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Faunal assemblages associated with living shorelines and implications for high-wave energy ecosystems

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Faunal assemblages associated with living shorelines and implications for high-wave energy ecosystems

By

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This study investigated the main and interactive effects of nearshore breakwaters and marsh vegetation on faunal abundance and diversity along an eroded shoreline in Bon Secour Bay, Alabama. In summer 2016, eight replicates of three vegetation treatments plots (naturally vegetated, planted, and open) were established along a breakwater-protected and an adjacent no breakwater shoreline. After which, three methods were used to evaluate nekton quarterly from summer 2016 to summer 2018; Breder traps along the shoreline and lift nets and trawls in nearshore waters. Data were analyzed using the Shannon-Weiner diversity index and ANOVA. Results showed breakwaters supported significantly more abundant and diverse communities along the shoreline and in parallel nearshore waters than similar no breakwater sites. However, the main vegetation treatment effects were not significant. These findings suggest that living shoreline projects with nearshore breakwater support can be beneficial for fisheries enhancement in high-wave energy environments.

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CHAPTER I

INTORDUCTION

Intertidal shorelines provide many ecosystem services such as nutrient filtration (Sparks et al. 2014), erosion control (Temmerman et al. 2013), and habitat for economically important fish and invertebrate species (Beck et al. 2001). However, shoreline erosion and the associated loss of intertidal habitats is a growing issue (Scyphers et al. 2011). Around the world, at least 90% of oyster reefs (Beck et al. 2011) and 67% of salt marshes (Lotze et al. 2006) have been lost due to natural and anthropogenic factors including sea level rise (Church et al. 2013), wave energy impacts (Kroeger 2012), and coastal urbanization (Gedan et al. 2009). A recent report estimates that over 70% of Gulf of Mexico (GoM) shoreline habitats are at high risk of degradation and may not be able to provide the ecosystem services necessary to sustain healthy faunal populations (Stockdon et al. 2012).

Traditionally, hardened structures, such as bulkheads, seawalls, revetments, and riprap (i.e., large, concrete rubble), are installed to combat shoreline erosion and prevent property loss (Munsch et al. 2015; Scyphers et al. 2011). Although capable of reducing erosion, many traditional methods not only fail to account for the ecological consequences of the structures (e.g. tidal restrictions and loss of fringing vegetation; Barnett and Wang 1989; Douglass and Pickel 1999), but also typically support a lower abundance and diversity of fauna than naturally vegetated areas (Airoldi et al. 2008; Gittman et al. 2016). For instance, hardened shorelines can limit the structural complexity of benthic habitats as a result of reciprocated wave energy removing vegetation and soft sediment seaward of the barrier (Douglass and Pickel 1999; Birben et al. 2007). By reducing shelter availability and influencing spatial competition, benthic communities can become intermittent or absent (Chapman 2003).

As an alternative to hardened shorelines, living shorelines have been used to reduce erosion while maintaining a suite of ecosystem services (Bilkovic and Mitchell 2013; Hoellein et al. 2015; Sparks et al. 2014). Living shoreline projects often incorporate vegetation and other natural materials to increase shoreline stability and recover fishery habitat in degraded areas (Odum and Odum 2003; Beck et al. 2011; Sutton-Grier et al. 2015). For example, Scyphers et al. (2011), established oyster reefs and saltmarsh plants along an eroding shoreline to mitigate land recession and promote faunal recruitment. In that study, oyster reefs were shown to enhance the structural complexity of the benthic areas by providing low-wave energy protection and increased refuge for smaller nekton. Likewise, studies have shown that faunal recruitment relies heavily on available habitat. Specifically, as opposed to restrictive shoreline barriers, even small vegetation patches and open areas lacking vegetation can support a large diversity of infauna and epifauna (Jones et al. 2002; Partyka and Peterson 2008).

Subtidal and intertidal breakwaters can support living shoreline projects where wave energy and sediment deposition may impede faunal establishment (Harris 2009; Douglass et al. 2015). Numerous studies credit breakwaters with increased faunal abundance and diversity due to the subsequent habitat complexity and protection they provide (Bohnsack 1989; Meyer et al. 1997; Spalding et al. 2013). Complementarily, shoreline vegetation can augment the protection provided by breakwaters (Roland and Douglas 2005); however, few studies have assessed the main and interactive effects of breakwaters and restored shoreline vegetation at providing suitable habitat to faunal communities, particularly in high-wave energy ecosystems.

In high-wave energy ecosystems, such as large bays and beaches, shorelines are subjected to increased wave energy leading to greater erosion that can influence restoration projects. Projects in these areas may require significant planting efforts and large-scale breakwater support to reduce the effects of high-impact waves (> 1 m) on restored habitats (Dillon et al. 2015). Unfortunately, restoration projects of this magnitude are scarce due to the increased uncertainties around the project size, cost, and success (Sparks et al. 2013; Dillon et al. 2015; Sutton-Grier et al. 2015). Such uncertainties have led many coastal land managers and property owners to continue to rely on traditional methods of shoreline armoring to reduce erosion, regardless of the impacts on faunal communities.

The effects of traditional shoreline protection on faunal communities can be seen in Mobile Bay, AL and the surrounding areas. Mobile Bay represent a large estuarine system frequently subjected to intense wave energy from wind and storms (Jones 2009). Due to historic shoreline armoring, approximately 38% of the bays natural shorelines have been lost (Douglas and Pickel 1999; Jones 2009) causing habitat restrictions and considerable declines in shrimp and blue crab harvest (Valentine 2006; Perry 2007; Perry 2008). These declines are projected to continue; therefore, it is necessary to consider how living shoreline projects in high-wave energy areas might benefit faunal recruitment and restore lost intertidal habitats.

This study analyzed the effect of large-scale breakwaters on nearby faunal communities and the interactive effects of breakwaters and shoreline vegetation on nearshore communities following the implementation of a living shoreline project in Bon Secour Bay, AL. Faunal abundance, diversity, and species richness were measured seasonally for two years to assess breakwater and vegetation effects.

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Methods

Study Site

The study site, known as Swift Tract, is located along the heavily eroded shoreline of an estuarine salt marsh system in Bon Secour Bay, AL (Figure 1). In 2012, The Nature Conservancy (TNC) and Weeks Bay National Estuarine Research Reserve (WBNERR) collaborated to install 575 m of large-scale breakwaters near the Swift Tract shoreline (Figure 1) with the goal of protecting existing salt marsh stands and associated ecosystem services. The breakwaters are divided into five segments. The southernmost four are 125 m x 3.5 m, while the northernmost one is 75 m x 3.5 m. All are approximately 1.5 m tall, separated by a 12 m gap and placed 30 m offshore. Each breakwater was constructed from wire caging, filled with medium-large rocks, and topped with loose oyster shell rubble (Figure 2). Overall, the Swift Tract study site contains nearly 1.5 km of continuous shoreline to include the breakwater sites and adjacent no breakwater sites to the south (Figure 1)

To analyze the main and interactive effects of breakwaters and shoreline vegetation on faunal assemblages, the study included two breakwater treatments (i.e., breakwater and no breakwater), three vegetation treatments (i.e., planted, naturally vegetated, and open), and four seasonal treatments (i.e., fall, winter, spring, and summer). The vegetation treatment plots (2 m × 2 m; 4 m2) were established in summer 2016 using Real Time Kinematic (RTK) positioning to mark the seaward edge of each plot 0.3 m above the mean water level (MWL). Planted plots contained 64 Spartina alterniflora sods (3.8 L pots) and were planted in a checkerboard pattern to achieve 50% plant coverage (Sparks et al. 2013; Sparks et al. 2015). Natural plots (4 m2) were established in areas dominated by S. alterniflora stands and open plots were set in areas lacking vegetation coverage. The breakwater and no breakwater shorelines each contained 8 replicates of each vegetation treatment plot resulting in 48 total plots (Figure 3).

Faunal Surveys – Sampling Zones

The sampling area was subdivided into four sampling zones to include breakwater and vegetative influences on intertidal and nearshore faunal abundance, diversity, and species richness (Figure 4). Zone 1, the most shoreward sampling zone, corresponded to the 4 m^2 vegetation plots. Zone 2 began at the mean higher high water (MHHW) level and extended 0.5 m seaward of the lowest edge of the vegetation plots. Data from Zones 1 and 2 were used to compare the main and interactive influences of breakwater and vegetation plots on fauna residing near the intertidal shoreline. Zone 3 occupied the shoreward side of the breakwaters and extended 15 m towards the shoreline. Zone 4 began at the seaward side of the breakwaters and extended 15 m seaward of the structures. Data from Zones 3 and 4 were used to analyze the breakwater effects on nearshore fish and invertebrate communities. Each sampling zone used distinct sampling methods to assess faunal communities in both the breakwater and no breakwater sites.

