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ARTICLE

Special Feature: Honoring Charles H. Peterson, Ecologist

Fish and invertebrate use of restored vs. natural oyster reefs in a shallow temperate latitude estuary

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Abstract

Coastal marine habitats continue to be degraded, thereby compelling large-scale restoration in many parts of the world. Whether restored habitats function similarly to natural habitats and fully recover lost ecosystem services is unclear. In estuaries, oyster reefs have been degraded by multiple anthropogenic activities including destructive fishing practices and reduced water quality, motivating restoration to maintain oyster fisheries and other ecosystem services, often at relatively high cost. We compared fish and invertebrate communities on recently restored (0–1 year post-restoration), older restored (3–4 years post-restoration), and natural oyster reefs to determine if and when restored reefs support functionally similar faunal communities. To test the influence of landscape setting on the faunal communities, the restored and natural reefs, as well as a control without reef present, were distributed among three landscapes (on the edge of salt marsh away from seagrass [salt marsh landscape], on mudflats [mudflat landscape], and near to seagrass and salt marsh [seagrass landscape]). Oyster density and biomass were greatest on restored reef habitat, as were those of non-oyster bivalve species. Total abundance of invertebrates was much greater on oyster reefs than in control plots, regardless of reef or landscape type, yet were frequently highest on older restored reefs. Meanwhile, juvenile fish densities were greatest on natural reefs, at intermediate densities on older restored reefs, and least abundant on controls. When comparing the effects of reef age and landscape setting, juvenile fish densities were greatest on younger reefs within the mudflat landscape. Collectively, these results indicate that oyster reefs harbor higher densities of resident invertebrate prey, which may explain why reef habitat is also important for juvenile fish. Laboratory and field experiments supported the notion that gag grouper (a predatory demersal fish) forage more effectively on oyster reefs than on unstructured mud bottom, whereas our experiments suggest that

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flounders that utilize oyster reefs likely forage on adjacent mud bottom. Because landscape setting influenced fish and invertebrate communities on restored reefs, the ecological consequences of landscape setting should be incorporated into restoration decision making and site selection to enhance the recovery of ecosystem goods and services.

KEYWORDS
benthos, habitat restoration, nekton, oyster reefs, salt marshes, seagrass beds,
Special Feature: Honoring Charles H. Peterson, Ecologist

INTRODUCTION

Estuarine and marine habitats are among the most valuable on earth because they provide numerous ecosystem services that coastal communities rely upon (Barbier et al., 2011). For instance, seagrass beds, salt marshes, mangroves, and oyster reefs provide nursery habitat for fishes and mobile invertebrates, thereby supporting economically valuable and culturally important recreational and commercial fisheries (Breitburg et al., 2000; Coen et al., 1999; Grabowski et al., 2012; Peterson et al., 2003). These habitats also enhance water quality by removing excess nitrogen, and a subset of them promote carbon burial and storage (Fourqurean et al., 2012; Piehler & Smyth, 2011; Röhr et al., 2018; Smyth et al., 2013). Coastal wetlands also reduce shoreline erosion and flooding, which in turn reduces damages to coastal property (Narayan et al., 2017). The provision of ecosystem services explains in part why coastal habitats are a major focus of conservation and restoration decision making.

Coastal and estuarine habitats face numerous threats, with many having been reduced to less than 50% of their historic extent (Lotze et al., 2006). Habitat loss will certainly be exacerbated by impending sea-level rise and other climate risks (Airoldi & Beck, 2007; Beck et al., 2011; Grabowski et al., 2012; Waycott et al., 2009). Anthropogenic threats include dredge and fill activity, diseases, eutrophication, and destructive harvesting practices, all of which tend to reduce the structural complexity of coastal habitats via conversion to unconsolidated mud and sand bottom (Lenihan & Peterson, 1998, 2004). Widespread degradation of coastal habitats globally has coincided with the loss of the valuable ecosystem services that coastal communities rely upon (Beck et al., 2011; Grabowski et al., 2012; Lotze et al., 2006; Orth et al., 2006). Thus, large-scale habitat restoration will likely be necessary in many coastal regions of the United States and elsewhere to rehabilitate coastal ecosystems and recover these lost ecosystem services.

The degree to which restored habitats function similarly to natural habitats is often unclear, in part because restoration science is relatively nascent (Peterson & Lipcius, 2003). A critical function of restored habitat is the recovery and/or maintenance of biodiversity, which can be assessed by quantifying the species assemblages that develop or emerge and then comparing those with natural habitat. In temperate latitude estuaries and lagoons, oyster reefs were historically a ubiquitous subtidal and intertidal biogenic habitat that provided substrate and refuge for a plethora of species in addition to massive oyster populations (Jackson et al., 2001). About 85% of oyster reef habitat has been lost globally due to anthropogenic disturbance (Beck et al., 2011). Oyster reefs are widely recognized for providing multiple ecosystem services that humans rely upon (Peterson & Lipcius, 2003). In addition to providing habitat for economically and ecologically valuable finfish and invertebrates that support several fisheries, oyster reefs stabilize and protect shorelines (Meyer et al., 1997; Piazza et al., 2005; Scyphers et al., 2011). Oyster habitat also removes excess nutrients from coastal ecosystems by promoting denitrification (Kellogg et al., 2014; Piehler & Smyth, 2011; Smyth et al., 2013). Collectively, these valuable services explain why there have been widespread efforts to restore oyster reefs (Breitburg et al., 2000; Coen et al., 1999). Over the last few decades, broad understanding of the value of reef restoration for recovering oyster populations and associated ecosystem services has emerged (Grabowski et al., 2012; Harding & Mann, 1999; Harding & Mann, 2001; Lenihan, 1999; Schulte et al., 2009). Looking forward, determining the environmental factors and habitat characteristics that are most critical in predicting if restored habitats recover lost ecosystem services will fundamentally advance the field of restoration ecology.

In recent years, there has been a growing awareness that landscape-scale processes can mediate coastal communities and ecosystem functioning. The spatial configuration of habitat patches and different habitats within a landscape can influence species movement, foraging, and community assembly. For instance, Micheli and Peterson (1999) found that seagrass beds serve as

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corridors between the edge of salt marsh and intertidal oyster reef habitat, and consequently facilitate blue crab *Callinectes sapidus* access to bivalve prey on the reefs. Meanwhile, the landscape setting of restored oyster reefs can influence whether it provides key functions, such as habitat for juvenile and adult fishes (Geraldi et al., 2009; Grabowski et al., 2005; Lenihan et al., 2001). Studies that address how the landscape setting of restored habitats affects if they perform the ecosystem functions and services associated with natural habitats will help guide future restoration decision making.

It is widely accepted that estuarine and marine habitats function as important refuge and nursery grounds for juvenile fishes and invertebrates (Hollweg, Christman, Lipton, et al., 2020; Irlandi & Crawford, 1997; Lefcheck et al., 2019; Peterson et al., 2003; Peterson & Lipcius, 2003; Rozas & Minello, 1998; Thayer et al., 1978; Thayer et al., 1982; Zu Ermgassen et al., 2016). Lefcheck et al. (2019) reviewed nekton use of estuarine habitats and determined that almost all structured habitats enhance juvenile fish and invertebrate densities, but the magnitude of enhancement was greatest within seagrass beds and mangroves. Meanwhile, Zu Ermgassen et al. (2021) found that enhanced fish and mobile invertebrate productivity derived from seagrass beds and salt marshes in the Gulf of Mexico was greater than that of oyster reefs. Thus, while they all provide important refuge habitat for juvenile fish, the most common biogenic habitats vary in the degree to which they provide key ecosystem functions such as augmenting secondary production. However, it is often unclear whether and how specific landscape contexts (e.g., presence or absence of adjacent biogenic habitats) influence the ecosystem services provided by natural and restored habitats (Grabowski et al., 2005; Lenihan et al., 2001).

In this study, we conducted a series of field surveys to test whether fish and invertebrate communities differ between restored and natural reefs, as well as from mud bottom where structure is largely absent. Prior work has largely examined restored and natural reefs in relatively deepwater subtidal habitat (Lenihan et al., 2001), so here we explore differences observed in shallow subtidal and intertidal areas in which the majority of extant oyster habitat in coastal North Carolina is found. We further examined whether the landscape setting (i.e., presence of seagrass and salt marsh vegetation) influences the fish and invertebrate utilization of restored and natural reefs and if the age of restored reefs affects the resident and transient species utilizing the habitat. We coupled our community surveys with stomach content analyses of fish and experiments to investigate the importance of reefs as foraging habitat for juvenile and adult fishes. This study builds on our earlier efforts examining how landscape setting influences and oyster reef restoration influence fish and invertebrate communities (Grabowski et al., 2005) in two key ways: by comparing restored reefs to natural reefs and examining if restored reef age influences associated communities. A better understanding of how landscapes (or "seascapes") influences the community structure of reef assemblages, and their trophic interactions, will help reveal the potential mechanisms underlying augmented fish and invertebrate production in natural and restored reefs. Collectively, these efforts aim to enhance our understanding of oyster reef habitat community structure and help guide restoration decision making.

MATERIALS AND METHODS

We sampled oyster reefs and soft-sediment control areas without reef habitat to compare fish and invertebrate communities on preexisting "natural" versus restored reefs. We conducted sampling on natural reefs, newly restored reefs (0–1 year after construction), older restored reefs (3–4 years after construction), and controls in the fall of 2000 and throughout 2001. Fish and invertebrate communities were sampled using core excavations, pop-up nets, gillnets, and hook-and-line gear, while stomach contents of adult and juvenile fishes were also examined. In addition, we conducted a series of manipulative experiments in field enclosures and laboratory mesocosms to test whether oyster reef habitat influences fish growth and prey survival rates, and thus ultimately functions as critical foraging and/or refuge habitat.

