Habitat assessment of a restored oyster reef in South Texas.

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Highlights:

- An oyster reef complex consisting of reef mounds and corridors was constructed.
- High oyster densities were observed at the restored reef complex.
- Nekton recruited to the restored complex quickly after construction.
- Nekton use of between-reef corridors suggest these are important design elements.
- The complex reef design likely contributed to the high level of project success.

Abstract

Oyster reefs are important foundational habitats and provide many ecosystem services. A century of habitat degradation has resulted in substantial reductions in the extent and quality of oyster reefs in many estuaries, thus spurring restoration efforts. In this study, a 1.5 ha oyster reef complex was constructed in Copano Bay, Texas to restore habitat for oysters and associated fauna. Oysters and resident and transient fishes and crustaceans were monitored at the restored reef as well as at nearby natural oyster reef and unrestored bottom (i.e., dense mud with shell hash) habitats for two years following reef construction. The restored reef had substantial oyster recruitment and growth, with oyster abundance and size comparable to nearby habitats within the first year. Resident and transient fauna communities recruited to the restored reef within six months post-construction, and abundance and diversity were comparable to nearby habitats. Significant changes observed in oyster densities between the first and second year post-restoration demonstrate the importance of monitoring over multiple years to capture multiple recruitment cycles and growth to market size. Nekton densities did not change significantly after the first year, but changes in community assemblages were observed through the end of the study. The high densities of oysters and resident nekton relative to other studies indicate that this restoration project was successful in restoring suitable habitat. The design of the reef complex, consisting of relatively high-relief reef mounds and deeper corridors, likely contributed to the relatively high oyster and nekton densities observed in this study. Overall, the restored reef in this study showed tremendous near-term success in providing important ecological functions associated with habitat provision and oyster production.

1. Introduction

Marine ecosystems have experienced critical levels of degradation over the past century through various natural and anthropogenic stressors (e.g., climate change, coastal development, increased nutrient loading, extraction of natural resources) (Aubrey 1993; Montagna et al. 2002; Stegeman & Solow 2002; Lotze et al. 2006; Bricker et al. 2008). Seagrass and mangrove habitats have experienced global losses of about 30% from historic estimates; salt marsh habitats have declined by 50% world-wide (Jackson 2008; Barbier et al. 2011). Oyster reefs are the most imperiled marine habitat on Earth, exhibiting estimated losses of 85% from historic abundances (Jackson 2008; Beck et al. 2011; zu Ermgassen et al. 2012). Habitat degradation and loss is of concern because of associated losses in biodiversity and the provision of ecosystem services (Worm et al. 2006; Grabowski & Peterson 2007; Rey Benayas et al. 2009). Restoration projects have increased in an effort to reverse losses of habitat and decreases in ecosystem service provision.

Eastern oysters (*Crassostrea virginica*) are the most common oysters in North America, forming extensive reefs in estuaries throughout their range (Atlantic coast from Canada throughout the Gulf of Mexico to Brazil) (EOBRT 2007; Beck et al. 2009). As a foundation species, oysters contribute to the integrity and functionality of estuarine ecosystems, and are an important ecological and economic resource. Oysters have been an important food source for humans for centuries, but have recently gained recognition for many other services they provide (Luckenbach et al. 1999; Brumbaugh et al. 2006; Grabowski & Peterson 2007; Coen et al. 2007). In particular, the complex structure of oyster reefs provides essential habitat for a variety of fish and invertebrates (Zimmerman et al. 1989; Breitburg 1999; Peterson et al. 2003; Plunket & La Peyre 2005; Tolley & Volety 2005; Stunz et al. 2010; Reese Robillard et al. 2010). Oyster reefs can have 50 times the surface area of an equally sized flat bottom, and provide important structure in often otherwise barren landscapes (Coen et al. 1999; Henderson & O'Neil 2003). Young oysters depend upon the hard shell substrate provided by reefs for attachment and growth, and this is the mechanism by which oyster reefs are formed and maintained. Many commercially important fishes and crustaceans depend on oyster reefs during some part of their life, whether as nursery habitat or foraging areas (Beck et al. 2003; Coen & Grizzle 2007). Thus, oyster reefs can enhance tertiary productivity of estuaries and fishing opportunities for humans.

Efforts to restore oyster reef habitat have increased, and often include goals of providing suitable habitat for the many resident and transient fishes and crustaceans that use reefs (Breitburg 1999; Peterson et al. 2003; Plunket & La Peyre 2005; Baggett et al. 2014). However, relatively little is still known about reef and community development following restoration. It is important to understand how long it may take for the goals to be met, if they are met, and whether oyster reef restoration is a good investment (Grabowski et al. 2012, La Peyre et al. 2014a). Better understanding will improve knowledge of what metrics to monitor and at which timescales for assessing project success. Additionally, reef design can be a critical precursor for restoration success. Vertical relief of reef structures can be critical for oyster recruitment and survival, as sedimentation can impede attachment and growth (Jordan-Cooley et al. 2011; Colden et al. 2016). Also, considering the diversity of organisms that use oyster reef habitats, it is important to consider structural complexity and function at a variety of scales and employ reef designs that will benefit a variety of resident and transient reef-associated species (Breitburg 1999; Eggleston et al. 1999; Bostrom et al. 2011).

The goal of this study is to determine success of a restored oyster reef in Copano Bay, Texas, in terms of habitat provision and oyster production. Oysters and resident and transient fishes and crustaceans were monitored at the restored reef in addition to nearby natural oyster reef and unrestored bottom (consisting of dense mud and shell hash) habitats. The natural oyster reef represents the minimum end goal of restoration, while the unrestored bottom allows examination of the connecting landscape within natural and restored oyster reef habitats. An understanding of the dynamics of habitat provisioning by restored reefs is essential for assessing whether these habitats can function similarly to natural reefs, and how reef design elements can enhance habitat use by a variety of organisms.

2. Material and methods

2.1. Study area

The Mission-Aransas Estuary is a bar-built estuary in South Texas composed of several shallow bays, the largest being Copano Bay and Aransas Bay (Fig. 1A). The area is characterized by a semi-arid, subtropical climate with infrequent rain events. The average tidal range is small (0.15 m) and water movement is predominantly wind-influenced (Evans & Morehead Palmer 2012). Oyster reefs are common throughout the system (Fig. 1A). Reefs are primarily subtidal, and more prominent in areas of low to moderate salinity (Beseres Pollack et al. 2011, 2012). The Mission-Aransas estuary is the southern-most extent of commercial oyster harvest in Texas, and oysters are the most profitable fishery in the estuary (NMFS 2009).

2.2. Reef construction

An oyster reef complex was constructed in Copano Bay in July-August, 2011, to restore habitat for oysters and associated fauna (Fig. 1B). The restoration site (28.13°N, 97.05°W) was chosen based on previous efforts to identify suitable areas for oyster reef development (e.g., water quality, oyster health, substrate characteristics) (Beseres Pollack et al. 2012). The three-dimensional reef complex was designed to maximize available resources and create a structurally complex habitat that incorporates hills and valleys as essential design elements (Lenihan &

Peterson 1998; Lenihan 1999; Stunz et al. 2010). These valleys create important corridors that can increase habitat use across a larger spatial scale (Lenihan & Peterson 1998; Lenihan 1999; Darcy & Eggleston 2005; Stunz et al. 2010). Eight reef mounds, each measuring 20 x 30 m (0.06 ha), were constructed of a concrete rubble base topped with oyster shell to achieve a vertical relief of 0.3 m. Concrete was reclaimed from chutes and hoppers of concrete trucks and crushed to class 3 riprap size to resemble the size of large oysters and maintain natural interstitial space within the reef. Oyster shell was reclaimed from Alby's seafood wholesaler in Fulton, Texas and through the Oyster Recycling Program founded by the Harte Research Institute (HRI 2009). All shell material was sun-bleached for at least six months before use to ensure shells were free of oyster tissue and harmful bacteria (Bushek et al. 2004; Cohen & Zabin 2009). Construction occurred using barges with excavators during July 2011. The footprint of the restored reef complex encompasses approximately 1.6 ha, and is situated in close proximity to a subtidal natural oyster reef complex (Fig. 1B). Commercial harvesting via oyster dredges maintains a low vertical relief (~ 0.1 m) across much of the reef. The surrounding unrestored bottom is characterized by muddy sediments with dense shell hash and few scattered oysters. Though dredging in the area was not restricted during this study, experiment signage prevented harvest disturbance to the actual sampling sites.

2.3. Experiment setup

Six sites were haphazardly chosen at the restored reef as well as at natural reef and unrestored bottom habitats for a total of 18 fixed sampling sites (depth 0.6-1.7 m; Fig. 1B). Plastic sampling trays (0.64 x 0.70 m; 0.44 m^2) were lined with 0.6 cm aquaculture mesh and used to assess colonization and habitat use by oysters and resident crustaceans and fishes (Eggleston et al. 1998; Plunket & La Peyre 2005; Rodney & Paynter 2006; Gregalis et al. 2009).

In August 2011, following reef construction, trays were filled with approximately 20 L of corresponding substrate and secured in place with rebar hooks by divers. Trays deployed on restored reefs were filled with reclaimed oyster shell to match the veneer of the constructed reefs. An oyster dredge was used to collect natural reef material (i.e., oysters and shells), and this material was used to fill trays deployed on the natural reef. For the unrestored bottom habitat, trays were first deployed, secured and then filled with surrounding substrate (i.e., mud, shell hash, oysters) by divers using shovels. Six trays were deployed at each site so that sampling could occur for two years without tray replacement. This was done to ensure that sampling captured successional trends in reef development. Three additional sites were haphazardly chosen within each habitat type (9 sites total; Fig. 1B) for sampling of transient crustaceans and fishes using a beam trawl (2 m wide, 6 mm stretch mesh; Froeschke 2011).

