

RESEARCH ARTICLE

Salt marsh shoreline geomorphology influences the success of restored oyster reefs and use by associated fauna

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Restoration is increasingly implemented as a strategy to mitigate global declines in biogenic habitats, such as salt marshes and oyster reefs. Restoration efforts could be improved if we knew how site characteristics at landscape scales affect the ecological success of these foundation species. In this study, we determined how salt marsh shoreline geomorphologies (e.g. with variable hydrodynamic energy, fetch, erosion rates, and slopes) affect the success of restored intertidal oyster reefs, as well as how fauna utilize restored reefs and forage along marsh habitats. We constructed oyster reefs along three marsh shoreline geomorphologies in May 2012: 1) “creek” (small-fetch, gradual-sloped shoreline), “ramp” (large-fetch, gradual-sloped shoreline), and “scarp” (large-fetch, steep-sloped shoreline). Following recruitment, oyster spat density was greatest on ramp reefs; however, 2 years later, the highest adult oyster densities were found on creek reefs. Total nekton and blue crab catch rates in trawl nets were highest in the creek, while piscivore catch rates in gill nets were highest along the scarp shoreline. We found no difference in predation on snails in the salt marsh behind constructed reef and nonconstructed reference sites, but there were more snails consumed in the creek shoreline, which corresponded with the distribution of their major predator—blue crabs. We conclude that oyster reef construction was most successful for oysters in small-fetch, gradual-sloped, creek environments. However, nekton abundance did not always follow the same trends as oyster density, which could suggest constructed reefs may offer similar habitat-related functions (prey availability and refuge) already present along existing salt marsh borders.

Key words: landscape, nekton, oyster recruitment, structured habitat, tidal creek

Implications for Practice

- We recommend restoration practitioners consider constructing loose cultch shell oyster reefs along low-energy shorelines, such as in tidal creeks, where we found constructed reefs had the highest adult oyster densities.
- If the restoration goal is to enhance habitat use for fauna, one may consider building oyster reefs in areas without other structured habitats nearby.
- The geomorphology of the marsh shoreline (including slope and fetch) should be considered when siting and restoring intertidal oyster reefs. Along steep-sloped, high-exposure shorelines, reef restoration may require more robust substrates than loose shell.

Introduction

The production and sustainability of fishes and mobile crustaceans (nekton hereafter) is routinely linked to the abundance and quality of structured habitats that serve as essential refuge or foraging areas within estuaries (e.g. oyster reefs, seagrass, salt marsh, and mangroves; Gibson 1994; Gratwicke & Speight 2005; Humphries et al. 2011). However, the area of these habitats has declined globally, and in many places disappeared

completely, potentially contributing to lost service delivery (Grabowski et al. 2012), particularly fishery production (sensu Keller et al. 2017). In response, managers across local, national, and international scales have significantly increased restoration efforts to reestablish vital habitat for fauna (Bersosa et al. 2018). Oyster reefs (*Crassostrea virginica*) are a critical habitat to restore in the United States because they have experienced

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declines of up to 85% (Zu Ermgassen et al. 2012) and provide essential nursery habitat to a plethora of species.

However, evidence that constructed oyster reefs will enhance nekton production has been equivocal, with some studies showing strong enhancement (Peterson et al. 2003), while others have found no change (Grabowski et al. 2005; Geraldi et al. 2009). One hypothesis for no nekton enhancement is that additional biogenic habitat may offer similar habitat refuge and thus is functionally redundant habitat for mobile or transient nekton (Geraldi et al. 2009). In contrast, studies that did find enhancement with restoration speculated that predators like blue crabs and mobile fishes (e.g. sheepshead) might be attracted to reef structure, which could ultimately increase predation in adjacent salt marsh edge habitats (Humphries et al. 2011) and affect transfer of energy from marshes to the open estuary (Abrantes et al. 2015). Given the importance of habitat connectivity (Micheli & Peterson 1999), the placement of restored oyster reefs may be a particularly important determinant of habitat use and foraging patterns by mobile fauna and ultimately the amount of nekton production resulting from oyster restoration.

In addition to efforts to enhance nekton production, intertidal oyster restoration is increasingly being employed to protect eroding salt marsh shorelines (e.g. living shorelines), with case studies demonstrating reduced marsh shoreline erosion postreef restoration (Piazza et al. 2005; Currin et al. 2010; Smith et al. 2018). Eroding marsh shorelines are characteristically affected by exposure to wind-generated sheer stress, which depends on the unobstructed distance over which the wind can blow (i.e. fetch), water depth, and duration of the wind events (Fagherazzi & Wiberg 2009; La Peyre et al. 2015). Recent research suggests that fringing oyster reefs have a high impact on shoreline retreat at high-exposure shorelines, reducing marsh edge erosion an average of 1.0 m/year (La Peyre et al. 2015). However, along high-exposure eroding marsh shorelines, loose cultch reefs do not typically halt shoreline erosion (Scyphers et al. 2011; La Peyre et al. 2015). Differences in the slope, elevation, fetch, and hydrodynamics (termed “geomorphology”) of marsh shorelines may affect the development and nekton use of restored oyster reefs, as well as their effectiveness at reducing marsh erosion over time. Oyster reef development can be influenced by a variety of factors such as aerial exposure (Fodrie et al. 2014), water quality (salinity, temperature, oxygen concentration; Dickinson et al. 2012), sedimentation (Taylor & Bushek 2008), or the location where reefs are placed within a mosaic of habitat patches (i.e. landscape setting; Grabowski et al. 2005; Ziegler et al. 2018). Thus, understanding how different shoreline geomorphologies within a salt marsh landscape might regulate oyster reef development and salt marsh habitat use is critical for designing future restoration efforts and shoreline protection.

The hydrodynamic environment of exposed, eroding marsh shorelines can differ substantially from less-exposed, noneroding marsh shorelines (Allen & Rae 1987; Marani et al. 2011; Fig. 1). Highly exposed, eroding salt marsh shorelines are often characterized with a steep, near vertical or “scarp” morphology (also referred to as cliffs; Marani et al. 2011). Benthos adjacent to bulkheads (i.e. manmade vertical walls) can be exposed to increased wave energy reflected off the wall,

causing bottom scour and increasing the amount of suspended sediments (Patrick et al. 2014), which may result in displaced or buried restored reefs. Therefore, oyster reef development may be reduced or slowed along high-exposure, steep-sloped shorelines.

The objective of this study was to monitor the success (oyster density) and habitat function (nekton density) of oyster reefs constructed along shorelines with distinct salt marsh geomorphologies: creek, ramp, and scarp shorelines. To determine whether salt marsh shoreline geomorphology would affect the development of these reefs, we quantified the density of live oyster spat and adult oysters during August 2012 (3 months postconstruction) and in September 2014 (28 months postconstruction) on nonconstructed reference sites (2012 and 2014), constructed oyster reefs (2012 and 2014), and natural oyster reefs (only in 2014). We hypothesized that the creek shoreline would produce the highest spat and adult oyster survival and growth, but not necessarily recruitment. In 2014, we determined the influence of oyster reef construction and marsh shoreline geomorphology on habitat use by mobile fauna and trophic transfer by sampling nekton density on oyster removal, nonconstructed reference sites, constructed reefs, and natural reefs as well as measured predation rates on the marsh periwinkle, *Littoraria irrorata*, in the marsh immediately landward of reef and reference sites over 2 years postconstruction. We hypothesized that constructed oyster reefs located along the creek shoreline (with small fetch) would have the highest nekton density augmentation as the added structure of the reefs would attract nekton, and previous literature shows high nekton utilization of intertidal creeks (Allen et al. 2007). We hypothesized that reef presence would increase predation rates along marsh edges compared to other locations, as predators (e.g. blue crabs, mud crabs, etc.) would be attracted to the greater structural complexity of reefs adjacent to the marsh for foraging.