Study site

This project was conducted in Middle Marsh, a marsh complex within Back Sound, North Carolina (Figure 1). In June 1997, we constructed 12 intertidal reefs using oyster shell provided by the North Carolina Division of Marine Fisheries (NC-DMF) (Grabowski et al., 2005). In June 2000, we constructed eight more reefs in Middle Marsh again using shell from NC-DMF. Each experimental reef contained approximately 750 gallons (2836 L, ~60 bushels) of oyster shell and was 5 m long × 3 m wide × 0.3 m tall in total size. Restored reefs extended almost completely out of the water at low tide, ~0.1 m above the mean low tide, which is within the optimal growth zone for intertidal oyster reefs (Rodriguez et al., 2014). Reefs were positioned in each of the three intertidal landscapes (the spatial configurations of seagrass, salt marsh, and mudflat habitats) where intertidal reefs are commonly found in the South Atlantic

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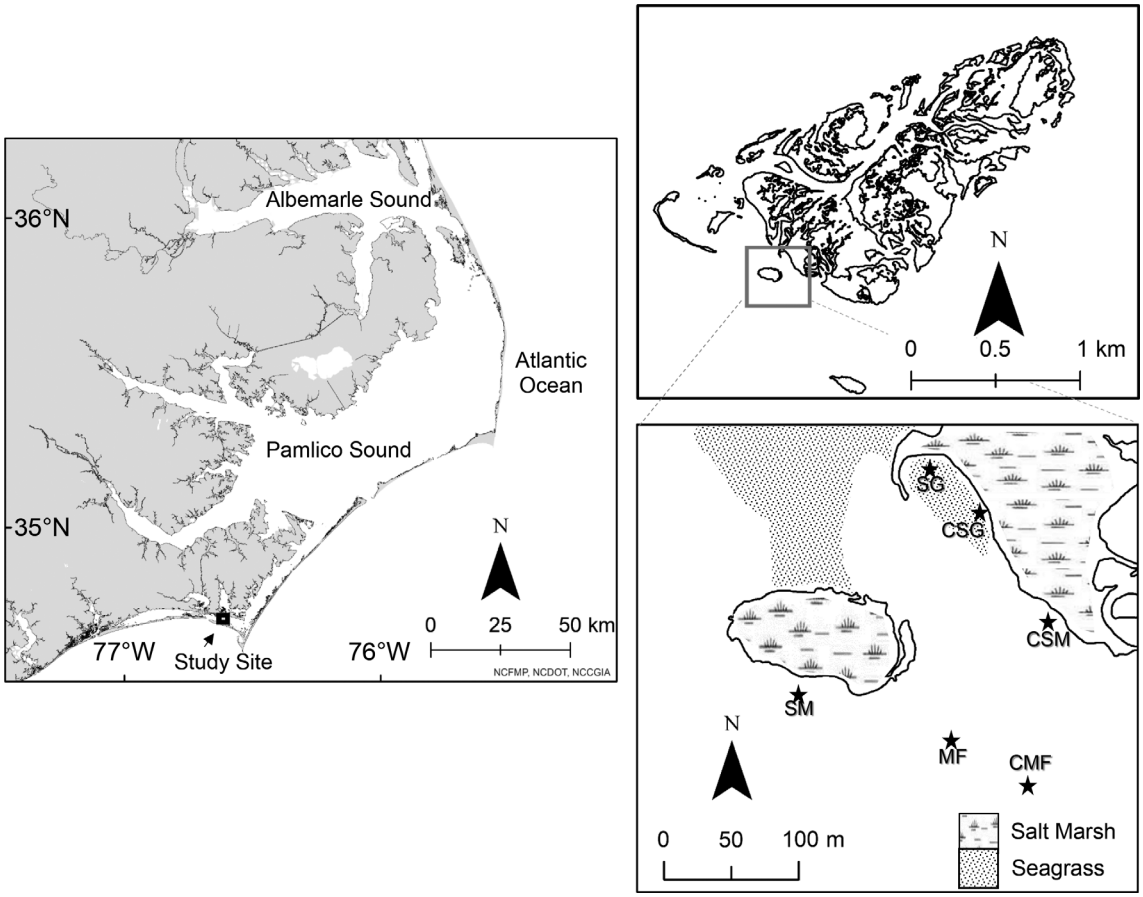

FIGURE 1 Map of field sites in Middle Marsh, Back Sound, Carteret County, North Carolina. In the bottom right panel, restored reefs were placed in salt marsh (SM), mudflat (MF), and seagrass (SG) landscapes; CSM, CMF, and CSG refer to the same landscapes, respectively, but without a restored reef present

Bight (Bahr & Lanier, 1981): on the fringes of salt marshes and bordered by seagrass beds on the opposite side (referred to throughout as the "seagrass landscape"); on the sandy points that extend outward from salt marshes not near seagrass habitat ("salt marsh landscape"); and on tidal flats isolated from vegetated habitat ("mudflat landscape").

Four replicate reefs were constructed in each of these landscapes in 1997 as well as in the mudflat and seagrass landscape types in 2000 (Grabowski et al., 2005). Four replicate natural reefs with similar dimensions were chosen for both the seagrass and salt marsh landscapes (there were no naturally occurring mudflat reefs in this study area). In addition, we selected four replicate control sites without reef habitat in each of the three landscapes (see Figure 1; Appendix S1: Table S1).

Reef sampling

Surveying juvenile and adult fishes, mobile invertebrates, and resident epifauna and infauna required use of a suite of sampling methods, including core excavations, pop-up nets, gillnets, and hook-and-line gear. Sampling was conducted in the fall of 2000 (gillnets and hook-and-line only) and seasonally in the spring, summer, and fall of 2001 (all collection methods). Sampling coincided with the seasons in which target organisms generally use shallow estuarine habitats in North Carolina.

Gillnets (10 m long × 1.5 m tall: 7.5-cm stretch) were used to sample large fishes. The lead line of the net outlined half of the reef (one 5-m side and one 3-m side) and was oriented to open fully during flood tide when catch rates are highest in this region (sensu Grabowski et al., 2005). Gillnets were deployed midflood tide and retrieved 6 h later at mid-ebb tide. Sampling days were selected to target the evening period when catch rates typically are high (Grabowski et al., 2005). Sampling was conducted monthly from September through November 2000 and April through November 2001, avoiding those months in which colder temperatures restrict fish from using shallow water habitats (Baillie et al., 2014). All captured fishes were identified, measured, and weighed. In addition, stomach contents were removed and preserved

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in 10% formalin for analysis in the laboratory (see Appendix S1 for more details on stomach content analysis and hook-and-line sampling).

To sample juvenile fishes as well as juvenile and adult shrimp and crabs, we used pop-up (5 m long × 3 m wide × 2 m tall) nets to surround and enclose experimental and control sites. The pop-up net consisted of 3-mm mesh net that formed a curtain around the sample area when deployed from the substrate to above the water surface. The bottom of the net was anchored to the substrate with sandbags that had been implanted around the edge of the reef, flush with the surrounding habitat. The rest of the net was then buried so as to not impede any organisms from entering the area, or artificially augment numbers by creating structure. Connecting ropes ran from the top edge of the buried net through eyeholes on the top of PVC rebar stakes surrounding the reef, and out away from the sample area. This method minimized human interference by allowing us to deploy the nets remotely. By pulling on the ropes at high tide, the net was lifted simultaneously on all sides of the reef, encircling the reef and trapping organisms as the water drained out with the ebbing tide. Organisms were collected at low tide when the reef or control substrate was exposed, and they were returned to the laboratory where they were identified to species and counted. Bird netting (1.0-cm mesh) was used to cover the enclosed area to deter mobile species from escaping, while the water level was near the top of the net and to prevent sea birds from preying on any enclosed organisms.

Core sampling was conducted at all natural and restored reefs and controls to quantify and analyze the resident infaunal and epifaunal community. Sampling occurred in the spring, summer, and fall of 2001. A haphazardly positioned 15-cm-diameter core was used to sample the top 10 cm of subsurface material within each core. This sampling procedure provided sufficiently high oyster and infaunal densities to detect differences among habitat treatments at the coarse taxonomic level and allowed us to mitigate damaging the natural reefs through mass excavation. Excavated material was sieved with 0.5-mm mesh sieves, and invertebrates were preserved in 10% formalin before being identified to the lowest possible taxonomic level and quantified in the laboratory. Species were then aggregated into the following taxonomic groupings: bivalves other than oysters, gastropods, resident crabs, and amphipods, all measured in densities, and the wet biomass of polychaetes. In addition, oysters and shell material from each core were used to assess characteristics of the oyster community. In particular, we quantified total weight (oysters and shell material), cluster weight (all shell material with at least two oysters extending 5 cm vertically from the shell), number and weight of living, legal size oysters (>7.6 cm in shell height [SH]), number of living large juvenile and adult oysters (≥5.1 cm SH), and number of living new recruits (<5.1 cm SH). Cluster weight is a quantification of living oysters on a reef that create vertical relief and has been used in previous studies as a proxy for structural complexity (Grabowski et al., 2005; Meyer et al., 1997).

Growth and survival experiments

Field experiments were conducted in Middle Marsh to determine the effect of oyster reefs on juvenile fish growth and survivorship. Square 1-m^2 enclosures were constructed using 1.3-cm mesh hardware cloth lined with 0.6-cm mesh Vexar cloth. Enclosures were placed in the shallow subtidal (0.1–0.2 m below mean low water) so as to include either reef habitat or mud bottom (i.e., control) and allow enough water for fish to survive at low tide. All enclosures were deployed on reef and control habitats late in the fall of 2001. We used juvenile gag *Mycteroperca microlepis* for experimental trials because it preferentially uses oyster reefs and other structured habitats over soft sediments as young-of-year (Peterson et al., 2003). One juvenile gag was measured (total length), weighed, and released within each enclosure in early November. After 6 weeks, gag were measured and weighed again, and their stomach contents were removed and preserved in 10% formalin. Gag stomach contents were identified to the lowest possible taxonomic level, quantified, and weighed in the laboratory.

Additionally, a series of prey survival experiments were conducted in a 6 m long × 9 m wide × 1 m tall settling tank behind the University of North Carolina's Institute of Marine Sciences (UNC-IMS). Twelve circular (1.5 m diameter × 0.4 m deep) pools were positioned within the settling tank, and each pool was filled with ~151 L of sand. Circular 1-m^2 enclosures were constructed using 1.3-cm mesh hardware cloth lined with 0.6-cm mesh Vexar cloth. One enclosure was positioned in the center of each pool, and the bottom 10 cm of the enclosure was buried into the sand. Oyster reef habitat was constructed in six of the 12 pools by adding 18.9 L of individual shells and 56.8 L of highly aggregated shell clusters with greater vertical relief typical of intact reefs. Experiments were conducted using juvenile gag and flounder *Paralichthys* spp. because they are common predators that forage in coastal estuaries in North Carolina and with gag predominately occupying a range of structured habitats, while flounder employing lie-and-wait foraging strategies in mud and seagrass habitats. For experiment trials with gag, mesocosms consisted of mud bottom (mudflat) and complete cover of oyster reef

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habitat (Reef). For experiments with flounder, we included an additional habitat treatment that involved splitting the mesocosm equally between oyster reef and mud bottom (Edge). Each experiment consisted of one predator (juvenile gag [mean: 139 mm Standard Length] or flounder *Paralichthys* spp. [mean: 241 mm Standard Length]) and one prey (adult white shrimp *Litopenaeus setiferus* or killifish *Fundulus heteroclitus*) species. A total of four experiments were conducted with each possible predator–prey combination represented. During each trial, one predator and either 10 white shrimp or 20 killifish individuals were added to each replicate pool. After 6 days, mesocosms were disassembled and the number of surviving prey was quantified. Control trials were conducted under the same experimental conditions without the presence of either predator species to assess prey natural mortality.

