TRAIT-MEDIATED EFFECTS IN ROCKY INTERTIDAL FOOD CHAINS: PREDATOR RISK CUES ALTER PREY FEEDING RATES

GEOFFREY C. TRUSSELL,[1,2,3] PATRICK J. EWANCHUK,[2] AND MARK D. BERTNESS[2]

[1]*Marine Science Center, Northeastern University, 430 Nahant Road, Nahant, Massachusetts 01908 USA*
[2]*Department of Ecology and Evolutionary Biology, Brown University, Providence, Rhode Island 02912 USA*

Abstract. The influence of predation on rocky intertidal community structure has long emphasized the importance of indirect interactions. Most efforts in this area have focused on the density-mediated, or lethal effects, of predators on prey density. Recently, there has been growing interest in trait-mediated indirect interactions (TMIIs): the presence of a predator in the environment influences the interaction between two other species (prey and their resource) by altering a trait of the prey species. For example, waterborne cues released by predators can cause changes in prey species behavior, such as feeding rates, thereby altering the impact of the prey species on their resources. Thus, TMIIs represent the non-lethal effects of predators that contrast with the more traditional emphasis on lethal indirect effects. Marine ecologists are just beginning to explore the role of TMIIs in their systems.

We examined whether risk cues released by a ubiquitous crab predator (*Carcinus maenas*) influence the abundance of two dominant species in the rocky intertidal zone (barnacles [*Semibalanus balanoides*] and fucoid algae [*Ascophyllum nodosum*]) by altering the behavior of two of its snail prey (*Nucella lapillus* and *Littorina littorea*). We found that the presence of green crab risk cues can have strong cascading indirect effects on the abundance of barnacles and fucoid algae. *N. lapillus* exposed to risk cues consumed up to 29% fewer barnacles compared to conspecifics feeding in the absence of risk cues, whereas *L. littorea* exposed to risk cues consumed 459% fewer fucoids compared to conspecifics feeding in the absence of risk cues. These cascading interactions appear to reflect suppression of snail feeding by predator risk cues. In both food chains, snails exhibited more refuge-seeking behavior and grew less in the presence of risk cues. Our experiments suggest that TMIIs may have an important and underappreciated influence on species interactions that shape community dynamics on rocky intertidal shores.

Key words: barnacles; community structure; crab predator; food chains; fucoid algae; indirect effects; plasticity; prey species behavior; rocky intertidal zone; snails; trait-mediated indirect interactions.

INTRODUCTION

In freshwater and marine communities studies of the importance of species interactions to community structure have been significantly influenced by the classic work of Brooks and Dodson (1965) and Paine (1966). These studies were the precursors of the trophic cascade concept, which has fostered a prolific body of work in terrestrial (Schmitz 1992, 1993, 1994, 1998, Belovsky and Slade 1993, Beckerman et al. 1997, Schmitz et al. 1997), freshwater (Carpenter et al. 1985, Mills et al. 1987, McQueen et al. 1989), and marine systems (Estes and Palmisano 1974, Paine 1980, Estes et al. 1998, Menge 2000*a*). In simplest terms, a trophic cascade describes how top predators, by regulating herbivore density via consumption, exert an indirect effect on the abundance of primary producers (Pace et al. 1999). For example, the intensity of fish predation on

herbivorous zooplankton can indirectly influence levels of primary production in lake ecosystems (Threlkeld 1988, Carpenter and Kitchell 1993, Vanni et al. 1997).