Zone 1 – Infauna Core Sampling

Infaunal assemblages were sampled along the shoreline using sediment corers during the 2017 winter and summer sampling seasons. Prior to sampling, each 4 m^2 vegetation plot was divided into sixteen 0.25 m^2 subplots (Figure 5). Two subplots, one from the upper section of the plot (i.e., subplots 1-8) and one from the lower section of the plot (i.e., subplots 9-16), were randomly selected to be sampled for infauna during each sampling season. Exactly 96 cores were collected during the winter 2017 sampling season. The number of cores was then reduced to 1 randomly selected subplot for the summer 2017 sampling season to minimize secondary disturbance to the vegetation plots. Exactly 48 sediment cores were collected during the summer 2017 sampling season, totaling 144 cores for the study.

Sediment cores were collected using a 5 cm × 25 cm cylinder corer with mechanical and powered driver attachments. Driver type was chosen according to site-specific characteristics. Powered drills were necessary for coarse, firm, and densely rooted areas and mechanical drivers for fine, loose sediment. Post collection, each core was placed into an empty 1-gallon Ziploc® bag labeled with the collection date, plot id, and subplot location. In the field, samples were kept on ice and transferred to the WBNERR laboratory to freeze until processing.

In the laboratory, core samples were thawed and sieved through 500 µm steel mesh to separate infauna from sediment and debris. The samples were transferred into laboratory dishes, stained with Rose Bengal solution (1 mL/L of water), and refrigerated for 12 hours to allow the stain to set. After setting, the dish contents were rinsed with water through a clean 500 µm sieve and transferred to a white sorting tray for analysis. Invertebrates and tissue debris appeared bright pink post stain to allow distinction from sediment and other debris. The specimens collected were identified to the lowest possible taxonomic level following Heard and Lutz (1982) and Carpenter and Nicoletta (2002).

Zone 2 – Breder Trap Sampling

Marsh nekton were sampled using 0.6 cm thick, clear plastic Breder traps (Breder 1960; Fulling et al. 1999; Figure 6). One trap was set 0.5 m seaward of each vegetation treatment plot with the trap opening facing shoreward. A U-shaped bracket, made of 1.27 cm diameter PVC, was inserted over the trap and into the ground until resistance, supporting the top, rear, and 2 sides of the trap (Figure 6). All 48 traps were deployed at MHHW and recovered at either low tide or when the water levels had receded past the trap opening. Breder trap sampling took place once every three months for exactly 8 sampling sessions during the study.

All specimens caught in Breder traps were fixed in a 1-gallon Ziploc® bag containing 2 cups of premixed 10% neutral buffered formalin (NBF). Bags were marked using a permanent marker with appropriate labels of collection date, plot number, and sampling method. Samples remained in the NBF solution for one week at the WBNERR to ensure fixation. In the laboratory, individuals were separated by location and treatment level, identified to the lowest possible taxonomic level following Carpenter and Nicoletta (2002), and measured for length and blotted wet mass. Data were recorded manually then transferred to an electronic spreadsheet.

Zone 3 – Lift Net Sampling

Nearshore fish and invertebrate communities were compared throughout the breakwater and no breakwater sites using 2.25 m^2 lift nets with 0.6 cm mesh (Figure 7). During each sampling session, 15 nets were deployed 40 m apart, parallel to the shoreward side of breakwaters and 15 nets were set at equal distances from the shoreline in the no breakwater sites (i.e., approximately 15 m offshore) totaling 30 nets. The nets were deployed 2 hours before MHHW and retrieved 4 hours later with the falling tide. Lift net sampling began in winter 2017 and occurred every 3 months until the end of the study, totaling 6 sampling sessions.

All specimens were immediately fixed in 1-gallon Ziploc® bags containing 2 cups of premixed 10% NBF and labeled with a number identifying in which net they were caught, the date of collection, and the appropriate breakwater treatment. Samples remained in the NBF solution for 1 week at the WBNERR to ensure fixation. In the laboratory, individuals were separated by location and treatment level, identified to the lowest taxonomic level following Carpenter and Nicoletta (2002), and measured for length and blotted wet mass.

Zone 4 – Trawl Sampling

A 3.6 m trawl net with 2.54 cm mesh was used to measure faunal communities seaward of the breakwater sites and at similar distances from the shoreline in the no breakwater sites (i.e., approximately 36 m offshore). Three, 200 m long tows were conducted at a low speed, 3 m seaward of the breakwaters. Tows were parallel to the breakwaters during MHHW and were set to a 5:1 m tow-rope length to water depth ratio. This was repeated 3 times in no breakwater sites, totaling 6 trawls per sampling quarter along the entire study site. After each tow, collected specimens were placed in a 5-gallon bucket and fixed with 10% NBF solutions. In the laboratory, specimens were separated by net identification number and breakwater treatment level, individually identified following Carpenter and Nicoletta (2002), and measured for length and blotted wet mass.

Data Analyses

Faunal data were analyzed separately within each sampling zone to determine the effect of breakwaters on nearby faunal communities, and the interactive effects of breakwaters and shoreline vegetation on nearshore communities over a 2-year study. Differences in the total and mean abundance (± 1 SE), diversity, and species richness, were measured at each sampling site (i.e., Breder trap, lift net, or trawl) and compared to determine treatment effects. Faunal diversities were calculated within each sampling site for all zones using the Shannon-Weiner Diversity Index. Species populations (> 1% of the total abundance) were then categorized into benthic and nekton communities and analyzed to determine breakwater effects on different community types using the non-parametric Kruskal-Wallis H Test (Grossman and Freeman 1987).

For sampling Zones 1 and 2, the main and interactive effects of breakwaters (i.e., present or absent), vegetation plot type (i.e., planted, naturally vegetated, or open), and sampling season (i.e., fall, winter, spring, or summer) on faunal mean abundance (± 1 SE), diversity, and species richness were determined using 3-way analysis of variance (ANOVA). If significant 2-way and 3-way interactions ($p < 0.05$) were detected in addition to the main effects of breakwater presence, vegetation plot, and sampling season, then post-hoc Tukey tests were conducted to determine the factor driving significance. Because of a lack of specimens collected in Zone 1, where less than 2 individuals per plot were collected, this zone was not included in any data analyses.

For sampling Zones 3 and 4, two-way ANOVAs were used to determine the effects of breakwater treatment and sampling season on faunal mean abundance and diversity. If significant 2-way interactions ($p < 0.05$) were detected between breakwater treatments and season in either sampling zone, post-hoc Tukey tests were conducted for multiple comparisons. All data analyses and figure generations were performed on the R statistical platform, version 3.4.3

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Results

Community Compositions

From fall 2016 to summer 2018, 2,922 individual specimen representing 41 different species of vertebrates and invertebrates were collected along the Swift Tract shoreline and in its parallel waters. Of those individuals, 1,105 were vertebrates and represented 30 different species such as *Arius felis* (28.4%), *Anchoa mitchilli* (10.1%), and *Gobionellus oceanicus* (10%) (see Appendix A1). Invertebrate communities were comprised of 11 different species accounting for 1,817 specimens collected over the length of the study. *Palaemonetes* spp. (56%) had the highest abundance among the invertebrates followed by *Litopenaeus setiferus* (15.8%), *Penaeus aztecus* (10.6%), and *Callinectes sapidus* (10.1%) (see Appendix A2). Overall, the most abundant species collected were *Palaemonetes* spp. (34.9% of the total abundance), followed by *Arius felis* (10.7%), *Litopenaeus setiferus* (9.8%), *Penaeus aztecus* (6.5%), and *Callinectes sapidus* (6.3%) (see Appendix A3).

Zone 2 – Breakwater and Vegetation Treatment Plot Effects

The interactive effects of breakwater and vegetation treatment plots on faunal assemblages were assessed at each of the 48 vegetation plots. Vegetation treatment plots had no significant effect on faunal abundance or diversity, regardless of the breakwater treatment (Figure 8a and 8b; Table 1 and Table 2). However, the breakwater sites supported a significantly higher abundance of fish and invertebrate communities along the shoreline than the no breakwater sites ($p < 0.001$; Figure 9a; Table 1). Seasonally, the breakwater sites maintained significantly larger faunal communities during 2 of the 8 sampling seasons, specifically the winter 2016 ($p < 0.001$) and spring 2018 ($p = 0.04$) seasons (Figure 9a).

The breakwater sites supported a significantly higher diversity of fish and invertebrates along the shoreline compared to the no breakwater sites ($p < 0.001$; Figure 9b; Table 2). However, there were no significant breakwater and seasonal interactions on faunal diversity reported over the duration of the study (Figure 9b). Similarly, there were no significant main or interactive breakwater and seasonal effects on species richness along the shoreline (Figure 10) though significant increases in *Palaemonetes vulgaris* ($p = 0.003$), *Palaemonetes pugio* ($p < 0.001$), *Callinectes sapidus* ($p < 0.001$), *Talitridae* spp. ($p = 0.007$), *Fundulus grandis* ($p = 0.04$) and *Mugil cephalus* ($p = 0.05$) populations were detected (Table 3).

