COMPLEX PREDATOR–PREY INTERACTIONS WITHIN AN ESTUARINE BENTHIC COMMUNITY[1]

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Abstract. Indirect predator–prey interactions have been suggested to be important in a variety of communities. However, we still understand little about the factors determining the relative importance of indirect and direct effects of predation or what forms indirect predator–prey interactions may take. We examined the direct effects of predation by an omnivorous grass shrimp, *Palaemonetes pugio,* and the indirect effects for prey species of interactions between this shrimp and other predators in an estuarine benthic community. Direct and indirect effects of predation were examined in the field using a combination of large- and small-scale enclosure/exclosure experiments. Specific interactions and mechanisms of effects were examined in laboratory predation studies, utilizing both two-species and multi-species systems.

Grass shrimp predation reduced the densities of a variety of benthic fauna, but the effects varied seasonally and with prey size. Interactions between grass shrimp and other predators took two forms: reduction of an infaunal predator by shrimp predation and predation on grass shrimp by fish. Both types of interactions had a mixed effect on lower trophic levels, with enhancement of certain benthic prey and no effect on other species. Interactions between grass shrimp and their fish predators resulted in changes in shrimp distribution independent of changes in shrimp abundance, creating spatial refugia for shrimp prey. The dynamics of indirect interactions in this community are strongly affected by the omnivorous nature of the major predators. Our results emphasize the general importance of omnivory in regulating predator–prey interactions and in predicting the relative importance of indirect predator effects.

Key words: benthic; benthic food webs; Chesapeake Bay; estuarine near-shore communities; field experiments; omnivory; Palaemonetes; *predation; shrimp predation on benthic fauna.*

INTRODUCTION

Complex trophic interactions are inherent in communities where consumers affect multiple species at lower trophic levels, or where the impact of a consumer upon a prey is mediated by other species. Multi-species interactions in food webs may be complex not only because of higher order interactions (Levine 1976), but also because indirect effects modify direct effects in unexpected ways (Sih et al. 1985), and indirect mechanisms producing even predicted effects are often unforeseen or easily misinterpreted (Holt 1977, 1984). The relative importance of direct vs. indirect effects in food webs is a matter of theoretical debate (Paine 1980, Patten 1982, 1983, Abrams 1984, Wiegert and Kozlowski 1984, Higoshi and Patten 1989, Pelitte 1989), but the indirect effects of predation are recognized as being of similar magnitude to direct effects in many field studies (Paine 1966, Estes and Palmisano 1974, Simenstad et al. 1978, Abrams 1984, Kerfoot and Sih 1987, Powers 1990). The mechanisms of indirect effects can involve major changes in the abundance, be-

havior, habitat utilization, distribution, and even the physiology and morphology of prey and predators (Werner et al. 1983, Hovel 1987, Mittelbach and Chesson 1987), and may affect competition among predators or prey (Levine 1976, Holt 1977, 1984, Vandermeer 1980, Pecharsky and Penton 1985, Schoener and Spiller 1987, Van Buskirk 1988). Indirect effects of predators have been variously termed "keystone predator effect" (Paine 1966), "three-trophic-level effect" (Hurlbert et al. 1972), and "cascading trophic interactions" (Carpenter et al. 1985).

This paper explores complex trophic interactions in a shallow soft-bottom community in a temperate estuary (Chesapeake Bay). We focus both upon direct and indirect effects of a small omnivorous grass shrimp, *Palaemonetes pugio,* preying on infaunal invertebrates, and on interactions between this shrimp and other omnivorous predators (killifish and sea anemones) (Fig. 1). We selected this system for study for a variety of theoretical and pragmatic reasons that allow us to investigate the fundamental importance of direct and indirect interactions in structuring natural communities.

Though they have strong similarities to marine and lotic systems, estuarine communities appear to differ from many other ecosystems in some fundamental aspects of food web structure, particularly maximum food
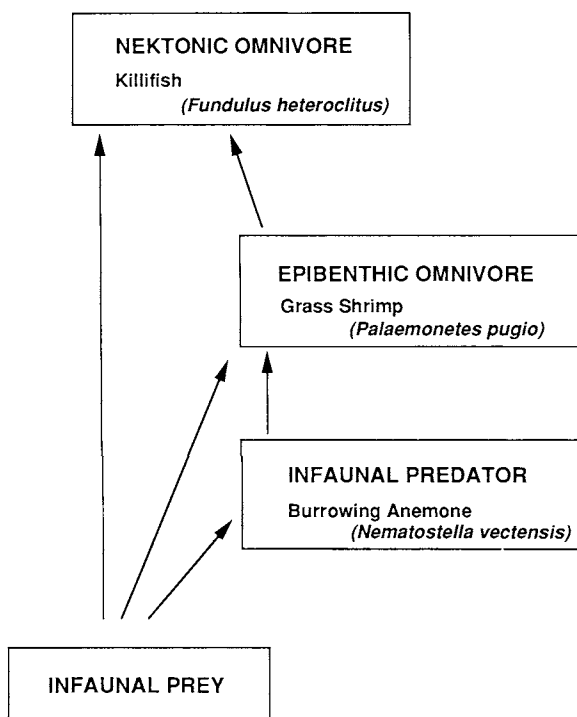
FIG. 1. Schematic diagram of the nearshore food web in the Rhode River, Chesapeake Bay, Maryland, indicating major trophic interactions examined in this study.

chain length, "loose-knitness," fraction of basal species, and degree of omnivory (Schoener 1989). In contrast to the pattern proposed for terrestrial and certain riverine systems (Hairston et al. 1960, Powers 1990), the prevalence of omnivores in marine and estuarine food webs leads to increasing predator control over lower trophic levels (Menge and Sutherland 1976, 1987, Menge et al. 1986, Schoener 1989). The prevalence of small- to medium-sized omnivores also may increase the importance of indirect interactions (Pimm and Lawton 1978, Schoener 1989). Predator–prey interactions may be particularly complex in soft-bottom marine and estuarine communities because of dominance by guilds of rather-generalized predators and the lack of a single competitively dominant prey species capable of monopolizing resources (Reise 1978, Peterson 1979, Virnstein 1980, Kneib and Stiven 1982, Levinton 1982, Ambrose 1984, Commito and Ambrose 1985, Martin et al. 1989, Hines et al. 1990). Significant omnivory and the importance of predation in controlling lower trophic levels suggests that both strong direct and indirect predation effects will be important in estuarine soft-bottom communities.

More pragmatically, the low species diversity in our study system facilitates the identification and manipulation of key species without potential artifacts from trophic grouping (Paine 1980, Schoener 1989). Grass shrimp (*Palaemonetes pugio*) are among the most abundant epibenthic decapods, and killifish (*Fundulus*

spp.) are among the most abundant fish in shallow-water areas of estuaries and salt marshes along the Atlantic and Gulf coasts of North America (Welsh 1975, Abraham 1985). Both killifish and grass shrimp are omnivores, consuming both detritus and benthic fauna (Fritz 1974, Welsh 1975, Valiela et al. 1977, Baker-Dittus 1978, Bell and Coull 1978, Morgan 1980, Nelson 1981, Weisberg et al. 1981, Weisberg and Lotrich 1982, Kneib 1985, Gibbons and Blogoslawski 1989), and both can be experimentally manipulated with relative ease (Bell and Coull 1978, Weisberg et al. 1981, Kneib 1985, 1986, Smith and Coull 1987). Moreover, killifish consume grass shrimp (Heck and Thoman 1981), which may have significant indirect consequences for the benthos. Experimental exclusion of killifish can result in the reduction of some benthic fauna (Kneib and Stiven 1982), a result attributed to enhancement of grass shrimp when killifish are absent. However, a study of killifish predation on grass shrimp in a Georgia salt marsh showed clear indirect effects for only one shrimp prey, the burrowing anemone *Nematostella vectensis* (Kneib 1988). The anemone is also a predator with potential, but unassessed, impacts on recruitment of benthic fauna.

