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REVERSING A RAPID DECLINE IN OYSTER REEFS: EFFECTS OF DURABLE SUBSTRATE ON OYSTER POPULATIONS, ELEVATIONS, AND AQUATIC BIRD COMMUNITY COMPOSITION

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ABSTRACT Offshore oyster reefs in the Big Bend Coast of Florida have declined by 88% during the last 30 y, with the most likely mechanism being repeated die-offs due to predation and disease during high-salinity periods, driven by episodic and increasing periods of reduced freshwater input to estuaries. These die-off events have led to a conversion from shell to sandbar substrate and rapid loss of elevation (ca 8 cm/y). This process appears to be nonreversible, because oyster spat are unable to colonize sandy substrate. It is hypothesized that the addition of durable hard substrate would make reefs more resilient to periodic declines in freshwater flow by providing a persistent settlement site for extant larvae. This article reports a test of the assumption that oyster populations on these reefs are limited by substrate, and documents key effects on oysters, elevation, and avian usage associated with the addition of substrate. Durable substrate was added in the form of limerock cobbles and recycled clam *Mercenaria mercenaria* (Linnaeus, 1758) aquaculture bags filled with cultch, live oysters, and associated fauna to eight paired treatment and control sites spaced along a highly degraded offshore reef chain. Elevation on treatment reefs increased postconstruction by an average of 16 cm. Mean oyster density on treatment sites increased by 2.65× on rock, 14.5× on clam bags, and 9.2× overall compared with control sites. Recycled clam bags contributed approximately 25% of the surface area on treatment reefs, but accounted for 52% of the oysters observed. Oyster densities on treatment sites were between 89× and 125× those measured at a larger sample of nearby natural reefs, and exceeded the 89th percentile of reported densities at natural and restored reefs in the Gulf of Mexico. Total bird use was higher on treatment sites, but when controlled for elevation, all species but double-crested cormorants [*Phalacrocorax auritus* (Lesson, 1831)] and bald eagles [*Haliaeetus leucocephalus* (Linnaeus, 1766)] preferred control (sand bar) sites. These results indicate that (1) oyster recruitment can be strongly limited by available, durable substrate, especially in high-energy environments; (2) aquaculture byproduct materials can play a significant role in the process of restoration; and (3) restoration of oyster reefs and other living shorelines may have impacts on avian community composition. Future research should be aimed at understanding whether durable substrate can also confer longer term resilience to oyster reef communities.

KEY WORDS: oyster, reef restoration, avian response, durable substrate, birds, restoration methods, resilience

INTRODUCTION

Oyster reefs are biological communities that support considerable biodiversity, provide habitat for juvenile fish, forage fish, invertebrates, and birds, and support economically important fisheries (Coen et al. 2007, Beck et al. 2011, Grabowski et al. 2012). Oyster reefs can also function to dampen wave action, reducing coastal erosion and protecting coastlines from erosion and storm damage (Piazza et al. 2005, Scyphers et al. 2011), and counteract the effects of nutrient runoff through filtration and sequestration (zu Ermgassen et al. 2013, Kellogg et al. 2013). Oyster reefs are probably the most highly impacted marine habitat in the world, and are declining rapidly due to a variety of stressors ranging from overharvest to pollution and disease introduction (Beck et al. 2011). Partly because of the recognition of coastal resilience derived from ecological and economic functions associated with healthy reefs, interest in restoration of reef function has been rapidly growing (French McCay et al. 2003, Grabowski et al. 2012, La Peyre et al. 2014). Many of the techniques for restoring reefs involve the provisioning of suitable substrate to provide settlement sites for larval oysters (spat) or increase reef elevation to escape anoxic bottom conditions. These efforts can dramatically increase settlement and survival of oysters (Schulte et al. 2009, La Peyre et al. 2014), and the maintenance of oyster substrate to promote persistence of oyster reefs has long been recognized (Swift 1898, Pine et al. 2015).

Although the stressors causing oyster reef declines can sometimes be directly affected through restoration activities (e.g., rebuilding shell stocks or elevation and improving water quality), stressors are frequently multiple, and are often characterized by feedback loops (e.g., harvest and elevation, water quality, and oyster density, see Pine et al. 2015). A common paradox of reef restoration is that although fully restored reefs are likely to be self-sustaining and may even reverse the effects of some stressors, restoration activities must often proceed in an environment that may be considerably less than ideal for oyster recruitment and survival (Beck et al. 2011). Examples of persistent stressors include managed harvest (Powers et al. 2009), diseases (Stokstad 2009, Powell et al. 2012), and elevation loss (Schulte et al. 2009).

Oyster reef restoration has been linked with changes in other parts of the trophic structure of reefs, including fish and macroinvertebrate populations (Rodney & Paynter 2006,

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Scyphers et al. 2011). Birds often forage and roost on intertidal oyster reefs and are widely used as indicators of marine ecosystem health (Furness & Greenwood 1993). Birds can also have top-down effects on estuarine vertebrate and invertebrate populations (Frank 1982, Quammen 1984, Hamilton 2000); however, the effects of oyster reef restoration efforts on bird usage and community structure have not been examined to date.

