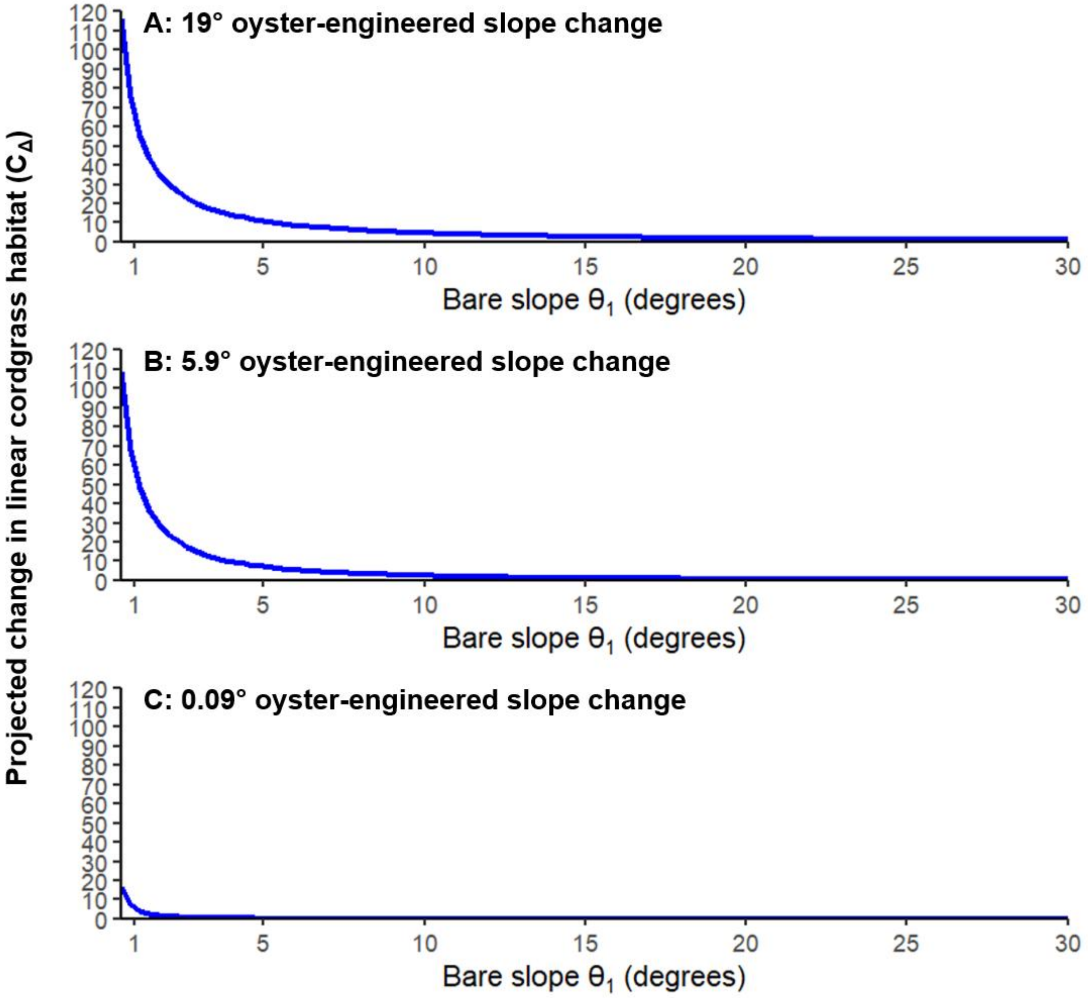

Figure 4.5. Projected cordgrass habitat change (C_Δ) as a function of bare bank slope (θ_1) for three different oyster-engineering slope change scenarios (θ_Δ). Panel (A) θ_Δ= 19° (maximum oyster-engineered slope change empirically measured across our 30 field sites). (B) θ_Δ = 5.9° (mean engineered slope change across the 30 field sites). (C) θ_Δ = 0.09° (minimum engineered slope change across 30 field sites).

