

Effects of landscape setting on oyster reef structure and function largely persist more than a decade post-restoration

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Long-term monitoring is vital to understanding the efficacy of restoration approaches and how restoration may enhance ecosystem functions. We revisited restored oyster reefs 13 years post-restoration and quantified the resident and transient fauna that utilize restored reefs in three differing landscape contexts: on mudflats isolated from vegetated habitat, along the edge of salt marsh, and in between seagrass and salt marsh habitat. Differences observed 1–2 years post-restoration in reef development and associated fauna within reefs restored on mudflats versus adjacent to seagrass/salt marsh and salt marsh-only habitats persisted more than 10 years post-restoration. Reefs constructed on open mudflat habitats had the highest densities of oysters and resident invertebrates compared to those in other landscape contexts, although all restored reefs continued to enhance local densities of invertebrate taxa (e.g. bivalves, gastropods, decapods, polychaetes, etc.). Catch rates of juvenile fishes were enhanced on restored reefs relative to controls, but to a lesser extent than directly post-restoration, potentially because the reefs have grown vertically within the intertidal and out of the preferred inundation regime of small juvenile fishes. Reef presence and landscape setting did not augment the catch rates of piscivorous fishes in passive gill nets, similar to initial findings; however, hook-and-line catch rates were greater on restored reefs than non-reef controls. We conclude that ecosystem functions and associated services provided by restored habitats can vary both spatially and temporally; therefore, a better understanding of how service delivery varies among landscape setting and over time should enhance efforts to model these processes and restoration decision-making.

Key words: context dependency, ecosystem services, habitat restoration, mudflats, salt marshes, seagrass beds

Implications for Practice

- Ecosystem services delivered by a restored habitat can be largely context dependent based on the landscape setting of the restoration.
- Furthermore, the type and magnitude of service delivery may be related to age of the restored habitat with some services building and others diminishing over time.
- Long-term monitoring of restoration projects is rare and hard to fund but may be critical for accurately assessing the return on these natural capital investments.

Introduction

Biogenic habitats or foundation species can mediate both community structure and ecosystem function (Dayton 1972; Bruno et al. 2003). Most coastal biogenic habitats exist as components of functionally connected mosaics, and the spatial arrangement of these habitats can determine the distribution of and interactions between organisms within an ecosystem (Boström et al. 2011). For example, seagrass meadows adjacent to salt marsh habitat can act as corridors for predators to access shellfish reef habitat, which could consequently alter predator foraging behavior and prey survival (Micheli & Peterson 1999).

Coastal and estuarine habitats, such as seagrass beds, oyster reefs, coral reefs, salt marshes, and mangroves are highly threatened with losses in global cover ranging between 30 and 85% (Wilkinson 2008; Waycott et al. 2009; zu Ermgassen et al. 2012). If a habitat is lost or becomes degraded, the integrity of neighboring patches and the ecosystem as a whole can become impaired. In Indonesia, for instance, the presence of seagrass was found to significantly reduce the incidence of bacterial pathogens in fishes and invertebrates occupying adjacent habitats such as coral reefs (Lamb et al. 2017). To reduce or reverse biogenic habitat loss, managers and conservationists have focused on both preservation and restoration of structurally complex habitats (Peterson & Lipcius 2003).

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Oyster reefs are important biogenic habitats that once were a common component of temperate estuaries; however, it is estimated that approximately 65–85% of oyster reefs have been lost in the United States, and in many areas the species is considered functionally extinct (zu Ermgassen et al. 2012). In addition to their extractive value for commercial fisheries, oysters provide a variety of ecosystem services, such as the enhancement of water quality, removal of excess nitrogen, shoreline stabilization, and provision of essential habitat for invertebrates and fishes (Meyer et al. 1997; Grabowski et al. 2012). Therefore, the loss of oyster reefs has negatively impacted estuaries globally, resulting in reduced habitat for valuable fishes and invertebrates, increased erosion rates, and reduced water quality (Peterson et al. 2003; Beck et al. 2011; Grabowski et al. 2012). The loss of this critical habitat has motivated oyster reef restoration efforts aimed at restoring ecosystem functioning and recovering associated valuable ecosystem services.

Even though landscape setting can influence the reestablishment of restored oyster reefs and the fish and invertebrate communities that utilize them, oyster reef restoration often proceeds without explicit consideration of the broader landscape setting in which it is being conducted. The restoration of oyster reefs directly adjacent to another biogenic habitat may impact habitat quality, subsequent ecosystem service delivery, and the overall success of the restoration effort. For instance, Grabowski et al. (2005) restored oyster reefs in three differing landscape settings: on isolated mudflats, adjacent to salt marsh with no seagrass present, and between seagrass and salt marsh habitats. During the first 2 years post-restoration, Grabowski et al. (2005) found that isolated mudflat reefs tended to support the highest density of oysters, other bivalves, and resident decapods. In addition, reefs constructed on mudflats also augmented catch rates of juvenile fishes potentially due to the increased structure, whereas reefs adjacent to other biogenic habitats did not enhance catch rates of juvenile fishes perhaps because the reefs were redundant to the adjacent structured habitats. In contrast to other findings, regardless of landscape setting, restored oyster reefs did not augment piscivorous fishes in any landscape setting (Grabowski et al. 2005).