In the Big Bend region of Florida, oyster reefs exist largely as intertidal structures (Hine et al. 1988, Fig. 1) within a complex of low-energy shoreline habitats (extensive sea grass meadows, salt marshes, and mudflats) in a region of low human population density, and a high percentage of coastline under management for conservation. Oyster reefs in this area have been reduced by 66% overall during the past 30 y (Seavey et al. 2011), with the greatest loss on the more valuable offshore reefs (88%). This loss has been coincident in time with increasing severity and frequency of episodic low freshwater flow events, whereas many other stressors (storm erosion, overharvest, pollution) are largely absent in the region. Although the full explanation for decline remains open, oyster density is highly correlated with salinity gradients (Bergquist et al. 2006) and the leading hypothesis is that episodic declines in freshwater input cause extended high-salinity events, leading to high oyster mortality and low recruitment through predation and disease. An important feature of the pattern of loss is the conversion from reef to sandbar habitat at over 30 long-term monitoring stations in the area. This suggests that the loss of oyster shell coverage following near-complete oyster mortality is a critical event in this sequence, leading to an inability to recruit and retain juvenile oysters in ensuing years. This sequence appears to be irreversible through natural dynamics, and is a considerable departure from historical dynamics, because these reefs are thought to be ca 3,500 y old (Grinnell 1972).

Although the restoration of freshwater inputs through increased regulation on surface and subsurface water in the Suwannee River basin is a long-term regional conservation goal (Farrell et al. 2005), it is unclear when or whether this will be fully implemented. At the same time, under a variety of climate change scenarios, drought frequency and intensity is predicted to increase in this region, perhaps approaching severity not observed for the previous 300 y (Pederson 2012). For these reasons, any timely oyster restoration strategy must focus on promoting resilience of reefs to these changes in freshwater availability (Petes et al. 2012, Camp et al. 2015). It was hypothesized that, during the current era of episodic low flow events, resilience of oyster populations on these reefs could be improved by adding durable substrate to the reef surfaces. On the basis of our prior assessments of oyster spatfall, the Suwannee Sound area does not appear to be limited by available oyster larvae, many of which probably come from inshore populations of oysters that are more buffered from the effects of freshwater discharge (P. Frederick and L. Sturmer, unpublished data). Instead, it is hypothesized that recruitment is limited by survival of postlarvae spat that settle on suitable substrate. A key to this problem is that below some critical population density, oyster shell substrate disappears almost entirely (Lipcius et al. 2015, Pine et al. 2015), probably due to wave action and burying. In this context, the introduction of substrate that persists between die-off events (= "durable" substrate) could be an important intervention, allowing reefs to recolonize following die-offs, effectively increasing their resilience. The main prediction of this intervention is not that durable substrate will prevent oyster death during periods of low freshwater flow, but that it will provide a mechanism for repeated recolonization following periods of extended episodic mortality which could lead to widespread loss of shell material due to burying. This should result in repeated episodes of die-off and recruitment to reefs, rather than the permanent loss currently occurring.

This prediction will obviously take several iterations of low freshwater flow events to test, which will be investigated in future years. A key assumption, however, is that oyster reef recruitment in this situation is primarily limited by substrate in both short and long terms. Further, it is unclear whether the introduction of durable substrate on isolated, high-energy sandbars will have a stabilizing influence, or will result in burying and erosion. This work reports on a controlled addition of durable substrate that mimics the topographic variability of the original reef to understand the effect on oyster size and densities, and elevation profiles (Walles et al. 2016) over the course of 18 mo. In addition, this article examines for the first time habitat use patterns by birds on augmented and degraded reefs.

MATERIALS AND METHODS

Study Area

The study site was located at the Lone Cabbage Reef (LC) along Florida's Big Bend, in Levy County approximately 3 km south of the mouth of the Suwannee River and 14 km north of Cedar Key, FL (Lat: 29° 14′ 53.86″N, Long: 83° 6′1.21″W, Fig. 1). As recently as the early 1990s, the chain extended from East Pass south to Buck Island (6.2 km), with as many as 38 individual reefs. By 2010, the reef extended 3.7 km, with only 13 individual reefs. Further, the size and depth of the inlets had changed markedly, with expansion in width from 27 to 984 m on average. The elevation of reefs prior to 2010 is unknown, but post-2010 trends in elevation (–7.2 cm/y), suggest a considerable loss of reef height since the early 1980s. Lone Cabbage has been closed to harvest since the late 1970s.

Study Design

A simple paired design of treatment (degraded oyster reefs with addition of durable substrate) and control (degraded reefs with no treatment) was used. Durable substrate was defined as materials that last more than 10 y in marine environments and that persist in the presence of strong currents and wave action. As described below, two materials were used, limerock cobbles and clam aquaculture bags containing live oysters, clam and oyster shells, and associated fauna. The first major inlet at the north end of the LC chain was designated as a treatment site, and then treatment and control were alternated at sites moving south. Edges of reefs adjoining these inlets were then numbered so that the northernmost pair (treatment) was 1 and 2, the next pair (control) was 3 and 4, and so on. Four total inlet treatments were compared, with sites 1 and 2, and 5 and 6 being treatment sites, and 3 and 4, and 7 and 8 being the intervening control sites (Fig. 1).