Traditionally, studies on the role of predators in trophic cascades have focused on direct consumer–resource interactions (Sih et al. 1985). Hence, it is the effect of predator consumption rates (i.e., lethal effects) that propagate through the food chain, leading to changes in the density of prey species and the abundance of the prey's resources. Growing evidence suggests, however, that trophic interactions are not solely driven by density changes in trophic assemblages caused by direct consumer–resource interactions. Instead, predators also can alter prey traits (nonlethal effects), such as behavior and morphology, resulting in large impacts on competitive interactions (Peacor and Werner 1997, 2000, 2001) and community structure (Turner and Mittlebach 1990, McIntosh and Townsend 1996, Beckerman et al. 1997, Schmitz et al. 1997, Raimondi et al. 2000, Turner et al. 2000). Indirect interactions caused by nonlethal predator effects have been termed trait-mediated indirect interactions (TMIIs, Abrams et al. 1996), interaction modifications

(Wootton 1993), or behavioral indirect interactions (Miller and Kerfoot 1987) to differentiate them from the more commonly known density-mediated indirect interactions (DMIIs, Abrams et al. 1996) describing effects propagated via changes in density caused by interacting species.

Although a relatively new area of research, ecologists are making rapid progress in understanding the ecological importance of TMIIs. In general, TMIIs describe how a predator affects a trait of a second species, which in turn affects the interaction of the second species with a third species. TMIIs constitute a form of higher order interaction that will likely influence the direct interactions between prey and their resource and overall community dynamics (Abrams 1983, Wootton 1993, 1994, Adler and Morris 1994, Billick and Case 1994, Kareiva 1994). TMIIs between predators and prey may be important at both high and low predation rates because nonlethal effects can (1) occur independently of lethal effects and (2) be transmitted throughout the prey's life even though they may be eventually consumed (Peacor and Werner 2001). Thus, a better understanding of TMIIs will improve our empirical understanding of the processes shaping ecological communities and our ability to model community dynamics.

In aquatic systems, TMIIs often occur because of changes in prey traits that are induced by exposure to waterborne predator risk cues (Tollrian and Harvell 1999). Modified traits can be morphological and life historical, but considerable emphasis has been placed on predator-induced changes in prey behavior (Werner 1991, 1992). This is not surprising because unlike morphological responses, which may be constrained by ontogeny or growth rate, behavioral responses are often immediate. Predator-induced changes in prey behavior that reduce their risk of predation, such as alterations in feeding rate or habitat use (Dill 1987, Lima 1988a, b, Werner and Anholt 1993, 1996, Turner 1996, Turner et al. 1999) also may modify the prey's impact on its resources (Turner and Mittlebach 1990, Turner 1997, Turner et al. 2000) and ultimately the overall structure of the community (McIntosh and Townsend 1996, Beckerman et al. 1997, Schmitz et al. 1997, Raimondi et al. 2000).

Rocky intertidal food chains: predatory crabs, snails and barnacles and algae

Considerable work indicates that many factors, including predation (Paine 1966, Menge 1976), herbivory (Lubchenco 1978), competition (Connell 1961), environmental stress (Dayton 1971, Sousa 1979), and recruitment (Gaines and Roughgarden 1985) are important in structuring rocky intertidal communities (see Menge and Branch 2001 for review). Recently there is growing interest in the role of indirect interactions in producing community patterns (Wootton 1992, 1993, 1994, Menge 1995). However, despite this elegant work

on interaction chains and interaction modifications (a form of TMII), our understanding of the importance of TMIIs to rocky intertidal community pattern and dynamics is still limited (but see Raimondi et al. 2000).

Inducible defenses in intertidal snails

The invasive green crab, *Carcinus maenas*, is a voracious predator common to sheltered rocky intertidal shores in southern New England. This crab's broad diet includes the herbivorous snail *Littorina littorea* and the carnivorous snail *Nucella lapillus*, two species that can strongly influence the recruitment success and population dynamics of perennial (e.g., *Ascophyllum nodosum*, *Fucus vesiculosus*) and ephemeral algae (e.g., *Ulva* sp., *Enteromorpha* sp.) and barnacles (*Semibalanus balanoides*) (Menge 1976, 1978a, b, Lubchenco 1978, Leonard et al. 1998, 1999, Bertness et al. 2002). However, while the green crab can indirectly influence algal and barnacle communities via its density-mediated effects on *N. lapillus* and *L. littorea*, the role of TMIIs in these food chains has not been explored (but see Trussell et al. 2002).

