HOW HABITAT SETTING INFLUENCES RESTORED OYSTER REEF COMMUNITIES

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Abstract. Integrating how habitat heterogeneity influences food web dynamics is critical to enhance our understanding of community structure. This study quantified resident (invertebrates) and transient (juvenile and piscivorous fish) fauna within restored intertidal oyster reefs and analogous control sites without reef habitat in each of three habitats (on the edge of salt marsh away from seagrass, on mudflats isolated from vegetated structures, and in between seagrass and salt marsh habitat). Reefs enhanced the abundance of resident invertebrates (e.g., polychaetes, nemerteans, epibenthic anemones, bivalves, and resident decapods) that comprise >90% of juvenile fish prey biomass. However, the increase in food availability due to reef presence did not affect abundance of juvenile fish in either of the vegetated habitats, suggesting that resources may not limit juvenile fish when restored in these habitats. Only mudflat reefs augmented juvenile fish abundances, most likely due to a combination of greater resource availability and relative isolation from functionally equivalent habitats. In addition, lower abundances of piscivorous fish in mudflat reefs relative to control areas likely contributed to this pattern. Thus, community structure and important ecosystem functions such as secondary production depend on the spatial configuration of surrounding habitats, in much the same way that species interactions can depend on their biotic and abiotic context.

Key words: consumer-resource dynamics; context dependency; ecosystem goods and services; habitat restoration; mudflats; oyster reefs; salt marshes; seagrass beds.

INTRODUCTION

Ecologists have begun to recognize that both the strength and direction of species interactions can differ on spatial and temporal scales as a consequence of variation in abiotic and biotic factors (Bronstein 1994, Travis 1996, Valentine et al. 2002). For instance, variability in predation pressure along the east coast of the United States influences the strength of positive associations between decorator crabs and defended algal species (Stachowicz and Hay 2000). Variation in the risk of predation can thus strongly influence prey behavior as well as mediate prey densities, growth rates, and reproductive effort (Werner and Anholt 1996, Mills and Gorman 1997, Krupa and Sih 1998, Sanford et al. 2003). Similarly, resource (i.e., prey) availability and the energetic benefits and constraints of different types of prey can dictate predator foraging behavior (MacArthur and Pianka 1966). In fact, patterns of habitat use by organisms often reflect trade-offs between resource availability and predation risk (Werner et al. 1983, Beck and Watts 1997, Cowlishaw 1997, Heithaus

and Dill 2002). These factors consequently have the potential to influence the value of a particular habitat, suggesting that the degree to which a habitat provides particular functions (e.g., secondary production) is likely to be dependent on the context in which it is found. Therefore, determining the appropriate scale at which to evaluate the quality of a particular habitat is critical to both conservation and restoration efforts.

Investigation of how predators and prey distribute among habitat patches of varying quality requires knowledge of the size and spatial arrangement of habitat patches (Turner 1989). For instance, the spatial arrangement of habitats can alter the foraging behavior of an individual predator, including which habitat patches and associated prey it has access to (Micheli and Peterson 1999, Lenihan et al. 2001). Even if relatively low food availability or a higher risk of predation deters species from residing within a particular habitat, that same area may serve as an important corridor or barrier to habitats with greater refuge and food availability. Belisle and Desrochers (2002) demonstrated that resident and migratory forest birds rarely stray (>25 m) from the forest edge and choose longer routes to maintain forest cover when called, presumably to avoid predation. Such evidence of the importance of habitat connectivity and arrangement indicates the need for empirical studies to address how the location of a

habitat influences predator–prey dynamics across multiple trophic levels.

Physical factors such as water and air currents influence transport and exchange of particles and organisms among interconnected habitats, which subsequently can mediate community structure in recipient habitats (Polis et al. 1997). Within temperate estuaries, the ebbing tide requires most fish species that forage in intertidal habitats at high tide to relocate to nearby subtidal areas as these intertidal habitats emerge from the water. If the availability of prey resources or predator regimes of adjacent subtidal and intertidal habitats differs, the setting in which a particular intertidal habitat is located may affect the distribution and abundance of organisms within it and thus the overall function of that habitat. In estuaries, complex habitats such as salt marshes or mangroves, seagrass beds, and oyster reefs exist in combination with unstructured sand and mud bottom. Linkages among these estuarine habitats affect prey mortality and growth (Robbins and Bell 1994, Irlandi and Crawford 1997, Micheli and Peterson 1999). For instance, blue crabs utilize seagrass beds as corridors to access oyster reefs and consume hard clams, so that hard clam survivorship is reduced on reefs that are adjacent to seagrass habitat and indirectly connected to salt marshes where crab densities are greater (Micheli and Peterson 1999). Although oyster reefs recently have been recognized as important habitat for fish and mobile crustaceans (Coen et al. 1999, Lenihan et al. 2001), it is uncertain how the setting of an oyster reef influences interactions among piscivorous fish, juvenile fish, and resident epifaunal and infaunal communities. Oyster reef restoration efforts that are attempting to recover ecosystem goods and services such as nursery habitat for juvenile fish should consider if these functions are dependent upon where an oyster reef is located.