Treatments

All sites were squares 21.3 m on a side (the approximate average width of the reef chain based on historical imagery), with one side oriented normal to the direction of flow through

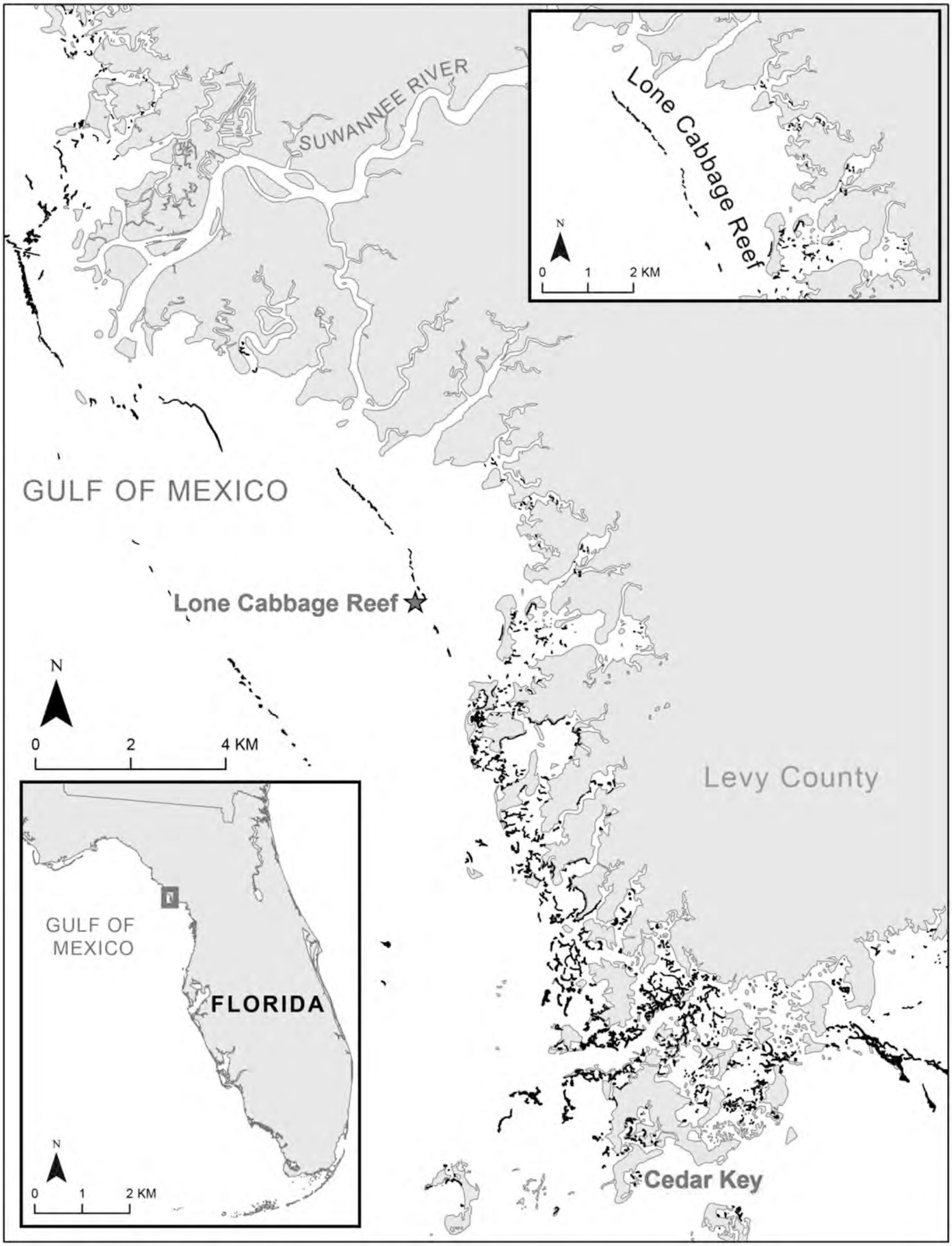

Figure 1. Map showing approximate location of the LC chain of reefs in Suwannee Sound. Oyster reefs are shown in black.

the inlet; all squares were oriented the same relative to one another. The middle of each square at each site was determined through real-time kinematic mapping as true elevation, with squares centered on –0.425 m ortho elevation (see Elevation Determinations below). Corners were marked with 10-cm-diameter polyvinyl chloride (PVC) poles that were approximately 2 m in length driven into the substrate.

Prior to construction, elevation, oyster density, and oyster size were measured on each of the treatment and control sites. Following this preconstruction assessment, we cleared all live oysters from the treatment sites and placed them to the northern side of the construction area. These oysters were then redistributed by random placement onto the construction footprint once construction was complete. The same activity was then carried out in a mock manner (picking up but not moving oysters) at control sites.

Because of low gradient and absence of sediment to form barrier islands (Hine et al. 1988), oyster reefs in this region are ocean facing and thus receive strong wave action and currents. A medium riprap size (generally 10–20 cm diameter) was chosen because it was thought to be sufficient to minimize displacement and burying during storms. Limerock is often used in various sizes for oyster restoration (Petes et al. 2012), and exposed limestone is a common feature in submerged habitat in this region (Hine et al. 1988), often forming nucleation sites for oyster reefs. Limerock cobbles were placed on treatment sites to an approximate depth of 0.3 m. Limerock was moved to the site using a 23-m barge equipped with spuds and placed onsite using a 13.7-m articulated hydraulic arm with bucket during the last 2 wk of September 2013. The use of the pivoting arm created linear ''arcs'' or rows of higher and lower elevation surface on treatment sites. These were not considered undesirable, because natural reefs also have considerable variation in elevation.