Our experiments had three main objectives and were designed to provide a mechanistic assessment of direct and indirect effects of predation in the nearshore community typical of Chesapeake Bay. First, we conducted an array of field and laboratory experiments to test for the direct effects of predation by grass shrimp. Field enclosure experiments assayed the effect of manipulating shrimp abundance on natural assemblages of infaunal prey. Laboratory experiments were used to test for direct consumption of infauna affected in the field, including size-dependent components of prey vulnerability to grass shrimp. Second, we tested for the indirect effects on infaunal recruitment of grass shrimp limitation of a burrowing sea anemone. These tests were conducted in the field with anemone transplant experiments and in the laboratory with observations of predation upon selected infaunal species. Third, we examined the indirect effects of predation on grass shrimp by predatory killifish, both in combination with the field shrimp enclosure experiments and with laboratory and field experiments examining the behavioral responses of shrimp to fish predators, and the indirect effects of these behavioral responses on grass shrimp prey. This combined field and laboratory approach allows us to distinguish direct and indirect effects, as well as to identify the principal mechanisms responsible for complex trophic interactions.

METHODS

Study area

Field studies were conducted within the Rhode River subestuary of the Chesapeake Bay, with experimental work occurring in an embayment dominated by fine

sands (Canning House Bay). The Rhode River is a shallow, well-studied estuary along the western shore of the Chesapeake Bay in Maryland (Hines and Comtois 1985, Hines et al. 1987, Hines et al. 1990), with salinities generally ranging from 12–15 g/L in summer to 4–8 g/L during winter and water temperatures ranging from 0° to 30°C. *P. pugio* is a common epibenthic species, and the killifish *Fundulus heteroclitus* is its most abundant predator at the site.

Grass shrimp abundance

Ambient grass shrimp abundances were monitored monthly with sweep nets at a site 50 m east of the Smithsonian Environmental Research Center pier in the central Rhode River. A single sweep of constant length was made along the bottom in 0.2–0.6 m depth water with a 25 cm wide rectangular net. Since grass shrimp are primarily benthic, the area for densities was calculated as a rectangle, using net width and sweep length. Since some shrimp may avoid a net, these values were viewed as an underestimate of true shrimp density.

Direct effects of grass shrimp predation on benthos

Community effects. — To assess direct grass shrimp effects on benthic fauna, shrimp enclosure experiments were conducted during late summer (August–September 1987 and 1988), spring (April–May 1988), and early summer (June 1988). Winter experiments were not run because of low shrimp abundances and ice cover. Cages were placed in shallow subtidal areas that were covered by 5–10 cm of water at extreme low water (grass shrimp in the Rhode River are most abundant in shallow, nearshore locations).

Cages were 0.25 m² and constructed of 1.25-cm mesh galvanized hardware cloth covered with 3-mm plastic netting. Cages were pressed 10 cm into the sediment and extended 20 cm into the water column. Grass shrimp were added through a resealable slit in the top of the cage. Three treatments were initiated during each period: high shrimp densities (100 individuals/cage), shrimp exclusion (0 shrimp/cage), and uncaged control areas. Effects of varying grass shrimp densities were examined using medium shrimp-density treatments (50 shrimp/cage) during summer and fall 1988 runs and low shrimp-density treatments (10 shrimp/cage) during the summer 1988 run. Five replicates of each treatment were used in summer 1987 and seven replicates of each during all other runs.

Grass shrimp used in the cages were a mixture of sizes representing ambient densities (mean lengths ranging from 32.1 mm in May to 35.6 mm in August). All cages were left in place for 21 d and then benthic fauna within each treatment plot were sampled with two 0.008-m² cores. Cores were seived on a 0.5-mm mesh screen. Shrimp survivorship during fall 1987 was estimated from dipnet catches with 75–95% recovery

of shrimp in enclosures and no shrimp found in exclusion cages.

To examine the influence of grass shrimp in deeper areas where they are normally less abundant, enclosures were placed at a depth of 2.5 m in August 1988. Five cages containing 100 shrimp and five control cages without shrimp were maintained for 21 d and sampled as described above.

Since grass shrimp effects may vary seasonally, statistical comparisons among treatments were done separately for each time period. Paired cores from a single cage were averaged. Faunal abundances were log-transformed, and abundances of common species (comprising > 1% total individuals) were compared among treatments using a one-way ANOVA.

Predation as the mechanism of direct grass shrimp effects. — To determine whether predation or disturbance was responsible for effects observed within enclosure cages, laboratory predation studies were conducted on the bivalves *Macoma mitchelli* (0.25–4.0 mm), *Mya arenaria* (0.25–4.0 mm), and *Mulinia lateralis* (0.25–2.0 mm), the polychaete *Streblospio benedicti* (5 mm), and the anemone *Nematostella vectensis* (15–20 mm). All are numerically dominant members of the benthic community or become common after shrimp exclusion (see *Results: Direct effects of grass shrimp predation on benthos*; Hines and Comtois 1985, Hines et al. 1987). Predation on all species was observed in the absence of sediment, while predation on *M. mitchelli, S. benedicti,* and *N. vectensis* was also examined after these species burrowed in 2 cm of sediment (2 cm was below the probing depth of *P. pugio*; M. H. Posey, *personal observation*). Known numbers of prey were placed into 10 replicate 18 cm diameter × 12 cm deep dishes. A single grass shrimp was added after 12 h to each of five dishes, with five additional dishes serving as controls, and prey survivorship was recorded after 48 h.

Grass shrimp were maintained on commercial fish food until 1 d prior to experiments and then were fed a mixture of fish food and experimental prey. Effects of shrimp size on predation rates were examined for 0.33-mm *M. mitchelli* using small (15–25 mm body length) and large (35–50 mm) grass shrimp. Only 35–50 mm shrimp were used for other experiments. The number of prey recovered from treatments with shrimp were compared to controls using ANOVA on log-transformed data.

Indirect effects of reducing a benthic predator

Sea anemones have been reported as predators on recruiting larvae (Rumrill 1987). If the anemone *Nematostella vectensis* also preys upon recruiting larvae, then grass shrimp predation on this anemone could indirectly enhance numbers of certain benthic fauna. The effects of *N. vectensis* on the recruitment of macrofauna in the field were examined using transplants

during July and late August 1988. Twenty-five *N. vectensis* were transplanted into 50-cm² cups containing sterile sediment. After 48 h to allow burrow formation, cups containing anemones and paired control cups lacking anemones were buried flush with the sediment surface in the field. Each treatment pair (one control and one anemone transplant) was caged to prevent predation by shrimp. After 2 wk the contents of the cups were preserved in 10% formalin and later seived on a 0.125-mm mesh screen. Abundances (log-transformed) of recruiting infauna were compared between treatment pairs using a paired *t* test.

Laboratory experiments examined predation by *Nematostella vectensis* on two benthic fauna, adult *Streblospio benedicti* and larval *Macoma mitchelli*. *S. benedicti* was affected by *Nematostella* in field transplants, while *M. mitchelli* was chosen as a representative species that has small planktonic larvae potentially impacted by the anemones. For both prey, equal numbers were introduced into dishes either containing a single anemone or containing no anemones, and abundances after 12 h were compared between the two treatments using ANOVA.