Restoration projects provide an ideal opportunity to test how the adjacency of differing habitats influences community structure and habitat quality. Our understanding of how estuarine and marine communities are structured is still evolving as degradation from destructive fishing practices, removal of top predators, land development, and reduced water quality continue to threaten the integrity of these habitats (Jackson et al. 2001). The capacity of marine habitat preservation to sustain provision of ecosystem goods and services is imperiled by dramatic alterations in the environmental and biological quality of coastal ecosystems (Hobbs and Harris 2001). In fact, habitat recovery from impairment is often inhibited after such severe disturbances, so that habitat restoration may be the only viable solution. Therefore, restoration experiments must identify the mechanisms that structure ecological communities and maintain the provision of ecosystem goods and services.

Intertidal oyster reefs are typically located in three habitats in coastal North Carolina: on the fringes of salt marshes with seagrass habitat on the lower end (i.e., ''seagrass''), on points extending outward from the edge of salt marsh habitat (i.e., ''salt marsh''), and on sandy and muddy bars isolated from vegetated habitats (i.e., ''mudflat'') (Bahr and Lanier 1981). In this study, we restored intertidal oyster reefs in each of these settings to determine how the habitat in which a reef is restored influences abundances of piscivorous fish, juvenile fish, and resident invertebrates. In particular, we tested whether habitat influences resource availability (prey and refuge) and predatory risk (piscivorous fish abundance). We also investigated the collective effects of reef presence, habitat setting, resource availability, and predatory risk on patterns of juvenile fish abundance within shallow estuaries. Thus, the restoration of reef habitat permitted an investigation of the effects of reef location on community structure within oyster reefs.

METHODS

Study site

Restoration of reef habitat occurred at four sites in Middle Marsh, which is a series of seagrass beds, salt marshes, and mudflats located in Back Sound, Carteret County, North Carolina (Fig. 1; Appendix A). Reefs were constructed during July 1997 using oyster shell provided by the North Carolina Division of Marine Fisheries (NC-DMF). Each reef was constructed with ~4.5 m³ (~60 bushels) of oyster shell, resulting in final dimensions of 5 × 3 × 0.30 m. Natural intertidal reefs in this region of coastal North Carolina range from below this size to much longer (i.e., up to ~100 m) and wider (i.e., up to ~10 m) reefs, though our restored reefs are similar in proportion to several of the natural intertidal reefs in Middle Marsh. We also selected a size that is similar to that of intertidal reefs constructed by local managers and advocacy groups attempting to recover ecosystem goods and services such as biofiltration and nursery habitat. Our restored reefs emerged completely from the water at low tide, corresponding to the tidal height of regional intertidal oyster reefs (the base of the reefs are ~0.1 m above the mean low tide line). At each site, we identified two locations separated by at least 50 m in each of three habitats, and then randomly chose one of the locations in each habitat in which to construct the experimental oyster reefs (12 reefs total): (a) with the longer reef edge abutting the fringe of *Spartina alterniflora* marsh habitat and directly adjacent to subtidal seagrass habitat (mixed beds of *Halodule wrightii* and *Zostera marina*), (b) with the longer reef edge abutting the salt marsh fringe and adjacent to mud bottom (isolated from seagrass habitat by >50 m), and (c) on mud bottom isolated from either vegetated habitat by >50 m). Thus, the reefs could be compared to the corresponding controls without experimental reefs in each habitat (12 controls total) to determine how restoring reef habitat affected fish (pi-
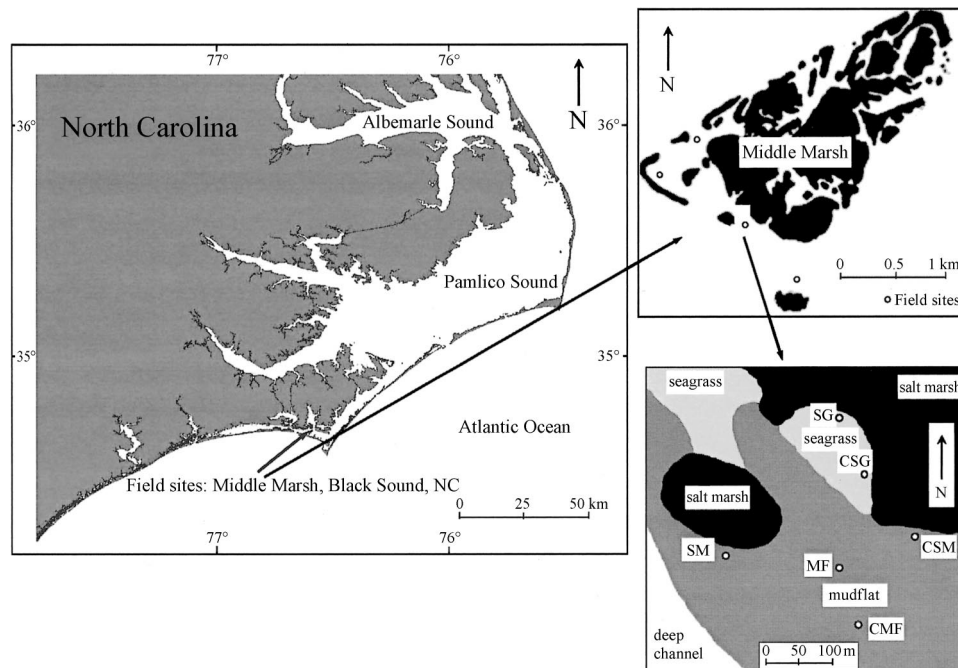
FIG. 1. Study location (left graph): Middle Marsh, situated in Back Sound, Carteret County, North Carolina, USA. Location (top right graph) of the four sites within Middle Marsh where reefs were restored. Diagram (bottom right graph) of a particular site. Restored reefs and controls without reef habitat were sampled in each of three different habitats: SM indicates a reef on the edge of salt marsh isolated from seagrass habitat, and CSM indicates a control station within this habitat; MF indicates a reef on a mudflat without either vegetated habitat present, and CMF marks the location of a mudflat control station; SG indicates a reef on the edge of a seagrass bed and salt marsh, and CSG marks a control station within this habitat.

scivorous and juvenile) and invertebrate utilization patterns within each habitat.