Following limerock placement, the four edges of all treatment sites were lined with clam aquaculture bags that contained live oysters, clam and oyster shell, and associated fauna (December 2013 to June 2015). Polyester mesh aquaculture bags (9- to 10-mm openings) were taken from submerged hard clam aquaculture leases (''Gulf Jackson'') approximately 10 km south of LC, removed directly from the lease and placed on LC on the same tidal cycle. The clam crop inside these bags ($0.3 \times 0.3 \times 0.2$ m) had died, and the remaining shells and bag material had been colonized by oysters and other meiofauna. Although live oysters were not quantified in these bags at the time of placement, earlier counts in 2005 had indicated an average of 7,000 live oysters per bag. On the basis of the condition of the bags used in this study, live oyster densities at the time of installation seemed substantially lower and in many cases, the bags contained no live oysters. Bags were laid against the edge of the limestone rock next to one another, and tied to their neighboring bags at each corner using large cable ties to ensure a cohesive mass.

Monitoring

Elevation Determinations

Benchmarks were created for each site by first establishing a local area benchmark using a base-rover pair of survey-grade global positioning system (GPS) units (Magellan Mark V). The base was allowed to record over the closest surveyed United States Geological Survey (USGS) benchmark approximately 8 km distant for 3.2 h, whereas the rover recorded over the benchmark on the reef; the solution for the reef benchmark showed a mean estimated vertical error of 1.8 cm. From this benchmark on the reef, a different base–rover pair (Topcon HiPer Lite + GPS receiver, TDS Nomad data collector) was used in Bluetooth-enabled real-time kinematic mode to establish 91-cm-deep concrete benchmarks on the other reefs in the chain. Using a laser level, elevations were measured on each reef relative to the appropriate reef benchmark, the four corners of each site, and every 5 m along each of the transects established.

Oyster Density and Size

Oyster density and size sampling was performed at each site during low tides preconstruction (April 23–24, 2013) and postconstruction (May 16–18, May 31–June 1, 2015). On each sampling date, live and dead oysters were counted within temporary belt transects (21 m $\times$ 15.4 cm wide) marked using stakes and string. Transects were spaced evenly across each site (ends were 5.34, 10.68, and 16.02 m from northeast and southeast corners), and oriented along an elevation gradient moving away from the inlet. Using click counters, live and dead oysters were then counted along the transect assuming detection probability was equal to 1.0. Dead oysters were defined as having two valves that were clearly open with no evidence of a living oyster within. All size classes were counted including live spat. Only oysters that could be distinguished visually from above or to the side were counted: oysters on the undersides of clumps were not counted, and clumps were not picked up. The temporary belt transects were removed after each sampling event.

Using the same transect, sizes of oysters were measured within randomly placed 0.0625 m^2 quadrats formed out of PVC pipe. Quadrats were placed at random lengths (with replacement) along transects (1.0-m increments), and distances normal to transects (0–4 m, in 0.1-m increments). All live and dead oysters within the quadrat were measured using either dial calipers or a sewing seam gauge to the nearest mm, from umbo to point of longest dimension. On the basis of previous oyster monitoring efforts in this area, to detect a 20% difference in size structure between reefs, quadrat sampling would have to continue until 50 oysters were measured or a maximum of 20 total quadrats were used for each transect on each site.

Sampling Oysters in Clam Bags

The surface of clam bags from aquaculture leases used in restoration was usually fouled with algae and it was not possible to measure or count oysters without cutting the bags open. On the last sampling (late May/early June 2015), oyster density and size were sampled within clam bags that had been on the reef for at least 9 mo. We cut open the upward facing side so that a 0.0625-m^2 quadrat could be placed on top of the contents. The same methods were used for counting density and measuring size as above. Clam bags were chosen to sample by randomly selecting a side of each square site (1–4 with replacement), and then randomly selecting a number of clam bags (0–25 with replacement) from each corner to sample. Clam bags were stitched closed following sampling using plastic cable ties.

Bird Sampling

Trail cameras were used in time-lapse mode to estimate usage of control and treatment sites by aquatic birds. Cameras

(Bushnell Trophy Cam 119467 with solar charging panels) were placed 2.5 m above the substrate within a weatherproof housing mounted on 15.2-cm-diameter PVC poles driven into the substrate. Cameras were deployed following placement of the limerock, between October 22 and December 17, 2013. This period coincides with the maximum period of both fall migration and of winter residence for most of the aquatic birds in Gulf coastal Florida. Each of eight cameras (one per site) was oriented to face either northeast or southwest along the axis of the reef chain depending on the site to be viewed; all cameras were oriented to face toward the nearest inlet and were placed far enough away from the edge of each study site to be able to clearly see the four corners of each site. Pictures were taken once every 5 min with motion detection turned off, and daytime operation only. Cameras were variously reliable, with usable pictures of birds from each camera between 1 and 68 days, depending on the site and camera.

