

Using plant-bivalve inter-specific facilitation to enhance coastal restoration
by

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Salt marshes and oyster reefs are critical ecosystems which are being lost or degraded at an alarming pace around the world. Current restoration efforts are insufficient to compensate for past and current habitat degradation, with restoration often ending in failure or only partial recovery. Increasingly, ecologists are calling for the inclusion of facilitation in coastal restoration efforts as a method to bolster success. Facilitation is a positive interaction in which a habitat modifier reduces local abiotic or biotic stressors, allowing organisms which were previously excluded to persist. Inter-specific positive interactions are predicted to be particularly important in areas of high physical stress.

In North Carolina, fringing oyster reefs and salt marsh vegetation facilitate each other's growth and persistence through attenuation of wave energy and substrate stabilization. These positive interactions represent a promising method to address pressing issues in coastal restoration, specifically, marsh restoration in environments stressed by high wave energy and excessive nutrient enrichment. To date, coastal restoration has largely failed to incorporate the benefits of positive interactions, despite research indicating that such facilitation may increase restoration success.

I examined the ability of oyster reefs to mitigate hydrodynamic and nutrient enrichment stress on marsh vegetation (smooth cordgrass, *Spartina alterniflora*) in two studies at an eroding salt marsh in Beaufort, North Carolina. In Study 1, I constructed restored oyster reefs from two

restoration substrates (Oystercatcher, OC; and shell bags, SB) on low- and high-energy shorelines, and compared their abilities to mitigate shoreline retreat, accrete and retain marsh sediment, and promote robust oyster communities. In Study 2, I investigated whether oyster reef presence can mitigate detrimental impacts of nutrient over-enrichment by transplanting and experimentally fertilizing *S. alterniflora* at a subset of the OC reef sites, comparing their growth and survival to that at control non-reef sites. Study 1 took place from May 2018 to August 2020, while Study 2 occurred in Summer 2019, with each study period including at least one extreme storm event (i.e. hurricane or tropical storm).

In Study 1, constructed reefs mitigated marsh retreat on both shorelines, with the OC reefs outperforming SB reefs on the high-energy shoreline. SB reefs on that shoreline were severely damaged by storm events, while OC reefs on both shorelines exhibited steady oyster recruitment and growth. OC reefs hosted higher densities of larger oysters. In Study 2, transplanted vegetation experienced high rates of mortality, which were impacted by a complex interaction between elevation, fertilization, and reef presence. Unsurprisingly, the most waterward portions of plots experienced greatest elevation loss. Reef presence fostered both higher plant survival and higher shoot density, while clonal expansion was greater at control sites. Shoot density decreased over the course of the study, while clonal expansion peaked in late July before also declining. Overall, any effect of fertilization was swamped by the high hydrodynamic stress impacting transplanted vegetation.

Conventional restoration approaches are often ineffective in areas of high stress. I highlight the ways in which deliberate decisions regarding oyster reef substrate and siting can maximize protection to salt marsh edges, and critical considerations for future research regarding mitigation of nutrient over-enrichment in threatened salt marsh systems. Harnessing of inter-

specific facilitation between native foundation species represents a promising avenue to restore and protect these critical habitats.

Using plant-bivalve inter-specific facilitation to enhance coastal restoration

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LIST OF SYMBOLS OR ABBREVIATIONS

| | | |
|------|---|---|
| NNBI | Natural and nature-based infrastructure | 1 |
| OC | Oystercatcher™..... | 2 |
| SB | Shell bag..... | 3 |
| RTK | Real-time kinematic..... | 4 |
| GNSS | Global navigation satellite system | 4 |

CHAPTER 1: REEF RESTORATION

INTRODUCTION

Increasingly frequent and intense storms compounded by rising sea levels pose a significant and growing threat to coastal shorelines (Hauer et al. 2016, Lin et al. 2012). Typically, so-called “grey” infrastructure (e.g., bulkheads and seawalls) has been used to provide protection and prevent erosion. However, with mounting evidence that these structures increase the erosion and loss of waterward habitats (Douglass and Pickel 1999) and negatively impact associated faunal communities (Gittman et al. 2016a), demand for alternative solutions has grown. One such solution is natural and nature-based infrastructure (NNBI) (Sutton-Grier et al. 2018). Coastal NNBI, such as salt marshes and oyster reefs, capitalizes on the protective capabilities inherent to coastal ecosystems (Koch et al. 2009), while simultaneously maintaining provision of other beneficial services such as water quality improvement (Brin et al. 2010, Smyth et al. 2015), carbon sequestration (Chmura et al. 2003, Fodrie et al. 2017), and nekton habitat (Humphries and La Peyre 2015, Minello et al. 2003). In addition, unlike static, grey infrastructure, NNBI approaches incorporating ecosystem engineers (Jones et al. 1997), like marsh plants and oyster reefs, can reduce wave energy, trap sediments, and accrete at rates which keep pace with sea level rise (Kirwan and Temmerman 2013, Rodriguez et al. 2014).

The simplest coastal NNBI approach is planting of native vegetation. However, the protective benefits provided by marsh vegetation (Möller and Spencer 2002) may be reduced by factors like shoreline slope (NRC 2007) and seasonal decreases in biomass (Möller 2006). Where wave energy, fetch, or bathymetry exceed the thresholds at which marsh plants can survive (Roland and Douglass 2005), additional structural components – like low sills built from oyster shell or rock - may be necessary. These oyster and rock sills can reduce marsh shoreline retreat (Polk and Eulie 2018) and may both be more resilient to storm damage (Smith et al. 2018) and

host more native bivalves (Gittman et al. 2016b), than un-augmented marshes or traditional shoreline hardening structures. However, sill construction necessitates conversion of ecologically valuable subtidal habitat (Bilkovic and Mitchell 2013), and the secondary production of sill-associated oysters may not attain the level of oyster reefs themselves (Wong et al. 2011). As such, oyster-based NNBI is becoming increasingly popular. Oyster reefs can enhance the protective services of marshes by facilitating the establishment and growth of emergent vegetation (Chowdury et al. 2019, Fodrie et al. 2017) and attenuating wave energy (Kroeger & Guannel 2014). However, oyster reefs' ability to successfully attenuate waves and stabilize shorelines is context-dependent, hinging on local hydrodynamic energy, reef design, and distance from shore (La Peyre et al. 2015, Zhu et al. 2020, La Peyre et al. 2014). While reefs built from loose or bagged oyster shell successfully mimic the structure of natural oyster reefs, they are susceptible to failure in the years following restoration when oyster growth and recruitment have not yet bound cultch to itself and its substrate (Keller et al. 2019). When cultch or shell bags are dislodged, young oysters which have recruited to the shells can die (Theuerkauf et al. 2015a) and the protective benefits of the reef are obviated (Ysebaert et al. 2019).

Further, because oyster shell is often a limited resource (Powell & Klinck 2007), restoration practitioners may turn to a variety of alternative substrates, including concrete pre-fabricated structures like Oyster Castles™ and Oyster Domes™ (Theuerkauf et al. 2015a). Concrete- or cement-based alternative substrates negate the issue of limited shell availability and can be tailored to the hydrodynamic, larval, and sedimentation processes at a given site (Graham et al. 2017, O'Beirn et al. 2000), providing greater substrate stability than loose shell (Goelz et al. 2020). One such novel substrate is Oyster Catcher™ (OC), a biodegradable material made from plant-fiber cloth dipped in cement (Sandbar Oyster Company 2018). OC reefs can be

constructed at specific heights to reduce the likelihood of fatal sedimentation (Theuerkauf et al. 2015a, Walles et al. 2016) and attain an elevation optimal for oyster growth (Ridge et al. 2015). Despite the predicted benefits of these alternative substrates, their biological efficacy (i.e. the degree to which they recruit and sustain oyster populations) and their performance as compared directly to conventional shell-based approaches is largely unknown (Goelz et al. 2020).

The goal of this study was to compare the performance, in terms of marsh stabilization and oyster reef formation, of alternative (e.g., OC) and conventional (e.g., shell bag) reef substrates in “high” and “low” wave exposure conditions in eastern North Carolina (Fig. 1). I monitored reef evolution (i.e., vertical and horizontal reef expansion/subsidence, oyster community characteristics) and assessed how these characteristics related to migration and elevation of the landward marsh shoreline. I hypothesized that OC reefs would recruit oysters and facilitate their growth to a greater degree than would shell bag (SB) reefs, due to their increased structural stability and configuration allowing for vertical accretion in additional directions relative to SB reefs (Fig. 1C, D, Fig. 1.2). I predicted that, when compared to unaltered control shoreline, sites protected by either reef substrate would experience comparatively less retreat. I further hypothesized that wave energy constrains the magnitude of marsh retreat. Namely, that reefs would provide greater protection at high-energy compared to low-energy sites (La Peyre et al. 2014), and that exposure would moderate this protection, with OC reefs reducing marsh erosion in both low and high exposure settings but SB reefs succeeding only in low exposure settings.

METHODS

Study Site

I conducted this study at Carrot Island within the Rachel Carson National Estuarine Research Reserve (NERR) in Beaufort, North Carolina, USA (34°42'12.96"N, 76°37'33.96"W). Carrot Island is located to the north of Back Sound, a large, shallow sound in Carteret County, NC (Fig. 1.1). Carrot Island marshes are experiencing both an increasing tidal range (Zervas 2003) and high levels of ambient erosion, losing up to 2 m annually in some areas (Theuerkauf et al. 2015b). The Island's intertidal salt marsh is dominated by *Spartina alterniflora* and exhibits scarped, ramped, and tidal creek shoreline geo-morphologies (Keller et al. 2019). The exposed "ramp" shoreline abutting Back Sound is characterized by the presence of a disaggregated oyster shell berm shoreward of *S. alterniflora* and experiences high wave energy resulting from storms, persistent southwesterly winds in summer, and boat wakes from a nearby channel (Theuerkauf et al. 2015b). The sheltered, tidal "creek" shoreline, which is characterized by a greater occurrence of aggregated clumps of oysters, receives hydrodynamic energy largely from tidal exchange. The fetch of the creek shoreline is much smaller fetch than that of the ramp (50 m vs. 2,472 m; Keller et al. 2019), resulting in a lesser degree of annual retreat (Theuerkauf et al. 2015). There is an abundant larval supply to the area, with the largest larval pulse occurring in August or September following maximum summer water temperatures (Ortega & Sutherland 1992).

Experimental Reef Siting and Construction

In August 2017 and April 2018, I used a Trimble R10 Real-Time Kinematic (RTK) GNSS (GPS; 0.5-1.0 cm horizontal and 1.0-4.0 cm vertical resolution) to identify sites on both shorelines with surface elevations falling in a previously-identified local "optimal growth zone"

(OGZ, -0.6 m to -0.3 m NAVD88; Ridge et al. 2015). In May 2018, I delineated four experimental blocks along both the relatively high energy ramp and relatively low energy creek shorelines of Carrot Island. Within each block I constructed one SB and one OC reef (2 m × 4 m) under a General Permit for marsh toe revetments (NCDRCM #69643, n=16). These reef dimensions were chosen to approximate those of both existing restored (Grabowski et al. 2005) and natural patch reefs (Keller et al. 2019) in the area. I also established four control sites (no reef) along each of the two shoreline types (n=8, Fig. 1.1B).

All reefs are shore-parallel and located within the OGZ (Ridge et al. 2015), positioned 0.14-0.69 m and 0-1.38m from the marsh edge in the creek and ramp respectively, mimicking the formation of natural fringing oyster reefs in North Carolina (Grabowski et al. 2005). OC reefs in the creek were constructed to stand 0.25 m above the sediment and were of a two-tiered lattice design, consisting of Y-shaped supports sunk ~0.25 m into the sediment, across which horizontal rows of rods were laid and bound together with galvanized wire. I constructed OC reefs along the ramp in a similar design, with coir logs placed on the sediment beneath the rod lattice and anchored with rebar (Fig. 1.1D, Fig. 1.2). Rods used in reef construction were pre-seeded with wild oyster spat prior to deployment. SB reefs were constructed from 143-176 shell bags, with each bag roughly measuring 44 × 28 × 17 cm. All SB reefs had an initial height of approximately 0.25 m and contained four bags that had been pre-seeded in the same manner as seeded rods.

Shoreline and Reef Monitoring

During the study period, our site was subjected to four severe storm events – Hurricane Florence (landfall Sep. 14, 2018, Category 1), Tropical Storm Michael (landfall Oct. 11, 2018), Hurricane Dorian (landfall Sep. 6, 2019, Category 1), and Hurricane Isaias (landfall Aug. 3,

2020, Category 1). In 2018, prior to reef construction, I established permanent transects extending from the landward edge of each reef's footprint to 5 meters shoreward of the marsh. I demarcated four permanent sampling stations along the transect at 0, 1, 3, and 5 m from the landward reef edge (or control site marker). Following reef construction, I assessed change in marsh surface elevation at each transect station using the RTK relative to NAVD88. I collected these elevation data in May 2018 and May 2020. Also using the RTK, I mapped the horizontal position of the marsh shoreline during the period of peak aboveground marsh vegetation biomass on both the ramp and creek in September 2018 and August 2020. Marsh shoreline edge was classified as the most waterward extent with a density of ~50 stems per m². I quantified live *S. alterniflora* stems within a 0.0625-m² quadrat at each transect station, then converted these densities to 1-m². To monitor changes in reef area (m²), I collected continuous (maximum sampling interval of 0.5 m) backpack-mounted RTK measurements while walking the perimeter of each reef. Finally, in August 2020 I assessed reef height by collecting discrete RTK measurements on the top of the reef corners and on the substrate immediately outside of each corner to assess change in vertical relief through time (n=8 points per reef).

I collected marsh shoreline position measurements in September 2018 (immediately pre-Florence) and in August 2020 (post-Isaias). *S. alterniflora* stem density data were collected concurrent with marsh position measurements. I quantified site-level shoreline change at each reef and control site by converting the aforementioned marsh shoreline positional data into line files in ArcMap (ESRI, version 10.7.1). Using the Distance tool, I calculated the mean shoreline retreat at each site by collecting triplicate measurements of the difference between the 2018 and 2020 shorelines. As a complement to this analysis, I used the software package Analyzing Moving Boundaries Using R (AMBUR) to perform assessments of shoreline change on the

larger creek and ramp shorelines (Jackson et al. 2012). I compared the vegetation lines from September 2018 and August 2020, casting transects at 0.5 m intervals. I retained AMBUR's calculated end-point rate (hereafter, shoreline change rate) and calculated the annualized shoreline position uncertainty following the methods of Eulie et al. (2013).

Given my interest in reef evolution and performance over a multi-annual time scale, I assessed oyster characteristics annually. I assessed reef area 4 times: in May 2018 (immediately post-construction and pre-Florence), in September 2018 (post-Florence), in September 2019 (post-Dorian), and in August 2020 (post-Isaias). Reef footprints were converted to polygons, from which I could extract their area in ArcMap. I assessed live and dead oyster demographics at reef and control sites in October 2018 (post-Florence), September 2019 (post-Dorian), and August 2020 (post-Isaias). Oysters from representative samples of each treatment were grouped into two size classes: juveniles (10–24 mm), and adults (≥ 25 mm, La Peyre et al. 2014). Densities were calculated based on the number of juveniles and adults (both living and dead) divided by the total surface area available for recruitment and then standardized per m^2 (Moore et al. 2020). Because smaller spat were difficult to enumerate in OC samples, I did not examine spat measuring <10 mm. At control sites, the density of adult and juvenile oysters was assessed within the excavated contents of a $0.0625\text{-}m^2$ quadrat placed in the center of the plot. To allow accurate inter-substrate comparisons of SB and OC samples, I based density calculations upon their respective surface areas (and therefore, area available for oyster settlement and growth). At SB sites, one bag was removed from the midpoint of the reef and measured to calculate an average surface area based on the formula of a rectangular solid (in m^2). All juvenile and adult oysters within the sample were enumerated and their totals divided by the calculated surface area, accounting for the fact that a majority of oyster settlement occurs on the bag exterior

(Moore et al. 2020). At each OC site, I removed a 10-cm linear section of rod from one corner of the reef using a hacksaw or reciprocating saw and calculated its surface area using the formula of a cylinder (in m^2). Juvenile and adult oyster densities were calculated based on the number of individuals from each size class present in the average surface area (in m^2). In addition, I measured the length of the first 10 live and dead juveniles and adults encountered in a sample, or the total number present if it was less than 10. I removed rod segments and SBs from the same location on each oyster reef to ensure consistency.