Resource availability

Sampling of resident invertebrates was conducted to quantify and compare resource availability for juvenile fish on reefs and controls in each habitat. Sampling was conducted semiannually in the winter (December 1997 and 1998) and summer (June 1998 and 1999) to sample just after peaks in spring and fall settlement occur. During each sampling period, two randomly chosen 0.25-m^2 plots within each reef and control site were sampled by excavating the top 10 cm of subsurface material. Prior to excavation, each 0.25-m^2 plot was subsampled in its center for polychaetes and amphipods with a 15 cm diameter core to a depth of 10 cm. Polychaetes and amphipods in core samples were sieved with a 0.5-mm mesh sieve, then preserved in 10% formalin, and identified and quantified in the laboratory. Unattached invertebrates and fish (except for polychaetes and amphipods) from each 0.25-m^2 plot were sieved on 1-mm mesh sieves, separated from the remaining coarse material, preserved in 10% formalin, and identified and quantified in the laboratory. Sample plots where excavation had already occurred during a previous sampling date were excluded from later sampling events, and data from the two samples within each plot during a sampling date were pooled. Cluster shell, defined as planted shell containing at least two living oysters that extend vertically upward >5 cm, was weighed to provide a measure of habitat complexity as a proxy for potential refuge availability. Cluster shell is considered a measure of potential refuge availability because it correlates positively with the amount of vertical relief and physical complexity of the reef (Meyer et al. 1996).

Juvenile fish

Trap sampling was conducted to assess abundance patterns of juvenile fish. Sampling was conducted with minnow traps (44.5 cm long × 24.3 cm diameter with 5-mm mesh screen and ~2.5-cm openings on two opposing sides) and modified Morton fish traps (0.7 m long × 0.6 m wide × 0.25 m high, with steel rebar frames and 5-mm nylon mesh walls containing two opposing 7 cm diameter tunnel openings). Unbaited traps were used to avoid potential biases associated with bait scent plumes attracting fish from outside of a particular habitat. Sampling was conducted monthly during the day and at night from April through November in 1998 and 1999. Trap sampling was discontinued from December through March because of the relative scarcity of juvenile fish and mobile invertebrates within shallow, estuarine waters during this time period. Two traps of each type were deployed on each reef and control site near the full moon of each month

during the sampling period. Traps were deployed at midflood tide and retrieved approximately six hours later at midebb tide. During retrieval, each captured organism was identified to species, quantified, measured, and released.

Piscivorous fish

Gill nets (10 m long × 1.5 m tall; 7.5 cm maximum slit opening) were utilized to sample piscivorous fish. Gill nets were stretched from the corner of the reef or control plot along the 5 m wide edge and then continuing along the 3 m edge on the downstream side of the flood tide. Nets were oriented with the current so that they opened during the flood tide when greatest catch rates were expected (J. Grabowski, *personal observation*). Gill nets were deployed at midflood tide and retrieved six hours later, midway on the ebb tide. Gill net sampling occurred monthly both during the day and at night from April through November in 1998 and 1999. Similar to trap sampling, gill net sampling was not conducted in December through March because colder water temperatures preclude fish from using shallow water habitats (J. Grabowski, *personal observation*). All captured fish were identified, measured, and weighed.

Statistical analyses

The effects of season (summer vs. winter), habitat (salt marsh, mudflat, or seagrass), and reef presence on the density of the five most abundant categories of resident invertebrates collected during core and 0.25-m² resident invertebrate sampling were analyzed collectively using multivariate analysis of variance (MANOVA) and then separately using analysis of variance (ANOVA) for each response variable (Underwood 1981). The effect of habitat on cluster shell mass in June 1999 was tested using a one-factor ANOVA. Although trap sampling for juvenile fish abundances was conducted during the day and in the evening, trap sampling attempted at night was inefficient (Grabowski 2002), so we excluded night sampling data from our analyses. Because gill net efficiency may differ with time of day, we only included night-sampling data in our analyses (when fish detection and avoidance of gill nets are likely lower). The effects of month, habitat, and reef presence on the abundance of piscivorous fish sampled by gill nets and juvenile fish caught in traps were tested using separate three-way ANOVAs for each of the two response variables (piscivorous and juvenile fish). We also analyzed both of the fish abundance data sets separately with repeated-measures ANOVAs, but did not present these results because qualitative comparison of each pair of analyses (standard three-way ANOVA vs. repeated-measures ANOVA) was identical for both response variables. All data sets were tested for heterogeneity of variances for each main effect using Cochran's test (Underwood 1981). Heterogeneous data were transformed using root transformations until

variance groups of transformed data were homogeneous. 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 experiment was balanced in design with a priori predictions and fixed factors (Day and Quinn 1989).