2.4. Field sampling

Sampling commenced in February 2012 (six months following experiment setup) and occurred three times per year through September 2013, for a total of six sampling periods (February 2012, June 2012, September 2012, March 2013, June 2013, and September 2013). Environmental parameters were measured at each tray sampling site. Water temperature (°C), salinity (psu) and dissolved oxygen (mg L^{-1}) were measured 0.1 m from the bottom with a handheld Hydrolab data sonde. Water clarity was measured by Secchi depth (m). Discrete water quality samples were collected 0.1 m from the bottom using a horizontal van Dorn water sampler. Water samples were stored in amber Nalgene bottles and placed on ice until further processing in the lab to quantify chlorophyll-*a* and total suspended solids (TSS).

One tray was retrieved by divers from each site during each sampling period (i.e., total of six trays per habitat type per sampling period). Once lifted out of the water and onto the boat, each tray was quickly emptied into a large tub, and contents were rough sorted in the field. Oysters were thoroughly rinsed within the tub to dislodge mobile fauna and then stored on ice for transport to the lab. All crustaceans and fish were then collected from the tub and preserved in buffered formalin (10%) for laboratory analysis. Transient species were sampled at each habitat type using a beam trawl. The trawl was towed at approximately 1 m second^{-1} for an average of 90 seconds at each site (average sampled area of 174 m^2). Samples were rough sorted in the field, and all fishes and crustaceans were preserved in buffered formalin (10%).

2.5. Laboratory analyses

In the laboratory, water samples were analyzed for chlorophyll-*a* using a non-acidification technique (Welschmeyer 1994; EPA method 445.0), and total suspended solids were also quantified (EPA method 160.2). Oysters were counted and measured for shell height from the umbo to posterior margin of the right valve (nearest 0.1 mm). Oyster abundance was transformed to density (ind. m^{-2}). Nekton samples were rinsed through a 1 mm-mesh sieve, identified to the lowest relevant taxonomic unit, enumerated and measured (standard length (or carapace width for crabs) to nearest 0.1 mm). For abundant species groups, a randomly selected subset (22 individuals, including smallest and largest specimens) was measured (Stunz et al. 2010; Reese Robillard et al. 2010). For each tray and trawl sample, faunal abundance was transformed to density (ind. m^{-2}), and diversity was calculated using Hill's N1 diversity index (Hill 1973).

2.6. Data analysis

The effects of sampling period and habitat type on environmental parameters, oyster densities, oyster size, nekton densities, and N1 diversity were analyzed using two-way analysis of variance (ANOVA, $\alpha = 0.05$) models. Data were tested for normality and homogeneity of variances using Shapiro-Wilk and Levene tests, respectively. Fourth-root transformations were applied where needed to improve normality and homogeneity of variances. Significant interactions were examined using simple main effects analyses. Tukey's honestly significant different (HSD) multiple-comparison test was used to examine differences among treatment levels. Additional analyses were performed separately for the most abundant families and species. All data were analyzed in R 3.0.1 (R Core Team 2013).

Similarities in nekton communities among habitat types and sampling periods were examined in PRIMER version 7 (Clark & Gorley 2015). Non-metric multidimensional scaling (MDS) was performed based on a Bray-Curtis similarity matrix. The SIMPROF routine was used to determine significant differences among clusters, and cluster groups were superimposed on the plot for interpretation. ANOSIM was used to determine significant differences in communities among habitat types and sampling periods (Clark & Warwick 2001).

3. Results

3.1. Environmental parameters

Salinity ranged from 26.6-38.8 psu, water temperature from 13.8-30.1 °C, and dissolved oxygen from 4.6-8.7 mg L^{-1} over the course of the study period. Chlorophyll-*a* levels ranged from 0.1-7.8 μg L^{-1}. TSS concentrations ranged from 6.8-50.3 mg L^{-1} across all sampling dates. No significant differences in environmental parameters were observed between habitat types. Differences observed between sampling periods reflected expected seasonal trends.

3.2. Oysters

Oysters were analyzed by size class: spat (< 25 mm), submarket (25-76 mm), and market (> 76 mm). Significant interaction terms between habitat type and sampling period in the two-way ANOVA models for both spat and submarket oyster densities required simple main effects analysis. Throughout 2012, spat oyster densities remained low (< 600 ind. m^{-2}) and did not differ significantly between habitat types during any of the three sampling periods (Fig. 2A). In March 2013, spat densities at the restored reef were significantly higher than densities observed at the natural reef ($p = 0.005$) and unrestored bottom habitat ($p < 0.001$). Substantial recruitment was observed in June 2013, with spat densities greater than 1,000 ind. m^{-2} across all habitats. Spat density at the restored reef surpassed that at the natural reef and unrestored bottom habitats by September 2012 and remained highest through the end of the study period.

Submarket oyster density was significantly higher at the natural reef in February 2012 compared to the unrestored bottom habitat ($p = 0.011$; Fig. 2B), but not significantly different from the restored reef ($p = 0.067$). In June 2012, oyster densities decreased across all habitats, followed by increased densities in September 2012. No significant differences were observed between habitat types during June or September 2012. In March 2013, submarket oyster densities at the restored reef increased greatly. Submarket oyster density was significantly greater at the restored reef compared to unrestored bottom habitats ($p < 0.032$) throughout 2013, but was not significantly greater compared to the natural reef ($p > 0.15$). Similar to the pattern demonstrated by spat oysters, submarket oyster density at the restored reef surpassed that at the natural reef and unrestored bottomhabitats by September 2012 and remained highest through the end of the study period.

Densities of market-sized oysters differed significantly among sampling periods ($p < 0.0001$), but not between habitats ($p = 0.078$) over the study (Fig. 2C). Market oysters were first observed at the restored reef during September 2012, approximately 13 months following reef construction. Market-sized oyster density at the restored reef surpassed that at the natural reef and unrestored bottom habitats by March 2013 and remained higher than the natural reef through the end of the study period. The lowest densities of market oysters were observed during June 2012, and were significantly lower than densities observed throughout 2013 ($p < 0.02$). No significant differences were observed between habitats during any sampling periods.

Shell height was examined for submarket and market oysters combined (Fig. 3). A significant interaction existed between habitat type and sampling period in the two-way ANOVA model for oyster shell height, and thus analysis of the main effects was required. At the beginning of the study (February 2012), oyster size was significantly different between all habitats ($p < 0.003$), with largest oysters (50.9 ± 1.9 mm) collected from the unrestored bottom habitat, and smallest oysters (30.4 ± 0.3 mm) at the restored reef habitat (Fig. 3). Oysters at the restored reef continued to be significantly smaller than those at both the natural reef and unrestored bottom habitats ($p < 0.005$) in June 2012. In September 2012, there were no significant differences in oyster size among habitats ($p > 0.18$). Oyster sizes remained largest at the unrestored bottom habitat throughout the remainder of the study, and in March 2013 were significantly larger compared to the restored ($p = 0.024$) and natural ($p = 0.046$) reef habitats. At the end of the study in September 2013, oyster shell height was comparable across all habitats ($p \geq 0.99$). In general, oyster size increased over the duration of the study from an average of 41.6 mm in February 2012 to 55.7 mm in September 2013 across all habitats.

3.3. Nekton

A total of 1,245 fish from 25 species and 21,832 crustaceans from 17 species groups were collected from tray and trawl samples throughout the study (Table 1). The greatest numbers of organisms were collected from the restored reef, with 556 fish from 21 species and 8,381 crustaceans from 14 species (Tables 2 and 3). The unrestored bottom habitat had the next highest abundance overall, with 391 fish from 21 species and 6,769 crustaceans from 15 species collected throughout the study (Tables 2 and 3). The fewest organisms were collected from the natural reef, with 298 fish from 19 species and 6,682 crustaceans from 15 species (Tables 2 and 3). However, the natural reef appears to be performing just as well as the unrestored bottom habitat when excluding a school of Atlantic croaker (n = 70) that was captured at the unrestored bottom habitat in February 2012. Across all habitats, the most abundant crustaceans were porcelain crabs (*Porcellanidae*, 46.8% RA (relative abundance)), mud crabs (*Xanthidae*, 34.6% RA) and snapping shrimp (*Alpheus heterochaelis*, 4.3% RA) (Table 1). The most abundant fishes were the code goby (*Gobiosoma robustum*, 1.3% RA) and the Gulf toadfish (*Opsanus beta*, 0.9% RA) (Table 1). Resident nekton (i.e., tray samples) were much more abundant than transient nekton (i.e., trawl samples) across all habitat types and sampling periods (Fig. 4). Additionally, crustaceans were much more abundant than fishes, for both tray and trawl samples.