Following most restoration projects, constructed habitats are typically monitored for 1–3 years, if at all (Bayraktarov et al. 2016; Zhao et al. 2016). While this time frame captures what is occurring on restored habitats immediately after restoration occurs, managers and practitioners would benefit from a deeper understanding of how communities may respond to restoration over decadal scales (Connell & Slatyer 1977). There are very few examples of long-term (>5 years) monitoring data investigating the trajectory of restoration in marine environments (Borja et al. 2010), which may bias our ability to maximize the long-term return on investments from restoration efforts. Long-term studies that do exist suggest that, in salt marsh and seagrass systems, the full effects of restoration may not be apparent within the typical 2- to 3-year time frame of most post-restoration monitoring grants (Bell et al. 2014). For instance, in salt marsh systems, “living shoreline” projects primarily designed to dampen shoreline erosion (i.e. marsh planting combined with a seaward oyster/rock sill) may

also support greater densities of fishes and crustaceans than surrounding areas, but this additional benefit may not be realized until 3–8 years post-construction (Gittman et al. 2016).

In this study, we examined whether landscape setting influences oyster reef communities using restored oyster reefs. In particular, we sampled oyster reefs restored in the three different landscape settings described above 13 years post-restoration (Grabowski et al. 2005). To make direct comparisons against initial observations made 1–2 years post-restoration, we followed the same sampling methodology as Grabowski et al. (2005). The objective of this study was to explore how landscape setting affects community structure on restored oyster reefs many years post-construction, as well as reefs’ functional role as essential habitat that promotes “secondary” production of fishes and decapods.

Methods

Study Site

Restored oyster reefs were sited in Middle Marsh, Back Sound, North Carolina (34°41′32″N, 76°37′16″W). Middle Marsh is part of the Rachel Carson National Estuarine Research Reserve (RC NERR) and is comprised of several marsh islands fringed by oyster reefs and seagrass beds. In the summer of 1997, 12 intertidal oyster reefs were constructed in three landscapes: on isolated mudflats (mudflat), immediately between salt marshes and seagrass (seagrass), and on sandy points immediately adjacent to salt marshes with no seaward seagrass present (salt marsh; described fully in Grabowski et al. 2005). Each reef was constructed with 60 bushels (4.5 m³) of cultch oyster shell, resulting in initial reef dimensions of 5 m × 3 m × 0.30 m (*l* × *w* × *h*). At the time of restoration, the reefs generally extended out of the water at low tide, corresponding with the tidal height at the base of natural intertidal oyster reefs. Each restored reef was paired with an unrestored control site at least 50 m away, with control sites mirroring the landscape setting of paired restored reefs. Restored reef and control sites were crossed within the three landscapes in a fully orthogonal design, with each unique treatment combination included in one of four replicate blocks around Middle Marsh.

Sampling Methods

Prey Resources. Sampling of living oysters and resident invertebrates was conducted to evaluate reef condition and quantify resource availability for higher predators (e.g. fishes) within restored and control plots of each landscape type. This sampling was conducted twice—once in July 2010 and once in December 2010. During each sampling event, two randomly chosen 0.25 m² plots within each reef or control were sampled by excavating to 10 cm below the sediment interface. Excavated material was sieved with a 1-mm sieve, after which all sessile and mobile fauna were identified and quantified. The number and weight of live oysters per 0.25 m² were also quantified from each sample plot.

Juvenile Fishes. Sampling began in July 2010 and continued each month until November 2010 to capture seasonal trends. Commercial crab pots, minnow traps (44.5 cm long \times 24.3 cm diameter; 5 mm mesh screen with two approximately 2.5 cm openings), and modified Morton fish traps (0.7 m long \times 0.6 m wide \times 0.25 m high, steel rebar frames with 5 mm nylon mesh walls containing two opposing 7 cm diameter tunnel openings) were used to quantify juvenile fish, shrimp, and crab utilization of the restored reef and control sites. Multiple trap types were utilized to quantify the nekton community, targeting species of varying sizes and with different life history strategies. Two traps of each type were deployed on each reef and corresponding control during each sampling event. Traps were deployed at mid-flood tide (always after sundown) and retrieved approximately 6 hours later at mid-ebb tide (always before sunrise). All captured individuals were identified to species, quantified, and measured during retrieval of the traps.

Piscivorous Fishes. Gillnets (10 m long \times 1.5 m tall; 7.62 cm stretch mesh) were utilized to sample more mobile, transient (often predatory) fishes each month from July 2010 until November 2010. Nets were stretched from one corner of the reef or control site along the seaward 5-m edge and then continuing along the 3-m edge on the downstream side relative to the flood tide. Nets were oriented with the current so that they opened during the flood tide when greatest catch rates were expected. Nets were deployed at mid-flood tide (always after sundown) and retrieved approximately 6 hours later at mid-ebb tide (always before sunrise). During retrieval of nets, each captured organism was identified to species, counted, measured, and released.

Hook-and-line sampling was conducted monthly July–November 2010. Nine volunteer fishermen representing a range of fishing experience were identified by the RC NERR. Optimal fishing days were selected for July–November 2010 based on occurrence of morning or evening high tides. Each month, each fisherman visited two of the four (randomly selected) study blocks in Middle Marsh (12 of the 24 reef or control sites). During each fishing excursion by any individual fisherman, at least one complete block of six reef or control sites was sampled. Fishermen were at liberty to choose tackle combinations, but were required to: (1) use the same tackle across all six reef or control sites within a study block; (2) fish within 2 hours of sunrise or sunset; (3) fish each reef or control site for 15 minutes; and (4) make all casts within 10 m of the reef or control site being sampled. All captured fishes were identified to species, counted, measured, and released.