RESULTS

Prey resource availability

Patterns of resource availability were largely influenced by reef presence. Invertebrates were divided into five functional groups based on their morphologies and similarities as fish prey: (1) soft-bodied infauna (i.e., polychaetes, nemerteans, and epibenthic anemones); (2) bivalves other than oysters; (3) gastropods; (4) resident decapods; and (5) arthropods other than decapods (i.e., amphipods, isopods, tanaids, and chironomids). The results of the MANOVA on the densities of the five prey groups were significant for the effects of season, habitat, and reef presence (Wilks' lambda test: $P < 0.05$ for all main effects); therefore, we proceeded with separate ANOVAs for each of the five response variables. ANOVA of the effects of season, habitat setting, and reef presence on combined densities of polychaetes, nemerteans, and epibenthic anemones revealed no significant interactions or main effects at $P = 0.05$. However, variance in polychaete size was very large, so total soft-bodied infauna biomass was also analyzed (Appendix A). Biomass of soft-bodied infauna was 30.4% higher in the summer than in the winter ($F_{1,84} = 6.3$, $P = 0.01$; Fig. 2a [left]) and 436% higher on reefs than controls ($F_{1,84} = 30.7$, $P < 0.0001$; Fig. 2a [right]), but did not differ with habitat ($F_{2,84} = 1.1$, $P = 0.33$).

The effects of reef presence and season on gastropod densities were similar to, yet more pronounced than, those for soft-bodied infauna (Appendix A). Gastropod densities were 175% higher in the winter than during the summer ($F_{1,84} = 10.9$, $P = 0.001$; Fig. 2b [left]), and reef presence increased gastropod densities by 1058% over control densities ($F_{1,84} = 56.0$, $P < 0.0001$; Fig. 2b [right]). There was also a nonsignificant trend of greater gastropod densities on mudflats than the other habitats ($F_{2,84} = 2.5$, $P = 0.09$).

In contrast to the results for polychaetes and gastropods, densities of bivalves other than oysters were influenced by both habitat setting and reef presence (Appendix A). ANOVA revealed a two-way interaction between habitat and reef presence ($F_{2,84} = 11.2$, $P < 0.0001$; Fig. 2c). SNK post hoc tests indicated that bivalve densities were augmented by reef presence only on mudflats; densities on mudflat reefs were 348% greater than on mudflat controls. Reef presence on mudflats also increased bivalve densities relative to salt marsh or seagrass reefs. There was no difference in control densities among all three habitats. Neither of
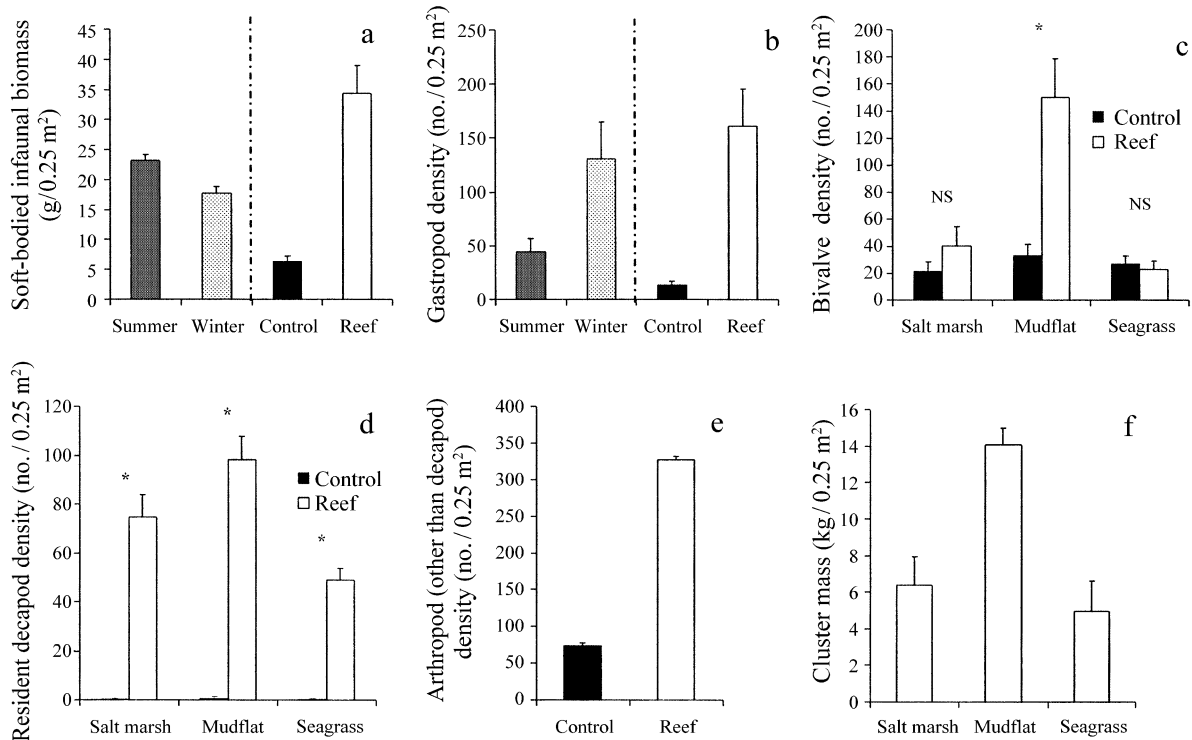
Fig. 2. Semiannual sampling for resident invertebrates and reef cluster mass was conducted on reefs and controls in each of three habitats from December 1997 to June 1999 in Middle Marsh, North Carolina. Sampling was conducted with two pooled 0.25-m^2 quadrats (gastropods, bivalves other than oysters, resident decapods, and reef cluster mass) and 15 cm diameter core samples (soft-bodied infauna and resident arthropods other than decapods) per reef and control during each sampling period. All values are means + SE. (a) The effects of season (left) and reef presence (right) on soft-bodied infaunal biomass (season, $n = 48$ reefs and controls sampled in the winter or summer with cores; reef presence, $n = 48$ reefs or controls sampled with cores). (b) The effects of season (left) and reef presence (right) on gastropod density ($n = 48$ sets of quadrat samples). (c) The two-way interaction between habitat setting and reef presence on bivalve (other than oyster) density ($n = 16$ reef or control quadrat samples within each habitat setting). Significance levels (*$P < 0.05$; NS, $P > 0.05$) presented above bars are from Student-Newman-Keuls (SNK) post hoc tests conducted to explore the cause of the significant habitat × reef interaction. (d) The two-way interaction between habitat setting and reef presence on the density of resident decapods ($n = 16$ sets of quadrat samples). (e) The effect of reef presence on total arthropod (other than decapod) density ($n = 48$ sets of core samples). (f) The effect of habitat on cluster mass ($n = 4$ reefs sampled with quadrats within each habitat setting). SNK post hoc tests revealed that cluster mass was greatest on mudflat reefs and did not differ in the two vegetated habitats.