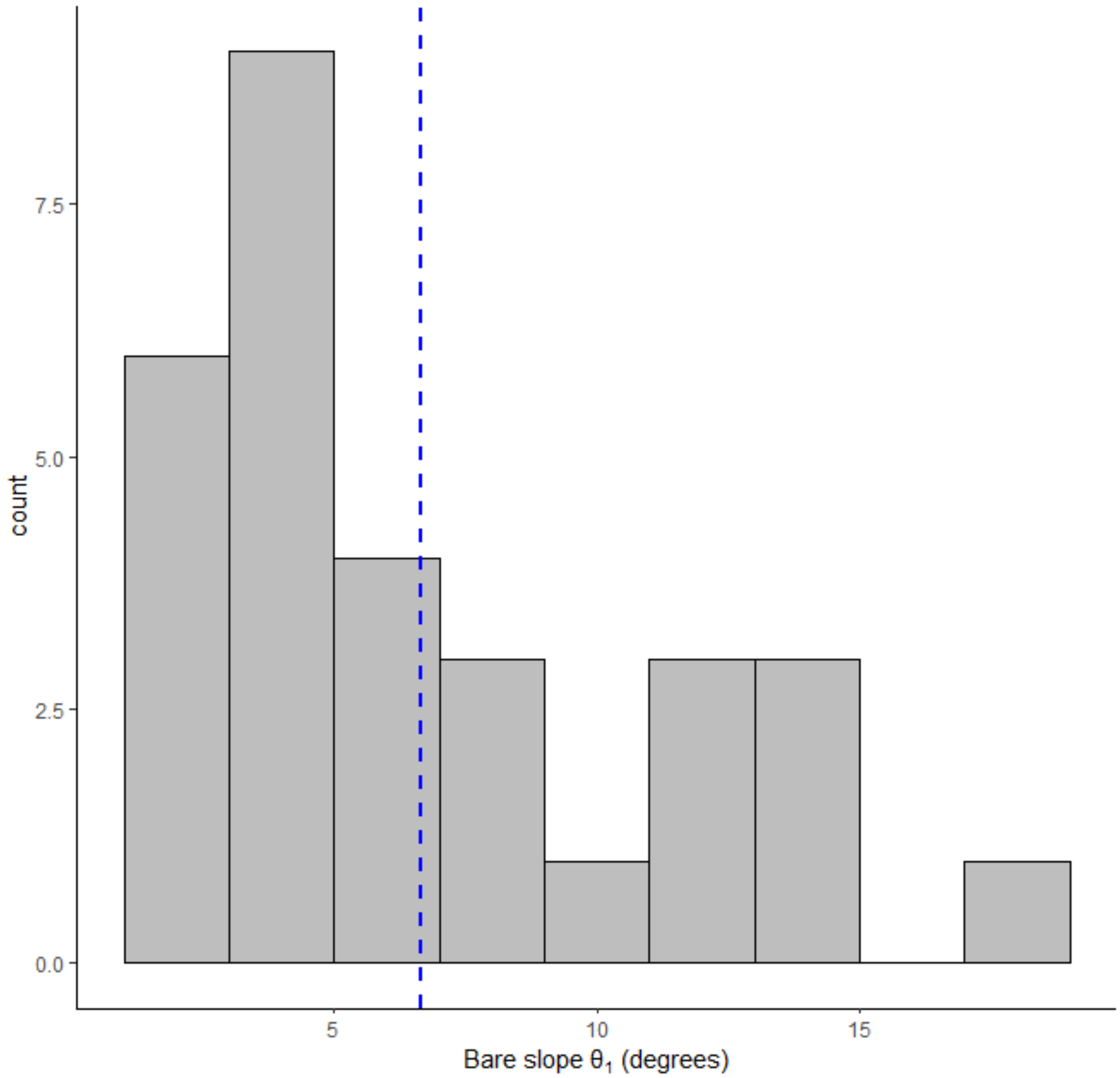

Figure 4.6. The distribution and mean (dashed blue line) of bare bank slopes across our 30 study sites.