Statistical Analysis

I performed exploratory visualization to determine the distributions of our data and, based on those distributions, selected the appropriate statistical modeling approaches (Bolker 2007). I used Bayesian linear mixed effects models to analyze the fixed effects of shoreline (creek, ramp), treatment (control, OC, SB) and transect station (1 m, 3 m, or 5 m into the marsh) on change in marsh surface elevation between May 2018 and May 2020. A Bayesian approach was necessary to overcome issues associated with singularity in our random effect, Block (representing spatial position of sites along the shoreline).

I used linear mixed effect models to analyze: 1) the fixed effects of shoreline (creek, ramp) and treatment (control, OC, SB) on change in shoreline position at each site between September 2018 and August 2020; and 2) the fixed effects of shoreline (creek, ramp), timestep (May 2018, September 2018, September 2019, and August 2020), and reef type (OC, SB) on the areas of our restored reefs. I included Block as a random effect in both models.

I used negative binomial generalized linear mixed effect models to analyze the fixed effects of shoreline (creek, ramp), treatment (control, OC, SB), year (2018, 2020), and transect

station (3 m or 5 m into the marsh) on *S. alterniflora* shoot density. Because *S. alterniflora* was rarely present at the 1 m transect station, I omitted the 1 m station data in this analysis. Block was included as a random effect. The negative binomial distribution is well-suited for patchy, over-dispersed data, mimicking a Poisson distribution but allowing for greater heterogeneity (Bolker 2007). I fit all models using maximum likelihood estimation through Template Model Builder (TMB).

To analyze the effect of substrate type on reef height, I used two-way Analysis of Variance (ANOVA) with the interaction term of shoreline (creek, ramp) and reef substrate (OC, SB). Data required no transformation to meet model assumptions (Levene's Test, $P > 0.05$).

To analyze differences in adult and juvenile oyster density across treatments, I used a two-step hurdle model for each age class. First, I determined whether oyster restoration – regardless of substrate – enhanced oyster densities beyond those hosted by the unaltered control plots. I created a new binomial response variable of oyster presence, scoring samples which included at least one live oyster in the given age class as 1, and those with no live oysters as 0. Hurdle models analyze data in two components: first, using an initial model to determine the probability of obtaining a zero outcome, then proceeding to model the non-zero outcomes (Cragg 1971). As such, zero and non-zero outcomes are treated as separate categories of data. I analyzed our presence-absence data using a binomial generalized linear model with a fixed effect of simplified treatment (comparing reef and no reef). Based on model results as interpreted from likelihood-ratio chi-square tests, I proceeded with Bayesian linear mixed effect models to examine the effects of shoreline (creek, ramp), year (2018, 2019, 2020), and reef type (OC, SB) on those data which indicated oyster presence. I log-transformed all data prior to analyses to meet model assumptions, and included Block as a random effect in all candidate models.

Lastly, I used Bayesian linear mixed effect models to analyze the fixed effects of shoreline (creek, ramp), year (2018, 2019, 2020), and reef type (OC, SB) on oyster length, examining adult and juvenile samples in separate models. As with my analysis of shore elevation, I used a Bayesian linear mixed effect model to overcome issues associated with singularity in my random effect, Block. I log-transformed all adult length data prior to analysis to meet model assumptions. Because I treat oyster length as a proxy for age and therefore growth rate, I omitted control plots from this analysis. Although I retrieved small numbers of live oysters from control samples, these individuals were often singletons of uncertain origin (e.g., could have been washed into the plot rather than having settled and grown there), and therefore did not contribute to my understanding of restored reef evolution.

I used likelihood ratio testing to evaluate mixed model performance and select the optimal model for each analysis. I initiated each analysis with a fully-crossed interaction model, sequentially reducing model complexity and removing higher-order terms based on the outcome of likelihood ratio tests. I then used Tukey's post-hoc comparisons and Kenward-Roger degrees of freedom approximation to assess pairwise differences for any significant treatment or interactive effects indicated by our models. I used an alpha level of 0.05 for all hypothesis testing, and performed all analyses in the R statistical computing environment (v. 3.5.2, R Core Team 2018) using the packages lme4 (Bates et al. 2015), blme (Chung et al. 2013), lsmeans (Lenth 2016), car (Fox and Weisberg 2019) and glmmTMB (Brooks et al. 2017).

RESULTS

Marsh Elevation Change

Changes in marsh surface elevation between 2018 and 2020 varied according to shoreline, treatment, and distance into the marsh (transect station, Appendix S1: Table S1). At creek sites, overall elevation loss over the two-year period was greater at control sites (-8.0 ± 1.3 cm) compared to SB reefs (-1.8 ± 1.2 cm, $P=0.04$, Fig. 2A-C, Appendix S1: Table S2). Creek OC reefs also experienced less elevation loss relative to creek controls (-5.2 ± 0.75 cm), but this difference was not statistically significant ($P>0.05$). Elevation change at creek reef sites did not differ among reef substrates ($P>0.05$, Fig. 2, Appendix S1: Table S2). At ramp sites, the elevation loss at control sites (-21.8 ± 4.0 cm) was greater than that at OC reefs, which incurred losses of -2.3 ± 3.9 cm (Fig. 2, Appendix S1: Table S2). SB reefs at ramp sites gained an average of 1.1 ± 2.9 cm in elevation, but this increase did not differ from elevation change at OC reefs ($P>0.05$). Along both shorelines, change in marsh elevation immediately landward of SB and OC reefs (1m-station) was less than that at the equivalent position at control sites ($P<.001$ and $P=0.008$ respectively, Appendix S1: Table S2). However, marsh elevation change did not differ between the two reef substrates (Appendix S1: Table S2). While control sites and OC reefs exhibited elevation loss across all transect stations, average loss of elevation was only observed at the mid-transect station (3m-station) behind SB reefs (Fig. 2).

Shoreline Position Change

Shoreline change analyses revealed that both the creek and ramp shorelines experienced horizontal retreat during our study period, with average annual retreat rates of -0.89 ± 0.14 m and -1.65 ± 0.02 m, respectively (Fig. 1B, Fig. 3, Appendix S1: Table S3). As such, reef substrate

and presence did not mitigate marsh retreat along the entirety of these shorelines. However, on the ramp, the marsh behind OC reefs retreated at an annual rate of 1.29 ± 0.11 m, which was less than the annual retreat at control 1.62 ± 0.04 m ($P = 0.019$) and SB sites 1.64 ± 0.08 m ($P = 0.008$). In the creek, SB reefs tended to decrease the degree to which landward marsh retreated as compared to control and OC sites, although this trend was not statistically significant ($P > 0.05$, Appendix S1: Table S3).

Marsh Vegetation

Between 2018 and 2020, aggregated *S. alterniflora* shoot density declined on both shorelines, although this difference was statistically significant only along the ramp shoreline (Fig. 1.5, Tables 1.4, 1.5). In both the initial and final years of sampling, creek sites maintained higher shoot density than those on the ramp (2018: $P = 0.028$, 2020: $P < 0.001$, Fig. 1.5).

Reef Characteristics

Both substrate and shoreline mediated changes in reef area over time (particularly pre- and post-Michael) (Fig. 1.6, Table 1.6). Along both shorelines, OC reefs demonstrated steady expansion over the course of the study (Fig. 1.6, Table 1.7), attributable to horizontal accretion of the reef community on a stable substrate (Tables 1.10, 1.11). The footprints of creek SB reefs decreased over the course of 2.5 years (Table 1.7), likely as a result of sediment infilling edge SBs (Fig. 1.6A, 1.6C). Conversely, between post-Florence and post-Dorian samplings, average areal extent of SB reefs along the ramp shoreline dramatically increased ($P < 0.001$, Fig. 1.6D). The time interval between these two measurements included the passage of Michael, which

scattered and critically de-stabilized three of the ramp SB reefs (Fig. 1.6F). As such, increases in ramp SB reef area were accompanied by a concomitant loss of vertical relief.

While SB reefs lost vertical relief on both shorelines, the heights of OC reefs during their terminal sampling hinged on shoreline type ($F_{1,58}=30.71$, $P < 0.001$). Specifically, two years post-construction, the heights of creek SB and OC reefs did not differ from one another (SB: 0.190 ± 0.018 m, OC: 0.199 ± 0.018 m, Tukey's post-hoc, $P = 0.985$). However, ramp OC reefs (0.415 ± 0.023 m) were taller than creek OC reefs and the SB reefs on either shoreline (ramp SB: 0.190 ± 0.016 m, Tukey's post hoc, $P < 0.001$).

Oyster Demographics

Regardless of reef substrate, restored reefs were more likely to support both juvenile ($P < 0.001$) and adult ($P < 0.001$) oysters as compared to control sites (Table 1.8). Between 2018 and 2020, the adult oyster densities on OC reefs increased by $>400\%$ ($P < 0.001$, Fig. 1.7, Table 1.10), while the adult density on SB reefs remained unchanged ($P = 0.779$, Table 1.10). By the final year of sampling, OC reefs hosted $>800\%$ higher densities of oysters than did SB reefs ($P > 0.001$, Fig. 1.7, Table 1.10). Additionally, adult oyster densities were mediated by the interaction between treatment and shoreline, though this effect was marginal (Table 1.9, $P = 0.058$). OC reefs hosted higher adult oyster densities than their SB counterparts on both shorelines (creek: $P < 0.001$, ramp: $P = 0.0281$, Table 1.10). However, while densities of adult oysters on OC reefs did not differ between the two shorelines ($P = 0.371$), ramp SB reefs had elevated adult oyster densities compared to their creek counterparts ($P = 0.028$).

The trends in juvenile densities were more complex (Table 1.9). While SB reefs had greater juvenile densities than OC reefs in 2019 ($P < 0.001$), I did not observe a similar trend in

the subsequent year's sampling ($P = 0.230$, Fig. 1.7, Table 1.10). Further, high juvenile density on SBs in 2019 was decoupled from adult oyster density in 2020, indicating either particularly slow growth or, more likely, elevated mortality relative to OC reefs. Further, while OC reefs hosted higher densities of juvenile oysters in 2020 as compared to 2018 ($P < 0.001$), SB reefs did not demonstrate a similar trajectory ($P = 0.998$). Juvenile densities on ramp reefs in 2018 exceeded those on creek reefs in that year, but no inter-shoreline difference was observed in 2019 or 2020 (Table 1.10). While both creek and ramp reefs hosted higher densities of juvenile oysters in 2020 as compared to 2018, this difference was statistically significant on creek reefs only (Creek: $P < 0.001$, Ramp: $P = 0.932$, Fig. 1.7, Table 1.10).

The effect of reef substrate on adult oyster length was mediated separately by shoreline and sampling year (Table 1.9, Fig. 1.7). Adult oysters on both substrates were longer in 2020 than they had been in 2018 ($P < 0.001$, Table 1.11). However, the lengths of OC adults exceeded those of SB adults in both the initial and final years of sampling (2018: $P < 0.001$, 2020: $P < 0.001$, Table 1.11) and on both shorelines ($P < 0.001$, Table 1.11). While adult oysters on the creek OC reefs exceeded the length of those on ramp reefs ($P < 0.001$, Table 1.11), the length of SB adults did not vary across shorelines ($P = 0.333$, Table 1.11). The lengths of juvenile oysters found on SB and OC reefs held steady across years, with a slight – but statistically insignificant – decline in 2020 as compared to the previous years (Table 1.11).

DISCUSSION

Coastal ecosystems can provide protective and shoreline stabilization benefits only if the ecosystem engineer upon which their structure depends can grow and persist in a given environment (Walles et al. 2016), which is not necessarily the case for heavily engineered oyster NNBI substrates (Morris et al. 2019a). Here, I demonstrate that oyster-based NNBI can both foster growth of a robust oyster community, while also reducing retreat of landward salt marshes. However, as my comparison of SB and OC performance demonstrates, such benefit provisioning is only possible through designs that account for the interaction of substrate characteristics and configuration with physical forcing to influence post-settlement processes. OC reefs were also better able than SB reefs to withstand the four severe storm events which occurred during the study period. These findings indicate that NNBI substrates like OC, which are highly stable but also provide high-quality oyster habitat, may offer a path forward for restoration in high-energy systems. Further, our results indicate a trajectory of increasing oyster densities associated with OC reefs, which will hopefully translate into increased structural footprint, and therefore protective efficacy, in coming years (*sensu* Morris et al. 2019a). Given the structural integrity of these reefs and recent findings that natural fringing reefs in the same system are growing at a rate exceeding local sea-level rise (Rodriguez et al. 2014), it is not unreasonable to expect that OC reef growth will continue.

Failure to incorporate principles of both ecology and engineering in the design of oyster-based NNBI can undermine its ability to deliver sustained protective benefits (Morris et al. 2019a). In order to continuously deliver ecosystem services and protect threatened shorelines, the structural make-up and configuration of oyster-based NNBI must be designed with an eye towards oyster recruitment and growth. There are, however, inherent trade-offs to be balanced

based on project priorities, including desired composition of ecosystem service portfolios and the temporal scale over which they are delivered (La Peyre et al. 2014). Marsh edges often require several years to demonstrate a positive response to reef-based protection, as evidenced by advancement or ceased retreat (Polk and Eulie 2018, Meyer et al. 1997).

Both study shorelines at Carrot Island are experiencing dramatic retreat (Fig. 1B, Fig. 3). In nearby marshes, *S. alterniflora* has expanded around and enveloped restored fringing oyster reefs (Fodrie et al. 2017). However, the high ambient rates of retreat at Carrot Island render such advancement and increased shoot density unlikely (Fig. 4). *S. alterniflora* landward of reefs is unlikely to rebound until sediment accretion (i.e. vertical elevation gain) is sufficient to allow persistence at its optimum elevation (Voss et al. 2013). If positive elevation change (Fig. 2A, 2C) continues, I hypothesize that shoot density will follow suit, although such a rebound was not observed during our study period. At our high-energy site (ramp), our findings support meta-analytical (Gagnon et al. 2020) and empirical evidence (La Peyre et al. 2015) suggesting that the restored reefs are better able to attenuate wave energy and provide protective benefits at exposed sites. As hypothesized, I observed both the highest shoreline retreat at unprotected control sites and superior mitigation of such retreat by OC as compared to SBs on the exposed ramp. Robust, high-stability substrates thus will likely play an important role in high-energy environments, where previous research has identified an energy threshold above which intertidal oyster survivorship and growth is limited (Theuerkauf et al. 2017).

In the challenging, high-energy ramp environment, the resilience of OC reefs starkly contrasted with the structural failure of their SB counterparts (Fig. 1.6E, F). Specifically, SB reefs were under-engineered for the ramp's hydrodynamic environment, incurring substantial displacement of bags beyond their initial footprints during storm events. This displacement from

ramp SB reefs not only reduced vertical relief but likely resulted in mortality of juvenile oysters from tumbling action (Keller et al. 2019, Scyphers et al. 2011). In contrast, development of robust adult oyster populations supported by the structural stability of OC reefs facilitated vertical and horizontal reef growth; accretion which appeared to have reduced transmitted wave energy to a level suitable for marsh persistence (Roland and Douglass 2005).

Oyster community data collected from shell bags sampled from reefs which had not suffered storm-induced damage indicate that mortality due to displacement alone cannot explain the decoupling of juvenile and adult oyster densities between 2019 and 2020. Rather, I argue that the open lattice-work design of OC reefs allows larvae to access – and grow out from – all surfaces of the structure, which is only possible for larvae on the outermost SBs (Fig. 1.1, 1.2). As such, lower numbers of smaller oysters on SB reefs in the creek could be due in part to heavy sediment deposition (Fig. 1.6B, C). Although oysters are somewhat resistant to burial, survival declines significantly once 70% or more of the oyster is buried (Colden et al. 2015).

