Importance of low-relief nursery habitat for reef fishes

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Abstract. Coastal restoration projects to mitigate environmental impacts have increased global demand for sand resources. Unfortunately, these resources are often extracted from sand/shell banks on the inner continental shelf, resulting in significant alteration or loss of low-relief reefs in coastal oceans. Experimental reefs (oyster shell, limestone rubble, composite) were deployed in the western Gulf of Mexico to assess their potential value as nurseries for newly settled reef fishes. Occurrence, abundance, and species richness of juvenile fishes were significantly higher on all three types of low-relief reefs compared with unconsolidated sediment. Moreover, reefs served as nursery habitat for a range of reef fish taxa (angelfishes, grunts, sea basses, snappers, and triggerfishes). Red snapper (*Lutjanus campechanus*) was the dominant species present on all experimental reefs (100% occurrence), and mean density of this species was markedly higher on each of the three low-relief reefs (>40.0 individuals/reef) relative to comparable areas over unconsolidated sediment (0.2 individuals). Our results suggest creation or restoration of structurally complex habitat on the inner shelf has the potential to markedly increase early life survival and expedite the recovery of exploited reef fish populations, and therefore may represent a critical conservation tool for increasing recruitment and maintaining reef fish diversity.

Key words: coastal restoration; continental shelf; dredging; Gulf of Mexico; juvenile; low-relief reef; nursery habitat; oyster shell; red snapper; reef fish; shoals; trawling.

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Introduction

Density-dependent processes (e.g., growth, predation, competition) during early life are important determinants of recruitment for marine fishes (Fogarty et al. 1991). Because mortality is greatest during early life stages, habitats or habitat complexes that minimize mortality while maximizing growth potential are generally thought to serve as nurseries (Nagelkerken et al. 2015). Given the increasing impacts of habitat degradation in coastal ecosystems, there is a pressing need to identify and conserve marine nursery habitats (Beck et al. 2001). To date, the majority of conservation efforts have focused on nearshore nurseries in estuaries or tropical coral reef systems (e.g., seagrasses, mangroves, oyster reefs; Adams et al. 2006, Mumby 2006, Sheaves et al. 2015), while relatively little is known about nursery habitats in open waters of the continental shelf, despite the fact that these areas likely play an important role in sustaining demersal fish populations (Woodland et al. 2012).

Low-relief habitats (relic oyster reefs, sand/shell shoals) on the inner continental shelf serve as refuge for a wide variety of reef-dependent

fishes during early life (Rooker et al. 2004, Wells et al. 2009), including several taxa of high ecological and economic value (e.g., snappers, groupers, triggerfishes). Unfortunately, low-relief habitat is frequently altered or lost due to anthropogenic disturbances (i.e., dredging, trawling; Fogarty and Murawski 1998, Watling and Norse 1998, Thrush and Dayton 2002), and as a result, the limited availability of this valuable nursery may represent a population bottleneck for reef fishes. Coastal land loss and beach erosion have increased the demand for shelf sand resources, with ~28 million m^3 of sand mined per year from U.S. waters over the past decade for the purposes of beach renourishment (Elko et al. 2021). These dredging activities have significant impacts on the structural complexity of low-relief habitats that consolidate sand, such as those created by epifaunal communities (e.g., bivalves, sponges, ascidians). Because the presence of structurally complex habitat enhances settlement and increases early life survival of reef-dependent fauna (Scharf et al. 2006, Johnson 2007), recruitment success and population dynamics of reef fishes are inherently linked to the availability of low-relief habitat (Johnson 2007). Moreover, improved survival due to the presence of low-relief habitat may also serve to increase genetic diversity within a cohort, which, in turn, can improve a population's ability to adapt to changing environmental conditions (e.g., oil spills, climate change; Schindler et al. 2010).