Only images that had some substrate showing were counted, and images that were too dark to detect birds or for which the lens was occluded by precipitation or fog were not counted. Viewers scanned both for images of birds, and for apparent movement while toggling among adjacent images. Birds were identified to species if possible, and were lumped into categories of pelicans, gulls, cormorants, shorebirds (small, large), terns, ducks, and raptors. "Large shorebirds" were as large or larger than a ruddy turnstone *Arenaria interpres* (Linnaeus, 1758), and generally were willets [*Catoptrophorus semipalmatus* (Gmelin, 1789)], marbled godwits [*Limosa fedoa* (Linnaeus, 1758)], or whimbrels [*Numenius phaeopus* (Linnaeus, 1758)]. "Small shorebirds" included semipalmated sandpipers [*Calidris pusilla* (Linnaeus, 1766)], western sandpipers [*Calidris mauri* (Cabanis, 1857)], least sandpipers [*Calidris minutilla* (Viellot, 1819)], plovers, and other small "peeps." Although the vast majority of gulls were ring billed [*Larus delawarensis* (Ord, 1815)] and laughing [*Leucophaeus atricilla* (Linnaeus, 1758)], all gull species were lumped into one category because gulls were difficult to distinguish when roosting together. White pelicans [*Pelecanus erythrorhynchos* (Gmelin, 1789)] and brown pelicans [*Pelecanus occidentalis* (Linnaeus, 1766)] were also lumped because they were sometimes silhouetted and difficult to distinguish in roosting flocks. Although usage was expressed as bird habitat usage per hour observed, the treatment sites were much more frequently exposed in any tide cycle compared with controls because their surface had been elevated as a result of adding limerock. This effect was controlled by comparing bird usage only during those time during which the lowest of the control sites were exposed above tide level.

RESULTS

A total of 360 m^3 of limestone rock was placed in aggregate on the four treatment reefs at a cost of \$186/m^3 or a total of \$67,184, and 407 clam aquaculture bags were placed at a cost of \$13,051, resulting in a total cost of \$176.25/m^2. By comparison with the longer term record, the period postconstruction was characterized by relatively high rainfall, average to high discharge from the Suwannee River, and intermediate to low salinities (Fig. 2).

Oyster Density

Between pre- and postconstruction, oyster densities increased on the control reefs (increase of 10–43 oysters/m^2 or 0–64× increase), likely because the salinity conditions had improved compared with relatively saline conditions in 2011 to 2013 (Table 1). Oyster densities on limerock on treatment sites, however, increased much more, with absolute increases of 107–199 oysters/m^2 or 15–157×. Oyster densities and sizes were measured in a total of 43 clam bags that had been in place for at least 9 mo, averaging 474 oysters/m^2 (SD = 19.8). Total oysters on limerock and clam bags were estimated based on expansion from average oyster densities and total areas of limerock and clam bags. Reefs had on average 25 bags per side, or 100 bags total, with an estimated flat bag surface area of 1.46 m^2. The limerock on treatment sites was estimated to contain between 49,076 and 96,514 oysters total, whereas the clam bags on a single reef were estimated to contain 70,159 oysters. Using an average of the limerock on the four sites (63,701 oysters), clam bags contributed 52.4% of the individual oysters on the reef. Because densities on the bottoms of either limerock or bags were not estimated, these are likely to be underestimates of true densities.

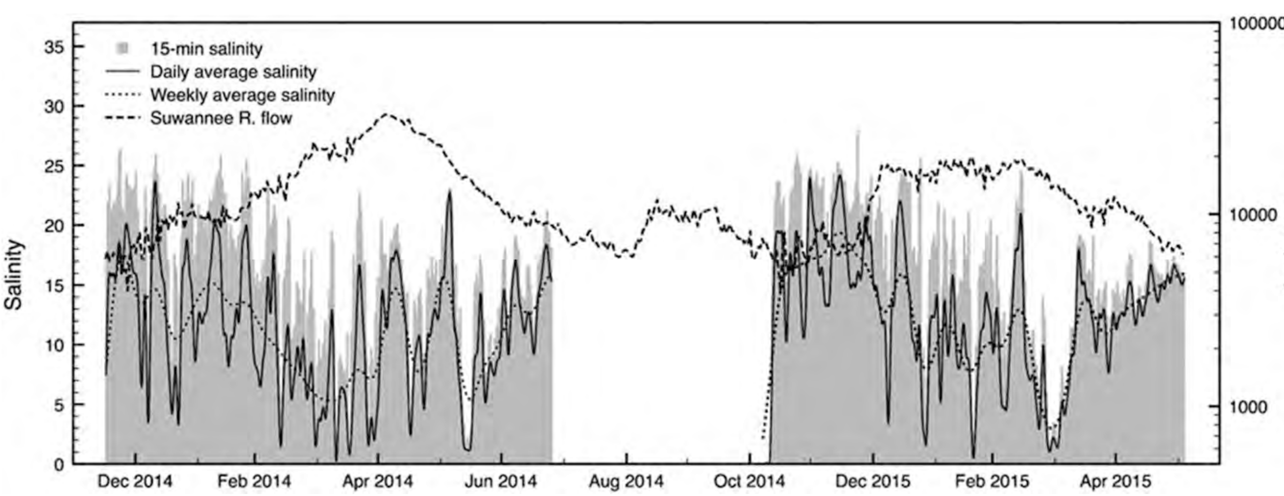

Figure 2. Graph of Suwannee River discharge (dashed line, Gopher River USGS station ID: 02323592) and average weekly and daily salinities at a station on the seaward side of restoration Site 2 on LC reef. The salinity sensor was not in the water during July–October 2014.

TABLE 1.

Live oyster densities by treatment and date sampled at LC.