Zone 3 – Shoreward Breakwater Effects

Faunal abundance and diversity shoreward of the breakwater sites were found to be significantly higher than those in the no breakwater sites (p = < 0.001 and p = < 0.001, respectively) (Figure 11a and 11b; Table 4 and Table 5). Significant breakwater and seasonal effects were detected on faunal abundance only during the spring 2017 sampling season (Figure 11a; Table 4). Of the 1,376 specimens collected in Zone 3, 70% were caught in the breakwater sites and 30% were caught in the no breakwater sites (Table 6). Breakwater presence significantly increased the abundance of benthic fish and invertebrates such as *Gobionellus oceanicus* ($p < 0.001$), *Callinectes sapidus* ($p = 0.007$), and *Polychaeta* spp. ($p < 0.001$) assemblages (Table 7). Other species significantly influenced by breakwater presence included *Arius felis* ($p = 0.04$), *Mugil cephalus* ($p = 0.001$) and *Cynoscion arenarius* ($p = 0.03$) communities that were captured more frequently in the breakwater sites (Table 3).

Zone 4 – Seaward Breakwater Effects

Faunal concentrations seaward of the breakwater sites were not found to be significantly different from those in the no breakwater sites ($p > 0.05$; Table 8 and Table 9). The mean abundance and species diversity varied seasonally ($p = 0.001$ and $p < 0.001$, respectively; Table 8 and Table 9) and were highest during the fall sampling seasons than all other seasons (Figure 12a and 12b). In total, 736 specimens were collected in Zone 4 (46% in the breakwater sites and 54% in the no breakwater sites) with *Arius felis* comprising approximately 40% of the total abundance in both treatments (Table 10). There were no significant breakwater effects on any species seaward of the breakwater and no breakwater sites over the duration of the study (Table 3).

Discussion

Intertidal habitats are being lost at concerning rates due to natural and anthropogenic processes (Gedan et al. 2009; Waycott et al. 2009; Church et al. 2013). Restoring and conserving shoreline vegetation and establishing nearshore breakwaters may provide sufficient wave energy mitigation and increase the likelihood for more robust faunal communities (Moschella et al. 2005). For example, Toft et al. (2013) found that shoreline enhancement projects coupled with intertidal wave mitigation can increase the richness and abundance of juvenile and larval crustaceans in areas experiencing erosion. By analyzing changes in faunal communities, this study investigated the effect of nearshore breakwaters and the interactive effects of breakwaters and shoreline vegetation on intertidal communities.

Nearshore breakwater influenced faunal assemblages

All vegetation plots were frequently inhabited by marsh nekton, but the abundance and diversity of fauna were often greater in the breakwater sites than in the no breakwater sites. Increases in faunal populations, such as *Palaemonetes* spp. and *Callinectes sapidus*, in the breakwater sites could reflect a larger amount of refuge provided by complimentary breakwater and vegetation support. For example, the spatial distribution of *Callinectes sapidus*, particularly juveniles, relies on the availability of refuge as the structural complexity of intertidal habitats has been shown to augment their growth and survival (Hay 1907; Moksnes and Heck 2006; Rodrigues et al. 2019). Thus, the habitat provided by the breakwaters combined with vegetative refuge allowed for more abundant and diverse shoreline communities, which is in line with most literature describing shoreline restorations and nearshore breakwater recruitment (Weaver and Holloway 1974; Peterson et al. 2000; Kroger et al. 2012).

While the breakwater sites had an increased abundance and diversity of nearshore nekton, no statistically significant effects of vegetation treatment plots were detected on faunal communities. Plot size and shoreline sampling methods (i.e., Breder traps), spatially, may have been too small or too reclusive to adequately gauge faunal preferences between plot types (Fulling et al. 1999). Furthermore, wave energy impacts, degraded vegetation, and urban debris (e.g., plastics, wreckage, and trash) along the shoreline could have caused many nekton that use saltmarsh surfaces as habitat, such as *Gambusia affinis* and *Palaemonetes* spp., to move out of the study area (Hettler 1989).

Heavy mud and detritus accumulation in the intertidal regions were anecdotally observed as an apparent result of reduced wave energy in the breakwater sites. A significant increase in substrate dependent fish and invertebrates, such as *Gobionellus oceanicus* and *Polychaeta* spp., were documented in the breakwater sites, which could suggest habitat influenced by sediment depositions (Martin et al. 2005; Birben et al. 2007). Comparatively, these species were found in low numbers in the no breakwater sites; thus, the increased organic matter and ensuing shelter for smaller organisms could account for higher faunal populations residing in the breakwater sites (Martin et al. 2005).

Nearshore predator and scavenger abundances (i.e., *Mugil cephalus*, *Micropogonias undulatus*, and *Callinectes sapidus*) were higher in the breakwater sites than in the no breakwater sites likely due to the breakwater protection provided to vegetated habitats and subsequent trophic resources. The increased predator abundance is supported by studies such as Micheli and Peterson (1999), which showed that shoreline vegetation influenced the recruitment of smaller prey species and indirectly severed as corridors for nearshore predation. In this study, *Palaemonetes* spp., a common genus of prey that feed primarily on saltmarsh epiphytes (Morgan

1980), were significantly more abundant in the breakwater sites than in the no breakwater sites. The increased abundance of *Palaemonetes* spp. suggests that the breakwaters may have supplied enough shoreline protection to limit vegetation disturbance, recruit prey, and increase predation, which could contribute to the higher abundance of specimens found in the breakwater sites.

Faunal abundance and diversity seaward of the structures were not significantly influenced by breakwater presence, likely due to disturbances caused by reciprocated wave energy off the breakwaters. Previous research has shown that reciprocated wave energy can displace benthic communities and limit potential habitat usage to passing nekton (Seitz and Lawless 2006). Similarly, nekton populations, such as *Brevoortia patronus*, and *Litopenaeus setiferus* and *Penaeus aztecus* adults, have been shown to avoid nearshore structures and pursue migration patterns to offshore feeding grounds (Deegan 1990; O'Conner and Matlock 2005). The presence of nearshore breakwaters may interrupt migrations, which could have led to the relatively higher abundance of specimens found in the seaward no breakwater sites (approximately 36 m offshore).

Implications for high-wave energy environments

Support for breakwater installment in high-wave energy environments is often based on shoreline stabilization effects and the production of important fishery habitat (Sheridan et al. 1998; Morrison 2002; Ruiz-Jaen and Aide 2005). In this study, large-scale breakwaters enhanced faunal productivity and increased the abundance of economically important fish and invertebrates in the area. Valuable species, such as *Callinectes sapidus*, *Litopenaeus setiferus*, and *Penaeus aztecus* that were found in greater numbers shoreward of the breakwaters were likely influenced by altered wave energy, which may have improved food and shelter resources (Munsch et al. 2015). Pastor et al. (2013) showed by improving food and shelter availability, nearshore breakwaters can support valuable communities and provide essential nursery habitats to growing juveniles. However, the habitat resources provided by breakwaters always depends on the response of certain assemblages inhabiting the area (Salas et al. 2006). For example, artificial structures, including breakwaters, are often colonized by selective groups and potentially invasive species that can outcompete native ones for food and shelter resources (Chapman and Underwood 2011). Although no invasive species were detected in this study, the establishment of unique habitats in a high energy environment could pose a threat to key faunal communities (Martin et al. 2005). For this reason, altered areas such as Swift Tract must continuously be monitored for changes in faunal assemblages to account for the influxes of new species. Despite the potential for adverse recruitment, the restored intertidal shorelines with large-scale breakwaters significantly enhanced faunal abundance and diversity in the degrading environment.

Conclusion

In this study, the large-scale breakwaters increased faunal abundance and diversity, regardless of vegetation coverage and erosion along the shoreline. There were no significant effects of the vegetation treatment plots on the communities measured, suggesting similar habitat capabilities between planted, naturally vegetated, and open saltmarsh stands. While most species in the intertidal environments were not affected by vegetation treatments, the relative abundance of those species may be sensitive to habitat loss by shoreline hardening. The 575 m of large-scale breakwaters improved nursery habitats, increased trophic resources, and increased the faunal biodiversity throughout the intertidal area. Based on these results, and the known relationships between shoreline hardening and ecosystem functions, coastal land managers can increase fish and invertebrate populations by implementing large-scale breakwaters without the need for restoring shoreline vegetation.

Tables

Table 1 Summary of ANOVA results for the main and interactive effects of vegetation plot type, breakwater presence, and sampling season on the mean abundance of fauna captured in Zone 2. Table abbreviations: Df = degrees of freedom; Sum Sq = sums of squares; Mean Sq = mean squares; F = F value; Pr(>F) = p-value.

Analysis of Variance Table

	Df	Sum Sq	Mean Sq	F	Pr(>F)	
Vegetation Plot Treatment	2	79.8	39.89	1.7271	0.179377	
Breakwater Treatment	1	515.7	515.69	22.3299	3.38e-06	***
Sampling Season	7	475.4	67.92	2.9410	0.005299	**
Plot:Breakwater	2	44.4	22.20	0.9612	0.383485	
Breakwater:Season	7	368.4	52.62	2.2787	0.028012	*
Plot:Season	14	314.9	22.49	0.9738	0.434236	
Breakwater:Plot:Season	14	329.2	23.52	1.0183	0.434236	
Residuals	336	7759.6	23.09			

Asterisks denotes significance.