Here, we develop an innovative approach to explore the potential benefits of low-relief habitat as nurseries for fishes on the inner continental shelf in the western Gulf of Mexico. While artificial reefs have been deployed in many regions of the world to mitigate habitat loss and create or restore hard bottom habitat for reef fishes, the majority of these deployments provide high-relief habitat (>1 m) for adult fishes targeted in recreational or commercial fisheries. As a result, catch rates at artificial reef sites are often high and there is debate over the conservation value of these structures (Powers et al. 2003). In contrast, similar creation or restoration of low-relief habitat for newly settled or juvenile reef fishes is relatively rare and often overlooked, despite the fact that such habitat is often limiting, and additional structure may increase early life survival

(Santiago et al. 2019). The goal of the current study was to develop low-relief reefs using both natural and fabricated materials to evaluate their potential value as nursery habitat for reef-dependent fishes. Specifically, we quantified occurrence and abundance of a model species, red snapper (*Lutjanus campechanus*), within and away from created low-relief nurseries, and characterized assemblage structure of juvenile fishes. Our working hypothesis was that species richness and abundance of red snapper recruits would be higher at created low-relief reefs than adjacent natural bottom (unconsolidated sediment), which is the dominant habitat type found on the inner shelf in the western GoM.

METHODS

The study was conducted within a recently established reef permit area on the inner shelf (depth 21–23 m) of the western GoM near the U.S.–Mexico border (Fig. 1A). The natural benthic habitat in the western Gulf of Mexico is largely mud/sand bottom; however, this region of the shelf was historically characterized by several low-relief habitats associated with relic barrier islands composed of scattered shell and sand shoals (Rodriguez et al. 2000). Recent studies indicate that this area represents a critical nursery habitat for red snapper and other exploited reef fishes in the northern GoM (Dance and Rooker 2019); however, this region of the shelf is also heavily impacted by shrimp trawling and is subject to dredging for sand resources, both of which can scour and/or alter the structure of low-relief habitats and may threaten the nursery function of this region (Wells et al. 2008). The placement of experimental reefs within a reef permit area (no trawl zone) was done in part to ensure that trawling did not occur at study sites, and reefs were created at two different locations within the permit area using the three material types: oyster shell, limestone (7–13 cm diameter rubble), and composite (concrete base with limestone and oyster shell) reefs (Fig. 1B–D). Experimental reefs comprised exclusively of oyster shell and limestone rock were deployed as bulk mounds (volume = 0.79 m^3, height ~ 20–25 cm, diameter ~ 2+ m), while prefabricated composite reefs (volume ~ 0.84 m^3, height ~ 10–15 cm, diameter ~ 3 m) were deployed on the seafloor as
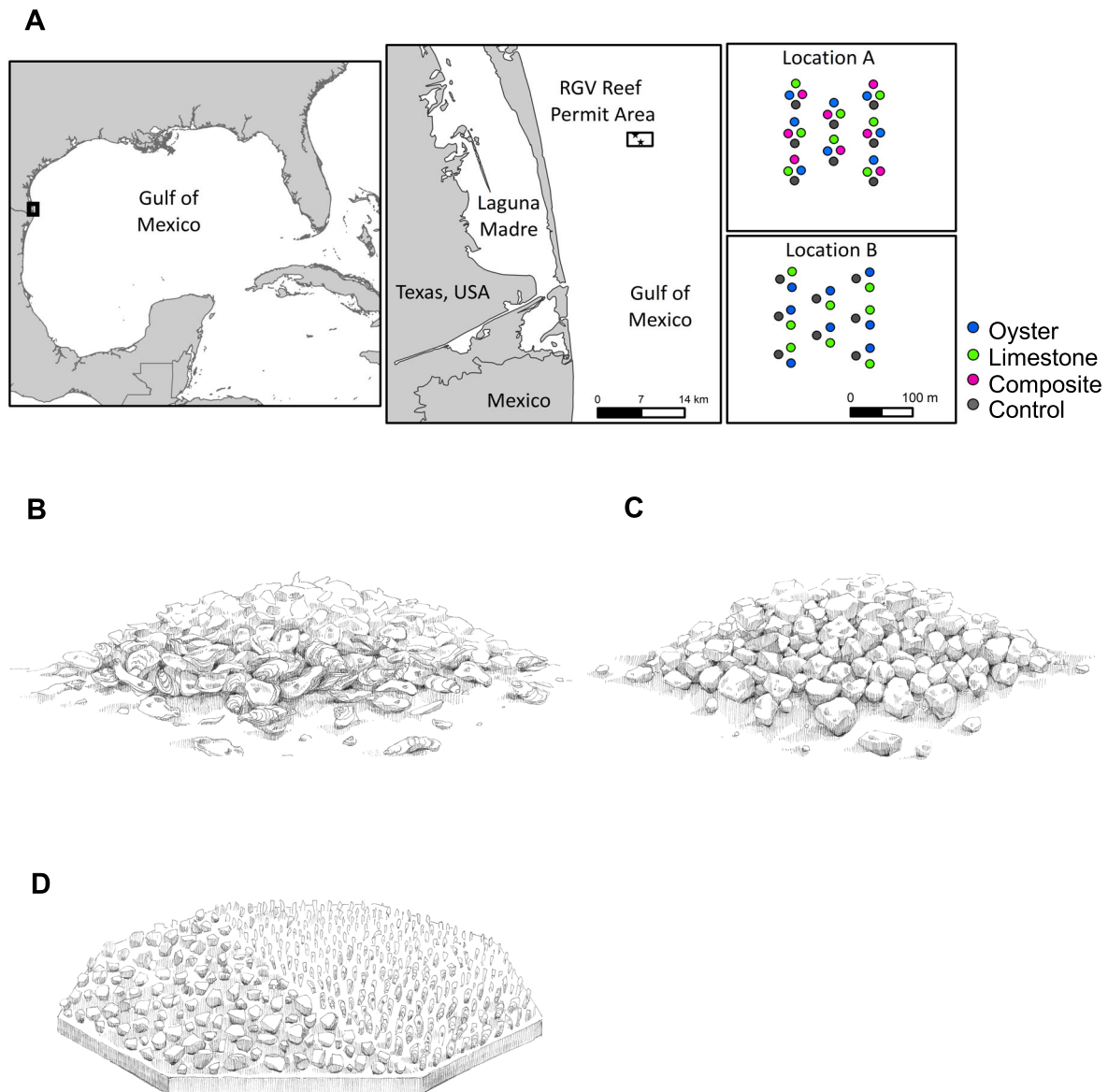
Fig. 1. Map showing study locations in the Rio Grande Valley (RGV) reef permit area off the United States–Mexico coast (A). Each study location is represented by a star inside of a rectangular box indicating the perimeter of the RGV reef permit area. Location A consisted of four low-relief reef treatments: oyster, limestone, composite (concrete base with limestone and oyster shell) reefs, and controls consisting of unconsolidated sediment (open). Location B consisted of three treatments: limestone reef, oyster reef, and controls. Diagrams depict deployed experimental reefs composed of oyster shell (B), limestone rock (C), and composite (concrete base with limestone and oyster shell) reefs (D).