Methods

Study Location

We conducted our study in the Rachel Carson National Estuarine Research Reserve (NERR) in Beaufort, NC, United States (34°42'14.99"N, 76°37'25.41"W) (Fig. 1A). The Rachel Carson NERR is approximately 5 km² and dominated by smooth cordgrass, *Spartina alterniflora*, along the shoreline. Our study was conducted on the south-facing shoreline of Carrot Island, which experiences high erosion (Riggs & Ames 2003) resulting from a large fetch and dominant south-southwest summer winds (Pietrafesa et al. 1986; Theuerkauf et al. 2015). Furthermore, the study area is exposed to waves from frequent boat traffic in a nearby channel. Within the study area, we classified the *S. alterniflora* marsh shorelines into three shoreline geomorphologies: creek, ramp, and scarp (Fig. 1). We measured the fetch (m) of each shoreline using the distance from the shoreline to the nearest landmass at 90, 135, 180, and 225° using Google Earth and averaged these distances. Shoreline slopes were calculated using elevations of terrestrial-light detection and ranging (LIDAR)-derived profile (see Theuerkauf et al. 2015). Sample

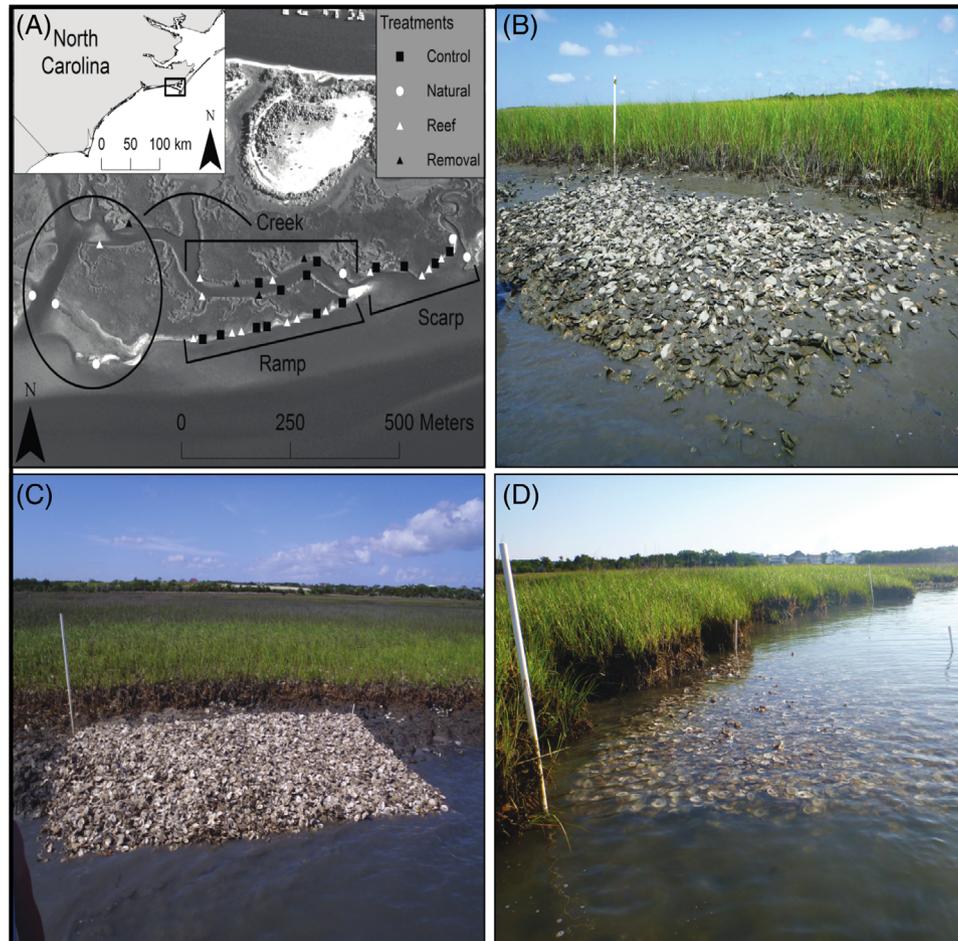


Figure 1. (A) Map of study area within a salt marsh at Carrot Island, part of the Rachel Carson National Estuarine Research Reserve in Beaufort, NC, USA ($34^{\circ}42'14.99''\text{N}$, $76^{\circ}37'25.41''\text{W}$). Sampling treatments include nonconstructed reference sites (“controls”: black squares), natural reefs (white circle), constructed reefs (“reefs”: white triangle), and oyster removal sites (black triangle) within different salt marsh shoreline geomorphologies (B) creek, (C) ramp, and (D) scarp (shown with constructed oyster reef).

elevations were regressed with their shore perpendicular distances, and then slopes were averaged across plots. The salt marsh creek shoreline (i.e. “creek,” Fig. 1B) has a gradual slope (average slope = 0.07 m/m) and small fetch (50 m) relative to the scarp and ramp shorelines, with little to no landward retreat (Theuerkauf et al. 2015). The salt marsh ramp (i.e. “ramp,” Fig. 1C) is a gradual-sloping (average slope = 0.09 m/m) and large-fetch (2,472 m) shoreline resulting in landward retreat (0.65 m/year since 1958: Theuerkauf et al. 2015). The salt marsh scarp shoreline (i.e. “scarp,” Fig. 1D) has a steep slope (nearly vertical) (average slope = 0.49 m/m), with an average height of approximately 0.5 m, and is also relatively large fetch (2,161 m), and has been retreating landward at a faster rate than the ramp (0.76 m/year since 1958: Theuerkauf et al. 2015; see Fagherazzi et al. 2012 for a description of the processes associated with the formation of scarp and ramp marsh shoreline geomorphologies). The wave exposure is similar between the ramp and the scarp (based on fetch, wind, and nearshore bathymetry), but the shoreline geomorphology (gradient) and the resulting distribution of wave energy differs (Fig. S1). The main premise

for choosing these three settings is to compare the development of constructed oyster reefs and habitat use by associated fauna and trophic transfer along shorelines with varying hydrodynamics (high-exposure environments—ramp and scarp, vs. low-exposure environments—creek) and shoreline morphologies (gradual-slope dissipative and steep-slope reflective). A dissipative shoreline is a gradual-slope, flat shoreline where wave energy is dissipated across a large area. A reflective shoreline is steep, in our case almost vertical shoreline, and wave energy is expended across a small area.

Oyster Reef Construction

In early May 2012 we constructed 14 oyster reefs along the three salt marsh geomorphologies: creek ($n = 4$), ramp ($n = 6$), and scarp ($n = 4$) (Fig. 1A). Prior to reef construction, we used a Trimble Real-Time Kinematic (RTK) high-resolution mapping system (0.5–1.0 cm horizontal and 1.0–4.0 cm vertical resolution) to identify locations immediately adjacent (within 1 m) to each of the three salt marsh shorelines with surface elevations

between -0.54 and -0.46 m relative to the North American Vertical Datum of 1988 (NAVD88). These elevations correspond to the “optimal growth zone” for oyster reefs in this system (Ridge et al. 2015). Following methods outlined by Grabowski et al. (2005), we placed adult oyster cultch to form 3-m-wide (perpendicular to the shoreline) by 5-m-long (parallel to shore) by 0.15-m-tall reefs at each site in May 2012 (Fig. 1B–D shows cultch reef immediately postconstruction).