Date sampled	Treatment	Oysters/m^2	SD	SE
April 24, 2013	Control 3	14.2	24.21	4.66
May–June 2015	Control 3	24.7	19.54	3.76
April 24, 2013	Control 4	2.6	3.19	0.61
May–June 2015	Control 4	29.8	16.59	3.19
April 24, 2013	Control 7	0.5	1.44	0.28
May–June 2015	Control 7	31.9	33.78	6.50
April 24, 2013	Control 8	0.8	1.40	0.27
May–June 2015	Control 8	44.6	34.18	6.58
April 24, 2013	Restore 1	12.7	17.36	3.34
May–June 2015	Restore 1	212.0	118.52	22.81
April 24, 2013	Restore 2	3.0	4.39	0.84
May–June 2015	Restore 2	114.7	70.72	13.61
April 24, 2013	Restore 5	0.7	1.53	0.30
May–June 2015	Restore 5	107.8	116.68	22.46
April 24, 2013	Restore 6	4.8	5.39	1.04
May–June 2015	Restore 6	125.2	81.41	15.67
May–June 2015	Clam bags	474.0	316.80	48.31

Dates in April 2013 are 5 mo before construction; dates in May–June 2015 are 19 mo postconstruction.

Estimated total densities on treatment sites (limerock + bags, calculated from total oyster estimates) averaged 303.5 oysters/m^2, whereas oysters on control sites in June 2015 averaged 32.8 oyster/m^2. Thus, oyster densities on treatment sites were 9.26× densities on control sites. Densities on the LC treatment sites were also compared with those at unmanipulated oyster reefs in the surrounding area (Wacassassa Bay to Horseshoe Beach, Seavey et al. 2011, Figure 3). Inshore reef densities in the unmanipulated sites were highest (39.9/m^2), and offshore reef densities lowest (3.01/m^2), with offshore reefs being most comparable in wave energy and hydrodynamics to the LC sites. Densities on treatment sections of LC were 89–125 times higher than the other offshore sites, and 7–9 times higher than the inshore reef densities (Fig. 3). It should be noted that the non-LC sites from Seavey et al. (2011) were often within oyster harvest areas, whereas LC was not. Very few of the oysters on LC were, however, harvestable size by the end of the study. Oyster densities on all of the LC treatment sites were higher than 89% of all the natural and restored sites in the Gulf of Mexico reported in a recent meta-analysis (LaPeyre et al. 2014; Fig. 4).

Oyster Size

Variable response was seen by treatment and time in the average sizes of oysters measured at the sites at LC. At one of the treatment sites, only one live oyster fell within our sampling quadrats in the preconstruction sampling, so size characterization was not reasonable. In the three treatment sites at which comparisons could be made pre- and postconstruction, all three sites had significantly larger mean oyster size postconstruction. Of the control sites, size comparisons were not possible due to small sample size in pre- or postconstruction condition. One of the two remaining sites (Control 3) had significantly larger mean oyster size preconstruction, and the other (Control 4) had significantly smaller oysters postconstruction (Table 2).

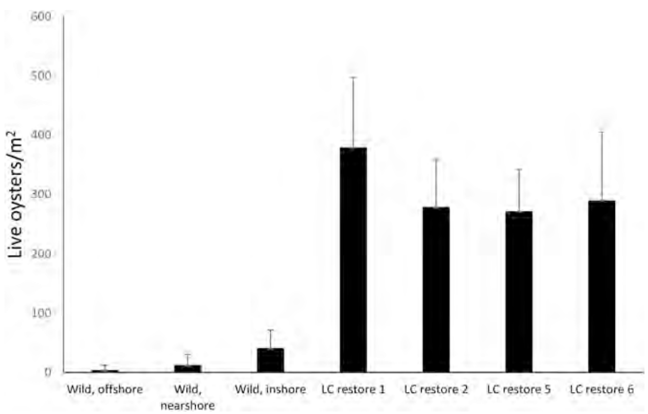

Figure 3. Mean oyster densities on restored sites at the LC reef with densities from 38 oyster reefs in the area between Wacasassa Bay and Horseshoe Beach collected in 2010, representing a gradient of conditions from offshore to inshore locations.

During the final sampling in May/June 2015, treatment sites had significantly larger oysters (mean 33.9 mm, $n = 819$, SD = 12.67, $P < 0.01$) than did control sites (mean 27.4 mm, $n = 361$, SD = 8.46, $P < 0.01$), though the difference in mean size was not large (6.5 mm, Table 2). Clam bags also had the largest mean oyster size of any treatment or substrate (mean 39.43 mm, SD = 13.94, $n = 1{,}306$) and were significantly larger than oysters on control sites (t-test, $P << 0.001$).

Reef Elevation

Treatment sites showed average absolute increases in elevation across the reef of 16.05 cm (range: –0.51 to 32.6 cm) whereas mean elevation change on control sites was 3.1 cm (range:–18.7 to 14.8). It is difficult to tell how much of this difference was due to placement of limerock (possibly followed by some settling), and how much was accretion of sediment onto the limerock. Patterns of sediment accretion were difficult to portray with the relatively coarse grid of measurements taken, but it appeared that sediment either accreted slightly or generally decreased in elevation on control sites, and accreted considerably on the treatment sites. In two cases, the surface-elevation benchmarks were found buried under 8–10 cm of

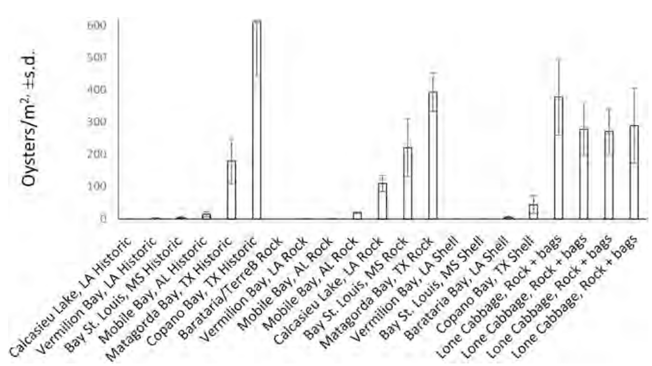

Figure 4. Oyster densities at restored and historic sites in the Gulf of Mexico (from LaPeyre et al. 2014).