Indirect effects of a nektonic predator on grass shrimp

Indirect effects resulting from changes in shrimp abundance. — Indirect effects on benthic macrofauna of reducing grass shrimp abundance were examined in enclosure experiments along with the caging studies examining direct shrimp effects. During fall 1987 and fall 1988, 0.25-m² cages containing two *F. heteroclitus* (one male and one female, 80–85 mm total length) plus 100 *P. pugio* were placed with the shrimp enclosure and control cages discussed previously (see *Direct effects of grass shrimp predation . . .: Community effects,* above). Because these small cages offered only edges as refuge, we assumed grass shrimp abundances would decline from killifish predation. Construction and placement of cages and sampling of benthic fauna were the same as described before. Abundances of grass shrimp and killifish in cages at the end of the fall 1987 experiments were estimated using dipnets. The effects of adding fish on benthic prey were analyzed as described for direct effects of shrimp predation, using ANOVA to compare log-transformed abundances between shrimp enclosure, cage control, uncaged, and fish + shrimp treatments. Where significant effects occurred, Ryan's *Q* test (Day and Quinn 1989) was used to compare individual treatments.

Indirect effects of shrimp distributional changes. — In addition to potential density changes, grass shrimp may exhibit distributional shifts in the presence of predators (Thorp 1976, Heck and Thoman 1981, Nelson 1981, Kneib 1988). We examined behavioral and distributional responses of *P. pugio* to *F. heteroclitus* addition, and the indirect effect of such responses for shrimp prey, in laboratory and field model systems.

Because of the sparsity of fringing marsh, the major spatial refuge for grass shrimp in the Rhode River is shallow water. This habitat was simulated in 130-L aquaria by dividing the bottom into five depth zones, using plexiglass with sand glued to its surface (Fig. 2). Paired aquaria—one experimental tank to which both fish and shrimp were added and a control to which only shrimp were added—allowed observation of killifish effects on shrimp distribution. Twenty grass shrimp (25–40 mm length) were added to each tank and allowed to acclimate for 15 h before adding two killifish (80–85 mm total length) to the experimental tank. Shrimp distribution in each depth zone was recorded in both tanks 1, 2, 4, 6, and 24 h after fish addition. After 24 h fish were removed, and shrimp distribution was monitored for an additional 6 h. Five trials were conducted, alternating which tank was used as a control.

The indirect effects of changes in grass shrimp distribution for benthic fauna were examined by repeating the above experiments with patches containing clam prey (*Mulinia lateralis,* 0.75 mm) in the shallow, intermediate, and deep portions of the aquaria. Triplicate runs of three treatments were used: (1) 20 shrimp added to a tank, (2) 20 shrimp + 2 killifish added, and (3) 0 shrimp and 0 fish added (a control for prey survival). A fish-only treatment was not used since preliminary observations indicated that killifish did not feed within the patches. Acclimation of grass shrimp and addition of fish was the same as for experiments without clam prey. Ninety *Mulinia* were placed in patches of defaunated sediment, 0.5 cm deep × 4 cm in diameter, and patches were placed simultaneously into all aquaria immediately before adding fish to the fish + shrimp treatment. The patches were covered for 1 h to allow fish and shrimp to recover from disturbance and then the covers were removed using attached strings. After 24 h shrimp distributions were recorded and the number of clams remaining in each patch was counted.

To determine whether indirect effects on shrimp prey observed in the laboratory occurred in the field, shallow fence enclosures were constructed in Canning House Bay. Four fence enclosures, 10 m long by 1.5 m wide, were placed with the long axis perpendicular to the shoreline. The upper end of each bordered extreme high tide level while the lower portion was covered with 0.5–1.5 m of water. Fences were constructed of 3-mm plastic mesh with hardware cloth reinforcing the bottom 15 cm. Fences were sunk 10 cm into the sediment, and exposed mesh was cleaned weekly.

Four predator treatments were used: (1) 0 killifish + 0 shrimp, (2) 0 killifish + 3000 shrimp, (3) 30 killifish + 0 shrimp, and (4) 30 killifish + 3000 shrimp. These densities are within the range observed in the Rhode River (high tide densities: 2 killifish/m² and 200 grass shrimp/m²; Fig. 3; A. H. Hines, M. H. Posey, and G. Ruiz, *unpublished data*). Prey patches were obtained by taking 50-cm² plugs from an area where pred-
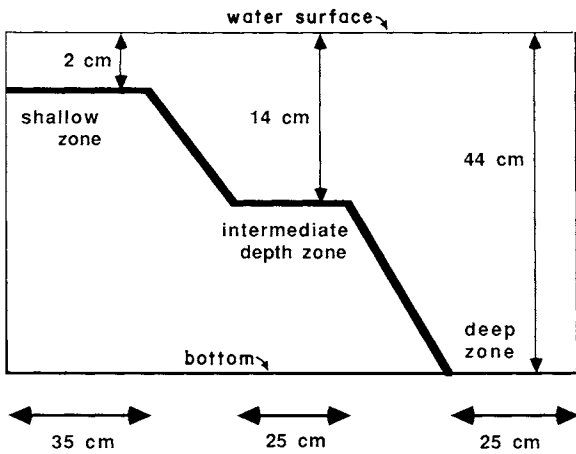
FIG. 2. Diagram of one of the experimental aquaria used to examine depth distribution of grass shrimp (*Palaemonetes pugio*) in the presence and absence of fish predators (*Fundulus heteroclitus*) and the indirect effects of distribution patterns on benthic prey.

ators had been previously excluded for 3 wk. We buried two patches flush with the sediment surface in the deep portion of each fence enclosure (pooling data from patches within the same enclosure for later statistical analyses). Runs included one replicate of each predator treatment, and were repeated over three 1-wk intervals between April and June 1989. At the end of 1 wk all patches were removed from the fences and seived on a 0.5-mm screen. We removed fish, shrimp, and other natant predators from each fence with sweep nets (sweeping until three sweeps yielded no fish or shrimp for two consecutive days). Treatments were reassigned among fences for each run, and new predators and prey patches were used.

Predator effects were analyzed only for common species (> 1% of the total individuals) and for total abundances. Numbers were log-transformed, and infaunal abundances were compared among treatments using ANOVA, blocking for differences among experimental sets. Individual treatments were contrasted with Ryan's *Q* test.

RESULTS

Grass shrimp abundance

Palaemonetes pugio abundances varied temporally. Highest abundances occurred in summer and fall, with few shrimp collected during winter (Fig. 3). Densities ranged from 0 shrimp/m² in December and January to >900 shrimp/m² in late November. Densities of 200–400 shrimp/m² were consistently observed during summer.

Direct effects of grass shrimp predation on benthos

Community effects.—We predicted that grass shrimp, as abundant epibenthic omnivores, would directly reduce numbers of common benthic prey. Total macro-

infaunal abundances were lower within high-density shrimp enclosures (100 shrimp/cage) compared to control cages lacking shrimp for all time periods (Table 1). Eighteen species were common during at least one period, and 10 of these responded to shrimp addition. All species affected were less abundant when shrimp were present, but the responses varied between periods (Table 1). The clam *Macoma mitchelli* was affected only during the two fall periods, when it recruited into the community. The anemone *Nematostella vectensis* was common from fall 1987 through summer 1988, consistently exhibiting lower densities in the presence of shrimp. *N. vectensis* disappeared from the community in fall 1988. Amphipods and chironomid insect larvae were only common during spring 1988, showing a negative correlation with shrimp presence. The only infaunal polychaetes responding to shrimp presence were the burrowing *Heteromastus filiformis* in summer and fall 1988 and the tube-dwelling *Streblospio benedicti* in fall 1988.