Table 2 Summary of ANOVA results for the main and interactive effects of vegetation plot type, breakwater presence, and sampling season on the diversity of fauna captured in Zone 2. Table abbreviations: Df = degrees of freedom; Sum Sq = sums of squares; Mean Sq = mean squares; F = F value; Pr(>F) = p-value.

Analysis of Variance Table

	Df	Sum Sq	Mean Sq	F	Pr(>F)	
Vegetation Plot Treatment	2	0.083	0.04172	0.4042	0.6678	
Breakwater Treatment	1	2.397	2.39692	23.2218	2.189e-06	***
Sampling Season	7	4.069	0.58126	5.6314	3.693e-06	***
Plot:Breakwater	2	0.012	0.00615	0.0596	0.9422	
Breakwater:Season	7	0.874	0.06240	0.6046	0.8612	
Plot:Season	14	0.750	0.10720	1.0386	0.4037	
Breakwater:Plot:Season	14	1.441	0.10292	0.9971	0.4557	
Residuals	336	34.681	0.10322			

Asterisks denotes significance.

Table 3 Breakwater effect on each species collected over the duration of the study by collection method. Reported p-values following Kruskal-Wallace H Test.

Total Species	**Breder Trap**	**Lift Net**	**Trawl**
Palaemonetes vulgaris	0.003	0.4	
Palaemonetes pugio	2.9e-06	0.02	
Arius felis		0.04	0.7
Litopenaeus setiferus	0.4	0.9	0.2
Farfantepenaeus aztecus	0.07	0.4	0.7
Callinectes sapidus	0.0005	0.007	0.3
Anchoa mitchilli	0.3	0.4	
Gobionellus oceanicus	0.2	5.6e-05	
Micropogonias undulatus	0.2	0.07	0.7
Gambusia affinis	0.2		
Leiostomus xanthurus	0.2		0.4
Mugil cephalus	0.05	0.001	
Polychaeta spp.	0.3	0.0002	
Talitridae spp.	0.007		
Bagre marinus	0.3		0.3
Cynoscion arenarius	1	0.03	0.8
Brevoortia patronus	0.3		0.3
Sphoeroides parvus			0.8
Anchoa hepsetus	0.3		0.4
Citharchthys spilopterus	0.2	1	0.9
Trinectes maculatus			0.6
Clibanarius vittatus		0.8	
Cynoscion nebulosus	1		0.7
Eruytium limosum	1	1	0.2
Lagodon rhomboides		0.3	0.4
Menticirrhus littoralis			0.4
Panopeus herbstii	1	0.3	
Fundulus grandis	0.04		3
Chloroscombrus chrysurus		0.3	
Dasyatis sabina			1
Chaetodipterus faber	0.6		
Gobiosoma bosc		0.08	
Symphurus civitatium	0.3		0.2
Prionotus tribulus			0.2
Anguilla rostrata	0.3		
Etropus crossotus			0.3
Menticirrhus americanus		0.3	
Oligoplites saurus		0.3	
Paralichthys lethostigma		0.3	
Selene vomer			0.3
Sesarma cinereum	0.3		

Table 4 Summary of ANOVA results for the main and interactive effects of breakwater presence and sampling season on the mean abundance of fauna captured in Zone 3. Table abbreviations: Df = degrees of freedom; Sum Sq = sums of squares; Mean Sq = mean squares; F = F value; Pr(>F) = p-value.

Analysis of Variance Table

	Df	Sum Sq	Mean Sq	F	Pr(>F)	
Breakwater Treatment	1	1608.0	1608.0	34.842	1.925e-08	***
Sampling Season	5	18566.8	3713.4	80.459	2.2e-16	***
Breakwater:Season	5	5767.4	1153.5	24.993	2.2e-16	***
Residuals	168	7753.6	46.2			

Asterisks denotes significance.

Table 5 Summary of ANOVA results for the main and interactive effects of breakwater presence and sampling season on the diversity of fauna captured in Zone 3. Table abbreviations: Df = degrees of freedom; Sum Sq = sums of squares; Mean Sq = mean squares; F = F value; Pr(>F) = p-value.

Analysis of Variance Table						
	Df	Sum Sq	Mean Sq	F	Pr(>F)	
Breakwater Treatment	1	1.7900	1.78997	12.8006	0.000453	***
Sampling Season	5	12.2305	2.44610	17.4927	6.297e-14	***
Breakwater:Season	5	2.6430	0.52878	3.7814	0.002285	***
Residuals	168	23.4924	0.13984			

Asterisks denotes significance.

Table 6 Percentage of species collected shoreward of the breakwater sites and in the no breakwater sites (Zone 3).

Lift Net Species	**Breakwater**	**No Breakwater**
Palaemonetes vulgaris	35.21%	31.03%
Palaemonetes pugio	17.24%	15.51%
Anchoa mitchilli	4.49%	16.23%
Litopenaeus setiferus	5.02%	13.37%
Gobionellus oceanicus	10.14%	
Penaeus aztecus	3.76%	12.41%
Callinectes sapidus	4.70%	3.34%
Mugil cephalus	5.75%	
Polychaeta spp.	5.43%	
Micropogonias undulatus	2.93%	3.10%
Arius felis	2.51%	1.43%
Clibanarius vittatus	0.73%	1.67%
Cynoscion arenarius	1.15%	0.24%
Eruytium limosum	0.21%	0.48%
Gobiosoma bosc	0.31%	
Panopeus herbstii	0.31%	
Chloroscombrus chrysurus		0.24%
Citharchthys spilopterus		0.24%
Lagodon rhomboides		0.24%
Menticirrhus americanus		0.24%
Oligoplites saurus		0.24%
Paralichthys lethostigma	0.10%	
Total	70%	30%

Table 7 Species populations (> 1% of the total abundance) categorized into benthic and nekton communities to determine breakwater significance on different species types.

	Scientific name	Common name	p-value	Pooled p-value
Nekton	*Palaemonetes vulgaris*	Marsh grass shrimp	0.01	0.0002
	Palaemonetes pugio	Daggerblade grass shrimp	5.41e-07	
	Arius felis	Hardhead catfish	0.16	
	Litopenaeus setiferus	White shrimp	0.99	
	Farfantepenaeus aztecus	Brown shrimp	0.82	
	Anchoa mitchilli	Bay anchovy	0.53	
	Micropogonias undulatus	Atlantic croaker	0.04	
	Gambusia affinis	Mosquitofish	0.24	
	Leiostomus xanthurus	Spot	0.97	
	Mugil cephalus	Flathead grey mullet	0.0004	
	Bagre marinus	Gafftopsail catfish	0.49	
	Cynoscion arenarius	Sand weakfish	0.14	
	Brevoortia patronus	Gulf menhaden	0.17	
Benthic	*Callinectes sapidus*	Blue crab	4.38e-06	1.168e-09
	Gobionellus oceanicus	Highfin goby	0.0001	
	Polychaeta spp.	Polychaete worm	0.0002	
*	*Talitridae* spp.	Marsh hoppers	0.01	0.01

Asterisk denotes terrestrial amphipod captured in vegetation plots.

Table 8 Summary of ANOVA results for the main and interactive effects of breakwater presence and sampling season on the mean abundance of fauna captured in Zone 4. Table abbreviations: Df = degrees of freedom; Sum Sq = sums of squares; Mean Sq = mean squares; F = F value; Pr(>F) = p-value.

Analysis of Variance Table

	Df	Sum Sq	Mean Sq	F	Pr(>F)	
Breakwater Treatment	1	69.4	69.43	0.3234	0.57411	
Sampling Season	6	6523.1	1087.19	5.064	0.00125	**
Breakwater:Season	6	682.6	113.76	0.5299	0.78080	
Residuals	28	6011.3	214.69			

Asterisks denotes significance.

Table 9 Summary of ANOVA results for the main and interactive effects of breakwater presence and sampling season on the diversity of fauna captured in Zone 4. Table abbreviations: Df = degrees of freedom; Sum Sq = sums of squares; Mean Sq = mean squares; F = F value; Pr(>F) = p-value.

Analysis of Variance Table

	Df	Sum Sq	Mean Sq	F	Pr(>F)	
Breakwater Treatment	1	0.2382	0.23817	1.9086	0.1780	
Sampling Season	6	14.6826	2.44710	19.6108	7.599e-09	***
Breakwater:Season	6	0.6376	0.10627	0.8516	0.5417	
Residuals	28	3.4939	0.12478			

Asterisks denotes significance.

Table 10 Percentage of species collected seaward of the breakwater complex and in the no breakwater sites (Zone 4).

