

HABITAT COMPLEXITY DISRUPTS PREDATOR–PREY INTERACTIONS BUT NOT THE TROPHIC CASCADE ON OYSTER REEFS

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Abstract. Despite recognition of the significance of both food web interactions and habitat complexity in community dynamics, current ecological theory rarely couples these two processes. Experimental manipulations of the abundance of the two predators in an oyster-reef trophic cascade, and the structural complexity provided by reefs of living oysters, demonstrated that enhanced habitat complexity weakened the strengths of trophic interactions. The system of tri-trophic interactions included oyster toadfish (*Opsanus tau*) as the top predator that consumed the mud crab (*Panopeus herbstii*), which preys upon juvenile oysters (*Crassostrea virginica*). On reefs of low complexity, toadfish controlled mud crab abundances and indirectly determined the level of mortality of juvenile oysters. The indirect effects of toadfish on oysters emerged through their influence on how intensely mud crabs preyed on oysters. Augmentation of habitat complexity by substituting vertically oriented, living oysters for the flat shells of dead oysters disrupted both of the direct trophic linkages but did not alter the magnitude of the indirect effect of toadfish on juvenile oysters. This paradox can be understood by partitioning the mechanisms by which toadfish influence mud crabs and ultimately juvenile oysters. Trait-mediated indirect interactions (TMIs; i.e., predator-avoidance behavior in mud crabs) accounted for 95.6–98.2% of toadfish indirect benefits to oyster survival and, consequently, were a much greater contributor than density-mediated indirect interactions (DMIs; i.e., the reduction in crab abundance by toadfish). Avoidance behavior was unaffected by modification in habitat complexity. Complex reefs increased total oyster survival because added habitat complexity reduced mud crab predation on oysters. Additionally, the magnitude of this effect was much greater than the increase in oyster mortality as a result of complex reefs disrupting toadfish predation on mud crabs. This experimental demonstration of how habitat complexity modifies trophic interactions in a temperate reef community has fundamental implications for our understanding of species interaction webs and community structure. The influence of habitat complexity on the strength of a trophic cascade generally may depend upon whether physical complexity provides actual and perceived refuges for component predator–prey pairs.

Key words: density-mediated indirect interactions (DMIs); habitat complexity; indirect effects; mud crabs; oysters; predator-avoidance behavior; predator–prey dynamics; toadfish; trait-mediated indirect interactions (TMIs); trophic cascades.

INTRODUCTION

While trophic cascades have been documented in a wide diversity of aquatic and terrestrial systems (reviewed in Pace et al. 1999), the relative importance of top-down control within wet vs. dry food webs continues to be debated fervently. Evidence of strong top-down control in marine (Estes and Palmisano 1974) and freshwater (Carpenter et al. 1985, Power et al. 1985, Brett and Goldman 1996) communities has encouraged several ecologists to conclude that trophic cascades occur predominately in aquatic systems with low species diversity (Strong 1992, Polis et al. 2000). It has also been posited that aspects of terrestrial systems such as more reticulated food webs, primary pro-

ducers with longer life spans, and greater plant defenses tend to attenuate the strength of trophic cascades in terrestrial systems (Strong 1992, Polis et al. 2000, Shurin et al. 2002, Duffy 2002; but see Schmitz 1998). However, these particular attributes have complicated empirical investigations of top-down control within terrestrial food webs (Strong 1992, Holt 2000, Polis et al. 2000, Power 2000, Duffy 2002). Recent meta-analyses that reviewed the relative strength of trophic cascades initially reached some conflicting conclusions (Schmitz et al. 2000, Halaj and Wise 2001), but have begun to resolve this issue (Shurin et al. 2002). Although predators can have strong indirect effects on species composition and producer condition within terrestrial communities (Schmitz et al. 2000), evidence of top-down control on total plant biomass is limited in comparison to aquatic systems (Halaj and Wise 2001, Shurin et al. 2002). Yet the paucity of empirical manipulations of vertebrate predators in terrestrial systems is still a confounding factor in our understanding of this apparent

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contrast between terrestrial and aquatic systems (Duffy 2002).

Predators can affect prey populations directly through reducing prey abundance or biomass (e.g., Hairston et al. 1960, Paine 1966, Connell 1972), or indirectly through altering how a prey species interacts with its competitor (Paine 1966, Hughes 1994, Werner and Anholt 1996) or its own prey (Carpenter et al. 1985, Power et al. 1985, Ambrose 1986). In addition to these density-mediated (direct and indirect) effects where one species influences the abundance or biomass of one or several other species, a species can also mediate trophic interactions through behavioral, chemical, and environmental pathways (Wootton 1993, Menge 1995). These trait-mediated indirect interactions (TMIIs) can modify trophic interactions with important implications for community structure. For example, an organism that changes a predator's foraging behavior can indirectly affect several prey species by altering their susceptibility to predation (Schmitt 1987, Wootton 1993). Conversely, a predator or competitor that alters prey behavior may influence its susceptibility to other predators (Morin 1995, Crowder et al. 1997). Palatable species often are located near chemically defended organisms because these defenses deter predators from foraging in the general vicinity (e.g., Hay 1986, Pfister and Hay 1988, Stachowicz and Hay 1999). Organisms also can influence a predator's ability to capture prey by modifying habitat complexity (Estes and Palmisano 1974, Werner et al. 1983, Summerson and Peterson 1984, Wootton 1993, Schriver et al. 1995).