It is important to note that the timescale over which marsh shorelines respond positively to NNBI exceeds the duration of this study. Although assessment of the long-term outcomes of oyster-based NNBI in this system will require monitoring over the coming years, I have demonstrated promising reef development and resultant reductions in marsh retreat. Furthermore, I acknowledge the relatively small footprint of the restored reefs in this study (8-m² footprint) as compared to the linear extent of even a modestly sized living shoreline. Small oyster reefs are more likely to be negatively impacted by scour, given that oncoming waves can fully wrap around the structure and meet immediately landward of it (Piazza et al. 2005). However, despite their small size, ramp SB and OC reefs attenuated wave energy and promoted sediment deposition in the area between their footprint and the marsh edge, forming tombolos - small

landforms (here, oyster reefs) attached to the mainland by narrow spits (Fig. 2E, F). Although larger reefs may certainly have mitigated shoreline retreat at our sites to a greater degree than our patch reefs, I am encouraged by the observed reduction in shoreline retreat relative to controls on both shorelines (Fig. 3) The distance from the shoreline at which NNBI projects are constructed is therefore a critical consideration, as this distance is inversely proportional to sediment accretion, and subsequent growth, in landward marshes (Vona et al. 2020). The scale and quantity of oyster restoration projects has outpaced the science and substrate-specific assessments necessary to inform them (Goelz et al. 2020). Practitioners must surmount many obstacles to promote wider use of NNBI (Morris et al. 2019b), and project failure stemming from poor ecological and engineering planning undermines such promotion and adoption. Further, NNBI practitioners are faced with an ever-growing selection of restoration substrates from which to choose (Goelz et al. 2020). Our results highlight the need to consider local oyster ecology, wave energy conditions, and the likelihood of severe weather events when designing and deploying oyster-based NNBI. Resultant high-stability, high-quality oyster substrates can address joint ecological and engineering imperatives to a degree that traditional substrates are not able. Although our results certainly merit future studies on a larger scale – and involving reefs constructed with greater footprints – I provide immediate valuable insight regarding the interactive effects of NNBI substrate, siting, and configuration on protection of essential, threatened coastal ecosystems.

CHAPTER 2: EXPERIMENTAL FERTILIZATION

INTRODUCTION

Studies of nutrient enrichment have found this phenomenon to have both beneficial and deleterious effects on ecosystem stability. In terrestrial and aquatic systems, enrichment may fundamentally shift community composition and either increase (Kraufvelin et al. 2010) or potentially irreversibly reduce (Isbell et al. 2013) species diversity. Nutrient enrichment has also been shown to increase primary productivity, causing increases of up to 50% in plants (Gough et al. 2000). However, in marine systems, hypoxia resulting from metabolism of this increased primary production may destabilize critical system attributes like trophic structure and habitat connectivity (Deegan 2002). In addition to potential mitigation through nutrient regulation and management strategies, further research is necessary to untangle these competing effects of enrichment on different systems.

Despite decades of study, the impacts of nutrient enrichment on salt marsh stability remain variable and, at times, contradictory. Marsh response may depend on whether the system is initially nutrient-poor or -rich, with the former demonstrating a drastic shift in species composition (Verhoeven et al. 2006). Enrichment can induce shifts in marsh macrophyte zonation and/or abundance, with potential habitat fragmentation resulting from enrichment-induced subsidence (Deegan 2002, Turner 2011). Accordingly, though not found universally, it is generally believed that excess nutrients increase a plant's ratio of above- to belowground biomass (Valiela et al. 1976). Some studies have implicated excess nutrients in the decreased production of stabilizing belowground organs (Turner et al. 2009, Alldred et al. 2017), potentially to the point of weakening marsh structure enough to cause collapse and conversion (Deegan et al. 2012). However, in some cases enrichment has no negative effects on marsh

elevation (Davis et al. 2017) or belowground biomass (Crosby et al. 2021, Anisfeld & Hill 2012). Typically, fertilization increases aboveground biomass (Graham & Mendelsohn 2016, Anisfeld & Hill 2012, Silliman & Zieman 2001), though gains in cordgrass aboveground biomass may be cancelled out by reduced shoot density (Johnson et al. 2016). Further complicating matters, strategic fertilization of nutrient-poor sediments may greatly enhance success and survival of restored marsh vegetation, jumpstarting their productivity and encouraging rapid growth (Broome et al. 1983). However, given that drag per unit surface area is highest in stiffer vegetation like *Spartina* cordgrasses, increased productivity may prove detrimental for transplants at high-energy restoration sites, especially those along the marsh edge (Bouma et al. 2010). This increased drag may place transplants at a greater risk of being uprooted. Therefore, to reap benefits from strategic marsh fertilization while ensuring transplant longevity, additional stabilization measures – like restored oyster reefs – may be necessary to protect newly-transplanted vegetation. In sum, the conditions under which nutrient enrichment may destabilize or benefit salt marshes are not definitively known.

Given the pervasiveness of anthropogenic nutrient enrichment, it is necessary to evaluate strategies to mitigate potential negative effects of enrichment on marsh stability. One approach may be the harnessing of inter-specific facilitation, as provided by aforementioned restored oyster reefs. Given the ability of oyster reefs to attenuate wave energy, enhance sediment deposition, stabilize adjacent shorelines (Fodrie et al. 2017), and keep pace with sea-level rise (Rodriguez et al. 2014), oyster reefs could be a promising strategy to support nutrient-stressed marshes.

In this study, I examined the ability of restored oyster reefs to mitigate the presumed negative effects of nutrient over-enrichment on transplanted marsh vegetation in high-energy

environments. I experimentally planted salt marsh seedlings on a high-energy exposed shoreline to examine the interacting effects of physical protection (i.e. proximity to an oyster reef) and nutrient over-enrichment on plant growth and survival. I hypothesized 1) that all seedlings landward of Oystercatcher (OC) reefs, regardless of fertilization treatment, would experience lower mortality and higher growth than those landward of control sites; 2) that fertilized seedlings landward of OC reefs would enjoy the highest growth and survival, benefiting from both nutrient subsidies and reef-induced shoreline stabilization; and 3) that fertilized control plots would experience the greatest elevation loss, due to the absence of reef stabilization and fertilizer-induced reduction of belowground production.

METHODS

Vegetation Transplantation, Fertilization, and Monitoring

I conducted this study on the ramp shoreline at Carrot Island, at which restored oyster reefs were constructed in Chapter 1 (see Chap. 1 Methods, Chap. 1 Fig 1). In May 2019, I delineated two 1-m² plots landward of OC (n=4) and control sites (n=4) on the ramp shoreline (Fig 1.1B). At each OC and control site, these two plots were sited 0.5 m landward of the reef or the farthest waterward extent of vegetation respectively, and randomly assigned to fertilized or non-fertilized treatments (n=8 per fertilization treatment). Culms of *S. alterniflora* were obtained from a local nursery and trimmed to a height of 30 cm to standardize height and initially reduce drag following transplantation. All plots were planted at an approximate initial shoot density of 74 shoots m⁻¹ in 4 shore-parallel rows of 6 planting holes, with row 1 closest to the water, and, therefore, lowest in elevation. Plants were tagged with numbered zip ties and their initial heights recorded. In plots assigned to the fertilized treatment, each hole received 3.5 grams of Osmocote™ slow-release fertilizer (15% N, 9% P, 12% K₂O) prior to planting (84 grams m⁻¹). This level of nutrient application was chosen based on the findings of Broome et al. (1983), who determined that application of Osmocote at quantities of ~25 g m⁻¹ benefited survival and growth of transplanted *S. alterniflora*. I trebled the quantity of fertilizer in an attempt to induce increased aboveground production, thus increasing drag and stress on the transplants (Deegan et al. 2012). Belowground fertilization prevents removal of nutrients by tidal action (Mendelssohn 1979), while slow-release fertilizer ensures a sustained dosage of belowground organs over time and can be safely placed in direct contact with *S. alterniflora* belowground structures (Broome et al. 1983). Plants in each plot were monitored from June 2019 to September 2019, with the maximum elapsed time between monitoring events not exceeding 14 days. At each monitoring

event, I recorded the total shoot density, the number of live plants present per row (a proxy for survival), the number of clonal shoots, and the height of any tagged plants. Total shoot density included all green, living plants within the experimental plot (including clonal shoots), while clonal shoots were young plants attached via rhizomes to transplanted culms. I verified clonal expansion by carefully removing sediment and confirming rhizomal connection to a transplanted culm either visually or manually. Shoot density was not assessed during the second monitoring event (June 14, 2019) due to logistical issues. Due to high plant mortality, I was unable to track growth of tagged plants with sufficient resolution to report inter-treatment differences in aboveground biomass production. Indeed, the final monitoring event revealed that no tagged plants remained in any experimental plots. As such, I was also unable to assess differences in plant above-to-belowground biomass ratios due to insufficient replication (i.e., remaining living plants). Hurricane Dorian made landfall in North Carolina on September 6, 2019 over Cape Hatteras as a Category 1 storm, occurring between the 12th and 13th monitoring events. The initial and final elevation of each row of plants relative to NAVD88 was determined using a Trimble R10 RTK in June 2019 and September 2019 (post-Dorian). I additionally sited and planted plots at all creek sites but found that one week post-planting, all transplanted culms were absent. I attribute this mass loss to the positive buoyancy of the dry, nursery-raised *S. alterniflora* culms. This buoyancy likely allowed the strong tidal forces in the creek to dislodge culms from the loose, muddy sediment.

Statistical Analysis

I assessed differential risk in plant survival through time based on planting row (1-4, with 1 the farthest waterward), fertilization treatment (fertilized, control) and reef treatment (OC, control) using Cox Proportional hazard regression analysis (R package “survival”, Therneau

2015). I then plotted Kaplan–Meier survival curves to visualize the outcomes of survival during the course of the study (“survminer”, Kassambara and Kosinski 2018).

To examine the impacts of fixed effects of monitoring date (June 3, 2019 through September 16, 2019), fertilization treatment (fertilized, control) and reef treatment (OC, control) on a) total *S. alterniflora* shoot density and b) clonal expansion, I used Poisson and negative binomial generalized linear mixed models respectively. All candidate models were fit using Template Model Builder (TMB) and included block (see Ch. 1), reef treatment, and subplot (i.e. fertilization treatment) as crossed random effects. In order to improve model parameterization, the fixed effect of time was scaled to its median value.

Lastly, I used linear models to analyze the effect of fertilization treatment (fertilized, control), planting row (1-4), and reef treatment (OC, control) on change in elevation between June and September 2019. Data required no transformation to meet model assumptions (Levene’s Test, $P > 0.05$).

To determine relative support for the candidate models describing proportional plant survival, shoot density, clonal expansion, and elevation, I used a model selection approach based on sample size-corrected Akaike Information Criterion (AICc) (Burnham and Anderson 2003). I used Tukey’s post-hoc comparisons and Kenward-Roger degrees of freedom approximation (package “emmeans”, Lenth et al. 2021) to assess pairwise differences for any significant treatment effects. I used an alpha level of 0.05 for all hypothesis testing, and performed all analyses in the R statistical computing environment (v. 3.5.2, R Core Team 2018)

RESULTS

Plant Mortality

The model which best explained proportional survival of transplants incorporated the interactive effects of row, fertilization treatment, and reef treatment (Tables 2.1, 2.2, Fig. 2.1). Cordgrass transplants in control sites faced a higher risk of mortality than those at OC sites ($P < .001$), as did those located in row 1 (as compared to Rows 2, 3, and 4; Table 2.3). As such, placement a) behind restored reefs and b) higher in the tidal frame appeared to increase plant survival. Plant mortality in fertilized plots was mediated by reef presence, with risk of mortality in fertilized control sites exceeding that in fertilized OC sites ($P = 0.005$). Unfertilized plants at control sites also suffered higher mortality than fertilized plants protected by OC reefs ($P = 0.0045$). However, this differential risk based on treatment was not observed for plants in unfertilized plots ($P = 0.547$). Similarly, mortality risk between fertilized and unfertilized plants within control and OC plots did not differ, indicating that reef presence did not equalize survival between fertilized and unfertilized subplots (Table 2.3). Fertilized plants in row 1 experienced higher mortality than those in the other three rows, though this difference was significant only between rows 1 and 3 (Row 1 vs. Row 3: $P = 0.004$, Table 2.3). Mortality among unfertilized plants trended similarly, with mortality of plants in Row 1 significantly exceeding that in the other rows (Table 2.3).

Shoot Density

Total shoot density in this study varied according to the additive effects of time and fertilization treatment (Table 2.1). Total shoot density declined steadily over the course of the experiment, with an average of only 3.8 ± 1.2 shoots m^{-1} recorded on the final date of sampling

(Fig. 2.2). Throughout the study, fertilized plots maintained higher shoot densities than did unfertilized plots (Table 2.5, $P < 0.01$).

Clonal Expansion

Clonal expansion at experimental plots differed only according to time (Table 2.1). The quantity of clonal shoots peaked in late July and early August, coincident with the period of peak *S. alterniflora* growth in the study area, before declining (Fig. 2.3). On average, unfertilized plots hosted slightly more clonal shoots than their unfertilized counterparts (Unfertilized: 0.9 ± 0.2 , Fertilized: 0.7 ± 0.1), as did control sites relative to OC sites (Control: 1.0 ± 0.2 , OC: 0.6 ± 0.1).

Elevation

The additive effects of fertilization and planting row best explained changes in elevation at my study site (Table 2.1), although only the effect of row was significant (Table 2.5). The two rows of plants sited the farthest waterward (1 and 2) declined in elevation more than did row 4 (which was farthest landward; Table 2.6). In fact, average elevation loss in Row 1 (8.8 ± 1.2 cm) was almost double that of Row 4 (4.6 ± 0.6 cm). Although elevation loss at rows 1 and 2 at control sites (Row 1: 10.2 ± 1.8 cm, Row 2: 8.9 ± 1.0 cm) exceeded those at OC sites (Row 1: 7.4 ± 1.7 cm, Row 2: 7.0 ± 0.9 cm), the change of elevation of the upper rows (3 and 4) was similar among treatments.

DISCUSSION

The interacting effects of nutrient fertilization and high energy could have serious ramifications for marshes and landward communities if belowground production – and, therefore, coastal protection (Silliman et al. 2019) - is compromised. Studies which specifically enriched erosive shorelines to examine the interaction between enrichment and hydrodynamic energy regime are lacking (but see Broome et al. 1983). Thus, although short in duration and characterized by high plant mortality, this study can offer initial lessons learned on which future researchers and restoration practitioners can build. My results suggest that although OC reefs reduced mortality of fertilized plants as compared to control sites, within individual control and OC sites, fertilization did not differentially impact plant mortality. This finding indicates that a) transplants did not persist for sufficient time to react to fertilizer, and/or b) my fertilizer dosage was insufficient to alter plant growth. Although fertilized plants appeared to suffer increased risk of mortality than their unfertilized counterparts, total *S. alterniflora* shoot density was higher in fertilized plots (Fig. 2.2). However, I found no evidence of a beneficial interaction between reef presence and fertilization.

Although transplantation of nursery-raised seedlings alone may be an effective marsh restoration technique in low-energy settings, my findings indicate that transplantation, regardless of reef presence or fertilizer treatment, is less successful in high-energy systems. Typically, plants within the marsh edge will prograde naturally once restored reefs have sufficiently stabilized the substrate, often after several years (Safak et al. 2020, Chowdury et al. 2019). This plant growth in turn stabilizes marsh sediments (Feagin et al. 2009). Restoration practitioners should therefore consider optimizing transplantation using planting designs which promote intra-specific facilitation (Silliman et al. 2015) or structures which foster growth by mimicking emergent traits (Temmink et al. 2020). If permitted, mature cordgrass plugs (*sensu* Broome et al.

1983) may be preferable transplants, given that their complex extant belowground structures will likely be more receptive to fertilizer than those of young nursery-raised plants. This increased responsiveness would benefit future investigations of both nutrient enrichment stress and fertilizer application as a method of restoration enhancement, helping identify thresholds between the two. In addition, given the high rates of transplant dislodgment due to wave action, quick-release fertilizer may have better suited this study site, helping plants overcome the “slow start” associated with slow-release fertilizers (Broome et al. 1983).

Further, although fertilized plots tended to suffer greater elevation loss than unfertilized areas, partially supporting my third hypothesis, I hesitate to attribute this change to impoverishment of belowground plant structures due to nutrient loading. While such impoverishment can indeed occur and, in severe cases, result in marsh collapse (Deegan et al. 2012), the short duration and massive loss of transplants render this mechanism unlikely. Rather, extreme shoreline retreat at the site (Fig. 1.1B) likely drove elevation change.