the other two-way interactions or the effect of season were significant (ANOVA, Appendix A).

Of the five prey functional groups, oyster reef augmentation was greatest for resident decapods. Xanthid crabs constituted 94.0% of resident decapods collected during 0.25-m^2 excavation sampling for resident invertebrates, 99.9% of which resided within reef habitat. Decapod shrimp comprised 4.5% of resident decapods, 92.6% of which were on reefs. Of the remaining 1.5% of resident decapods, which consisted of nonxanthid crabs, 79.8% were found within reef habitat. There was an interaction between habitat and reef presence on the density of resident decapods (Appendix A; $F_{2,84} = 5.7$, $P = 0.005$; Fig. 2d). Resident decapod density was greater on reefs than on controls within all three habitats, and densities on controls did not differ among the three habitat settings. Mudflat reefs augmented the density of resident decapods more than either salt marsh or seagrass reefs, whereas densities were greater

on salt marsh reefs than on seagrass reefs (SNK tests, $P < 0.05$). Oyster reefs also enhanced densities of arthropods other than decapods. Amphipods comprised >95% of total amphipod, isopod, tanaid, and chironomid density captured in 15 cm diameter core samples. Densities of amphipods and associated organisms required fourth-root transformation to homogenize variances. Reef presence increased densities of amphipods and associated organisms by 344% over control sites ($F_{1,84} = 40.1$, $P < 0.0001$; Fig. 2e), whereas season ($F_{1,84} = 0.1$, $P = 0.81$) and habitat ($F_{2,84} = 0.3$, $P = 0.71$) had no effect (Appendix A).

Habitat setting was an important determinant of cluster mass, which is an indirect measure of the relative habitat complexity of oyster reefs. Cluster mass (mean ± SE) ranged from 14.1 ± 0.9 kg on mudflat reefs to 6.4 ± 1.6 kg on salt marsh reefs and 5.0 ± 1.6 kg on seagrass reefs. Cluster mass of mudflat reefs was greater than that of seagrass or salt marsh reefs (SNK tests,
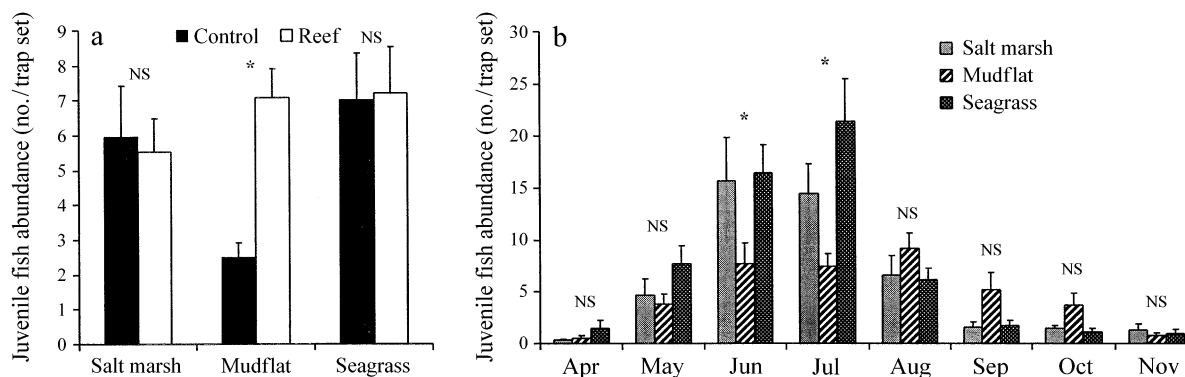
FIG. 3. Trap sampling was conducted monthly for juvenile fish from April to November in 1998 and 1999 on reefs and controls in each of three habitats in Middle Marsh, North Carolina. All values are means + SE. (a) The two-way interaction between habitat and reef presence on the total abundance of juvenile fish ($n = 64$ reef or control sampling events conducted with trap sets in each habitat setting). (b) The two-way interaction between month and habitat on total abundance of juvenile fish ($n = 16$ reef and control sampling events conducted with trap sets in each habitat setting during each sampling month). Significance levels (*$P < 0.05$; NS, $P > 0.05$) presented above bars are from SNK post hoc tests conducted to explore the cause of each significant interaction.