In marine and freshwater aquatic systems, the relative importance of cascading top predator effects for community dynamics has been investigated thoroughly. Menge's (1995) review of 23 food webs in rocky intertidal systems found that indirect effects explain ~40% of the change in community structure when manipulating biotic and abiotic factors, and that keystone predation was the most common type of indirect effect within these food webs. However, Menge (1995) focused primarily on density-mediated indirect interactions (DMIIs) because of the paucity of studies addressing whether TMIIs are also important for community structure. Having demonstrated that TMIIs can influence community structure, ecologists must now grapple with how physical and biological factors affect the relative importance of TMIIs vs. DMIIs more broadly (Schmitz 1998, Werner and Peacor 2003).

Strong top-down control within complex habitats such as kelp forests and coral reefs can cause dramatic habitat modifications and subsequent shifts in community composition (Estes and Palmisano 1974, Hughes 1994). Removal of top predators has demonstrated how physical complexity created by these biogenic habitats is integral for the communities associated with them. Habitat refuge, a common feature among complex habitats, is recognized as an important component of food web dynamics (Pace et al. 1999).

Several previous investigations have demonstrated that habitat complexity can reduce predator efficiency and influence community structure (Littler et al. 1989, Diehl 1992, Schriver et al. 1995, Beukers and Jones 1997). Yet whether habitat complexity strengthens or weakens top predator effects within trophic cascades remains largely untested empirically.

Refuge availability also structures communities within shallow estuarine and marine habitats. Sea grass beds, salt marshes, and oyster reefs maintain high densities of infaunal organisms in part because habitat complexity provides refuge from predation (Menge and Lubchenco 1981, Summerson and Peterson 1984). Eastern oysters, *Crassostrea virginica*, grow collectively and form bars or reefs that provide an important habitat along the east coast of the United States within temperate estuaries and are inhabited by a dense and diverse assemblage of fishes, crustaceans, polychaetes, and mollusks (Wells 1961, Coen et al. 1999, Lenihan et al. 2001, Grabowski 2002). Xanthid crabs such as the mud crab, *Panopeus herbstii*, are an important predator of juvenile oysters (Menzel and Nichy 1958, Meyer 1994), whereas oyster toadfish, *Opsanus tau*, forage primarily on mud crabs (McDermott and Flower 1952, Schwartz and Dutcher 1963, Wilson et al. 1982). Previous studies of toadfish–mud crab–bivalve interactions have been motivated almost entirely by economics in order to facilitate biological control of intermediate predators on juvenile oysters and the hard clam *Mercenaria mercenaria* (Gibbons and Castagna 1985, Bisker et al. 1989, Abbe and Breitburg 1992). While both of the earlier two culture studies documented that toadfish increased survival of the hard clam, Abbe and Breitburg (1992) found no cascading effects of toadfish presence on mud crab and oyster mortality.

I experimentally manipulated habitat complexity and toadfish presence to determine their effects on crab and oyster mortality and to address whether habitat complexity attenuates or enhances cascading interactions among these predators and their prey. I hypothesized that toadfish would indirectly benefit oysters by reducing mud crab densities. I also predicted that toadfish would forage less effectively on mud crabs residing within complex reefs because increased habitat complexity enables crabs to escape from predation. Finally, I posited that habitat complexity would disrupt this trophic cascade by releasing mud crabs from toadfish predation to forage on juvenile oysters. I observed the relative proportion of visible crabs in the presence and absence of toadfish to determine if toadfish induce predator-avoidance behavior and indirectly benefit juvenile oysters by reducing mud crab foraging on oysters. An understanding of how refuge produced by habitat complexity affects predator–prey components of food webs and ultimately cascading effects across multiple trophic levels could advance conceptual models of food web interactions. Complex habitats that are valued for the variety of unique ecosystem goods and

services they provide have been widely reduced and degraded by anthropogenic disturbances (Lenihan et al. 2001). Therefore, this research also has implications for management strategies that rely on the predictability of these models.

METHODS

Experiments were conducted at the University of North Carolina, Institute of Marine Sciences (UNC-IMS) laboratory in Morehead City, North Carolina between July and October of 1997. To test the effects of fish presence and habitat complexity on crab mortality as well as fish presence, crab presence, and habitat complexity on oyster mortality, I submerged eight cylindrical, plastic pools (1.7 m wide \times 0.3 m tall) within a concrete settling tank (6 \times 9 \times 1.2 m). Unfiltered seawater from Bogue Sound, North Carolina, was pumped (0.27–0.29 L/s) into the concrete tank continuously during the experiment, maintaining a constant depth of 1.2 m. Each individual pool was enclosed with a 6-mm mesh plastic fence extending from the top of the pool to 20 cm above the water surface, and was covered with 10-mm mesh bird-netting to prevent fish and crabs from escaping.