Natural reefs ($n = 6$) were sampled for oyster and fauna density, as well as predation at the marsh edge, as a reference for how “successful” each constructed reef would be in providing habitat and foraging access (i.e. “positive” controls; Fig. 1A). We also identified nonconstructed reference sites along each shoreline ($n = 4$ creek, $n = 6$ ramp, $n = 4$ scarp) that were greater than 10 m from constructed reefs and within the elevation range described above. These reference sites were characterized by unstructured bottom (mudflat) adjacent to salt marsh (i.e. “negative” controls; Fig. 1A). Within some of the nonconstructed reference sites inside the creek, there were higher densities of fringing oyster clumps relative to the nonconstructed reference sites in the other shoreline treatments (Fig. 1B, see Fig. S2B). We suspected the increased biogenic structure associated with these clumps might attract higher densities of nekton and modify landscape-scale differences. To test this idea, we conducted a field manipulation, where we removed oysters from 3×5 -m areas only at the creek edge (termed oyster removal hereafter, $n = 4$) in June 2014 (Fig. S2A). Thus, we could more thoroughly compare the effect of reef type (oyster removal, nonconstructed reference site, constructed oyster reef, natural oyster reef) on fauna density and predation rates. In May 2014, we used a real-time kinematic global positioning system (RTK GPS) to take the three elevation measurements at the sediment surface of each nonconstructed reference site and on the top of each constructed reef and natural reef (creek only) along a shore-perpendicular transect to estimate the vertical relief of each reef or reference site.

Oyster Density

We quantified the density of live oysters on constructed reefs during August 2012 (3 months postconstruction), and in September 2014 (28 months postconstruction). We grouped oysters by size: spat (<25 mm), juveniles (25–75), and adults (>75 mm) to determine how constructed reefs were developing and how many of the oysters were recruits (sensu La Peyre et al. 2014). In August 2012, 3×5 -m grids were mapped over each constructed reef and nonconstructed reference sites and three points were randomly selected for sampling within each grid (at 1-m resolution along the x and y axes). Cultch shells were collected by hand from each point on the constructed reef to fill the bottom of a 20×20 -cm² (0.04 m²) tray. The number of oysters (all spat) were counted on these shells as a measure of initial recruitment intensity. We anticipated that reef structure would change and that cultch material and growing oysters would cement together over time; therefore, we adapted our sampling method in 2014 to also sample deeper layers of the reef. We again used a grid (same method as above) to

randomly select three points to place quadrats (0.0625 m²; scaled to 1 m² for analysis). Within each quadrat, we excavated all shell material until we reached the black, anoxic sediment layer devoid of live oysters. We counted the abundance of live oysters and also measured the length (mm) from the anterior to the posterior of each live oyster at oyster removal (creek only), nonconstructed reference sites, constructed reefs, and natural reefs (creek only). Our sampling methods were similar to previous oyster construction projects in this area (Fodrie et al. 2014).

Nekton Density

We quantified nekton densities at each constructed reef and nonconstructed reference site monthly from June to September in 2012 and July to October in 2014 using gill and fyke nets. During the 2014 sampling effort, we also quantified nekton densities at oyster reef removal sites and natural reef sites using the same methods. Sampling took place at night because fish abundance has been shown to increase on high tides, especially in the evening and after dark (Ross et al. 1987; Layman 2000; Pessanha & Araújo 2003). For two nights each month, we randomly selected a reef type (e.g. natural reefs [$n = 6$], oyster removal sites [$n = 4$], constructed reefs [$n = 6$], and nonconstructed reference sites [$n = 6$]) to sample nekton with gill and fyke nets, using a different gear for each reef type, across all three salt marsh morphologies (not all sites were sampled each month).

Gill nets were 9 m long and 1.5 m tall to capture the entire water column. During high tide, one end of the gill net was placed at the marsh edge and stretched at a 45° angle from shore such that the ebb-tide current would funnel fish toward the acute angle formed by the marsh and net. Fyke nets were deployed at high tide along each shoreline to capture organisms exiting the marsh platform with the falling tides. The ends of each fyke net wing (5.1 m long) were placed 0.25 m into the marsh and set for a total mouth width of 8 m following Gittman et al. (2016). All organisms leaving the marsh were funneled into a $1 \times 1 \times 5$ -m³ compartmentalized, 3.2-mm-mesh bag. Gill net and fyke net sampling occurred during nighttime falling tides to capture animals as they egressed from the marsh platform or approached the marsh edge to prey upon egressing nekton.

We also sampled nekton occupying the shallow subtidal habitat adjacent to each marsh shoreline where oyster reef construction occurred using a 5-m-wide otter trawl (2-cm mesh size, 0.6-cm cod end mesh, with no tickler chain; Baillie et al. 2015; Yeager et al. 2016). We completed two–three 2-minute tows (150–200 m in length) each month along each salt marsh shoreline within 3 hours of a diurnal high tide. The location of each tow was haphazard but within the boundaries of each distinct shoreline geomorphology (creek, ramp, or scarp). Trawl surveys were conducted between June–October in 2012 and May–October in 2014. The trawl was used to explore potential differences in nekton community between salt marsh shoreline geomorphologies at the landscape scale (approximately 100–500 m), rather than at the reef scale (approximately 5 m). Although this precluded reef versus nonrestored reference site comparisons, trawl sampling was valuable, as we wanted

an estimate of the potential periwinkle predators within each shoreline to evaluate the potential drivers of our predation rates (see below).

Predation Rates

We conducted predation assays using a common prey species, the marsh periwinkle (*Littoraria irrorata*), along the three salt marsh shoreline geomorphologies with and without constructed oyster reefs to understand if constructed oyster reefs reduce or enhance trophic transfer between the intertidal marsh and subtidal bottom habitat. Periwinkles (11–20 mm in shell length) were attached to a 10-cm monofilament tether with marine epoxy and placed in the field by tying the line to a metal stake secured in the marsh surface. This tethering technique allowed snails to forage on the marsh surface in a 10-cm radius without tangling tethers and permitting natural behavior (e.g. climbing up and down cordgrass stems with the tide (sensu Silliman & Bertness 2002)). Tethered periwinkles ($n = 10$ per plot) were deployed within paired open and caged plots located along the vegetated marsh edge at each reef or nonreef reference site. Cages (0.65 m tall \times 0.5 m wide \times 0.5 m wide, 5-mm mesh hardware cloth) were used to account for loss of periwinkles as a result of factors other than predation (e.g. wave energy, tether failure). The average number of periwinkles lost from the caged plots was subtracted from paired open plots to estimate periwinkle predation within each plot. Predation assays were conducted June–September in 2012 ($n = 4$ trials) and June, July, and September in 2014 ($n = 3$ trials). During the 2014 sampling effort, we also quantified predation rates at the marsh edge of oyster reef removal sites and natural reef sites using the same methods as above. Additionally, we quantified *S. alterniflora* stem heights (average of five tallest stems [cm]) and stem densities within each open and control plot (0.25 m²) during each trial to account for any behavioral differences between crabs and snails due to spatial heterogeneity in *S. alterniflora* densities (Lewis & Eby 2002).

Statistical Analyses

To determine how much the oyster reefs grew vertically, we measured the vertical relief, or height, of each constructed reef and nonconstructed reference sites (elevation of sediment surface) along each shoreline in 2014. We ran a mixed effects model with two fixed factors: geomorphology (creek, ramp, scarp) and reef type (constructed and nonconstructed reference sites), the interaction of geomorphology and reef type, and a random factor: site. We also compared the natural reefs to the constructed and nonconstructed reference sites in the creek shoreline using a mixed model with a fixed factor, reef type, and the random factor site.