$P < 0.05$ for both comparisons; $F_{2,21} = 11.9$, $P = 0.0003$; Fig. 2f), but cluster mass of reefs within vegetated habitats did not differ from each other.

Juvenile fish

The effect of oyster reefs on juvenile fish abundances varied among the three habitats. Juvenile pinfish (*Lagodon rhomboides*), pigfish (*Orthopristis chrysoptera*), killifish (*Fundulus* spp.), oyster toadfish (*Opsanus tau*), spot (*Leiostomus xanthurus*), gray snapper (*Lutjanus griseus*), spottail pinfish (*Diplodus holbrooki*), flounder (*Paralichthys* spp.), and gag grouper (*Mycteroperca microlepis*) collectively accounted for >95% of the total catch. There was a significant two-way interaction between habitat and reef presence (ANOVA, $F_{2,336} = 9.2$, $P = 0.0001$; Appendix B; Fig. 3a). Reef presence increased the abundance of juvenile fish over control abundances only within the mudflat habitat. Abundances of juvenile fish on reefs did not differ among habitats, but seagrass and salt marsh controls had significantly greater abundances of juvenile fish than did mudflat controls.

ANOVA of juvenile fish abundance also revealed a significant two-way interaction between month and habitat ($F_{14,336} = 3.2$, $P < 0.0001$; Appendix B; Fig. 3b). Juvenile fish abundance was greater in the seagrass than in the mudflat habitat in July, but did not differ during the other seven sampling months. In addition, juvenile fish abundance in the salt marsh habitat did not differ from the other two habitats during any of the eight sampling months. Juvenile fish abundances peaked from June to July in both of the vegetated habitats and between June and August in the mudflat habitat.

Piscivorous fish

In contrast to the results for prey resources and juvenile fish, total abundance of piscivorous fish was not augmented by oyster reefs. Twenty-two species of piscivorous fish were captured with gill nets, and the seven most common (ordered from most to least abundant) species were gulf flounder (*Paralichthys albigutta*), bluefish (*Pomatomus saltatrix*), Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*), red drum (*Sciaenops ocellatus*), speckled trout (*Cynoscion nebulosus*), blacktip sharks (*Carcharhinus limbatus*), and southern flounder (*P. lethostigma*). Piscivorous fish abundances were greater during the night than during the day, whereas all other piscivorous fish abundance patterns (i.e., reef and habitat effects) were consistent between day and night sampling (Grabowski 2002). The only significant two-way interaction was between habitat setting and reef presence ($F_{2,240} = 4.2$, $P = 0.02$; Appendix C; Fig. 4a). Piscivorous fish were more abundant on controls than on reefs within the mudflat habitat (SNK test, $P < 0.05$), but did not differ with reef presence within salt marsh and seagrass habitats. Differences in abundances of piscivorous fish between mudflat reefs and controls were due to sharks and bluefish, which were common on mudflat controls but did not frequent mudflat reefs. Piscivorous fish abundance on controls did not differ among habitats, whereas the abundance of piscivorous fish on reefs was greater within the seagrass habitat than on reefs located in salt marsh or mudflat habitats. Bluefish, flounder, sharpnose sharks, red drum, and speckled trout were all more common on seagrass reefs than on reefs in the other habitats. Finally, piscivorous fish were more abundant in July than in all other months ($F_{7,240} = 3.5$, $P = 0.002$; Appendix C; Fig. 4b). Abundance of piscivorous fish was also greater in September than in November, but abundances of piscivorous fish in all remaining months did not differ from each other or from September or November.
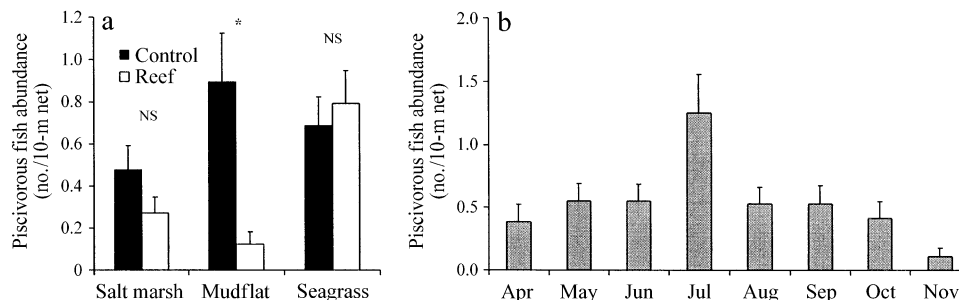
FIG. 4.   Gill net sampling for piscivorous fish was conducted monthly from April to November in 1998 and 1999 on reefs and controls in each of three habitats in Middle Marsh, North Carolina. Values are means + SE. (a) The two-way interaction of habitat and reef presence on total abundance of piscivorous fish ($n = 48$). Significance levels (*$P < 0.05$; NS, $P > 0.05$) presented above bars are from SNK post hoc tests conducted to explore the cause of the significant reef × habitat interaction. (b) The effect of month on total abundance of piscivorous fish ($n = 36$).