I conducted a 2 \times 2 \times 2 factorial design with two levels of toadfish (present or absent), mud crabs (present or absent), and habitat complexity (low or high), requiring eight pools to provide one set of all possible combinations. I constructed \sim 2-m² reefs within each pool, depositing 75.7 L of unaggregated oyster shell in each of four pools (simple reefs), and 56.8 L of oyster clusters on top of 18.9 L of unaggregated shell in each of the other four pools (more complex reefs). Oyster clusters extended 10–30 cm upward from the unaggregated shell, and created high vertical relief in contrast to the thin veneer of shell (<5 cm vertical relief) that comprised the simple reefs. Using super glue gel, I attached 10 juvenile oysters (13.5 \pm 0.1 mm shell height, mean \pm 1 SE) to the concave portion of dead oyster shells to mimic juvenile oysters that had settled within the past three months (Ortega and Sutherland 1992). Four oyster-containing shells (for a total of 40 juvenile oysters) were deposited within each of the eight pools and positioned vertically upright \sim 10 cm from the edge of the pool with juvenile oysters facing inward. Forty adult mud crabs (21.5 \pm 0.9 mm carapace width, [CW]) were released within each of two pools containing simple reefs and two with more complex reefs. Crab density (\sim 20 crabs per m²) and mean size corresponded to those that have been observed on oyster reefs locally (*unpublished data*) as well as regionally (10–49 crabs/m², 19.4 mm CW; McDonald 1982). I then added one adult toadfish (147 \pm 14.3 mm standard length) to one pool of each reef complexity level with only juvenile oysters and to one of each type containing both mud crabs and juvenile oysters.

Space limitations within the tank prohibited replication of treatments in any given experimental trial; therefore, I conducted five replicate 6-d trials and treated each experimental trial as a block. After each 6-d experimental trial was completed, living, dead, and missing mud crabs and juvenile oyster mortality were quantified in each pool by sieving all shell material in order to retrieve animals. Missing oysters and crabs rarely occurred in pools without predators, and remnants of dead organisms were retrieved in pools with predators. I then released surviving animals from the previous experimental run, randomly reassigned treatments, and reconstructed pool environments with recently collected organisms. In the absence of toadfish, oyster mortality in pools with mud crabs present was 96%, so that prey depletion inhibited determination of mud crab foraging rates in the absence of toadfish. For all other treatments, prey depletion was <50%. Therefore, I ran a complimentary assay with only mud crabs and quantified oyster mortality after 24 h. For this assay, five replicate reefs of each habitat complexity were constructed within separate pools and organisms (crabs and oysters in each enclosure) were added using methods identical to the 6-d experimental runs. Consequently, oyster mortality levels for all other treatments were divided by six in order to standardize (to number per day) all oyster mortality results for statistical analysis. Laboratory and field results (Grabowski 2002) support the assumption that mortality rates during the first 24 hours are consistent with rates during subsequent 24-h intervals.

Mud crabs and toadfish were collected on oyster reefs in Back Sound, Carteret County, North Carolina, and were stored for \sim 3–4 days in separate upwellers and offered crushed ribbed mussels (*Geukensia demissa*) prior to initiation of each experimental run. To provide an alternative food source for all predators in the experiment and avoid starvation-induced predator effects, \sim 100.0 g of crushed ribbed mussels were deposited in each pool at the beginning of each experimental run. Several additional small prey organisms entered the individual enclosures via the UNC-IMS water pumping system (Martin et al. 1989; *personal observation*).

To test whether toadfish influence mud crab behavior, I observed mud crab presence on the shell surface while conducting the fifth experimental run of the experiment. In order to compare night to day observations, I attached 0.8 mm phosphorescent stars (Star Glows, Illuminations, Derry, New Hampshire) onto the carapace of all mud crabs used in the fifth experimental run. Before beginning this final run, I conducted laboratory assays and determined that mud crab feeding rates and survivorship were unaffected by the addition of stars (Grabowski 2002). During the final experimental run, I quantified the numbers of visible mud crabs within each of the four pools containing crabs using a 50-cm fluorescent light held directly over the

pool for 15 s and repeated this procedure every 10 min for 1 h during each day and each night for all six 24-h intervals of the fifth experimental run. All seven observations within each pool from a 1-h sampling period were averaged to obtain an estimate of the number of crabs visible in each pool during the observational hour. I standardized crab observations by dividing the total number of observed crabs by the average crab density within each particular pool to account for differences in mud crab mortality during the experiment. Therefore, estimates of the numbers of visible crabs reflect differences in crab behavior, not toadfish predation and mud crab mortality.