Trawl Species	**Breakwater**	**No Breakwater**
Arius felis	40.47%	36.96%
Leiostomus xanthurus	12.32%	7.09%
Penaeus aztecus	8.21%	9.11%
Litopenaeus setiferus	2.05%	11.14%
Bagre marinus	5.28%	5.32%
Brevoortia patronus	0.29%	8.10%
Micropogonias undulatus	4.69%	3.29%
Callinectes sapidus	4.11%	3.04%
Sphoeroides parvus	3.52%	3.54%
Cynoscion arenarius	4.99%	1.27%
Anchoa hepsetus	4.40%	1.27%
Citharchthys spilopterus	2.05%	2.53%
Trinectes maculatus	2.35%	2.28%
Cynoscion nebulosus	1.76%	1.27%
Lagodon rhomboides	0.59%	1.01%
Menticirrhus littoralis	0.59%	1.01%
Dasyatis sabina	0.59%	0.51%
Chloroscombrus chrysurus	0.29%	0.51%
Eruytium limosum	0.59%	
Prionotus tribulus		0.51%
Symphurus civitatium	0.59%	
Etropus crossotus		0.25%
Selene vomer	0.29%	
Total	46%	54%

Figures

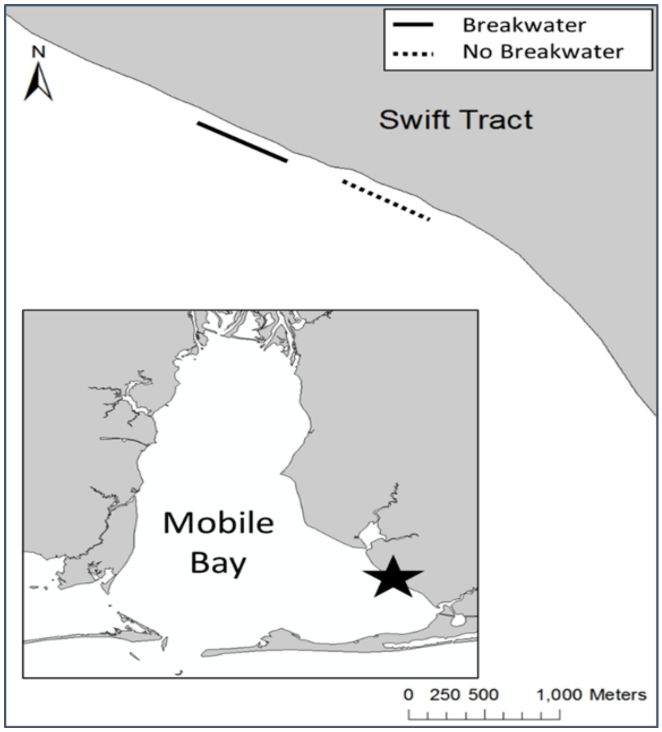

Figure 1 Swift Tract shoreline including the 575 m breakwater sites and adjacent no breakwater sites (approximately 1.5 km).

Figure 2 Living shoreline breakwater during MHW tide at Swift Tract in Bon Secour Bay, Alabama, showing wave reducing effects.

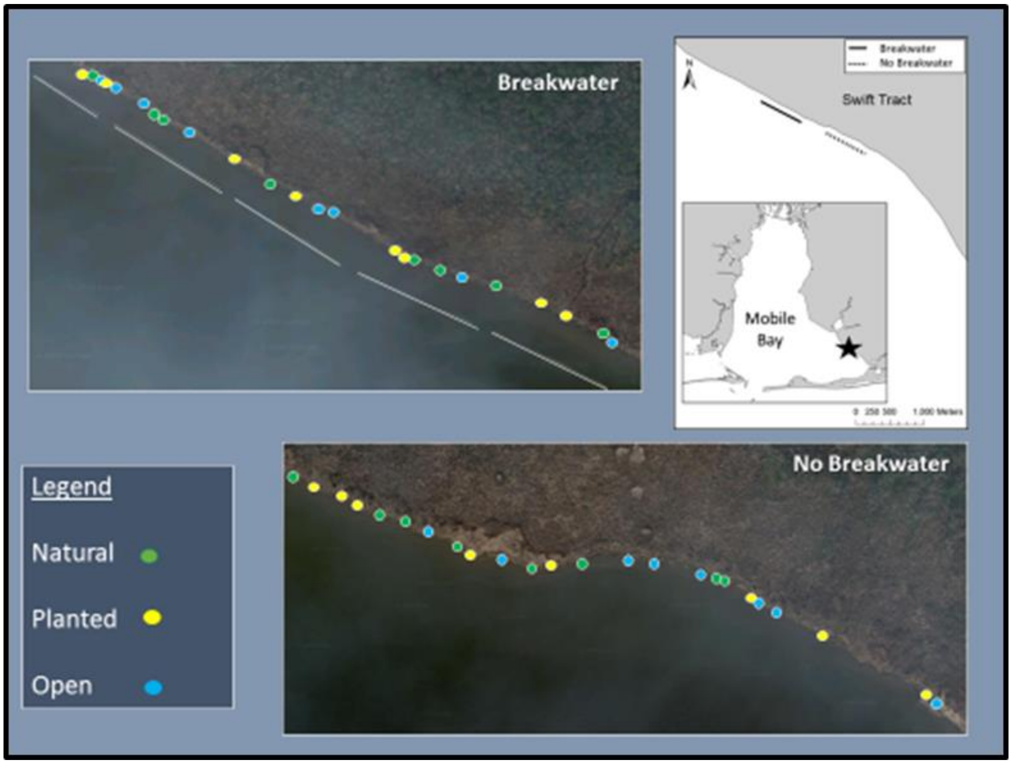

Figure 3 Map of the vegetation treatment plots along the Swift Tract study site.

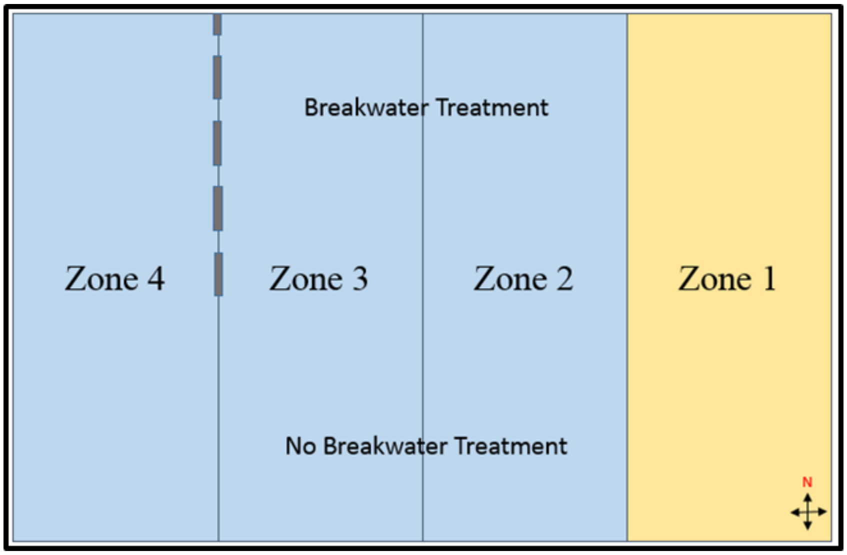

Figure 4 Faunal sampling zones relative to breakwater positions and the shoreline.

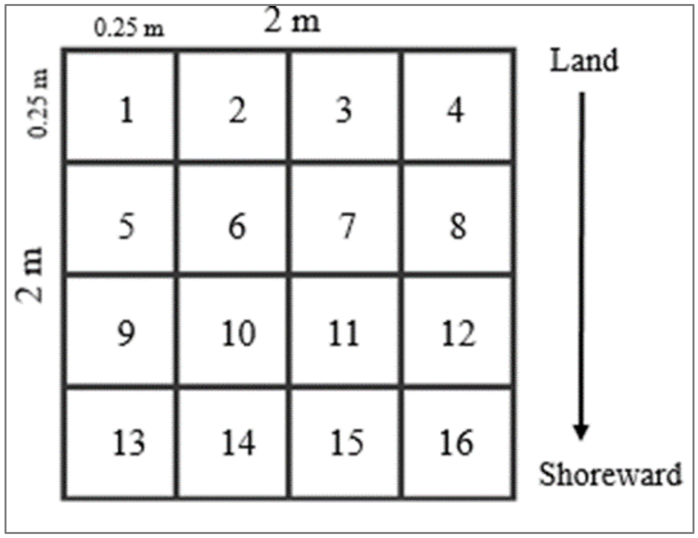

Figure 5 Experimental plot subset for core sampling.

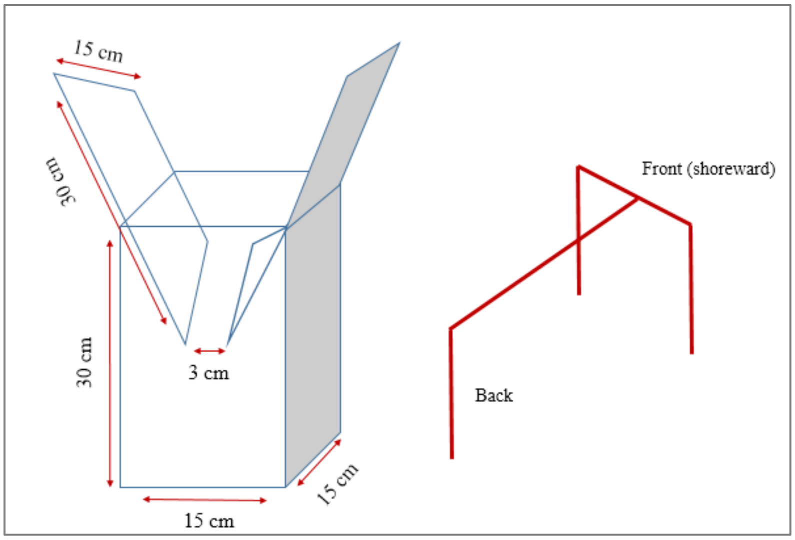

Figure 6	Breder trap dimensions with set wings and support bracket illustration.