Contrary to my first hypothesis, neither total *S. alterniflora* shoot density nor clonal expansion increased in the presence of OC reefs. Wave attenuation by OC reefs may therefore have been insufficient to protect transplants. I sited rows of transplants based on proximity to reefs, and, therefore, presumed protection from wave energy. However, transplanted *S. alterniflora* may have enjoyed greater growth and survival if located at a higher elevation at the expense of reef adjacency. Although *S. alterniflora* tolerates, and may thrive, in flooded conditions, aboveground production declines dramatically at levels of extreme inundation (Voss et al. 2013, Ober and Martin 2018). Nursery-raised seedlings unaccustomed to natural marsh environments may have been overwhelmed by the compounded effects of high wave energy and

water levels. This inundation stress was likely exacerbated by elevation loss which occurred over the course of the experiment (Fig. 2.4).

In fact, the raised latticework design of OC reefs (Fig 1.2) may have allowed sufficient wave run-up beneath its platform to scour and stress transplants. However, my assessments of ramp OC reefs in Fall 2020 indicate that oysters have grown more fully into the open space underneath the reef, likely minimizing wave throughput. Contrary to trends in growth, plant mortality risk was indeed lower at OC sites relative to control sites (Table 2.3), partially supporting my first hypothesis. Reef presence may have reduced wave energy to a degree that plants remained in place, but not sufficiently to promote growth or expansion. As such, future reef-adjacent planting efforts may enjoy increased success when sited near reefs which fully block wave access, perhaps either mature OC-style or shell bag reefs.

Unfortunately, I was unable to assess relative plant growth (tracked over time through plant tagging) and above- to belowground biomass ratios due to transplant mortality. However, analyses of belowground biomass are critical, especially in eroding salt marshes like Carrot Island. In marshes subjected to high wave energy, loss of belowground structures could reduce sediment trapping and substrate stabilization, increasing vulnerability to wave attack and exacerbating retreat (Mariotti and Fagherazzi 2010). Typically, scarped shoreline morphologies are considered to be hallmarks of such retreat (Mariotti and Fagherazzi 2010). Although the shoreline studied here is largely of ramped geomorphology (Keller et al. 2019), several areas are developing more dramatic scarps (E. Wellman, *pers. obs.*), increasing the likelihood of sediment loss and so-called “mass failure” (calving events, Wang et al. 2017). When located waterward of scarps, pioneer vegetation (like *S. alterniflora*) can slow marsh edge retreat (Wang et al. 2017). However, at sites experiencing dramatic ambient erosion and high energy (Fig. 1.1B), plantings

of marsh vegetation alone are unlikely to be able to hold the line (Roland and Douglass 2005). Deployment of natural and nature-based infrastructure (NNBI), like restored oyster reefs, may protect and enhance success of these restoration efforts through shoreline stabilization and attenuation of wave energy. Future research should build upon my findings, perhaps by planting landward of more solid, less permeable NNBI structures (i.e. sills), or planting vegetation at a greater depth or in greater numbers to reduce risk of dislodgment. In sum, identification of the a) settings and b) application levels at which nutrient enrichment bolsters versus hinders marsh restoration success will help inform management of coastal wetlands, including potential enrichment mitigation strategies.

TABLES AND FIGURES

Table 1.1: Mixed model results for change in landward marsh elevation between 2018 and 2020
Significant p values ($P < 0.05$) are shown in bold.

| Fixed Factors | χ^2 | DF | Prob > χ^2 |
|-----------------------------|----------|----|-----------------|
| Shoreline (Ramp, Creek) | 17.5528 | 1 | < 0.0001 |
| Treatment (CTRL, SB, OC) | 20.7068 | 2 | < 0.0001 |
| Station (1, 3, 5m) | 3.8838 | 2 | 0.1434 |
| Shoreline*Treatment | 10.6974 | 2 | 0.0048 |
| Shoreline*Station | 16.6735 | 2 | 0.0002 |
| Treatment*Station | 11.2724 | 4 | 0.0237 |
| Shoreline*Treatment*Station | 1.5037 | 4 | 0.826 |

Table 1.2: Results of Tukey’s post-hoc tests to examine pairwise comparisons in marsh elevation change mixed model. Control, Oystercatcher, and shell bag substrates are abbreviated as CTRL, OC, and SB respectively. Significant p values ($P < 0.05$) are shown in bold.

| Model term | Contrast | Estimate | Standard error | DF | T ratio | P value |
|---------------------|-------------------------|----------|----------------|--------|---------------|------------------|
| Shoreline*Treatment | CTRL Creek v. OC Creek | -0.0249 | 0.0193 | 44.1 | -1.286 | 0.7908 |
| | CTRL Creek v. SB Creek | -0.0594 | 0.0193 | 44.1 | -3.069 | 0.0400 |
| | CTRL Creek v. CTRL Ramp | 0.1402 | 0.0208 | 44.1 | 6.735 | <.0001 |
| | OC Creek v. SB Creek | -0.0345 | 0.0188 | 44.0 | -1.836 | 0.4543 |
| | OC Creek v. OC Ramp | -0.0173 | 0.0233 | 44.6 | -0.742 | 0.9755 |
| | SB Creek v. SB Ramp | -0.0285 | 0.0188 | 44.0 | -1.517 | 0.6557 |
| | CTRL Ramp v. OC Ramp | -0.1824 | 0.0245 | 44.4 | -7.460 | <.0001 |
| | CTRL Ramp v. SB Ramp | -0.2281 | 0.0204 | 44.4 | -11.163 | <.0001 |
| | OC Ramp v. SB Ramp | -0.0457 | 0.0233 | 44.6 | -1.963 | 0.3791 |
| Shoreline*Station | Creek 1m v. Creek 3m | 0.00425 | 0.0188 | 44.0 | 0.226 | 0.9999 |
| | Creek 1m v. Creek 5m | 0.003886 | 0.0193 | 44.1 | 0.201 | 1 |
| | Creek 3m v. Creek 5m | -0.00036 | 0.0193 | 44.1 | -0.019 | 1 |
| | Creek 1m v. Ramp 1m | 0.053135 | 0.0238 | 44.9 | 2.232 | 0.2439 |
| | Creek 3m v. Ramp 3m | 0.125581 | 0.0193 | 44.1 | 6.49 | <.0001 |
| | Creek 5m v. Ramp 5m | -0.08425 | 0.0199 | 44.3 | -4.231 | 0.0015 |
| | Ramp 1m v. Ramp 3m | 0.076696 | 0.0241 | 44.6 | 3.18 | 0.0301 |
| | Ramp 1m v. Ramp 5m | -0.1335 | 0.0242 | 44.8 | -5.514 | <.0001 |
| | Ramp 3m v. Ramp 5m | -0.21019 | 0.0199 | 44.3 | -10.555 | <.0001 |
| Treatment*Station | CTRL 1m v. CTRL 3m | 6.25E-04 | 0.0249 | 44.0 | 0.025 | 1 |
| | CTRL 1m v. CTRL 5m | -0.124 | 0.0258 | 44.1 | -4.815 | 0.0006 |
| | CTRL 3m v. CTRL 5m | -0.125 | 0.0258 | 44.1 | -4.839 | 0.0005 |
| | OC 1m v. OC 3m | 0.0208 | 0.0309 | 44.8 | 0.673 | 0.9989 |
| | OC 1m v. OC 5m | -0.0825 | 0.0309 | 44.8 | -2.667 | 0.1889 |
| | OC 3m v. OC 5m | -0.103 | 0.023 | 44 | -4.486 | 0.0016 |
| | SB 1m v. SB 3m | 0.1 | 0.023 | 44 | 4.345 | 0.0024 |
| | SB 1m v. SB 5m | 0.0122 | 0.023 | 44 | 0.532 | 0.9998 |
| | SB 3m v. SB 5m | -0.0877 | 0.023 | 44 | -3.812 | 0.0115 |
| | CTRL 1m v. OC 1m | -0.124 | 0.0316 | 44.7 | -3.938 | 0.0079 |
| | CTRL 1m v. SB 1m | -0.222 | 0.024 | 44.2 | -9.254 | <.0001 |
| | OC 1m v. SB 1m | -0.0981 | 0.0309 | 44.8 | -3.173 | 0.0616 |
| | CTRL 3m v. OC 3m | -0.104 | 0.024 | 44.2 | -4.333 | 0.0025 |
| | CTRL 3m v. SB 3m | -0.123 | 0.024 | 44.2 | -5.118 | 0.0002 |
| | OC 3m v. SB 3m | -0.0189 | 0.023 | 44 | -0.82 | 0.9956 |
| | CTRL 5m v. OC 5m | -0.0825 | 0.0249 | 44.2 | -3.308 | 0.0443 |
| CTRL 5m v. SB 5m | -0.0859 | 0.0249 | 44.2 | -3.444 | 0.0313 | |
| OC 5m v. SB 5m | -0.00337 | 0.023 | 44 | -0.147 | 1 | |

Table 1.3: Results of Tukey’s post-hoc tests to examine pairwise comparisons in shoreline change mixed model. Control, Oystercatcher, and shell bag substrates are abbreviated as CTRL, OC, and SB respectively. Significant p values ($P < 0.05$) are shown in bold.

| Contrast | Estimate | Standard error | DF | T ratio | <i>P</i> value |
|-------------------------|----------|----------------|----|---------|------------------|
| Creek CTRL v. Ramp CTRL | 1.6223 | 0.199 | 63 | 8.148 | <.0001 |
| Creek SB v. Ramp SB | 2.1214 | 0.199 | 63 | 10.654 | <.0001 |
| Creek OC v. Ramp OC | 0.9283 | 0.199 | 63 | 4.662 | 0.0002 |
| Creek CTRL v. Creek OC | 0.0375 | 0.199 | 63 | 0.188 | 1.000 |
| Creek CTRL v. Creek SB | -0.4427 | 0.199 | 63 | -2.224 | 0.2418 |
| Creek OC v. Creek SB | -0.4803 | 0.199 | 63 | -2.412 | 0.1679 |
| Ramp CTRL v. Ramp OC | -0.6565 | 0.199 | 63 | -3.297 | 0.0192 |
| Ramp CTRL v. Ramp SB | 0.0563 | 0.199 | 63 | 0.283 | 0.9997 |
| Ramp OC v. Ramp SB | 0.7128 | 0.199 | 63 | 3.58 | 0.0084 |

Table 1.4: Mixed model results for analysis of *S. alterniflora* shoot density. Significant p values ($P < 0.05$) are shown in bold.

| Response variable | Fixed Factors | χ^2 | DF | Prob > χ^2 |
|-------------------|-------------------------|----------|----|------------------|
| Shoot density | Shoreline (Ramp, Creek) | 8.1062 | 1 | 0.0044 |
| | Year (2018, 2020) | 2.0831 | 1 | 0.1489 |
| | Shoreline*Year | 35.6827 | 1 | <.0001 |

Table 1.5: Results of Tukey’s post-hoc tests to examine pairwise comparisons in *S. alterniflora* shoot density mixed model. Significant p values ($P < 0.05$) are shown in bold.

| Contrast | Estimate | Standard error | DF | T ratio | P value |
|--------------------------|----------|----------------|----|---------|------------------|
| 2018 Creek v. 2020 Creek | -0.419 | 0.29 | 89 | -1.443 | 0.4761 |
| 2018 Creek v. 2018 Ramp | -0.784 | 0.275 | 89 | -2.847 | 0.0276 |
| 2018 Creek v. 2020 Ramp | 1.169 | 0.345 | 89 | 3.387 | 0.0057 |
| 2020 Creek v. 2018 Ramp | -0.365 | 0.193 | 89 | -1.897 | 0.2366 |
| 2020 Creek v. 2020 Ramp | 1.588 | 0.28 | 89 | 5.671 | <.0001 |
| 2018 Ramp v. 2020 Ramp | 1.953 | 0.275 | 89 | 7.106 | <.0001 |

Table 1.6: Mixed model results for analysis of changes in reef areas. Oystercatcher and shell bag substrates are abbreviated as OC and SB respectively. Significant p values ($P < 0.05$) are shown in bold.

| Fixed Factors | χ^2 | DF | Prob > χ^2 |
|---|----------|----|------------------|
| Shoreline (Ramp, Creek) | 0.0969 | 1 | 0.7556 |
| Treatment (CTRL, SB, OC) | 28.6536 | 1 | <.0001 |
| Time (Post-Construction, Post-Florence, Post-Dorian, August 2020) | 23.2252 | 3 | <.0001 |
| Shoreline*Treatment | 26.5979 | 1 | <.0001 |
| Shoreline*Time | 0.594 | 3 | 0.8978 |
| Treatment*Time | 18.7345 | 3 | 0.0003 |
| Shoreline*Treatment*Time | 23.8136 | 3 | <.0001 |

Table 1.7: Results of Tukey’s post-hoc tests to examine pairwise comparisons in reef area mixed model. Oystercatcher and shell bag substrates are abbreviated as OC and SB respectively. Significant p values ($P < 0.05$) are shown in bold.

| Contrast | Estimate | Standard error | DF | T ratio | P value |
|--|----------|----------------|----|---------|------------------|
| OC Aug-20 Creek v. SB Aug-20 Creek | 4.49266 | 0.839 | 45 | 5.353 | 0.0003 |
| OC Aug-20 Creek v. OC Aug-20 Ramp | -0.26122 | 0.839 | 45 | -0.311 | 1 |
| SB Aug-20 Creek v. SB Aug-20 Ramp | -6.38265 | 0.839 | 45 | -7.605 | <.0001 |
| OC Post-Construction Creek v. SB Post-Construction Creek | -0.05346 | 0.839 | 45 | -0.064 | 1 |
| OC Post-Construction Creek v. OC Post-Construction Ramp | -0.73493 | 0.839 | 45 | -0.876 | 0.9999 |
| SB Post-Construction Creek v. SB Post-Construction Ramp | -1.16777 | 0.839 | 45 | -1.391 | 0.9883 |
| OC Post-Dorian Creek v. SB Post-Dorian Creek | 3.84205 | 0.839 | 45 | 4.578 | 0.0033 |
| OC Post-Dorian Creek v. OC Post-Dorian Ramp | -0.02975 | 0.839 | 45 | -0.035 | 1 |
| SB Post-Dorian Creek v. SB Post-Dorian Ramp | -6.0883 | 0.839 | 45 | -7.254 | <.0001 |
| OC Post-Florence Creek v. SB Post-Florence Creek | 3.97605 | 0.839 | 45 | 4.737 | 0.002 |
| OC Post-Florence Creek v. OC Post-Florence Ramp | -0.80385 | 0.839 | 45 | -0.958 | 0.9998 |
| OC Aug-20 Ramp v. SB Aug-20 Ramp | -1.62877 | 0.839 | 45 | -1.941 | 0.8431 |
| OC Post-Construction Ramp v. SB Post-Construction Ramp | -0.4863 | 0.839 | 45 | -0.579 | 1 |
| OC Post-Dorian Ramp v. SB Post-Dorian Ramp | -2.2165 | 0.839 | 45 | -2.641 | 0.3979 |
| OC Post-Florence Ramp v. SB Post-Florence Ramp | 3.80693 | 0.839 | 45 | 4.536 | 0.0038 |
| SB Aug-20 Creek v. SB Post-Construction Creek | -0.86721 | 0.839 | 45 | -1.033 | 0.9995 |
| OC Aug-20 Creek v. OC Post-Construction Creek | 3.67891 | 0.839 | 45 | 4.383 | 0.006 |
| OC Aug-20 Ramp v. OC Post-Construction Ramp | 3.20521 | 0.839 | 45 | 3.819 | 0.0301 |
| SB Aug-20 Ramp v. OC Post-Construction Ramp | 4.83397 | 0.839 | 45 | 5.76 | 0.0001 |
| SB Post-Dorian Ramp) v. SB Post-Florence Ramp | 6.08034 | 0.839 | 45 | 7.245 | <.0001 |

Table 1.8: Generalized linear model results for analysis of juvenile and adult oyster presence. Significant p values ($P < 0.05$) are shown in bold.

