

BEHAVIORAL INDIRECT INTERACTIONS: MULTIPLE PREDATOR EFFECTS AND PREY SWITCHING IN THE ROCKY SUBTIDAL

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Abstract. The high trophic connectivity of many communities can produce large numbers of indirect interactions. Although many trait-mediated indirect interactions (TMII) are caused by changes in prey behavior, less is known about the effects of changes in predator behavior such as prey switching or multiple predator effects (MPE) on indirect interactions, especially in marine systems. We performed a series of field caging experiments off the Isles of Shoals, Maine (USA) from 2000 to 2002 to test for the presence of behaviorally mediated indirect effects in a shallow subtidal food web. Specifically, crab (*Cancer borealis*) predation on sea urchins (*Strongylocentrotus droebachiensis*) was quantified in three habitats (*Codium fragile* algal beds, barrens, and mussel beds) representing differing combinations of food and shelter to examine the effects of prey switching by crabs. A second predator (the lobster, *Homarus americanus*) was added to the crab treatments to examine MPE effects.

Urchin mortality was significantly lower in the mussel habitat than in the *Codium* and barren habitats. Mussels produced a positive indirect effect on urchins by changing the behavior of crabs; crabs fed on mussels instead of urchins (prey switching). In the barrens, crab predation on urchins indirectly increased the abundance of the introduced ascidian, *Diplosoma* sp., whereas *Codium* density did not change among treatments.

A significant risk reduction for urchins occurred in *Codium* and barren habitats, but not in mussel habitats when crabs and lobsters were combined. Lobsters also produced a positive indirect effect on mussels by reducing crab predation. Thus, lobsters modify crab behavior and dampen changes in community structure.

Our results illustrate the importance of predator behavior and habitat context in modifying consumer pressure and community structure, and argue for the consideration of these factors in other multi-predator systems where habitats represent food and/or shelter.

Key words: *Cancer borealis*; *Homarus americanus*; indirect effects; Isles of Shoals, Maine; multiple predators; predation; prey switching; shallow rocky subtidal; *Strongylocentrotus droebachiensis*; structural complexity; trait-mediated indirect interaction; trophic cascade.

INTRODUCTION

Understanding variation in species interactions is essential to predicting community change. Indirect effects are a main source of this variation and their impact on community structure through changes in species densities (i.e., density-mediated indirect interactions [DMII] such as trophic cascades, keystone predation, exploitative competition) is well supported (Paine 1966, 1980, Carpenter et al. 1985, Kerfoot and Sih 1987, Menge 1995). The complexity, variety, and magnitude of these DMII make them difficult to model (Yodzis 1988) and a continuing challenge for experimental ecology. In addition to DMII, trait-mediated indirect interactions (TMII) can add even more complexity to our understanding of community structure (e.g., Werner and Anholt 1996, Schmitz et al. 1997, Swisher et al. 1998, Wootton 2002, Trussell et al. 2003). TMII occur when a trait (e.g., behavior), rather

than the density, of the intermediate species changes in the presence of another species, causing the abundance of a third species to be modified. The occurrence of these behavioral indirect effects is becoming well recognized (Werner and Peacor 2003), but their relative importance and pervasiveness in a variety of communities compared to other density-mediated indirect interactions and direct effects are not well understood (but see Peacor and Werner 2001).

TMII may arise through a wide variety of mechanisms and may occur at any level(s) within a food web. Commonly, TMII are produced through behavioral changes as the community context, such as the presence of a potential predator, changes. For example, interaction strengths of herbivores on their resource may decrease (Schmitz et al. 1997, Bernot and Turner 2001, Trussell et al. 2003), or the competitive interactions between two species may decrease (Werner and Anholt 1996, Peacor and Werner 2001) in the presence of a predation risk (i.e., no lethal effect). In addition, predator efficiency may change depending on the structural complexity of the habitat (Swisher et al. 1998) or the availability of an alternative food source (Huang and

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TABLE 1. Predicted sea urchin mortality rates for three common subtidal habitats in relation to the structural complexity and the alternative food sources they provide.

Habitat	Structural complexity	Alternative food source	Predicted mortality
Mussel	low	present	low
<i>Codium</i>	high	absent	low
Barren	low	absent	high

Note: Predictions are based on the premises that structural complexity generally decreases prey mortality by decreasing predator efficiency (e.g., Witman 1985, Swisher et al. 1998) and that alternative food sources release prey from predation pressure (e.g., Huang and Sih 1991).