Statistical analyses

Cochran's test for homogeneity of variance was conducted on all main effects in each analysis (Underwood 1981). Oyster mortality data required arcsin transformation to remove heterogeneity (geometric means are reported in the *Results*). I performed a three-way blocked ANOVA on percentage crab mortality with habitat complexity, toadfish presence, and experimental run (block) as fixed factors. I conducted a four-way blocked ANOVA on juvenile oyster mortality with habitat complexity, toadfish presence, mud crab presence, and experimental run (block) as fixed factors. For each of these two ANOVAs, block effects that were not significant at $P > 0.25$ were removed from the analysis and data were reanalyzed (Underwood 1981). I conducted a two-way repeated-measures ANOVA on crab visibility for toadfish presence and habitat complexity with experimental day as the repeated measure. Because the proportion of visible crabs during the day and in the evening did not differ substantially after the initial 24 hours of the experimental run, time of day was not included in this analysis. Student-Newman-Keuls (SNK) post hoc tests were conducted for all significant interaction terms. The SNK test was selected because I conducted a balanced experiment with a priori predictions and fixed factors (Day and Quinn 1989).

RESULTS

There was a trend of lower crab mortality in the presence of toadfish during the middle three experimental runs (block \times toadfish interaction: $F_{1,4} = 5.7$, $P = 0.06$; Appendix A). Mud crab mortality varied with habitat complexity and fish presence (habitat complexity \times toadfish interaction: $F_{1,4} = 9.5$, $P = 0.04$). Toadfish significantly increased mud crab mortality on simple reefs, but did not affect mud crab mortality on more complex reefs (SNK test: $P < 0.05$; Fig. 1). Enhanced complexity reduced mud crab mortality in the presence of toadfish, while habitat complexity did not affect crab mortality in the absence of toadfish. Toadfish increased mud crab mortality on average from 4.0% to 11.5% on simple reefs, whereas mud crab mor-

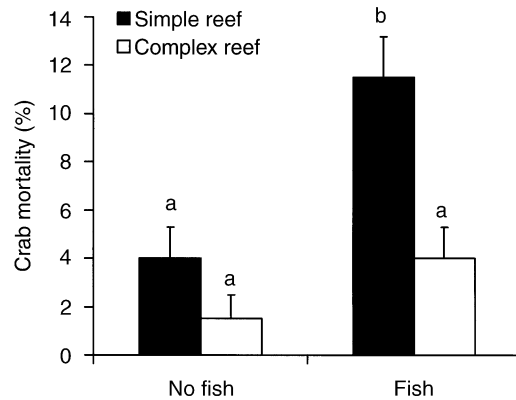


FIG. 1. The effect of toadfish presence and habitat complexity on percentage mud crab mortality. Percentage crab mortality is the mean percentage of crabs per experimental run from the original 40 crabs that did not survive the experimental run. SNK post hoc results are represented with letters above the error bars (bars with different letters above them are significantly different at $P < 0.05$). Error bars indicate $+1$ SE.

tality in the absence of toadfish ranged from 1.5% (more complex reefs) to 4.0% (simple reefs).

Oyster mortality did not differ significantly among experimental runs ($P > 0.25$ for block), so data were reanalyzed without the blocking factor (Underwood 1981). Oyster mortality varied with mud crab presence, toadfish presence, and structural complexity (three-way interaction: $F_{1,32} = 5.9$, $P = 0.02$; Appendix B). When mud crabs were absent, average oyster mortality was 0.5% per day and did not vary with habitat complexity or toadfish presence (SNK test: $P > 0.05$; Fig. 2). Conversely, mud crabs increased average oyster mortality per day from 0.5% to 59.0% without toadfish vs. 7.7% with toadfish present. Toadfish significantly decreased oyster mortality in the presence of mud crabs from 72.5% to 9.7% per day on simple reefs and from 45.5% to 5.7% per day on more complex reefs. Habitat complexity reduced mud crab predation on oysters by 41.4% per day with toadfish present and 37.2% per day without.

The percentage of visible mud crabs varied with each main effect: experimental day ($F_{5,5} = 6.1$, $P = 0.001$; Appendix C), habitat complexity ($F_{1,5} = 8.5$, $P = 0.033$), and toadfish presence ($F_{1,5} = 25.1$, $P = 0.004$). Both of the interaction terms were not significant (i.e., experimental day \times toadfish, $F_{5,5} = 0.1$, $P = 0.99$; experimental day \times habitat complexity $F_{5,5} = 0.6$, $P = 0.72$). A greater proportion of crabs were visible during the first experimental day than the following five days (Fig. 3a). Habitat complexity increased mud crab visibility by 44.4% (Fig. 3b). Toadfish reduced the percentage of visible mud crabs by 66.9% (Fig. 3c).