Statistical Analyses

To determine the effect of reef restoration and landscape context on the density of oysters and resident invertebrates, two-way analysis of variance (ANOVA) was serially employed on the following response variables: oysters, bivalves (except oysters), decapods, nondecapod crustaceans (i.e. barnacles, amphipods, and isopods), gastropods, and soft-bodied infauna. Three-way ANOVAs were conducted to determine how reef restoration, landscape, and month affect relative catch rates

of juvenile fishes, piscivorous fishes caught in gillnets, and hook-and-line-caught fishes. All response variables were tested for normality (Shapiro–Wilk test, $p > 0.05$) and heterogeneity of the variances using a studentized Breusch–Pagan test ($p > 0.05$). Heteroscedastic data (i.e. oysters, nonoyster bivalves, decapods, nondecapod crustaceans, gastropods, soft-bodied infauna, juvenile fishes, piscivorous fishes, and hook-and-line-caught fishes) were transformed using square-root transformations and then retested to ensure homogeneous variance. Following square-root transformations, only modest violations of homoscedasticity were found for oysters, nonoyster bivalves, and decapods. Therefore, to maintain consistency in our statistical approach, we employed ANOVAs uniformly across response variables. All analyses were conducted in R version 3.2.2 (R Core Team 2015). Differences in densities were considered statistically significant at $p < 0.05$, except in cases in which homoscedasticity was violated; in those cases, we considered differences in abundance statistically significant at $p < 0.01$. Fisher’s least significant difference (LSD) post-hoc tests were used to conduct pairwise comparisons between treatments for significant main effects and interactions. Due to the high number of zeros present in the hook-and-line data, we also utilized the delta approach (Fletcher et al. 2005). We constructed two datasets from the original metric of recreationally prized species (i.e. sharpnose sharks, pigfish, flounder, bluefish, speckled trout, spot, kingfish, red drum, and gag grouper): one indicating presence of a captured fish in a 15-minute fishing bout (occurrence), and the other the mean catch rate when present (concentration). The occurrence and the mean concentration values were multiplied together to generate an index for relative density known as “delta-densities” of recreationally prized species (Serafy et al. 2007).

We used nonmetric multidimensional scaling (NMDS) ordination to assess how community composition varied as a function of reef restoration and landscape context. NMDS analyses were conducted with the Vegan and LabDSV packages in R (Oksanen et al. 2016; Roberts 2016). The NMDS ordinations were run with Bray–Curtis dissimilarity measures. In total, three NMDS ordinations were conducted: one including all species (quadrats/cores, traps, and nets pooled at each reef or control site), one with invertebrate species only (from quadrats/cores), and one with juvenile and piscivorous fishes (traps and gill nets pooled at each reef or control site).

Results

Prey Resources. There was a significant interaction between restoration and landscape on oyster density ($F_{[2,90]} = 14.99$, $p < 0.001$). Oyster densities were on average 360 times greater in all restored reef sites compared to control sites. In addition, oyster densities in restored reefs located on mudflats (874.1 oysters 0.25 m^{-2}) were significantly greater than densities on reefs in either salt marsh (81.3 oysters 0.25 m^{-2}) or seagrass (124.6 oysters 0.25 m^{-2}) landscapes (LSD, $p < 0.001$ for both

