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SETBACKS AND SURPRISES

Do restored oyster reefs benefit seagrasses? An experimental study in the Northern Gulf of Mexico

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Oyster reefs and seagrass beds are being lost worldwide at alarming rates. These habitats provide many services to humankind and, thus, much effort has been dedicated to their restoration. Here, we examine the efficacy of created oyster reefs at enhancing seagrass beds through the amelioration of hydrographic conditions and water quality. We carried out a field experiment in the Northern Gulf of Mexico where we compared areas shoreward of created reefs with adjacent reef-free areas over several years using a before-after control-impact (BACI) design. The reefs were built with oyster shell, measured 65 m, and were placed at circa 100 m from the shoreline to ensure subtidal conditions and enhance oyster recruitment. The BACI results showed few and disparate effects of the reefs, even when distance from the reef was factored in. However, we found a temporal increase in seagrass cover throughout all the experimental area (i.e. including both reef and control plots) following reef deployment. Interestingly, further analysis with satellite imagery showed the experimental area had higher seagrass cover 5 years after reef deployment than it did before reef deployment, but such increase was not observed for nearby areas. In concert, the results suggest "shadow" effects for the reefs examined, where positive effects on seagrass beds extend beyond the area directly shoreward from the reef. Oyster reef restoration may have positive impacts on shallow seagrass beds in turbid, high-energy systems; however, more work on the extent and mechanisms for this interaction is needed.

Key words: BACI design, ecosystem services, living shorelines, shoalgrass, water quality, widgeongrass

Implications for Practice

- The positive effects of reefs on seagrass beds may expand beyond the reef and "spill over" adjacent areas.
- Confirmation of "shadow effect" of restored reefs on adjacent control areas requires studies at large scales with controls areas sufficiently far from the reefs.

Introduction

The importance of shellfish reefs as nursery grounds for commercially and ecologically important fish species has been well established (Beck et al. 2001). The complex 3-dimensional reef structures provide refugia for prey species and predatory grounds for predators. Many ecosystem services are associated with shellfish reefs, namely water quality enhancement, nutrient cycling, and assimilation; benthic-pelagic coupling and protection and enhancement of adjacent emergent and submerged vegetation (Peterson & Lipcius 2003; Newell & Koch 2004; Newell et al. 2005; Plutchak et al. 2010). Despite their importance, oyster reefs are among the most exploited habitats with a global areal loss of 85% within the past 130 years (Beck et al. 2011). Within the last century, losses have amounted to 64% for reef extent and 88% for oyster biomass in the United States alone (Zu Ermgassen et al. 2012). Unsustainable harvesting practices (Rotschild et al. 1994), sedimentation (Coen & Luckenbach 2000), degraded water quality and hypoxia (Lenihan & Peterson 1998), and salinity alteration (Volety 2008) are the major causes of oyster reef degradation. Degraded reefs provide lower levels of ecosystem service than healthy reefs, which has become a major concern (Beck et al. 2011).

To mitigate the adverse impacts of oyster loss, restoration and research efforts have accelerated in the Atlantic and the Gulf coasts (Schulte et al. 2009; La Peyre et al. 2014). The Atlantic and the Gulf coast native, the eastern oyster (*Crassostrea virginica*), is one of the most commonly restored shellfish species, because it forms more extensive and complex reefs than any other bivalve species (Rotschild et al. 1994). Restored oyster reefs are considered an important "living shorelines" component, that is, an ecological alternative to traditional shoreline stabilization structures (bulkheads, riprap revetments, etc.; Scyphers et al. 2011).

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Success in restoration projects is often gauged as the degree to which the restored habitat provides the goods and services of their natural counterparts. Assessing restoration progress may require long-term comprehensive monitoring, which may be challenging to maintain due to budgetary and regulatory constraints (Suding 2011). Further, some restoration projects require preemptive preparatory measures (i.e. adaptive management) for unpredictable outcomes, thus complicating the progress assessment. Monitoring programs that are restricted in time and space may overlook recovered benefits from restoration programs (Bell et al. 2014). Most monitoring of restored oyster reefs has focused on enhancing shellfish and finfish abundance, along with increased market values for fisheries (Gregalis et al. 2009). Other benefits of restored oyster reefs, such as enhanced water quality and shoreline protection, have also been monitored (Plutchak et al. 2010; La Peyre et al. 2014). However, assessments of effects of restored reefs on adjacent seagrass beds are rare, although seagrasses and oysters typically co-occur in nearshore estuarine waters of Northern Gulf of Mexico (nGOM).