Because a cage would exclude predators other than grass shrimp (e.g., fish and blue crabs), the above comparisons were made only between cages containing grass shrimp and cages lacking shrimp. We assumed that uncaged areas, where other predators are present, would have significantly lower faunal densities than shrimp enclosures. However, abundances of most taxa affected by shrimp presence did not differ between uncaged areas and shrimp enclosures (Ryan's *Q* test and Duncan's multiple range test, *P* > .05). There were no significant differences between shrimp enclosures and uncaged areas for total faunal abundance during September 1987–June 1988 runs, for *Nematostella* in May–June 1988 runs, and for those amphipods, isopods, and insect larvae that were affected by shrimp presence during May–June 1988. These results suggest that grass shrimp may have as great an impact upon infauna as
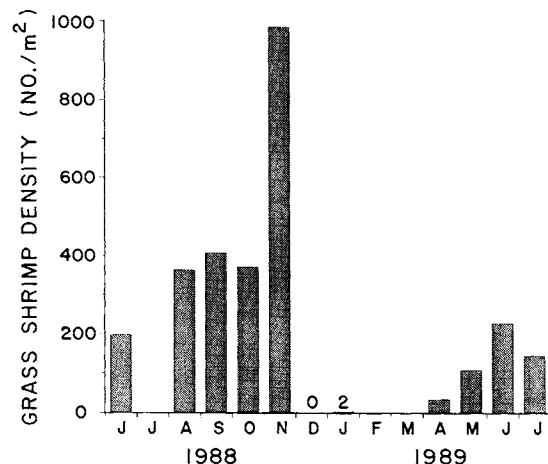

FIG. 3. Monthly abundance of *Palaemonetes pugio* from sweep-net catches in the Rhode River, Chesapeake Bay, Maryland.

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TABLE 1. Effect of grass shrimp presence on abundances of common† fauna in 0.25-m² shallow cage enclosures in the Rhode River (Chesapeake Bay, Maryland). Data (means ± 1 SE) are from sediment cores from control cages lacking predators and cages each containing 100 grass shrimp.

Taxa	September 1987		May 1988	
	Control	Shrimp	Control	Shrimp
	Abundance of infauna (no./0.01 m²)			
Bivalves				
Macoma mitchelli	42.6 ± 3.9	16.8 ± 2.0**	7.6 ± 2.5	3.8 ± 0.7 NS
Macoma balthica			3.1 ± 0.8	1.4 ± 0.4 NS
Mulinia lateralis			0.9 ± 0.3	0.9 ± 0.3 NS
Polychaetes				
Heteromastus filiformis	25.8 ± 2.3	24.4 ± 2.4 NS	61.0 ± 7.6	43.6 ± 4.1 NS
Streblospio benedicti	22.2 ± 4.5	13.9 ± 2.7 NS	2.6 ± 0.6	1.7 ± 0.5 NS
Laeoneris culveri	27.3 ± 4.2	22.8 ± 2.3 NS	8.6 ± 0.9	11.2 ± 1.3 NS
Scolecolepides viridis	3.1 ± 0.7	4.1 ± 1.4 NS	11.8 ± 1.6	14.0 ± 1.3 NS
Eteone heteropoda	4.9 ± 1.3	1.8 ± 0.4 NS	2.2 ± 0.5	1.1 ± 0.2 NS
Polydora ligni			5.7 ± 1.7	2.2 ± 0.6 ns
Oligochaetes			13.1 ± 2.2	8.9 ± 1.5 NS
Arthropods				
Cyathura polita	7.8 ± 1.4	5.4 ± 0.8 NS	4.3 ± 0.6	4.2 ± 0.6 NS
Gammarus mucronatus			23.4 ± 5.3	2.4 ± 1.0***
Leptocheirus plumulosus			7.3 ± 1.9	1.8 ± 1.0*
Monoculoides spp.			5.4 ± 1.0	2.5 ± 0.6*
Corophium lacustre			4.2 ± 1.5	0.9 ± 0.2**
Chironomus spp.			13.4 ± 4.3	2.1 ± 0.6**
Cnidarians				
Nematostella vectensis	53.7 ± 9.1	7.8 ± 4.1**	35.6 ± 9.1	8.9 ± 1.6**
Nemerteans				
Carinoma tremaphorus	2.3 ± 0.5	2.6 ± 0.3 NS	2.2 ± 0.5	1.4 ± 0.2 NS
Total faunal abundance	194.1 ± 16.2	103.4 ± 5.3***	213.6 ± 25.2	113.5 ± 7.0**

* $P < .05$, ** $P < .01$, *** $P < .001$; NS = no significant difference (ANOVA comparing control and shrimp-addition cage treatments for each date).

† Species comprising at least 1% of the fauna.

other epibenthic predators and indicate that cage artifacts were minimal compared to predation effects.

The effects of lower grass shrimp densities were examined for those prey responding to high shrimp densities. During June runs there was only a graded increase in the magnitude of density depression with increased shrimp density (Fig. 4), and there was no difference in the response to high vs. medium shrimp densities during September runs.

The response of infauna in deeper water (>1.5 m) with muddier sediments (Hines and Comtois 1985) was similar to that in shallow areas (<0.5 m) (Table 2). Both the clam *Macoma mitchelli* and the polychaete *Streblospio benedicti* were reduced in shrimp enclosures compared to control cages. The only difference between depths was a lack of response by the polychaete *Heteromastus filiformis* in deeper areas. For all species, abundances did not differ significantly between shrimp enclosures and uncaged areas ($P > .05$, Ryan's Q test and Duncan's multiple range test).

Predation as the mechanism of direct shrimp effects. — Laboratory studies indicated that the response of certain infauna to grass shrimp addition is due to direct shrimp predation rather than substrate disturbance. Individual shrimp (>35 mm length) consumed

significant numbers of small (<1 mm) *Macoma mitchelli* in the absence of sediment (Fig. 5). Predation rates declined for larger clam size classes, with no detectable effect for clams >1.35 mm length (ANOVA, $P > .05$). A similar pattern of predation on small *M. mitchelli* was seen in sand and silt substrates (Fig. 5). There was no obvious influence of substrate type on predation patterns and no detectable difference in predation rates between 15–25 mm and 35–50 mm shrimp feeding on 0.33 mm clams ($t = 0.6$, $P > .1$, $n = 7$ for both). Grass shrimp also consumed significant numbers of only small sizes of the clams *Mya arenaria* (0.5 mm length: 100% consumed; 1.0–2.0 mm length: $\bar{X} \pm 1$ SE = 32 ± 3.1% consumed; >2 mm length: 5 ± 0.2% consumed) and *Mulinia lateralis* (0.34 mm length: 98.8% consumed).

Grass shrimp also exhibited significant predation on *Streblospio benedicti,* even after these worms had established tubes in sediment (Fig. 6). However, there was only a marginally significant effect of shrimp predation on the anemone *Nematostella vectensis* in the absence of sediment (shrimp treatment: $\bar{X} \pm 1$ SE = 22.2 ± 2.2 anemones recovered; control: 24.9 ± 3.7 recovered, $n = 5$ for both, $t = 2.57$, $P < .05$), and shrimp predation was not significant when anemones burrowed in 1–2 cm of fine sand (shrimp treatment:

TABLE 1. Continued.

	June 1988		September 1988	
	Control	Shrimp	Control	Shrimp
	Abundance of infauna (no./0.01 m²)			
	1.2 ± 0.2	1.1 ± 0.3 NS	3.3 ± 0.7	1.6 ± 0.3**
	54.7 ± 3.6	42.7 ± 3.4**	42.8 ± 3.5	31.5 ± 2.5***
	2.1 ± 0.5	1.5 ± 0.3 NS	98.5 ± 8.5	63.8 ± 8.1***
	32.1 ± 6.2	22.3 ± 4.5 NS	15.8 ± 1.4	18.8 ± 2.3 NS
	12.4 ± 1.3	11.4 ± 1.2 NS	1.8 ± 0.4	2.3 ± 0.5 NS
	4.9 ± 1.1	6.3 ± 3.3 NS	14.7 ± 2.6	10.9 ± 2.2 NS
	3.5 ± 1.1	2.2 ± 0.5 NS	7.6 ± 2.0	8.1 ± 2.5 NS
	20.6 ± 3.1	7.0 ± 1.9*		
	16.1 ± 3.4	3.6 ± 1.0**		
	2.0 ± 0.3	1.6 ± 0.3 NS		
	155.2 ± (13.2)	103.1 ± (10.0)***	186.1 ± (12.5)	138.4 ± (12.5)***

24 ± 2.4 anemones recovered; control: 25.7 ± 1.6 recovered, $n = 20$, $t = 1.07$, $P > .1$), even when the sand experiments were repeated over several time periods and with several size classes of anemones. The small direct predation effect on *Nematostella* is surprising given the strong effect of grass shrimp on its abundance during three of our enclosure experiments and reports of shrimp control of its occurrence in a salt marsh (Kneib 1988).