TABLE 2.

Mean lengths of oysters by treatment and date sampled at LC.

Date sampled	Treatment	Mean (mm)	Number of oysters	SD	SE
April 23, 2013	Control 3	36.2	20	11.89	2.66
May 16, 2015	Control 3	28.9	100	9.79	0.98
April 23, 2013	Control 4	34.5	6	6.66	2.72
May 17, 2015	Control 4	27.2	123	8.53	0.77
April 24, 2013	Control 7	23.1	1	0	0
May 31, 2015	Control 7	25.9	138	6.82	0.58
May 31, 2015	Control 8	27.7	143	6.02	0.50
April 23, 2013	Restore 1	32.2	20	13.02	2.91
May 17, 2015	Restore 1	38.8	156	14.40	1.15
April 23, 2013	Restore 2	27.5	9	8.51	2.84
May 16, 2015	Restore 2	34.8	149	11.75	0.96
April 24, 2013	Restore 5	37.7	1	0	0
May 18, 2015	Restore 5	30.0	155	9.32	0.75
April 24, 2013	Restore 6	29.7	4	7.16	3.58
June 1, 2015	Restore 6	36.3	227	14.59	0.97
May 18, 2015	Clam bags	39.1	1,306	13.94	0.39

Dates in April 2013 are 5 mo prior to construction; dates in May–June 2015 are 19 mo postconstruction.

sediment on treatment sites, whereas the benchmarks on the control sites were all elevated by 1–14 cm above the surface of the sediment by the end of the observation period.

Avian Use and Community Composition

After excluding image frames from trail cameras in which the reef was covered by tide or that had poor visibility, a total of 163 h of potential avian observation were recorded on control sites, and 530 h on treatment sites. Due in part to this large difference in availability of the sites (treatment sites were higher elevation and remained out of the water longer), 62% of bird observations occurred on restored sites (Table 3).

Observations were then standardized for tide level to allow direct comparison of sites when all were available simultaneously (Table 4). Under these conditions, only 49% of all bird observations occurred on restored sites. Most species overwhelmingly used the control sites when the choice was available, including osprey *Pandion haliaetus* (Gmelin, 1788), shorebirds, gulls, pelicans, and terns. Cormorants and bald eagles used the restored sites more frequently.

DISCUSSION

The prediction that oyster populations on this reef were limited by recruitment through substrate availability was directly tested in this study. Placement of durable substrate on the reef resulted in an increase in mean oyster density on treatment sites by 2.65× on limerock. Because limerock was clean cultch when it was placed, all of the oysters recruited clearly came from the site itself. For clam bags, we were unable to distinguish between oysters that recruited to the bags prior to placement (on clam leases) or postplacement on LC. Nonetheless, the addition of clam bags resulted in an increase of oyster density of 14.5× for the surface area of bags, by comparison with nearby control sites. Overall, the combination of oysters on limerock and oysters in clam bags represented a 9.2× overall increase in density compared with nearby control sites. Because this study provided local and temporal controls, the conclusion that substrate limits local recruitment to this population seems well supported. Durable substrate treatments were also associated with a moderate increase in mean oyster size on limerock (6.5 mm, 23.7% increase over controls) and a more substantial one in clam bags (12.0 mm, 44% increase over controls).

The effects on oyster density were the most consistent and striking of these effects, with absolute densities greater than the 90th percentile of restored sites within the Gulf of Mexico, and greater than 89th percentile of restored and natural sites. These densities are not directly comparable because the sites reported in LaPeyre et al. (2014) were all subtidal and measured using diver-recovered quadrats counted in the laboratory, whereas the LC sites were counted *in situ* without disturbance from above, suggesting our estimates are likely undercounts. Further, the LaPeyre et al. (2014) sites were of various ages (generally

TABLE 3.

Summary of camera trap surveys of birds on control and restored oyster reefs at LC, October–December 2013.

	Total time observed		Total time bird frames per hour		Total time proportion	
Species	Control	Restore	Control	Restore	Control	Restore
Osprey	178	207	1.04	0.38	0.46	0.54
Large shorebird	66	199	0.39	0.37	0.25	0.75
Small shorebird	479	27	2.81	0.05	0.95	0.05
Gull	1,425	1,946	8.35	3.61	0.42	0.58
Cormorant	2,567	6,007	15.04	11.13	0.30	0.70
Bald eagle	42	275	0.25	0.51	0.13	0.87
Pelican	449	119	2.63	0.22	0.79	0.21
Tern	356	365	2.09	0.68	0.49	0.51
All species	5,562	9,145	32.59	16.95	0.38	0.62

"Frames" were photos taken every 5 min. "Bird frames" are numbers of frames with birds × numbers of birds/frame. These results include all observations and are uncorrected for elevation relative to tide.