Sih 1991, Norbury 2001). Lastly, the addition of a second predator species can create either increased or decreased prey mortality rates on a common prey through changes in either predator or prey behavior (multiple predator effects [MPE]; Sih et al. 1998). Thus in communities with multiple predators, prey, and habitats, changes in predator behavior may have markedly different effects on the community (e.g., ranging from no effect to strong top-down control).

Although many of the indirect effects have been described from a wide variety of systems, the diversity of indirect effects within a system is poorly known (but see Huang and Sih 1991). Variation in species interactions within a community is important to understanding and predicting community change (Menge et al. 1994, Power et al. 1996). Because most communities encompass multiple habitats and have multiple predator species that have broad overlapping diets, we expect these effects to be common.

To address the importance and diversity of indirect effects within a community, we examined how direct predation changed in relation to prey switching, structural complexity, and MPE. Specifically, we examined variation in the mortality rate of the green sea urchin, *Strongylocentrotus droebachiensis*, due to the Jonah crab, *Cancer borealis*, with a series of field caging experiments. Both species have large ranges in the western North Atlantic (Gosner 1971), occur in many biogenic habitats, tolerate wide fluctuations in temperatures, and co-occur with other important consumer

species (e.g., the American lobster, *Homarus americanus*). We first examined the effect of three common biogenic habitats (beds of *Codium*, an invasive green alga; barrens; and mussel beds) on urchin mortality due to crab predation. Each habitat had unique combinations of structural complexity and alternative food sources to address the relative influence of these attributes (Table 1). Second, we hypothesized that the addition of the lobster, *H. americanus*, as a second predator species would produce a significant MPE (e.g., a risk reduction) in each of the three habitats.

METHODS

Study site

All fieldwork was conducted at the Isles of Shoals, a group of small islands 10 km offshore of Portsmouth, New Hampshire, USA. All caging experiments were conducted at Smith's Cove (42°59.105' N; 70°37.150' W) off the southeast side of Appledore Island, on gently sloping bedrock surfaces 3–8 m below mean lower low water.

Field predation

Natural predation by crabs, *Cancer borealis*, on urchins, *Strongylocentrotus droebachiensis*, was assessed in the field using haphazard searches at two naturally occurring barren habitats. Searches lasted for the duration of a dive (45–60 min) and covered ~200 m². Predation events were defined as a crab grasping an urchin in its chelipeds, although typically a wedge-shaped portion of the urchin test was removed and crabs were actively removing soft tissue (Appendix A). Predation events were counted on six days between 13 August and 15 September 1999, and the maximum body dimension of the crabs and urchins was measured.

Caging experiments

We conducted a series of six caging experiments between July 2000 and October 2002 (Table 2) to test the effects of habitat and multiple-predator effects (MPE) on the crab–urchin interaction in the shallow rocky subtidal zone. Each experiment was independent from the others; newly collected organisms were used

TABLE 2. Parameters for all caging experiments conducted between July 2000 and October 2002, showing the hypotheses and habitats tested, predators used, and mean temperature over the experimental duration.

Date performed	Hypotheses tested	Habitat(s)	Predators	Temperature (°C)	
				Mean	1 SD
17 Jul–9 Aug 2000	habitat	barren, <i>Codium</i> , mussel	crabs	16.51	0.81
4 Sep–17 Sep 2000	MPE	barren	crabs + lobsters	14.85	0.41
23 Aug–9 Sep 2001	MPE	<i>Codium</i>	crabs + lobsters	14.45	0.21
20 Sep–29 Sep 2001	MPE	barren, <i>Codium</i>	crabs + lobsters	13.03	0.27
25 Jul–15 Aug 2002	MPE	mussel	crabs + lobsters	15.38	0.19
19 Sep–5 Oct 2002	MPE	mussel	crabs + lobsters	15.31	0.23

Note: Water temperature data were collected in situ at 10-min intervals over the course of the experiments using a Tidbit data logger (Onset Computer Corporation, Bourne, Massachusetts, USA) attached to one of the cages or a nearby eyebolt.

and cages were placed in different areas for each experiment. Five-sided, bottomless cages were constructed to allow consumer species unencumbered access to a 1.0 m² area of substratum. The cages consisted of a 1 × 1 × 0.5 m (L × W × H) base onto which a heavy flexible skirt was attached to fit the irregular contours of the bedrock substrate. Detailed cage designs and tests for cage artifacts are described in Appendix B.