3.3.1. Nekton Densities

Resident crustacean density averaged 1,097 ind. m^{-2} across habitats in February 2012, and was significantly lower throughout the rest of the study, averaging 190-384 ind. m^{-2} ($p <$ 0.001, Fig. 4A). No significant differences in total resident crustacean densities were observed between habitat types during the study ($p = 0.085$). The most abundant resident crustacean was the porcelain crab (*Porcellanidae*), and densities were significantly higher in February (average 601 ind. m^{-2}) than any other sampling period (range 101-201 ind. m^{-2}; $p < 0.0001$). Significant differences in porcelain crab densities were observed between habitat types, with the natural and restored reef habitats similar to each other ($p > 0.2$) but both greater than the unrestored bottom habitat ($p < 0.05$). Over the duration of the study, porcelain crab densities averaged 140 ind. m^{-2} at unrestored bottom habitats, 238 ind. m^{-2} at the natural reef, and 275 ind. m^{-2} at the restored reef. Mud crabs (*Xanthidae*) were the second most abundant resident crustacean, and were also significantly more abundant in February 2012 (average 475 ind. m^{-2}) than any other sampling period (range 46-135 ind. m^{-2}; $p < 0.001$). Throughout 2012, mud crab densities were significantly higher at the unrestored bottom habitat compared to the natural oyster reef ($p < 0.01$). Throughout 2013, no significant differences in mud crab densities were observed between habitats. Snapping shrimp (*Alpheus heterochaelis*) were the third most dominant crustacean. Densities of snapping shrimp were initially low (average 5.1 ind. m^{-2} in February 2012) and increased over the course of the study (range 14.3-33.4 ind. m^{-2}). In general, snapping shrimp were more abundant in natural and restored reef habitats (24.6-29.7 ind. m^{-2}) compared to the unrestored bottom habitat (16.2 ind. m^{-2}) over all sampling periods. The only significant difference between habitat types was observed during March 2013, when snapping shrimp densities were significantly higher at the restored reef (43.6 ind. m^{-2}) compared to the unrestored bottom (11.3 ind. m^{-2}; $p = 0.016$).

Resident fish densities were highest at the restored reef during February 2012 (mean 30.8 ind. m^{-2}) (Fig. 4C). Significant differences were observed between sampling periods ($p = 0.035$) and between habitats ($p = 0.049$) in the two-way ANOVA model. Tukey's post-hoc test identified the only significant difference in resident fish densities occurred between the restored reef in February 2012 and the unrestored bottom habitat in June 2012 ($p = 0.034$; Fig. 4C). Resident fish assemblages were dominated by *Gobiidae* species. Significant differences in *Gobiidae* densities were observed between habitats during February 2012 ($p < 0.04$) due to high densities at the restored reef (mean 30.4 ind. m^{-2}) compared to unrestored bottom (7.9 ind. m^{-2}) and natural reef (8.6 ind. m^{-2}) habitats. During the remainder of the study, goby densities ranged from 5.6-12.5 ind. m^{-2} across all habitat types. The oyster toadfish (*Opsanus beta*) was the second most abundant resident fish species. Densities of *O. beta* increased over the course of the study across all habitat types, from an average of 2.3 ind. m^{-2} in February 2012 to 10.1 ind. m^{-2} in September 2013. Densities observed in September 2013 were significantly higher than in February ($p = 0.044$) and June ($p = 0.004$) 2012. No differences between habitat types were observed over the duration of the study ($p > 0.5$).

Transient faunal densities observed in trawl samples were much lower than resident faunal densities observed in trays (Fig. 4A-D). A significant interaction term in the two-way ANOVA model for transient crustaceans required simple main effects analysis. High densities of crustaceans were observed at the unrestored bottom habitat during February 2012 (Fig. 4B), and crabs from the *Xanthidae* and *Portunidae* families were dominant. Over the remainder of the study, transient crustacean densities were generally highest at the restored reef (except during June 2013) and were dominated by grass shrimp (*Palaemonetes* spp.). No significant differences in transient crustacean densities were observed between habitat types during any sampling period.

Significant differences in transient fish densities were observed between sampling periods ($p < 0.0001$), but not habitats ($p = 0.097$) (Fig. 4D). These differences were attributable to high densities observed at the unrestored bottom habitats during February 2012 and at the restored reef during June 2012 (Fig. 4D). Atlantic croaker (*Micropogonias undulatus*) represented over half of all fishes identified at the unrestored bottom habitats in February 2012. In June 2012, high fish densities observed at the restored reef were due to the collection of a school of spot croaker (*Leiostomus xanthurus*). Lowest densities of transient fishes were observed in June and September 2013 (Fig. 4D).

3.3.2. Nekton Diversity

A significant interaction term between sampling period and habitat in the two-way ANOVA model for resident faunal diversity required simple main effects analysis. A general trend of increased diversity over time was observed for resident nekton (Fig. 4E). During June 2012, diversity observed at the natural reef was significantly higher than at the restored reef or unrestored bottom habitats ($p < 0.02$). No other significant differences between habitat types were observed during the study.

Transient faunal diversity was slightly higher and more variable than resident faunal diversity (Fig. 4E-F). Transient faunal diversity showed significant differences between sampling periods ($p < 0.0001$) in the two-way ANOVA model. Faunal diversity was significantly lower during June 2013 than during any of the previous four sampling periods ($p < 0.002$), and remained low in September 2013 (Fig. 4F). No significant differences were observed between habitat types overall ($p = 0.326$), nor within any sampling period.

MDS analysis of resident faunal communities identified two distinct clusters, with communities at least 60% similar to each other (SIMPROF: $p = 0.001$; Fig. 5A). Resident communities were significantly different among sampling periods (ANOSIM: $R = 0.619$, $p = 0.001$), but not among habitat types (ANOSIM: $R = 0.069$; $p = 0.826$). One cluster contains all habitat types during the first sampling period (February 2012) and unrestored bottom habitat communities observed during the second sampling period (June 2012). The other cluster is segregated into two groups: all remaining communities observed in 2012 are on the left, and all communities observed during the second year of the study (March, June and September 2013) are together on the right (Fig. 5A). Communities within each of these groupings are at least 75% similar to each other (SIMPROF: $p = 0.058$). MDS analysis of transient faunal communities identified five clusters, with communities at least 50% similar to each other (SIMPROF: $p < 0.05$; Fig. 5B). Transient communities were significantly different among sampling periods (ANOSIM: $R = 0.255$, $p = 0.01$), though not as strongly separated as resident communities. No significant differences were observed among habitat types (ANOSIM: $R = 0.065$, $p = 0.204$).

4. Discussion

A major goal of oyster reef restoration is to restore suitable habitat to support oyster recruitment and growth, and also the faunal communities associated with oyster reefs (Brumbaugh et al. 2006; Baggett et al. 2014). Oysters and associated fauna communities support desired ecosystem functions, such as providing critical habitat and supporting secondary and tertiary production (Coen et al. 1999; Peterson et al. 2003), and are often linearly associated with ecosystem services such as nutrient regulation, augmented potential oyster harvest and recreational fishing opportunities (Breitburg 1999; Grabowski et al. 2012). The results of this study indicate success of the restored oyster reef. Recruitment both of oysters and reef-associated fauna was observed in comparable numbers to reference habitats.

4.1. Oyster production

As restoration efforts continue to increase, restoration projects face more scrutiny (Mann & Powell 2007; Choi 2007). Oyster densities observed at the restored reef in the present study are at the high end of the spectrum of observations from other restoration projects. By the end of the study (2 years post-restoration), oyster densities totaled over 4,000 ind. m^{-2} (approximately 3,700 spat and 400 adults; Fig. 2). A restoration effort in Virginia regarded as highly successful (3 years post-restoration) reported oyster densities at high-relief (0.25-0.45 m) and low-relief (0.08-0.12 m) reefs just over 1,000 and 250 ind. m^{-2} respectively (approximately 350 spat and 700 adults, and 100 spat and 150 adults, respectively; Schulte et al. 2009). The restoration of these reefs in Virginia is considered unprecedented, with typical densities observed at sanctuary reefs in the Chesapeake Bay ranging from 100-150 ind. m^{-2} (Schulte et al. 2009; Bullock et al. 2011; Nyström et al. 2012). Thus, oyster densities observed at the restored reef in the present study reflect a similar degree of success as the highly celebrated project in Virginia (Schulte et al. 2009). Oyster densities observed in this study were substantially higher than any of the restored reefs sampled across the Gulf of Mexico by La Peyre et al. (2014b), who reported oyster densities at 11 restored reefs across seven bays throughout Texas, Louisiana, Mississippi and Alabama ranging from 0-392 ind. m^{-2} (spat and adults; La Peyre et al. 2014b). Oyster densities observed at a suite of constructed reefs within oyster sanctuary areas in North Carolina were generally lower than densities observed in the present study, with spat oyster densities less than 40 ind. m^{-2} and submarket oyster densities less than 250 ind. m^{-2} (Powers et al. 2009). Densities of market-sized oysters at the most successful reefs were over 100 ind. m^{-2} (Powers et al. 2009). These reefs have been protected for 3-30 years in no-harvest sanctuaries, and observed densities of market-sized oysters reflect the success of sanctuary designation (Powers et al. 2009).

In the present study, declines in oyster densities were observed across all size classes and habitats during June 2012. This was particularly evident for submarket oysters at the natural reef (Fig. 2B). This may have been due to mortality induced by the protozoan parasite, *Perkinsus marinus*, which causes the disease known as dermo (Ray 1966; Andrews & Ray 1988; Soniat 1996). Oysters collected from the natural reef in the study area exhibited high weighted prevalence values in both submarket and market-sized oysters (2.65 and 4.71, respectively) in January 2012 (Oyster Sentinel 2015). In June 2012, submarket oysters exhibited similar weighted prevalence values (2.65) and no market oysters were observed (Oyster Sentinel 2015). Market oysters were observed in November 2012, and exhibited high weighted prevalence values (3.21), as did submarket oysters (3.07) during this period (Oyster Sentinel 2015). Sharp increases in salinity coincident with increasing temperatures observed during summer 2012 indicate favorable conditions for the proliferation of *P. marinus* disease (Powell et al. 1992). Fortunately, subsequent increases in oyster density were observed across all size classes and habitats during September 2012. Highest oyster densities across all size classes were observed at the restored reef throughout 2013 (Fig. 2).