Indirect effects of reducing a benthic predator

A potential indirect effect of predation by epibenthic omnivores such as grass shrimp upon benthic prey involves increased abundances of some infauna when infaunal predators are reduced. Although sea anemones were absent in the surrounding areas during fall 1988, *Nematostella vectensis* survivorship within caged transplant cups was high (final density: $\bar{X} \pm 1$ SE = 26.4 ± 2.91 anemones/cup in transplants; 0.2 ± 0.15 anemones/cup in controls). Thirteen taxa were observed to recruit into the cups during July and August. *Heteromastus filiformis*, *Laeoneris culveri*, *Polydora ligni*, and *Streblospio benedicti* comprised >95% of the total individuals. *S. benedicti* was the only common

taxon to exhibit significant density responses, with lower numbers in anemone transplants compared to controls (Fig. 7, $t = 3.13$, $n = 7$, $P < .05$). *N. vectensis* readily consumed *S. benedicti* in the laboratory.

Although the clam *Macoma mitchelli* was not common during the transplant experiments (<1% of total fauna), laboratory experiments indicated that settling larvae of this species were susceptible to anemone predation. *N. vectensis* ingested significant numbers of *M. mitchelli* pediveliger larvae (Fig. 8), with shells of digested clams found within anemone regurgitate pellets.

Because *Nematostella* most likely affects settling larvae, true assessment of its importance as a potential predator is difficult without long-term experiments that span several recruitment seasons. However, the studies reported here indicate that this anemone did significantly reduce numbers of certain benthic prey in the field and may affect numbers of other species under certain conditions. Its reduction would thus enhance numbers of these prey species.

Indirect effects of a nektonic predator on grass shrimp

Indirect effects resulting from changes in shrimp density. —Grass shrimp were observed in enclosure cages
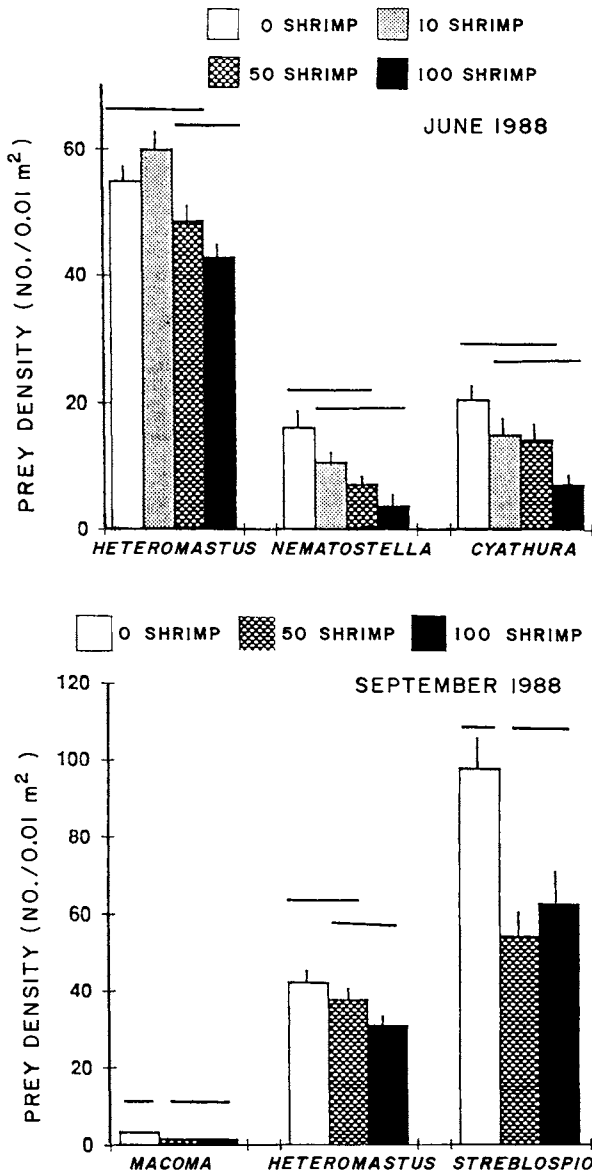
FIG. 4. Effect of varying grass shrimp density (0, 10, 50, and 100 shrimp/0.25-m² cage) for abundances of grass shrimp benthic prey in the Rhode River. Histogram bars indicate number per treatment (mean and 1 SE); those sharing a horizontal line above them do not differ significantly (Ryan's Q test).

containing killifish during the initial 2 wk of experiments. However, sweep-net catches at the end of fall 1987 runs indicated <10% final survivorship of shrimp in the presence of killifish.

We predicted that killifish predation on grass shrimp would indirectly increase abundances of benthic prey. Compared to treatments where only shrimp were added, adding killifish to the cages produced a mixed effect for benthic prey species. Both the polychaete *Streblospio benedicti* and the burrowing anemone *Nematostella vectensis* had significantly lower numbers in shrimp-

only treatments, but displayed no difference in abundances between cages containing killifish + shrimp and those containing no predators (Fig. 9). In contrast, the addition of killifish did not affect numbers of *Macoma mitchelli* or *Heteromastus filiformis* relative to shrimp-only treatments. For both *M. mitchelli* in 1988 and *H. filiformis* the trend was for lower numbers in killifish + shrimp treatments compared to cages containing only shrimp or with no added predators. Other infauna showed no significant response to killifish addition.

Indirect effects of shrimp distributional changes. — Indirect effects of a nektonic predator on benthic prey of the grass shrimp may be caused by behavioral changes in shrimp microhabitat utilization rather than actual consumption of shrimp. In the absence of predators, shrimp occurred in all depth zones of laboratory tanks (2–44 cm depth). However, when killifish were added, shrimp quickly shifted to the shallowest zone (Fig. 10a). Most shrimp moved into the shallow zone within 2 h after fish addition, and few shrimp were observed in deeper areas 24 h after fish addition. Killifish were never observed to enter the shallow zone. Shrimp in paired control tanks (Fig. 10b) did not move into shallow water and the number of shrimp in the shallow zone was significantly less in controls compared to fish-addition treatments (paired t test, $t = 9.77$, $P < .001$). Movement of shrimp into shallow areas occurred even without apparent attacks by fish. Final numbers of grass shrimp in control and killifish-addition treatments did not differ significantly ($\bar{X}$ recovered with fish = 18.3; $\bar{X}$ without fish = 19.1; $t = 1.06$, $P > .1$).

The changes in shrimp distribution in the presence of killifish also indirectly affected survivorship of bivalve prey. Survival of juvenile *Mulinia lateralis* differed between treatments with no predators, with

TABLE 2. Effect of grass shrimp on abundances of common fauna within deep cage enclosures (>2.5 m depth) in the Rhode River in August 1988. Data (means ± 1 SE) are from sediment cores from control cages lacking predators and cages each containing 100 grass shrimp.