Statistical analyses

For all field sampling efforts, we performed two separate sets of analyses to account for the fact that we did not have restored and natural reef treatments in all three landscapes. First, we analyzed if communities associated with restored oyster reefs differed from those on natural reefs in either the seagrass or salt marsh landscapes using the reefs that were restored in 1997. Next, we examined whether reef age influenced fish and invertebrate communities on oyster reefs in either the mudflat or seagrass landscapes using reefs restored in 1997 versus 2000. In both sets of analyses, we also compared reefs to unrestored controls within each landscape to examine the degree to which restored reef, natural reef, and soft-sediment communities differ from each other.

To compare restored versus natural reefs, the effects of season (spring, summer, and fall), habitat type (1997 reefs, natural reefs, and control), and landscape setting (salt marsh and seagrass) were analyzed first using multivariate analysis of variance (MANOVA) and then separate ANOVAs on: (1) total weight of oyster and shell material, weight of oyster clusters, and densities of legal and newly recruited oysters in core samples; (2) the densities of bivalves other than oysters, gastropods, resident crabs, and amphipods, and biomass of polychaetes in core samples; and (3) densities of spot *Leiostomus xanthurus*, all benthic fishes excluding spot, and grass shrimp collected using pop-up nets. There were no living oysters and little shell material in the cores from the control habitat; therefore, the control treatment was excluded from all oyster analyses. Because over 90% of juvenile spot were captured in spring, and pop-up nets in the vast majority of habitat type–landscape combinations in summer and fall caught no spot, we decided to analyze spot captured in spring separately from all other benthic fishes as separate response variables. We utilized the same tests to examine the importance of age of restored reefs on the aforementioned response variables, using habitat type based on the presence and age of restored reefs (1997 reefs, 2000 reefs, and control), and landscape setting (mudflat and seagrass) as fixed factors. In all of the above cases, MANOVAs resulted in significant main effects; thus, we proceeded with all of the individual ANOVAs, which are presented in the "Results" section.

All datasets were tested for heterogeneity of variances using Cochran's tests (Underwood, 1981). Heterogeneous data were transformed using root transformations until variance groups of transformed data were homogenous for all main fixed effects. Student-Newman-Keuls (SNK) post hoc tests were conducted for all significant interactions and main effects with more than two levels. The SNK post hoc test was selected because the study design was balanced with a priori predictions and fixed factors (Day & Quinn, 1989).

For the growth experiment in the field, the effect of habitat type (reef or mud bottom) on the growth of gag was analyzed using ANOVA. Prey mortality from mesocosm experiments was analyzed using separate one-factor ANOVAs (gag experiments with two treatments: reef or mud bottom; flounder experiments with three treatments: reef, reef edge, and mudflat) with habitat type as the independent variable (Underwood, 1981). Trends in the stomach contents of gag from the field experiment were examined. Student-Newman-Keuls post hoc tests were performed on all significant ANOVA results for interaction terms or main effects with more than two levels.

RESULTS

Comparing oyster reef communities of restored (1997) reefs versus natural oyster reefs

Oyster properties in restored and natural reefs

Habitat type and season were the main driver of differences among oyster properties on restored and natural reefs in the seagrass and salt marsh landscapes (see MANOVA results in Appendix S1: Table S2). Total oyster and shell weight were significantly greater on restored (3.9 ± 0.3 [mean ± SE] kg) than on natural reefs (1.8 ± 0.1 kg; $p < 0.0001$) but did not differ among landscapes ($p = 0.76$; Appendix S1: Table S3a). Total oyster and shell weight also varied by season ($p = 0.04$); it was greater in the fall (3.4 ± 0.5 kg) than the spring

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(2.5 ± 0.2 kg) or summer (2.6 ± 0.4 kg), which did not differ from each other. Cluster weight varied only as function of habitat type ($p = 0.01$), and it was 50% greater on restored (1.4 ± 0.2 kg) than on natural (0.9 ± 0.1 kg) reefs (Appendix S1: Table S3b). Similar to cluster weight, the density of legal oysters was significantly greater on restored (8.9 ± 1.5 oysters/core) than on natural (4.7 ± 0.6 oysters/core) reefs ($p = 0.02$; Appendix S1: Table S3c). Oyster recruits did not differ by season, landscape, or reef status or their interactions (Appendix S1: Table S3d).

Resident invertebrate communities in restored and natural reefs and mud habitat

There were 13 species of crabs, 10 species of shrimp, three species of echinoderms, and three species of tunicates and anemones identified in core samples. Twenty-four families of polychaete worms also were identified in the core samples, with a majority of the biomass coming from the Eunicidae, Nereidae, and Terebellidae families. For the analysis of restored (1997) reefs versus natural reefs, gastropod densities varied significantly by season, habitat type, and landscape, but not any of their interactions (Appendix S1: Table S5a). Gastropod densities in the spring (27.7 ± 5.0 gastropods/core) were higher than those in summer (17.2 ± 3.4 gastropods/core) and fall (13.7 ± 2.3 gastropods/core), which did not differ from each other (Figure 2a). Gastropod densities did not differ between restored (1997) reefs (18.9 ± 3.0 gastropods/core) and natural reefs (25.9 ± 4.9 gastropods/core), but both were significantly higher than control (13.8 ± 3.2 gastropods/core) sites. Gastropod densities in the seagrass landscape (23.6 ± 3.9 gastropods/core) were over twice those in the salt marsh landscape (9.7 ± 1.6 gastropods/core). Bivalve (other than oyster) densities varied by season and habitat type (Appendix S1: Table S5b). Bivalve densities in the spring (26.3 ± 4.5 bivalves/core) were more than double those in the summer (12.2 ± 3.8), while fall (17.2 ± 8.7 bivalves/core) densities did not differ from either season (Figure 2b). Bivalve densities on 1997 restored reefs (30.0 ± 9.0 bivalves/core) were almost three times more abundant than those on controls (10.3 ± 3.1 bivalves/core), but densities on natural reefs (15.4 ± 3.9 bivalves/core) did not vary from those on 1997 reefs or controls. Habitat type also significantly affected resident crab densities (Appendix S1: Table S5c). Resident crab densities on natural reefs (11.0 ± 1.2 crabs/core) and restored (1997) reefs (14.3 ± 2.0 crabs/core) did not differ from each other but were both two orders of magnitude greater than those on controls (0.1 ± 0.1 crabs/core). The densities of resident crabs were not significantly different in the spring and summer but were

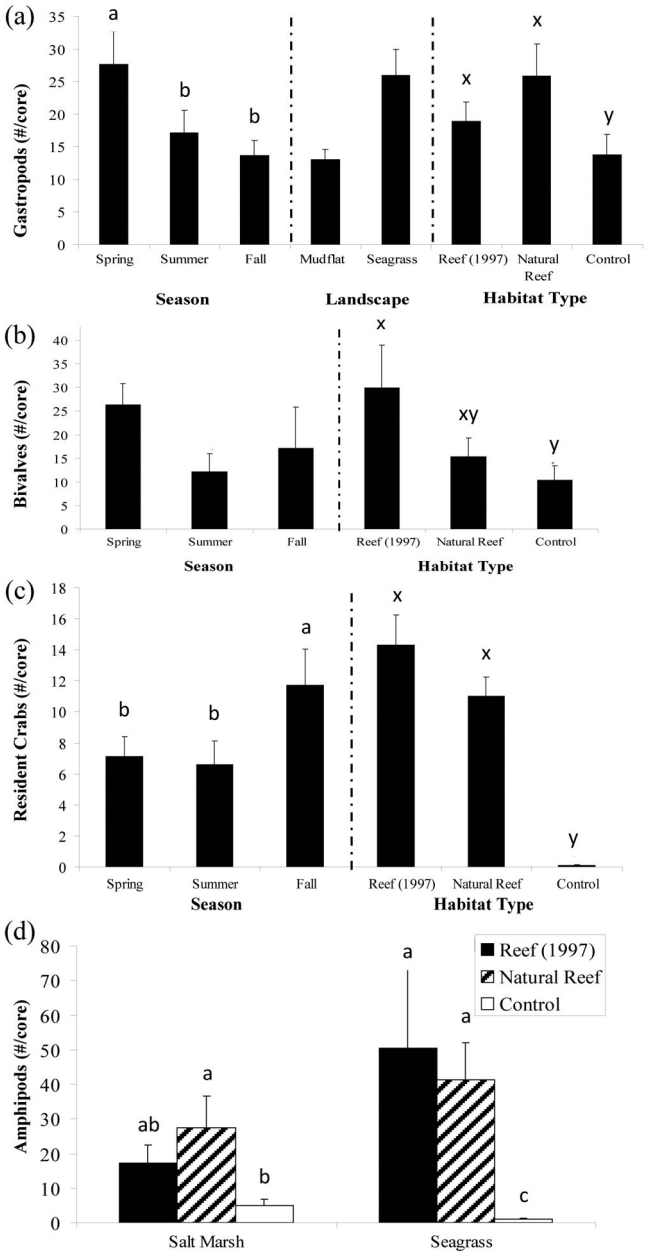

FIGURE 2 Core sampling: restored versus natural reefs. The independent effects of (a) season, landscape, and habitat type on gastropod densities; season and habitat type on (b) bivalves and (c) resident crab densities; and the interaction between landscape and habitat type on amphipod densities. Student-Newman-Keuls (SNK) post hoc results are represented with letters above the error bars (bars with different letters above them are significantly different at $p < 0.05$). Error bars are +1 SE

marginally higher in the fall ($p = 0.06$; Figure 2c). Habitat type was the only factor that significantly influenced polychaete biomass (Appendix S1: Table S5d). Polychaete biomass on restored (1997) reefs (1.9 ± 0.3 kg/core) did not vary from natural reefs (1.7 ± 0.2 kg/core), but both habitat types increased polychaete biomass by a factor of four over controls (0.4 ± 0.1 kg/core). There was a

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significant interaction between habitat and landscape types for amphipod densities (Appendix S1: Table S5e). Amphipod densities on 1997 reefs were not different from those on controls in the salt marsh landscape, but over 50 times greater than the controls in the seagrass landscape (Figure 2d). Amphipod densities on salt marsh natural (27.3 ± 9.2 amphipods/core) and restored (17.3 ± 5.2 amphipods/core) reefs were three to six times greater than those on salt marsh controls (4.9 ± 1.8 amphipods/core), whereas seagrass natural (41.3 ± 10.8 amphipods/core) and restored (50.6 ± 22.7 amphipods/core) reef densities were over 40 times greater than those in seagrass controls (0.9 ± 0.3 amphipods/core). Amphipod densities on the 1997 reefs and natural reefs did not differ from each other in either landscape. Amphipod density also varied with season, with the densities in the summer (11.5 ± 3.2 amphipods/core) less than those in the spring (20.8 ± 5.2 amphipods/core) or fall (38.8 ± 12.9 amphipods/core).