Urchins were haphazardly distributed into each cage prior to adding predators. The mean urchin test diameter for all experiments was 62.4 ± 6.2 mm (mean ± 1 SD; *n* = 453 urchins). Using the largest size class of urchins eliminated any size-dependent mortality and minimized their escape through cage openings. All test animals (urchins, crabs, and lobsters) were measured to the nearest millimeter using vernier calipers for each experiment. Predator densities for all experiments were within the natural range for the southern Gulf of Maine (Siddon 2004).

Habitat variation

We tested the hypothesis that the mortality rate of *S. droebachiensis* from *C. borealis* predation differed among habitats. In total, 42 cages were placed in areas dominated by *Codium fragile* (*Codium*), bare space (barren), or *Mytilus edulis* (mussel), at Smith's Cove and were stocked with either two crabs and 14 urchins (Crabs) or only 14 urchins (Control). Seven replicate cages were used for the six predator-habitat combinations. Smith's Cove was dominated by *C. fragile*, with a nearly uniform layer of *M. edulis* underneath. We selectively removed all of the *M. edulis* from under the *Codium* and, conversely, pruned *Codium* from areas to create monospecific habitats of *Codium* and mussels, respectively. We removed all macrofauna and flora except crustose coralline algae to create barren habitats. All areas remained undisturbed for at least 24 hours before predators were added and cages were visually inspected every 2–3 days. Crab predation was quantified by comparing the overall mortality rates between the Crab and Control treatments (the number of urchins lost divided by the experimental duration for each habitat). Mortality rate was analyzed using a two-way ANOVA, with predator (levels: Crab, Control) and habitat (levels: *Codium*, Barren, Mussel) treatments defined as fixed effects. Data were log-transformed to meet assumptions of normality and homoscedasticity (Underwood 1997). All analyses were done using JMP statistical software Version 4.0.4 (SAS Institute 2001).

Multiple-predator effects

Similar caging experiments were used to test the importance of multiple-predator effects (MPE) on urchin mortality and community structure. Due to logistical constraints, experiments were conducted in consecutive summers. Care was taken to ensure that each experiment was initiated as close to the same dates and water temperatures as possible to minimize yearly var-

iation (Table 2). To test for MPE, we employed a substitutive design in which total consumer density in each treatment was held constant, thus eliminating the confounding effect of density-dependent predation (Sih et al. 1998). Each experiment consisted of four predator treatments: Control (2 urchins + 14 urchins), Crabs (2 crabs + 14 urchins), Lobsters (2 lobsters + 14 urchins) and Crab + Lobster (1 crab + 1 lobster + 14 urchins).

The effect of predator treatment was quantified as a per capita mortality rate, the number of urchins lost per predator (irrespective of species) divided by the experimental duration (days). The experiments were analyzed separately using one-way ANOVAs to first test for treatment effects. We then compared the mortality rate of the Crab + Lobster treatment to a predicted value using a *t* test to test for a significant, non-linear MPE (Schmitz and Sokol-Hessner 2002). The predicted value was calculated as the mean per capita mortality rate of the two single-species treatments. Thus, if the mortality rate of the Crab + Lobster treatment was significantly lower than the predicted value, a risk reduction occurred. Conversely, if the Crab + Lobster treatment was significantly greater than the predicted value, we would conclude that the addition of the lobster produced a risk enhancement for the urchins.

The change in benthic community structure was quantified photographically for each experiment, except for Trial 1 in the mussel habitat. Four photographs (0.25 m² each) inside each cage were taken at the beginning and end of the experiments with a quadrupod system (Witman 1985). The percent cover of macro-invertebrate and algal species (excluding crustose coralline algae) on each slide was quantified by identifying their presence under 200 randomly placed dots (Witman et al. 2003). Initial percent cover was 0 ± 0%, 76 ± 10%, and 71 ± 18% (mean ± 1 SD) for barren, mussel, and *Codium* beds, respectively.