Taxa	Treatment	
	Control	Shrimp
	Abundance of infauna (no./0.01 m²)	
Bivalves		
Macoma mitchelli	5.4 ± 1.0	0.9 ± 0.4***
Polychaetes		
Heteromastus filiformis	7.2 ± 0.8	9.0 ± 1.1 NS
Streblospio benedicti	15.1 ± 2.7	8.0 ± 1.8***
Laeonereis culveri	0.1 ± 0.1	0.5 ± 0.2 NS
Scolecolepides viridis	2.1 ± 0.5	1.4 ± 0.4 NS
Polydora ligni	0.6 ± 0.2	1.7 ± 1.0 NS
Oligochaetes	2.1 ± 0.7	3.4 ± 1.1 NS
Total faunal abundance	36.0 ± 3.2	27.5 ± 3.4*

* $P < .05$, *** $P < .001$; NS = no significant difference (ANOVA comparing control and shrimp-addition cage treatments).
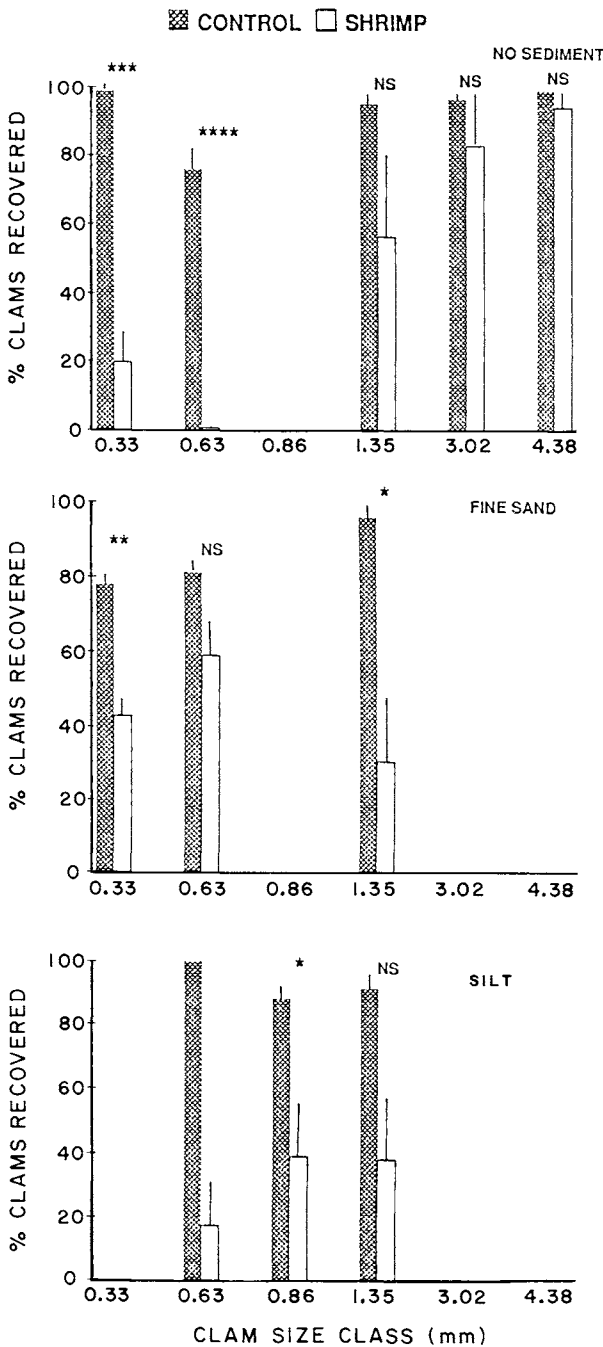
FIG. 5. *Palaemonetes pugio* predation on juvenile *Macoma mitchelli* under laboratory conditions of no sediment, fine sand, or silt substrate. Histogram bars indicate mean and 1 SE; significance levels are from one-way ANOVA (*$P < .05$; **$P < .01$; ***$P < .001$; ****$P < .0001$).
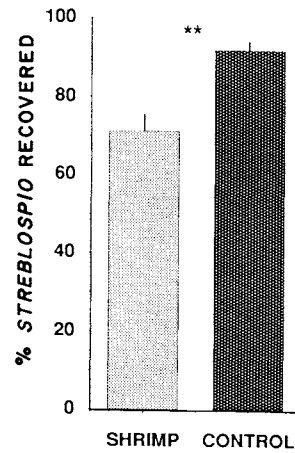

FIG. 6. Survivorship of *Streblospio benedicti* in the laboratory in the presence and absence of *Palaemonetes pugio* ($F = 15.9$, **$P < .01$). Histogram bars indicate mean and 1 SE.

shrimp+killifish treatments was not significant in the deepest zone. The intermediate effect of shrimp+killifish treatments may be related to shrimp foraging in deeper areas at night when killifish were not active (M. H. Posey, *personal observation*). Killifish were never observed to feed on prey patches.

A field test utilizing natural shallow refugia within large fence enclosures yielded results analogous to those in the laboratory. Unlike the small, subtidal enclosure cages described previously (lacking a shoreline refuge), final grass shrimp densities within the fence enclosures spanning the natural near-shore depth gradient did not differ significantly between treatments with only shrimp

shrimp only, and with fish+shrimp ($F = 281.4$, $P < .0001$). In general, clam survival was greatest when predators were absent, intermediate when killifish+shrimp were present, and significantly lower when only shrimp were present (Fig. 11; Ryan's Q test, $P < .05$), though the difference between shrimp-only and
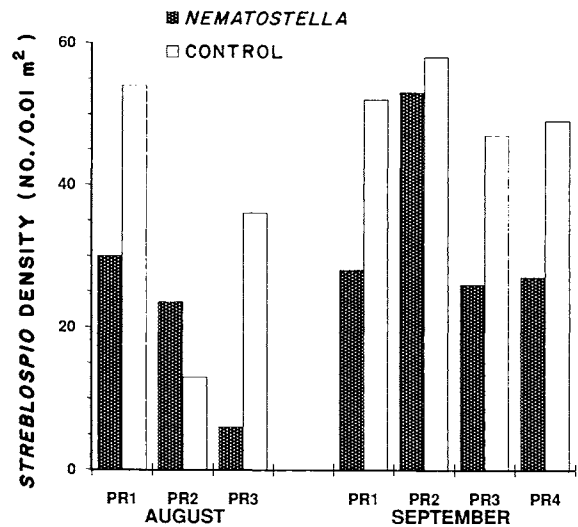

FIG. 7. Recruitment of *Streblospio benedicti* into defaunated sediment in the presence and absence of *Nematostella vectensis*. Treatment pairs during each time period reflect paired placement of anemone transplant and control (no anemone) cups of sediment in shrimp exclusion cages in the Rhode River, Chesapeake Bay, Maryland.
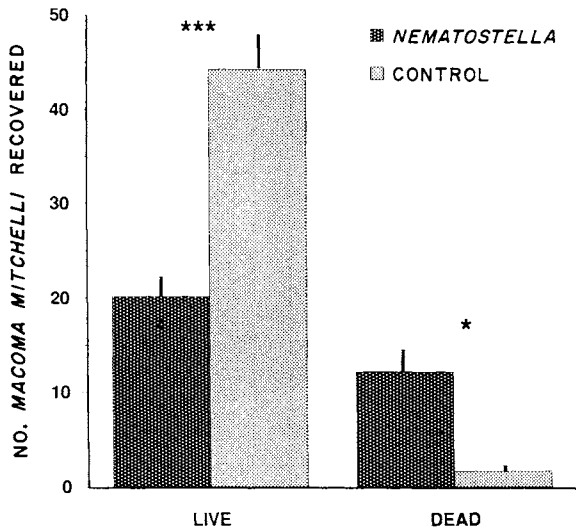
FIG. 8. Survivorship (mean and 1 SE) of settling *Macoma mitchelli* (live) and number of empty *M. mitchelli* shells (indicating mortality during settlement) in the presence and absence of *Nematostella* in laboratory arenas. *P < .05; ***P < .001.

added and those with killifish + shrimp added (shrimp-only fences: $\bar{X} \pm 1$ SE = 869 ± 239 shrimp recovered; killifish + shrimp fences: 690 ± 239 shrimp recovered). Total macrofaunal abundances were greatest in control treatments (no added predators) and fish-only treatments, and were least in shrimp-only additions (Fig. 12). Macrofaunal abundances were intermediate in kil-

lifish + shrimp treatments (Ryan's Q test, P < .05), indicating an indirect enhancement of benthic prey due to shrimp distributional shifts, not density changes, as seen in the laboratory experiments. The species showing the strongest contributions to changes in total macrofaunal abundances were chironomid insect larvae, *Polydora ligni, Streblospio benedicti,* and oligochaetes—most of which also responded to grass shrimp addition within the 0.25-m² enclosure cages. However, densities of individual species were low compared to previous years (M. H. Posey, *unpublished data*), possibly related to unusually low salinities in 1989, and consequently we could not detect differences in the densities of individual species among the four treatments.