Juvenile fish and motile invertebrates on restored reefs, natural reefs, and mud habitat

Nineteen species of fish were captured by pop-up nets collectively on 1997 reefs, natural reefs, and controls. Of the 2785 fishes captured in total on these three treatments, 69.7% were spot and 24.1% were pinfish, *Lagodon rhomboides*. A total of 580 shrimp were captured, 95% of which were grass shrimp and 2.7% were penaeid shrimp. Of the two species of crabs caught, 50.0% were blue crabs and 47.4% were hermit crabs, *Clibanarius vittatus*. Total densities of benthic fish other than spot was significantly affected by season and habitat type, and marginally by landscape (Appendix S1: Table S7a). Total benthic fish densities were five times greater in the spring (41.8 ± 14.5 benthic fish/reef) than in the fall (8.6 ± 2.1 benthic fish/reef; Figure 3a), while benthic fish densities in the summer (16.6 ± 4.5 benthic fish/reef) did not differ significantly from either season. Benthic fish densities on 1997 reefs (14.8 ± 3.5 benthic fish/reef) were twice that of controls (7.3 ± 2.4 benthic fish/reef), whereas densities on natural reefs (44.9 ± 14.2 benthic fish/reef) were six times greater than those on controls (Figure 3a). Benthic fish densities were marginally ($p = 0.05$) higher in the seagrass landscape than in the salt marsh landscape. There was a trend of higher spot densities in the salt marsh than the seagrass landscape (Appendix S1: Table S7b; $p = 0.06$). The density of grass shrimp varied by landscape (Appendix S1: Table S7c). Densities of grass shrimp were an order of magnitude greater in the seagrass (27.9 ± 11.8 grass shrimp/reef) than in the salt marsh (2.7 ± 1.2 grass shrimp/reef) landscape (Figure 3b).

Large fish and crabs on restored reefs, natural reefs, and mud habitat

The abundances of fish caught in gillnets were not analyzed due to low overall catch rates and preliminary analyses consistently violating the assumption of homogeneity of variances. Gillnets regularly caught more than nine species of fishes, as well as blue crabs, stone crabs (*Menippe mercenaria*), hermit crabs, and whelks *Busycon* spp. (Appendix S1: Table S8). The number of total fish (not including spot, menhaden *Brevoortia tyrannus*, mullet *Mugil cephalus*, or sharks) caught in the seagrass landscape was 97% higher than in the salt marsh landscape and 47% higher than in the mudflat landscape regardless of reef presence. Total fish densities collected from gillnets were similar across restored reefs, natural reefs, and controls.

Examining how reef age influences oyster reef communities

Oyster properties in recently restored versus older restored reefs

Oyster properties on older versus recently restored reefs in the mudflat and seagrass landscapes often varied as a function of season, landscape, and reef age. Total shell weight varied significantly by season ($p < 0.0001$; Appendix S1: Table S10a) and predictably was lowest in spring (4.1 ± 0.4 kg), intermediate in summer (5.8 ± 0.5 kg), and greatest in fall (6.9 ± 0.4 kg). Total shell weight was also significantly greater in the mudflat (6.5 ± 0.3 kg) than the seagrass (4.8 ± 0.4 kg) landscape ($p = 0.0002$). In addition, total shell weight was significantly greater on restored 2000 reefs (6.2 ± 0.4 kg) than on restored 1997 reefs (5.1 ± 0.4 kg), but none of the interactions were significant.

Cluster weight significantly varied with season ($p = 0.001$) and the interaction between habitat type and landscape type ($p = 0.007$; Appendix S1: Table S10b). Cluster weight was greater in fall (2.3 ± 0.4) than in spring (1.2 ± 0.3 kg) and summer (1.6 ± 0.3 kg), which did not differ from each other. Meanwhile, mudflat 1997 reefs (3.4 ± 0.2 kg) had greater cluster weight than that of either 2000 mudflat (1.3 ± 0.3 kg) or 1997 seagrass reefs (1.4 ± 0.3 kg), and both of these were greater than the cluster weight of 2000 seagrass reefs (0.6 ± 0.3).

Similar to cluster weight, legal oyster densities varied with season ($p = 0.0007$) and the interaction between

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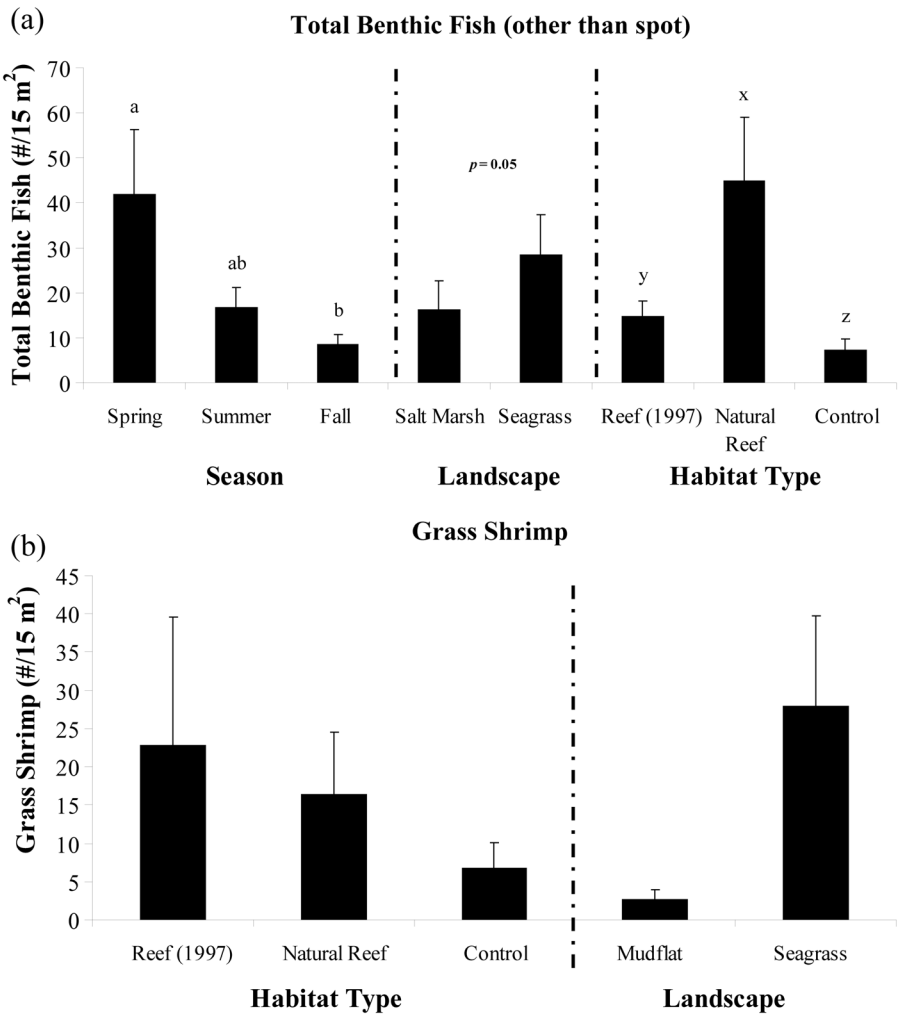

FIGURE 3 Pop-up sampling: restored versus natural reefs. The independent effects of (a) season, landscape, and habitat type on densities of benthic fish other than spot and (b) habitat type and landscape on grass shrimp densities. Student-Newman-Keuls (SNK) post hoc results are represented with letters above the error bars (bars with different letters above them are significantly different at $p < 0.05$). Error bars are +1 SE

habitat type and landscape type was also significant ($p = 0.002$; Appendix S1: Table S10c). Legal oyster densities were higher in the fall (17.3 ± 3.4 oysters/core) than in the spring (6.9 ± 2.3 oysters/core) or summer (9.4 ± 2.7 oysters/core). In addition, legal oyster densities were higher on 1997 mudflat reefs (25.9 ± 2.4 oysters/core) than on 2000 mudflat reefs (6.1 ± 2.1 oysters/core) or 1997 seagrass reefs (8.8 ± 2.3 oysters/core). Meanwhile, the densities on 2000 seagrass reefs (3.7 ± 2.9 oysters/core) were lower than those on 1997 seagrass reefs, but they did not differ from those on 2000 mudflat reefs.

Both landscape ($p < 0.0001$) and habitat type ($p < 0.0001$) independently affected the densities of oyster recruits significantly (Appendix S1: Table S10d). Densities of recruits were approximately twice as great on 2000 restored reefs (118.7 ± 11.4 oysters/core) than on 1997 restored reefs (65.0 ± 10.4 oysters/core). Furthermore, densities of recruits were also much higher on mudflat reefs (126.2 ± 10.2 oysters/core) than on seagrass reefs (54.8 ± 9.1 oysters/core).