The number of small crabs (<80-mm carapace width) within each cage was also counted. Small crabs were able to enter and exit the cages freely, which was a necessary trade-off of the large mesh size required to minimize other experimental artifacts due to flow and irradiance. Small crabs do not consume large urchins during summer months (when these experiments were conducted), but they become important predators in late autumn (Siddon 2004).

RESULTS

Field predation

Crab predation on urchins was commonly observed in late summer. We witnessed an average of 6.67 ± 3.89 (mean ± 1 SD) predation events per dive. Crabs ranged from 50 to 120 mm in carapace width, whereas the consumed urchins ranged from 15 to 65 mm test diameter. There was no correlation between crab car-

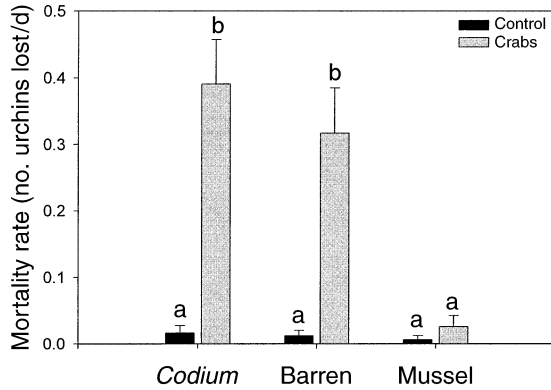


FIG. 1. Mean (+1 SE) mortality rate of sea urchins in 1.0-m² cages within the *Codium*, Barren, and Mussel bed habitats in treatments with crabs (two crabs + 14 urchins) feeding on urchins vs. control treatments (14 urchins). Different letters indicate significant differences between treatment combinations (Tukey test, $P < 0.05$). $N = 7$, except for the Crab/*Codium* ($n = 3$) and the Crab/Mussel ($n = 5$) treatment combinations.

space width and urchin test diameter ($F_{1,38} = 1.26$, $P = 0.27$, $n = 40$).

Habitat variation

Caging experiments indicated that crabs were a significant source of mortality for urchins, that mortality varied significantly with habitat, and that there was a significant predator–habitat interaction (Fig. 1; Appendix C). Post hoc Tukey tests showed that urchin mortality rate in the *Codium* and barren habitats did not differ from each other, but both were significantly higher than in the mussel habitat (Fig. 1). Only 4.3% of the urchins were consumed in the mussel habitat, compared to 36% and 48% consumed in the *Codium* and barren habitats, respectively. There was no significant difference in crab carapace widths among treatments ($F_{2,33} = 0.118$, $P > 0.89$, $n = 12$), with an overall mean of 105.7 ± 1.8 mm (mean \pm 1 SE).

Multiple-predator effects

The results from the multiple-predator effect (MPE) experiments showed that crabs and lobsters were significant predators on urchins when in isolation and that a significant risk reduction occurred for urchins in *Codium* and barren habitats when in combination. In addition, the community structure in the barren and mussel habitats changed significantly due to trait- and density-mediated indirect interactions.

In the *Codium* habitat, ANOVA on log-transformed data showed a significant difference in mortality rates among predator treatments ($F_{3,17} = 12.518$, $P < 0.001$; Fig. 2A). Post hoc Tukey tests showed that urchin mortality in all predator treatments was significantly higher than the Control treatment and the Crab treatment was significantly greater than the Lobster and the Lobster + Crab treatments (P values < 0.05). Similarly, in the

barren habitat, urchin mortality varied significantly with predator treatments ($F_{3,17} = 7.250$, $P = 0.0024$; Fig. 2B). Post hoc Tukey tests showed that the per capita mortality rate was significantly higher in the Crab treatment than any other treatment ($P < 0.05$). In the mussel habitat, however, there were no significant differences among treatments in either trial (for Trial 1, $P = 0.87$, $df = 3, 15$; for Trial 2, $P = 0.06$, $df = 3, 19$; Fig. 2C), although there was a significant increase in mortality between trials (data not shown).