To determine whether salt marsh shoreline geomorphology affected the development of constructed oyster reefs, we used mixed effects models. Our model included a fixed factor, geomorphology (creek, ramp, scarp), and a random factor, site, (replicate location), on the response variable spat density in 2012. Our main objective in 2012 was to quantify where the

spat settled along each salt marsh shoreline and therefore we monitored spat only on constructed reefs and not on nonconstructed reference sites. In 2014, we also included the fixed factor reef type (constructed and nonconstructed reference sites) and the interaction of geomorphology and reef type on spat, juvenile, and adult oyster density. We ran separate models for each year (2012 and 2014), as the location of where spat settle versus where the juvenile and adult oysters exist can often change over time (Fodrie et al. 2014). To determine if total oyster densities were similar between constructed and natural reefs, we ran a mixed effects model with the fixed factor reef type (oyster removal, nonconstructed reference site, constructed oyster reef, natural oyster reef) and the random factor site (to address the potential biases associated with each reef location) using only the 2014 creek data.

To determine whether salt marsh shoreline geomorphology and constructed oyster reefs would affect the density of nekton, we divided our catch data into three guilds that we thought may respond differently to oyster reef construction and could have variable impacts on reef community composition: total nekton, piscivorous fishes, and blue crabs (Table S1). We used mixed effects models to analyze total nekton, piscivore, and blue crabs catch rates separately for each gear type (gill and fyke nets) and each year (2012 and 2014). Mixed models included fixed factors: geomorphology (creek, ramp, scarp), reef type (constructed and nonconstructed reference sites), the interaction of geomorphology and reef type, month, and the random factor: site. Blue crabs were analyzed separately because they are one of the main predators of periwinkles (Silliman & Bertness 2002). Catch data were standardized to catch-per-unit-effort (CPUE) for gill and fyke nets (6 hour/soak) and for the trawl net (100 m per tow). As trawl nets were used to quantify the nekton catch rates along each marsh shoreline geomorphology, rather than at the individual reef or control plot scale, the mixed effects models only included a fixed factor: geomorphology (creek, ramp, scarp), and a random factor: tow replicate, with the following response variables: total nekton, piscivores, and blue crabs, separately for 2012 and 2014. To determine if constructed oyster reefs were serving as comparable habitat to natural reefs, we used a mixed effects model to analyze the effects of two fixed factors: reef type (oyster removal, nonconstructed reference sites, constructed oyster reef, natural oyster reef) and month, and a random factor, site, on both the gill and fyke net 2014 creek data.

We determined if predation on periwinkles (# of *L. irrorata* snails consumed in each plot) differed between constructed and nonconstructed reference sites at different salt marsh shoreline geomorphologies. We used mixed effects models separately for 2012 (June, July, August, September) and 2014 (June, July, September). Our models included fixed factors: geomorphology (creek, ramp, scarp), reef type (constructed and nonconstructed reference sites), the interaction of geomorphology and reef type, month, and the random factor site. To determine if predation on periwinkles differed between all reef types (oyster removal, nonconstructed reference sites, constructed oyster reef, and natural oyster reef), we used a mixed effects model with a binomial family link to analyze the effects of fixed factors reef

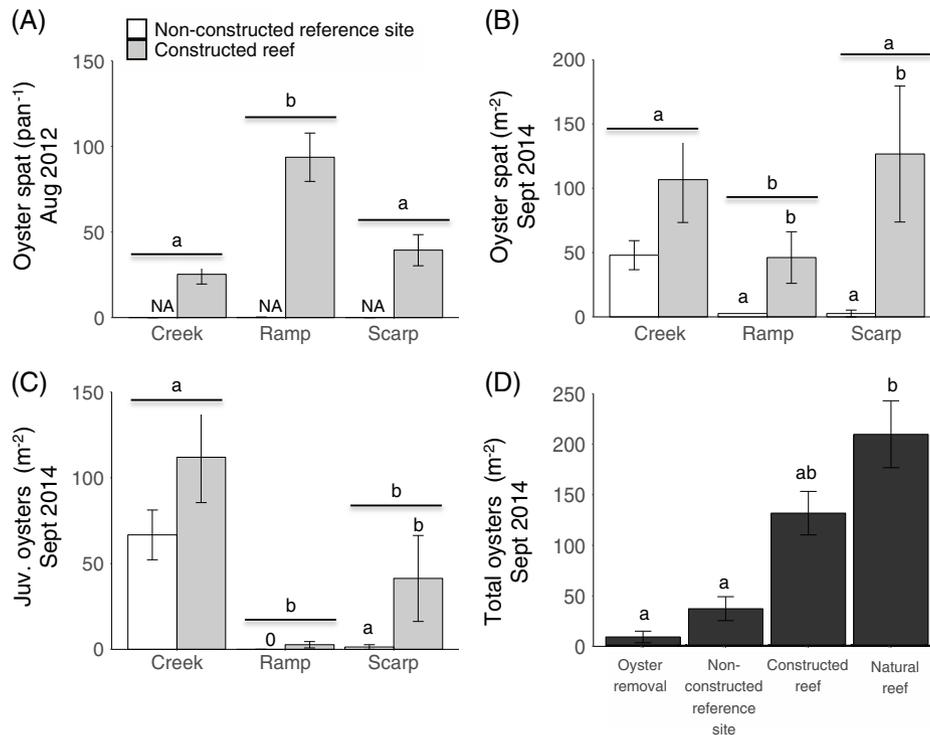


Figure 2. Number of oyster spat (A) per pan from August 2012 and (B) per m⁻² in September 2014, and (C) juvenile oysters m⁻² from September 2014 at each nonconstructed reference site (white bars) and constructed oyster reef (light gray bars) among three salt marsh shoreline geomorphologies: creek, ramp, and scarp. (D) Total oysters (m⁻²) from each reef type (oyster removal, nonconstructed reference site, constructed reef, and natural reef) in the creek morphology from September 2014. No oyster data was taken for the nonconstructed reference sites in the creek in August 2012, denoted by “NA.” Letters above horizontal lines represent significant differences across landscapes ($p < 0.05$) and letters above bars represent significant differences across reef types ($p < 0.05$). Data are shown as means \pm 1SE.

type and month, and the random factors site, *S. alterniflora* stem height, and *S. alterniflora* stem density, on predation of periwinkles along just the creek shoreline in 2014.

For all analyses we tested the assumptions of normality with the Shapiro–Wilk test and equal variance with the Bartlett test (if normally distributed) or Levene test (if not normally distributed) prior to analyses. Data were log (or log +1 when the dataset included zeros) transformed if data were not normal and/or heteroskedastic (see data transformations in Table S2). If there was a significant treatment effect (including interactive terms), we used Tukey’s post hoc comparative analysis to determine pairwise differences among all unique treatments. All analyses were conducted using R 1.0.143 (R Development Core Team 2009) and the packages lme4 and function lmer (Pinheiro et al. 2019).

Results

Overall, constructed reefs within the ramp and scarp shoreline had lower vertical relief compared to those along the creek shoreline (Fig. S3; Table S3). Constructed reefs had a higher vertical relief compared to nonconstructed reference sites in both the ramp and scarp, but no difference was found in the creek (Fig. S3; Table S3). Natural reefs had the highest vertical relief

reef compared to the constructed and nonconstructed sites in the creek shoreline (Fig. S3; Table S3).

Oyster Spat, Juvenile, and Adult Density

In August 2012, oyster spat density was highest on constructed reefs located adjacent to ramp marsh shorelines (Fig. 2A; Table S4; $p = 0.023$); however, 2 years postconstruction, the lowest spat densities were found on constructed reefs were along the ramp marshes (Fig. 2B; Table S4; $p = 0.006$). By September 2014, similar densities of oyster spat were found on constructed reefs along the scarp and creek (Fig. 2B). However, the creek constructed reefs had almost three times more adult oysters than the scarp and 42 times more than the ramp constructed reefs (Fig. 2C; Table S4; $p < 0.001$).