Submarket oysters were observed at similar densities at the restored reef during 2013 as were observed at the natural reef during the first sampling period (>300 ind. m^{-2}; Fig. 2B). This is a great indicator of success, as it would be expected to observe similar oyster densities at natural and successfully restored reefs (Brumbaugh et al. 2006; Baggett et al. 2014). However, it is unclear why submarket oyster densities at the natural reef do not return to former densities. Sedimentation was observed at the natural reef sites, though was not quantitatively measured. At the restored reef, sedimentation was not observed to the extent as observed at the natural reef. The restored reef complex was designed to achieve relatively high vertical relief (~0.3 m) to avoid the effects of sedimentation as much as possible (Lenihan 1999; Soniat et al. 2004). A previous restoration attempt in Copano Bay, constructed of oyster shell spread across mud bottom with minimal vertical relief, suffered from sedimentation (Beseres Pollack et al. 2009), and densities of oysters averaged 44 ind. m^{-2} (± 26.3 SE) three years post-construction (La Peyre et al. 2014b).

General trends of increased oyster size were observed over the course of the present study (Fig. 3). An unexpected observation was the larger size of oysters at the unrestored bottom sites. During the harvest process, oyster clumps must be culled (e.g., broken apart) and submarket oysters are required to be returned to the water (Quast et al. 1988). Many submarket oysters may be deposited on sediments surrounding the reefs from which they were collected, where they can then continue to grow. These non-reef areas likely experience less pressure during oyster harvest compared to reefs. It is possible that these areas may be serving as an important sanctuary for large oysters (Puckett & Eggleston 2012). Larger oysters contribute more eggs with each spawn, and thus their reproductive effort, or fecundity, is greater than smaller oysters (Galtsoff 1964; Hayes & Menzel 1981; Thompson et al. 1996; Dame 2012). Thus, these large oysters on sediments surrounding reefs may be an important source of larvae for the colonization of nearby reefs. More research in this area could further examine this hypothesis and offer insight on the designation of oyster sanctuaries.

4.2. Habitat use

Many estuarine species depend on structured habitats, such as oyster reefs (Zimmerman et al. 1989; Beck et al. 2003; Coen & Grizzle 2007), and habitat provision for crustaceans and fishes is often a primary goal of oyster reef restoration efforts (Breitburg 1999; Peterson et al. 2003; Plunket & La Peyre 2005). The results of this study indicate that the restored reef is successful in providing suitable nekton habitat. Over the course of the study, average densities of resident fishes (18.4 ± 2.1 SE ind. m^{-2}) and decapod crustaceans (453.9 ± 66.8 SE ind. m^{-2}) observed at the restored reef were consistent with, or greater than densities observed at natural and restored reefs elsewhere. Stunz et al. (2010) observed similar fish densities (17.2 ± 1.9 SE ind. m^{-2}) and lower crustacean densities (62.3 ± 9.9 SE ind. m^{-2}) at reef plots constructed of live oysters in Galveston Bay, Texas. Fish and decapod crustacean densities ranged from 80-100 ind. m^{-2} at live oyster cluster treatments in Tarpon Bay, Florida (Tolley & Volety 2005). Fish and crustacean densities observed at natural subtidal oyster reefs in Lavaca Bay and Sabine Lake, Texas were low (< 5 ind. m^{-2}; Reese Robillard et al. 2010; Nevins et al. 2014). Low densities were particularly surprising in Sabine Lake, considering the sampled reef represents the largest unfished oyster reef in the United States and is characterized by high vertical relief and substantial structural complexity (Nevins et al. 2014). However, the complexity of these reefs was so great that sampling was difficult, and low nekton densities are likely a reflection of poor gear efficiency (Nevins et al. 2014).

Over the course of the present study, differences in species assemblages between tray and trawl samples, and between habitat types, were observed. The most pronounced difference was observed for small swimming crabs (*Portunidae*). They represented the only crustacean to be collected exclusively in trawl samples, and were relatively abundant (1.2% RA). They were observed at all habitats, with mean densities higher at the unrestored bottom sites (0.05 ± 0.04 ind. m^{-2}) compared to the natural and restored reef sites (both 0.02 ± 0.01 ind. m^{-2}). Additionally, they were almost exclusively observed during winter (67.7% of total catch observed in February 2012) and early spring (29.7% of total catch observed in March 2013) sampling periods. This indicates that the bare sediment and shell hash habitats may be important settlement habitats for juvenile blue crabs (*Callinectes sapidus*), which are an important commercial species and have shown troubling declines over the past decade in this area (Sutton & Wagner 2007).

A surprising finding in this study was the high degree of nekton use of the unrestored bottom habitats. This is in contrast to many studies that have compared relative habitat density among estuarine habitats of various structural complexities, which overwhelmingly indicate higher nekton densities associated with structured habitat compared to bare sediment (Harding & Mann 2001; Lenihan et al. 2001; Tolley & Volety 2005; Plunket & La Peyre 2005; Stunz et al. 2010; Reese Robillard et al. 2010; Humphries et al. 2011). However, it has been shown that shell hash or rubble is an important and highly utilized habitat for estuarine species (Lehnert & Allen

2002; Shervette & Gelwick 2008). Bare sediments have also been shown to support similar or higher abundances of transient species compared to reefs (Gregalis et al. 2009; Pierson & Eggleston 2014).

It is possible that the unrestored bottom sites in this study performed so well due to their proximity or connectivity to the natural and restored reef sites. For example, Gregalis et al. (2009) observed higher numbers of transient fishes at unrestored bottom sites following reef construction compared to observations prior to construction. Similarly, Grabowski et al. (2005) observed increased fish abundances at mudflat habitat following the construction of oyster reefs in the area. Due to the fact that sampling at unrestored bottom and natural reef sites in the present study did not start before the construction of the restored reef, it is not possible to determine whether observed densities were due to increased use of the nearby restored reef. However, it has been widely demonstrated that landscape connectivity is critical to the dispersal and colonization of organisms, and habitat corridors can facilitate the movement of organisms between habitat patches (Taylor et al. 1993; Anderson & Danielson 1997; Kindlmann & Burel 2008; Bostrom et al. 2011). Unrestored bottom throughout the restoration area is characterized by shell hash, which may be providing enough structure to support movement of small organisms between reef mounds. Further, these corridors are likely traveled by transient predators as they forage on the edges of the reef mounds.

It has been shown that the presence of live oysters does not necessarily affect the habitat value for resident fishes and crustaceans (Tolley & Volety 2005). The micro-structure provided by oyster shells and shell hash may be enough structure to provide refuge for some species (Lehnert & Allen 2002). Also, it might be desirable habitat for certain functions. For example, empty shells are desired spawning substrate for several reef resident fishes (Crabtree &

Middaugh 1982; Breitburg 1999; Tolley & Volety 2005). During spawning, less structured habitat consisting of empty shells and shell hash may be a critical habitat for fishes such as gobies, blennies, and skilletfish.

Structured habitats (e.g., oyster reefs, seagrass beds, coastal marshes) receive more attention when discussing essential fish habitat, particularly for juveniles as nursery habitats (Beck et al. 2003; Coen & Grizzle 2007). Restoration efforts are increasing around the U.S. and globally to recreate structured habitats. In this study, bare sediments, or at least those with some micro-structure via shell hash, are providing similar habitat value as more structured reef habitats. Thus, further research to understand the relative value of bare substrates is warranted. Additionally, bare sediments should be included in restoration assessments. This would support return on investment analysis, and will be increasingly important as restoration efforts face more scrutiny for the large expense and perceived failure of some projects (Mann & Powell 2007; Choi 2007).

4.3. Monitoring timeframes

It is important to understand reef development following restoration in order to determine how long it takes for restoration goals to be met, and also to provide insight regarding the appropriate timeframes for monitoring various metrics of restoration success. In the present study, monitoring lasted for two years following reef construction in an effort to capture year-to-year variability and at least two oyster recruitment cycles. Interesting patterns were observed for oyster density and size from the first year to the second. It is evident that to assess the successful growth of adult oysters, monitoring needs to occur for at least two years. Oyster size and densities of submarket and market oysters did not approach similar values observed at the natural reef until after one year post-restoration. In colder waters where oyster growth is slower

(Shumway 1996; EOBRT 2007), longer monitoring timeframes (e.g., five years) may be warranted. Additionally, substantial increases in spat recruitment were observed across all habitats during the second year of monitoring. Spat recruitment can vary greatly from year to year (Kennedy 1996). Thus, monitoring over multiple years is important for understanding recruitment dynamics at restored reefs.

An interesting pattern was observed in relative densities between size classes. Spat, submarket, and market-sized oysters exhibit approximately an order of magnitude difference in densities (Fig. 2), indicating approximately 10% survival rates between size classes. This observation is supported by survival estimates of oysters in Texas (Quast et al. 1988) and other molluscs in Copano Bay (Cummins et al. 1986). Better understanding of survival rates between size classes of oysters could improve monitoring efficiency. For example, observations of spat oyster densities over short time frames could provide a basis for estimating potential densities of larger oysters that could only be observed over longer time frames.