constructed (Fig. 1B–D). Oyster shell and limestone material for each bulk mound were measured (by volume) into a hopper and lowered to the seafloor with steel cables—composite reefs were lowered to the seafloor in the same fashion.

Trials were conducted at two separate locations with the permit area and each location (A, B) contained eight separate sites. At location A, each site consisted of all three reef types and a control on natural bottom (unconsolidated

sediment, approximately 2–3 m in diameter). At location B, each site contained oyster shell mounds and limestone rubble mounds only as well as a control (unconsolidated sediment, approximately 2–3 m in diameter). Spacing of experimental reefs within each site was approximately 20 m, and all sites were a minimum of 40 m from other sites at a location (see Fig. 1A).

Experimental reefs were deployed in June 2017 during the primary spawning period for many reef fishes in the GoM, including red snapper (Rooker et al. 2004). Visual and video surveys were each conducted by divers using SCUBA on experimental reefs and controls in July and August to quantify the juvenile reef fishes present. Visual surveys at each reef consisted of two stationary counts conducted on either side of the structure (or plot area for unconsolidated control sites) by a diver. For the first count, the diver faced the reef structure on the seafloor and counted the individuals on the near half of the reef. The second count was subsequently performed on the opposite side of the reef in the same manner. Juvenile reef fishes were identified to species, and counts for each experimental reef were calculated as the sum of both counts. For

red snapper, juveniles were further classified as newly settled or age 0 (Fig. 2). Newly settled red snapper were identified as individuals possessing a clear white halo around the prominent dark spot below the second dorsal fin (Fig. 2B). A second diver performed a video survey (GoPro Hero 4) consisting of two parallel transects (one on each side of the reef) and a circular survey where the diver swam around the perimeter of the reef with the camera facing inward. Video surveys were analyzed in the laboratory and were used to account for small cryptic species missed in diver surveys and to validate counts of newly settled red snapper. Given the similarity in patch size (by volume) across experimental reefs, counts were not converted into a density and all analyses were performed on the raw abundance.