Seagrasses are important ecosystem engineers and provide various ecosystem services, such as, habitat provision (Heck et al. 2003); sediment stabilization (Christianen et al. 2013); wave attenuation (Fonseca & Cahalan 1992); carbon sinks (Duarte et al. 2013); and neighboring system subsidization (Heck et al. 2008). However, seagrasses are declining globally due to synergistic effects of natural and anthropogenic stressors (Orth et al. 2006; Waycott et al. 2009). Seagrass restoration typically involves seed sowing, seedling planting, and/or sod transplantation. Although, restoration techniques have improved substantially within the past decade, it remains expensive to restore seagrass beds. Further, such efforts often do not produce seagrass beds (Christiaen et al. 2013). The deployment of oyster reefs could, however, prove as an efficient technique to bring back seagrass beds into coastal systems or, alternatively, enhance existing beds shoreward of the reefs. Along with enhancing seagrass beds, oyster reefs could also generate other environmental benefits, therefore providing an "all-in-one" rather than "piece-meal" restoration approach. "All-in-one" approach considers restoration and conservation of key estuarine habitats collectively rather than focusing the conservational efforts on each habitat independently.

Oyster reefs provide physical protection on their leeward side, thereby ameliorating conditions for seagrass growth (Meyer et al. 1997; Piazza et al. 2005). Sedimentation (from buffered wave energy) and nutrient inputs (addition of feces and pseudo-feces from live oysters) may enhance seagrass growth (Newell & Koch 2004). Moreover, oysters may increase water clarity by filtering particulate organic matter, thus benefitting seagrasses (Peterson & Lipcius 2003; Plutchak et al. 2010). In this study, we evaluate the impacts of restored reefs on water quality and seagrass beds shoreward of the reefs.

We hypothesize that the deployed reefs will improve water quality (through water filtration and wave attenuation) and subsequently will enhance seagrass growth in comparison to reef-absent control areas (Fig. S1). To test these hypotheses, we deployed four oyster reefs in a coastal location of the nGOM. Our study encompassed 1.5 km of shoreline and compared the deployed reefs with adjacent control areas over more than 3 years. To assess the impacts of created reefs, we used a BACI design to compare reef and control plots. BACI designs account for ambient temporal and spatial variability between reefs and reef-free plots prior to reef deployment and include that variability into the analysis to describe more accurately the specific impacts of the reefs (Smith 2002). Such designs are useful in assessing restoration outcomes (Geraldi et al. 2009; Plutchak et al. 2010).

Methods

Study Site and Oyster Reefs

The study site was located in northeast Point-aux-Pins (NEPAP), a peninsula located in Portersville Bay in coastal Alabama (site center: 30.38°N, 88.30°W; Fig. S2A). Tides are diurnal (mean tidal amplitude: 0.43 m). Prevalent winds are from the south/southeast in spring/summer and from the north in winter accompanied by cold fronts. Mean wind speed averages 18 km/hour with high seasonal variability. Patches of seagrass, namely shoalgrass (*Halodule wrightii*) and widgeon grass (*Ruppia maritima*), occur only in shallow areas (<1 m) due to high water turbidity (Heck et al. 2001). The patches are usually small (a few m^2). Smooth cordgrass (*Spartina alterniflora*) spreads along the marsh fringes with a few intermittent escarpments. Oyster clumps are frequent through the intertidal marsh zone (Moody et al. 2013). Salinity oscillates within 20–27 ppt, although episodes of low salinity may occur.

Four reef complexes made of loose oyster shell were constructed perpendicular to the dominant wind direction in September 2009 by adding clean shells bought from a local shell-processing vendor. Our study followed a randomized paired design ($n = 4$), with each pair consisting of a reef complex and a control plot with no reef (Fig. S2B). Reefs and controls within the pairs were separated by 75 m, and adjacent pairs by 100 m (except Pairs 3 and 4: separated by 125 m). Each reef complex consisted of three trapezoidal units, each unit was 25 m long, 5 m wide, and 1 m tall (Fig. S2C). Biodegradable reinforcing fences were set up around the reefs for extra support. Reefs were constructed approximately 110 m from the shoreline (Fig. S3), where the mean lower low water depth corresponded to the height of the reefs, thereby submerging most of the reef area.

Sampling

Within each control and reef plot, three parallel transects separated by 25 m were established ($n = 24$). Each transect ran perpendicular from the shoreline to the deployed reef (or equidistantly in case of the controls). Along the three transects, fixed sampling stations were established at 1- (shore-), 55.5- (mid-), and 110-m (reef-stations) from the shoreline, for nine sampling stations within a plot (total sampling stations: $n = 72$; Fig. S3). At the nine sampling stations, water quality (total suspended solid, particulate organic matter, and water column chl-*a*), sediment (organic matter, silt-clay fraction, and benthic chl-*a*), seagrass, and polychaete samples were taken approximately monthly from April to October and once each in November, January, and March starting from December 2008. Standard sampling methods are provided as Supporting Information (Appendix S1).