Temporal variations in resident crustacean and fish densities were also observed. The highest densities of resident crustaceans and fishes at the restored reef were observed during the first sampling period (six months post-construction). A significant decline in resident nekton densities was observed during the following sampling period, and levels were sustained for the remainder of the study. Personal observations during experiment setup (one month post-restoration) suggest that resident nekton densities may have been even higher immediately following reef construction. During placement of the trays at the restored reef, substantial noise was observed, indicating high use of the habitat by resident species (Lillis et al. 2014). The soundscape of the restored reef was considerably loud compared to the natural reef and unrestored bottom habitats during experiment setup, and the same level of noise was not observed during any subsequent sampling periods, including the first sampling event in February 2012. This suggests that new structure attracts nekton quickly (Powers et al. 2003; Humphries et al. 2011). Attraction to the new reef habitat could also explain the relatively low numbers of nekton collected at the natural reef. Recruitment to the restored reef is likely due to movement from the nearby natural reef, resulting in a net loss of organisms from the natural reef habitat they previously occupied.

These observations also highlight important implications of replacing sampling trays between sampling events. Replacement of sampling units and substrates is common (Eggleston et al. 1998; Lehnert & Allen 2002; Tolley & Volety 2005; Plunket & La Peyre 2005; Gregalis et al. 2009; but see Humphries et al. 2011), and is likely due to budget constraints. However, replacement of sampling units between sampling events does not allow observations of succession patterns or development trajectories that are important to assessing success of restored habitats. This is further supported by analysis of resident community assemblages. As time progress, community assemblages become increasingly similar, and by the second year of monitoring, all samples exhibited 75% similarity to each other. By replacing sampling units between sampling events, observations may continually reflect initial attraction rather than sustained use.

4.4. Restoration design

Reefs of higher vertical relief have proven to provide superior habitat for oysters and resident fauna (Breitburg 1999; Lenihan 1999; Schulte et al. 2009; Jordan-Cooley et al. 2011). In this study, a reef complex design was employed to maximize the vertical relief of reefs with the substrate available. Eight individual reefs were constructed with a vertical relief of approximately 0.3 m. The relatively high vertical relief of the constructed reefs prevented the level of sedimentation observed across natural reef and unrestored bottom habitats in the study area. As filter feeders, oysters can be highly susceptible to sedimentation (Lenihan 1999; Jordan-Cooley et al. 2011). Results indicate that a vertical relief of 0.3 m was enough to prevent detrimental levels of sedimentation in this area. The vertical relief of reefs can also be important during periods of bottom-water hypoxia (Breitburg 1999; Lenihan 1999). Designing reefs that extend above hypoxia/stratification depths typical of an area can prevent total mortality of oysters and other sessile fauna, and enables mobile resident fauna to seek refuge in more elevated portions of reefs (Breitburg 1999; Lenihan 1999). Thus, increasing the vertical relief of reefs can increase survival of oysters and resident fishes and crustaceans.

The valleys, or corridors, between the reef mounds across the restoration footprint are also important design features. The creation of these corridors may have increased the use of unrestored bottom habitat by mobile fauna throughout the restored area. A majority of work examining estuarine habitat corridors focuses on vegetated habitats, such as seagrass beds (Eggleston et al. 1999; Darcy & Eggleston 2005; Bostrom et al. 2011). In the present study, the microstructure provided by the dense shell hash and scattered oysters comprising the unrestored bottom may be providing similar functions as vegetated corridors. Small resident organisms face better chances of survival when dispersing through corridors that provide some habitat structure similar to the patches they are traveling between (Anderson & Danielson 1997; Bostrom et al. 2011). Additionally, these corridors can be particularly desirable for transient fishes (e.g., croaker, sheepshead, drum) that forage at the edge of reef habitats (Beck et al. 2003; Coen & Grizzle 2007; Bostrom et al. 2011). These species are often targeted by recreational fishers, and thus, the inclusion of corridors in oyster reef design can enhance the recreational benefits provided by a restoration project (Coen et al. 2007; Grabowski et al. 2012).

Despite their important role as foundational, habitat-building species, oysters have been understudied with respect to seascape ecology (Bostrom et al. 2011). The reef mound-corridor design employed in this project likely contributed substantially to the success of the restored habitat. Traditionally, flat pavement-style reefs were constructed for oyster restoration projects in an effort to maximize the total restored area by spreading cultch material in a thin, continuous layer across the restoration footprint (Mann & Powell 2007; Beseres Pollack et al. 2009). Building higher-relief reef mounds with the same amount of cultch material results in a smaller actual restored area, and such projects may be compared unfavorably to pavement-style projects if acreage is the most influential metric used to assess potential success. In the present study, eight reef mounds were spaced less than 20 m apart from each other over a 1.5 ha restoration footprint. The total area comprised strictly of restored reef habitat was less than 0.5 ha. However, this project demonstrates that the reef complex design enhanced the functioning of the entire restoration footprint by incorporating both higher-relief reefs and connecting corridors.

5. Conclusion

In conclusion, the restored reef habitat shows remarkable success in terms of providing suitable habitat for oysters and nekton. Within the first year post-restoration, oyster densities observed at the restored reef were similar or greater than observations at reference habitats, and oyster sizes were similar between natural and restored reefs. Nekton densities were similar between all habitats throughout the study and community assemblages among the restored and nearby habitats became more similar over time. The high densities of oysters and resident nekton indicate that this restored reef was highly successful in providing important ecological functions associated with habitat provision and oyster production. Densities of oysters and nekton were on-par or higher than densities reported from several previous restoration efforts, and may be attributed to the complex reef design incorporating relatively high relief reef mounds with valleys that create corridors important for nekton use and habitat connectivity.

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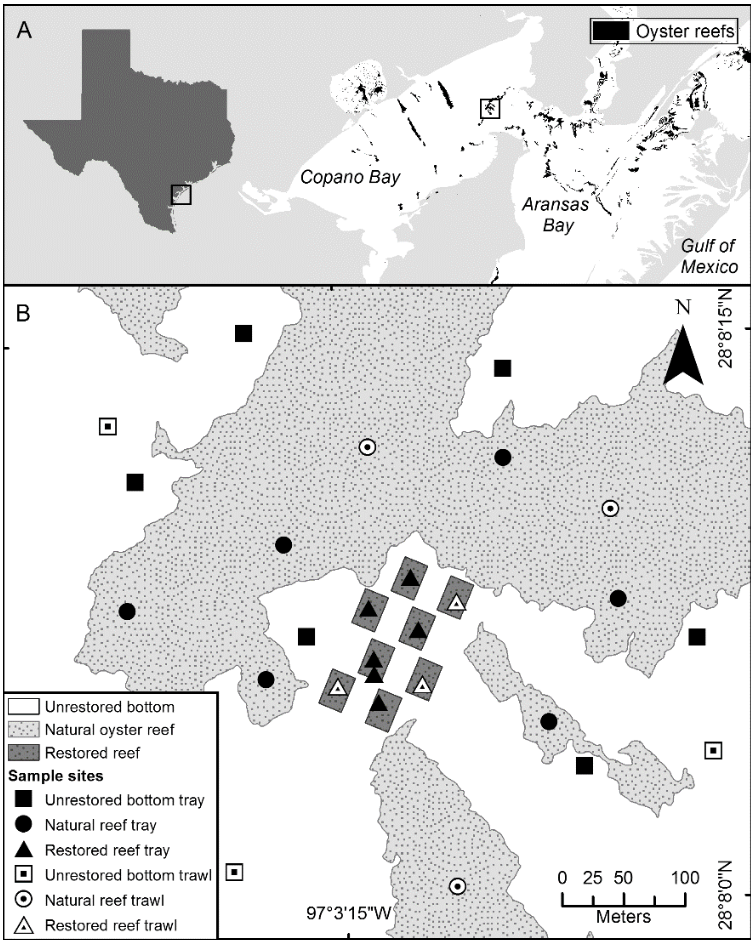

Fig. 1. Study area. A) Mission-Aransas Estuary, Texas; oyster reefs shown in black. The location of the restored reef complex in Copano Bay is indicated by the black box. B) Sampling sites.