Resident invertebrate communities on recently restored reefs, older restored reefs, and mud habitat

Similar to the comparison of restored versus natural reefs, our analyses examining the effects of reef age and landscape setting on oyster reef communities were highly varied but suggested that reefs are quickly colonized by diverse and abundant communities of resident and transient fauna. For the analysis of 1997 versus 2000 restored reefs on gastropod densities, none of the main effects or interactions were significant (Appendix S1: Table S12a). Meanwhile, there was a significant interaction between habitat type (1997 reefs, 2000 reefs, and controls) and

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landscape type (mudflat and seagrass) on bivalve (other than oyster) densities (Appendix S1: Table S12b). In the mudflat landscape, bivalve densities on 1997 reefs (173.9 ± 30.5 bivalves/core) were three times greater than those on 2000 reefs (57.2 ± 15.9 bivalves/core) and 15 times greater than those on controls (11.8 ± 3.2 bivalves/core). In the seagrass landscape, habitat type did not affect bivalve densities (Figure 4a). For resident crabs, there was a significant interaction between habitat type and landscape type ($p = 0.002$; Appendix S1: Table S12c). Resident crab densities were greatest on mudflat reefs restored in 1997 (47.0 ± 8.9 crabs/core), intermediate on 1997 seagrass reefs (12.6 ± 2.1 crabs/core) and 2000 reefs in both landscapes (2000 mudflat reefs: 18.8 ± 2.6 crabs/core; 2000 seagrass reefs: 15.3 ± 2.7 crabs/core), and lowest on controls in both landscapes (mudflat controls: 0.0 ± 0.0 crabs/core; 2000 seagrass controls: 0.1 ± 0.1 crabs/core; Figure 4b). In general, restored reefs augmented crab densities by two to three orders of magnitude over control mud bottom. Only habitat type affected polychaete biomass (Appendix S1: Table S12d), which was greatest on 1997 reefs (2.2 ± 0.3 kg/core), intermediate on 2000 reefs (0.8 ± 0.1 kg/core), and lowest on controls (0.3 ± 0.1 kg/core). Finally, amphipod densities varied with season, habitat type, and landscape type (Appendix S1: Table S12e). Amphipod densities in the spring (43.9 ± 10.4 amphipods/core) and fall (47.0 ± 14.1 amphipods/core) did not differ but were two times greater than the densities in summer (20.4 ± 5.2 amphipods/core; Figure 4c). Amphipod densities in mudflats (46.7 ± 8.7 amphipods/core) were almost twice as great as those in the seagrass landscape (27.4 ± 8.5 amphipods/core). Amphipod densities on both 1997 (58.0 ± 13.4 amphipods/core) and 2000 (50.1 ± 9.7 amphipods/core) reefs were over an order of magnitude greater than those on controls (3.1 ± 1.1 amphipods/core).

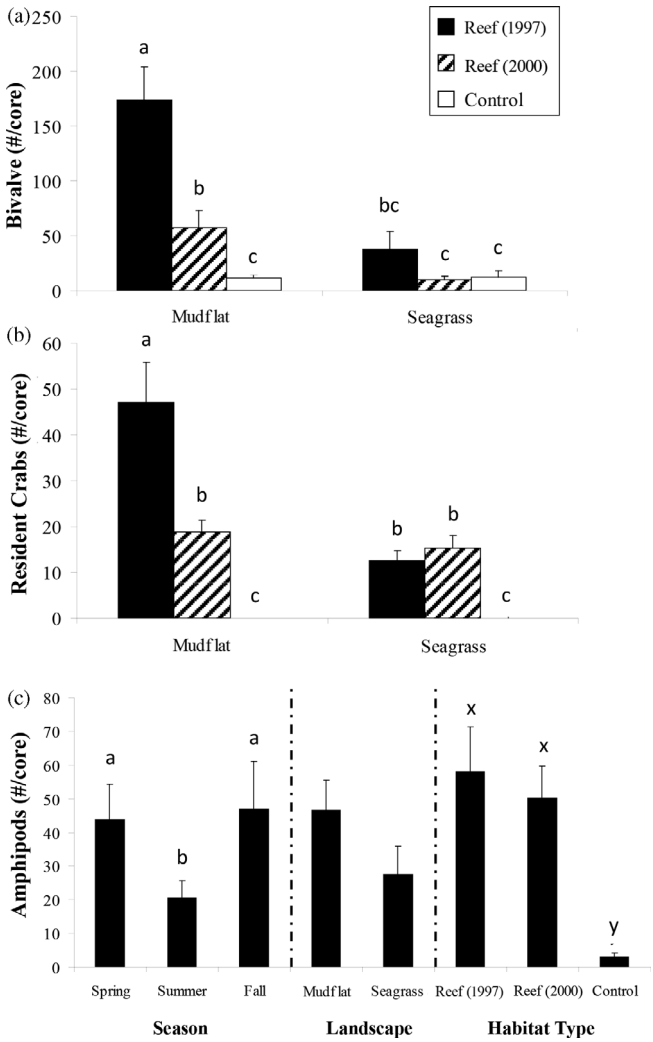

FIGURE 4 Core sampling: 1997 versus 2000 reefs. The interaction between landscape and habitat type on (a) bivalve and (b) resident crab densities and (c) the independent effects of season, landscape, and habitat type on amphipod densities. Student-Newman-Keuls (SNK) post hoc results are represented with letters above the error bars (bars with different letters above them are significantly different at $p < 0.05$). Error bars are +1 SE

Juvenile fish and mobile invertebrates on recently restored reefs, older restored reefs, and mud habitat

The densities of benthic fishes other than spot caught in pop-up nets were significantly affected by the three-way interaction among season, habitat type, and landscape type (Appendix S1: Table S14a). In the spring, benthic fish densities did not differ among 1997 reefs, 2000 reefs, and controls within each landscape (Figure 5a). Yet, fish densities in spring were greater on seagrass 1997 reefs than on mudflat 1997 reefs. Fish densities on control and 2000 reefs in the seagrass landscape were marginally greater than densities in respective habitats in the mudflat landscape. In the summer, total fish densities did not differ among treatments in the mudflat landscape, but densities of fish on seagrass restored reefs were greater than seagrass controls. Mudflat 2000 reefs had higher fish densities than on seagrass 2000 reefs in summer. Similarly, mudflat controls had higher fish densities than on seagrass controls, whereas fish densities on 1997 reefs did not differ significantly between the two landscapes in the summer. In the fall, fish densities on mudflat reefs were greater than on mudflat controls, but they did not differ within the seagrass landscape. Landscape only affected benthic fish densities of controls, with higher densities occurring in the seagrass landscape.

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Spot densities were marginally higher ($p = 0.07$) in the mudflat landscape than in the seagrass landscape (Appendix S1: Table S14b). Grass shrimp densities were affected by habitat type and marginally by season and landscape (Appendix S1: Table S14c). Grass shrimp densities were 10 times higher in summer than in spring, whereas their densities in the fall did not significantly differ from either of the other seasons (Figure 5b). Grass shrimp densities on 1997 reefs (65.3 ± 35.9 grass shrimp/reef) were 14 times greater than controls (4.8 ± 3.1 grass shrimp/reef), whereas 2000 reefs (134.5 ± 66.6 grass shrimp/reef) were 28 times greater than controls. Densities were also marginally higher ($p = 0.06$) in the mudflat landscape than in the seagrass landscape.

Large fish and crabs on recently restored reefs, older restored reefs, and mud habitat

Similar to above, the abundances of fish caught in gillnets were not analyzed. There was a trend of more flounder (*Paralichthys* spp.) and juvenile red drum (*Sciaenops ocellatus*) on restored reefs than on controls (Appendix S1: Table S8). Mullet (*M. cephalus*), whelks (*Busycon* spp.), and stone crabs (*M. mercenaria*) were also more commonly caught on restored reefs than on controls. Conversely, there was a trend of more bluefish (*Pomastomus saltatrix*), spot, juvenile sharks (F. Carcharhinidae), and blue crabs on control plots than on restored reefs, especially on mudflats.

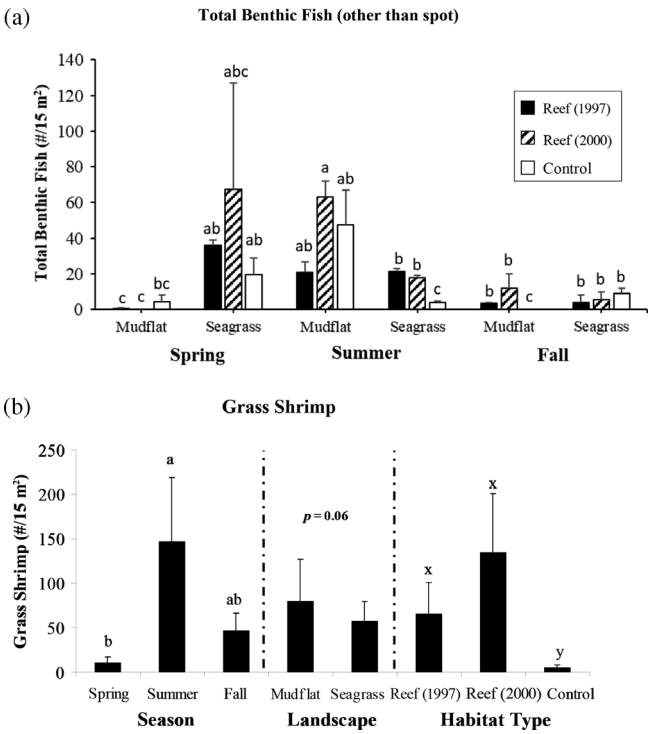

FIGURE 5 Pop-up sampling: 1997 versus 2000 reefs. (a) The interaction among season, landscape, and habitat type on densities of benthic fish other than spot and (b) the independent effects of season, landscape, and habitat type on grass shrimp densities. Student-Newman-Keuls (SNK) post hoc results are represented with letters above the error bars (bars with different letters above them are significantly different at $p < 0.05$). Error bars are +1 SE

Determining if oyster reef habitat influences the growth and foraging of juvenile fishes

In the field enclosure experiments, habitat type did not affect the growth of juvenile gag ($F_{1,7} = 1.3$, $p = 0.29$). Although we originally deployed six replicate cages each on mudflats and oyster reefs, the gag in three (two mudflat and one oyster reef) replicates did not survive the duration of the experiment; thus, $n = 5$ for the reef treatment, and $n = 4$ for the mudflat treatment. Gobies, killifish, and xanthid crabs were present in the stomachs of recovered fish from both habitat types.

In the foraging experiments with gag conducted at UNC-IMS, shrimp mortality did not differ between habitat treatments ($F_{1,16} = 0.1$, $p = 0.77$; $n = 9$), but there was a slight trend of higher mortality of killifish prey in the oyster reef treatment ($F_{1,22} = 1.8$, $p = 0.19$; $n = 12$) (Figure 6). Flounder in the mudflat treatment consumed more shrimp than those in edge and reef habitats, which did not vary from each other (SNK post hoc comparisons; ANOVA, $F_{2,14} = 5.3$, $p = 0.02$; $n = 6$ for the mudflat and reef treatments, $n = 5$ for edge treatment). Flounder did not forage effectively on killifish in any of the three habitat treatments; therefore, results of this experiment were not analyzed.