DISCUSSION

The context dependency of trophic interactions and habitat quality are increasingly recognized by ecologists. Yet coupling habitat heterogeneity and food web interactions poses a serious challenge to empirical and theoretical ecologists. In our study, oyster reef restoration was conducted to explore how the habitat setting in which an oyster reef is located influences community structure and consequently affects the provision of ecosystem goods and services. The habitat setting of an oyster reef impacts both resource availability and predator communities, as well as how these factors interact to mediate secondary production (i.e., juvenile fish abundance).

Oyster reef habitats are recognized for maintaining high densities of resident polychaetes, mollusks, and crustaceans (Arve 1960, MacKenzie 1979, Zimmerman et al. 2000, Lenihan et al. 2001). While restored oyster reefs in this study augmented the density of all five of the major functional groups of resident invertebrates, the habitat in which a reef is restored further influenced both bivalve and resident decapod densities. Increased bivalve and decapod densities on mudflat reefs may be due to the direct and indirect effects of higher current velocities in this habitat, as increased water velocity in oyster reef communities has been shown to enhance bivalve survivorship (S. Powers and J. H. Grabowski, *unpublished data*). Higher water flow could benefit bivalves and resident decapods directly by augmenting settlement rates or indirectly via decreasing predator detection and consumption of bivalves due to increasing dissipation of bivalve scent plumes (Zimmer-Faust and Tamburri 1994). Increased velocity rates on mudflats also may indirectly benefit bivalves and resident decapods by augmenting oyster growth from enhanced food delivery (Lenihan 1999), which increases structural complexity and refuge availability within the reef. Mudflat reefs contained significantly more cluster shell than reefs in either of the other two habitats, suggesting that oyster growth and survivorship is greatest on mudflats. Independent of flow velocity and reef structure,

mudflat reefs are isolated from vegetated habitats that are rich in blue crab predators, so that greater bivalve and resident decapod densities within mudflat reefs may be a consequence of reduced access by blue crabs to these reefs (Micheli and Peterson 1999). Thus, whether an oyster reef is located in a mudflat or next to salt marsh and/or seagrass habitat influences the communities associated with reef habitat.

Lenihan et al. (2001) found that subtidal oyster reefs in North Carolina are rich in invertebrate prey and serve as important foraging grounds for several recreationally and commercially harvested species of juvenile and adult fish. While our study found that intertidal oyster reefs did not augment piscivorous fish abundances in any of three habitats, a number of the important finfish species associated with oyster reefs (e.g., speckled trout, gag grouper, and red drum) have experienced stock declines because of overharvesting and degradation or loss of spawning and nursery habitat (Swingle et al. 1984, National Marine Fisheries Service 1998). Individual abundances of each of these three species (in addition to flounder, bluefish, and sharpnose sharks) on seagrass reefs were equal to or greater than the other two reef types or seagrass controls, suggesting that oyster reefs located near seagrass beds might be important habitat for all of these species.

The size of our restored reefs could have limited our ability to detect whether highly mobile predator fish species utilize oyster reefs. Although Lenihan et al. (2001) documented that subtidal reefs augment adult fish abundances using moderately sized (~20–30 m²) experimental reefs, they constructed more (~100) reefs at their study sites in the Neuse River than we constructed in this study (H. S. Lenihan, *personal communication*). Determining whether intertidal oyster reefs influence adult predatory fish abundances may require restoring much larger reefs or more reef habitat (i.e., networks of small reefs), and should include consideration of how these factors affect the functional response of predatory fishes. It will also be difficult to assess more generally if these species are limited by

reef habitat until restoration projects are conducted on much larger scales (e.g., basin-wide manipulations).

Polychaetes, bivalves, and resident decapods collectively account for >90% of the diet of juvenile fish within temperate estuaries (Grabowski 2002). Although oyster reefs augmented abundances of most of these prey items in all three habitats, juvenile fish abundances increased only in mudflat reefs. The lack of a response among juvenile fish to increased prey resources in either of the vegetated habitats suggests that bottom-up control may not be driving community dynamics in this system. However, because mudflat reefs increased bivalve and resident decapod densities relative to reefs in vegetated areas, it is also possible that these functional groups are an important component of bottom-up control. In addition to augmenting prey resources, the increased structural complexity of mudflat oyster reefs relative to vegetated reefs may contribute to enhanced abundances of juvenile fish observed in the mudflat habitat by providing greater refuge from predators. Alternatively, oyster reefs may be functionally redundant to existing seagrass beds and salt marshes as habitat for juvenile fish when located adjacent to them, because these vegetated habitats also offer greater prey densities and refuge availability than is provided by mudflat habitat without oyster reefs (Summerson and Peterson 1984, Irlandi and Crawford 1997, Rozas and Minello 1997).