Although 2 years postconstruction, oyster spat densities on the constructed reefs were significantly greater than densities on the nonconstructed reference sites in the ramp and scarp, spat densities on the constructed reefs in the creek were not significantly different than densities on creek reference sites (Fig. 2B, Table S4). Conversely, juvenile oyster densities were higher on constructed oyster reefs in the creek compared with the scarp and ramp constructed reefs (Fig. 2C, Table S4). Adult oysters were only found in the creek shoreline and were higher on constructed reefs (8 ± 1.5 oysters/m²) compared to nonconstructed

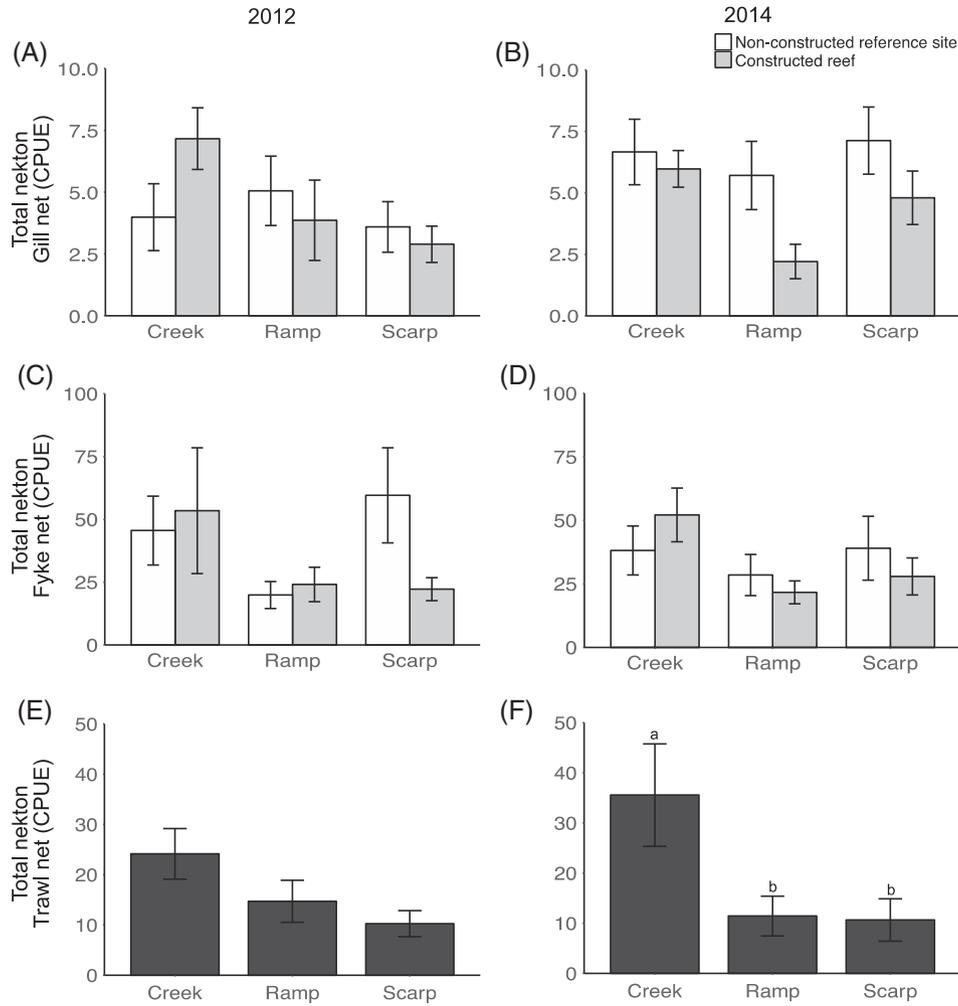


Figure 3. Average catch per unit effort (gill and fyke: 6-hour soak; trawl: 100 m/tow) of fishes and invertebrates (total nekton) in gill (A & B), fyke (C & D), and trawl (E & F) nets within nonconstructed reference sites (white bars) and constructed oyster reefs (light gray bars) across three salt marsh shoreline geomorphologies: creek, ramp, and scarp in 2012 (A, C, E) and 2014 (B, D, F). Letters represent significant differences across landscapes ($p < 0.05$). Data are shown as means \pm 1SE.

reference sites (1.3 ± 1.3 oysters/m²) (Table S4). Additionally, total oyster density (spat, juveniles, and adults) just within the creek shoreline was affected by reef type; natural reef sites were not statistically different from constructed reef sites (Tukey's honestly significant difference (HSD) post hoc test $p = 0.579$), but had almost six times more oysters than nonconstructed reference sites and 22 times more oysters than oyster removal sites (Tukey's HSD post hoc tests $p < 0.05$; Fig. 2D).

Nekton Density

There were no differences in CPUE of total nekton and piscivores between constructed reefs and nonconstructed reference sites across salt marsh geomorphologies for both the gill nets and fyke during both years sampled (Figs. 3A–D & 4A–D; Table S5). However, we did find higher blue crab gill net catch rates in the creek, compared to scarp and ramp, in 2014 (Fig. 5; Table S5). In 2014, total nekton and blue crab trawl catch rates

were higher in the creek than along ramp shorelines or scarp shorelines (Figs. 3F & 5F; Table S5). In contrast to the total nekton and blue crab trawl catches, piscivore catch rates in gill nets were highest along the scarp shoreline, followed by the ramp shoreline, and lowest along the creek shoreline in 2014 (Fig. 4B; Table S5). Within the creek shoreline, we found no difference in total nekton, piscivores, or blue crabs caught in gill nets or fyke nets across reef treatments (oyster removal, nonconstructed reference sites, constructed reef, natural reef) 2 years postrestoration (Fig. 6, Table S6, all $p > 0.114$).

Predation Rates

In both 2012 and 2014, there were more snails on average consumed along the creek shoreline compared to the ramp and scarp shorelines (Fig. 7; Table S7, both years $p < 0.01$). However, we found no difference in the number of snails consumed in the