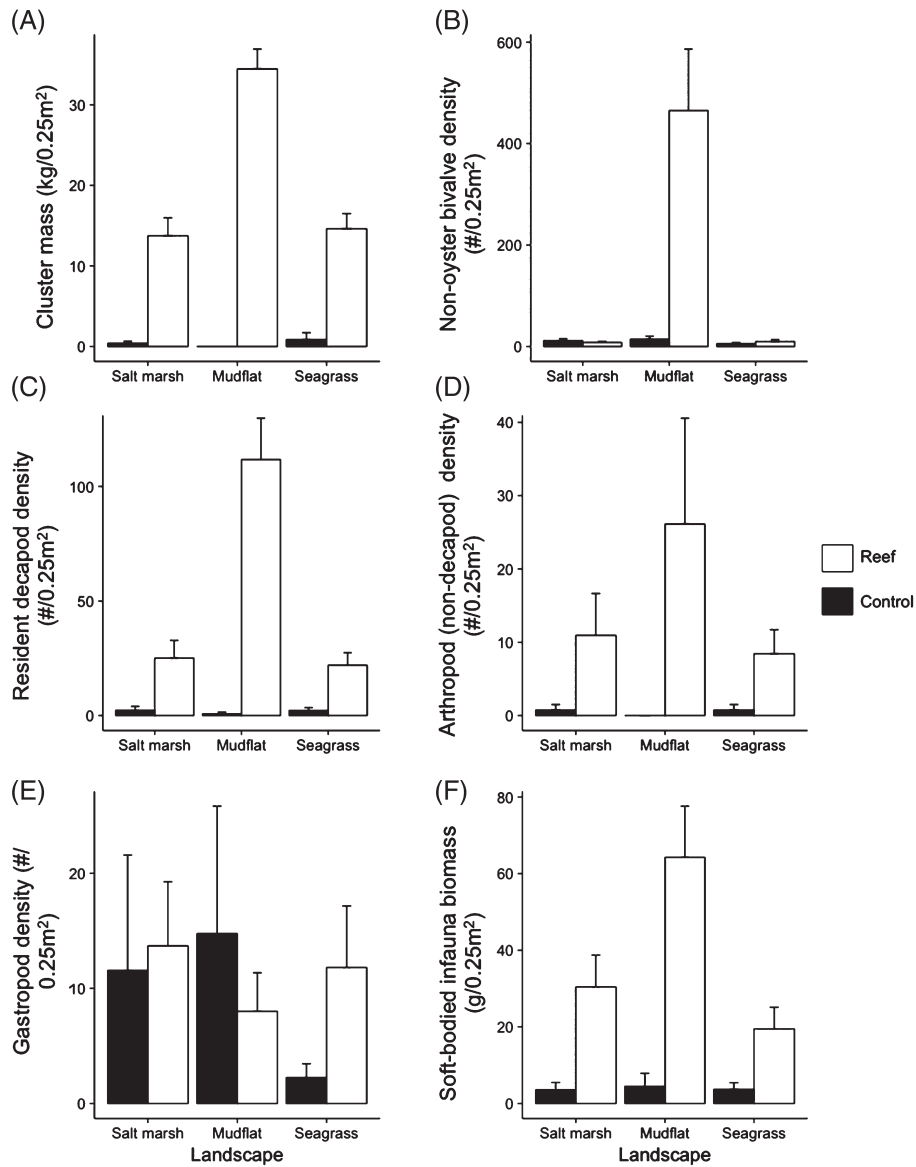


Figure 1. The effect of restoration and landscape context on (A) cluster mass of live oysters, (B) bivalve densities, (C) decapod densities, (D) non-decapod arthropod densities, (E) gastropod densities, and (F) infauna densities. All values are means (+SE). Black, control; white, restored reef.

comparisons). Similarly, the interaction between restoration and landscape influenced oyster cluster mass ($F_{[2,90]} = 49.96$, $p < 0.001$). Oyster cluster mass is the biomass of live oyster shell within the reef. Cluster mass of reefs on mudflats was about 2.5 times greater than that of reefs adjacent to salt marsh or seagrass (LSD, $p < 0.001$ for both comparisons; Fig. 1A), whereas we detected no differences between oyster reefs constructed immediately adjacent to either vegetated habitat setting (LSD, $p = 0.33$; Table 1). The increase in cluster mass can be visually observed by the total growth in reefs through time. Mudflat reef dimensions increased from the initial 5 m \times 3 m ($l \times w$) to approximately 8.5 m \times 6.5 m, whereas salt marsh and seagrass reefs remained similar in size to initial restoration measurements.

There was an interactive effect of restoration and landscape setting on density of bivalves other than oysters ($F_{[2,90]} = 23.53$, $p < 0.001$). LSD post-hoc tests revealed that only reefs restored on isolated mudflats enhanced bivalve densities (LSD, $p < 0.001$). Densities of non-oyster bivalves in mudflat reefs were about an order of magnitude greater than those of control sites, as well as seagrass or salt marsh reefs (Fig. 1B; Table 1), driven largely by the ribbed mussel *Geukensia demissa*. Similarly, decapod densities were approximately two orders of magnitude higher within mudflat reefs than nearby control habitats (driven largely by the mud crab *Eurypanopeus depressus*) ($F_{[2,90]} = 19.01$, $p < 0.001$). Although the enhancement derived from reef presence was greatest within mudflat landscapes, decapod densities were also elevated

Table 1. Direct comparison of results more than a decade after restoration (13 years) to results from 1 to 2 years (Grabowski et al. 2005) following the oyster reef restoration in three landscape contexts: mudflat reef (MF), seagrass reef (SG), and salt marsh reefs (SM). The direction of the sign indicates which group was greater in value (i.e. > for reef-control indicates restored reefs has a significantly greater abundance of that response variable than the control sites). Equal signs (=) indicate that there was no significant difference between groups. One greater than or less than sign (>, <) represents a $p < 0.05$. Two greater than or less than signs (>>, <<) signifies $p < 0.001$. Bolded and enlarged symbols represent a statistical difference from the initial sampling.

Response Variable	1997–1999				2010			
	Reef Setting				Reef Setting			
	Reef-Control	MF-SG	MF-SM	SM-SG	Reef-Control	MF-SG	MF-SM	SM-SG
Oyster cluster mass	>	>	>	=	>>	>>	>>	=
Non-oyster bivalves	>	>	>	=	>>	>>	>>	=
Infauna	>	=	=	=	>	>	>	=
Decapods	>	>	=	>	>>	>>	>>	=
Non-decapod arthropods	>	=	=	=	>>	=	=	=
Gastropods	>	=	=	=	=	=	=	=
Juvenile fishes	=	>	>	=	=	=	=	=
Piscivorous fishes	=	<	<	=	<	<<	=	<<

on salt marsh and seagrass reefs relative to controls (LSD, $p < 0.001$ for both; Fig. 1C). Decapod densities on mudflat reefs (111.7 individuals 0.25 m^{-2}) were significantly greater than on either seagrass reefs (22.0 individuals 0.25 m^{-2} ; LSD, $p < 0.001$), salt marsh reefs (25.1 individuals 0.25 m^{-2} ; LSD, $p < 0.001$), or control habitats (0–2 individuals 0.25 m^{-2} ; LSD, $p < 0.001$; Table 1). Non-decapod crustacean densities dominated by barnacles (*Balanus* sp.) and gammaridean amphipods were significantly elevated (on average 17 times greater) in restored reefs relative to non-reef control sites ($F_{[1,90]} = 24.97$, $p < 0.001$; Fig. 1D), but non-decapod crustacean densities did not differ among landscapes ($F_{[2,90]} = 1.19$, $p = 0.31$; Table 1).

