

RESEARCH ARTICLE

Diminishing returns in habitat restoration by adding biogenic materials: a test using estuarine oysters and recycled oyster shell

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Restoration of degraded estuarine oyster reefs typically involves deploying recycled oyster shell. In low-salinity, low-predation areas of estuaries, high-volume shell deployments are known to improve flow conditions and thus oyster survival and growth. It is also hypothesized that the physical structure of restored reefs could suppress foraging by oyster predators in high-salinity, high-predation zones. That hypothesis is untested. Given limited resources, it is important to determine how much shell is needed for successful restoration and whether there are diminishing returns in shell addition. In Apalachicola Bay, Florida, we manipulated shell volume on an oyster reef to create three 0.4 ha areas of low (no shell addition), moderate (153 m³ shell), and high (306 m³ shell) habitat structure. We repeated experiments and surveys over 2 years to determine if restoration success increased with habitat structure. Predation on oysters was greater on the non-shelled area than on the reshelled reefs, but similar between the two reshelled reefs. Oyster larval supply did not differ among the reef areas, but by the end of the experiment, oyster density (per unit area) increased quadratically with habitat structure, plateauing at high levels of structure. Model selection indicated that the most parsimonious explanation for these patterns was that increased habitat structure reduced predation and increased overall recruitment, but that the higher reshelling treatment did not have better outcomes than moderate reshelling. Thus, restoration could be optimized by deploying a moderate amount of shell per unit area.

Key words: ecosystem-level restoration, estuarine salinization, larval recruitment, predation threshold hypothesis, restoration metrics, structural complexity

Implications for Practice

- It is more cost-effective to restore oyster reefs by deploying moderate amounts of the recycled shell (per area) in multiple areas, rather than deploying high amounts of shell in fewer areas.
- In agreement with the predation threshold hypothesis, moderate and high amounts of recycled oyster shell equally promote oyster restoration at a landscape level by impeding predators.

Introduction

Historical evidence suggests that harvesting oysters has supported human sustenance and economies for millennia (Beck et al. 2011; Rick et al. 2014). Meanwhile, contemporary evidence suggests that the reef habitat formed by oysters also provides important ecosystem services by protecting shorelines, sequestering carbon, enhancing water quality, and supporting other fisheries (Jackson et al. 2001; Grabowski et al. 2005; Coen et al. 2007; Fodrie et al. 2017). When harvesting transitioned from hand to mechanical dredge over a century ago, oyster fisheries, and ecosystem services around the globe collapsed due to the efficient removal of the structural foundation to which successive generations of oyster larvae settle and grow (Rothschild et al. 1994; Lenihan et al. 2001). Over the past

several decades, this habitat loss increased due to oyster disease, sedimentation, water quality degradation, low spawning stock biomass, and predator outbreaks (Rothschild et al. 1994; Lenihan & Peterson 1998; Lenihan 1999; Garland and Kimbro 2015; Kimbro et al. 2017), such that the existing amount of oyster habitat represents only 15% of the historical global abundance (Beck et al. 2011; Zu Ermgassen et al. 2012).

Over the last four decades, efforts to reverse this alarming trend have focused mostly on eastern oyster (*Crassostrea virginica*) populations along the Atlantic and Gulf of Mexico coasts of the United States (Hernandez et al. 2018). Of the several different restoration methods and materials, the deployment of

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recycled or fossilized oyster shell is the most frequently used method and is also the method most associated with a positive return on investment (Hernandez et al. 2018). However, a substantial number of reshelling efforts have failed to regenerate enough reef habitat to produce positive returns on investment. Given this uncertainty in the outcome of reshelling as well as the rising costs and insufficient quantities of available recycled shell (La Peyre et al. 2014), empirically testing how to optimally deploy this limited resource may facilitate the recovery of oyster reef habitat and ecosystem services (Hernandez et al. 2018).

Community ecology theory is often used to identify mechanisms underlying restoration success (Wainwright et al. 2018) and may help improve our understanding of how to deploy recycled oyster shell. More specifically, the physical structure of a habitat such as a forest or coral reef has been theoretically and empirically associated with biodiversity patterns, predator–prey dynamics, and propagule recruitment (MacArthur & MacArthur 1961; Heck & Wetstone 1977; Gotceitas & Colgan 1989; Johnson 2007). For example, increasing habitat structure may increase the survival of prey, such as oysters, by reducing the foraging efficiency of predatory fishes, crabs, and snails (Grabowski et al. 2008; Grabowski et al. 2020). Meanwhile, ecological theory also highlights that community structure and, by extension, restoration success may depend on prey recruitment dynamics (Underwood & Fairweather 1989), with more habitat structure facilitating the success of local-scale recruitment (Johnson 2007). For example, oyster larvae in the laboratory recruited more to the interstitial spaces within an oyster shell aggregation, which reduced the shear stress that dislodges larvae, than to smoother surfaces (Whitman & Reidenbach 2012). Thus, a better understanding of the quantitative relationship between the volume of recycled shell (i.e. habitat structure) and either reductions in predation or increases in recruitment could help optimize restoration efforts. In particular, there may be diminishing returns in the volume of shell applied, allowing better use of this limited resource. Although the height of reefs restored with high shell volume deployments in a low-predation environment has been shown to benefit the growth and survival of individual oysters by altering hydrodynamics (Lenihan 1999), the influence of habitat structure on predation and recruitment for restoration success in high-predation environments has yet to be examined in the field.