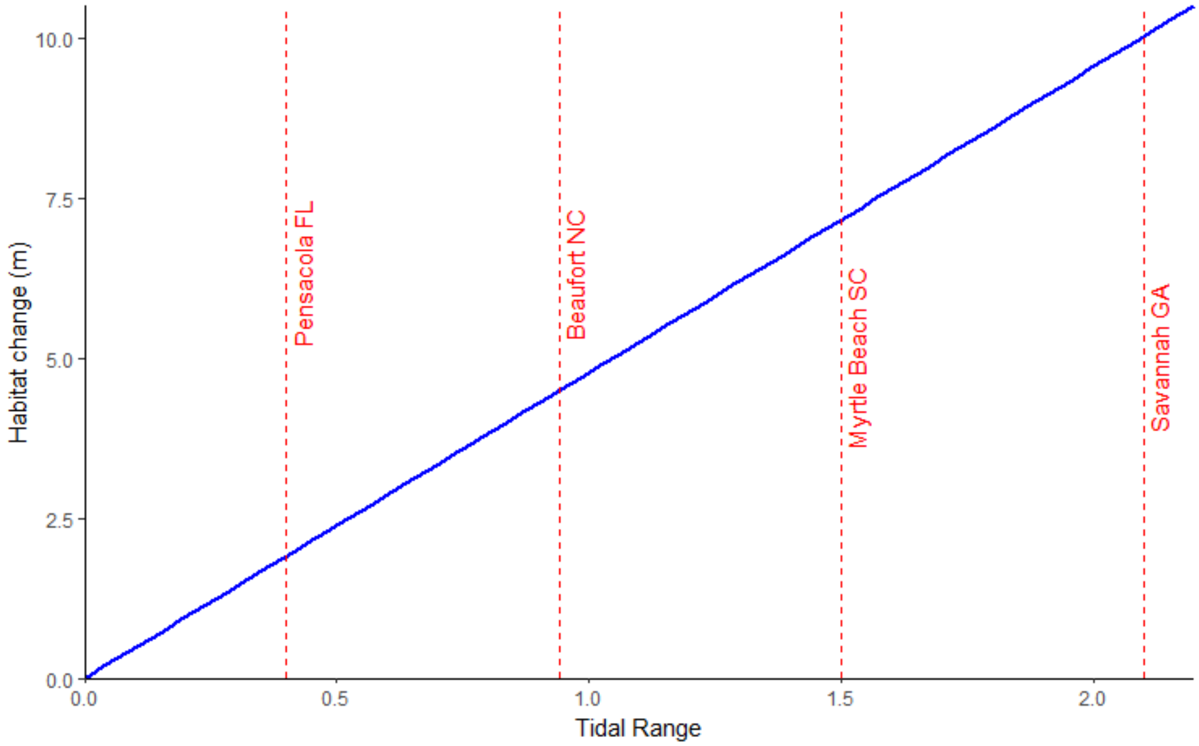

Figure 4.7. Predicted geometric effect of tidal range on habitat change (C_Δ), for bare bank slope of $\theta_1 = 2°$ and oyster-engineered slope change of $\theta_\Delta = 1°$. The tidal range over which oysters grow (v) is kept constant at 50% the height of the tidal range. The average tidal ranges of key locations in the South Atlantic Bight and Gulf of Mexico (Pensacola FL, Beaufort NC, Myrtle Beach SC, and Fort Pulaski near Savannah GA) are indicated in dashed red lines.

Tables

Table 4.1: Replication statement

Metric	Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Bare bank slope (θ_1)	Bank	Estuary	30
Fetch (F)	Bank	Estuary	30
Oyster-engineered slope change (θ_Δ)	Bank	Estuary	30
Cordgrass habitat change (C_Δ)	Bank	Estuary	30

Table 4.2: Subset of AICc model selection results. Global model with all interactions, and the top four models with the lowest AICc values.

Parameters	K	AICc	Delta AICc	AICc Wt.	Cumulative AICc Wt.	Log-likelihood	Adjusted R^2
θ_1	3	199.89	0.00	0.59	0.59	-96.48	0.38
θ_1 , θ_Δ	4	201.61	1.73	0.25	0.84	-96.01	0.38
θ_1 , θ_Δ, F	5	203.79	3.90	0.08	0.92	-95.64	0.37
θ_1 , θ_Δ , $\theta_1 * \theta_\Delta$	5	204.10	4.21	0.07	0.99	-95.80	0.36
θ_1 , θ_Δ, F, and all interactions	9	208.59	8.70	0.01	1.00	-90.80	0.46

CHAPTER 5

CONCLUSIONS

In the preceding chapters, I have shown that ecosystem engineering is context dependent. I demonstrated that ecosystem engineering outcome is affected by energy, as a result of both live and legacy engineering. While I predicted a positive correlation between engineering potential and energy, the results were more nuanced. I found that live engineering outcome had a unimodal response to energy, where live engineering outcome increased with positive effects on cordgrass habitat over low to mid wave energy. However, I found that when wave energy was high, engineering had a negative impact of cordgrass habitat. In contrast, as I predicted, legacy engineering did exert increasing negative impacts on cordgrass habitat with increasing energy. Consequently, the net effect of live and legacy engineering is difficult to predict. In this system, I found that net engineering outcome for the whole estuary had a positive effect on cordgrass habitat. This was because most of the coastline has low fetch values, where live engineering has a positive effect and negative legacy effects are small. For the rare sections of coast with mid to high wave energy I found the opposite relationship, where live positive effects switched sign and negative legacy effects were higher in magnitude than live effects, resulting in net negative engineering outcome.