Percent frequency of occurrence was calculated for each species at each reef type and month combination. For each location, two-way analysis of variance (ANOVA) models were developed to test the influence of reef treatment (oyster, limestone, composite, and control) and month on both species richness (S) and juvenile red snapper abundance. Because each site included one
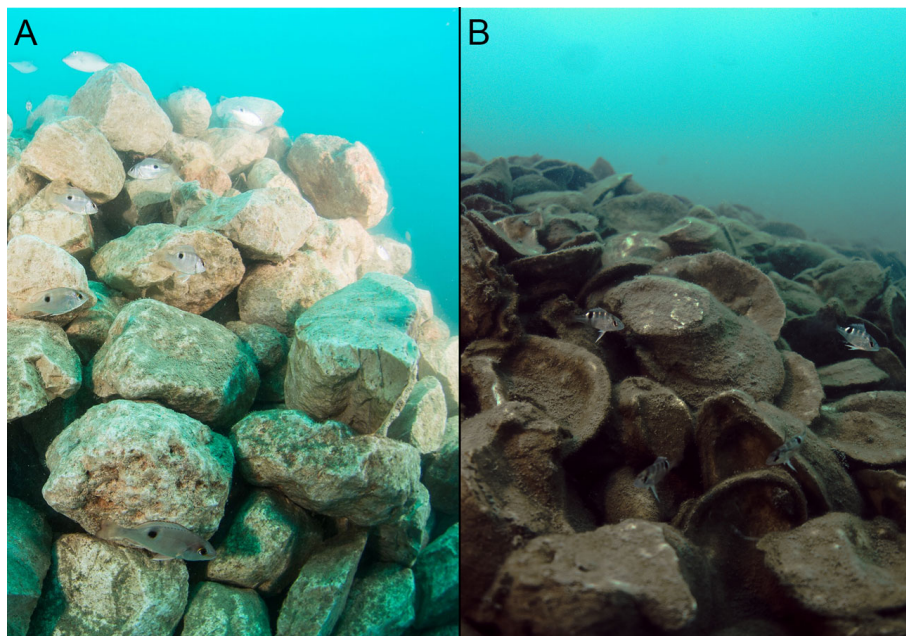

Fig. 2. (A) Juvenile red snapper at created limestone low-relief reefs and (B) newly settled red snapper at created oyster low-relief reefs.

replicate per treatment arranged in a group, site was included as random blocking term in both models to account for any site effects. For tests with a significant ANOVA, Tukey's honestly significant difference (HSD) was used to test for differences among reef treatments. At location B, only oyster, limestone, and control treatments were included in ANOVA models. The effects of reef type and month on newly settled red snapper abundance across both locations were tested using a paired *t*-test.

RESULTS

Nearly 3000 juvenile fishes representing 34 species were enumerated during July and August surveys of experimental reefs (Appendix S1: Table S1). Excluding controls (unconsolidated sediment), percent frequency of occurrence on all experimental reefs (*n* = 66) was highest for red snapper (100% of experimental reefs), dwarf sand perch *Diplectrum bivittatum* (93%), gray triggerfish *Balistes capriscus* (80%), lane snapper *Lutjanus synagris* (80%), and pigfish *Orthopristis chrysoptera* (71%). Species composition was similar across reef types; however, small differences in the most frequently encountered species were observed. Percent frequency of occurrence on oyster reefs was highest for red snapper (100%), dwarf sand perch (91%), lane snapper (84%), cocoa damselfish *Stegastes variabilis* (84%), and blue angelfish *Holocanthus bermudensis* (72%). In contrast, percent frequency of occurrence on limestone reefs was highest for red snapper (100%), gray triggerfish (97%), dwarf sand perch (94%), pigfish (75%), and lane snapper (69%). On prefabricated reefs, percent frequency of occurrence was highest for red snapper (100%), dwarf sand perch (94%), lane snapper (94%), gray triggerfish (88%), and pigfish (75%). Percent frequency of occurrence in July and August surveys was highly similar (≤5% different) for most of the dominant taxa including red snapper, dwarf sand perch, and gray triggerfish; nevertheless, the occurrence of some species was notably higher (≥20%) in one of the surveys (e.g., blue angelfish, lane snapper, pygmy sea bass, tomtate *Haemulon aurolineatum*; Appendix S1: Table S1).