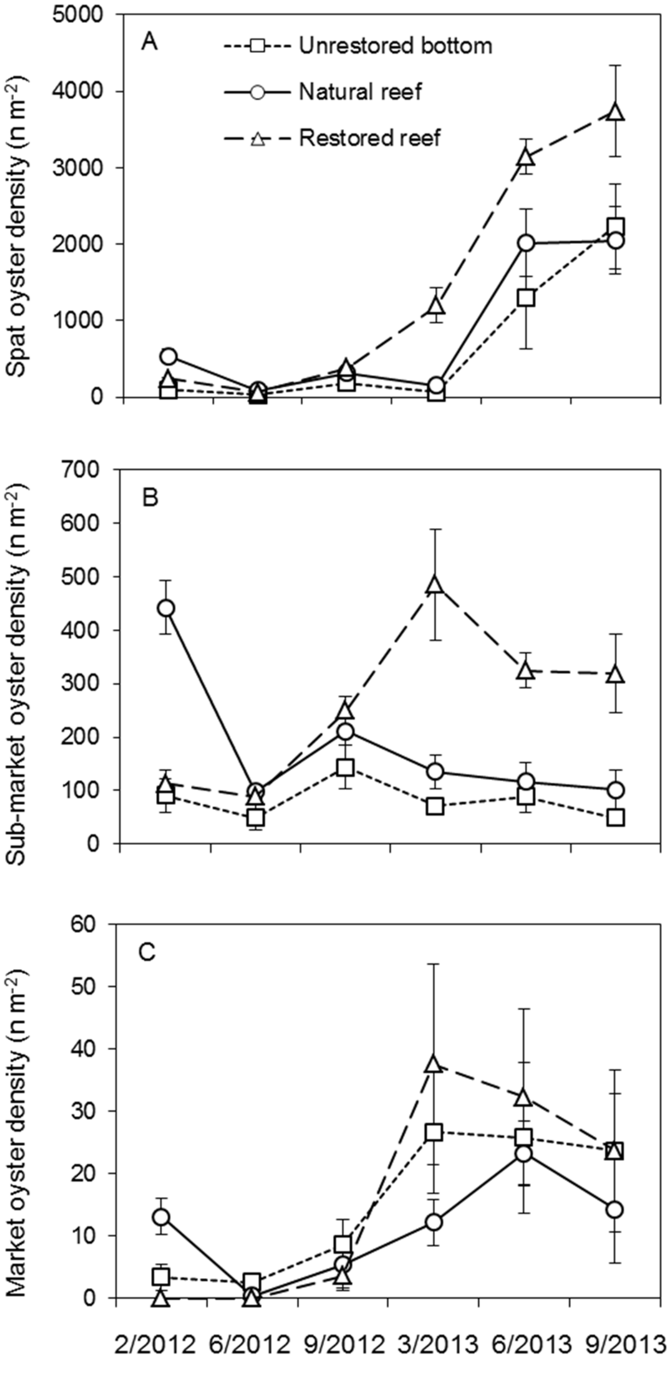

Fig. 2. Oyster density (mean ± SE) observed at unrestored bottom, natural reef and restored reef habitat types during each sampling period. A) Spat oysters (<25 mm). B) Sub-market oysters (25–76 mm). C) Market-sized oysters (>76 mm).

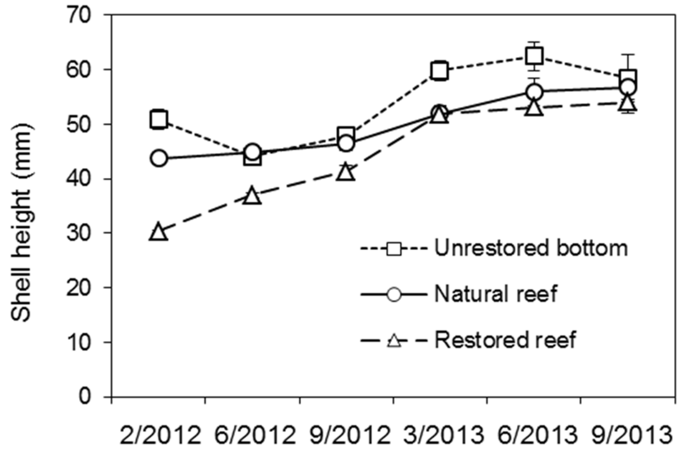

Fig. 3. Shell height (mean ± SE) of submarket and market oysters (> 25 mm) from unrestored bottom, natural reef and restored reef habitat types during each sampling period.

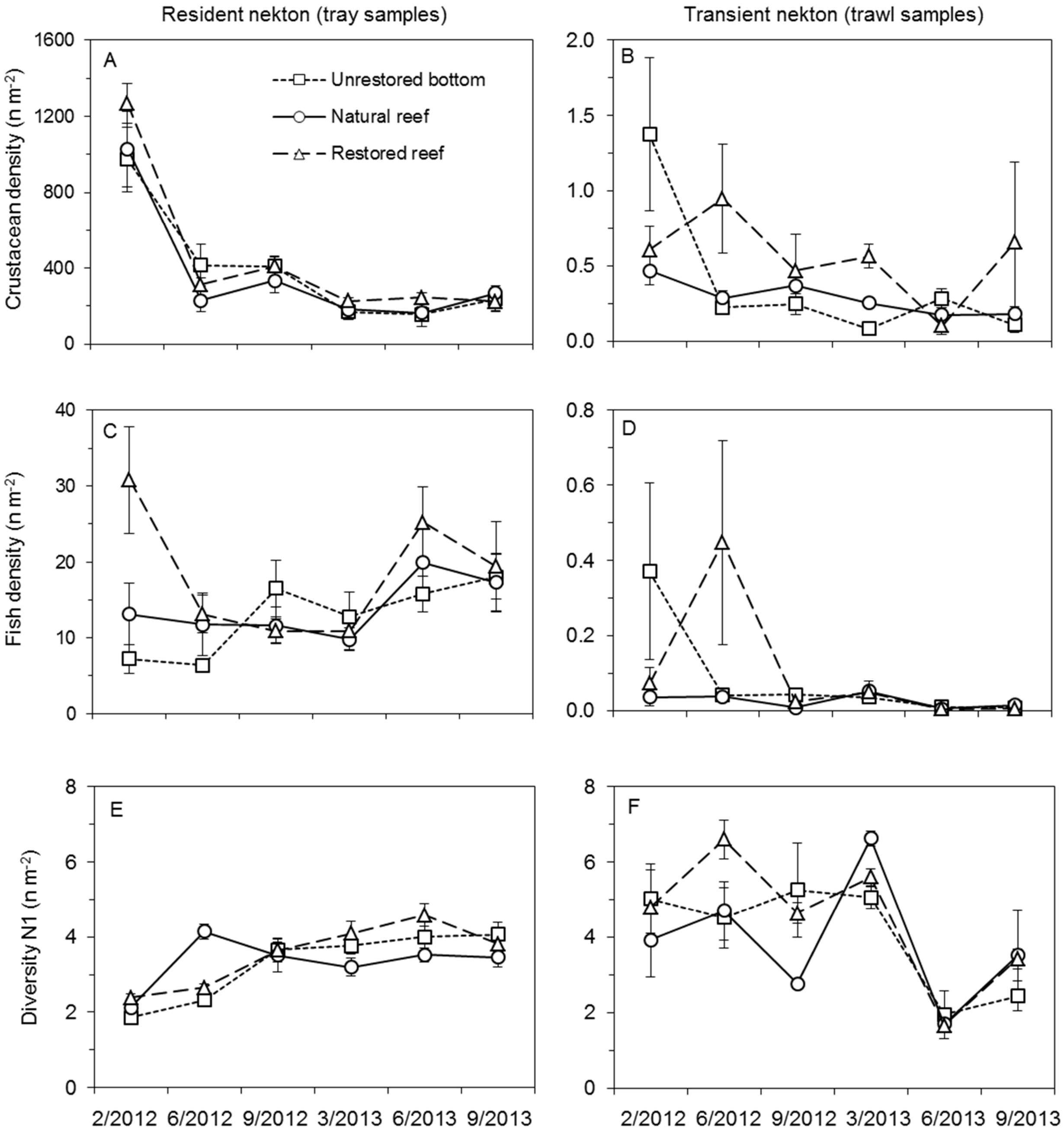

Fig. 4. Resident (A) and transient (B) crustacean density, resident (C) and transient (D) fish density, and diversity of resident (E) and transient (F) communities. Density reported in number of individuals per square meter; diversity reported as Hill's N1; all values reported as mean±SE.

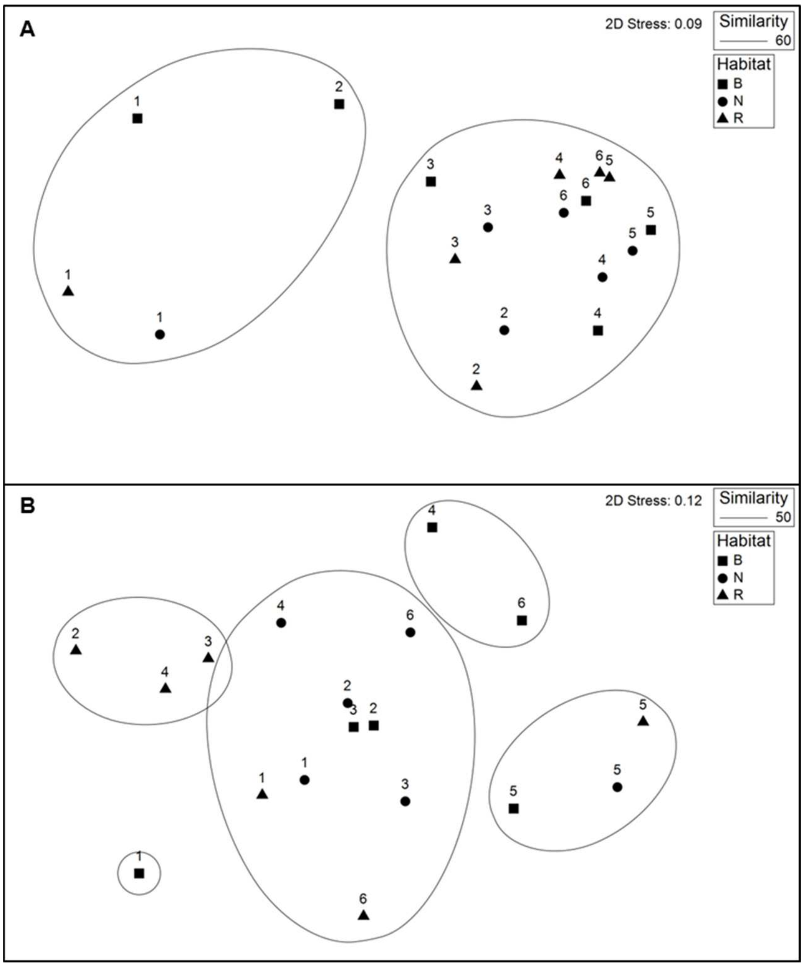

Fig. 5. Non-metric multidimensional scaling analysis of mean community structure of fish and crustaceans collected via trays (A) and trawls (B) for each habitat and sampling period combination. Symbols indicate unrestored bottom (B, squares), natural reef (N, circles) and restored reef (R, triangles) habitats. Numbers indicate sampling period, starting in February 2012 (1) through September 2013 (6). Lines show similarity grouping results related to community differences; similarity numbers indicate percent similarity of samples encompassed within each grouping.