The oyster fishery in Apalachicola Bay on the Gulf Coast of Florida was one of the healthiest in the nation, consistently providing 10% of U.S. oyster landings (Beck et al. 2011; Zu Ermgassen et al. 2012). But sharp oyster declines in 2012 resulted in the declaration of a federal fishery disaster (FFWCC 2013). Subsequent experiments and analysis suggested that the collapse was precipitated by a prolonged regional drought that was exacerbated in Apalachicola Bay by the upstream removal of freshwater from the Apalachicola-Chattahoochee-Flint watershed (Marella & Fanning 2011). Together, regional drought and freshwater removal facilitated a salinization-induced outbreak of predators and disease that contributed to the oyster population collapse during the anomalously high-salinity conditions of 2011–2013 (Fig. 1; Kimbro et al. 2017). Once drought and salinity conditions returned to normal in 2015, the state of Florida resumed reshelling efforts to promote oyster recovery.

As part of this reshelling effort, we advised the Florida Department of Agriculture and Consumer Services (FDACS 2012a, 2012b) regarding appropriate locations to deploy two available loads of recycled oyster shell ("cultch"): a moderate (153 m³) and a high (306 m³) volume load. Each was deposited on a 0.4-ha section of a historically productive oyster reef, which now experiences heavy losses to predation (Kimbrow et al. 2017). On these two reshelled areas, as well as on a non-shelled section of the same reef (low volume of ambient shell; Table S1), we repeatedly conducted predator-exclusion experiments over 2 years to determine how habitat structure modified predation rates. We also measured whether added habitat structure altered local-scale larval recruitment to individual oyster shell. Finally, 10 months after reshelling, we conducted surveys to determine whether the influence of habitat structure on local-scale predation and recruitment scaled up to reflect restoration success on the reshelled sections in terms of oyster size structure and the functional relationships between oyster density and habitat structure.

Methods

Study System

Apalachicola Bay is a large (400 km²) and shallow (2 m average depth) estuary located at the terminus of the Apalachicola-Chattahoochee-Flint (ACF) River system in the Florida panhandle (Fig. 1A). The headwaters of the ACF watershed (50,000 km²) begin in northeastern Georgia and flow through west-central Georgia before entering Florida. The dominant freshwater and nutrient sources to this bay are provided by the Apalachicola River (Mortazavi et al. 2000; Putland et al. 2013). As a result, the Apalachicola River is the primary cause of salinity variation throughout the bay (Livingston et al. 2000). While the maximum river flows in the winter are driven by rainfall amounts in the upper basin, minimum flows occur during the late summer months (Morey et al. 2009). In this estuary, oyster reefs cover approximately 5–13% of the bottom (16–24 km²) and are distributed from areas close to the river mouth (lower salinity) to those far from it (higher salinity; Fig. 1A; Twichell et al. 2007; ANERR Management Plan 2013; Zu Ermgassen et al. 2012).

Shell Addition

In September 2015, high-salinity conditions abated (Fig. 1B). On a historically productive oyster reef in the mid/western region of Apalachicola Bay (Dry Bar, Fig. 1A), FDACS used a barge to deploy recycled oyster shell into two 0.4 ha areas (approximately 63 × 63 m) separated by 100 m. At the time, the physical reef had little mass (mean ± standard deviation = 0.73 ± 0.41 kg/m²; Table S1) and pre-existing structure. This reef was also one of the study sites where Kimbro et al. (2017) conducted predator exclusion experiments from 2013 to 2015. The two deployments were 153 m³ and 306 m³ of recycled oyster shell.

Similar to a natural experiment, this large-scale reshelling effort created a gradient in habitat structure (low [ambient], moderate [153 m³], and high [306 m³]). Because we were