Further analyses of the MPE experiments showed significant risk reductions (TMII) of urchin mortality

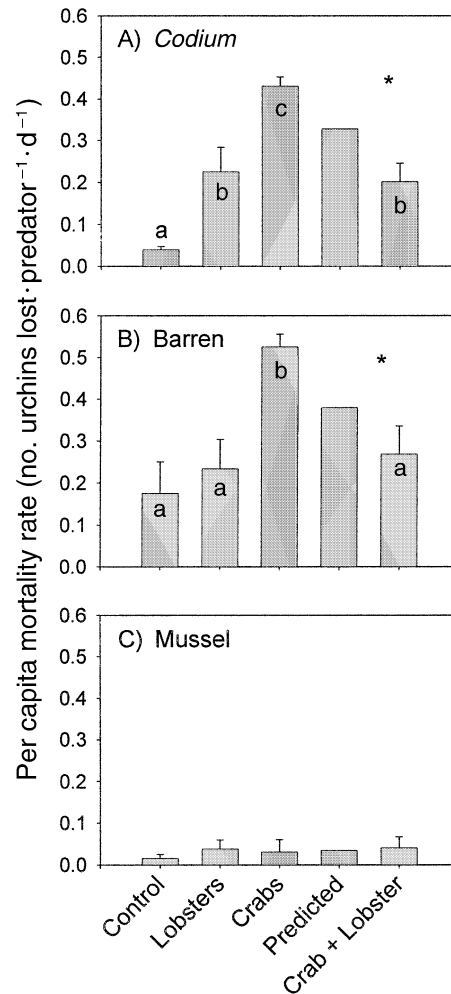


FIG. 2. Mean (+1 SE) per capita urchin mortality rate in control, single predator, and combined predator treatments in 1.0-m² cages for (A) *Codium*, (B) Barren, and (C) Mussel habitats (Trial 1). Different letters indicate significant differences between treatment combinations (Tukey test, $P < 0.05$). An asterisk indicates that the “Crab + Lobster” treatment was significantly different than predicted (risk reduction; t test, $P < 0.05$). The predicted bar was calculated as the mean per capita mortality rate of the “Lobsters” and “Crabs” treatments. $N = 5$, except for the Crab + Lobster treatment, where $n = 7, 6$, and 6 in the *Codium*, Barren, and Mussel habitats, respectively.

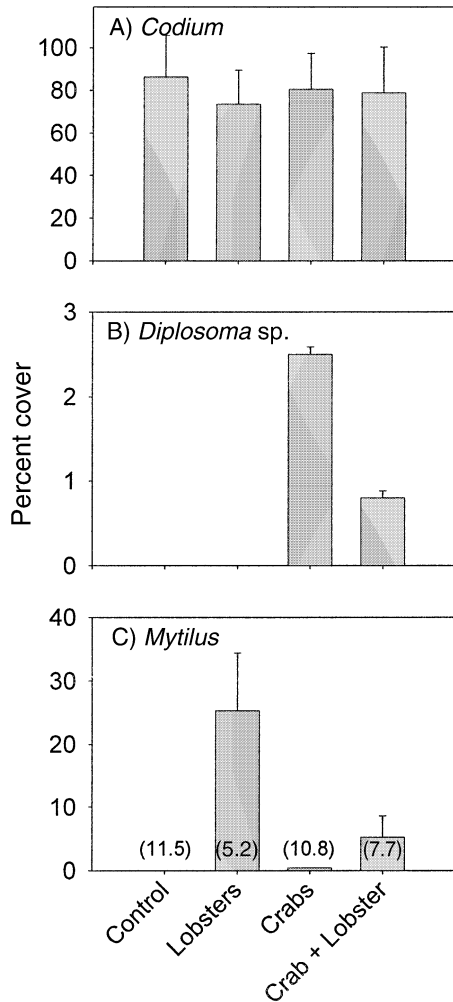


FIG. 3. Mean (+1 SE) differences in community structure, measured as percent cover in control, single predator, and combined predator treatments for (A) *Codium*, (B) *Diplosoma* sp., and (C) *Mytilus* in the *Codium*, Barren, and Mussel (Trial 2) habitats, respectively. Different letters indicate treatments that were significantly different from one another (Tukey test, $P < 0.05$). Values within parentheses indicate mean abundance of small crabs in each treatment. Sample sizes are the same as in Fig. 2.

in the barren and *Codium* habitats, but not in the mussel habitats (Fig. 2; Appendix D). The experimental Crab + Lobster treatment was significantly lower than the predicted average of the two single-species treatments. In the mussel habitat, no MPE was possible because there were no significant predator treatment effects.