| Response Variable | Fixed Factors | χ^2 | DF | Prob $> \chi^2$ |
|--------------------------|---------------------------|----------|----|------------------|
| Juvenile oyster presence | Treatment (reef, no reef) | 38.43 | 1 | <.0001 |
| Adult oyster presence | Treatment (reef, no reef) | 22.5 | 1 | <.0001 |

Table 1.9: Mixed model results for analysis of adult and juvenile oyster lengths and densities on OC and SB reef substrates. Oystercatcher and shell bag substrates are abbreviated as OC and SB respectively. Significant p values ($P < 0.05$) are shown in bold and marginal p values are shown in italics.

| Response variable | Fixed Factors | χ^2 | DF | Prob > χ^2 |
|--|--------------------------|----------|----|------------------|
| Adult oyster length (mm) | Shoreline (Ramp, Creek) | 10.671 | 1 | 0.0011 |
| | Treatment (SB, OC) | 28.6075 | 1 | <.0001 |
| | Year (2018, 2019, 2020) | 67.3569 | 2 | <.0001 |
| | Shoreline*Treatment | 9.0831 | 1 | 0.0026 |
| | Shoreline*Year | 1.9093 | 2 | 0.3849 |
| | Treatment*Year | 8.816 | 2 | 0.0122 |
| | Shoreline*Treatment*Year | 1.9673 | 2 | 0.3739 |
| | | | | |
| Juvenile oyster length (mm) | Year (2018, 2019, 2020) | 7.6586 | 2 | 0.0217 |
| | | | | |
| Adult oyster density (ind. m ²) | Shoreline (Ramp, Creek) | 1.9673 | 1 | 0.1607 |
| | Treatment (SB, OC) | 4.3546 | 1 | 0.0369 |
| | Year (2018, 2019, 2020) | 58.7549 | 2 | <.0001 |
| | Shoreline*Treatment | 3.5856 | 1 | <i>0.0583</i> |
| | Shoreline*Year | 2.7115 | 2 | 0.2578 |
| | Treatment*Year | 29.8334 | 2 | <.0001 |
| | Shoreline*Treatment*Year | 0.0413 | 2 | 0.9796 |
| | | | | |
| Juvenile oyster density (ind. m ²) | Shoreline (Ramp, Creek) | 6.0938 | 1 | 0.0136 |
| | Treatment (SB, OC) | 3.991 | 1 | 0.0457 |
| | Year (2018, 2019, 2020) | 73.7077 | 2 | <.0001 |
| | Shoreline*Treatment | 0.0824 | 1 | 0.7741 |
| | Shoreline*Year | 14.837 | 2 | 0.0006 |
| | Treatment*Year | 39.3098 | 2 | <.0001 |
| | Shoreline*Treatment*Year | 5.8491 | 2 | <i>0.0537</i> |

Table 1.10: Results of Tukey’s post-hoc tests to examine pairwise comparisons in adult and juvenile oyster density mixed models. Oystercatcher and shell bag substrates are abbreviated as OC and SB respectively. Significant p values ($P < 0.05$) are shown in bold. Examination of influential observations using Cooks distances indicated that two datapoints were highly influential in the models for both age classes. Both models were re-run following removal of these influential observations to confirm that model estimates were unchanged by their exclusion and are reported herein. Because both influential observations belonged to SB reef samples which hosted anomalously low densities of oysters, I consider the results reported here to be conservative estimates of that substrate’s ability to host and recruit oysters.

| Response variable | Model term | Contrast | Estimate | Standard error | DF | T ratio | P value |
|--|----------------|--------------------|----------|----------------|------|---------|------------------|
| Adult oyster density (ind. m ²) | Year*Treatment | | | | | | |
| | | 2018 OC v. 2019 OC | 0.103 | 0.185 | 31 | 0.559 | 0.993 |
| | | 2018 OC v. 2020 OC | -1.486 | 0.185 | 31 | -8.055 | <.0001 |
| | | 2019 OC v. 2020 OC | -1.589 | 0.185 | 31 | -8.613 | <.0001 |
| | | 2018 SB v. 2019 SB | 0.138 | 0.193 | 31.1 | 0.715 | 0.9786 |
| | | 2018 SB v. 2020 SB | 0.263 | 0.201 | 31.2 | 1.306 | 0.7794 |
| | | 2019 SB v. 2020 SB | 0.125 | 0.193 | 31.1 | 0.648 | 0.9862 |
| | | 2018 OC v. 2018 SB | 0.227 | 0.193 | 31.1 | 1.175 | 0.8451 |
| | | 2019 OC v. 2019 SB | 0.261 | 0.185 | 31 | 1.417 | 0.717 |
| | | 2020 OC v. 2020 SB | 1.976 | 0.193 | 31.1 | 10.248 | >.0001 |
| Juvenile oyster density (ind. m ²) | Year*Treatment | | | | | | |
| | | 2018 OC v. 2019 OC | 1.018 | 0.232 | 30.1 | 4.389 | 0.0016 |
| | | 2018 OC v. 2020 OC | -1.25 | 0.222 | 30 | -5.631 | 0.0001 |
| | | 2019 OC v. 2020 OC | -2.268 | 0.232 | 30.1 | -9.777 | <.0001 |
| | | 2018 SB v. 2019 SB | -0.246 | 0.232 | 30.1 | -1.061 | 0.8927 |
| | | 2018 SB v. 2020 SB | -0.105 | 0.242 | 30.4 | -0.435 | 0.9978 |
| | | | | | | | |

| | | | | | | | |
|--|----------------|-------------------------------|---------|-------|------|--------|------------------|
| | | 2019 SB v. 2020 SB | 0.141 | 0.232 | 30.1 | 0.607 | 0.9897 |
| | | 2018 OC v. 2018 SB | -0.614 | 0.232 | 30.1 | -2.646 | 0.1171 |
| | | 2019 OC v. 2019 SB | -1.878 | 0.232 | 30.1 | -8.095 | <.0001 |
| | | 2020 OC v. 2020 SB | 0.531 | 0.232 | 30.1 | 2.288 | 0.2299 |
| | Year*Shoreline | | | | | | |
| | | 2018 Creek - 2019 Creek | 0.1296 | 0.242 | 30.4 | 0.535 | 0.9942 |
| | | 2018 Creek - 2020 Creek | -1.1365 | 0.232 | 30.1 | -4.899 | 0.0004 |
| | | 2019 Creek - 2020 Creek | -1.2661 | 0.232 | 30.1 | -5.458 | 0.0001 |
| | | 2018 Ramp - 2019 Ramp | 0.6422 | 0.222 | 30 | 2.894 | 0.0695 |
| | | 2018 Ramp - 2020 Ramp | -0.2186 | 0.232 | 30.1 | -0.942 | 0.932 |
| | | 2019 Ramp - 2020 Ramp | -0.8608 | 0.232 | 30.1 | -3.711 | 0.0098 |
| | | 2018 Creek - 2018 Ramp | -0.7084 | 0.232 | 30.1 | -3.054 | 0.0485 |
| | | 2019 Creek - 2019 Ramp | -0.1958 | 0.232 | 30.1 | -0.844 | 0.9566 |
| | | 2020 Creek - 2020 Ramp | 0.2095 | 0.232 | 30.1 | 0.903 | 0.9427 |

Table 1.11: Results of Tukey’s post-hoc tests to examine pairwise comparisons in adult and juvenile oyster length mixed models. Oystercatcher and shell bag substrates are abbreviated as OC and SB respectively. Significant p values ($P < 0.05$) are shown in bold and marginal p values are shown in italics.

| Response variable | Model term | Contrast | Estimate | Standard error | DF | T ratio | P value | |
|----------------------|---------------------|----------------------|----------|----------------|------------------|---------|------------------|--|
| Adult length (mm) | Shoreline*Treatment | | | | | | | |
| | | Creek OC v. Ramp OC | 0.1289 | 0.0336 | 459 | 3.84 | 0.0008 | |
| | | Creek OC v. Creek SB | 0.4451 | 0.0331 | 459 | 13.463 | <.0001 | |
| | | Creek OC v. Ramp SB | 0.3894 | 0.0331 | 459 | 11.778 | <.0001 | |
| | | Ramp OC v. Creek SB | 0.3162 | 0.0336 | 459 | 9.42 | <.0001 | |
| | | Ramp OC v. Ramp SB | 0.2605 | 0.0336 | 459 | 7.76 | <.0001 | |
| | | Creek SB v. Ramp SB | -0.0557 | 0.0331 | 459 | -1.685 | 0.3326 | |
| | | Treatment*Year | | | | | | |
| | | OC 2018 v. SB 2018 | 0.1815 | 0.0414 | 459 | 4.382 | 0.0002 | |
| | | OC 2018 v. OC 2019 | -0.3179 | 0.0414 | 459 | -7.676 | <.0001 | |
| | | OC 2018 v. OC 2020 | -0.5189 | 0.0414 | 459 | -12.529 | <.0001 | |
| | | SB 2018 v. SB 2020 | -0.2331 | 0.0405 | 459 | -5.757 | <.0001 | |
| | | OC 2019 v. SB 2019 | 0.4095 | 0.0405 | 459 | 10.115 | <.0001 | |
| | | OC 2019 v. OC 2020 | -0.201 | 0.0405 | 459 | -4.964 | <.0001 | |
| OC 2019 v. SB 2020 | 0.2663 | 0.0405 | 459 | 6.577 | <.0001 | | | |
| SB 2019 v. OC 2020 | -0.6105 | 0.0405 | 459 | -15.079 | <.0001 | | | |
| SB 2019 v. SB 2020 | -0.1432 | 0.0405 | 459 | -3.538 | <i>0.0059</i> | | | |
| OC 2020 v. SB 2020 | 0.4673 | 0.0405 | 459 | 11.541 | <.0001 | | | |
| Juvenile length (mm) | Year | | | | | | | |
| | | 2018 v. 2019 | -0.0628 | 0.456 | 407 | -0.138 | 0.9896 | |
| | | 2018 v. 2020 | 0.9774 | 0.416 | 407 | 2.35 | <i>0.0503</i> | |
| | | 2019 v. 2020 | 1.0402 | 0.444 | 408 | 2.343 | 0.0512 | |

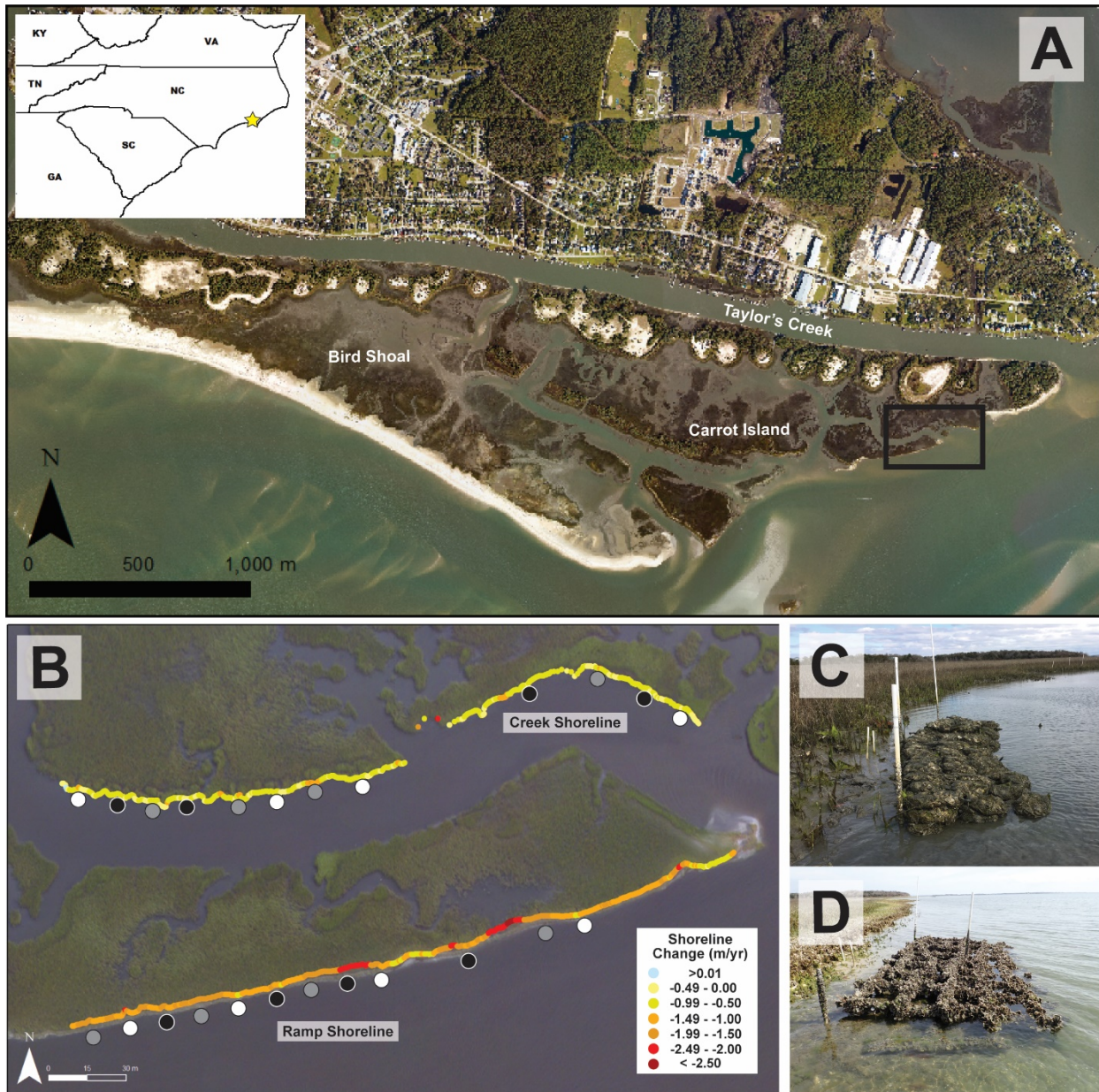


Figure 1.1: A) Map of study area near Beaufort, NC, USA in the Rachel Carson National Estuarine Research Reserve, with black polygon denoting study area. B) Reefs were constructed along two shorelines at Carrot Island: a sheltered tidal creek shoreline and an exposed “ramp” shoreline. Annual shoreline change rates over the study period were calculated with the AMBUR program (Jackson et al. 2012). Polygon color denotes experimental treatment: control (grey), SB (black), and OC (white). Photographs show intact C) SB and D) OC reefs in March 2019.



Figure 1.2: Schematic of a novel OC reef and its components. A) Each OC reef, such as this example on the ramp shoreline, was designed as a raised latticework composed of B) long, thin rods supported by C) thick, Y-shaped supports, which are sunk into the marsh sediment to the point of refusal. Photo C courtesy of N. Lindquist.