Further, we obtained continuous records of water temperature, salinity and dissolved oxygen from nearby weather stations at Dauphin Island Katrina Cut (2011–2012; 16 km from NEPAP; Fig. S2A) and Dauphin Island East End (2006–2012; 25.5 km from NEPAP). Additional hydrographic data were obtained from a YSI-probe stationed at Portersville Bay (2008–2010; 5 km away YSI Model: 6600 EDS V2–4 units, YSI Inc., Yellow Springs, Ohio, USA). These hydrographic parameters were measured at 0.5 m above the sediment.

We mapped reef footprint in November 2009, October 2010, and November 2011. Shellfish densities on the reefs were measured semiannually from April 2010 to May 2012 for five times. We measured water currents using SeaHorse tilt current meters by simultaneously deploying eight current meters in all plots at the central sampling station (station 5; Fig. S3). The current meters were deployed for three time-periods spanning from March 2012 to October 2012 (24 days in March; 30 days in April/May; and 23 days in September/October).

Similarly, we measured point photosynthetically active radiation (PAR) at the central sampling station. These measurements were taken at varying intervals (weekly prereef deployment and approximately monthly from April–October and bi-monthly from November–March postreef deployment). Additionally, continuous PAR was measured at the central sampling stations from March to November 2011. Along with the seagrass measurements taken at all nine stations in each plot, we also monitored specific seagrass patches located between the reef (or adjacent control) and the shoreline for 2 years. These measurements were taken postreef deployment approximately monthly from April to October and once each in November, January, and March.

Finally, we analyzed seagrass cover along the NEPAP shores using satellite imagery (orthoimagery) acquired from Landsat (Thematic Mapper) satellite and QuickBird and Ikonos imagery obtained from Google Earth (GE). GE imagery is easily available, has high-resolution and true color composition (24-bits depth), and is frequently used to map coasts (Collin et al. 2014). Our intent was to compare seagrass cover pre- and postreef deployment between the pairs and surrounding areas south and north of the pairs to gauge evidence of "shadow" effects by the reefs. We divided the shoreline in four areas (Fig. S4), (1) a south control area (south of the experimental pairs 1 and 2, past a man-made canal); (2) pairs 1 and 2 together; (3) pairs 3 and 4 together; and (4) a north control area (north of experimental pairs 3 and 4 by mouth of Little River). The four areas share a similar physical and environmental setting.

Statistical Analysis

Reef effects were analyzed following a paired before-after control-impact (BACI) design. For each sampling time, we calculated the difference between each of the sampling stations in the reef plot and the corresponding station in the control plot in the pair (e.g. station 1 in reef plot − station 1 in control plot; station 2 in reef plot − station 2 in control plot, and so forth; Fig. S3). Then we calculated the mean value of the nine differences, and those mean values were compared before and after reef deployment with a *t* test for each pair separately. For point PAR measurements, this was done for station 5 (mid-station) because those data were only obtained at that station. To see if there was any effect of distance from the reef, we carried out similar analysis using the average values for the three closest stations to the shoreline (1, 2, and 3), the three mid-distance stations (4, 5, and 6), and the three stations closest to the reef (7, 8, and 9; "reef-proximity" specific analysis).

One-way analysis of variance (ANOVA) was used to test the difference in bivalve densities among sampling dates followed by post hoc Tukey tests. Water-current velocity and continuous PAR were only measured at station 5 during a number of time intervals postreef deployment. To analyze these data, we used two-way repeated measures ANOVA with treatment as the among-subject factor and time as the within-subject factor. For these analyses, daily averages were used. For PAR, we considered the readings between 10:00 and 16:00 to calculate daily averages. A different repeated measures ANOVA (RMANOVA) was done for each time interval. Seagrass patch measurements were also analyzed with two-way RMANOVA with treatment as the among-subject factor and time as the within-subject factor. The measurements obtained for the three patches at each plot on each sampling time were averaged into one single replicate.

The temporal dynamics of *R. maritima* and *H. wrightii* were examined using two-way RMANOVA with time as the within-subject factor and species (*R. maritima* vs. *H. wrightii*) as the among-subject factor. The additional seagrass analysis was a follow-up of the BACI results (see justification in the Results section) and specifically focused on the temporal trends of both species in the study area. We pooled reef and control plots and considered each of the nine sampling stations within each plot as a single replicate. Post hoc paired *t* tests comparing density between the two species were done between control and reef plots separately for each sampling time when there was a significant interaction between time and treatment. We did these analyses for each pair separately.