DISCUSSION

Oyster reefs enhance structural complexity over adjacent soft sediments and provide refuge and foraging habitat for a wide diversity and high densities of crustaceans, polychaetes, mollusks, and fishes (Coen et al., 1999; Lenihan et al., 2001; Wells, 1961; Zu Ermgassen et al., 2016). Densities of most categories of resident species sampled in our study were generally higher on both restored and natural oyster reef habitats than on mud bottom. At the coarse taxonomic level used in this study, we found little difference between the densities of resident fishes and invertebrates on restored and natural reefs, similar to patterns observed on subtidal reefs (Harding & Mann, 1999; Harding & Mann, 2001; Lenihan et al., 2001). Our study suggests that restored reefs reestablish dense assemblages

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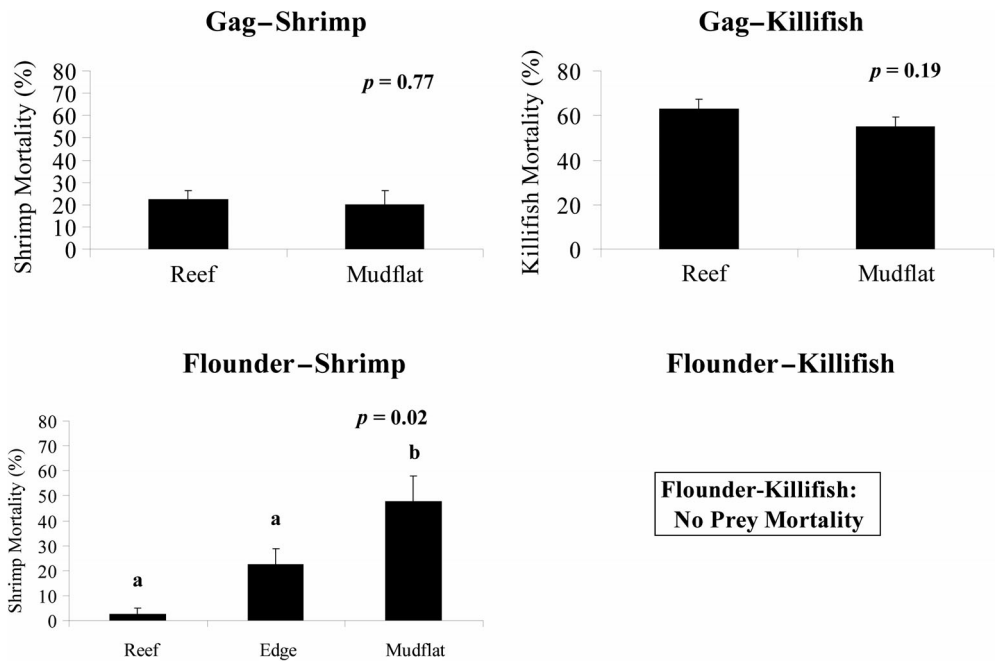

FIGURE 6 Predation experiments were conducted at the University of North Carolina's Institute of Marine Sciences exploring whether habitat type influences juvenile gag and flounder consumption of penaeid shrimp or killifish. Student-Newman-Keuls (SNK) post hoc results are represented with letters above the error bars (bars with different letters above them are significantly different at $p < 0.05$). Error bars are +1 SE

of resident species relatively quickly. Estimates of recovery times for fish and invertebrate communities for other coastal habitats have been variable in previous studies. For instance, Hollweg, Christman, Cebrian, et al. (2020) reviewed nekton recovery in restored salt marshes in the northern Gulf of Mexico and found that total nekton densities at restored marshes were half of those at natural marshes during the initial 5 years following restoration. Furthermore, they found that restored salt marshes required 13 years after restoration occurred to achieve comparable animal densities. Meanwhile, several studies have compared faunal recovery in restored versus adjacent seagrass beds and found that nekton reassembly occurs relatively rapidly, but it is dependent upon the successful recovery of the biogenic habitat (Fonseca et al., 1990; McSkimming et al., 2016; Orth et al., 2020; Sheridan, 2004). For instance, McSkimming et al. (2016) revealed that invertebrate richness and total abundance generally recover within a year, yet that composition and relative abundances did not match those of natural beds until full recovery of seagrass occurred, which typically required 3–5 years. The rapid recovery of oyster reefs and associated communities observed in our study could be explained in part by the high natural oyster recruitment and growth on restored reefs in Middle Marsh. Further investigation is needed to examine the drivers that determine whether restored oyster reefs and associated communities generally recover more quickly than other restored biogenic habitats in coastal and estuarine ecosystems.

One key difference between restored and natural reefs in our study is that juvenile fishes were more than twice as abundant on natural than on restored reefs. This finding disagrees with previous research, which generally found equal or higher fish densities on restored reefs (Davenport et al., 2021; Keller et al., 2019; Rodney & Paynter, 2006). Rodney and Paynter (2006) noted that unrestored reefs generally contain dead shell buried by silt. Natural oyster reefs throughout much of the United States have declined in extent and quality due to destructive harvesting practices, diseases, siltation, and bottom water hypoxia (Kirby, 2004; Rothschild et al., 1994; Zu Ermgassen et al., 2012), making comparisons among restored reefs and natural intact oyster habitat challenging. The natural reefs used in our study contained living oysters even if at slightly lower densities than on restored reefs. Future studies should explicitly test mechanisms driving different juvenile fish densities in natural and restored oyster reefs, which could be related to differences in recruitment, habitat preferences, and post-recruitment survival due to predation or competition (Breitburg, 1991; Laurel et al., 2003; Tupper & Boutilier, 1995).

There are no natural intertidal oyster reefs on mudflats at our study sites in Middle Marsh, NC; thus, we did not compare juvenile fishes caught on natural reefs to restored reefs in the mudflat landscape. Our previous research in this system suggested restored reefs on mudflats, both soon after and extending >10 years post-restoration, can support higher densities of juvenile fish

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relative to unstructured mud bottom, whereas restored reefs adjacent to vegetated habitats do not enhance juvenile fish abundances relative to nearby soft sediments (Grabowski et al., 2005; Ziegler et al., 2018). These and other past efforts have surmised that oyster reefs in vegetated landscapes may be functionally redundant to seagrass beds and salt marshes that are also important juvenile fish habitat. Yet, additional investigation into the mechanisms that potentially mediate differences between fish and invertebrate use of natural and restored habitats across landscapes could help advance future conservation and restoration efforts.

Restored reefs augmented juvenile fish densities in the summer and fall in the mudflat landscape and in the fall on seagrass landscapes. Benthic fish densities also varied strongly between the mudflat and seagrass landscapes, and this was largely driven by (1) seasonal pulses in recruiting spot and pinfish resulting in greater densities of fish on restored seagrass reefs, and (2) extremely high densities of pinfish on mudflat reefs restored in 2000. This finding disagrees somewhat with our previous study, which detected significant juvenile fish augmentation by restored reefs in mudflat landscape but not in landscapes containing seagrass or salt marsh habitat (Grabowski et al., 2005). Differences between these two studies may be a consequence of the two studies using different sampling methods to quantify juvenile fishes, with each gear type having different species- and size class-dependent sampling efficiencies. For example, Grabowski et al. (2005) used fish traps to sample reefs, which are likely more effective at sampling mobile species, but only provide data on relative abundance. By contrast, the current study used pop-up nets, which sample a known area and thus provide a quantitative estimate of density. Yet, this gear can be challenging to deploy and labor-intensive, and it is likely not very efficient at capturing more mobile species. Pop-up net sampling was also noisy in this study, and it is worth considering some of the potential confounding effects of this approach. For example, setting up the nets required burying them around the study plots and deploying poles around the plot that were used to draw up the net, thus adding structure around the controls where structure is otherwise absent (especially in the mudflat landscape). Moreover, when the methodological design interacts with the treatments, it can confound the interpretation of the results (Peterson & Black, 1994). In spite of these biases and limitations, we detected a general signal of enhanced fish densities on restored reefs. There was also a slight but consistent trend of higher juvenile fish densities on mudflat 2000 reefs than on mudflat 1997 reefs. However, Ziegler et al. (2018) revisited these reefs in 2010 and found that the mudflat 1997 reef augmentation of juvenile fish relative to controls was less than directly after reef restoration. This finding occurred perhaps because the reefs had continued to grow upward (Rodriguez et al., 2014), thereby leaving less vertical space above the reef during flood tide for juvenile fish. This difference could also be a function of Ziegler et al. (2018) sampling juvenile fishes at night, whereas Grabowski et al. (2005) analyzed catches during the day when they were highest. Keller et al. (2019) found higher predation rates on recently restored than on natural reefs, and they surmised that the high vertical relief of the natural reefs in their study may inhibit transient predator access to them. Collectively, these studies suggest that fish use of oyster reefs on mudflats is dynamic, and it may not continue indefinitely after the reef reestablishes.

In this study, we chose to aggregate species into coarse taxonomic groupings because we were interested in whether oyster reef restoration results in rapid reassembly of resident and transient fauna to inform oyster reef restoration. This approach is more readily implemented than identifying each organism to species, and we used it to describe a large swath of the fauna that occupy oyster reefs and mud habitats rather than focusing on a smaller subset of taxonomic groups. Moreover, it has been used effectively previously to describe differences among the communities associated with oyster reefs and other habitats (Grabowski et al., 2005; Lefcheck et al., 2019; Ziegler et al., 2018). Yet, it provides a limited understanding of how community structure differs among treatments and could overestimate the degree to which communities associated with restored habitats have recovered. Future studies that identify each taxonomic group to species will be more capable of addressing how community structure differs as a function of restoration and the age of a restored habitat. However, the fact that large abundances of fishes and invertebrates quickly recruit to restored oyster reefs above and beyond those found on mud bottom is important for restoration decision making.

Resident fishes and invertebrates sampled on reefs and soft sediments comprised the overwhelming majority of the diet of juvenile and adult estuarine fishes. Increased prey densities could result in greater trophic transfer to higher trophic levels if these prey species are accessible to predators. Prey accessibility likely increases initially with greater habitat complexity due to higher prey densities, but may eventually decline if habitat structural complexity increases to the point where it significantly reduces predator foraging efficiency (Crowder & Cooper, 1982; Grabowski et al., 2008). Although catch rates of adults were low, both hook-and-line and gillnet sampling coupled with stomach content analyses suggested that predatory fishes including red

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drum, black drum *Pagonia chromis*, and gag likely utilize oyster reefs as foraging grounds (Appendix S1: Tables S10 and S11). Fodrie et al. (2015) implanted acoustic tags in red drum and monitored their habitat use patterns in Middle Marsh, which suggested that they prefer reefs along the fringes of salt marsh over those near seagrass beds or on isolated sand and mudflats. Meanwhile, bluefish, spot juvenile sharks, and blue crabs were less abundant on reefs, indicating that oyster reefs may be less optimal foraging grounds for these species (but see Lenihan et al., 2001). Some species, such as flounders, were more common on oyster reefs but apparently were also foraging on adjacent mud bottom. This finding agrees with past studies demonstrating that species utilizing structured estuarine habitats as refuge emerge from them to forage on adjacent mud bottom presumably when predation risk is low (Summerson & Peterson, 1984). Restored reefs had higher densities of resident crabs and slightly higher densities of grass shrimp than natural reefs, both of which are important prey for higher trophic levels. A similar pattern was observed for subtidal oyster reefs (Lenihan et al., 2001). This could be related to restored reefs having greater habitat complexity, likely due to the higher amount of shell cluster biomass and legal oyster densities, than natural reefs. Lower shell cluster biomass and legal oyster densities in the natural reefs could be due to oyster harvesting occurring in our study site, though we were unable to quantify the degree to which oyster harvesting has occurred in Middle Marsh on natural reefs.