Species richness (*S*) was quantified to assess the effects of season and reef type on juvenile fish assemblages in each study location (Fig. 3A). Mean number of species observed at sites in location A differed by reef type and month (ANOVA, *P* < 0.001) with no interaction. Species richness was greater for all three reef types than controls (Tukey's HSD; *P* < 0.001); however, no differences were observed among the three reef types: oyster (7.9 ± 0.3; mean ± SE), limestone (mean = 7.7 ± 0.4), and composite (mean = 8.2 ± 0.5; *P* > 0.05). Also, *S* was higher in August (mean = 6.3 ± 0.5) relative to July (mean = 5.6 ± 0.5) across all sites at location A (*P* < 0.05). While *S* also differed among reef types at location B (ANOVA, *P* < 0.001), no seasonal trend in *S* was observed. Species richness was lower on controls (mean = 0.2 ± 0.1) relative to oyster (mean = 8.8 ± 0.3) and limestone (mean = 8.7 ± 0.5) reefs (Tukey's HSD; *P* < 0.05) at location B, and similar to location A, *S* was not significantly different between oyster and limestone reefs (*P* > 0.05).

Juvenile red snapper abundance differed by reef type at both locations (ANOVA, *P* < 0.001); however, no seasonal differences were observed between July and August surveys at either location (ANOVA, *P* > 0.05). Juvenile red snapper abundance (individuals per reef) at experimental reefs was markedly higher than on controls (0.2 ± 0.1; mean ± SE) at location A for all three reef types (Tukey's HSD; *P* < 0.001); however, juvenile red snapper abundance on oyster (45.3 ± 5.1), limestone (43.7 ± 3.9), and composite (40.4 ± 3.3) reefs was similar (*P* > 0.05; Fig. 3B). Likewise, juvenile red snapper abundance was significantly higher on oyster (37.4 ± 4.5) and limestone reefs (29.6 ± 2.7), compared with unconsolidated controls (0.0 ± 0.0) at location B (*P* < 0.001), with no significant differences observed between the oyster and limestone reefs (*P* > 0.05). The abundance of newly settled red snapper was also calculated for oyster and limestone reefs to assess the relative potential of these materials as suitable substrate for settlement. Newly settled red snapper were more commonly observed on oyster and limestone reefs in July (3.0 ± 0.5) than August (1.1 ± 0.3), and paired comparisons between oyster and limestone reefs indicated that newly settled red snapper were more abundant at oyster (3.0 ± 0.5) than limestone (1.1 ± 0.3) reefs across the entirety of the study (paired *t*-test; *P* < 0.001).
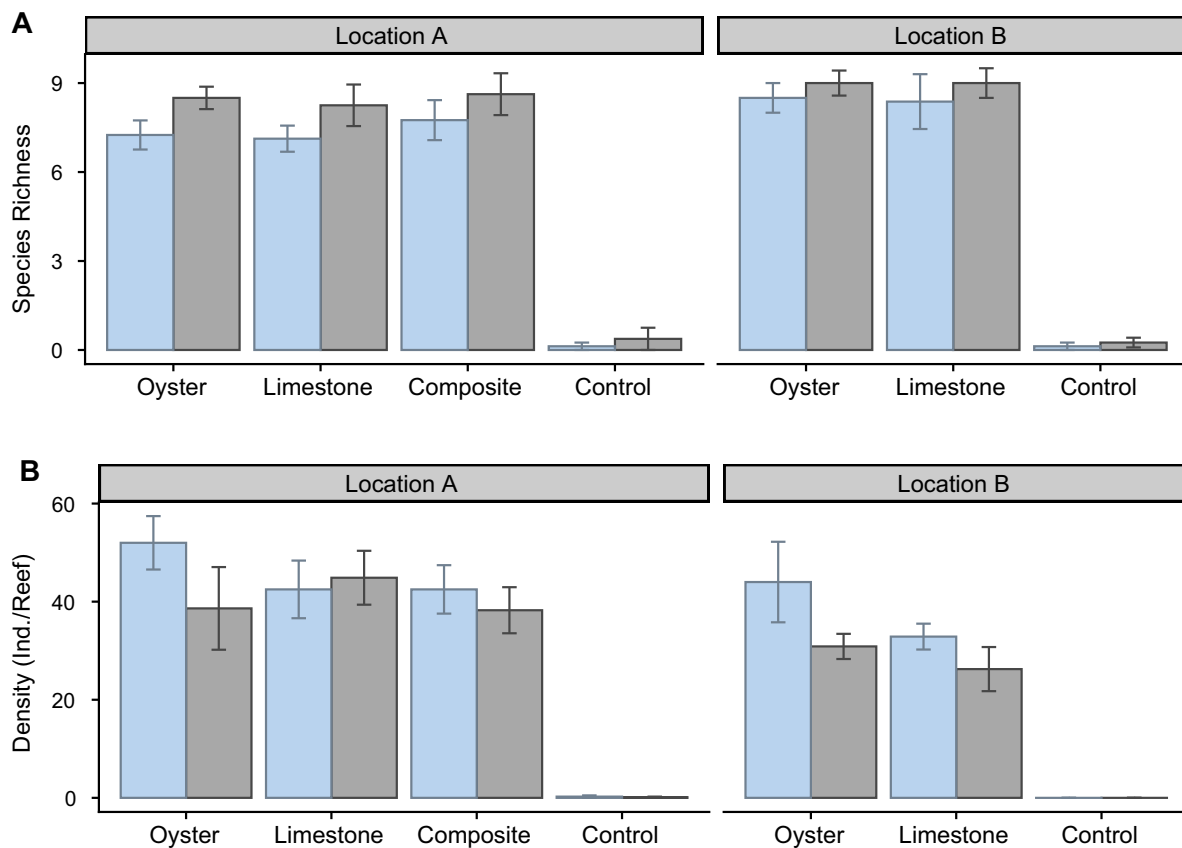
A