Compared with other taxa, densities of gastropods were low (<15 individuals 0.25 m^{-2}) and highly variable. The most common species of gastropod found was the Atlantic oyster drill (*Urosalpinx cinerea*). There were no statistically significant main or interactive ($F_{[2,90]} = 0.63$, $p = 0.535$) effects of restoration ($F_{[1,90]} = 0.14$, $p = 0.093$) or landscape ($F_{[2,90]} = 2.88$, $p = 0.873$) on gastropod densities; however, we did detect 1.5-fold higher gastropod densities on seagrass reefs than on controls in seagrass landscapes (LSD, $p < 0.095$; Fig. 1E). Reef presence had a significant effect on the biomass of soft-bodied infauna (predominantly nereididae worms and anemones) in all landscape settings ($F_{[1,90]} = 47.81$, $p < 0.001$). There was a marginally significant interaction of restoration and landscape on soft-bodied infauna biomass ($F_{[2,90]} = 2.99$, $p = 0.055$). On mudflat reefs there was approximately two to three times more soft-bodied infauna biomass (64.3 g 0.25 m^{-2}) than that of seagrass reefs (19.5 g 0.25 m^{-2}) and salt marsh reefs (30.4 individuals 0.25 m^{-2}), or any of the controls (3–4 g 0.25 m^{-2} ; LSD, $p = 0.002$; Fig. 1F; Table 1).

Juvenile Fishes. Juvenile fishes were dominated by pinfish (*Lagodon rhomboides*), pigfish (*Orthopristis chrysoptera*), oyster toadfish (*Opsanus tau*), spot (*Leiostomus xanthurus*), spot-tail pinfish (*Diplodus holbrooki*), and flounder (*Paralichthys*

spp.). Cumulative catch rates of juvenile fishes on reefs differed among landscapes in certain months but not in others. There were significant interactions between restoration and month ($F_{[4,209]} = 2.42$, $p = 0.049$), as well as between landscape and month ($F_{[8,209]} = 2.06$, $p = 0.041$) on densities of juvenile fishes. In August, reef presence increased the catch rates of juvenile fishes by 2-fold in all landscapes. In November, juvenile catch rates were six times greater on salt marsh and mudflat reefs than their respective controls and two times greater on seagrass controls than seagrass reefs. (Fig. 2A; Table 1).

Piscivorous Fishes. Total abundance of piscivorous fishes was affected by landscape ($F_{[2,90]} = 6.49$, $p = 0.002$), restoration ($F_{[1,90]} = 63.93$, $p = 0.05$), and month ($F_{[4,90]} = 2.49$, $p = 0.002$), but there were no interactions among any factors. Unexpectedly, piscivorous fishes on average were 3.5 times more abundant in control sites than restored reefs, although this difference appeared most extreme in the salt marsh landscape (Fig. 2B). Catch rates of piscivorous fishes were highest in seagrass landscapes (two times greater), regardless of reef presence, compared to those located in mudflats and salt marsh habitats (LSD, $p \leq 0.01$ for both; Table 1).

Hook-and-line efforts resulted in the capture of 83 recreationally prized fishes. There was no statistically significant effect of landscape ($F_{[2,528]} = 0.07$, $p = 0.932$), reef presence ($F_{[1,528]} = 1.33$, $p = 0.249$), or month ($F_{[4,528]} = 0.65$, $p = 0.627$) on the catch rates reported by recreational fishermen—unsurprising for zero inflated data. Delta densities, however, revealed that fisherman caught approximately 1.4 times more fish on restored reefs than at control sites (Fig. 2C). Additionally, there was a trend toward higher catch rates of mobile fishes in seagrass landscapes compared to those in either mudflat or salt marsh landscapes.

Nonmetric Multidimensional Scaling. Each of the three NMDS analyses conducted explained at least 75% of variation observed in the data (all species: $R^2 = 0.78$; invertebrates