The effect of predators on community structure also varied with habitat. In the *Codium* habitat, the percent cover of *Codium* was consistently high throughout the experiment ($78.8 \pm 4.4\%$; mean ± 1 SE; Fig. 3A) and there were no differences among predator treatments ($F_{3,11} = 0.43$, $P = 0.74$; data arcsine square-root transformed). In the barren habitat, percent cover of macroflora and fauna remained low overall ($<0.1\%$); how-

ever, there was a significant difference in abundance of the introduced ascidian, *Diplosoma* sp., among treatments ($F_{3,15} = 4.98$, $P = 0.01$; data arcsine square-root transformed). *Diplosoma* sp. was most abundant in the Crab treatment and absent from the Control and Lobster treatments (Fig. 3B). In the mussel habitat (Trial 2), the low mortality rate (0.28 ± 0.04 ; mean ± 1 SE) of urchins, as crabs switched to mussel prey, was associated with a dramatic decrease in mussel percent cover, which varied significantly within the predator treatment ($F_{3,19} = 5.15$, $P = 0.009$). Post hoc Tukey tests showed that percent cover of mussels was significantly higher in the Lobster treatment than the Crab and Control treatments (Fig. 3C). The percent cover of mussels was inversely related to the number of lobsters in each cage: treatments with no lobsters (Crab, Control), contained $<1\%$ mussel cover, the Crab + Lobster treatment (one lobster) contained 13% mussel cover, and in the Lobster treatment (two lobsters), 46% of the mussels remained at the end of the experiment. These data suggest that lobsters are indirectly influencing the abundance of mussels by modifying the feeding behavior of crabs (i.e., the interaction strength between crabs and urchins, a TMII).

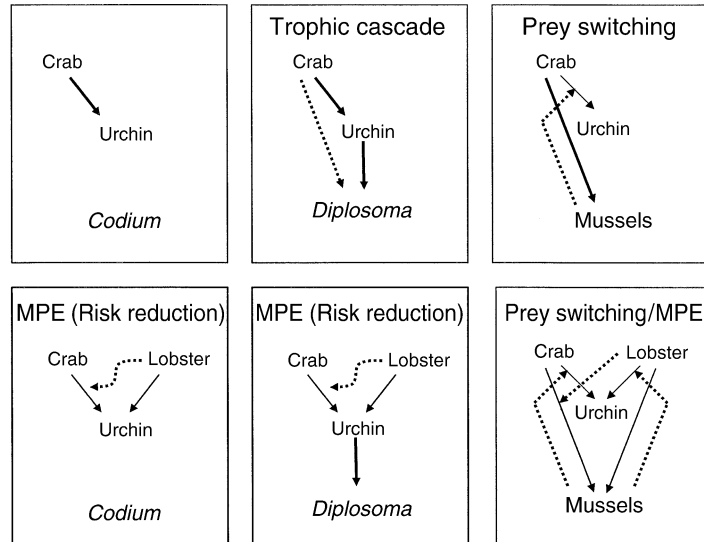
The number of small crabs (<80 -mm carapace width) found inside cages was negligible except in the mussel habitat, where a substantial alternative food source was available. Small crabs were nearly nonexistent in the barren habitat (0.43 ± 0.19 crabs/ 1 m^2 , mean ± 1 SE; $n = 21$). Small crabs were not counted in the *Codium* habitat due to its dense canopy, although few small crabs were seen when quantifying urchins. Small crabs were conspicuous in the mussel habitat (for Trial 1, 3.81 ± 0.87 crabs/ 1 m^2 , mean ± 1 SE, $n = 19$; for Trial 2, 8.70 ± 1.15 , $n = 23$; Fig. 3C). In the first trial (T1), the number of small crabs varied as a function of predator treatment ($F_{3,17} = 11.40$, $P = 0.002$; log-transformed data). A post hoc Tukey test showed that crab abundance was significantly lower in the Lobster treatment than in either the Crab or the Control treatments ($P < 0.05$). No small crabs were found in the Lobster treatment, whereas in the two treatments with no lobsters (Crab and Control treatments) 6 ± 1.14 and 7 ± 1.86 crabs (mean ± 1 SE) were found, respectively. Further analysis showed no significant MPE (i.e., risk reduction) on the number of small crabs (Appendix D).