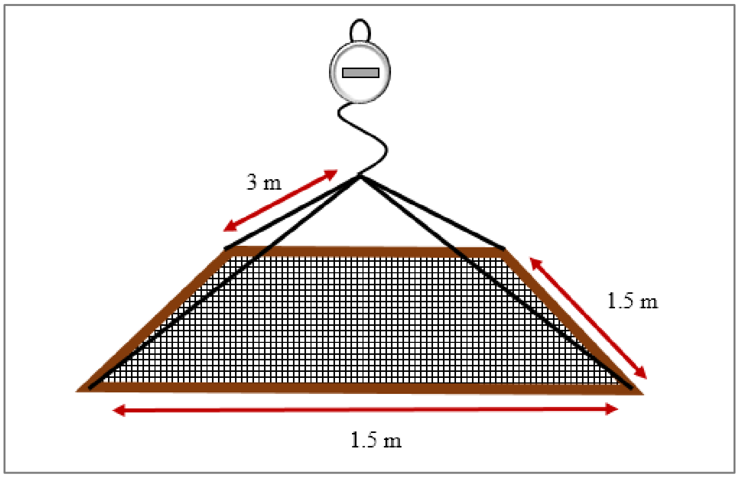

Figure 7 Lift nets dimensions; 2.25 m2 traps with 0.6 cm mesh netting.

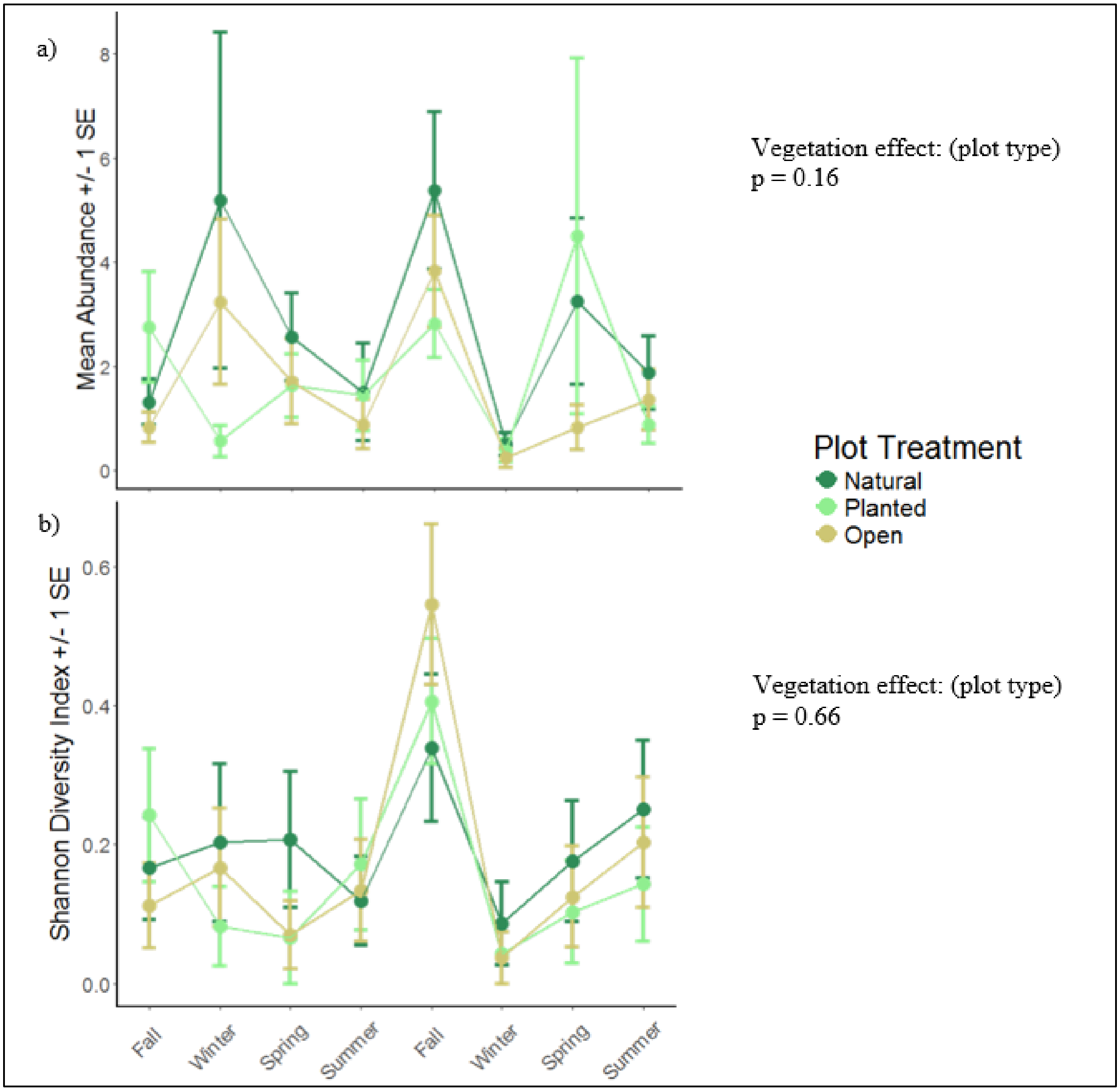

Figure 8 a) Mean abundance (± 1 SE) and b) species diversity (± 1 SE) of fauna captured in the planted, natural, and open plot treatments (Zone 2) from fall 2016 to summer 2018. P-value equals the vegetation treatment plot effect on faunal response.

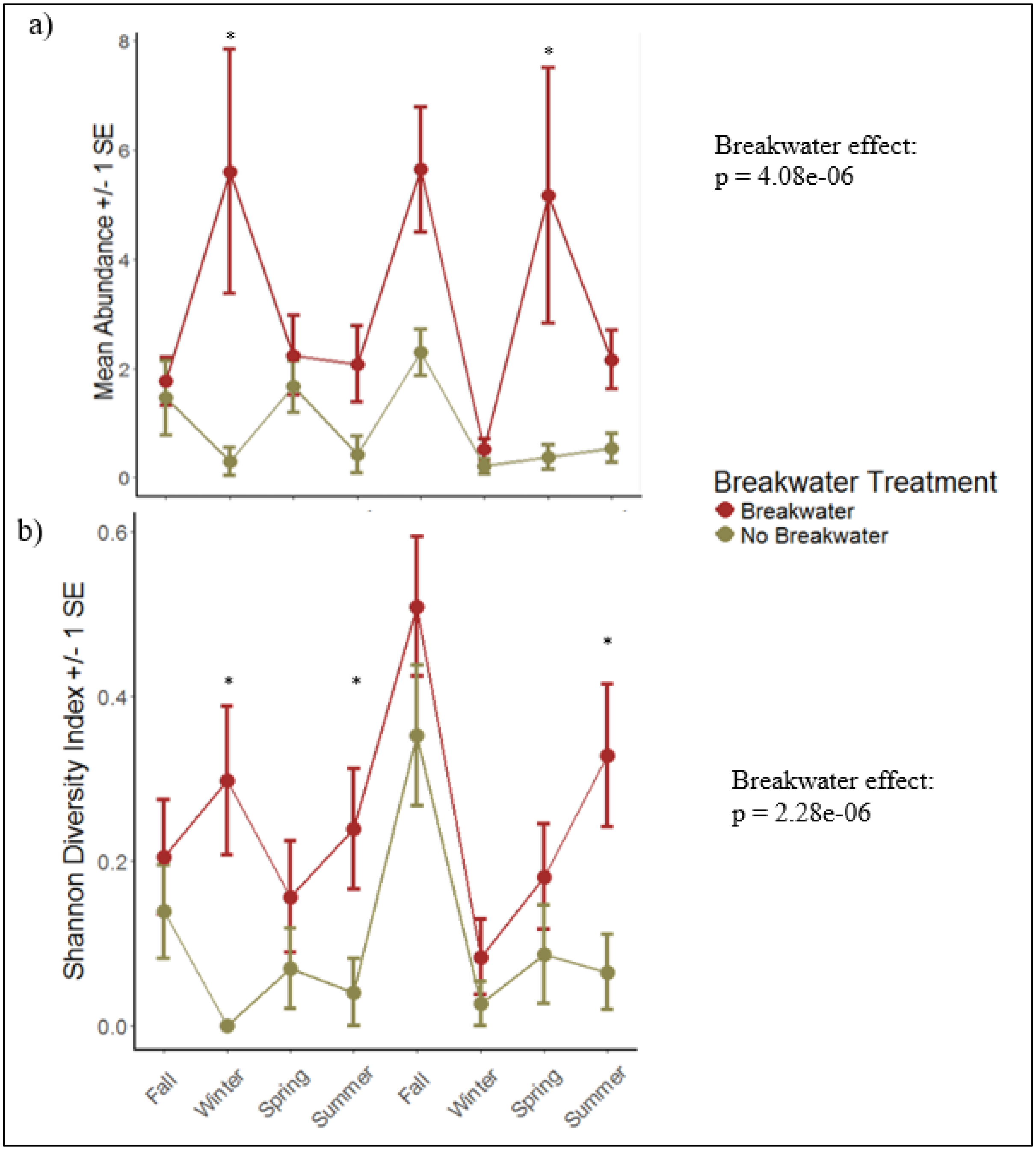

Figure 9 a) Mean abundance (± 1 SE) and b) species diversity (± 1 SE) of fauna captured in the breakwater sites and no breakwater sites along the shoreline (Zone 2) from fall 2016 to summer 2018. P-value equals the breakwater effect on faunal response. Asterisk denotes significant breakwater effects ($p < 0.05$).