B

Fig. 3. Mean species richness (A) and juvenile red snapper abundance (B) at experimental reef sites at location A and location B during July (blue) and August (gray) surveys. Experimental reefs consisted of limestone, oyster, composite reefs, and control sites of unconsolidated sediment (open). Error bars represent ± 1 SE of the mean.

DISCUSSION

The importance of benthic habitat to reef fishes is well-documented, and species composition of the juvenile fish community on experimental reefs reflected adult assemblages at nearshore and off-shore reefs in the western GoM (Rooker et al. 1997, Froehlich and Kline 2015, Streich et al. 2017, Wetmore et al. 2020). Mixed-species groupings of juveniles from several family groups (Lutjanidae, Serranidae, Haemulidae, Pomacanthidae, Pomacentridae, Balistidae, Chaetodontidae) representing critical components of the shelf-edge reef ecosystem were observed at study sites indicating that structurally complex habitat on the inner continental shelf may provide nursery habitat to a wider variety of reef fish taxa than previously thought. Interestingly, the habitat and trophic requirements for adults of these species vary

greatly, spanning a range of trophic guilds from herbivores and planktivores to piscivorous predators (Dance et al. 2011). A growing body of literature suggests that there are several benefits for juvenile fish in mixed-species groupings ranging from foraging, detection of predators, and reduced intraspecific competition (Seppänen and Forsman 2007, Gil et al. 2017, Haak et al. 2020), highlighting the complex ecological role that nursery habitats play in regulating reef fish communities. Thus, the loss or degradation of nurseries on the inner continental shelf may have wide-reaching consequences for the health and resilience of reef fish communities, and the creation of low-relief reefs may represent a valuable conservation tool to maintain reef fish productivity and diversity.