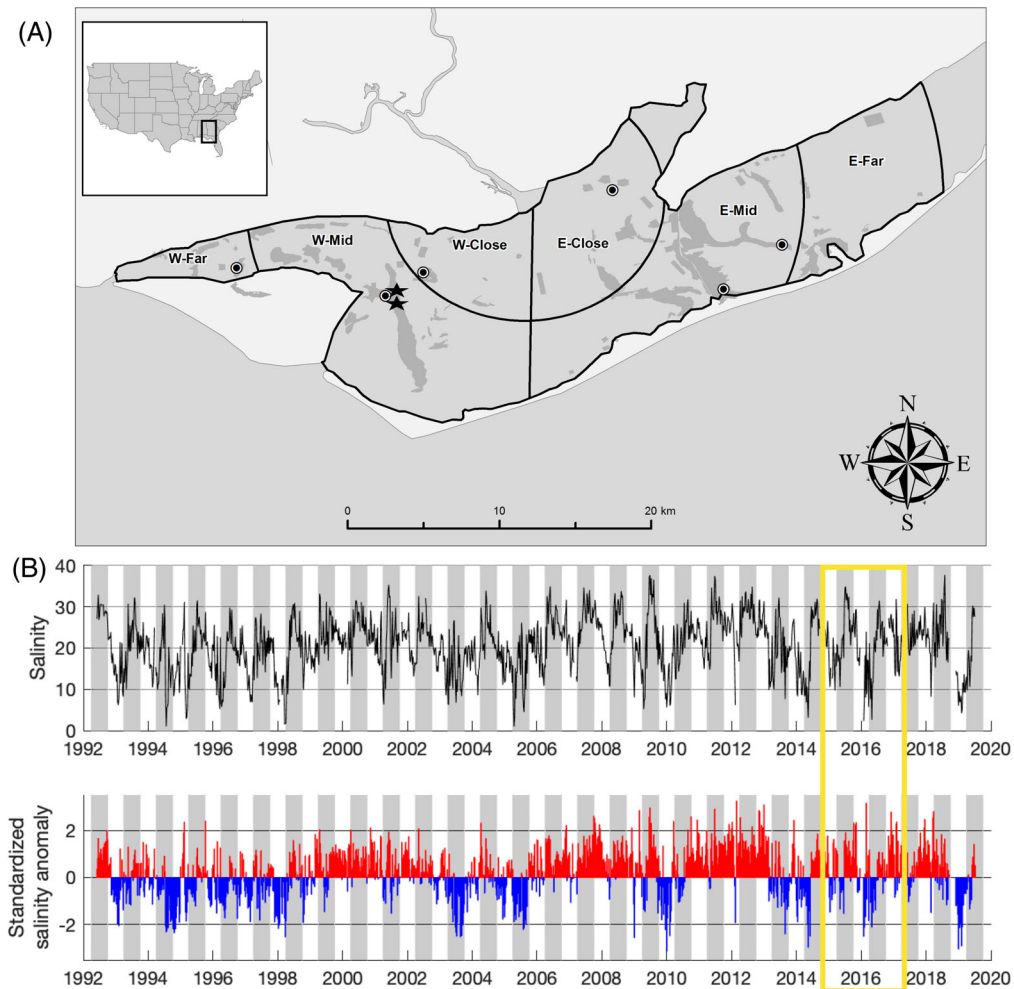


Figure 1. (A) Map of study sites in Apalachicola Bay, Florida. In Apalachicola, dark shading illustrates distribution of oyster reefs. Concentric circles illustrate proportional distances (close, mid, far) of oyster reefs from river discharge. In Apalachicola, proportional distances extend west (W) and east (E) of the river. Circles in each zone represent areas where repeated experiments were conducted in Kimbro et al. (2017). In the W-mid region, stars denote locations of reshelling. (B) Time series of weekly mean salinity and weekly salinity anomaly at Cat Point oyster bar in Apalachicola Bay from 1992 to 2019. Anomaly was calculated based on the climatological mean from 1992 to 2002; data obtained from Apalachicola National Estuarine Research Reserve (<http://cdmo.baruch.sc.edu>). Yellow rectangle highlights time frame of the experiment and surveys of this study.

unable to produce replicate habitat structure areas, we replicated our experiment four times over a 2-year period: experiment I (September–December 2015), experiment II (February–May 2016), experiment III (June–September 2016), and experiment IV (October 2016–January 2017). In our experiments, we focused on the variation in habitat structure that resulted from the different shell volumes, but recognize that higher resolution attributes of habitat structure such as reef height (Lenihan 1999) and structural rugosity (Kimbro & Grosholz 2006) were likely important.

Predator Exclusion Experiment

We conducted a predator exclusion experiment on oysters deployed in each of the three study locations (low, moderate, high habitat structure) to evaluate the role of habitat structure in impeding oyster predator foraging success. In the center and

on the edges of the two reshelled sections of the reef (moderate and high habitat structure) and also 100 m away from these center areas (low complexity), we deployed nine protective frames ($H \times L \times W$; 1.2 m \times 0.9 m \times 0.6 m) constructed of steel rebar (13 cm diameter) at 3.0 m increments from each other (18 frames \times 2 reef areas = 36 total frames). Meanwhile, the non-shelled section was sampled with 9 protective rebar frames, resulting in a total deployment of 45 rebar frames. These frames were used to protect the experiment from harvesting and boating activities (see Fig. S2 for further details). One side of each rebar frame contained three posts separated by 0.4 m. Three experimental units were attached to these posts and randomly assigned among three treatments: (1) control, (2) caged (predator exclusion), and (3) caged-control treatments. Thus, each experiment consisted of 135 experimental units that were constructed from 0.2 m \times 0.2 m squares of vinyl-coated wire mesh (5 mm \times 5 mm mesh opening). The control treatment consisted

Table 1. Summary of repeated experiments conducted in Apalachicola Bay (AB) on restored oyster reefs