Prior to ANOVA analysis, data were tested for normality using the Shapiro–Wilk test and homogeneity of variance using the Bartlett's test, and transformed when necessary to meet the assumptions of the test. We also confirmed that the sphericity requirement for RMANOVA was met. All statistical tests were considered significant at $p \leq 0.05$. All statistical analyses were done using SigmaPlot version 12.0.

Results

Overall, we recorded similar mean values and ranges of water temperature, salinity, and dissolved oxygen in the three nearest

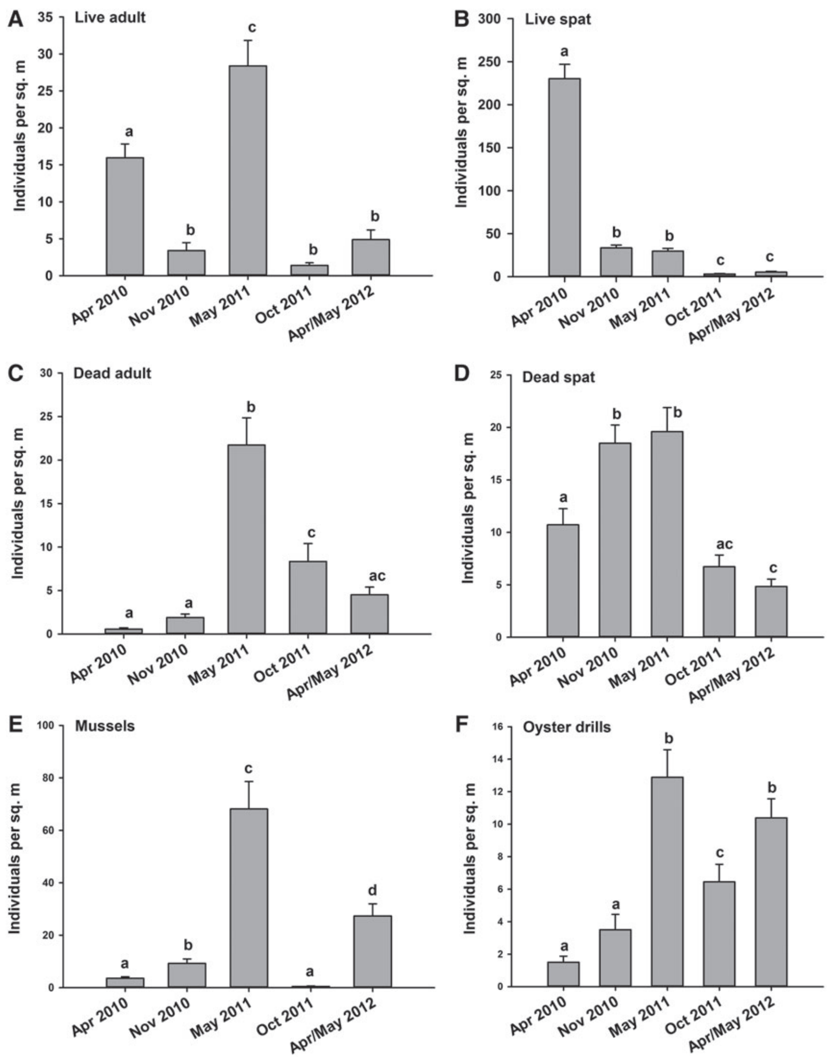

Figure 1. Density of (A) live adult oysters (SH > 3 cm); (B) live spat (SH < 3 cm); (C) dead adult oysters; (D) dead spat; (E) mussels; and (F) oyster drills. Letters denote significant differences following Post hoc Tukey tests. Bins represent means and bars ± SE.

hydrographic stations to NEPAP (Table S1). Water temperature values showed typical seasonal oscillations. Salinity remained most often within typical values for open coastal waters in the area, although large decreases to oligohaline levels occurred throughout the study period. Generally, waters remained well oxygenated, but hypoxic/anoxic levels were recorded in the stations. Our study site was very shallow and generally well mixed and, thus, anoxic/hypoxic conditions in the water column should have occurred rarely.

Densities of live and dead adult oysters were highly variable, with the peak in May 2011 (Fig. 1A & 1C). Lower adult oyster densities later in the sampling periods could be due in part to the decline in recruitment. The live spat density decreased consistently through the sampling period to <20 individuals m^{-2} on the last two sampling dates (Fig. 1B). The dead spat density was also low on the last two sampling dates (Fig. 1D). High oyster-drill densities were found later in the sampling period (Fig. 1F). Mussel densities also oscillated through the sampling period (Fig. 1E). Our reef footprint maps showed that the reefs were stable and stayed in place (Fig. S5).