In the mudflat landscape, older restored reefs contained higher densities of some important prey (i.e., bivalves and resident crabs) groups than more recently restored reefs, suggesting that establishment of reef invertebrate communities may be slower on mudflats. Conversely, prey densities did not differ between 1997 and 2000 restored reefs that were constructed within the seagrass landscape where oyster densities were generally low. Therefore, the timescale of reef community establishment apparently depends upon the landscape in which a reef is constructed. Shell cluster and legal oyster weights of 1-year-old reefs were less than half of that of 4-year-old reefs, indicating that oysters continued to recruit and survive on oyster reefs well after the initial year of restoration. Ziegler et al. (2018) revisited the 1997 reefs in 2010 and found that oyster cluster biomass had continued to increase between 2001 and 2010. Prey densities on mudflat reefs were generally much greater than those on seagrass reefs, which could be explained by greater reef complexity on mudflat reefs and the lack of alternative, structurally complex habitat nearby (Grabowski et al., 2005).

Our experiments suggest that oyster reefs can enhance (gag) and reduce (flounder) predator foraging efficiency. These findings may reflect that predator–prey interactions on oyster reefs, similar to other habitats, are dependent on predator foraging behavior (Horinouchi et al., 2009). Gag effectively preyed on killifish in both oyster reefs and mud bottom perhaps because reef structure reduced the ability of killifish prey to detect gag and/or did not impede gag foraging efficiency significantly. Conversely, oyster reefs drastically reduced flounder consumption of shrimp, which could be due to the structure associated with reefs reducing the ability of flounder to detect and capture prey effectively. These results agree with our stomach content analyses and suggest that flounder forage on mud bottom where their foraging behavior, which involves burrowing in sediments to camouflage themselves as they sit and wait before ambushing prey, is better suited. Higher foraging success in mudflat bottom translated to higher growth rates for flounders. In contrast, gag grew faster on oyster reef than on mudflat bottom, although their foraging success did not vary significantly between the two habitat types. However, there was a slight trend of gag consuming more prey on reefs than on mudflats. Future investigations should more explicitly test how natural and restored reefs and their landscape setting influence trophic transfer via predator–prey interactions and thus growth and performance of predatory fishes, especially during juvenile life stages.

Our study demonstrates that restored oyster reefs function as critical habitat for resident and transient benthos and nekton, and in some cases can outperform preexisting natural reefs. Therefore, reef restoration will be a vital tool for recovering the ecosystem goods and services that have been lost over the past century from destructive harvesting and degradation of oyster reef habitat (Beck et al., 2011; Lenihan & Peterson, 1998; Rothschild et al., 1994; Zu Ermgassen et al., 2012). Our findings further suggest that the landscape in which oyster reefs are restored influences the communities associated with them. Specifically, reefs restored on mudflats produced greater densities of harvestable oysters and resident prey, whereas reefs adjacent to seagrass beds seem to support greater abundances of recreationally and commercially valuable adult fish. Hence, restoration and management efforts for important coastal biogenic habitats such as oyster reef should increasingly consider landscape-scale processes (as well as other habitat quality characteristics) to enhance ecosystem functioning and recovery of lost services.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Grabowski, 2022) are available from the Knowledge Network for Biocomplexity: https://doi.org/10.5063/F1XS5STX.

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REFERENCES

Airoldi, L., and M. W. Beck. 2007. "Loss, Status and Trends for Coastal Marine Habitats of Europe." *Oceanography and Marine Biology Annual Review* 45: 345–405.

Bahr, L. M., and W. P. Lanier. 1981. "The Ecology of Intertidal Oyster Reefs of the South Atlantic Coast: A Community Profile." FWS/OBS-81/15, U.S. Fish and Wildlife Service.

Baillie, C., J. Fear, and F. Fodrie. 2014. "Ecotone Effects on Seagrass and Saltmarsh Habitat Use by Juvenile Nekton in a Temperate Estuary." *Estuaries and Coasts* 38: 1–17.

Barbier, E. B., S. D. Hacker, C. Kennedy, E. W. Koch, A. C. Stier, and B. R. Silliman. 2011. "The Value of Estuarine and Coastal Ecosystem Services." *Ecological Monographs* 81: 169–93.

Beck, M. W., R. D. Brumbaugh, L. Airoldi, A. Carranza, L. D. Coen, C. Crawford, O. Defeo, et al. 2011. "Oyster Reefs at Risk and Recommendations for Conservation, Restoration and Management." *Bioscience* 61: 107–16.

Breitburg, D. L. 1991. "Settlement Patterns and Presettlement Behavior of the Naked Goby, *Gobiosoma bosci*, a Temperate Oyster Reef Fish." *Marine Biology* 109: 213–21.

Breitburg, D. L., L. D. Coen, M. W. Luckenbach, R. Mann, M. Posey, and J. A. Wesson. 2000. "Oyster Reef Restoration: Convergence of Harvest and Conservation Strategies." *Journal of Shellfish Research* 19: 371–7.

Coen, L. D., M. W. Luckenbach, and D. L. Breitburg. 1999. "The Role of Oyster Reefs as Essential Fish Habitat: A Review of Current Knowledge and Some New Perspectives." *American Fisheries Society Symposium* 22: 438–54.

Crowder, L. B., and W. E. Cooper. 1982. "Habitat Structural Complexity and the Interaction between Bluegills and Their Prey." *Ecology* 63: 1802–13.

Davenport, T., A. R. Hughes, P. S. E. Z. Ermgassen, and J. H. Grabowski. 2021. "Recruitment Enhancement Varies by Taxonomic Group and Oyster Reef Habitat Characteristics." *Ecological Applications* 31: e02340.

Day, R. W., and G. P. Quinn. 1989. "Comparisons of Treatments after an Analysis of Variance in Ecology." *Ecological Monographs* 59: 433–63.

Fodrie, F. J., L. A. Yeager, J. H. Grabowski, C. A. Layman, G. D. Sherwood, and M. D. Kenworthy. 2015. "Measuring Individuality in Habitat Use across Complex Landscapes: Approaches, Constraints, and Implications for Assessing Resource Specialization." *Oecologia* 178: 75–87.

Fonseca, M. S., W. J. Kenworthy, D. R. Colby, K. A. Rittmaster, and G. W. Thayer. 1990. "Comparisons of Fauna among Natural and Transplanted Eelgrass *Zostera marina* Meadows: Criteria for Mitigation." *Marine Ecology Progress Series* 65: 251–64.

Fourqurean, J. W., C. M. Duarte, H. Kennedy, N. Marba, M. Holmer, M. A. Mateo, E. T. Apostolaki, et al. 2012. "Seagrass Ecosystems as a Globally Significant Carbon Stock." *Nature Geoscience* 5: 505–9.

Geraldi, N. R., S. P. Powers, K. L. Heck, and J. Cebrian. 2009. "Can Habitat Restoration Be Redundant? Response of Mobile Fishes and Crustaceans to Oyster Reef Restoration in Marsh Tidal Creeks." *Marine Ecology Progress Series* 389: 171–80.

Grabowski, J. 2022. "Fish and Invertebrate Use of Restored vs. Natural Oyster Reefs in Coastal North Carolina." Knowledge Network for Biocomplexity. https://doi.org/10.5063/F1XS5STX.

Grabowski, J. H., R. D. Brumbaugh, R. Conrad, A. G. Keeler, J. Opaluch, C. H. Peterson, M. F. Piehler, S. P. Powers, and A. R. Smyth. 2012. "Economic Valuation of Ecosystem Services Provided by Oyster Reefs." *Bioscience* 632: 900–9.

Grabowski, J. H., A. R. Hughes, and D. L. Kimbro. 2008. "Habitat Complexity Influences Cascading Effects of Multiple Predators." *Ecology* 89: 3413–22.

Grabowski, J. H., A. R. Hughes, D. L. Kimbro, and M. A. Dolan. 2005. "How Habitat Setting Influences Restored Oyster Reef Communities." *Ecology* 86: 1926–35.

Harding, J. M., and R. Mann. 1999. "Fish Species Richness in Relation to Restored Oyster Reefs, Piankatank River, Virginia." *Bulletin of Marine Science* 65: 289–300.

Harding, J. M., and R. Mann. 2001. "Oyster Reefs as Fish Habitat: Opportunistic Use of Restored Reefs by Transient Fishes." *Journal of Shellfish Research* 20: 951–9.

Hollweg, T. A., M. C. Christman, J. Cebrian, B. P. Wallace, S. L. Friedman, H. R. Ballestero, M. T. Huisenga, and K. G. Benson. 2020. "Meta-Analysis of Nekton Utilization of Coastal Habitats in the Northern Gulf of Mexico." *Estuaries and Coasts* 43: 1722–45.

21508925, 2022, 5, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/ecs2.4035 by University Of South Alabama, Wiley Online Library on [20/10/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Hollweg, T. A., M. C. Christman, J. Lipton, B. P. Wallace, M. T. Huisenga, D. R. Lane, and K. G. Benson. 2020. "Meta-Analysis of Nekton Recovery Following Marsh Restoration in the Northern Gulf of Mexico." *Estuaries and Coasts* 43: 1746–63.

Horinouchi, M., N. Mizuno, Y. Jo, M. Fujita, M. Sano, and Y. Suzuki. 2009. "Seagrass Habitat Complexity Does Not Always Decrease Foraging Efficiencies of Piscivorous Fishes." *Marine Ecology Progress Series* 377: 43–9.

Irlandi, E. A., and M. K. Crawford. 1997. "Habitat Linkages: The Effect of Intertidal Saltmarshes and Adjacent Subtidal Habitats on Abundance, Movement, and Growth of an Estuarine Fish." *Oecologia* 110: 222–30.

Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, et al. 2001. "Historical Overfishing and the Recent Collapse of Coastal Ecosystems." *Science* 293: 629–38.

Keller, D. A., R. K. Gittman, M. C. Brodeur, M. D. Kenworthy, J. T. Ridge, L. A. Yeager, A. B. Rodriguez, and F. J. Fodrie. 2019. "Salt Marsh Shoreline Geomorphology Influences the Success of Restored Oyster Reefs and Use by Associated Fauna." *Restoration Ecology* 27: 1429–41.