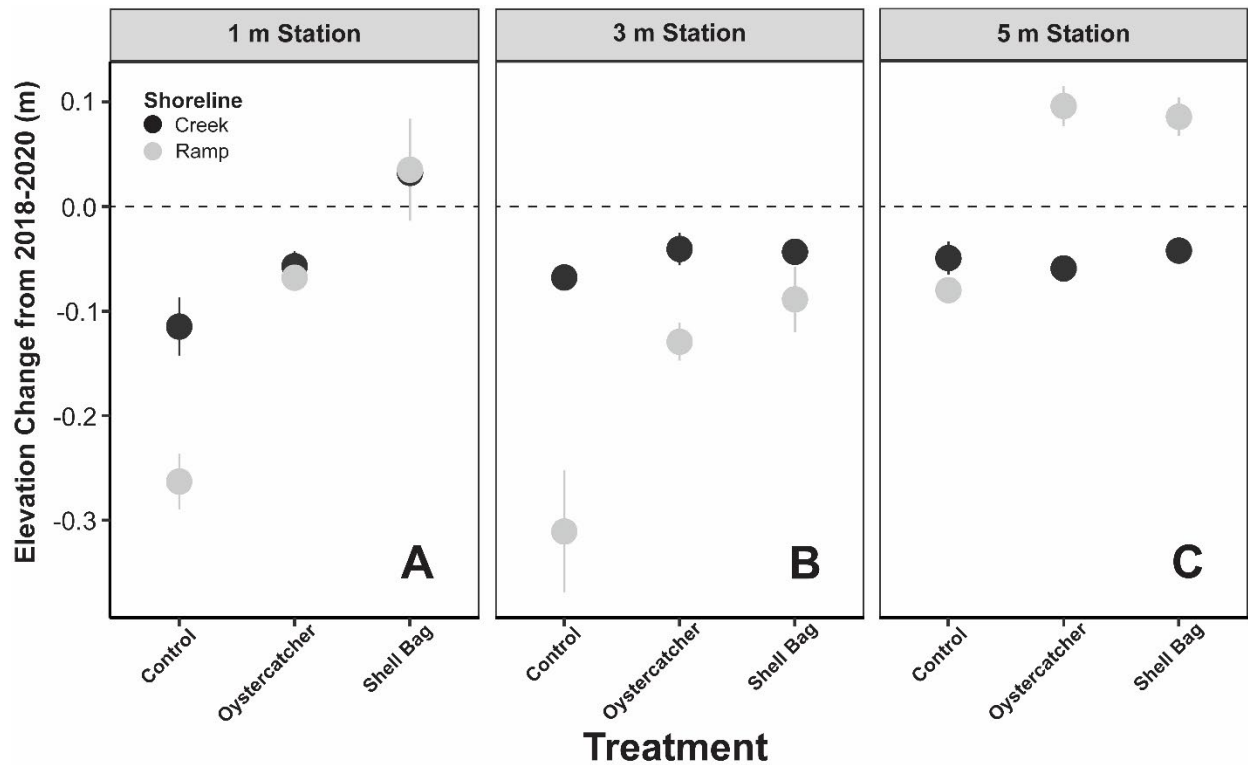


Figure 1.3: Mean change in landward marsh elevation relative to NAVD88 between May 2018 and May 2020 on both shorelines A) 1 meter, B) 3 meters, and C) and 5 meters into the marsh. D) Ramp control, E) OC, and F) SB sites are shown as they appeared in August 2020. Black polygon in D) represents footprint of control site. Horizontal dashed line indicates no elevation change. Error bars represent ± 1 SE.

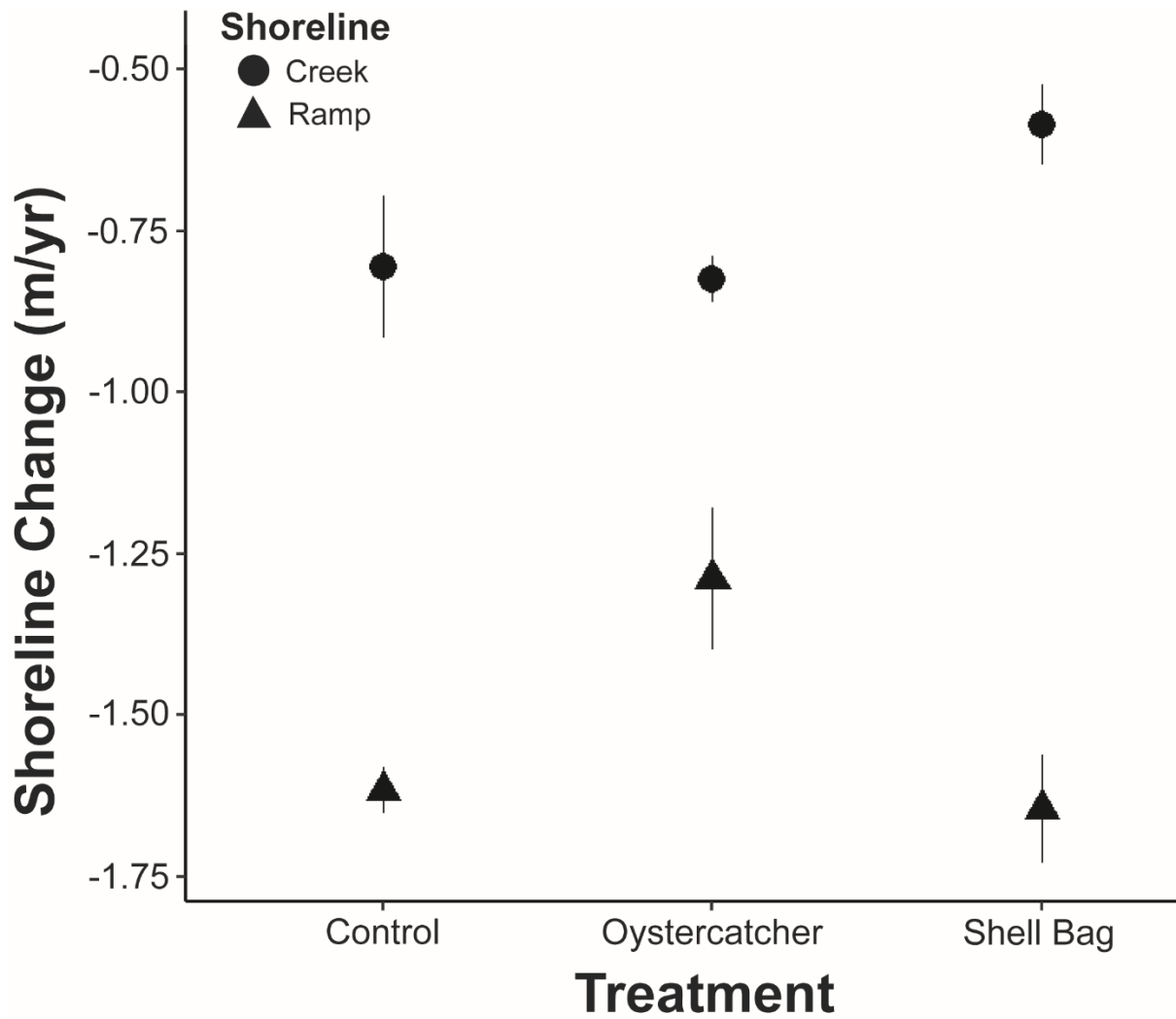


Figure 1.4: Mean annual shoreline change between May 2018 and May 2020 at Carrot Island experimental sites. Negative values indicate shoreline retreat, or landward movement of the marsh edge. Error bars represent ± 1 SE.

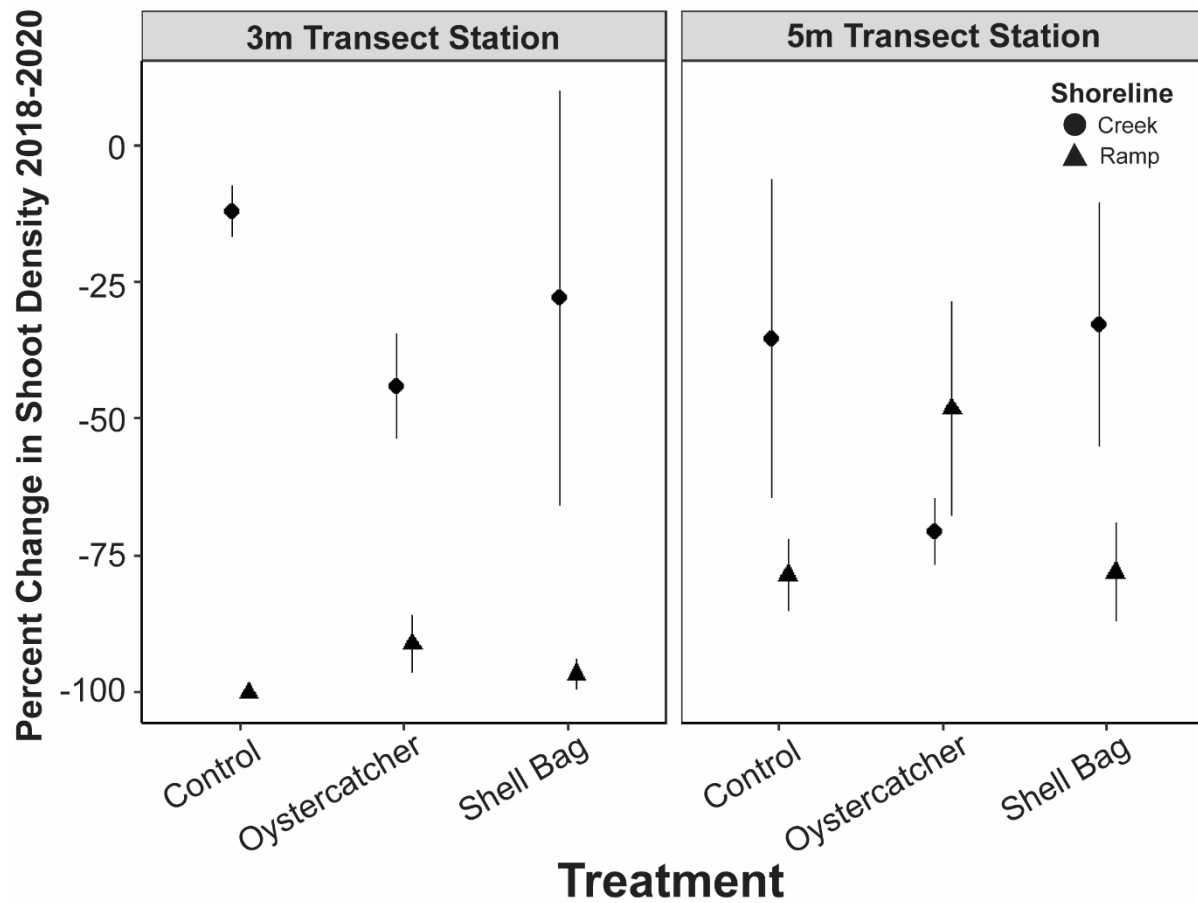


Figure 1.5: Mean percent change in *S. alterniflora* shoot density from September 2018 to August 2020 at all treatments on the creek and ramp shorelines. Error bars represent ± 1 SE.

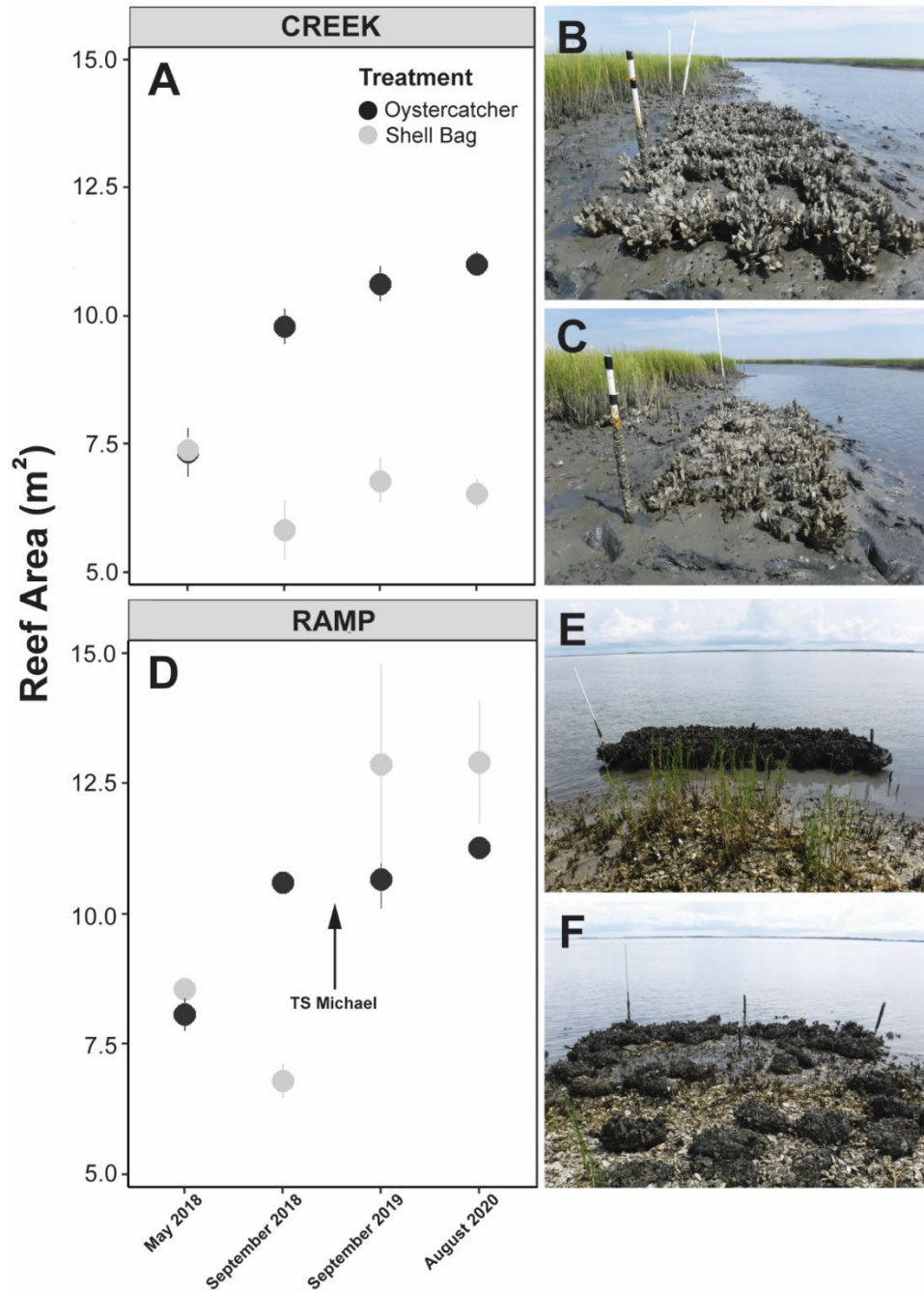


Figure 1.6: Change in mean reef area over time on the A) creek and D) ramp shorelines, with arrow indicating passage of Tropical Storm Michael in October 2018. B) Creek OC, C) creek SB, E) ramp OC, and F) ramp SB reefs are pictured as they appeared in August 2020. Error bars represent ± 1 SE. Cooks distances were used to identify influential datapoints, which were vetted and retained.

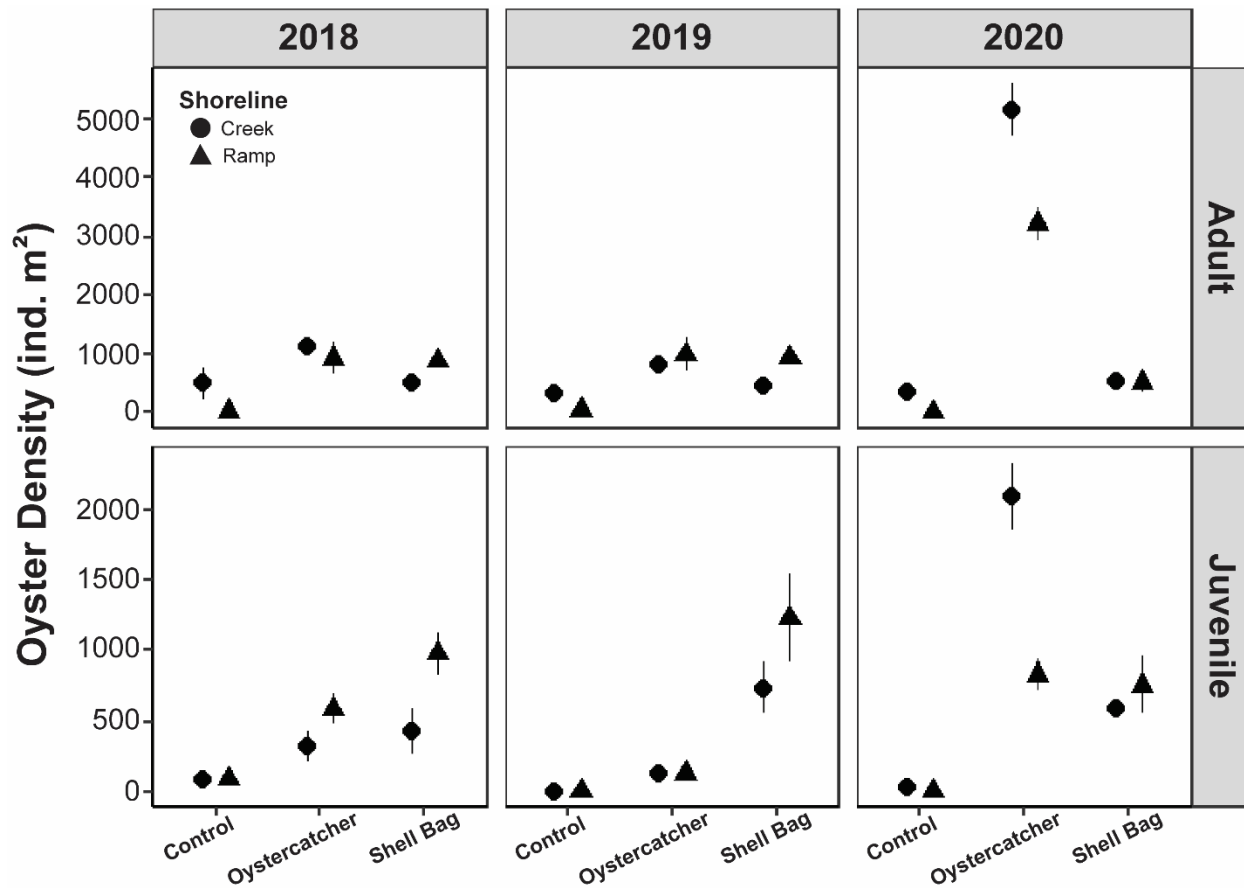


Figure 1.7: Mean adult and juvenile oyster densities at experimental sites from September 2018, September 2019, and October 2020. Juvenile and adult oysters were classified as those measuring 24 mm or less and 25 mm or more respectively. Error bars represent ± 1 SE.