We observed optimal water temperature, salinity, and dissolved oxygen; however, water-current velocity, total suspended solid (TSS), particulate organic matter (POM), chl-*a*, and PAR values did not show significant difference between reef and control plots (Tables S2, S4, S6; Figs. S6, S7A, S8). This was also the case for the separate "reef-proximity analyses," that is stations pooled as 1–3, 4–6, and 7–9 (Table S5; Fig. S3). Water depths at station 5 were similar among plots (Table S7).

Similarly, we did not observe significant impact of reef deployment in sediment metrics. (Table S4, S5; Fig. S7B). However, when all nine stations were considered, we found a significant impact of reef deployment in Pair 3, with higher polychaete density observed in the reef than in the control plot after reef deployment but not before reef deployment (Table S4; Fig. S7B). These across-plot differences for polychaete density

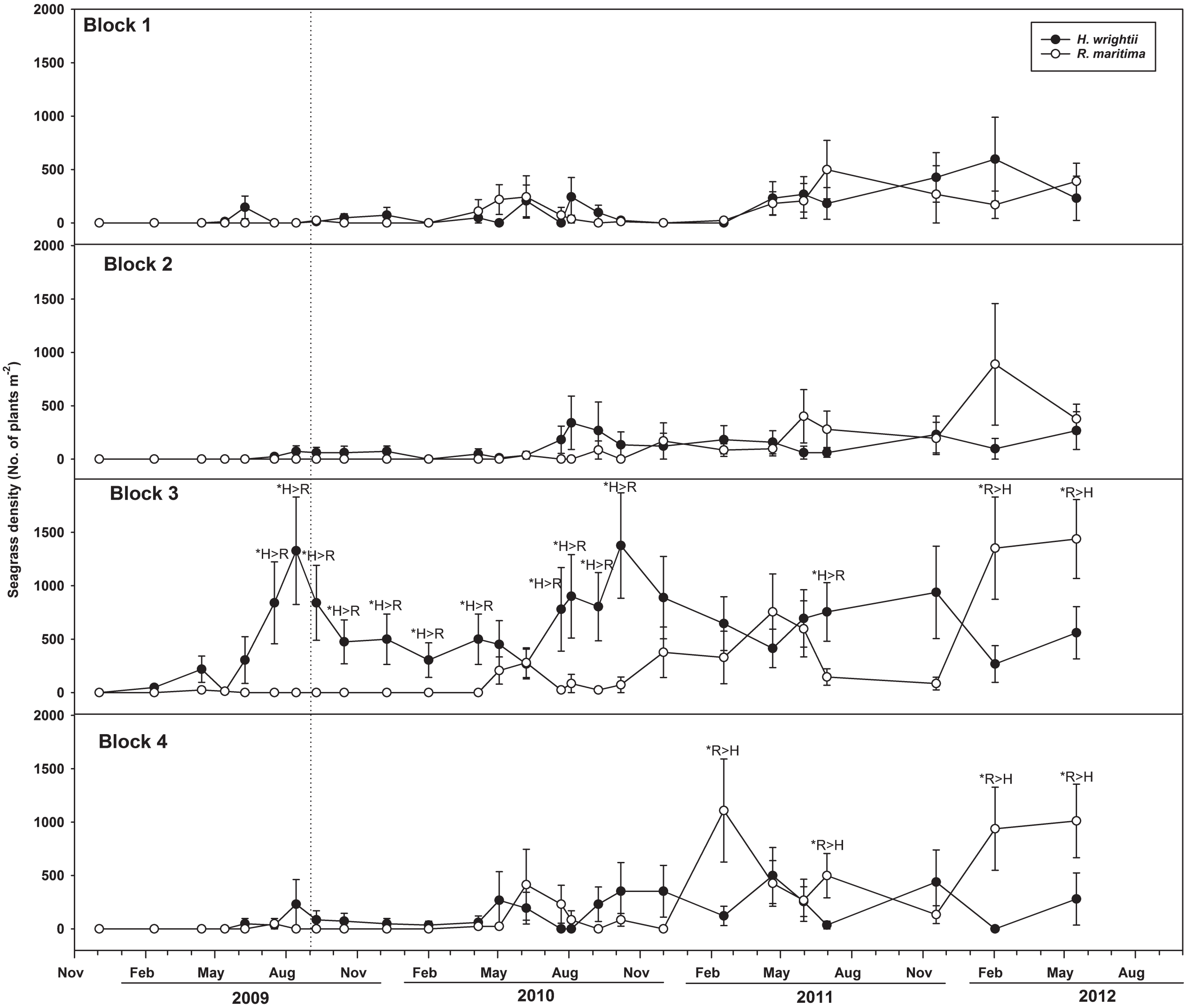

Figure 2. Seagrass density temporal dynamics. Bars represent ± SE. Dotted line represents the time of reef deployment.

were probably driven by the three stations closest to the reef (Table S5).