DISCUSSION

Our experiments on the benthic food web in the nearshore zone of Chesapeake Bay show that: (1) predation by the epibenthic omnivore *Palaemonetes pugio* has strong direct effects on the abundances of a variety of benthic invertebrates, and (2) interactions among grass shrimp, benthic predators (burrowing sea anemone), and nektonic omnivores (killifish) have strong indirect effects upon benthic faunal densities and community composition. Temporal variation in the response of benthos to grass shrimp probably reflected seasonal fluctuations in prey settlement and size-dependent predation, since shrimp consumed primarily small, newly settled individuals in the lab. Indirect interactions resulted both from predation by shrimp
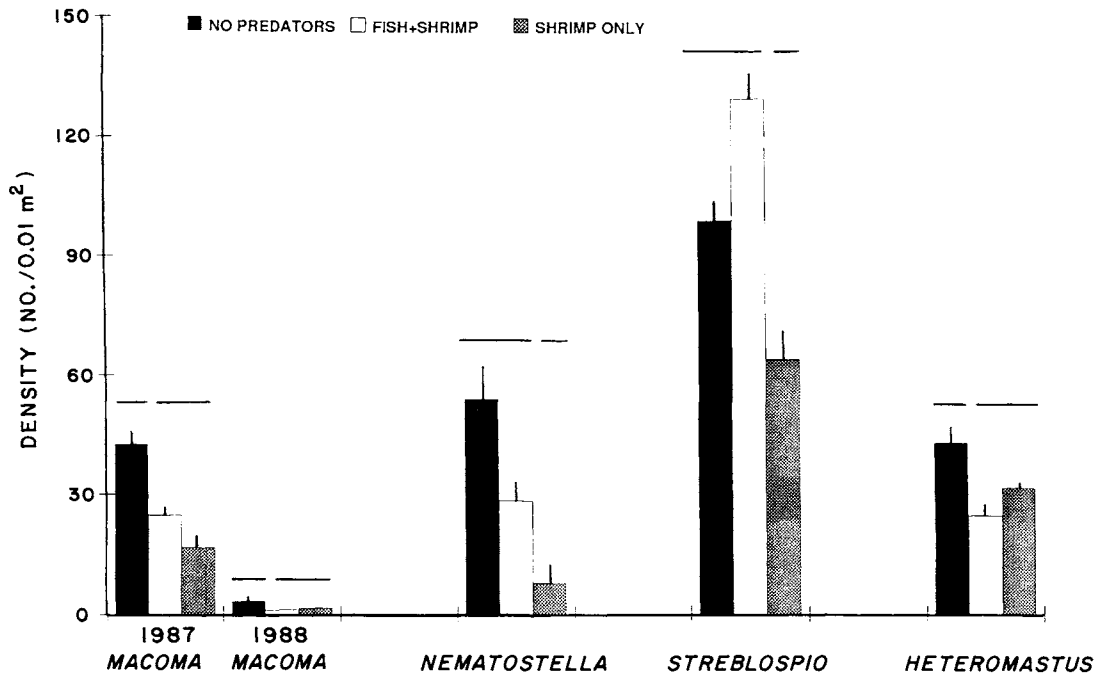

FIG. 9. Effect on benthic prey of adding *Fundulus heteroclitus* plus grass shrimp into field enclosure cages as compared to cages with only grass shrimp or with no added predators. Histogram bars indicate mean and 1 SE; means connected by a horizontal line above do not differ significantly (Ryan's Q test).
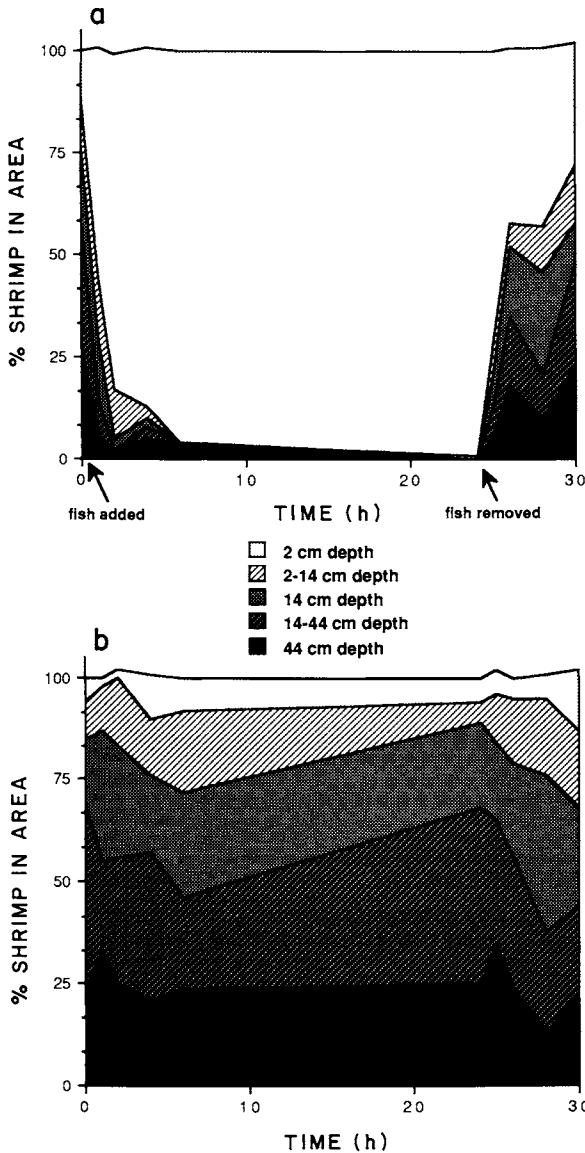
FIG. 10. Effect of *Fundulus heteroclitus* addition on the depth distribution of grass shrimp in laboratory mesocosms. Area plots indicate the percentage of grass shrimp in five depth zones before, during, and after fish addition (a) and in paired control tanks lacking fish (b). All points are means of five observations.

on a predatory sea anemone and from predation upon shrimp by killifish. When released from the effects of grass shrimp, burrowing anemones have the potential for regulating infaunal abundances by consuming settling larvae. Killifish indirectly affected infauna by altering epibenthic predation pressure both through consuming shrimp and through inducing shifts in shrimp distribution. For some benthic prey the indirect effects of these interactions were as strong as direct effects in determining infaunal abundances. Cage artifacts (Virnstein 1978, Hulberg and Oliver 1980) did not signifi-

cantly alter the results of field experiments; since the influence of shrimp was determined by comparing only caged treatments, the results were consistent across our array of field and laboratory experiments, and our results were consistent with those in other studies (Kneib 1985, 1988, Van Dolah 1978).