Kellogg, M. L., A. R. Smyth, M. W. Luckenbach, R. H. Carmichael, B. L. Brown, J. C. Cornwell, M. F. Piehler, M. S. Owens, D. J. Dalrymple, and C. B. Higgins. 2014. "Use of Oysters to Mitigate Eutrophication in Coastal Waters." *Estuarine, Coastal and Shelf Science* 151: 156–68.

Kirby, M. X. 2004. "Fishing down the Coast: Historical Expansion and Collapse of Oyster Fisheries along Continental Margins." *Procedures of the National Academy of Science, USA* 101: 13096–9.

Laurel, B. J., R. S. Gregory, and J. A. Brown. 2003. "Settlement and Distribution of Age-0 Juvenile Cod, *Gadus morhua* and *G. ogac*, Following a Large-Scale Habitat Manipulation." *Marine Ecology Progress Series* 262: 241–52.

Lefcheck, J. S., B. B. Hughes, A. J. Johnson, B. W. Pfirrmann, D. B. Rasher, A. R. Smyth, B. L. Williams, M. W. Beck, and R. J. Orth. 2019. "Are Coastal Habitats Important Nurseries? A Meta-Analysis." *Conservation Letters* 12: e12645.

Lenihan, H. S. 1999. "Physical-Biological Coupling on Oyster Reefs: How Habitat Structure Influences Individual Performance." *Ecological Monographs* 69: 251–75.

Lenihan, H. S., and C. H. Peterson. 1998. "How Habitat Degradation through Fishery Disturbance Enhances Impacts of Hypoxia on Oyster Reefs." *Ecological Applications* 8: 128–40.

Lenihan, H. S., and C. H. Peterson. 2004. "Conserving Oyster Reef Habitat by Switching from Dredging and Tonging to Diver-Harvesting." *Fishery Bulletin* 102: 298–305.

Lenihan, H. S., C. H. Peterson, J. E. Byers, J. H. Grabowski, G. W. Thayer, and D. R. Colby. 2001. "Cascading of Habitat Degradation: Oyster Reefs Invaded by Refugee Fishes Escaping Stress." *Ecological Applications* 11: 764–82.

Lotze, H. K., H. S. Lenihan, B. J. Bourque, R. Bradbury, R. G. Cooke, M. C. Kay, S. M. Kidwell, M. X. Kirby, C. H. Peterson, and J. B. C. Jackson. 2006. "Depletion, Degradation and Recovery Potential of Estuaries and Coastal Seas." *Science* 312: 1806–9.

McSkimming, C., S. D. Connell, B. D. Russell, and J. E. Tanner. 2016. "Habitat Restoration: Early Signs and Extent of Faunal Recovery Relative to Seagrass Recovery." *Estuarine, Coastal and Shelf Science* 171: 51–7.

Meyer, D. L., E. C. Townsend, and G. W. Thayer. 1997. "Stabilization and Erosion Control Value of Oyster Cultch for Intertidal Marsh." *Restoration Ecology* 5: 93–9.

Micheli, F., and C. H. Peterson. 1999. "Estuarine Vegetated Habitats as Corridors for Predator Movements." *Conservation Biology* 13: 869–81.

Narayan, S., M. W. Beck, P. Wilson, C. J. Thomas, A. Guerrero, C. C. Shepard, B. G. Reguero, G. Franco, J. C. Ingram, and D. Trespalacios. 2017. "The Value of Coastal Wetlands for Flood Damage Reduction in the Northeastern USA." *Scientific Reports* 7: 9463.

Orth, R. J., T. J. B. Carruthers, W. C. Dennison, C. M. Duarte, J. W. Fourqurean, K. L. Heck, Jr., A. R. Hughes, et al. 2006. "A Global Crisis for Seagrass Ecosystems." *Bioscience* 56: 987–96.

Orth, R. J., J. S. Lefcheck, K. S. McGlathery, L. Aoki, M. W. Luckenbach, K. A. Moore, M. P. J. Oreska, R. Snyder, D. J. Wilcox, and B. Lusk. 2020. "Restoration of Seagrass Habitat Leads to Rapid Recovery of Coastal Ecosystem Services." *Science Advances* 6: eabc6434.

Peterson, C. H., and R. Black. 1994. "An experimentalist's Challenge: When Artifacts of Intervention Interact with Treatments." *Marine Ecology Progress Series* 111: 289–97.

Peterson, C. H., J. H. Grabowski, and S. P. Powers. 2003. "Estimated Enhancement of Fish Production Resulting from Restoring Oyster Reef Habitat: Quantitative Valuation." *Marine Ecology Progress Series* 264: 249–64.

Peterson, C. H., and R. N. Lipcius. 2003. "Conceptual Progress towards Predicting Quantitative Ecosystem Benefits of Ecological Restorations." *Marine Ecology Progress Series* 264: 297–307.

Piazza, B. P., P. D. Banks, and M. K. La Peyre. 2005. "The Potential for Created Oyster Shell Reefs as a Sustainable Shoreline Protection Strategy in Louisiana." *Restoration Ecology* 13: 499–506.

Piehler, M. F., and A. R. Smyth. 2011. "Impacts of Ecosystem Engineers on Estuarine Nitrogen Cycling." *Ecosphere* 2: art12.

Rodney, W. S., and K. T. Paynter. 2006. "Comparisons of Macrofaunal Assemblages on Restored and Non-restored Oyster Reefs in Mesohaline Regions of Chesapeake Bay in Maryland." *Journal of Experimental Marine Biology and Ecology* 335: 39–51.

Rodriguez, A. B., F. J. Fodrie, J. T. Ridge, N. L. Lindquist, E. J. Theuerkauf, S. E. Coleman, J. H. Grabowski, M. C. Brodeur, R. K. Gittman, and D. A. Keller. 2014. "Oyster Reefs Can Outpace Sea-Level Rise." *Nature Climate Change* 4: 493–7.

Röhr, M. E., M. Holmer, J. K. Baum, M. Björk, K. Boyer, D. Chin, L. Chalifour, et al. 2018. "Blue Carbon Storage Capacity of Temperate Eelgrass (Zostera marina) Meadows." *Global Biogeochemical Cycles* 32: 1457–75.

Rothschild, B. J., J. S. Ault, P. Goulletquer, and M. Heral. 1994. "Decline of the Chesapeake Bay Oyster Population: A Century of Habitat Destruction and Overfishing." *Marine Ecology Progress Series* 111: 29–39.

Rozas, L. P., and T. J. Minello. 1998. "Nekton Use of Salt Marsh, Seagrass, and Nonvegetated Habitats in a South Texas (USA) Estuary." *Bulletin of Marine Science* 63: 481–501.

Schulte, D. M., R. P. Burke, and R. N. Lipcius. 2009. "Unprecedented Restoration of a Native Oyster Metapopulation." *Science* 325: 1124–8.

21508925, 2022, 5, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/ecs2.4035 by University Of South Alabama, Wiley Online Library on [20/10/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Scyphers, S. B., S. P. Powers, K. L. Heck, Jr., and D. Byron. 2011. "Oyster Reefs as Natural Breakwaters Mitigate Shoreline Loss and Facilitate Fisheries." *PLoS One* 6: e22396.

Sheridan, P. 2004. "Comparison of Restored and Natural Seagrass Beds Near Corpus Christi, Texas." *Estuaries* 27: 781–92.

Smyth, A. R., S. P. Thompson, K. N. Siporin, W. S. Gardner, M. J. McCarthy, and M. F. Piehler. 2013. "Assessing Nitrogen Dynamics Throughout the Estuarine Landscape." *Estuaries and Coasts* 36: 44–55.

Summerson, H. C., and C. H. Peterson. 1984. "Role of Predation in Organizing Benthic Communities of a Temperate-Zone Seagrass Bed." *Marine Ecology Progress Series* 15: 63–77.

Thayer, G. W., M. S. Fonseca, and W. J. Kenworthy. 1982. "Restoration and Enhancement of Seagrass Meadows for Maintenance of Nearshore Productivity." *Atlantica* 5: 118–9.

Thayer, G. W., H. F. Stuart, W. J. Kenworthy, J. F. Ustach, and A. B. Hall, eds. 1978. *Habitat Values of Salt Marshes, Mangroves, and Seagrasses for Aquatic Organisms*. Minneapolis, MN: American Water Resource Association.

Tupper, M., and R. G. Boutilier. 1995. "Effects of Habitat on Settlement, Growth, and Postsettlement Survival of Atlantic Cod (*Gadus morhua*)." *Canadian Journal of Fisheries and Aquatic Sciences* 52: 1834–41.

Underwood, A. J. 1981. "Techniques of Analysis of Variance in Experimental Marine Biology and Ecology." *Oceanography and Marine Biology Annual Review* 19: 513–605.

Waycott, M., C. M. Duarte, T. J. B. Carruthers, R. J. Orth, W. C. Dennison, S. Olyarnik, A. Calladine, et al. 2009. "Accelerating Loss of Seagrasses across the Globe Threatens Coastal Ecosystems." *Proceedings of the National Academy of Sciences of the United States of America* 106: 12377–81.

Wells, H. W. 1961. "The Fauna of Oyster Beds, with Special Reference to the Salinity Factor." *Ecological Monographs* 31: 239–66.

Ziegler, S. L., J. H. Grabowski, C. J. Baillie, and F. J. Fodrie. 2018. "Effects of Landscape Setting on Oyster Reef Structure and Function Largely Persist More than a Decade Post-Restoration." *Restoration Ecology* 26: 933–42.

Zu Ermgassen, P. S. E., B. DeAngelis, J. R. Gair, S. Z. Ermgassen, R. Baker, A. Daniels, T. C. MacDonald, et al. 2021. "Estimating and Applying Fish and Invertebrate Density and Production Enhancement from Seagrass, Salt Marsh Edge, and Oyster Reef Nursery Habitats in the Gulf of Mexico." *Estuaries and Coasts* 44: 1588–603.

Zu Ermgassen, P. S. E., J. H. Grabowski, J. R. Gair, and S. P. Powers. 2016. "Quantifying Fish and Mobile Invertebrate Production from a Threatened Nursery Habitat." *Journal of Applied Ecology* 53: 596–606.

Zu Ermgassen, P. S. E., M. D. Spalding, B. Blake, L. D. Coen, B. Dumbauld, S. Geiger, J. H. Grabowski, R. Grizzle, M. Luckenbach, and K. McGraw. 2012. "Historical Ecology with Real Numbers: Past and Present Extent and Biomass of an Imperilled Estuarine Habitat." *Proceedings of the Royal Society B: Biological Sciences* 279: 3393–400.

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