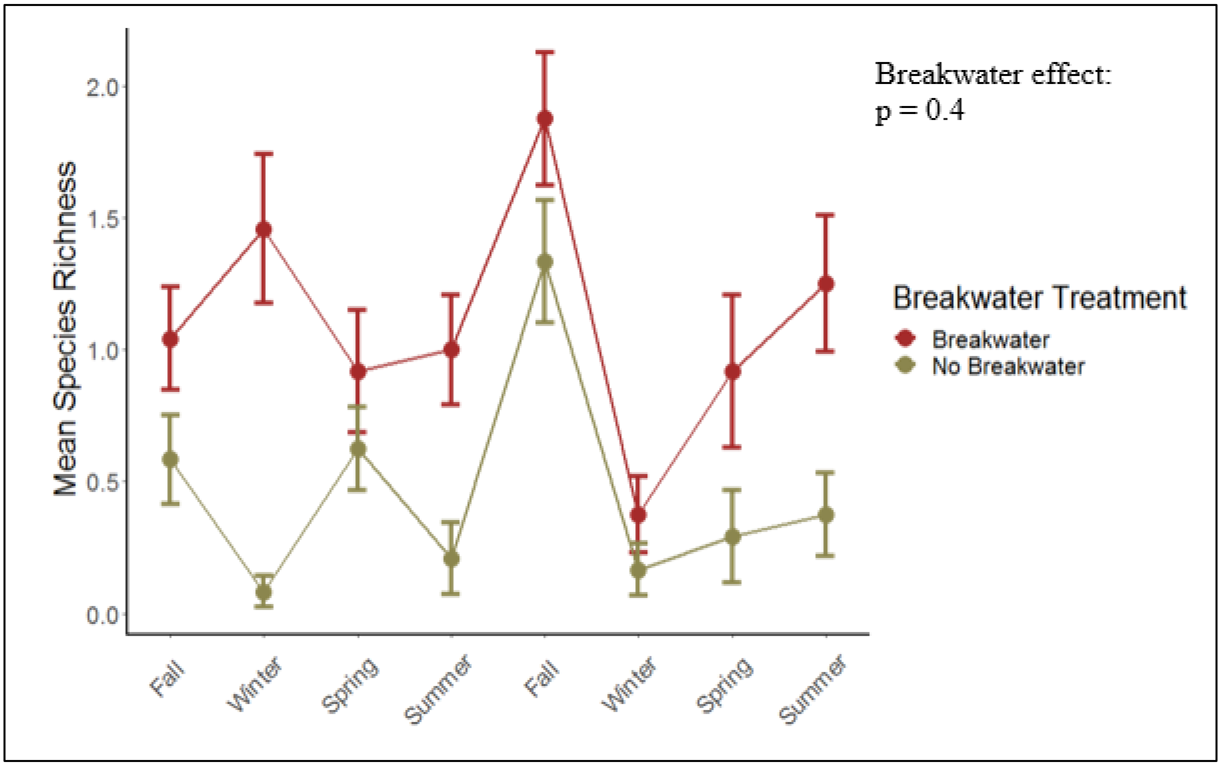

Figure 10 Mean species richness (± 1 SE) of fauna captured in the breakwater sites and no breakwater sites along the shoreline (Zone 2) from fall 2016 to summer 2018. P-value equals the breakwater effect on faunal response.

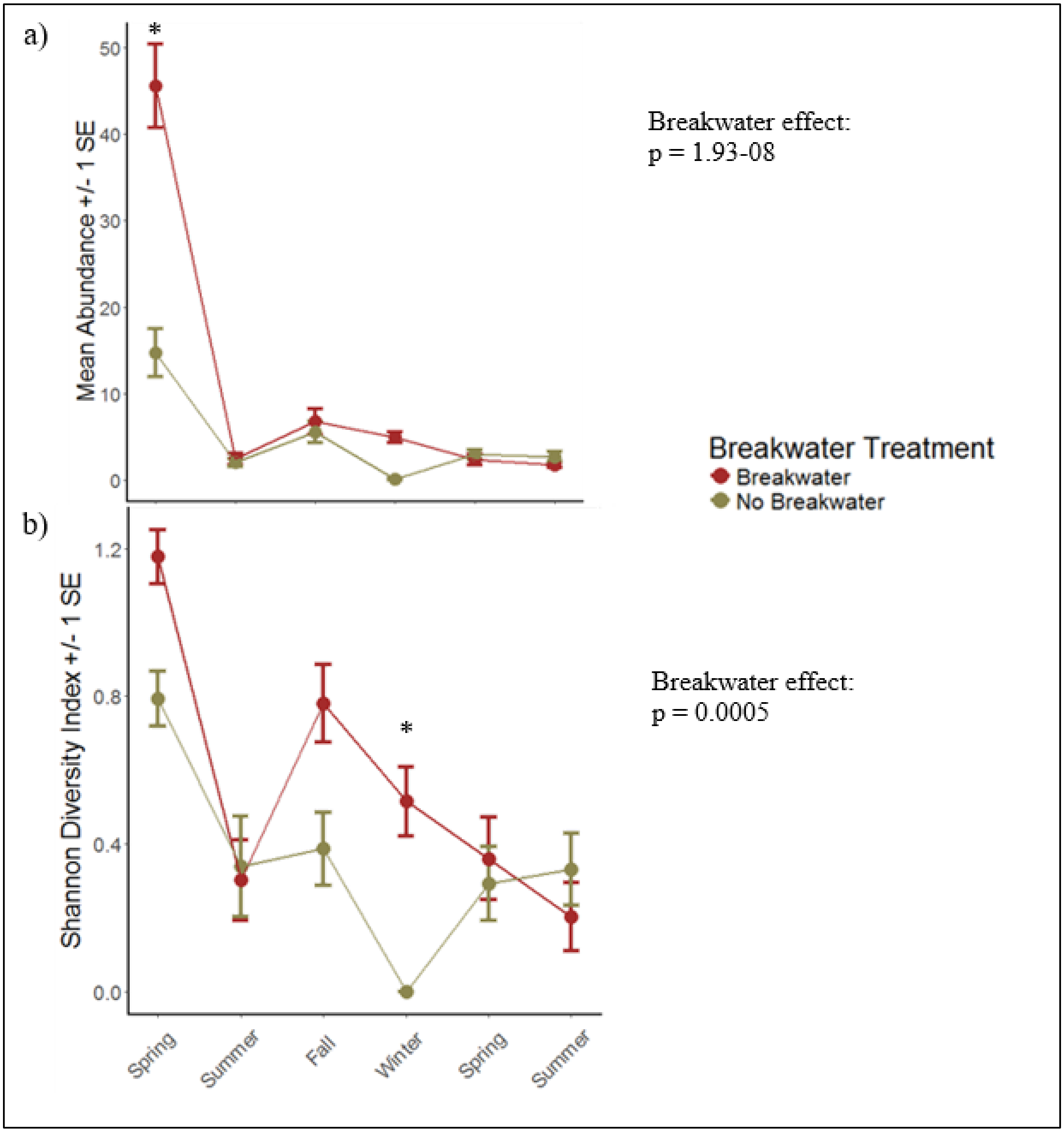

Figure 11 a) Mean abundance (± 1 SE) and b) species diversity (± 1 SE) of nearshore fauna captured shoreward of the breakwater sites and no breakwater sites (Zone 3) from spring 2017 to summer 2018. P-value equals the breakwater effect on faunal response. Asterisk denotes significant ($p < 0.05$) seasonal sampling effects.