The vast majority of fishes inhabiting experimental low-relief reefs in the current study were

juveniles, which is consistent with the notion that these habitats provide sufficient complexity for refuge for smaller individuals without attracting larger predators (Arney et al. 2017). All three experimental reef types had higher species diversity and juvenile red snapper abundance relative to adjacent unconsolidated sediment (i.e., control) that accounts for the majority (>90%) of available benthic habitat present on the continental shelf in the northwestern GoM. While the similarity in species diversity and red snapper abundance among oyster, limestone, and composite reefs may indicate that each material functions similarly as juvenile habitat, newly settled red snapper were notably more abundant at experimental reefs composed of oyster shell. Interestingly, several other species that primarily inhabited experimental reefs during the newly settled stage (e.g., blue angelfish, French angelfish, and cocoa damselfish) were also more frequently encountered on oyster mounds, suggesting this material may provide more suitable settlement habitat relative to limestone rubble or concrete composite reefs. The structural complexity of oyster shell is most similar to naturally occurring sand/shell banks of the northwestern GoM, which are areas of high juvenile recruitment for reef-dependent fishes (Rooker et al. 1997, Wells et al. 2009). It is possible that scattered shell provides the benefits of habitat complexity to newly settled fishes while minimizing the attraction of predators and the associated predation risk (Bradley et al. 2019). Previous studies indicate that the presence of predators and larger conspecifics negatively impacts the settlement success of new recruits due to both predation and competition for shelter (Almany 2003, Mudrack and Szedlmayer 2011). Indeed, our video surveys indicated that, although rare, larger (e.g., age 1+) reef fishes including red snapper, amberjacks, and gray triggerfish were more frequently encountered at experimental limestone and composite reefs relative to oyster reefs, potentially limiting the abundance of newly settled individuals.

Many reef fishes have protracted spawning seasons spanning several months with peak spawning occurring during more discrete time frames. As a result, we might expect to see seasonality in juvenile abundance at reef sites. Observed temporal variability in juvenile reef fishes on our experimental reefs likely reflected species-specific timing of spawning and recruitment patterns. For example, juvenile blue angelfish, cocoa damselfish, and tomtate occurred more frequently in August, while juvenile vermilion snapper *Rhomboplites aurorubens* and pigfish occurred more frequently in July. This notion was further supported by the patterns of occurrence for newly settled red snapper and lane snapper, which were reflective of previously published spawning and recruitment patterns (following 25- to 30-d pelagic larval duration) in the northern GoM. While both species spawn throughout the summer, newly settled red snapper were most common in July corresponding to the known peak spawning period of June in the western GoM (Rooker et al. 2004). In contrast, newly settled lane snapper were most common in August, which corresponds to the peak spawning period of mid-July described by Mikulus and Rooker (2008) in the western GoM.

Low-relief nursery habitat serves a vital function in the life cycle of many reef fishes (Hewitt et al. 2005). Unfortunately, land loss, hurricanes, and oil spills have resulted in a proliferation of coastal restoration projects that have increased the demand for sand resources, often extracted from these nurseries (e.g., shoals) on the inner continental shelf (Diaz et al. 2003). Given the increasing disturbance to benthic habitats in coastal ecosystems of the GoM and other regions of the world (Hiddink et al. 2017), the restoration of these habitats may be critical to the conservation of reef fish communities and to sustaining exploited species, such as red snapper. Our results clearly demonstrate that creation of low-relief, structurally complex habitat on the inner shelf greatly increases both the abundance and diversity of juvenile reef fishes. While juvenile abundance alone does not necessarily equate to habitat quality as created habitat could concentrate new settlers and increase predation risk, it should be noted that the presence of predators at study sites was quite rare. Moreover, recent studies indicate that this region of the inner continental shelf represents an important nursery area for reef-dependent species such as red snapper (Wells et al. 2009, Dance and Rooker 2019). Because the availability of high-quality juvenile habitat is likely an important determinant of survival and recruitment success, the restoration of

low-relief habitat within this region may improve the long-term resilience and stability of reef fish populations in the GoM. While future studies that improve our understanding of how these structures facilitate or improve growth and survival of resident taxa are needed, this study represents an important step in understanding the value of low-relief reefs as nursery habitat for key constituents of the reef fish assemblage.

Acknowledgments

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3542/full