Experiment	Start Date	Duration (months)	Initial Oyster Density	Sites Nested Within Habitat Complexity
I	Sept. 2015	3	1, 3, 5	(a) Low complexity (1) (b) Moderate complexity (2) (c) High complexity (2)
II	Feb. 2016	3	1, 3, 5	(a) Low complexity (1) (b) Moderate complexity (1) (c) High complexity (2)
III	June 2016	3	4	(a) Low complexity (1) (b) Moderate complexity (1) (c) High complexity (1)
IV	Oct. 2016	3	4	(a) Low complexity (1) (b) Moderate complexity (1) (c) High complexity (1)

For each experiment (I–IV), we provide the starting date, duration of the experiment (months), levels of oyster density tested, as well as the number of nested sites within each level of the factor habitat complexity.

of a single mesh panel to which adult oysters were attached; the panel was attached to a post and placed flat on the reef with oysters facing upwards. The caged treatment was similarly oriented, but it was enclosed by additional mesh panels to form a 0.2 m × 0.2 m × 0.2 m cage. For the caged-control treatment,

two mesh walls were removed from the full cage design to maintain caging material effects, while also allowing access by predators. For each experiment (I–IV), new adult oysters (mean ± sd length = 67.77 ± 17.21 mm) were collected from the east-mid zone of the bay (Fig. 1A).

For experiments I–II, we also manipulated oyster density because higher densities may increase predator attack rate (Sih 1984). Initial oyster density comprised three levels (1, 3, and 5 oysters), which were based on the minimum, average, and maximum densities of adult oysters (per unit area) on the primary commercial reefs in 2012 (FWCC 2013). The three levels of initial density were randomly assigned among the rebar frames within each re-shelled and non-shelled section of the reef so that each frame had the same initial density on all experimental units. Because initial density did not have a statistically significant effect on oyster survival in experiments I–II, we used a constant density of 4 oysters in experiment III–IV. See Table 1 for similarities and differences among experiments I–IV.

At monthly intervals, we quantified survival of oysters, with survival in the caged treatment reflecting the influence of the physiochemical environment and disease on oysters (e.g. Dermo, a disease caused by the protist *Perkinsus marinus*; Petes et al. 2012), while survival in the control treatment reflected the influences of both the environment and predators. Consequently, significantly lower survival in the control compared to the caged treatment was inferred to represent the strength of predation. During each monthly check, we also quantified the number of new oyster recruits to each individual adult oyster on the mesh panels, and focused our assessment of recruitment only on the caged treatment in order to control for the influence of post-settlement predation. Because we did not remove the oyster recruits on each monthly visit, we calculated an average number of recruits observed over the course of each three-month experiment. See *Data Analysis* below for further details.

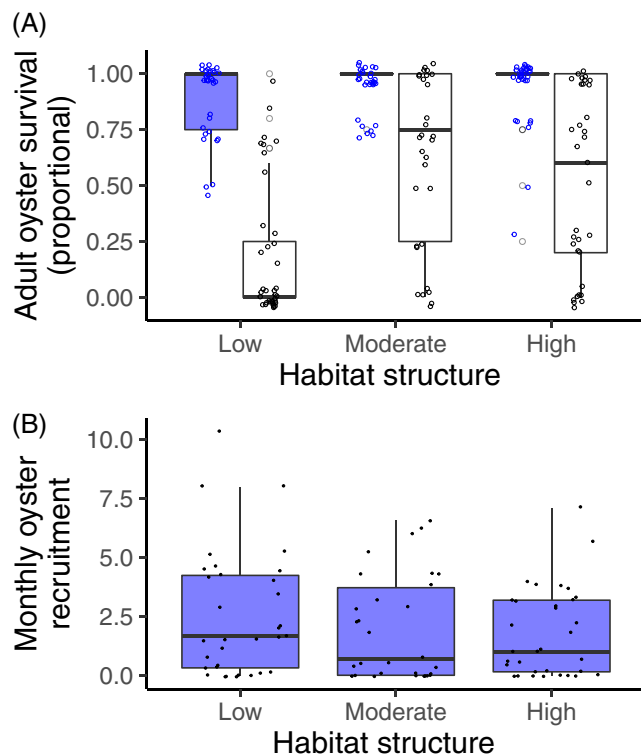


Figure 2. (A) Survival of adult oysters across different levels of structural complexity on a historically productive oyster reef as a function of caging treatment (open = control, blue = predator exclusion cage) to exclude predators. (B) Number of oyster recruits to adult oyster shell in predator exclusion cages as a function of habitat structure on a historically productive oyster reef. In (A) and (B), the thick black line on each box indicates the median, the box indicates the interquartile range, and the whiskers indicate the middle 95% of the data. Individual data are plotted as points.