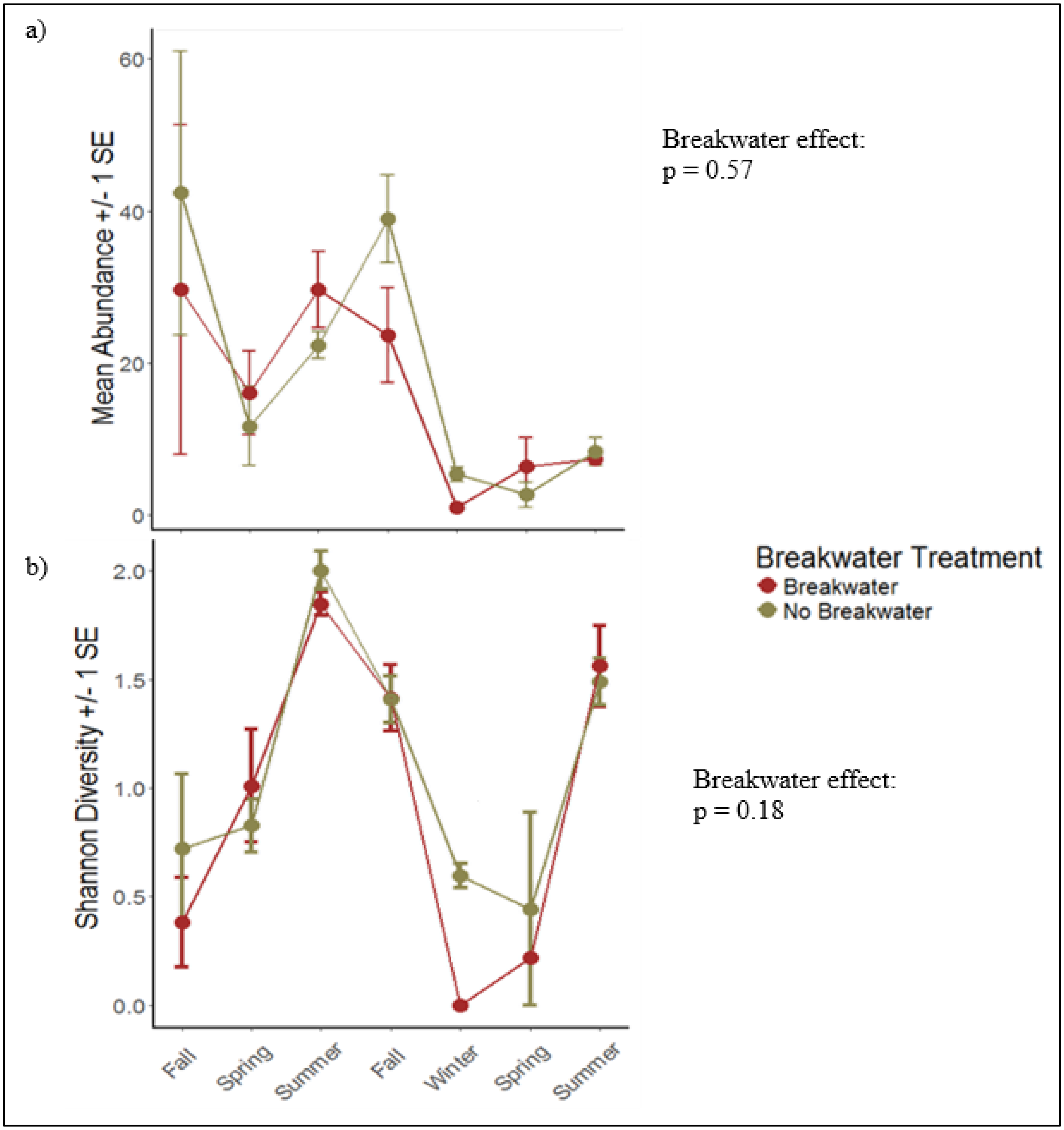

Figure 12 a) Mean abundance (± 1 SE) and b) species diversity (± 1 SE) of fauna captured seaward of the breakwater sites and no breakwater sites (Zone 4) from fall 2016 to summer 2018. P-value equals the breakwater effect on faunal response. Asterisk denotes significant ($p < 0.05$) seasonal sampling effects.

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APPENDIX

ADDITIONAL TABLES

Table A1 Total abundance and percent abundance of vertebrate specimens captured through the duration of the study

Total Vertebrate Species	Abundance	% Abundance
Arius felis	314	28.42%
Anchoa mitchilli	112	10.14%
Gobionellus oceanicus	110	9.95%
Micropogonias undulatus	97	8.78%
Gambusia affinis	80	7.24%
Leiostomus xanthurus	72	6.52%
Mugil cephalus	70	6.33%
Bagre marinus	40	3.62%
Cynoscion arenarius	36	3.26%
Brevoortia patronus	34	3.08%
Sphoeroides parvus	26	2.35%
Anchoa hepsetus	21	1.90%
Citharchthys spilopterus	20	1.81%
Trinectes maculatus	17	1.54%
Cynoscion nebulosus	13	1.18%
Lagodon rhomboides	7	0.63%
Menticirrhus littoralis	6	0.54%
Fundulus grandis	5	0.45%
Chloroscombrus chrysurus	4	0.36%
Dasyatis sabina	4	0.36%
Chaetodipterus faber	3	0.27%
Gobiosoma bosc	3	0.27%
Symphurus civitatium	3	0.27%
Prionotus tribulus	2	0.18%
Anguilla rostrata	1	0.09%
Etropus crossotus	1	0.09%
Menticirrhus americanus	1	0.09%
Oligoplites saurus	1	0.09%
Paralichthys lethostigma	1	0.09%
Selene vomer	1	0.09%
Total	1105	100.00%

Table A2 Total abundance and percent abundance of invertebrate specimens captured through the duration of the study

Total Invertebrate Species	**Abundance**	**% Abundance**
Palaemonetes vulgaris	602	33.13%
Palaemonetes pugio	416	22.89%
Litopenaeus setiferus	287	15.80%
Penaeus aztecus	192	10.57%
Callinectes sapidus	185	10.18%
Polychaete spp.	53	2.92%
Talitridae spp.	52	2.86%
Clibanarius vittatus	14	0.77%
Eruytium limosum	9	0.50%
Panopeus herbstii	6	0.33%
Sesarma cinereum	1	0.06%
Total	1817	100.00%

Table A3 Breakwater and no breakwater comparisons, total abundance, and percent abundance of all species captured throughout the duration of the study.

Total Species	Breakwater	No Breakwater	% Abundance
Palaemonetes vulgaris	501 (25.15%)	164 (16.52%)	20.60%
Palaemonetes pugio	329 (16.52%)	87 (8.76%)	14.24%
Arius felis	162 (8.13%)	152 (15.31%)	10.75%
Litopenaeus setiferus	148 (7.43%)	139 (14.00%)	9.82%
Penaeus aztecus	88 (4.42%)	104 (10.47%)	6.57%
Callinectes sapidus	131 (6.58%)	54 (5.44%)	6.33%
Anchoa mitchilli	44 (2.21%)	68 (6.85%)	3.83%
Gobionellus oceanicus	107 (5.37%)	3 (0.30%)	3.76%
Micropogonias undulatus	69 (3.46%)	28 (2.82%)	3.32%
Gambusia affinis	70 (3.51%)	10 (1.01%)	2.74%
Leiostomus xanthurus	42 (2.11%)	30 (3.02%)	2.46%
Mugil cephalus	66 (3.31%)	4 (0.40%)	2.40%
Polychaete spp.	53 (2.66%)		1.81%
Talitridae spp.	42 (2.11%)	10 (1.01%)	1.78%
Bagre marinus	19 (0.95%)	21 (2.11%)	1.37%
Cynoscion arenarius	28 (1.41%)	7 (0.70%)	1.23%
Brevoortia patronus	1 (0.05%)	33 (3.32%)	1.16%
Sphoeroides parvus	12 (0.60%)	14 (1.41%)	0.89%
Anchoa hepsetus	16 (0.80%)	5 (0.50%)	0.72%
Citharchthys spilopterus	9 (0.45%)	11 (1.11%)	0.68%
Trinectes maculatus	8 (0.40%)	9 (0.91%)	0.58%
Clibanarius vittatus	7 (0.35%)	7 (0.70%)	0.48%
Cynoscion nebulosus	8 (0.40%)	6 (0.60%)	0.44%
Eruytium limosum	6 (0.30%)	3 (0.30%)	0.31%
Lagodon rhomboides	2 (0.10%)	5 (0.50%)	0.24%
Menticirrhus littoralis	2 (0.10%)	4 (0.40%)	0.21%
Panopeus herbstii	4 (0.20%)	2 (0.20%)	0.21%
Fundulus grandis	5 (0.25%)		0.17%
Chloroscombrus chrysurus	1 (0.05%)	3 (0.30%)	0.14%
Dasyatis sabina	2 (0.10%)	2 (0.20%)	0.14%
Chaetodipterus faber	2 (0.10%)	1 (0.10%)	0.10%
Gobiosoma bosc	3 (0.15%)		0.10%
Symphurus civitatium	3 (0.15%)		0.10%
Prionotus tribulus		2 (0.20%)	0.07%
Anguilla rostrata		1 (0.10%)	0.03%
Etropus crossotus		1 (0.10%)	0.03%
Menticirrhus americanus		1 (0.10%)	0.03%
Oligoplites saurus		1 (0.10%)	0.03%
Paralichthys lethostigma	1 (0.05%)		0.03%
Selene vomer	1 (0.05%)		0.03%
Sesarma cinereum		1 (0.10%)	0.03%
Total	1929 (66%)	993 (34%)	100.00%

Parentheses denotes breakwater and no breakwater percent abundance.