In Trial 2, more small crabs were also found in the treatments with no lobsters than in the Lobster treatment, although differences were not significant ($F_{3,19} = 1.85$, $P = 0.17$). In addition, there were significantly more small crabs in Trial 2 than in Trial 1 (10.75 ± 1.43 and 6.55 ± 1.10 crabs, respectively; $t = -2.30$, $df = 21$, $P = 0.032$).

DISCUSSION

Our mechanistic approach to understanding community structure in the shallow rocky subtidal showed

FIG. 4. Summary of direct and indirect effects associated with the crab–urchin interaction when in different habitats and with the second (lobster) predator. Solid black arrows indicate direct trophic linkages, and dashed arrows indicate indirect effects. Indirect effect arrows that point to a species are density-mediated (i.e., interaction chains), and arrows that point at trophic linkages represent trait-mediated (i.e., interaction modifications). Curved arrows represent nonlinear MPE (risk reductions). Arrow thickness is proportional to the strength of the interactions.



that natural variation in predator–prey interactions can produce markedly different community dynamics through changes in habitat and the number of predator species. Most of the variations in consumer interactions were initiated by changes in predator behavior, and are a type of trait-mediated indirect interaction (TMII). Our approach also provides evidence that overfishing of two dominant benthic consumers may increase the abundance of non-native species in the subtidal Gulf of Maine (GOM).

Habitats and multiple predators

The variation found within one predator–prey interaction examined in different environmental contexts was striking. Our predicted mortality rates (Table 1) matched the results for two out of the three habitats tested (Fig. 1). Urchin mortality rates were relatively high in the barren habitat, as predicted, due to minimal search time and lack of alternate prey. Contrary to our predictions, however, the addition of a dense three-dimensional structure provided by *Codium* provided no spatial refuge for urchins from crab predation. The addition of an alternative food source (mussels) functionally eliminated crab predation on urchins in the mussel habitat. Mussels produced a positive indirect effect on the urchins by changing the behavior of crabs (prey switching). Thus, the availability of an alternative food source dramatically changed the interaction strength between the focal species (crabs and urchins) through a shift in predator behavior (a TMII; Fig. 4) and was more important than spatial refuges in this system.

The large variation in predator–prey interactions in the three habitats also indicates the importance of predator behavior (rather than prey behavior) in controlling the abundance of resource species in barren and mussel habitats. In the barren habitat, crabs had a positive

indirect effect on the abundance of a lower trophic level filter feeder, *Diplosoma* sp., by feeding on urchins (i.e., a trophic cascade; Fig. 4). This density-mediated indirect interaction resulted in the successful colonization of *Diplosoma* sp. in treatments where crabs fed on urchins (Crab treatment; Fig. 3B). The effect of crabs on mussels was dramatic. Crabs were able to remove all mussels within a 1 m² area within a three-week period and thus had a strong negative effect on the habitat that the mussels created. Although it was not apparent from the results of our relatively short (three-week) experiments, we assume that predation rates on urchins would increase shortly after all the mussels were consumed. However, even relatively short shifts in predator behavior may produce a significant temporal refuge, especially in highly seasonal communities (Coma et al. 2000, Siddon 2004) or in ecosystems characterized by large-scale episodic recruitment of prey species (Kelley 1994, Witman et al. 2003).

The importance of multiple predator species has gained significant recognition in recent years (Sih et al. 1998). In our system, lobsters generally dampened the foraging effectiveness of crabs, irrespective of habitat (Figs. 2 and 3). In both *Codium* and barren habitats, lobsters produced a significant, nonlinear risk reduction for the urchins, whereas this dampening effect was linear in the mussel habitat. Because no direct trophic linkage between crabs and lobsters existed (within the size classes tested), this reduction is attributed to a behavioral modification of crabs by lobsters (i.e., a TMII; Fig. 4). In the *Codium* habitat, this reduction in feeding served only to reduce the mortality rate of urchins and had no indirect effects on the community, as expected. In the barren habitat, lobsters decreased urchin mortality and effectively eliminated the trophic cascade set up in their absence by reducing the establishment of *Diplosoma* (Figs. 3B and 4). Lastly, in the

mussel habitat, mussels had a similar strong effect on both crab and lobster behavior. Mussels produced a positive TMII on urchins by decreasing the interaction strength of crabs and lobsters on urchins. Lobsters still modified crab behavior, although the effect was realized through the significant differences in mussel, rather than urchin, abundance (Fig. 3C).