When all nine sampling stations were considered in seagrass analysis, few and disparate significant impacts of reef deployment were found for density and biomass after reef deployment (Table S4, Fig. S7C). Reef-proximity analyses also showed similar effects (Table S5). Density within the patches changed over time (RMANOVA; $p < 0.05$ for time effect) but not between control and reef plots ($p > 0.05$ for treatment and interaction effects) for both seagrass species (Fig. S9).

Despite finding no significant impact of reef deployment on seagrass abundance using the BACI analysis, we noticed an overall increase in seagrass abundance after reef deployment across the area examined. Seagrass density generally increased over time after reef deployment in all four pairs (Table S8; Fig. 2). In Pairs 1 and 2, the pattern of increase was similar for *Halodule wrightii* and *Ruppia maritima,* and density did not differ between the two species during the experiment. In Pair 3, *H. wrightii* increased before reef deployment and showed higher densities than *R. maritima* during most of the study period. *Ruppia maritima* increased later and had higher densities than *H. wrightii* on the last two sampling dates. In Pair 4, the increase after reef deployment was similar for the two species in the first half of the experiment, but *R. maritima* increased to a larger extent and was often denser than *H. wrightii* during the second half of the experiment.

Our remote sensing analysis revealed that, 5 years after reef deployment, seagrass cover was higher than prereef deployment levels throughout the entire area covered by the experimental pairs (including both the control and reef plots). Seagrass cover area at Pairs 1 and 2 increased by 5.4 times from 2,613 m^2 (in June 2006) to 13,998 m^2 (in November 2013) and at Pairs 3 and 4 it increased by 14.1 times from 3,589 m^2 (June 2006) to 50,662 m^2 (November 2013). However, seagrass cover area at South Control decreased by 0.6 times from 3,363 m^2 (in June 2006) to 2,057 m^2 (in November 2013) and at North Control it