Survey

In July of 2016 (10 months after deployment of recycled oyster shell), we used SCUBA surveys to assess the size structure and abundance of the ambient oyster population in each reshelled

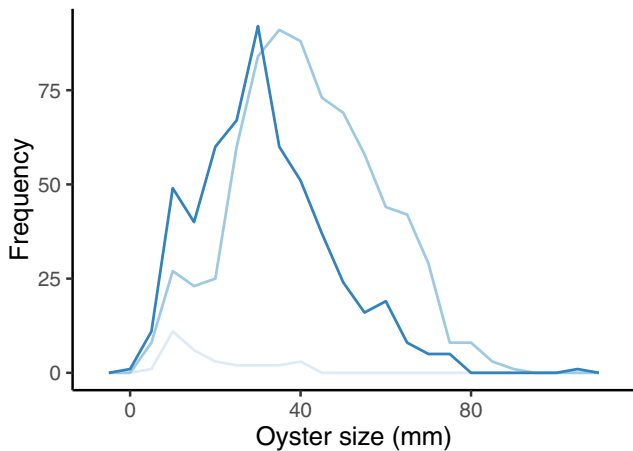


Figure 3. Results of oyster population census 10 months after reshelling showing the frequency of different oyster size classes (mm) on the low (light blue line), moderate (blue line), and high (dark blue line) habitat structure areas of a restored oyster reef.

area of the reef. On each reef (but away from the predator exclusion experiments), we obtained spatially balanced samples by extending three 20 m transects at 120° angles from a boat. Along each transect, we overlaid a 0.25 m² weighted quadrat at the 5, 10, 15, and 20 m marks. For each quadrat, we collected the entire contents of the quadrat into a uniquely labeled mesh bag, which was transported to the surface and placed on ice. The contents were excavated to ~5 cm depth to avoid remnant reef material that was no longer available for oyster settlement. In the laboratory, we processed each quadrat sample to obtain the total mass (kg) of reef habitat, the size of the first 100 oysters encountered (not all samples contained 100 oysters), the density of all juvenile oysters (length < 25 mm), and the density of all adult oysters (length ≥ 25 mm).

Data Analysis

This study represented an opportunistic investigation of a large-scale management intervention. Because shell deployment is expensive, shell was in limited supply, and because we did not have input on the logistics or magnitude of shell deployment other than on location, this study did not have the level of spatial replication of most ecological field experiments. This is a common problem in large-scale studies of ecosystem manipulation, and precludes the use of frequentist statistics and null hypothesis tests (Carpenter 1990; Reckhow 1990). Therefore, we followed the advice of Carpenter et al. (1998), and took an approach of comparing alternative explanations for the observed patterns in data. We used information-theoretic model selection to compare alternative models for our data and to identify the most parsimonious explanation for observed patterns (Carpenter et al. 1998; Burnham & Anderson 2002). All analyses were conducted using R 3.6.1 (R Foundation for Statistical Computing 2019).

This study produced four main results. The experimental oyster deployment generated results regarding adult oyster survival and recruitment. Separately, the reef surveys generated results

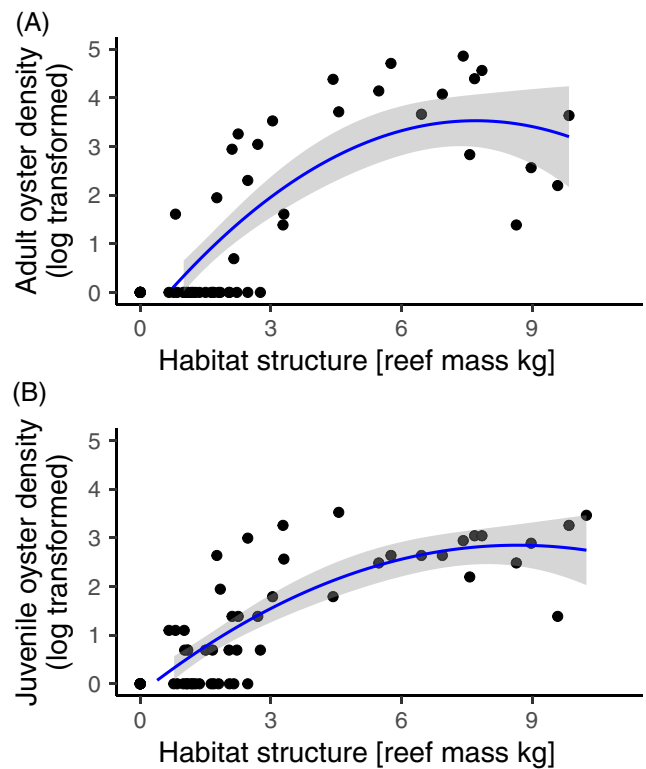


Figure 4. Results of oyster population census 10 months after reshelling showing the (A) quadratic relationship between adult oyster density (log-transformed) and habitat structure as well as the (B) quadratic relationship between juvenile oyster density (log-transformed) and habitat structure. In (A) and (B), gray shaded regions represent ±95% CI of the quadratic regression and each data point represents a pair of reef biomass (kg) and oyster density per 0.25 m² sampling area.

on the size-structure of the non-shelled and reshelled sections of the reef and on the relationship between oyster density and habitat structure across all reefs. We fitted a suite of models with different numbers of explanatory variables to each response variable and then used the Akaike information criterion corrected for small sample sizes (AICc) to identify the model with the most parsimonious fit to the data (Burnham & Anderson 2002). The models we considered were designed to answer three general questions: (a) did reshelling improve survival, recruitment, and the size structure of the oyster population; (b) did the "high" reshelling treatment produce a greater effect than the "moderate" reshelling treatment, or were there diminishing returns to adding extra shell; and (c) did improvements in survival on reshelled reefs depend on changes in predation (as measured by predator exclusion treatments). We now describe how we structured the model-selection analysis for each response variable.