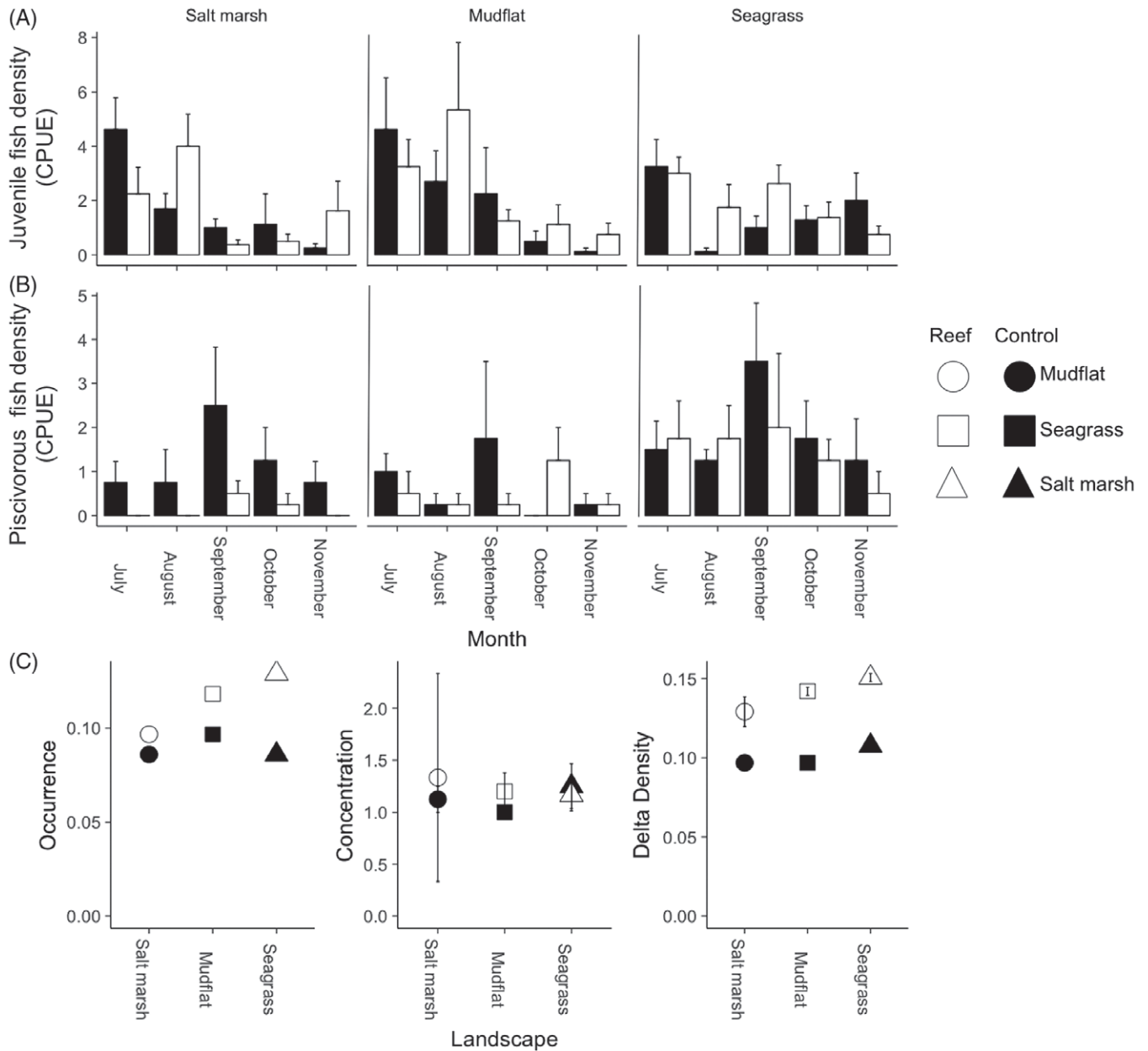


Figure 2. Trap sampling for juvenile fish and gill net sampling for piscivorous fish was conducted monthly from July to November 2010 on reefs and controls in all three landscapes. All values are means (+SE). The two-way interaction of month and restoration on (A) the total abundance of juvenile fish, (B) the total abundance of piscivorous fish, and (C) the occurrence, concentration, and delta densities for hook-and-line-caught fish. Black, control; white, restored reef.

only: $R^2 = 0.75$; fishes only: $R^2 = 0.79$). Two-dimensional axes were utilized for each NMDS analysis with a stress of 0.11, 0.09, and 0.13, respectively. Restoration accounted for 74% of the variation observed along axis 1 for the all species model (Fig. 3A). Similarly, restoration accounted for 71% of the differences in communities along axis 1 and 38% of the observed variation along axis 2 in the invertebrate taxa NMDS (Fig. 3B). In both the all species and invertebrate species NMDS, isolated mudflat reefs tended to group together (indicating the communities on these reefs were the most similar to one another) and were observed to have the most

dissimilar communities from other landscapes and/or restored reefs. Differences observed in mudflat reefs were largely driven by the ribbed mussel (*G. demissa*), mud crabs, and the Atlantic oyster drill (*U. cinerea*) (Fig. 3A & B). Neither axis 1 nor axis 2 from the fish species NMDS were driven by restoration, landscape setting, or month (0.0%). We note, however, that black drum (*Pogonias cromis*) and flounder (*Paralichthys* sp.) tended to be more characteristic of catches in seagrass landscapes, whereas sheepshead (*Archosargus probatocephalus*) were only observed in mudflat landscapes (Fig. 3C).