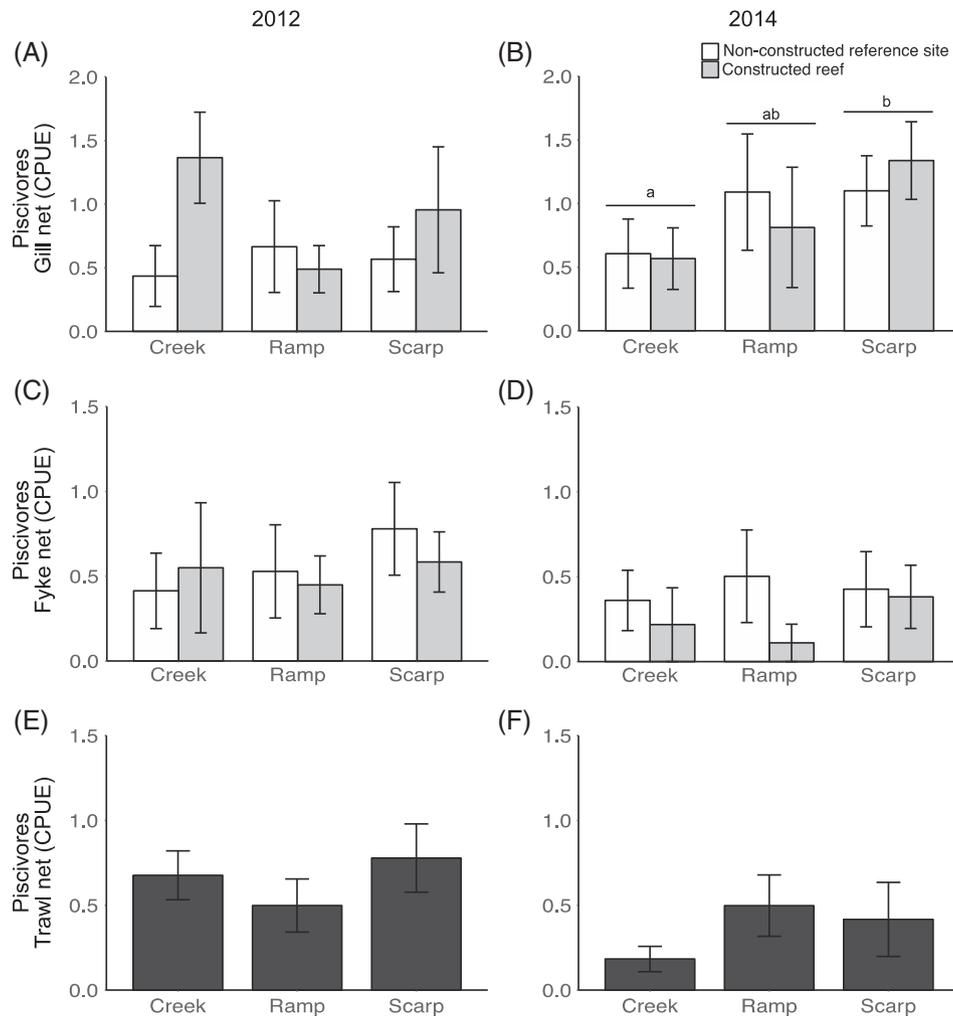


Figure 4. Average catch per unit effort (gill and fyke: 6-hour soak; trawl: 100 m/tow) of piscivorous fishes in gill (A & B), fyke (C & D), and trawl (E & F) nets within nonconstructed reference sites (white bars) and constructed oyster reefs (light gray bars) across three salt marsh shoreline geomorphologies: creek, ramp, and scarp in 2012 (A, C, E) and 2014 (B, D, F). Letters represent significant differences across landscapes ($p < 0.05$). Data are shown as means \pm 1 SE.

marsh adjacent to constructed reefs when compared to nonconstructed reference sites in both 2012 and 2014, regardless of the shoreline geomorphology (Fig. 7; Table S7, $p > 0.5$).

In 2012, snail consumption at the marsh edge was higher along the creek shoreline (Fig. 8A; Table S7). In 2014 we found a similar trend, although snail consumption was higher along the creek and the ramp, compared to the scarp shoreline (Fig. 8B; Table S7). In our 2014 study of reefs in the creek shoreline only, we observed lower consumption of snails in marsh adjacent to natural oyster reefs than oyster removal sites and constructed oyster reefs (Tukey's post hoc tests: $p > 0.04$), however, snail consumption adjacent to natural reefs was not different from reference sites (Tukey's post hoc test: $p = 0.219$; Fig. 8A). There was no effect of either stem density ($F_{[1,34]} = 0.55$, $p = 0.462$) or stem height of *Spartina alterniflora* ($F_{[1,30]} = 0.26$, $p = 0.614$) on the number of snails consumed in the creek in 2014, although there was a statistically nonsignificant trend of decreasing snail consumption with increasing stem density (Fig. 8B & 8C).

Discussion

We found that salt marsh geomorphology can influence the development and growth of constructed oyster reefs. While oyster spat densities were initially higher at constructed reefs along the ramp shoreline (compared to scarp and creek), within 2 years postconstruction, the trend reversed with the greatest adult oyster densities occurring in the creek and, to a lesser extent, scarp shorelines. Fodrie et al. (2014) also found a shift between where highest densities of spat and adult oysters were found along an aerial exposure gradient, which was associated with vertical gradients in the intensity of biofouling and predation pressure. Together, these results suggest that post-settlement factors, rather than larval supply, determine biogenic reef success in this environment (sensu Ólafsson et al. 1994). However, oyster reef success did not seem to regulate nekton density, which could suggest constructed reefs may offer similar habitat-related functions (prey availability and refuge) already present along existing salt marsh borders. Consequently, we recommend restoration practitioners

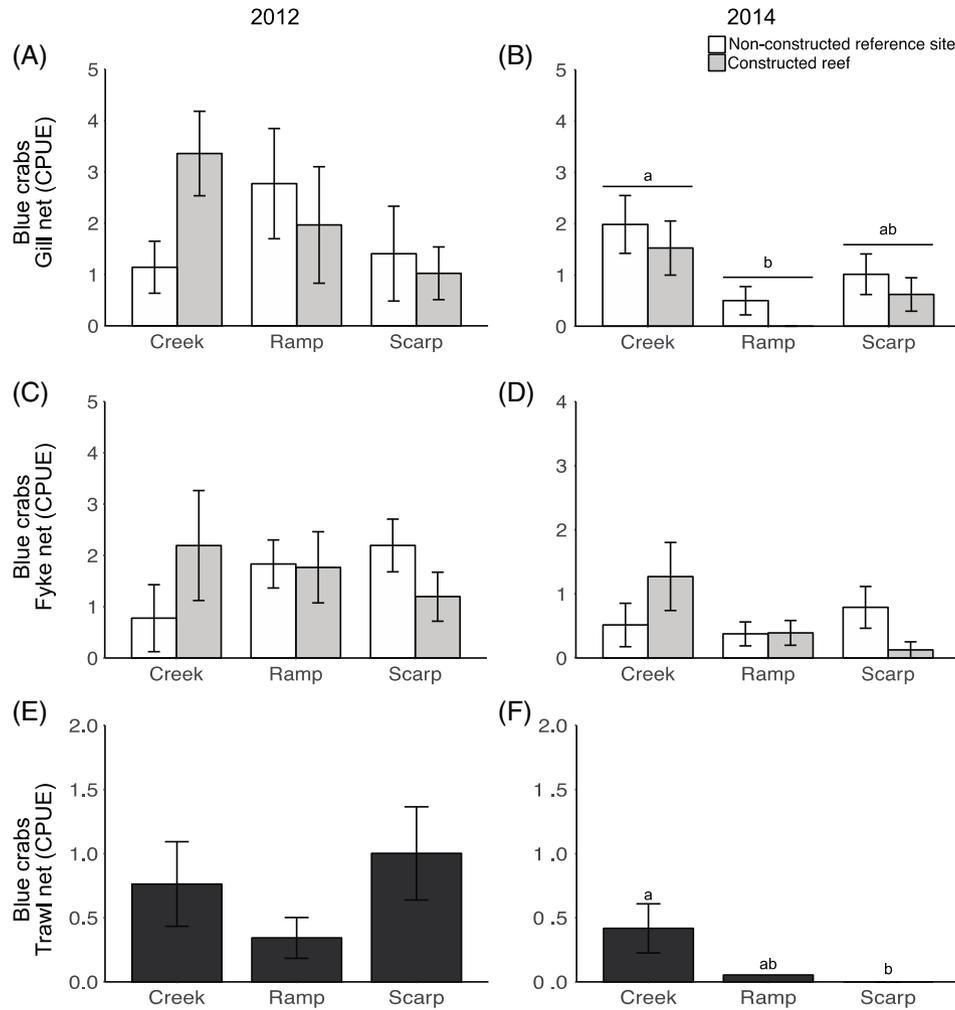


Figure 5. Average catch per unit effort (gill and fyke: 6-hour soak; trawl: 100 m/tow) of blue crabs in gill (A & B), fyke (C & D), and trawl (E & F) nets within nonconstructed reference sites (white bars) and constructed oyster reefs (light gray bars) across three salt marsh shoreline geomorphologies: creek, ramp, and scarp in 2012 (A, C, E) and 2014 (B, D, F). Letters represent differences across landscapes. Data are shown as means \pm 1 SE.

consider constructing loose cultch shell oyster reefs along gradual-slope, low-exposure shorelines, such as in tidal creeks. Along steep-sloped, high-exposure shorelines, reef restoration may require more robust substrates than loose shell.