Looking closer at the relationship between context, ecosystem engineer structure, and ecosystem engineer outcome, I found that in this system, although context is not correlated with engineered structure, context is correlated with engineered outcome. Specifically, I found that environmental context—in this case, unengineered intertidal bank slope— was highly correlated with cordgrass habitat, the outcome of oyster engineering, but not the actual change in slope resulting from engineered structure. Through simple geometric modeling, I found that if oysters engineer a slope increase to a bank with an existing large slope, its engineering has minimal effects on cordgrass habitat. However, when the unengineered bank slope is small, any oyster engineered structural change has large effects on cordgrass habitat.

Given that ecosystem engineers can exist in close proximity to one another, I looked at the reciprocal effects of engineering outcome between two ecosystem engineers. Specifically, I found that oysters and cordgrass facilitate one another. Cordgrass increased biomass and recruitment of upper reef oysters, but not oyster length. However, when oyster length was binned into separate size classes, cordgrass increased the length of large oysters. This distinction is important, as juvenile oysters are highly susceptible to desiccation and heat stress. The faster they can grow into larger oysters, the more likely they are to survive these stressors. The results show that cordgrass shading, rather than density (structural complexity), is the main driver of cordgrass engineering effects on oysters. Field surveys show a correlation between oyster engineering and cordgrass habitat, where cordgrass habitat extends by a mean 5.7m when oysters were present relative to unengineered shorelines. Additionally, I found that oyster and cordgrass habitat overlapped by a mean of 1.6m. Given that these species facilitate one another at the vertical edges of their habitat range, and the fact that both habitats overlap, it is likely that through this facilitation, the realized niche of both species is larger than that of their fundamental niche.

This research has direct implications for resource management. The finding that oysters and cordgrass facilitate one another indicates that oyster restoration and living shoreline projects are likely to benefit from planting both species in close proximity. Proximity is especially important for cordgrass to facilitate oysters because facilitation is limited to cordgrass shading effects. My data suggest that the benefits of oyster live engineering of cordgrass habitat may be limited to coastal areas with low and mid wave energy. My data also suggest that the practice of dumping loose shell to promote oyster habitat is unlikely to work in shorelines with mid to high wave energy, as the unconsolidated material is likely to wash away, and will likely wash up as a shell rake, smothering cordgrass.

This research highlights how the effects of live and legacy engineering are not always the same. It is likely that for most allogenic engineers, the effects of live and legacy engineering are relatively the same. This research suggests that this may be different for autogenic engineers. This research showed that live oyster engineering mainly had a positive effect on cordgrass habitat, whereas legacy oyster engineering had a negative effect. These differences were due to the fact that live oyster reefs are sessile, whereas legacy dead oyster shell is disarticulated from the reef, highly mobile, and subject to deposition as shell rakes. This highlights how focusing on trait differences between live and legacy engineering may help predict net engineering outcome. This work also highlights how environmental context may help predict ecosystem engineering outcome. By definition, engineers modify environments through structural change. It makes intuitive sense that the unengineered baseline structure, or environmental context, upon which the engineer acts would influence the impact of its engineering. I propose that measuring environmental context in the same unit used to measure engineered structure may be particularly informative.

APPENDIX A

CHAPTER 2

Table A.A.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 A.A.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 A.A.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 A.A.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		

APPENDIX B

CHAPTER 3

Intertidal hardened structures like manmade bulkhead shorelines or natural oyster reefs can affect shorelines downstream of the hardened structures footprint. This is known as flanking effects. To assess the linear extent of oyster flank engineering as a function of fetch, we selected 22 sites across a fetch gradient from St Catherines Estuary, Liberty County, Georgia, (64km^2 study domain; 31.660° N; 81.235° W). We created a 100 meter buffer of shoreline around each reef. Cordgrass and water's edge were digitized from NOAA (2013) aerial photography. Starting at the outer buffer limit and working inwards towards the reef, shore width (distance between cordgrass and water's edge) was measured every 5 meters. When width increased by 2 meters or more, we measured shore width every meter, to more finely resolve the extent of flanking effects. The shoreline distance between the reef edge and outer limit of flanking effects was measured for each reef. We found that at all sites, flank effects were contained within a 20-meter buffer of oyster reefs (Figure A.B.1). We also found that fetch was not correlated to the linear extent of flank engineering ($F_{1,20} = 1.69$, $p < 0.21$, $R^2 = 0.03$). It is important to note, that while we found that flanking effects could occur up to 20 meters from a reef, most reefs did not have any flanking effects.