Direct effects of predation

Direct predation exerts strong control over faunal abundances and community structure in most marine, estuarine, and freshwater ecosystems (Paine 1966, 1980, Sih et al. 1985, Kerfoot and Sih 1987). Although single predatory species exert key control of some communities (Paine 1966, Simenstad et al. 1978), guilds of predators regulate others, especially in soft-bottom habitats (Peterson 1979, Levinton 1982, Hines et al. 1990). The mechanism of direct regulation is through consumption of abundant prey (e.g., Paine 1966, Virnstein 1977) and, in some soft-bottom communities, sedimentary disturbance by predator activity (Woodin 1981, Hines et al. 1990, Posey 1990). In the nearshore habitat of central Chesapeake Bay, grass shrimp and killifish directly affect the composition of the infaunal community through consumption of benthic prey. For example, *Nematostella vectensis* has only been reported once from the Chesapeake Bay (Calder 1972), and we have not observed it specifically within the Rhode River during 10 yr of field sampling of infaunal communities. Our field exclusion experiments suggest that shrimp have played a major role in reducing densities of this otherwise conspicuous species to normally undetectable levels in Chesapeake Bay. However, direct
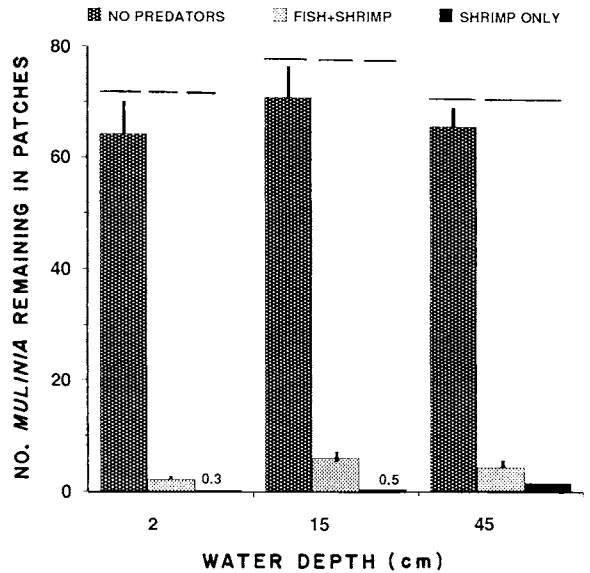

FIG. 11. Survival of *Mulinia lateralis* in three depth zones within laboratory mesocosms in the presence of no predators, grass shrimp only, and a mixed assemblage of grass shrimp and *Fundulus*. Histogram bars indicate mean and 1 SE and horizontal lines above them connect means that do not differ significantly (Ryan's Q test).
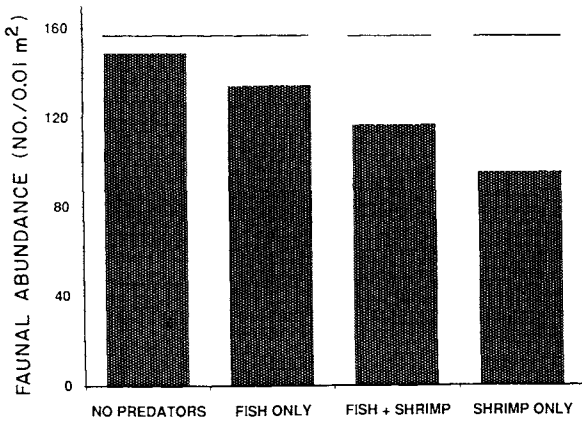
FIG. 12. Effect of single-species and mixed-species addition on total faunal abundance within fence enclosures. Histogram bars indicate mean total abundance and horizontal lines above them connect treatments that do not differ significantly (Ryan's Q test following ANOVA blocking for differences between experimental sets).

effects of predation explain only part of community regulation.

Indirect effects of predation on a benthic predator

The importance of epibenthic predators in controlling infaunal predators, and thereby indirectly enhancing abundances of infaunal prey, has been proposed in several soft-substrate communities (Levin 1982, Ambrose 1984, Commito and Ambrose 1985, Posey 1986, Luckenbach 1987, Hines et al. 1990). The infaunal anemone *Nematostella vectensis* was negatively affected by grass shrimp both in our experiments in Chesapeake Bay and in a Georgia salt marsh (Kneib 1988). *Nematostella* readily consumed settling larvae in the laboratory and reduced recruitment of the polychaete *Streblospio benedicti* in the field. More complexly, although shrimp preyed on *Streblospio* in the laboratory and reduced their numbers in the one field experiment when *Nematostella* was absent from the community, there was no significant effect of shrimp on *Streblospio* during the three periods when *Nematostella* was abundant in control cages. The lack of an overall direct effect of shrimp predation on *Streblospio* when *Nematostella* was present may reflect a balance between weak direct negative effects of low shrimp predation rates on *Streblospio* adults and the indirect positive effect of shrimp on *Streblospio* recruitment through predation on *Nematostella*. Net community effects in the balance of such opposing interactions will vary with seasonally fluctuating predator abundance and prey recruitment.

Indirect effects of interactions among epibenthic and nektonic omnivores

Interactions among mobile predators can also produce strong indirect effects that clearly regulate the structure of aquatic communities. Mechanistically, the indirect effect of one mobile predator consuming another is a cascading impact of reduced mortality in the prey species of the second predator. Such cascading trophic interactions appear to be common in freshwater lakes (Carpenter et al. 1985, Kerfoot and Sih 1987) and in marine rocky communities (Paine 1966, Estes and Palmisano 1974). In our study the relative importance of indirect effects on benthic infauna resulting from grass shrimp–killifish interactions varied among prey species, possibly reflecting diet overlap between these generalist predators. Neither *Streblospio* nor *Nematostella* have been reported commonly in killifish diets (Kneib and Stiven 1982, Kneib 1986), and *Fundulus* did not attack *Nematostella* in our laboratory even after they were starved. Numbers of both of these prey were enhanced by the presence of killifish compared to the presence of only shrimp. Juvenile bivalves, in contrast, have been reported as killifish prey (Kelso 1979), and in our experiments the clam *Macoma mitchelli* showed no increase in density when killifish were present in addition to shrimp. The extent of dietary overlap between these omnivores probably regulates the indirect impacts on the species composition of surviving prey.

Shifts in habitat utilization, independent of reduction in abundance, by a prey in the presence of a predator have been reported as another type of interaction among mobile predators for freshwater communities (Mittelbach 1988, Rahel and Stein 1988, Formanowicz and Bobka 1989, Turner and Mittelbach 1990) and for marine surfperch (Holbrook and Schmitt 1988). Such distributional shifts may indirectly affect prey abundances in freshwater systems (Gilliam 1989) in a manner similar to the influence of killifish–shrimp interactions on infauna in our study, indicating that indirect trophic interactions involving behavioral changes occur in a variety of systems (Sih et al. 1985). For these systems, spatial and/or structural refugia play an essential role of concentrating into certain microhabitats the indirect interactions that would be dispersed in the absence of the top predator.

Importance of omnivory in regulating indirect effects

The consistency of responses across our array of field and laboratory experiments, the correspondence of our results with aspects of other studies (Van Dolah 1978, Kneib 1985, 1988, Smith and Coull 1987), and the wide geographical distribution of these and analogous species indicate that the results of our study have broad applicability to similar communities along the Atlantic and Gulf coasts of North America. Despite the relatively low species diversity of these estuarine nearshore communities, the complexity of their direct and indirect trophic interactions emphasizes the importance of omnivory in regulating food-web structure. The omnivory of epibenthic grass shrimp and nektonic killi-

fish, as well as the breadth of larval species potentially taken by burrowing anemones, means that considerable dietary overlap exists among these regulatory species. By virtue of the large number of links produced by this dietary overlap, omnivory produces complex interactions and prevents broad trophic-level generalizations of the effects of predation. Moreover, as key linkages by one omnivore regulate another omnivore (killifish–shrimp, or shrimp–anemones), indirect effects of interactions become multiplicative. Since many food-web properties (predator–prey ratio, fraction of species in each trophic level, number of links per species, web "vulnerability," and web "generalization") appear to be independent of the number of species in a web (Schoener 1989), the regulatory importance of omnivory in these low-diversity webs may apply generally to high-diversity communities. The degree of omnivory in a food web should be a significant predictor of the relative strength of indirect vs. direct interactions.

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