Although the direct mechanisms controlling oyster density—and ultimately reef development—were not tested here, there are a number of factors, including wave disturbance (Scyphers et al. 2011; Theuerkauf et al. 2017), predation (Garton & Stickle 1980), and inundation time (Fodrie et al. 2014), that can affect reef development and success. Byers et al. (2015) suggested that areas of high tidal energy (e.g. water flow speeds) could drive higher accumulation of oysters and thus influence reef community dynamics. Wave energy is presumed to be high along the marsh-open estuary interface (ramp), where we initially saw the greatest spat settlement. However, we hypothesize the wave energy experienced by the ramp reefs may have been too high, with the waves dispersing the loose cultch shell from the reefs, leaving little hard substrate for settlement after 2 years. Additionally, shifting cultch shell

and wave energy may have increased mortality of the settled spat and decreased the ability for the reef to consolidate and develop. Furthermore, there is mounting evidence that oyster reefs in this shallow euhaline estuary are unlikely to be limited by larval supply, and recruitment patterns are not predictive of where adult densities will occur (Fodrie et al. 2014). Therefore, using loose cultch shell may not be the most suitable substrate in these large-fetch, high-energy environments and we suggest practitioners consider other forms of restoration, including oyster castles or other hard substrates such as sills or marsh-toe revetments in those environments.

Comparing oyster densities at constructed reefs with those at natural reefs can be one way of determining the success of oyster reef restoration. We found that oyster densities at our constructed creek reefs were comparable to natural reefs in the creek, though there was a nonsignificant trend of higher densities on natural reefs. Coen and Luckenbach (2000) found oyster densities on experimental (constructed) cultch shell reefs adjacent to marsh tidal creeks had only 17% of the oysters

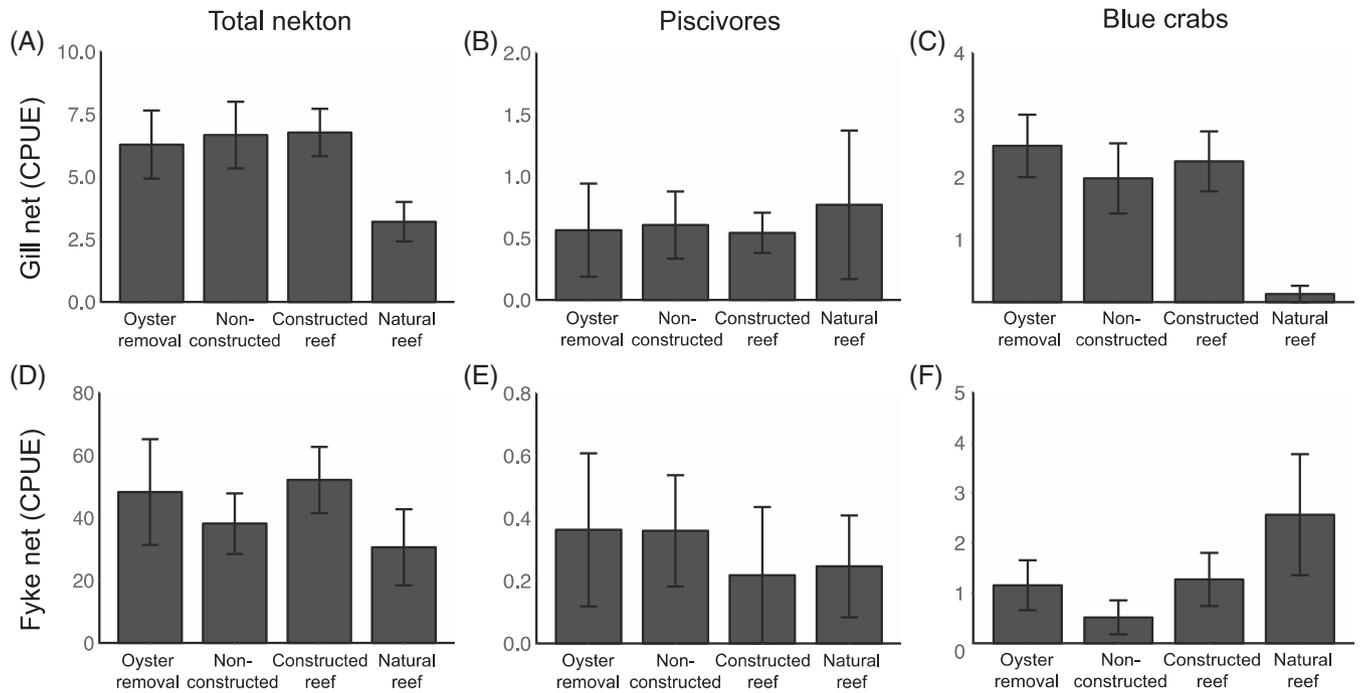


Figure 6. Average catch per unit effort (gill and fyke: 6-hour soak; trawl: 100 m/tow) of total nekton (A, D), piscivores (B, E), and blue crabs (C, F) caught in the gill nets (A–C) and fyke nets (D–F) in June–October 2014. Oyster removals, nonconstructed reference sites, and constructed reefs are taken from the salt marsh creek landscape only, while all natural reefs—regardless of location—are included.

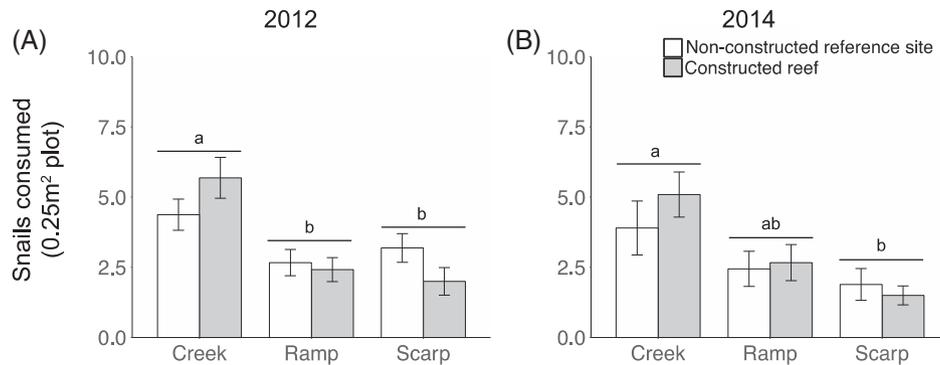


Figure 7. Predation rates (# of *Littoraria irrorata* snails consumed/0.25 m² plot) at the salt marsh edge adjacent to nonconstructed reference sites (white bars) and constructed oyster reefs (light gray bars) across three salt marsh shoreline morphologies—creek, ramp, and scarp—averaged across 2012 and 2014 sampling ($n = 10$ snails/0.25m² plot; $n = 7$ sampling periods). Letters represent differences across marsh shoreline morphology types. Data are shown as means \pm 1SE.

found on adjacent natural reefs after 3 years. We found similar oyster densities on constructed reefs compared to the natural reefs, which could indicate successful restoration. This is an important finding for future restoration, as the ecological structure and functioning of natural reefs in our area, and in many locations globally, have been dramatically reduced in coverage and biomass (Zu Ermgassen et al. 2012) due to multiple stressors such as harvest pressure, diminished water quality, climate change, and localized physical disturbances (Beck et al. 2011). Further research on healthy natural reefs to determine ecological functions, such as habitat use by nekton and trophic interactions, will provide more suitable measures for assessing oyster reef restoration.