Oyster Survival in the Predator Exclusion Experiment

For the evaluation of oyster survival, we combined the data from experiments I–IV and fit the data to a series of generalized linear mixed-effects models (GLMM) with binomial errors and logit link functions (i.e. logistic regression). In these models, the

experimental round (I–IV) was treated as a random effect (this is because we were not interested in seasonal differences among experiments per se, but rather used the four rounds to capture temporal variability in demographic rates).

Before proceeding with the model-selection approach of primary interest, we evaluated whether survival differed between the control and caged-control treatments, which would suggest a procedural artifact. This analysis was performed by excluding the caged treatment from the dataset and fitting the data to a null model (intercept-only fixed effect) and a model with a fixed effect of caging treatment (control or caged-control). Because the null model was the most parsimonious explanation of the data (AICc weight = 0.65), we concluded that procedural artifacts were not present. Therefore, in the subsequent analyses, we excluded the caged-control treatments and analyzed only the data from caged and control (uncaged) treatments.

For the survival of adult oysters at the end of the experiment, the model-selection approach of primary interest concerned a null model (intercept as the only fixed effect), and all possible single-factor and two-factor models given the possible fixed effects of reshelling, caging treatment, and initial oyster density. The fixed effect of initial density was evaluated because experiments I–III included variation in initial density but experiment IV did not. For the "reshelling" effect, we considered models with a binary variable (reshelled or not) and a variable with three levels (low [no reshelling], moderate, high). Model selection favoring the former over the latter would indicate a threshold, diminishing-returns relationship between the response and any level of reshelling. If a model with the caging treatment factor was identified as the most parsimonious explanation, then we calculated relative effect sizes between the caged treatment and the control treatment ($[\text{survival caged} - \text{survival control}] / \text{survival control}$); Kimbro 2012).

Experiments I–II also differed from experiments III–IV in that locations were nested within the two shelling sections during the former group of experiments, but not the latter (Table 1). Experiment I also differed from experiment II in that we lost all data from the center of the moderately reshelled section of the reef. To account for the lack of balance in nesting, we focused our analyses only on results from the center of each reef. To account for the missing data from the center of the moderately reshelled reef in experiment II, we used the other nested location as replacement data.

Oyster Recruitment in the Predator Exclusion Experiment

To evaluate oyster recruitment during the field experiment, we focused only on the caged treatment. Due to the initial differences in adult oyster density, replicates of the caged treatment often contained different numbers of adult oysters and therefore differing amounts of settlement substrate for larval oysters. As a result, for each mesh cage, we calculated the total number of recruits and divided that total by the number of adult oysters. Because we did not remove the oyster recruits on each monthly visit, we calculated an average number of recruits observed per adult oyster over the course of each three-month experiment. We combined the data from experiments I–IV and then fit the

recruitment data to a series of linear mixed-effects models that used experiments I–IV as a random effect. As in the survival analysis, the list of candidate models included a null intercept-only model, a model distinguishing among all three levels of reshelling, and a simpler model only distinguishing between the presence or absence of reshelling.

Oyster Size Structure From Survey Data

To evaluate the most parsimonious explanation for differences among the three reefs in the survey results, we bootstrapped 10^4 samples (with replication) of the median oyster size in each treatment. We then used AICc to compare three explanatory models for the results: a model distinguishing among all three levels of reshelling, and a simpler model only distinguishing between the presence or absence of reshelling, and a null model (intercept only).

Oyster Abundance and Habitat Structure From Survey Data

A second set of analyses of the survey results directly tested the relationship between oyster abundance and reef structure. Based on preliminary examinations of residuals, we log-transformed the density of adult (>25 mm length) and juvenile (≤ 25 mm) oysters per unit area (0.25 m^2) before analysis. We then fit each of these response variables to three linear models: a null model (intercept only), a model with a linear response to habitat structure in terms of reef mass (kg), and a more complicated model with a quadratic response to habitat structure. For these models, we used the post-hoc estimates of reef mass from field samples as an explanatory variable, rather than reshelling volume (low, moderate, and high) as a categorical variable.