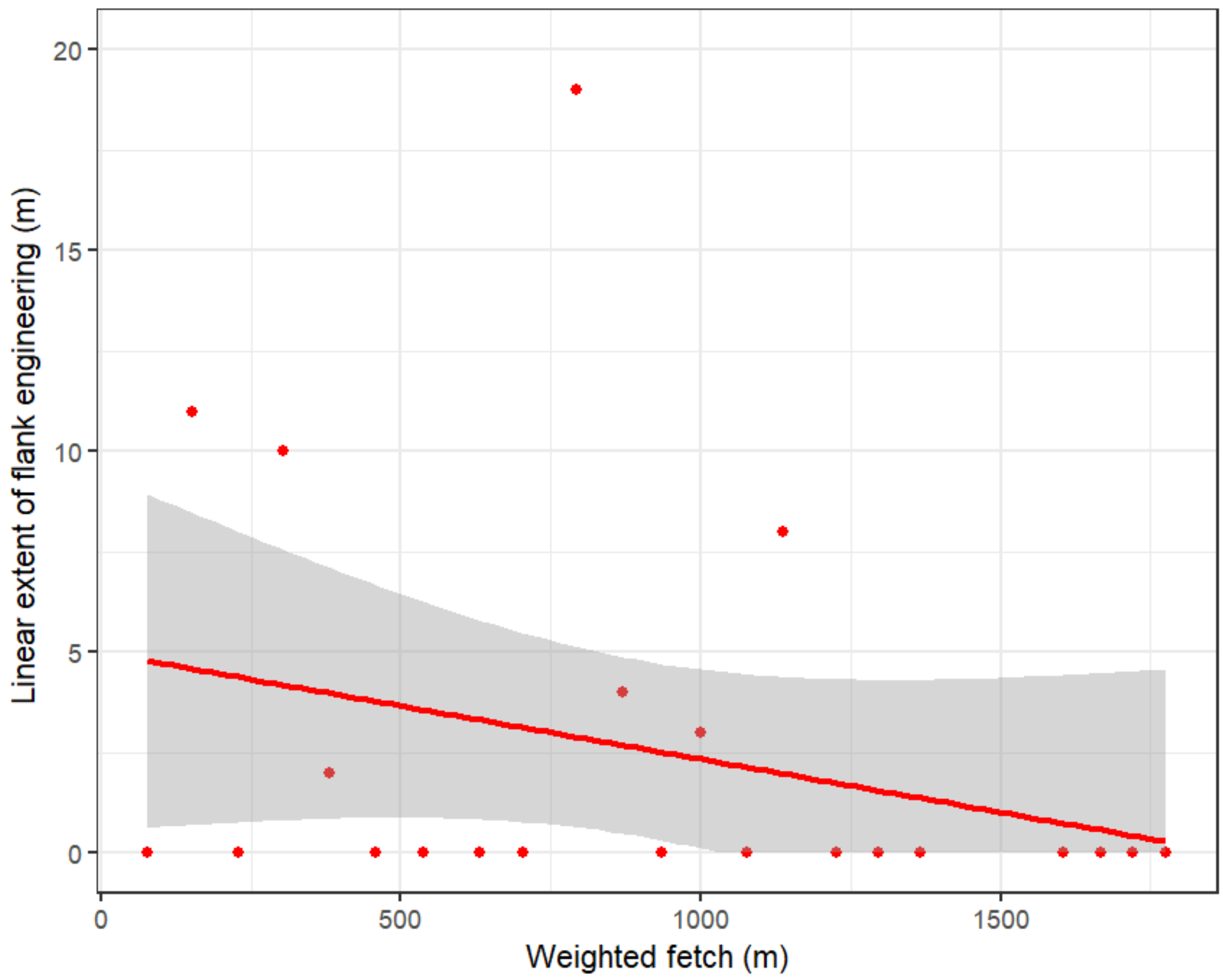

Figure A.B.1. Linear (shore-parallel) extent of oyster flank engineering as a function of fetch. At all 23 sites, the linear extent of oyster flank engineering was under 20m and usually much less than 10m. Model regression lines (red), data points (red), and 95% confidence intervals (grey shading) are shown.