Integrating how vertical reef height influences habitat-use dynamics and foraging rates is critical to enhancing our knowledge of how natural and constructed oyster reefs affect community structure. Although constructed reef sites did not support increased nekton densities relative to nonconstructed reference sites, we did find higher predation on periwinkle snails at oyster removal sites when compared to natural reefs along the creek shoreline. One possible explanation for this finding is that the greater height of the natural reefs may have served as a barrier and thus reduced the accessibility of transient nekton (i.e. blue crabs) to the creek shoreline where our snails were tethered (Byers et al. 2015). Community structure and important ecosystem functions such as secondary production

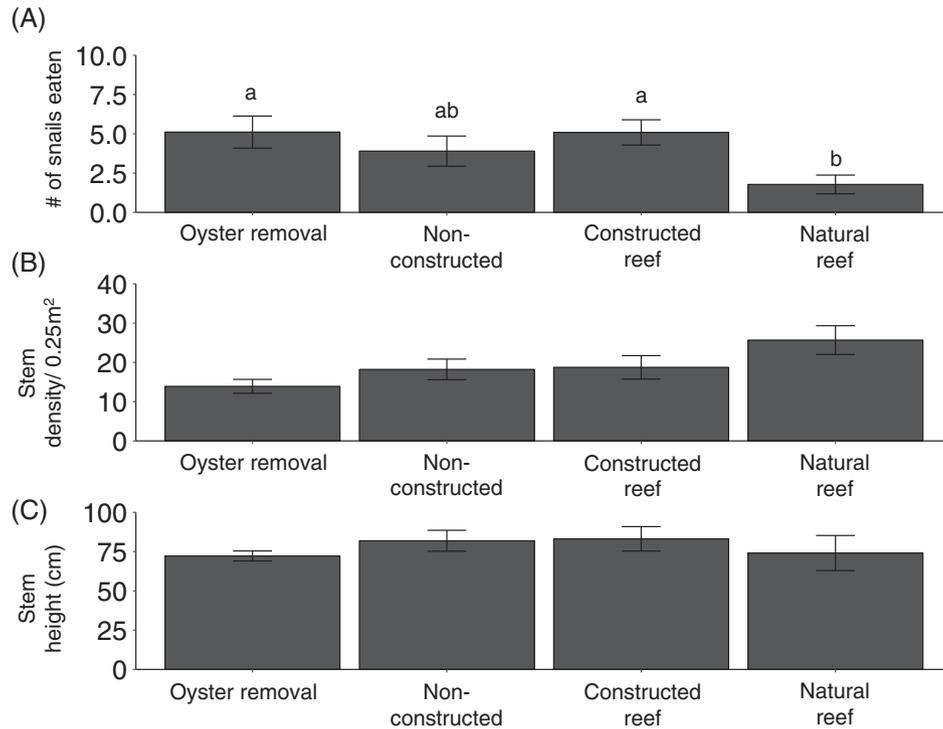


Figure 8. (A) Number of snails consumed, and *Spartina alterniflora* (B) stem density (per 0.25 m² plot), and (C) stem height (cm) where snail tethers were placed in the salt marsh creek in 2014 comparing the different reef types: oyster removal, nonconstructed reference sites, constructed oyster reef, and natural oyster reefs. Letters represent differences across reef types. Data are shown as means \pm 1 SE.

and predator–prey dynamics may depend on the physical elevation of constructed oyster reefs adjacent to salt marsh shorelines. Our reefs (natural and constructed) are shallow intertidal reefs that may have very different effects on fauna habitat use and trophic transfer compared to deep subtidal reefs found elsewhere (e.g. in Chesapeake Bay).

More work needs to be done to assess whether adding structured habitat along different salt marsh shorelines can enhance transient nekton, as the existing literature is equivocal (Grabowski et al. 2005; Geraldi et al. 2009; Scyphers et al. 2011; La Peyre et al. 2014; Gittman et al. 2016). We may not have seen a difference between the natural and constructed reefs and the nonconstructed reference and removal sites because most of the transient species we collected are habitat generalists and have a broad distribution and utilize many habitats (i.e. salt marshes, mudflats, seagrass beds, etc.). As transient fauna utilized all of the reef types (oyster removal sites, non-constructed reference sites, constructed reefs, and natural reefs) equally, the scale at which these organisms respond to environmental heterogeneity could possibly be larger than the scale of these reefs (Breitburg 1999). Furthermore, many of the transient fauna sampled utilize the salt marsh as habitat and thus adding oyster reef may have resulted in functionally redundant habitat for these species. Even if habitat is not enhanced when restoring oysters adjacent to salt marshes there are many other functions and services to consider including shoreline stabilization (Ridge et al. 2017), carbon sequestration (Fodrie et al. 2017; Ridge et al. 2017), and denitrification (Smyth et al.

2015). There may be a tradeoff between services provided by oyster reefs based on where they are located within the marsh landscape.

Restoration is increasingly implemented as a strategy to mitigate global declines in structured estuarine habitats, such as salt marshes and oyster reefs, and to increase fauna abundance. However, the ecological understanding of where and how to restore habitats has often lagged behind restoration practice. Often practitioners assume that if you build it [habitat], they [fauna] will come (Palmer et al. 1997); however, this may only be true in areas where functionally similar, structured habitat is no longer available. Similar to previous findings (Grabowski et al. 2005; Geraldi et al. 2009) we conclude that the interactive effects between mobile fauna density and oyster habitat are not guaranteed, and that the condition and proximity of other structured habitats is important in predicting the response of transient fauna to constructed oyster reefs. If the goal of oyster restoration is to increase oyster abundance in the area, then the geomorphology of the marsh shoreline (including shape and wave energy) should be considered. However, if the goal is to increase secondary production, one must consider how adding more habitat might affect species targeted for enhancement (i.e. consider if species are habitat-limited, recruitment-limited, or over-harvested, see Keller et al. 2017). Continuing investigation of the factors that influence biogenic habitat restoration and persistence will be vital to improving strategies for estuarine habitat and species conservation and restoration.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. List of species caught in gill net, fyke net, and trawl net in 2012 and 2014 across all landscapes and reef types.

Table S2. Description of data used including response species, type of net used for nekton catch, data type (if the models were run on raw, log, or log+1 transformed data), model used, including the fixed and random factors.

Table S3. Results of mixed effects models of elevations of the tops of constructed reefs and sediment surface of nonconstructed reference sites along the three salt marsh geomorphologies (creek, ramp, scarp).

Table S4. Results of mixed effects models of spat and adult oyster densities (restored oyster reefs vs. control sites) and salt marsh geomorphologies (creek, ramp, scarp).

Table S5. Effect of month, reef type, salt marsh morphology, and the interaction of reef and salt marsh morphology on total abundance (Total), piscivorous fishes (Pisc.), and blue crabs within gill, fyke, and trawl nets and by year (2012 and 2014).

Table S6. Effect of month and reef type (oyster removal, control, restored reef, and natural reef) in the salt marsh creek morphology on total abundance (Total), piscivorous fishes (Pisc.), and blue crabs within gill and fyke nets in July–October 2014.

Table S7. Effect of month, reef type, salt marsh morphology, and the interaction of reef and salt marsh morphology on *Littoraria irrorata* snails consumed/0.25m² plot at the salt marsh edge by year (2012 and 2014).

Figure S1. Bathymetric profiles showing similar nearshore gradients among ramp and scarp sites.

Figure S2. Salt marsh creek reef types including (A) oyster removal, (B) nonrestored reference site, (C) restored oyster reef, and (D) natural oyster reef located on Carrot Island, Beaufort, NC.

Figure S3. Reef surface elevations (m: NAVD88) taken with a Trimble Real-Time Kinematic (RTK) high-resolution mapping system (0.5–1.0 cm horizontal and 1.0–4.0 cm vertical resolution).

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