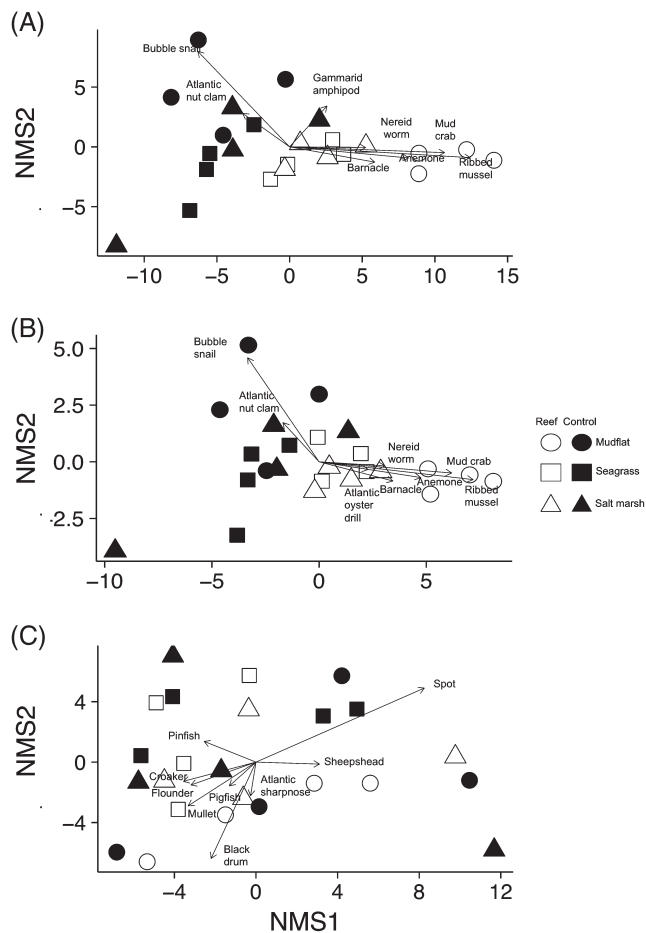


Figure 3. Non-metric multidimensional scaling ordinations of (A) all species sampled, (B) only invertebrate species, and (C) only fish species were conducted to visualize the similarity of community composition between reef and controls across all three landscape settings. Arrows indicate specific species driving observed trends. All values calculated with Bray–Curtis dissimilarity matrix.

Discussion

Restoration scientists have postulated that biological function of a restored habitat will increase through time for some period before eventually plateauing as the system reaches a new carrying capacity (Choi 2004). Therefore, to better understand if a restored habitat has fully reestablished, it is vital to continue monitoring over decadal scales. In our study, 13-year-old restored oyster reefs were resampled to explore if the restoration trends changed or remained consistent through time. To our knowledge, no other long-term study greater than 10 years has been conducted on restored oyster reefs. Our results indicate that mudflat reefs continued to support the highest densities of oysters and other resident invertebrate species and at greater levels than during the first 2 years post-restoration. In contrast, invertebrate densities on salt marsh reefs 13 years post-construction were relatively low compared to densities more immediately post-restoration. Collectively, our results suggest that communities on restored oyster reefs are highly influenced by the spatial

configuration of adjacent habitats or landscape setting, and to a lesser extent, time since construction.

There are several mechanisms that could influence the trajectory of invertebrate communities on restored reefs in different landscapes through time. In Middle Marsh, water velocity rates near mudflat reefs may have remained relatively consistent given the local stability of major shoal complexes, whereas marsh erosion-accretion over meter scales may have reduced hydrologic flow near salt marsh and seagrass reefs (detailed below). This could have resulted in consistently higher larval settlement rates of juvenile oysters and larval invertebrates near mudflat reefs but not in the other two landscape settings (Sanford et al. 1994). The higher flow would also consistently enhance food delivery to mudflat reefs, resulting in increased growth and survival on mudflat reefs (Lenihan 1999). Therefore, the higher densities of oysters and invertebrates on mudflat reefs could be expected during both the first 2 years post-restoration and 13 years after reef construction.

The tidal elevation of an oyster reef can mediate the success of restoration efforts (Powers et al. 2009; Fodrie et al. 2014). In North Carolina, intertidal oyster reefs are found in the low- to mid-intertidal, and landscape setting likely influences this variation. Specifically, seawater temperatures constrain many seagrass species, such as *Zostera marina*, to the shallow subtidal (Rozas & Minello 1998) so that oyster reefs adjacent to seagrass beds are typically found at slightly deeper elevations than those in the other two landscapes. The lower (approximately 5–10 cm) elevation of seagrass reefs may have initially increased the settlement of oysters but negatively impacted their post-settlement growth due to higher rates of predation with less aerial exposure (Bishop & Peterson 2006; Fodrie et al. 2014). This could explain why Grabowski et al. (2005) reported seagrass reefs to support the lowest density of oysters following reef construction. However, over time the advantage of higher elevation of salt marsh reefs over the seagrass reefs was apparently counterbalanced by the envelopment of the oyster reef by salt marsh cordgrass (*Spartina alterniflora*). The sediment stabilization and expansion of the salt marsh habitat around the oyster reef may have created a barrier to oyster and invertebrate settlement and resulted in the lower densities of oysters and invertebrate taxa on salt marsh reefs. Additionally, the increased predation pressure of juvenile oysters and spat by mesopredators, such as xanthid crabs that occupy the marsh edge (Carroll et al. 2015), may have lowered survival as the reefs aged. Increased predation pressure could also explain the lower oyster densities observed on salt marsh reefs compared to those on mudflat or seagrass reefs 13 years post-construction.

Initially after reef construction, only mudflat reefs enhanced juvenile fish densities, perhaps because oyster reef habitat is functionally redundant to seagrass and salt marsh habitat (Grabowski et al. 2005; Geraldi et al. 2009). Indeed, oyster reefs may provide similar functions (i.e. foraging grounds, protection, etc.) to fishes as other structured habitats, such as seagrass, salt marsh, and mangroves. In this study, however, we found that juvenile fishes were augmented by reefs in all landscapes, although this benefit was only apparent during a small window of time during our study. These differences in juvenile fish catch

rates 1–2 years versus 13 years after restoration could be a result of several interacting mechanisms. Initially, restored reefs in all three landscape settings were characterized by low vertical relief (30 cm tall), allowing for the regular inundation of the reefs at high tide. As the reefs have grown vertically (>75 cm tall; Rodriguez et al. 2014) they may be completely covered by water less frequently, resulting in a reduction from initial densities observed on mudflat reefs in certain months, yet it is unclear why catch rates would increase on salt marsh or seagrass reefs compared to initial findings. Moreover, the lack of enhancement of juvenile fish catch rates throughout the year, 13 years post-restoration, may be due to a shift in the preferential habitat from the top of the reef (where our traps were placed) to the edges that are more regularly flooded. Additional efforts to monitor older reefs will help resolve how the effects of landscape setting on juvenile fish catch rates and other important ecosystem functions evolve with reef age.