Mud crab consumption rates of oysters were quantified and used to partition the indirect effects of toadfish presence (direct removal of crabs vs. predator-

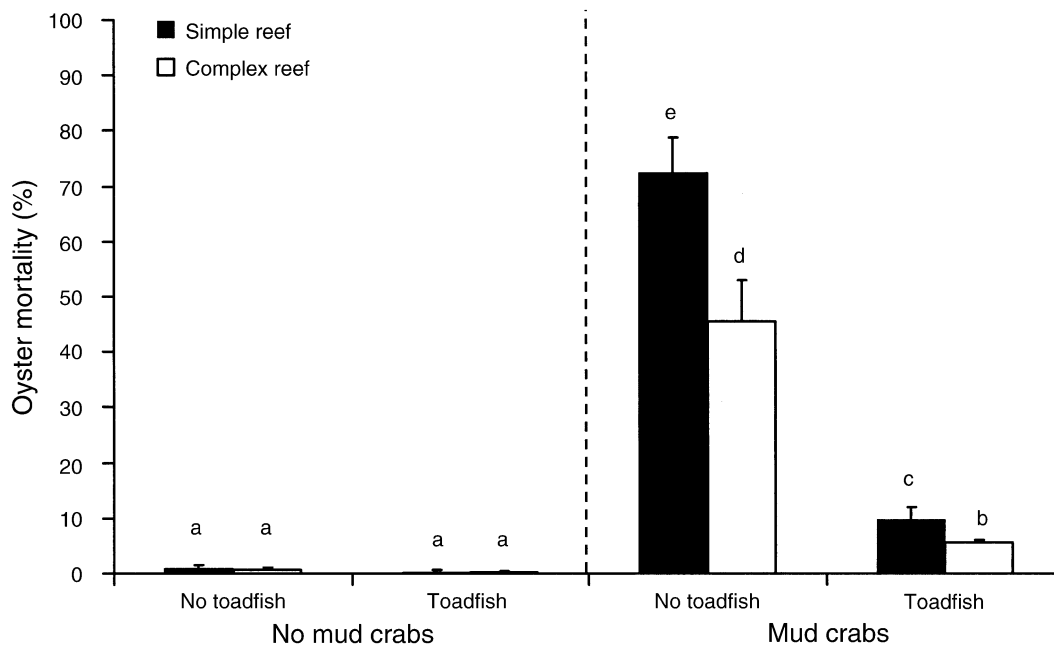


FIG. 2. The effects of mud crab presence, toadfish presence, and habitat complexity on juvenile oyster mortality. Oyster mortality was calculated by dividing the percentage of oysters consumed by 6 (the length of each experimental run) to determine the average oyster mortality per each 24-h period during an experimental run. 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 indicate $+1$ SE.

avoidance behavior) on mud crab consumption of oysters within low and more complex reefs (Table 1). Crab consumption rates of oysters were calculated by determining the average number of oysters eaten by crabs per day during each experimental run ([oyster mortality with crabs minus oyster mortality without crabs]/duration of experiment in days) and dividing it by the average number of crabs present during each particular experimental run. Toadfish presence decreased mud crab consumption of oysters by 86.5% on simple reefs and by 87.0% on more complex reefs. Toadfish effects on oysters then were partitioned between direct removal of crabs by toadfish (DMII) and predator-avoidance behavior of crabs (TMII). The effect of direct removal was estimated by determining the expected number of oysters per day that should have been released from mud crab predation as a consequence of toadfish consuming mud crabs and lowering their densities (daily rate of oysters consumed by crabs in the absence of toadfish multiplied by the average number of crabs consumed by toadfish during an experimental run). I also calculated the actual number of oysters that were released per day from mud crab predation when toadfish were present (actual release = direct removal and predator-avoidance behavior). Actual oyster release was calculated by subtracting the number of oysters consumed by mud crabs with toadfish present from the number consumed by mud crabs in the absence of toadfish. Using expected vs. actual oyster release, I quantified the proportion of oysters released from mud

crab predation as a consequence of toadfish removal of mud crabs (toadfish effect 1[DMII]: expected/actual oyster release) vs. the proportion of oysters released as a function of toadfish induced modifications in mud crab foraging behavior (toadfish effect 2[TMII]: [actual - expected]/actual). Although the effect of direct removal by toadfish is slightly greater on simple reefs where toadfish are more effective at capturing mud crabs, >95% of the reduction in mud crab foraging on oysters can be explained by toadfish modifying mud crab foraging behavior (TMII) on both reef types.

DISCUSSION

This study investigates how habitat complexity and induced modifications in prey behavior couple to influence predator-prey interactions and community structure. Habitat complexity attenuated the strength of component interactions within a trophic cascade, whereas predator-induced modifications in prey behavior reinforced this cascade (Fig. 4). Toadfish increased mud crab mortality only on simple reefs, suggesting that oysters enhance habitat complexity as they grow upright and create greater refuge availability for mud crabs (Fig. 1). Because toadfish did not affect mud crab mortality on more complex reefs, one might intuitively expect toadfish to influence juvenile oysters only within simple reefs; however, toadfish dramatically reduced mud crab removal of oysters on more complex reefs (Fig. 2). Estimation of mud crab foraging rates indicated that the decrease in mud crab abundance by toad-