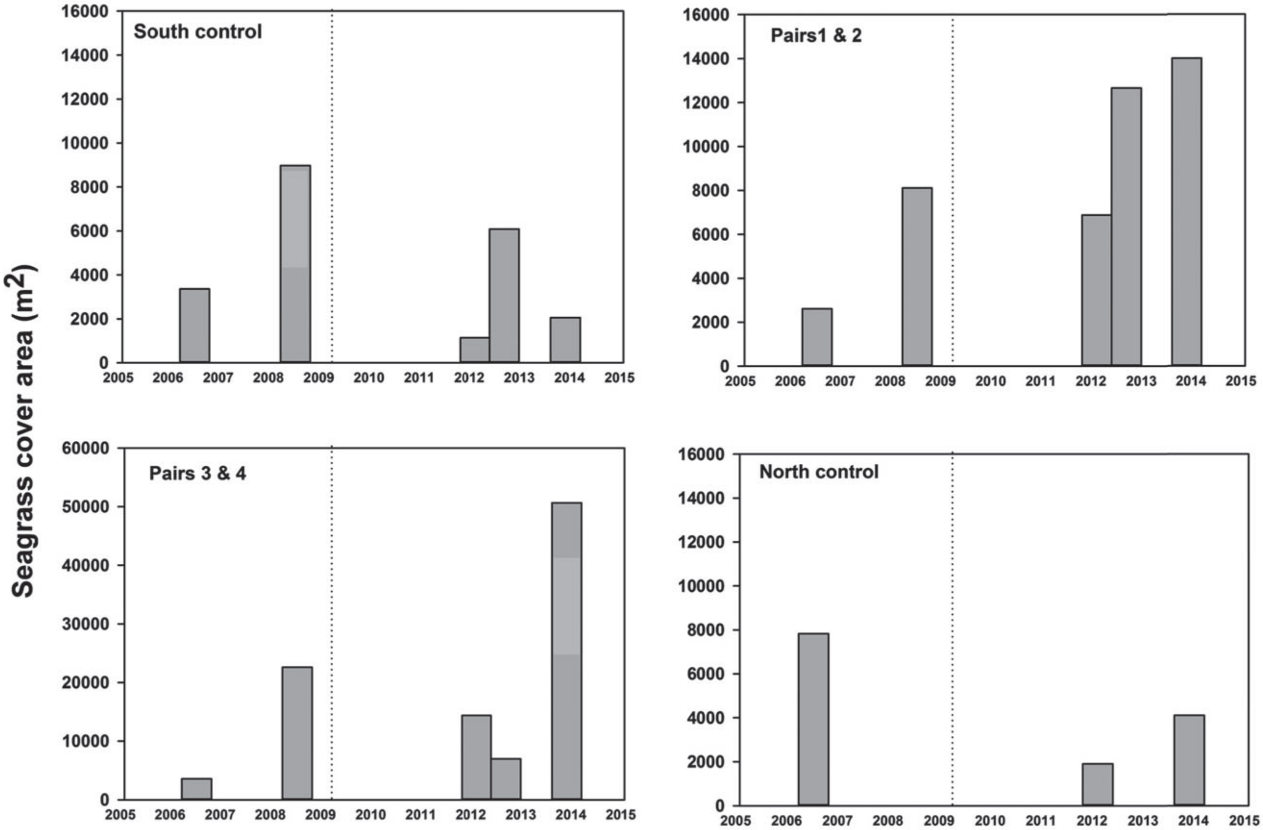

Figure 3. Seagrass cover in our experimental and adjacent areas. Dotted line represents the time of reef deployment.

decreased by 0.5 times from 7,823 m^2 (June 2006) to 4,100 m^2 (November 2013) (Fig. 3).

Discussion

Although oyster reefs are known to provide habitat for fish and crustaceans, yet their role in facilitating adjacent habitat expansion is less explored. Here, we report that created oyster reefs could potentially enhance seagrass cover in shallow waters in the nGOM.

Stability of restored reefs is crucial for quality ecosystem services and sustained oyster population, which may be dependent in part on availability of substrate for new spat recruitment (La Peyre et al. 2014). Hydrographic records generally showed favorable conditions for oyster growth around NEPAP and the created reefs maintained the structural integrity. Despite the prediction of high spat recruitment from physical and biological models around NEPAP, favorable hydrographic conditions and stable reefs did not translate into high oyster density (Hoese et al. 1972; Kim et al. 2010). Indeed, mean live oyster density of 35 individuals m^{-2} in this study represents only a fraction of values reported elsewhere, e.g. 728 ± 101.9 in Louisiana (La Peyre et al. 2014), 200–300 in Alabama (Geraldi et al. 2009), and 250.4–1026.7 in Chesapeake Bay (Schulte et al. 2009).

We suggest that predators played a role at our experimental site. Adapted to high salinity, oyster drills are one of the natural predators of the eastern oyster in the nGoM (Garton & Stickle 1980). Indeed, oyster drill density was highest in 2011, followed by 2012, corresponding with the most saline years around NEPAP. Other mobile predators of the eastern oysters such as black drums and blue crabs are not uncommon in the Gulf waters, and NEPAP is no exception (Brown et al. 2008; Gregalis et al. 2008). Decreased spat recruitment in the later sampling events coinciding with high mortality may be due to predation and/or physical disturbance (Scyphers et al. 2011). Predation, mortality, and physical disturbance probably resulted in low oyster density at our reefs.

Based on established premises, we expected that reefs abundant with live oysters would attenuate wave energy and increase water clarity, and consequently have positive impacts on the light-limited seagrass beds leeward of the reefs (Newell & Koch 2004). However, the BACI analysis did not support large or consistent reef effects on water quality and seagrass beds. This was also the case when distance from the reef was factored in and reef-proximity was analyzed. Based on these results, our reefs did not perform as expected. Limited wave attenuation efficiency of subtidal reefs coupled with low bio-filtration from sparse oysters resulted in nonsignificant reef effect on water-current velocity and water quality. Although reefs were deployed to coincide with the mean lower low water (to maximize larval recruitment), the intended recruitment level was not attained as predicted by previous studies (Hoese et al.

1972). The ratio of reef length to the reef deployment distance was probably too low to attenuate wave energy substantially. In wave-dominated open systems, such as NEPAP, frequent resuspension and constant intermixing of water may demand higher bio-filtration efficiency from large oysters (La Peyre et al. 2014); because our reefs were not densely populated, bio-filtration was limited. Further, an effect of live oysters on seagrass patches as modeled by Newell & Koch (2004) was not detected, perhaps because feces/pseudo-feces did not reach the seagrass sediment or accumulated away from the segrass beds (Booth & Heck 2009).