The results of our experiments highlight the important influence of both density- and trait-mediated indirect interactions in subtidal communities (Fig. 4). The characteristics of the habitats play a major role in determining the types of interactions between predator and prey species, whereas the inclusion of a second predator species acts to dampen or stabilize community change. This dampening effect is common in multiple-predator experiments (e.g., Wissinger and McGrady 1993, Crowder et al. 1997, Finke and Denno 2002) and adds to the growing empirical evidence that increased food web complexity can stabilize food webs (Kondoh 2003). Lastly, our results demonstrate the magnitude of variation possible through both direct and indirect pathways, and the importance of behavioral modifications in a relatively simple community. These effects should be even more common in communities with greater species richness than the GOM (Menge 1995). Thus, trait-mediated indirect interactions should be widespread and may contribute more to community dynamics than do direct or density-mediated indirect effects.

*Introduced species, overfishing,
and community change*

Understanding the ability of exotic species to invade a system and their subsequent impact on native communities is a pressing issue in ecology (Stachowicz et al. 1999, Bertness 2002). Our results provide insight into how increased fishing pressure may facilitate the establishment of an invading species (*Diplosoma* sp.) through the direct removal of a dominant consumer species (urchins) or changes in predator behavior (crabs) at a higher trophic level.

A novel result of the manipulative experiments was that crabs and lobsters are strong interactors (sensu Paine 1980), and this status was reconfirmed for urchins. Extraction of any of these species through commercial fishing is therefore likely to change benthic community structure. In the nearshore GOM, the American lobster makes up the majority of commercial take, followed by urchins, whereas crabs comprise only a minor fishery (NOAA fisheries database for 2001).² Thus, the combination of strong interacting species and intense commercial harvest for urchins and lobsters suggests that these fisheries may increase the abundance of *Diplosoma* through trophic and behavioral pathways.

The reduction of urchin density in our studies resulted in a significant increase of *Diplosoma* over the short experimental duration. *Diplosoma* density can be

modified through a DMII (trophic cascade) where the density of urchins is controlled through strong crab predation. Therefore, we hypothesize that the removal of urchins through commercial fishing (i.e., human predation) would also increase *Diplosoma* abundance through a trophic cascade.

The TMII produced when crab and lobster predators were combined significantly reduced the interaction strength between crabs and their prey. In the absence of lobsters, crab predation increased dramatically and provided bare substrate in the barren and mussel habitats for colonization. In the barren habitat, *Diplosoma* increased in abundance and, given that mussel beds are ultimately converted to bare substrate, *Diplosoma* or other fast-colonizing, invasive species should also increase after mussels are consumed. With many more lobsters than crabs being harvested annually, increased crab predation may be widespread, leading to an increase in *Diplosoma*, but through a behaviorally mediated pathway.

Strong predatory control of urchins by *Cancer borealis* is likely to have important consequences for community structure in the Gulf of Maine beyond the results reported here, because increased recruitment and abundance of macroalgae (usually kelp) is a predictable effect of urchin removal in the North Atlantic (Himmelman et al 1983, Witman 1987). We hypothesize that *Cancer borealis* drives a trophic cascade by controlling the abundance of herbivorous urchins in localized areas of the GOM. Historical effects of overfishing may partly account for the present important role of *C. borealis* predation in the GOM subtidal; Witman and Sebens (1992) hypothesized that overfishing of large predatory fish led to increased *Cancer* crab abundance via a release of top-down control.

In summary, our results illustrate the magnitude of variation possible through both direct and indirect pathways, and the importance of behavioral modifications and habitat context in a relatively simple community.

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APPENDIX A

A photograph of crab predation on a sea urchin is available in ESA's Electronic Data Archive: *Ecological Archives* E085-095-A1.

APPENDIX B

A description of the cage design and artifact testing is available in ESA's Electronic Data Archive: *Ecological Archives* E085-095-A2.

APPENDIX C

A statistical table for crab predation and habitat effects on urchin mortality is available in ESA's Electronic Data Archive: *Ecological Archives* E085-095-A3.

APPENDIX D

A statistical table for multiple predator effects is available in ESA's Electronic Data Archive: *Ecological Archives* E085-095-A4.