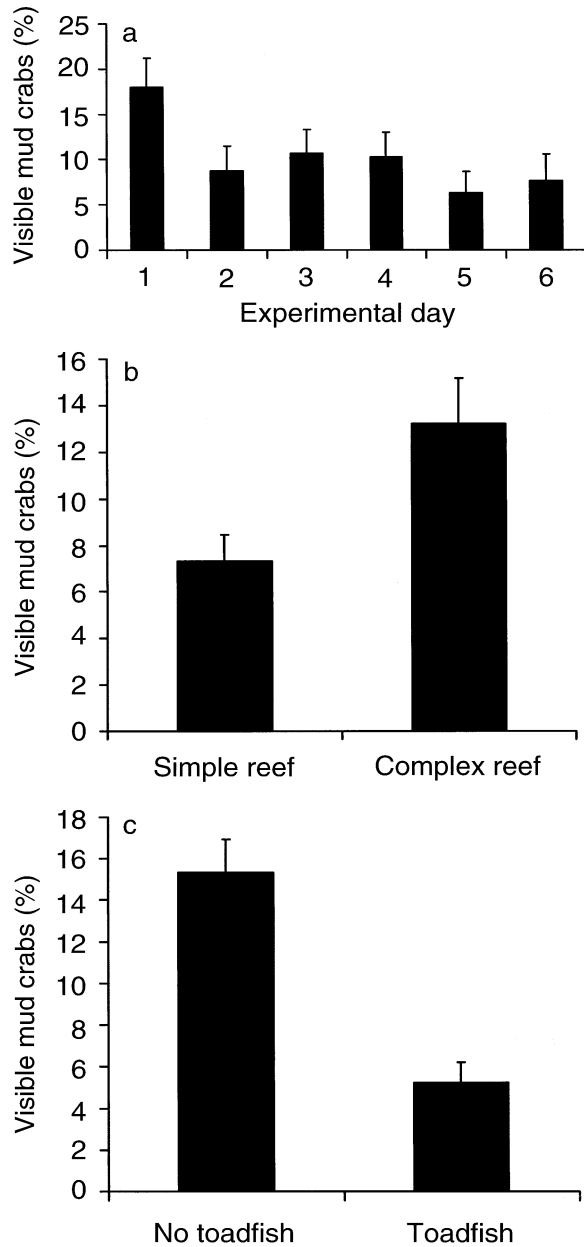


FIG. 3. The (a) percentage of visible mud crabs during each of the six experimental days, (b) effect of habitat complexity on the percentage of visible mud crabs, and (c) effect of toadfish presence on the percentage of visible mud crabs. The percentage of visible crabs was adjusted for differences in crab mortality within the observed pools. Error bars indicate +1 SE.

fish predation also could not explain the magnitude of toadfish reduction in oyster mortality on simple reefs (Table 1).

Toadfish decreased the percentage of visible mud crabs regardless of complexity level (Fig. 3c), suggesting that modifications in mud crab behavior reduces predation of oysters. Little difference between toadfish reductions in oyster mortality in simple and

more complex reefs indicated that predator-avoidance behavior did not vary with habitat complexity. Reef complexity also consistently reduced mud crab foraging on oysters independent of whether toadfish were present. The magnitude of the decrease in oyster mortality from enhancing habitat complexity as a consequence of reduced crab foraging efficiency and toadfish-induced behavioral responses was much greater than the opposing effect of increased oyster mortality from lower toadfish removal of mud crabs (DMII), explaining how habitat complexity reduced oyster mortality even with toadfish present (Fig. 2).

The initial peak in visible mud crabs across all pools suggested that crabs were still acclimating to the experimental arena during the first experimental day (Fig. 3a). Crab visibility was greatest during the first observation period, which was conducted at night six hours after releasing mud crabs within the pools. More crabs were visible in complex habitats where intact oyster reefs create vertical structure, which can reduce the ability of predators to maneuver within a reef to locate and capture prey. Thus, prey might be more mobile or hide less within complex habitats because they are either less susceptible to predation or less capable of recognizing predators. Toadfish reduced mud crab visibility in both habitats, indicating that prey were capable of detecting toadfish presence in both reef types. Because the percentage of visible mud crabs in complex habitats was fairly consistent during the six experimental days, mud crabs apparently did not respond to the reduced threat of toadfish predation in complex habitats. Strong behavioral effects on mud crab foraging rates independent of habitat type further supports the notion that mud crabs were incapable of deducing actual risk levels.

The results of my study suggest that toadfish indirectly benefit juvenile oysters by reducing mud crab predation, which is counter to the findings of Abbe and Breitburg (1992). Contrasting results may be attributable to important differences in the experimental design of these two studies. First, Abbe and Breitburg (1992) conducted their experiment in field exclosures, whereas I conducted experimental manipulations in a laboratory tank system flushed with unfiltered sea water. Manipulations of reduced species interaction webs exclude many important features of food webs, which could potentially confound the interpretation of oversimplified studies on food web dynamics (Polis and Strong 1996, Polis et al. 2000). Yet this reasoning can not fully elucidate our dramatically different results. Abbe and Breitburg (1992) deployed cages filled with dead shell cultch near oyster reefs to investigate applications of toadfish as a biocontrol for oyster culture rather than manipulate natural oyster reefs inhabited by intact communities to assess impacts of toadfish on community structure. In addition, although their cages were colonized by much larger organisms, I did observe a wide diversity of small polychaete, isopod, gastropod, and

TABLE 1. Partitioning the toadfish effects (direct removal of mud crabs vs. toadfish-induced mud crab behavioral changes) in each reef type (simple vs. complex) on the daily rates of oyster mortality induced by mud crabs (mud crab feeding rates).