The enhancement of fishes and mobile crustaceans is considered an important ecosystem service provided by restored oyster reefs (Coen et al. 1999; Breitburg et al. 2000; Peterson et al. 2003; Grabowski & Peterson 2007). Over the past three decades, several studies have investigated fish communities on oyster reefs and found that oyster reefs generally support higher densities of many juvenile and adult fishes and mobile crustacean species than non-oyster reef controls (Grabowski et al. 2005; Allen et al. 2007; Gregalis et al. 2009). Although we found some evidence of higher densities of juvenile fishes on reefs, densities of piscivorous fishes were higher on controls than on reefs and were generally higher in the seagrass than the other two landscapes regardless of reef presence. These results are similar to findings of functional redundancy of Grabowski et al. (2005) and Geraldi et al. (2009), in that they also found that oyster reefs did not augment adult fish catch rates. These results likely reflect the fact that the species that dominated our catch included many that are not obligate residents of oyster reefs, such as flounder and gag grouper. In addition, intertidal oyster reefs may not be easily accessed by larger fishes given the more limited inundation of intertidal oyster reefs relative to surrounding mudflats.

In general, the ability to detect whether reefs enhance fish densities may be confounded by inherent biases and selectivity of the methodologies used to quantify catch rates at the scales we studied. Specifically, the catch rate of nets ultimately depends on both the density of animals within the sampling domain, as well as the movement behavior of those individuals over 1–100s of meters (Rudstam et al. 1984). Acoustically tagged red drum (*Sciaenops ocellatus*) within Middle Marsh have been observed to preferentially utilize the same restored oyster reefs sampled with nets in this study, especially restored reefs near or adjacent to seagrass or salt marsh habitats (Fodrie et al. 2015). Acoustic data also demonstrated that red drum near reefs are more stationary and may not be as accessible to net-based approaches around reefs. In this regard, hook-and-line sampling is potentially a valuable, orthogonal method of assessing fish utilization of habitat patches within a landscape because hook-and-line sampling involves capturing fishes while they are actively foraging. In our system, we speculate that mobile fishes

may be using reefs for short periods of time to forage which could suggest a positive effect of reef presence on trophic transfer and, ultimately, recreational fishing harvest; however, this effect may not be detected by traditional net sampling.

The greater numbers of oysters on mudflat reefs created more habitat for invertebrate species, such as xanthid crabs, that likely impact food-web structure and function. Additionally, the increased numbers and biomass of living oysters on mudflat reefs influences their water filtration rates (Newell & Koch 2004) and nutrient cycling capacity (Smyth et al. 2015) relative to seagrass or salt marsh reefs. For instance, in salt marsh and seagrass landscapes, the addition of oyster reefs did not enhance levels of denitrification already occurring, yet reefs in mudflats greatly increased denitrification compared to that of control sites (Smyth et al. 2015). Carbon cycling of restored oyster reefs is also greatly affected by landscape setting. Salt marsh reefs and subtidal oyster reefs have been shown to be net carbon sinks due to the predominance of organic carbon burial, whereas intertidal mudflat reefs can be net carbon sources due to the high rates of biosynthesis and retention (burial) of inorganic carbon in shell (Fodrie et al. 2017). Salt marsh reefs also appear to promote sediment stabilization and accretion of shoreline habitats, including the salt marshes that they were located adjacent to. Efforts to restore oyster reefs in the intertidal zone should include consideration of how landscape setting and reef age influence the delivery of these different ecosystem services.

More than 10 years post-restoration, we found evidence that oyster reefs greatly influence fish and invertebrate communities by augmenting the densities of many ecologically and economically important species. Yet, these results are largely context dependent—the landscape setting of an oyster reef greatly influences these processes. Specifically, our findings in conjunction with others indicate that mudflat reefs have higher numbers of live oysters and associated sessile and mobile fauna, which can be related to increased water quality and denitrification rates (Smyth et al. 2015). The shift in structure and function of salt marsh reefs due to the envelopment of the reefs by marsh grass may be perceived as a negative impact, but these restored reefs can increase sediment stabilization and carbon sequestration (Fodrie et al. 2017). In addition, we have shown that these context-dependent effects may be directly related to period of observation. Therefore, these results provide additional support for evaluating restoration outcomes at expanded time-scales. Even when continuous monitoring of restoration sites may not be financially possible over longer time scales (e.g. decades), there are opportunities for periodic assessments (e.g. every 5–10 years) that can inform our understanding of restoration trajectories. Mounting evidence from long-term monitoring of salt marsh, seagrass, and now oyster reef restoration indicate that the typical 1- to 2-year post-restoration monitoring is likely insufficient for generalizing restoration trajectories (Borja et al. 2010; Zhao et al. 2016). Finally, we suggest that future investigations should consider how landscape setting and other environmental factors interact with oyster reef success to impact the timing of the delivery of associated ecosystem services.

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