Table 1. Total catch, relative abundance (RA), and gear, habitat and seasonal occurrence of fish and crustaceans collected during the study.

						Seasonal occurrence					
Common name	**Scientific name**	**Total catch**	**RA (%)**	**Gear occurrence**	**Habitat occurrence**	**Feb-12**	**Jun-12**	**Sep-12**	**Mar-13**	**Jun-13**	**Sep-13**
Total fish		**1,245**	**5.4**								
Code goby	*Gobiosoma robustum*	289	1.3	tray, trawl	B, N, R	X	X	X	X	X	X
Gulf toadfish	*Opsanus beta*	209	0.9	tray, trawl	B, N, R	X	X	X	X	X	X
Spot	*Leiostomus xanthurus*	177	0.8	tray, trawl	B, N, R		X	X			
Darter goby	*Ctenogobius boleosoma*	114	0.5	tray, trawl	B, N, R	X	X	X	X	X	X
Naked goby	*Gobiosoma bosc*	101	0.4	tray, trawl	B, N, R	X	X	X	X	X	X
Goby species	*Gobiidae*	95	0.4	tray, trawl	B, N, R	X	X	X	X		X
Atlantic croaker	*Micropogonias undulatus*	88	0.4	trawl	B, N, R	X			X		
Skilletfish	*Gobiesox strumosus*	73	0.3	tray, trawl	B, N, R	X	X	X	X	X	X
Green goby	*Microgobius thalassinus*	28	0.1	tray, trawl	B, N, R	X	X	X	X	X	
Stretchjaw blenny	*Chasmodes longimaxilla*	16	0.1	tray, trawl	B, N, R	X	X	X		X	X
Pipefish	*Sygnathidae*	14	0.1	tray, trawl	B, N, R	X	X	X	X		X
Bay whiff	*Citharichthys spilopterus*	12	0.1	trawl	B, N, R	X		X		X	X
Blackcheek tonguefish	*Symphurus plagiusa*	4	0.0	trawl	B, N, R				X		
Freckled blenny	*Hypsoblennius ionthas*	3	0.0	tray	N, R	X			X	X	
Gray snapper	*Lutjanus griseus*	3	0.0	tray	B, N				X		
Least puffer	*Sphoeroides parvus*	3	0.0	trawl	B, N, R		X				X
Pigfish	*Orthopristis chrysoptera*	3	0.0	tray	B, N			X			X
Speckled worm eel	*Myrophis punctatus*	3	0.0	tray, trawl	B, N, R		X		X		X
Feather blenny	*Hypsoblennius hentz*	2	0.0	tray	B, N	X					
Pinfish	*Lagodon rhomboides*	2	0.0	trawl	B, R			X			
Sheepshead	*Archosargus probatocephalus*	2	0.0	trawl	B, R	X	X				
Bay anchovy	*Anchoa mitchilli*	1	0.0	trawl	R				X		
Blackwing searobin	*Prionotus rubio*	1	0.0	trawl	R	X					
Spotfin mojarra	*Eucinostomus argenteus*	1	0.0	tray	B						X
Unidentified larval fish	*Unidentified larval fish*	1	0.0	tray	R			X			
Total crustaceans		**21,832**	**94.6**								
Porcelain crabs	*Porcellanidae*	10,791	46.8	tray, trawl	B, N, R	X	X	X	X	X	X
Mud crabs	*Xanthidae*	7,977	34.6	tray, trawl	B, N, R	X	X	X	X	X	X
Snapping shrimp	*Alpheus heterochaelis*	990	4.3	tray, trawl	B, N, R	X	X	X	X	X	X
PL penaeid shrimp	*Postlarval Penaeidae*	542	2.3	tray, trawl	B, N, R	X	X	X	X	X	X
Marsh grass shrimp	*Palaemonetes vulgaris*	442	1.9	tray, trawl	B, N, R	X	X	X	X		X
Grass shrimp	*Palaemonetes spp.*	390	1.7	tray, trawl	B, N, R	X	X	X	X		X
Gulf stone crab	*Menippe adina*	320	1.4	tray, trawl	B, N, R	X	X	X	X	X	X
Swimming crabs	*Portunidae*	266	1.2	trawl	B, N, R	X	X	X	X		X
Arrow shrimp	*Tozeuma carolinense*	57	0.2	tray, trawl	B, N, R	X	X	X	X		X
Brown shrimp	*Farfantepenaeus aztecus*	25	0.1	tray, trawl	B, N, R	X	X	X		X	
Olivepit porcelain crab	*Euceramus praelongus*	7	0.0	tray, trawl	B, N, R		X			X	X
Cleaner shrimp	*Hippolytidae*	7	0.0	tray, trawl	N, R				X		X
Daggerblade grass sh.	*Palaemonetes pugio*	6	0.0	tray, trawl	B, R	X	X				X
White shrimp	*Litopenaeus setiferus*	5	0.0	tray, trawl	B, N, R	X		X			X
Blue crab	*Callinectes sapidus*	3	0.0	tray, trawl	N				X		X
Longnose spider crab	*Libinia dubia*	3	0.0	tray	B, N	X		X		X	
Ghost shrimp	*Callianassa spp.*	1	0.0	tray	B	X					

RA = (no. individuals/total)*100. Habitat types: unrestored bottom (B), natural reef (N), restored reef (R). X indicates species was collected during sampling date.

Table 2. Overall mean species density and SE, mean size and SE, and total number collected from trays in unrestored bottom, natural reef and restored reef habitats during the study.

		Unrestored bottom					**Natural reef**					**Restored reef**				
Common name	**Scientific name**	**Mean density**	**SE**	**Mean size**	**SE**	***n***	**Mean density**	**SE**	**Mean size**	**SE**	***n***	**Mean density**	**SE**	**Mean size**	**SE**	***n***
Total fish						**186**					**217**					**285**
Code goby	*Gobiosoma robustum*	3.35	0.62	20.9	0.9	49	3.67	0.63	21.0	0.8	57	3.41	0.69	21.5	0.7	53
Gulf toadfish	*Opsanus beta*	4.37	0.66	91.9	8.1	64	4.44	0.84	56.9	6.8	69	4.77	1.02	40.8	3.2	74
Spot	*Leiostomus xanthurus*	-	-	-	-	-	0.06	0.06	38.5	-	1	-	-	-	-	-
Darter goby	*Ctenogobius boleosoma*	1.64	0.38	18.6	1.3	24	0.84	0.23	19.7	1.7	13	1.35	0.38	20.5	1.2	21
Naked goby	*Gobiosoma bosc*	0.75	0.32	25.6	1.9	11	1.67	0.54	26.2	0.9	26	3.09	0.84	24.7	0.7	48
Goby species	*Gobiidae*	1.64	0.98	18.1	1.5	24	0.39	0.24	11.0	2.4	6	3.29	1.95	24.5	0.8	51
Skilletfish	*Gobiesox strumosus*	0.34	0.14	26.5	4.3	5	1.55	0.45	28.7	2.5	24	1.42	0.56	28.4	1.8	22
Green goby	*Microgobius thalassinus*	0.14	0.14	17.6	0.9	2	0.19	0.14	19.7	1.4	3	0.77	0.26	21.6	1.7	12
Stretchjaw blenny	*Chasmodes longimaxilla*	0.07	0.07	30.9	-	1	0.71	0.34	44.7	4.2	11	0.06	0.06	33.3	-	1
Pipefish	*Sygnathidae*	-	-	-	-	-	0.06	0.06	57.5	-	1	-	-	-	-	-
Freckled blenny	*Hypsoblennius ionthas*	-	-	-	-	-	0.06	0.06	49.4	-	1	0.13	0.09	51.2	28.0	2
Gray snapper	*Lutjanus griseus*	0.14	0.10	86.1	8.4	2	0.06	0.06	59.7	-	1	-	-	-	-	-
Pigfish	*Orthopristis chrysoptera*	0.07	0.07	190.0	-	1	0.13	0.09	132.0	12.0	2	-	-	-	-	-
Speckled worm eel	*Myrophis punctatus*	0.07	0.07	172.1	-	1	0.06	0.06	203.0	-	1	-	-	-	-	-
Feather blenny	*Hypsoblennius hentz*	0.07	0.07	35.3	-	1	0.06	0.06	48.7	-	1	-	-	-	-	-
Spotfin mojarra	*Eucinostomus argenteus*	0.07	0.07	16.9	-	1	-	-	-	-	-	-	-	-	-	-
Unidentified larval fish	*Unidentified larval fish*	-	-	-	-	-	-	-	-	-	-	0.06	0.06	-	-	1
Total crustaceans						**5,676**					**5,769**					**7,046**
Porcelain crabs	*Porcellanidae*	140.19	20.78	4.8	0.0	2,052	237.76	47.87	5.2	0.0	3,691	275.31	44.58	5.8	0.0	4,274
Mud crabs	*Xanthidae*	218.14	43.52	7.8	0.1	3,193	94.95	18.59	9.8	0.1	1,474	126.06	26.41	9.0	0.1	1,957
Snapping shrimp	*Alpheus heterochaelis*	14.28	2.48	15.3	0.4	209	21.13	3.18	14.5	0.3	328	28.02	3.19	16.3	0.3	435
PL penaeid shrimp	*Postlarval Penaeidae*	6.76	1.88	5.6	0.1	99	4.19	1.18	5.6	0.3	65	9.28	1.95	5.0	0.1	144
Marsh grass shrimp	*Palaemonetes vulgaris*	3.62	1.66	13.4	0.5	53	6.76	2.49	14.4	0.3	105	3.86	1.17	14.3	0.4	60
Grass shrimp	*Palaemonetes spp.*	1.30	0.56	11.6	1.0	19	0.84	0.42	12.8	1.5	13	0.71	0.30	12.2	1.3	11
Gulf stone crab	*Menippe adina*	2.80	0.56	36.1	3.2	41	5.48	1.02	25.5	1.8	85	10.50	2.23	17.5	0.9	163
Arrow shrimp	*Tozeuma carolinense*	0.07	0.07	13.6	-	1	0.06	0.06	14.8	-	1	-	-	-	-	-
Brown shrimp	*Farfantepenaeus aztecus*	0.07	0.07	-	-	1	0.06	0.06	56.9	-	1	-	-	-	-	-
Olivepit porcelain crab	*Euceramus praelongus*	0.20	0.15	10.0	1.0	3	-	-	-	-	-	-	-	-	-	-
Cleaner shrimp	*Hippolytidae*	-	-	-	-	-	0.13	0.13	7.7	0.5	2	-	-	-	-	-
Daggerblade grass sh.	*Palaemonetes pugio*	0.14	0.14	9.1	0.4	2	-	-	-	-	-	0.06	0.06	6.9	-	1
White shrimp	*Litopenaeus setiferus*	-	-	-	-	-	0.13	0.13	10.2	0.1	2	0.06	0.06	15.1	-	1
Blue crab	*Callinectes sapidus*	-	-	-	-	-	0.06	0.06	33.1	-	1	-	-	-	-	-
Longnose spider crab	*Libinia dubia*	0.14	0.10	5.4	0.6	2	0.06	0.06	9.0	-	1	-	-	-	-	-
Ghost shrimp	*Callianassa spp.*	0.07	0.07	14.8	-	1	-	-	-	-	-	-	-	-	-	-