Toadfish presence	Habitat complexity level	Mud crab feeding rate† (oysters·crab ⁻¹ ·d ⁻¹)	Expected oyster release‡ (oysters/d)	Actual oyster release§ (oysters/d)	Toadfish effect 1: DMII (expected/actual oyster release)	Toadfish effect 2: mudcrab behavioral Δ TMII¶ ([actual – expected]/actual oyster release)
No toadfish	low	0.74 (0.07)				
	high	0.46 (0.08)				
Toadfish	low	0.10 (0.03)	1.17 (0.47)	25.13 (2.64)	4.4% (1.6%)	95.6% (1.6%)
	high	0.06 (0.01)	0.24 (0.12)	15.93 (3.13)	1.8% (0.8%)	98.2% (0.8%)

Note: Standard errors are presented in parentheses.

† Mud crab feeding rates are the average number of oysters consumed per crab present per day during an experimental run.

‡ Expected oyster release estimates the expected decrease in the average number of oysters consumed per day by mud crabs as a function of lowered crab densities in the presence of fish. Expected oyster release is calculated by multiplying the daily rate of crab removal of oysters in the absence of fish by the reduction in crab density induced by toadfish during an experimental run.

§ Actual oyster release calculations measure the actual number of oysters per day released from mud crab predation in the presence of toadfish. Actual release is calculated by subtracting the number of oysters consumed by mud crabs with toadfish present from the number consumed by mud crabs in the absence of toadfish.

|| Toadfish effect 1: DMII (density-mediated indirect interactions). This is the percentage of toadfish indirect effects on oyster mortality explained by toadfish removal of mud crabs.

¶ Toadfish effect 2: TMII (trait-mediated indirect interactions). This is the percentage of toadfish indirect effects on oyster mortality explained by toadfish induced modifications in mud crab foraging behavior.

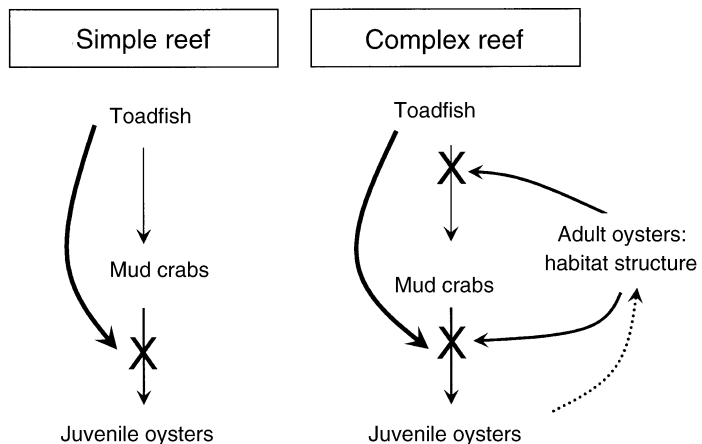
decapod prey settling and immigrating into the pools during each experimental run.

A second major difference between the two studies is that Abbe and Breitburg (1992) did not add mud crabs in their cages, instead opting to measure if toadfish affect mud crab colonization rather than mortality. Colonization by larger (>15 mm²) mud crabs during their two-week experimental runs was reduced in general, and average densities in their enclosures were very low (1987, 2.0 crabs/m²; 1988, 5.2 crabs/m²) in comparison to levels used in this study and reported in the wild (McDonald 1982; unpublished data). Lower crab abundances in their cages could also explain why they found much lower oyster mortality rates in general. Finally, they used a larger cage (2.5 cm) mesh that permitted large (100–120 mm total length) juvenile toadfish to enter several of their control cages. Smaller

toadfish may be less effective at capturing larger mud crabs, but juvenile toadfish were only slightly smaller than those used in my study. Because toadfish benefit oyster survival predominately through TMII rather than DMII, unwanted toadfish entry into control (no toadfish) cages could have suppressed mud crab foraging and masked the intended contrast between toadfish and control treatments. Determining whether the strength of the indirect mechanisms in my study are applicable to oyster-reef and other estuarine communities requires empirical studies in the field that are capable of detecting TMII in addition to DMII.