Seagrass patches restricted to the shallow waters of NEPAP are typically subjected to environmental stresses related to water temperature, wind speed, turbidity, and water-current velocity. Further, the shallow seagrass patches are often exposed at low tides during winter, imposing additional stress. We hypothesized that reefs would ameliorate the stressful conditions and have a positive impact on seagrasses by improving hydrological and water quality conditions. Despite the lack of support for this hypothesis, our study offers evidence that the constructed reefs may benefit the seagrass beds between the reefs and shoreline. Namely, we generally found an increase in seagrass abundance after reef deployment throughout the experimental area including all pairs and reef and control plots. These results suggest a "shadow" effect, that is, their effect may have cascaded to both sides of the reef toward the shore, thereby spilling over into the adjacent control plots.

The possibility of a "shadow" effect is supported by seagrass cover from satellite imagery in all four control and reef plots and two nearby areas on a number of dates before and after reef deployment. The nearby areas were also located in NEPAP and had similar environmental conditions to our experimental area, but were sufficiently far from the reefs to prevent "shadow" effects, at least to the same magnitude as they could have occurred in control plots adjacent to reef plots. Our control and reef plots had higher seagrass area 5 years after reef deployment than they did before reef deployment; however, such increases were not observed in nearby areas. These long-term, large-scale results also suggest that accurate assessment of oyster reefs impacts on environmental quality and status of surrounding habitats may require monitoring that extends well beyond the reefs and over several years (Bell et al. 2014). Thus, we cannot conclude unequivocally that the increase in seagrass cover after reef deployment is due to the reefs. We conclude that oyster reef restoration may have positive impacts on shallow seagrass beds in turbid, high-energy systems, but more work on the extent and mechanisms is needed. However, we iterate that significant effects of reefs could be found due to small improvements in water quality and shear (friction, wave energy), given the high natural levels of murkiness and wave energy that exist in the area (i.e. stringent limiting light and wave energy conditions for seagrass growth). To be able to detect this effect, we possibly need to work at large spatial scales with control areas sufficiently far so they are not "shadowed" by the reefs.

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Supporting Information

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

Table S1. Hydrographic parameters (mean ± SE) at nearby stations (see text for details). Mean values correspond to the average of all daily means recorded during the period. Values in the parentheses represent the range (min–max values)

Table S2. Two-way repeated measures ANOVA for water-current velocity (cm/second).

Table S3. Before-after, control-reef values of water quality, K_d, sediment metrics, polychaete density, and seagrass metrics for (A) Pairs 1 & 2 and (B) Pairs 3 & 4. Values represent the mean ± SE for the control or reef plot before or after reef deployment. Values in parentheses represent the range.

Table S4. BACI results for water quality, K_d, sediment metrics, polychaete density, and seagrass metrics including all plot stations (see text for details).

Table S5. BACI results for water quality, K_d, sediment metrics, polychaete density, and seagrass metrics including only the three closest stations to shore ("Shore," stations 1–3); mid-distance stations ("Mid," stations 4–6); and farthest stations from shore ("Reef," stations 7–9) (see text for details); ns, nonsignificant; +, positive reef effect; −, negative reef effect.

Table S6. Two-way repeated measures ANOVA for underwater bottom irradiance (μmoles/m^2/second).

Table S7. Water depth at the location (station 5) where bottom PAR measurements were recorded. Mean and range values have been calculated from depth measurements taken along with PAR point measurements at the station (see text for details).

Table S8. Two-way repeated measures ANOVA for seagrass density temporal dynamics.

Figure S1. Expected impacts of oyster reefs on water quality and seagrass beds shoreward of the reefs.

Figure S2. Study site and reef views. (A) Study site. Black dots represent hydrographic stations (1, Dauphin Island Station; 2, Katrina Cut Station; 3, Portersville Bay Station). (B) Paired control and reef complexes. (C) Aerial and cross-sectional views of the deployed reefs. Three reef units shown in aerial view and one unit in cross-sectional view.

Figure S3. Layout of sampling stations in a reef and control plot. Distances perpendicular to the shoreline are measured from the shoreline. S, M, and N denote south, mid, and north transects, respectively.

Figure S4. Areas compared for the seagrass cover analysis.

Figure S5. Reef footprints.

Figure S6. Mean daily water-current velocity. Bars represent ± SE.

Figure S7. BACI plots for (A) water quality and K_d; (B) sediment metrics and polychaete density; and (C) seagrass metrics. Values are means ± SE of the nine differences between stations in the reef plot and corresponding stations in the control plot (see text for details). Dotted line represents the time of reef deployment.

Figure S8. Mean daily continuous PAR. Bars represent ± SE.

Figure S9. Seagrass density in surveyed patches. Bars represent ± SE.

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