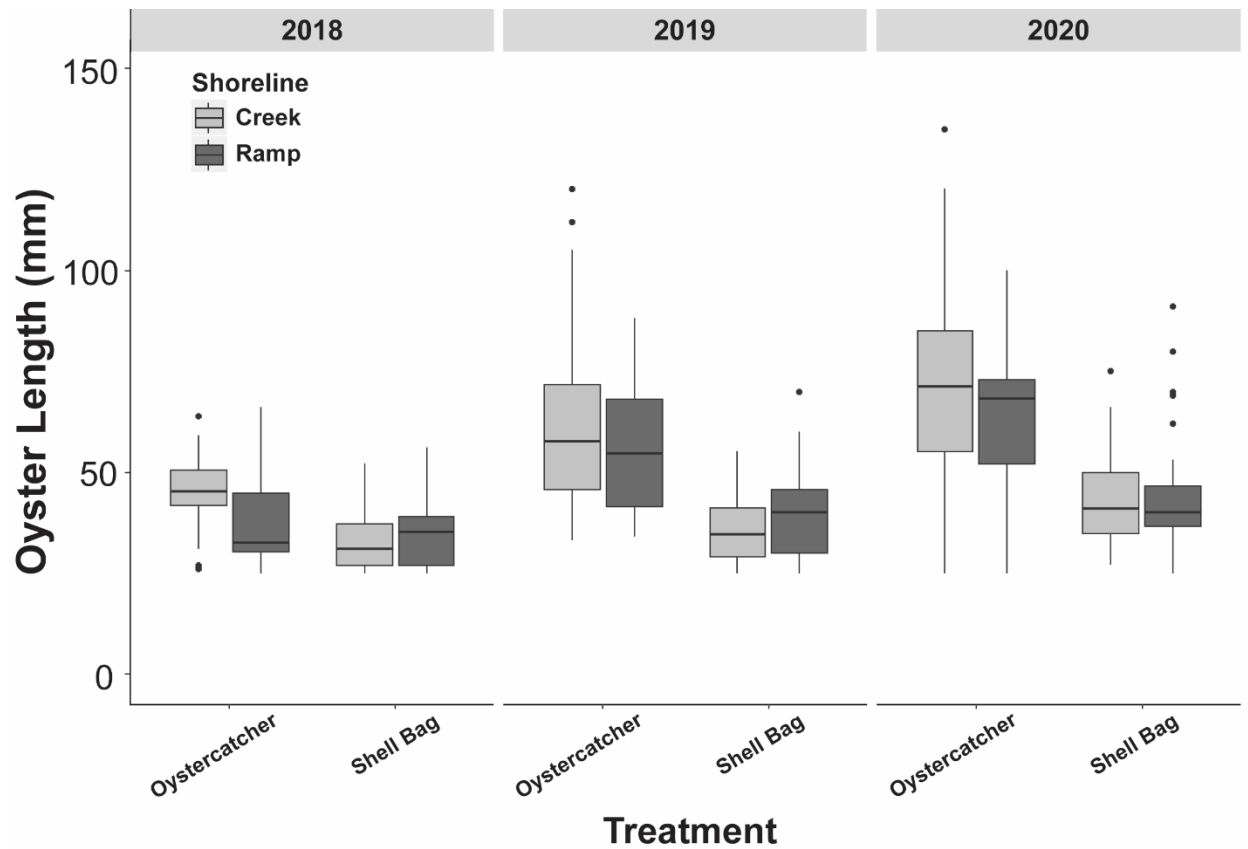


Figure 1.8: Lengths of adult oysters sampled from OC and SB substrates during September 2018, September 2019, and October 2020. Each box reports the median (dark black line), 25th and 75th percentiles (outer box edges), and \pm 95% confidence intervals (farthest extent of whiskers). Black dots represent outlier measurements.

Table 2.1: Results from sample-size corrected Akaike Information Criterion (AICc) model comparisons to determine best fit for assessment of plant mortality risk, shoot density, clonal expansion, and elevation change.

| Response | Model | Rank | dAICc | DF | Weight |
|--|---|------|-------|----|--------|
| Plant mortality risk | Fertilization treatment * reef treatment * row | 1 | 0 | 15 | 0.7413 |
| | Fertilization treatment + reef treatment + row | 2 | 4.1 | 5 | 0.0977 |
| | Reef treatment + row | 3 | 4.4 | 4 | 0.0821 |
| | Fertilization treatment * row | 4 | 5.2 | 7 | 0.0558 |
| | Reef treatment * row | 5 | 7.2 | 7 | 0.0204 |
| | Fertilization treatment + row | 6 | 12.4 | 4 | 0.0015 |
| | Row | 7 | 13.0 | 3 | 0.0011 |
| | Fertilization treatment * reef treatment | 8 | 38.7 | 3 | <0.001 |
| | Fertilization treatment + reef treatment | 9 | 41.6 | 2 | <0.001 |
| | Reef treatment | 10 | 42.0 | 1 | <0.001 |
| | Fertilization treatment | 11 | 49.8 | 1 | <0.001 |
| Shoot density (no. ind. per m ²) | Time + fertilization treatment | 1 | 0 | 6 | 0.225 |
| | Time * fertilization treatment | 2 | 0 | 6 | 0.225 |
| | Reef treatment * time * fertilization treatment | 3 | 0.3 | 7 | 0.190 |
| | Reef treatment + time + fertilization treatment | 4 | 0.3 | 7 | 0.190 |
| | Time | 5 | 2.1 | 5 | 0.079 |
| | Reef treatment + time | 6 | 2.4 | 6 | 0.067 |
| | Reef treatment * time | 7 | 4.4 | 7 | 0.205 |
| | Reef treatment * fertilization treatment | 8 | 598.1 | 7 | <0.001 |
| | Fertilization treatment | 9 | 616.5 | 5 | <0.001 |

| | | | | | |
|---|---|----|-------|----|--------|
| | Reef treatment + fertilization treatment | 10 | 616.8 | 6 | <0.001 |
| | Reef treatment | 11 | 618.9 | 3 | <0.001 |
| Clonal expansion (no. ind. per m ²) | Time | 1 | 0 | 6 | 0.4446 |
| | Reef treatment + time | 2 | 1.6 | 7 | 0.2002 |
| | Time + fertilization treatment | 3 | 2.1 | 7 | 0.1562 |
| | Reef treatment + time | 4 | 3.7 | 8 | 0.0694 |
| | Reef treatment * time | 5 | 3.8 | 8 | 0.0679 |
| | Time * fertilization treatment | 6 | 4.1 | 8 | 0.0571 |
| | Reef treatment * time * fertilization treatment | 7 | 9.2 | 12 | 0.0046 |
| | Reef treatment | 8 | 26.7 | 6 | <0.001 |
| | Fertilization treatment | 9 | 27 | 6 | <0.001 |
| | Reef treatment + fertilization treatment | 10 | 28.7 | 7 | <0.001 |
| | Reef treatment * fertilization treatment | 11 | 29.5 | 8 | <0.001 |
| Elevation change | Fertilization treatment + row | 1 | 0 | 6 | 0.3063 |
| | Row | 2 | 0.2 | 5 | 0.2837 |
| | Fertilization treatment + reef treatment + row | 3 | 1 | 7 | 0.1885 |
| | Row + reef treatment | 4 | 1.1 | 6 | 0.1767 |
| | Row * reef treatment | 5 | 6.2 | 9 | 0.0139 |
| | Fertilization treatment | 6 | 7.3 | 3 | 0.0081 |
| | Fertilization treatment * reef treatment | 7 | 7.6 | 5 | 0.0068 |
| | Fertilization treatment * row | 8 | 7.8 | 9 | 0.0061 |
| | Reef treatment | 9 | 8.1 | 3 | 0.0052 |

| | | | | | |
|--|--|----|------|----|--------|
| | Fertilization treatment + reef treatment | 10 | 8.3 | 4 | 0.0048 |
| | Fertilization treatment * reef treatment * row | 11 | 23.7 | 17 | <0.001 |

Table 2.2: Results for mixed models describing plant mortality risk, shoot density, and clonal expansion. Significant p values ($P < 0.05$) are shown in bold.

| Response | Fixed Factors | χ^2 | DF | Prob > χ^2 | |
|---|--|-------------------------|---------|------------------|------------------|
| Plant mortality risk | Fertilization treatment | 0.3313 | 1 | 0.5649 | |
| | Reef treatment | 4.1775 | 1 | 0.041 | |
| | Row | 19.2119 | 3 | 0.0002 | |
| | Fertilization treatment * reef treatment | 3.8546 | 1 | 0.0496 | |
| | Fertilization treatment * row | 11.3537 | 3 | 0.01 | |
| | Reef treatment * row | 3.6307 | 3 | 0.3042 | |
| | Fertilization treatment * reef treatment * row | 3.9797 | 3 | 0.2637 | |
| | Shoot density (no. ind. per m ²) | Time | 592.754 | 1 | <0.001 |
| | | Fertilization treatment | 22.629 | 1 | <0.001 |
| Clonal expansion (no. ind. per m ²) | Time | 25.5619 | 1 | <0.001 | |

Table 2.3: Results of Tukey’s post-hoc tests to examine pairwise comparisons in plant mortality risk model. Control and Oystercatcher sites and Fertilized and Unfertilized treatments are abbreviated as CTRL, OC, Fert, and Unfert respectively. Significant p values ($P < 0.05$) are shown in bold.

| Model term | Contrast | Estimate | Standard Error | DF | Z ratio | P value |
|--|-----------------------------|----------|----------------|-----|---------|------------------|
| Reef treatment | CTRL vs. OC | 0.421 | 0.126 | Inf | 3.339 | <.0001 |
| Row | 1 vs. 2 | 0.747 | 0.162 | Inf | 4.609 | <.0001 |
| | 1 vs. 3 | 0.977 | 0.174 | Inf | 5.614 | <.0001 |
| | 1 vs. 4 | 0.642 | 0.159 | Inf | 4.033 | 0.0003 |
| | 2 vs. 3 | 0.230 | 0.196 | Inf | 1.174 | 0.6436 |
| | 2 vs. 4 | -0.105 | 0.183 | Inf | -0.571 | 0.9407 |
| | 3 vs. 4 | -0.335 | 0.194 | Inf | -1.728 | 0.3089 |
| Fertilization treatment * reef treatment | Fert. CTRL vs. Unfert. CTRL | 0.0013 | 0.159 | Inf | 0.008 | 1.00 |
| | Fert. CTRL vs. Fert. OC | 0.6179 | 0.187 | Inf | 3.302 | 0.0053 |
| | Fert. CTRL vs. Unfert. OC | 0.2256 | 0.172 | Inf | 1.308 | 0.5578 |
| | Unfert. CTRL vs. Fert. OC | 0.6166 | 0.184 | Inf | 3.350 | 0.0045 |
| | Unfert. CTRL vs. Unfert. OC | 0.2243 | 0.169 | Inf | 1.324 | 0.5473 |
| | Fert. OC vs. Unfert. OC | -0.3923 | 0.196 | Inf | -2.003 | 0.1870 |
| Fertilization treatment * row | Fert. 1 vs. Unfert. 1 | -0.511 | 0.189 | Inf | -2.701 | 0.1222 |
| | Fert. 2 vs. Unfert. 2 | 0.0453 | 0.263 | Inf | 0.172 | 1 |

| | | | | | | |
|--|-------------------------|---------------|--------------|-----|--------------|------------------|
| | Fert. 3 vs. Unfert. 3 | -0.6529 | 0.291 | Inf | -2.247 | 0.3234 |
| | Fert. 4 vs. Unfert. 4 | 0.3367 | 0.256 | Inf | 1.316 | 0.8933 |
| | Fert. 1 vs. Fert. 2 | 0.4685 | 0.235 | Inf | 1.991 | 0.4878 |
| | Fert. 1 vs. Fert. 3 | 1.0476 | 0.277 | Inf | 3.788 | 0.0038 |
| | Fert. 1 vs. Fert. 4 | 0.2181 | 0.23 | Inf | 0.95 | 0.9811 |
| | Unfert. 1 vs. Unfert. 2 | 1.0248 | 0.223 | Inf | 4.605 | 0.0001 |
| | Unfert. 1 vs. Unfert. 3 | 0.9057 | 0.21 | Inf | 4.313 | 0.0004 |
| | Unfert. 1 vs. Unfert. 4 | 1.0658 | 0.22 | Inf | 4.834 | <.0001 |
| | Fert. 2 vs. Fert. 3 | 0.579 | 0.295 | Inf | 1.96 | 0.509 |
| | Fert. 2 vs. Fert. 4 | -0.2504 | 0.252 | Inf | -0.992 | 0.9757 |
| | Unfert. 2 vs. Unfert. 3 | -0.1191 | 0.257 | Inf | -0.463 | 0.9998 |
| | Unfert. 3 vs. Unfert. 4 | 0.041 | 0.266 | Inf | 0.154 | 1 |
| | Fert. 3 vs. Fert. 4 | -0.8295 | 0.291 | Inf | -2.848 | 0.0835 |
| | Unfert. 3 vs. Unfert. 4 | 0.1601 | 0.255 | Inf | 0.627 | 0.9985 |

Table 2.4: Results of Tukey's post-hoc tests to examine pairwise comparisons in shoot density mixed model. Significant p values ($P < 0.05$) are shown in bold.

| Model term | Contrast | Estimate | Standard Error | DF | T ratio | <i>P</i> value |
|-------------------------|-----------------------------|----------|----------------|-----|---------|------------------|
| Fertilization treatment | Fertilized vs. Unfertilized | 0.186 | 0.0391 | 186 | 4.757 | <.0001 |

Table 2.5: Results for linear model describing change in site elevation. Significant p values ($P < 0.05$) are shown in bold.

| Fixed Factor | Sum of Squares | DF | F value | Prob > F |
|---------------|----------------|----|---------|---------------|
| Fertilization | 0.0029 | 1 | 2.4393 | 0.1237 |
| Row | 0.0174 | 3 | 4.9376 | 0.0039 |
| Residuals | 0.0694 | 59 | | |

Table 2.6: Results of Tukey's post-hoc tests to examine pairwise comparisons in elevation change linear model. Significant p values ($P < 0.05$) are shown in bold.

| Contrast | Estimate | Standard Error | DF | T ratio | <i>P</i> value |
|----------|----------|----------------|----|---------|----------------|
| 1 vs. 2 | -0.00866 | 0.0121 | 59 | -0.714 | 0.8912 |
| 1 vs. 3 | -0.02866 | 0.0121 | 59 | -2.363 | 0.0959 |
| 1 vs. 4 | -0.04203 | 0.0121 | 59 | -3.466 | 0.0053 |
| 2 vs. 3 | -0.02000 | 0.0121 | 59 | -1.649 | 0.3595 |
| 2 vs. 4 | -0.03338 | 0.0121 | 59 | -2.753 | 0.0382 |
| 3 vs. 4 | -0.01337 | 0.0121 | 59 | -1.103 | 0.6891 |