Mean values were calculated from 33 samples for unrestored bottom and 35 samples each for natural reef and restored reef habitats. Density values in number ind. m^{-2}. Size values in mm. Dash indicates no catch.

Table 3. Overall mean species density and SE, mean size and SE, and total number collected from trawls in unrestored bottom, natural reef and restored reef habitats during the study.

		Unrestored bottom					**Natural reef**					**Restored reef**				
Common name	**Scientific name**	**Mean density**	**SE**	**Mean size**	**SE**	***n***	**Mean density**	**SE**	**Mean size**	**SE**	***n***	**Mean density**	**SE**	**Mean size**	**SE**	***n***
Total fish						**205**					**81**					**271**
Code goby	*Gobiosoma robustum*	0.01	0.00	20.2	1.0	42	0.01	0.01	23.4	1.2	43	0.01	0.01	22.0	1.2	45
Gulf toadfish	*Opsanus beta*	-	-	-	-	-	0.00	0.00	43.8	-	1	0.00	0.00	150.0	-	1
Spot	*Leiostomus xanthurus*	0.00	0.00	25.9	-	1	-	-	-	-	-	0.07	0.05	32.1	0.7	175
Darter goby	*Ctenogobius boleosoma*	0.01	0.01	17.6	0.9	32	0.00	0.00	20.5	1.8	9	0.00	0.00	18.8	2.1	15
Naked goby	*Gobiosoma bosc*	0.00	0.00	29.0	1.4	5	0.00	0.00	27.3	2.7	8	0.00	0.00	26.9	1.0	3
Goby species	*Gobiidae*	0.00	0.00	19.9	1.5	13	-	-	-	-	-	0.00	0.00	5.0	-	1
Atlantic croaker	*Micropogonias undulatus*	0.04	0.03	15.1	0.9	79	0.00	0.00	15.6	3.6	2	0.00	0.00	18.0	2.8	7
Skilletfish	*Gobiesox strumosus*	0.00	0.00	31.4	3.1	7	0.00	0.00	24.2	1.7	8	0.00	0.00	30.1	4.0	7
Green goby	*Microgobius thalassinus*	0.00	0.00	18.5	1.3	9	0.00	0.00	16.4	1.2	2	-	-	-	-	-
Stretchjaw blenny	*Chasmodes longimaxilla*	-	-	-	-	-	0.00	0.00	52.3	2.5	2	0.00	0.00	55.5	-	1
Pipefish	*Sygnathidae*	0.00	0.00	89.0	8.5	4	0.00	0.00	134.7	38.8	3	0.00	0.00	62.5	1.4	6
Bay whiff	*Citharichthys spilopterus*	0.00	0.00	39.2	10.2	8	0.00	0.00	15.7	-	1	0.00	0.00	20.7	5.5	3
Blackcheek tonguefish	*Symphurus plagiusa*	0.00	0.00	18.9	0.3	2	0.00	0.00	14.1	-	1	0.00	0.00	19.0	-	1
Least puffer	*Sphoeroides parvus*	0.00	0.00	36.7	-	1	0.00	0.00	72.3	-	1	0.00	0.00	39.1	-	1
Speckled worm eel	*Myrophis punctatus*	-	-	-	-	-	-	-	-	-	-	0.00	0.00	147.0	-	1
Pinfish	*Lagodon rhomboides*	0.00	0.00	45.1	-	1	-	-	-	-	-	0.00	0.00	120.0	-	1
Sheepshead	*Archosargus probatocephalus*	0.00	0.00	54.7	-	1	-	-	-	-	-	0.00	0.00	109.8	-	1
Bay anchovy	*Anchoa mitchilli*	-	-	-	-	-	-	-	-	-	-	0.00	0.00	19.3	-	1
Blackwing searobin	*Prionotus rubio*	-	-	-	-	-	-	-	-	-	-	0.00	0.00	45.8	-	1
Total crustaceans						**1,093**					**913**					**1,335**
Porcelain crabs	*Porcellanidae*	0.10	0.02	4.7	0.1	267	0.10	0.02	4.7	0.1	300	0.12	0.05	4.4	0.1	207
Mud crabs	*Xanthidae*	0.20	0.08	8.1	0.2	593	0.13	0.02	8.4	0.2	431	0.12	0.03	7.8	0.2	329
Snapping shrimp	*Alpheus heterochaelis*	0.00	0.00	18.3	3.7	5	0.00	0.00	13.9	1.9	8	0.00	0.00	14.4	1.7	5
PL penaeid shrimp	*Postlarval Penaeidae*	0.01	0.01	12.5	1.3	22	0.01	0.01	11.7	0.8	23	0.08	0.03	6.6	0.2	189
Marsh grass shrimp	*Palaemonetes vulgaris*	0.00	0.00	12.9	0.8	10	0.01	0.00	15.4	1.0	23	0.07	0.02	14.5	0.3	191
Grass shrimp	*Palaemonetes spp.*	0.01	0.01	8.0	0.4	26	0.01	0.00	8.6	0.3	34	0.11	0.04	8.1	0.1	287
Gulf stone crab	*Menippe adina*	0.00	0.00	15.4	2.2	9	0.00	0.00	16.7	2.4	15	0.00	0.00	21.8	8.9	7
Swimming crabs	*Portunidae*	0.05	0.04	9.0	0.6	133	0.02	0.01	9.4	0.7	65	0.02	0.01	8.6	0.7	68
Arrow shrimp	*Tozeuma carolinense*	0.00	0.00	12.5	0.8	14	0.00	0.00	12.9	2.2	6	0.01	0.01	13.7	0.5	35
Brown shrimp	*Farfantepenaeus aztecus*	0.00	0.00	47.9	2.5	11	0.00	0.00	39.5	4.0	3	0.00	0.00	46.4	4.2	9
Olivepit porcelain crab	*Euceramus praelongus*	0.00	0.00	6.3	-	1	0.00	0.00	7.7	0.6	2	0.00	0.00	8.8	-	1
Cleaner shrimp	*Hippolytidae*	-	-	-	-	-	0.00	0.00	9.2	-	1	0.01	0.01	17.4	4.7	4
Daggerblade grass sh.	*Palaemonetes pugio*	-	-	-	-	-	-	-	-	-	-	0.00	0.00	13.0	3.7	3
White shrimp	*Litopenaeus setiferus*	0.00	0.00	30.8	5.4	2	-	-	-	-	-	-	-	-	-	-
Blue crab	*Callinectes sapidus*	-	-	-	-	-	0.00	0.00	45.9	3.1	2	-	-	-	-	-

Mean values were calculated from 18 samples per habitat type. Density values in number ind. m^{-2}. Size values in mm. Dash indicates no catch.