Direct and indirect biological interactions within temperate estuaries are still not well understood, and models derived from rocky intertidal systems might not be appropriate because competitive exclusion is rare within soft-sediment habitats (Peterson 1979, Wilson

FIG. 4. Diagram of direct and indirect interactions (DMIIs and TMIIIs) within oyster-reef communities. On simple reefs, toadfish reduce mud crab densities and induce greater hiding in mud crabs, thereby reducing the magnitude of mud crab predation on juvenile oysters. In more complex environments, increased habitat complexity inhibits toadfish from feeding on mud crabs. Yet toadfish-induced effects on crab behavior maintain the indirect effect of toadfish on juvenile oysters in complex habitats. Habitat complexity also reduces mud crab predation on oysters, thereby further releasing juvenile oysters.



1991). Furthermore, the predominance of generalist feeders tends to diminish the strength of trophic interactions within these habitats across multiple trophic levels (Peterson 1979). Although toadfish are not specialist feeders, they are fairly selective predators (Gudger 1910, Schwartz and Dutcher 1963, Wilson et al. 1982) in a system in which fishes, crabs, and birds historically have been grouped as predators and benthic infauna as prey (Peterson 1979, Ambrose 1984). In a review of several estuarine caging studies, Ambrose (1984) noted that exclusion of top predators (i.e., epibenthic macroinvertebrates) resulted in increased abundances of intermediate infaunal predators, and suggested that exclusion of top predators could benefit infaunal prey within soft-sediment habitats. Kneib (1988) manipulated killifish *Fundulus heteroclitus* (top predator) and grass shrimp *Palaemonetes pugio* (intermediate predator) in a factorial experiment to test for indirect effects in a Georgia salt marsh and found that killifish indirectly benefit the dwarf mud anemone *Nematostella vectensis*. However, the densities of most invertebrate prey in this system were not affected by any combination of predator treatments. He posited that entry by other intermediate predators that were not controlled for may have dampened the magnitude of predator treatment effects. More explicit detection of the strength of food web interactions within estuarine systems will benefit from investigations that couple laboratory experiments that can control for these confounding factors with field manipulations of entire communities.

Estuarine studies focused on direct predator-prey interactions may be overlooking more complex interactions that are common within terrestrial and marine systems (Martin et al. 1989, Crowder et al. 1997). Furthermore, when mortality is the only predator effect quantified, important sublethal effects such as siphon nipping, growth rate changes, and induced modifications in prey behavior might be ignored (Irlandi and Peterson 1991, Werner and Anholt 1996, Nakaoka 2000). Freshwater aquatic scientists have documented predator-induced modifications in prey behavior ranging from utilization of alternate or multiple habitats (Sih 1980, Werner et al. 1983, Krupa and Sih 1998) to increased migration rates (Peckarsky and Dodson 1980, Forrester 1994) and decreased activity levels (Werner and Anholt 1996, Krupa and Sih 1998). Predator-induced modifications in prey behavior can alter how processes such as predation and competition structure ecological communities. In this study, mud crabs responded to the presence of toadfish by reducing movement presumably to increase hiding activity. McNamara and Houston (1987, 1994) developed a general model assessing the trade-off between access to food and the threat of predation, predicting how prey organisms will choose between the relative risks of predation vs. starvation. Werner and Anholt's (1996) study on anuran community assemblage provides an empir-

ical test of this model, with the trade-off between predation and starvation moderated by activity levels. In their study, as activity level decreased in response to higher predation threats, the avoidance of predators resulted in limited food access and subsequent higher risk of starvation.

Whether community structure can be explained by a series of predictable outcomes or described as increasingly random interactions is of critical importance given that comprehending ecological systems frequently requires multifactorial analyses that rely on interpretation of complicated interaction terms. Disentangling these interactions within complex habitats requires inclusion of appropriate trait-mediated factors such as animal behavior and habitat complexity within oyster reefs to investigate the relative strength of and interactions between DMIs and TMIs. Habitat complexity disrupts predator-prey interactions across multiple levels and generally weakens trophic cascades. Conversely, induction of predator-avoidance behavior reinforces predator-prey interactions and strengthens cascading effects. Intermediate predators capable of determining the relative risk of predation could completely disrupt top-down control within complex habitats. Empirical manipulations of other predator communities and habitat complexity simultaneously will elicit a greater understanding of how habitat complexity influences the relative strength of TMIs vs. DMIs in determining food web dynamics.

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APPENDIX A

A table showing the three-way ANOVA comparing the effects of block, toadfish presence, and reef complexity (simple vs. complex) on mud crab (*Panopeus herbstii*) mortality is available in ESA's Electronic Data Archive: *Ecological Archives* E085-027-A1.

APPENDIX B

A table showing the three-way ANOVA testing the effects of toadfish presence, mud crab presence, and reef complexity (simple vs. complex) on daily mortality of stocked juvenile oysters (*Crassostrea virginica*) is available in ESA's Electronic Data Archive: *Ecological Archives* E085-027-A2.

APPENDIX C

A table showing the repeated-measures ANOVA assessing whether toadfish presence and structure complexity (simple vs. complex) influence the percentage of visible mud crabs is available in ESA's Electronic Data Archive: *Ecological Archives* E085-027-A3.