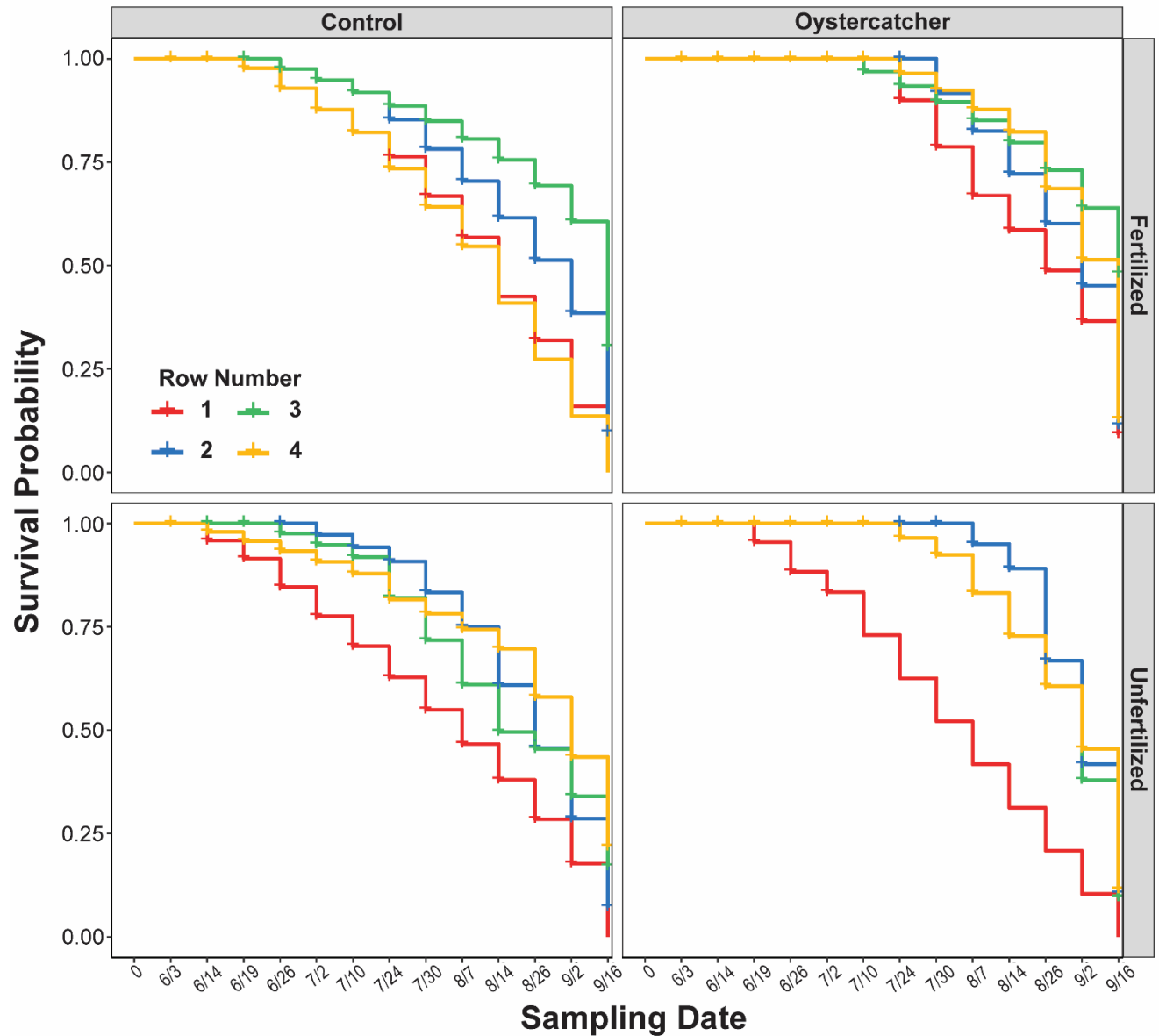


Figure 2.1: Kaplan-Meier survival curves showing *S. alterniflora* survival over the study period. Figure panels represent all levels of fertilization and reef treatments, with curve color corresponding to row. All sampling dates refer to 2019.

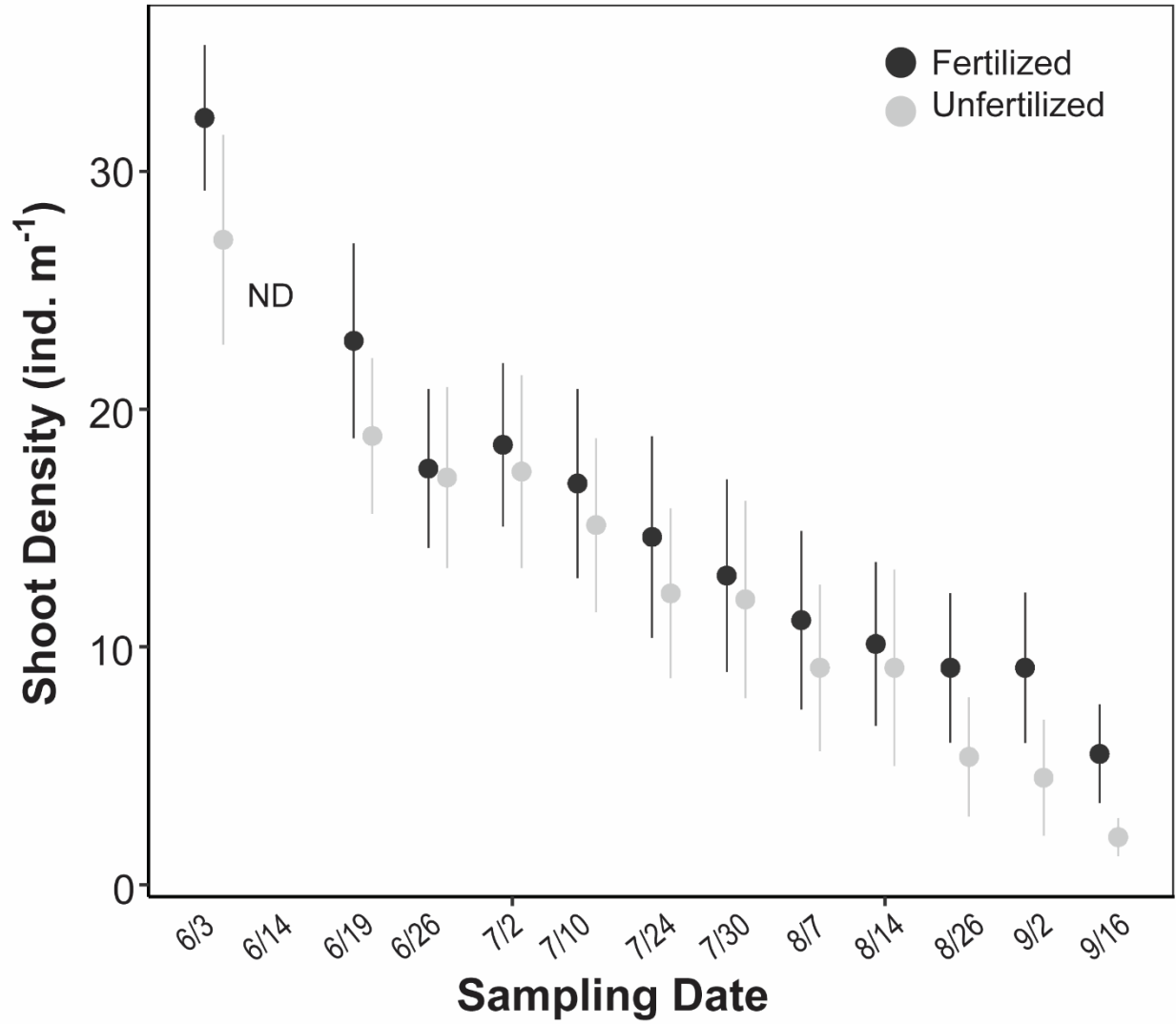


Figure 2.2: Mean *S. alterniflora* shoot density over the study period, as influenced by time and fertilization treatment. Error bars represent ± 1 SE. All sampling dates refer to 2019. No data were collected on June 14, 2019 (ND=No data).

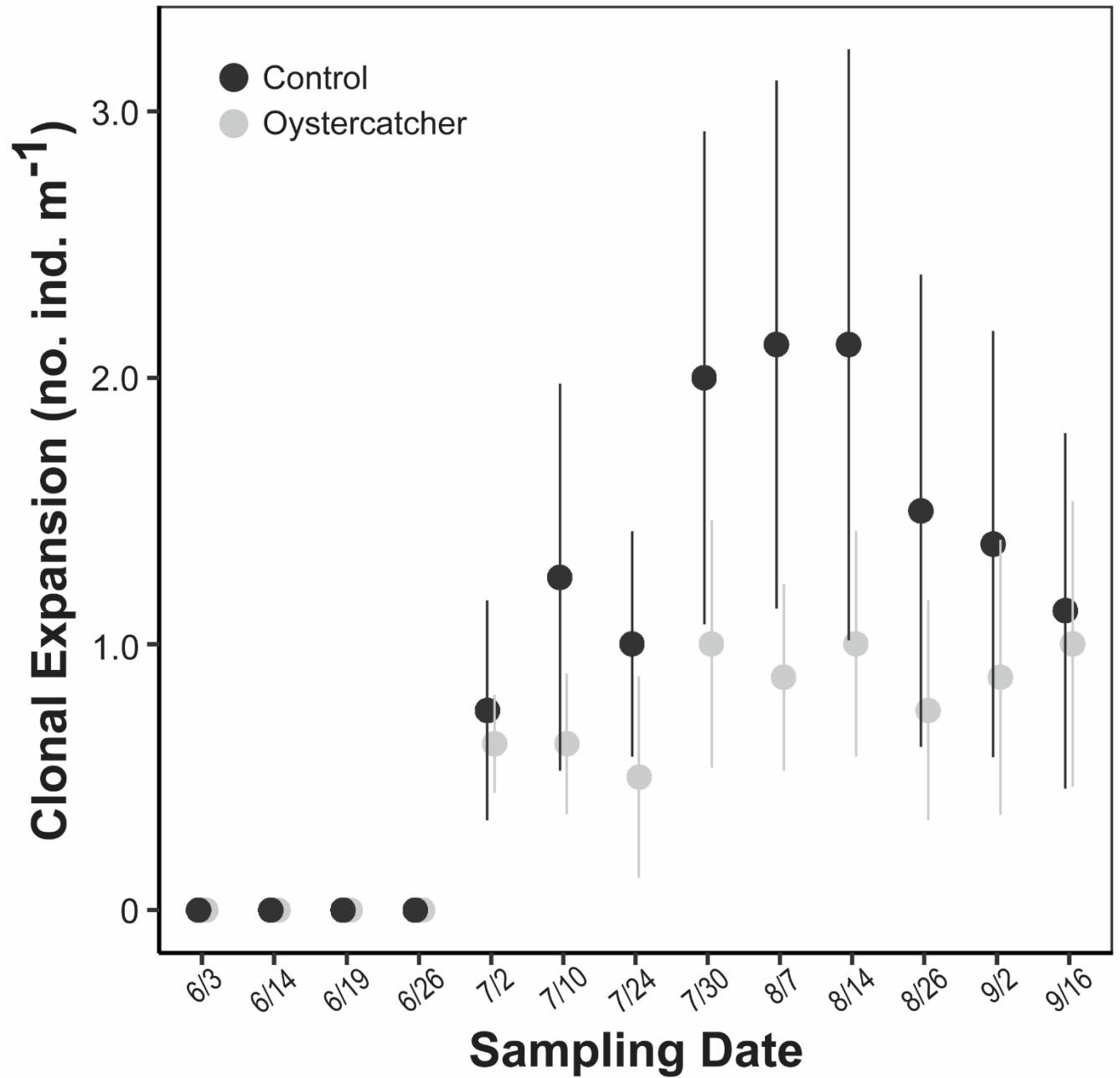


Figure 2.3: Mean number of clonal shoots present over the study period at control (black circles) and OC sites (grey circles). Error bars represent ± 1 SE. All sampling dates refer to 2019.

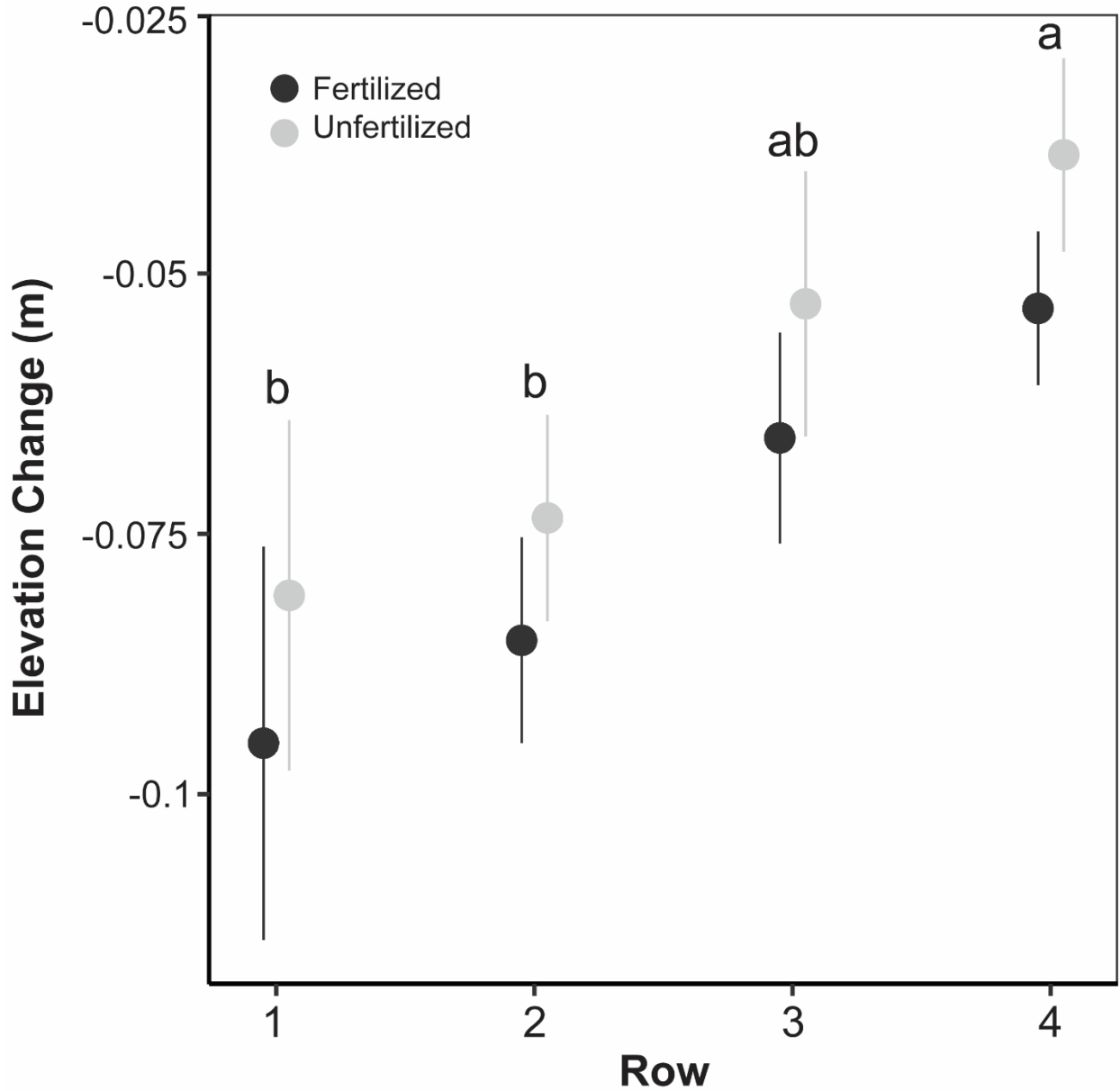


Figure 2.4: Mean change in elevation relative to NAVD88 between June and September 2019 at fertilized and unfertilized sites according to row. Error bars represent ± 1 SE. All sampling dates refer to 2019. No data were collected on June 14, 2019 (ND=No data).

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