Results

The most parsimonious explanations of adult oyster survival in our experiments included a model with an interaction between the effects of caging treatment and the presence of reshelling (AICc weight = 0.56) and a similar model with an interaction between the effects of caging treatment and all three levels of reshelling (AICc weight = 0.35). Because the combined AICc weight of these two similar models was 0.91, we focus our results on the simpler model with higher AICc distinguishing between presence and absence of reshelling (Fig. 2A; see Table S2 for all model-selection results). Oyster survival was high in predator exclusion cages, regardless of reshelling. But in control treatments where predators were present, very strong predation (effect size = 3.65) reduced oyster survival on the unshelled portion of the oyster reef. Predation strength was reduced by 89% with moderate or high reshelling (predation effect size = 0.66). In the same experiments, the larval recruitment to individual oyster shells was best explained by the null model that did not distinguish among the levels of reshelling (AICc weight = 0.68, Fig. 2B).

In a survey of the ambient oyster population (outside of the predator enclosure experiment) 10 months after reshelling, the most parsimonious explanation of the oyster size structure was

a model that distinguished only between reshelled and non-shelved sections of the reef (AICc weight = 0.99, Fig. 3). Across all three sections of the reef, the most parsimonious explanation of the relationship between the density of adult oysters and habitat structure was a quadratic relationship ($y = -0.50 + 0.88x - 0.04x^2$; $R^2 = 0.68$; AICc weight = 0.91; Fig. 4A). Similarly, the most parsimonious explanation of the relationship between the density of juvenile oysters and habitat structure was a quadratic relationship ($y = -0.17 + 0.68x - 0.04x^2$; $R^2 = 0.68$; AICc weight = 0.99; Fig. 4B).

Discussion

This study demonstrated that the habitat structure of recycled oyster shell promoted oyster restoration success by decreasing predation intensity and increasing the overall success of oysters recruiting into the population (but not by increasing the supply of oyster larvae). When a prolonged and regional-scale drought abated to allow for a return to pre-drought water salinities in Apalachicola Bay, FL, the deployment of both moderate and high volumes of recycled oyster shell onto a historically productive oyster reef initiated a recovery 10 months later in terms of enhanced densities of adult and juvenile oysters. As predicted by community ecology theory, this initial recovery was facilitated by the physical structure of the reshelled sections of the reef, which decreased the intensity of predation relative to the non-shelved, low-habitat structure area of the reef. Because the high volume of recycled shell did not decrease predation intensity any more than did the moderate volume of recycled shell, the important relationship between habitat structure and predation intensity in this system appeared to be asymptotic. Taken together, the observational and experimental results of this study suggest that restoration of oyster reefs in Apalachicola Bay, FL, may be optimized by deploying a moderate amount of recycled shell (per area) in multiple locations, rather than deploying high amounts of shell in fewer areas. This is an important consideration of the diminishing returns produced by this valuable restoration resource.

It has been suggested that a negative threshold relationship between predation intensity and habitat structure is a general feature of ecological systems (Gotceitas & Colgan 1989). This concept, the *threshold hypothesis* of predation (Gotceitas & Colgan 1989), is that increasing habitat structure does not impair predator foraging until a certain threshold of physical structure is reached, at which point, further increases in habitat structure do not alter foraging rate. This relationship has been supported by a number of experiments in a diversity of systems, such as predatory roach (*Rutilus rutilus*) foraging on zooplankton in freshwater systems (Winfield 1986), predatory pinfish (*Lagodon rhomboides*) foraging on amphipods in marine systems (Nelson 1979; Stoner 1979), and ladybird beetles (*Coccinella septempunctata*) foraging on aphids (Legrand & Barbosa 2003). While many of these studies were conducted at small scales in the lab or field, our study provides support for this general relationship at a much larger landscape level (hectare).

Given the agreement between our results and the threshold hypothesis, it is worth considering why the results of our study

did not support the complement of this hypothesis: that prey should select habitats with high physical structure as a refuge to reduce predator foraging. This complementary relationship between prey abundance and habitat structure has been empirically demonstrated in terrestrial, freshwater, and marine systems as well as with prey taxa from vertebrate to invertebrates (Ritchie & Johnson 2009). In the laboratory, planktonic larval oysters (the life stage in which oysters can behaviorally select a habitat) settle more readily on more structurally complex surfaces (Whitman & Reidenbach 2012). In our experiment, we did not observe any enhanced settlement on the reshelled areas of the oyster reef with more habitat structure. We offer three explanations to reconcile that result with the prior expectation of habitat selection. First, the identity of the predator whose foraging was affected by the habitat structure may have been one that selectively focuses on adult-sized oysters, such as the stone crab (*Menippe adina*; Brown & Haight 1992) and the southern oyster drill (*Stramonitina haemastoma*; Pusack et al. 2018). In fact, our unpublished laboratory trials suggest that increasing habitat structure (surface rugosity) reduces the foraging success of the oyster drill. Accordingly, oyster larvae may not have responded to the habitat structure of the reshelled areas because predators on juvenile oysters may not be inhibited by physical structure. A second explanation may be that the scale of the reshelling on the oyster reef (0.4 ha) may have exceeded the scale at which larvae respond to differences in surface rugosity. In our field experiment, the individual shell of adult oysters used to quantify larval settlement may have already exceeded the rugosity threshold for larval settlement, and consequently the larvae responded to the rugosity at the scale of individual shells rather than at the scale of the reshelled areas. Third, hydrodynamic forces across all areas of the reshelled reef may have overwhelmed any effects of predation risk cues. There are complex costs associated with habitat selection by settling larvae, such as the risks of deferring settlement and traveling to sample alternative habitats, that complicate simple tests of settlement habitat preference (e.g. Stamps et al. 2005; Hamman et al. 2018).