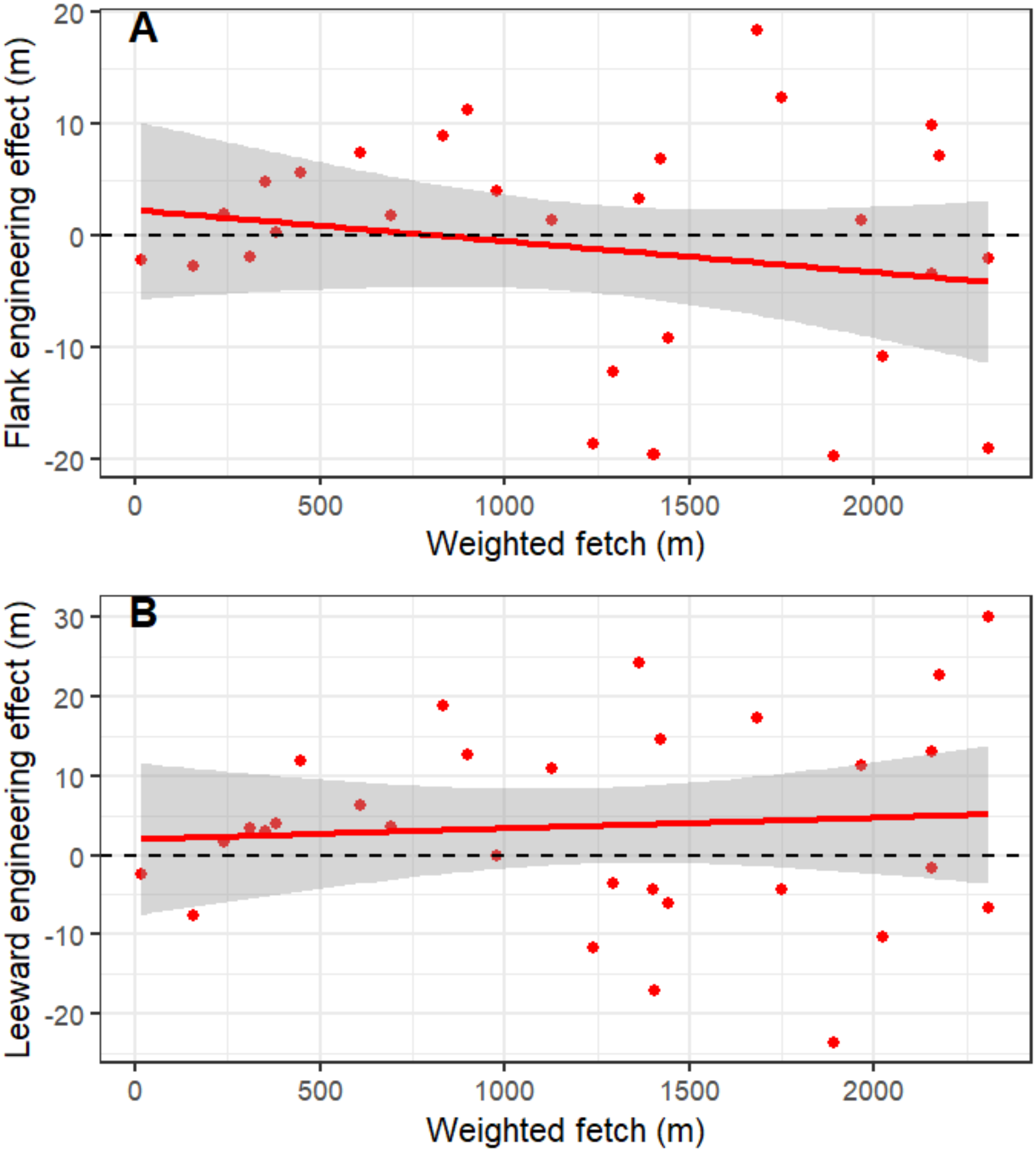

Figure A.B.2. Effect of weighted fetch on oyster engineering of cordgrass habitat (WOI). (A) Flank (WOI_f) and (B) leeward (WOI_l) engineering for all 30 sites. Sites were chosen to represent all weighted fetch classes (and not based on the commonality of weighted fetch classes). Increased variability in engineering effects for sites with mid to high fetch, can be seen (A and B). Model regression lines (red), data points (red), and 95% confidence intervals (grey shading) are shown.