TABLE 4.

Summary of camera trap surveys of birds on control and restored oyster reefs at LC, October–December 2013.

	Total standardized time		Standardized time bird frames per hour		Standardized time proportion	
Species	Control	Restore	Control	Restore	Control	Restore
Osprey	138	28	1.18	0.31	0.83	0.17
Large shorebird	53	13	0.45	0.14	0.80	0.20
Small shorebird	412	2	3.53	0.02	1.00	0
Gull	903	357	7.73	3.96	0.72	0.28
Cormorant	2,027	3,611	17.36	40.05	0.36	0.64
Bald eagle	42	61	0.36	0.68	0.41	0.59
Pelican	370	0	3.17	0	1.00	0
Tern	242	0	2.07	0	1.00	0
All species	4,187	4,072	35.86	45.16	0.51	0.49

"Frames" were photos taken every 5 min. "Bird frames" are numbers of frames with birds × numbers of birds/frame. These results portray bird usage only when all reefs were exposed simultaneously.

years) postconstruction, whereas the LC sites were sampled only 19 mo postconstruction. It is unclear whether one should expect higher densities at sites with longer postconstruction histories or not, because weather events and harvest could easily depopulate those sites over time. Further, early colonization sites like LC may have generally small, higher density oysters, and as multiple age classes develop on the oyster reef, densities may typically decline. Nonetheless, the densities found at LC appeared to fulfill a designation of high densities of oysters compared with other restoration sites in the Gulf of Mexico, and compared with all of the natural sites measured in the Big Bend study area.

The limerock substrate showed an increase in oyster density over nearby control sites and was resistant to movement and sinking into the sandy substrate. Oysters also cemented themselves across the cracks between some limerocks, or to one another across those gaps, further stabilizing the limerocks and creating a cohesive mass. It is perhaps unsurprising that clam bags showed higher oyster densities than the limerock because many clam bags arrived on site with live oysters, and the mesh bags excluded most of the large predators of oysters. Oyster growth within clam bags may, however, also be eventually limited by competition of densely crowded oysters, and reduction of flow created by the mesh of the bags (Bouchillon 2015). The durability of the bags themselves is limited to 6–10 y and eventually the contents of the bags will not be contained. At least in the early stages postconstruction, the bags contributed disproportionately to oyster populations on treatment reefs (52% of oysters despite being less than 25% of the area of the treatment reefs) in part because of their protected and high growth environment. Thus, although they may not be as durable as limerocks long term, clam bags probably provided a substantial early boost to oyster ecosystem services (Kellogg et al. 2013), and may aid in local recruitment through attracting spat.

The changes in habitat and substrate that were initiated through the addition of limerock and clam bags also affected use by avian species. Although bird use overall appeared to be considerably greater on treatment sites, this effect was reversed when reef availability due to elevation was controlled for, and most species preferred the sandy control sites. One effect of the addition of limerock was therefore to apparently decrease suitability of roosting and feeding habitat for most species. Double-crested cormorants and bald eagles were the only two species to prefer the rocky substrate to sandy substrate when both habitats were available, whereas all other avian groups were more commonly found on sandy substrate. These differences probably represent a mix of preferences for roosting/loafing habitat (bald eagle, cormorants, gulls, terns, and pelicans) or feeding habitat (shorebirds), because our observations did not attempt to categorize behavior. Most of the shorebirds typically feed on sandy or muddy substrate at low tide, whereas cormorants are known to roost on either limerocks or sand (Dorr et al. 2014).

However, the decrease in suitability may be offset somewhat by the increased availability of the treatment sites due to higher elevation. On the basis of average rates of increase on rising tides of 15.8 cm/h at the nearby Cedar Key tide gauge, the 16 cm average increase in elevation should give birds nearly an hour more per rising or falling tide to forage and roost than on lower control sites. Over the course of a 3-mo winter period for migratory birds with one extra hour on rising and falling tides, this effect could amount to an additional 170 h of foraging and roosting. In addition, the control sites are generally decreasing in elevation at an average rate of 7.2 cm/y (P. C. Frederick, unpublished data), indicating that suitability of the unrestored sites for birds may ultimately go to zero in the longer term. It is also important to note that the bird study took place during the first 4 mo following the installation of limerock, and when very few of the clam bags had been placed, oysters had not become established on the limerock. Thus, our study really compares limerock with sand substrate, rather than functional reef versus sand bar. For some aquatic bird groups, functional oyster reefs might offer a wider variety and greater density of avian food sources than does either limerock or sand.

This work supports the hypothesis that oyster recruitment to degraded reefs in this area is strongly limited in the short term by available substrate, which must initially be durable enough to withstand wave and tidal action. This knowledge is a key step in understanding the process of introducing longer term resilience to oyster reefs in this area in the face of declining freshwater discharge.

This study also demonstrated that byproducts of clam aquaculture materials can play an important part in the restoration of natural reefs. Encrusted clam bags provided both an immediate population of oysters and their reef associates (Kellogg et al. 2013), and refugia from predation for new recruits. Finally, this study illustrated that restoration of oyster reefs can have important impacts on avian usage. Although restoration of oyster reefs is known to affect fish and invertebrate community composition and abundance (Scyphers et al. 2011), this is the first report of effects on aquatic birds. It is suggested that future research should be aimed at understanding longer term impacts of reef restoration on reef resilience and avian usage.

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