Throughout the long history of restoring oyster reefs, a lack of accepted metrics to assess outcomes has been seen as an obstacle to detecting general trends and devising best practices (Baggett et al. 2015). Consequently, a group of experts advised that future restoration efforts should quantify four metrics including reef areal dimensions, reef height, oyster density, and oyster size-frequency distribution (Baggett et al. 2015). With these data, practitioners can evaluate whether a restoration outcome was successful by achieving a reef with vertical relief >20 cm in height, >10 living oysters m⁻², and evidence of recent recruitment in the size structure of the oyster population (Powers et al. 2009). Ten months after the reshelling of a historically productive oyster reef, the re-shelved areas achieved all of these metrics except for the vertical relief metric, which we did not measure. While the reshelled areas certainly contained structure heights >20 cm vertical relief, this relief was due to the height of the recycled oyster shell, not the living reef. Nevertheless, the other three restoration success metrics were met on areas of the reef with experimental support for the predator-threshold

hypothesis, suggesting that the local-scale relationship between predation and habitat structure scaled up to the oyster population at a landscape level.

Although this study suggests that oyster restoration in Apalachicola Bay, FL may be optimized by deploying a moderate amount of recycled shell (per area) in multiple locations, this strategy may be compromised by two other environmental contexts. First, regardless of the volume of shell deployed per unit area, oysters would not have recruited to the reshelled sections of the reef had the reshelling been conducted during the prolonged drought from 2012 to 2014, which caused a severe failure in oyster larval recruitment (Pine et al. 2015). Consequently, the threshold relationship between predation and structural complexity would have been rendered moot. Second, under warming temperatures and water stratification, oysters on subtidal reefs in some estuaries suffer higher mortality despite ideal salinity conditions because of low oxygen or hypoxic conditions on the benthos. In these locations, high amounts of recycled shell (per area) create tall reefs that provide a refuge for oysters and associated invertebrates closer to the water surface and away from the benthic hypoxic conditions (Lenihan & Peterson 1998). Thus, in estuaries with recurring hypoxia, a high reshelling volume may be needed to not only increase recruitment and decrease predation, but to also mitigate the effects of hypoxia/anoxia.

Although this study supports the growing consensus that community ecology theory can inform restoration practices, this study has several limitations that should be considered when evaluating its results. The first is that logistical constraints precluded a fully replicated experimental design. We followed best practices for making inferences from opportunistic low-replication studies (Reckhow 1990; Carpenter et al. 1998), but nonetheless we would encourage additional replication of this type of study to confirm our findings and better characterize the threshold level of oyster shell where returns diminish. Ideally, this would take the form of an adaptive management learning-by-doing process (Walters & Holling 1990). The second limitation of our study is that the reshelled areas may have promoted restoration success (in terms of adult and juvenile oyster density) both by reducing predation pressure and by altering hydrodynamics, with reef heights of the reshelled areas optimizing flow and the delivery of phytoplankton in a manner that enhances oyster condition and growth (Lenihan 1999). In fact, higher growth out of vulnerable size classes may promote an interaction between the effects of habitat structure on predation and physical-biological coupling that future experiments can tease apart. Finally, we were only able to follow the course of the experiment over 10 months, but restoration goals are much longer term. We hope that future funding opportunities will allow us to revisit these experimental reefs and assess the longer-term, generation-scale outcomes of these restoration activities.

It has become increasingly apparent that community ecology theory can be used to help predict the success of restoration efforts (Wainwright et al. 2018). However, many of the experimental approaches to test community ecology are often conducted at much smaller scale than are ecosystem-level

restoration activities. Here, we took advantage of an opportunistic ecosystem-level restoration of oyster reefs to obtain experimental evidence that moderate and high volumes of recycled oyster shell decrease local-scale predation on oysters by the same amount, supporting the threshold hypothesis of predation (Gotceitas & Colgan 1989). The implication of our findings is that oyster restoration is better served by deploying a moderate amount of recycled shell (per area) in multiple locations, rather than concentrating shell in fewer areas. This is an important consideration of the diminishing returns provided by this valuable restoration resource.

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Supporting Information

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

Figure S2. Image of rebar frames used in experiments to protect oysters from boating and harvesting activities (A). Diagram of rebar frame with dimensions (B). Image of oysters in an experimental cage made of wire mesh that was attached to one rebar post with cable ties (C)

Table S1. Summary of survey results from oyster reefs in Apalachicola Bay just prior to the reshelling experiment (summer 2015).

Table S2. Model-selection results for response variables from the field experiment (A–C) and survey (D–F).

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