Mudflat reefs decreased the abundance of piscivorous fish relative to mudflat control sites, indicating that release from top-down control may also be an important determinant of juvenile fish abundances and food web dynamics in this system. By providing critical foraging and refuge habitat for juvenile fish in an otherwise unstructured environment, mudflat reefs may serve as nursery habitat for juvenile fish, a function that traditionally has been attributed only to seagrass beds and salt marshes (Thayer et al. 1978, Thayer et al. 1982). Restoring oyster reefs on mudflats could increase the amount of nursery habitat for juvenile fish, and as a result, increase secondary productivity of the estuary. However, if the amount of mud bottom habitat limits the foraging efficiency of juvenile sharks and bluefish, mudflat reefs could simultaneously decrease production of these piscivorous species.

Resident epifauna and infauna responded most dramatically to the presence of oyster reef habitat. For instance, the reef effect was highly significant and explained a large proportion of the variance for all five prey groups (Appendix A). Only bivalves responded more strongly to the interaction between reefs and landscape. Resident decapod densities on reefs regardless of habitat type were far greater than control densities, which is why the reef effect explains the vast majority of the variation in this analysis. Yet part of the reason the amount of variance in resident decapod abundances explained by habitat is relatively small is simply because the presence of a reef has such a dramatic effect on their abundances that any other factor will be dwarfed. Salt marsh and mudflat reefs increased resident decapod densities by 50% and 100% over sea grass reef densities. We feel these proportional increases are biologically significant, and thus support our claim that where a reef is restored matters, particularly when taken in context with the rest of the analyses. In addition to influencing bivalve densities, the habitat × reef interaction explained a substantial proportion of the variance in juvenile fish and piscivorous fish abundances (Appendices A, B, and C). Oyster reefs generally increase prey resources, but the effect of habitat setting on oyster reef community structure is important, especially when considering prey resources, juvenile fish, and adult fish collectively.

Our results suggest that colonization of oyster reefs occurs rapidly because the interaction between season/month and reef was never significant. Previous studies of restored oyster reefs have also documented rapid response to created reefs (Coen et al. 1999, Lenihan et al. 2001, Peterson et al. 2003). Yet longer term studies of oyster reef succession should be conducted to assess if restored oyster reef functioning and delivery of ecosystem goods and services is consistent through time. Differences among prey communities within mudflat reefs vs. the other two reef habitats could be due to the faster rates at which oysters are growing if resident prey densities scale with oyster reef growth. If reefs in vegetated habitats compensate for initially slower growth rates and eventually achieve levels of complexity equivalent to mudflat reefs, differences among reef communities in the three habitats could decrease over longer time scales. However, revisiting our experimental reefs in 2002 determined that mudflat reefs still contain substantially more cluster shell than reefs in either of the other two habitats (Grabowski, *unpublished data*). Comparison of restored reef communities with those of natural reefs would enhance our understanding of the timing of reef colonization. Unfortunately, natural reefs have been severely degraded by oyster harvesting efforts throughout the southeastern United States.

In balancing the trade-off between predator risk and resource availability, organisms will often avoid habitats rich in resources that are also rich in predators (Sih 1980, Abrams 1982, Werner et al. 1983). Yet previous investigations have illustrated the importance of understanding how animal behavior and mobility influence patterns of prey mortality (Underwood and Denley 1984, Peterson 1991, Micheli 1997). Isolation of a reef from vegetated habitats may afford use by more mobile intermediate predators such as juvenile fish, but remain inaccessible to others that require vegetated corridors to move between habitats (i.e., blue crabs; Micheli and Peterson 1999). Collectively, Micheli and Peterson (1999) and this study suggest that animal mobility is a key determinant in whether intermediate predators will traverse high-risk, resource-

poor habitats to access relatively isolated habitat patches rich in prey resources. Therefore, organism mobility combined with the habitat setting of a particular habitat can strongly influence the value of that habitat as foraging grounds or refuge.

Oyster reefs are an important component of estuaries that are rich in resident prey as well as of potential importance as juvenile and adult fish habitat. Given that habitat restoration efforts are being implemented faster than the conceptual foundation for the field is being developed (Allen et al. 1997), studies that address how restoration influences ecological interactions and ecosystem functioning are critical. Restoration of oyster reefs is justified by ancillary benefits to fisheries, but our results show that the magnitude and even the existence of these benefits are highly dependent on the habitat in which the restoration occurs. Further investigations should consider how habitat scale processes influence variation in species interactions and their consequences for our general understanding of community structure. Such studies will continue to increase our conceptual understanding of the factors that mediate community structure within ecosystems, which subsequently will increase our ability to model and manage these systems (Polis et al. 1997).

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APPENDIX A

Results from three-way ANOVAs comparing the effects of season, habitat setting, and reef presence on the density/biomass of five resident prey categories are available in ESA's Electronic Data Archive: *Ecological Archives* E086-102-A1.

APPENDIX B

Results from a three-way ANOVA testing the effects of season, habitat setting, and reef presence on juvenile fish abundance are available in ESA's Electronic Data Archive: *Ecological Archives* E086-102-A2.

APPENDIX C

Results from a three-way ANOVA comparing the effects of season, habitat setting, and reef presence on piscivorous fish abundance are available in ESA's Electronic Data Archive: *Ecological Archives* E086-102-A3.