Several studies have shown that carnivorous (*N. lapillus*) and herbivorous (*L. littorea*, *L. obtusata*) snails exhibit inducible increases in shell thickness in response to waterborne risk cues released by the green crab (Appleton and Palmer 1988, Palmer 1990, Trussell 1996, 2000, Trussell and Smith 2000, Trussell and Nicklin 2002). These inducible defenses are thought to reduce snail vulnerability to crab predation, thus modifying the impact of crabs on snail density and, in turn the impact that snails have on the community. Perhaps equally important, however, are the strong behavioral responses that accompany these morphological changes. Snails exposed to predatory crab risk cues exhibit reduced activity, reduced feeding levels, and increased use of inconspicuous or "refuge" habitats (Palmer 1990, Marko and Palmer 1991). Palmer (1990) noted that *N. lapillus* feeding in the presence of green crab risk cues preferred to consume barnacles located on the underside rather than on top of stones placed within his experimental chambers. In contrast, *N. lapillus* feeding in the absence of these cues showed little discrimination with respect to the position of their barnacle prey and they consumed significantly more barnacles. The presence of inducible defenses, whether morphological or behavioral (also see Hadlock 1980), in multiple snail species in response to green crab risk cues suggests that TMIIs may be operating in these systems.

We examined the importance of behaviorally based TMIIs to species interactions in two simple, but important, rocky intertidal food chains. Using manipulative experiments in laboratory mesocosms, we allowed *Nucella lapillus* to feed on experimental barnacle communities and *Littorina littorea* to feed on experimental fucoid algal communities in the presence and absence of green crab risk cues. Our data revealed that

predator risk cues led to increased barnacle and fucoid abundance by inducing both reductions in snail feeding rates and increases in their use of refuge habitats. Hence, our results represent an important first step in understanding the potential importance of TMIIs to species interactions and community dynamics on rocky intertidal shores.

MATERIALS AND METHODS

Establishment of experimental barnacle and fucoid algal communities

To examine the effects of predator risk cues on snail feeding and behavior and subsequent effects on barnacle and fucoid abundance, we first created initial community states on experimental granite tiles. To establish barnacle (Semibalanus balanoides) communities, 120 granite tiles (15 × 15 cm) were anchored with bolts to a granite outcropping (Upper River Narrows) in the intertidal zone in the Damariscotta River, a tidal estuary in central Maine, in late February 2000. We chose this site because previous work has shown that it typically has high barnacle recruitment (Leonard et al. 1998, Bertness et al. 2002). Barnacle settlement commenced in mid-March, lasted for several weeks, and was remarkably uniform across all tiles. All tiles were returned to the laboratory in late March and maintained in seawater tables until the experiment began.

To create fucoid algal communities, 120 granite tiles (15 × 15 cm) were anchored with bolts at another granite outcropping (Lowes Cove) having dense (90–100% of available surface area) Ascophyllum nodosum cover in late February. Tiles were left in the field until early June to ensure adequate recruitment. Because snails (Littorina littorea) begin to emerge from the subtidal in late spring in response to warming air and water temperatures, it was necessary to enclose all tiles with galvanized hardware cloth to prevent snail grazing from impacting fucoid recruitment success.

Trait-mediated effects on barnacle density: experimental design

To ensure that barnacle densities were similar among all experimental treatments at the beginning of the experiment, we made initial estimates of barnacle density on each tile by counting the total number of barnacles in three quadrats (9 cm²) randomly placed on each tile. Of the original 120 tiles, we identified 96 tiles having similar barnacle densities (13.70 ± 0.21 barnacles/cm², mean ± 1 SE). From these 96 tiles, we established 48 pairs of tiles having similar barnacle densities (13.69 ± 0.10 barnacles/cm²). Each pair of tiles was then randomly allocated to 48 independent replicate chambers (35 × 15 × 15 cm), each having an independent water supply. Hence, there were two tiles per experimental chamber. Preliminary analysis of estimates of the total initial number of barnacles on each pair of experimental tiles detected no significant differences among our ex-

perimental treatments (Snail Density and Risk Cue, see below) and their interaction (ANOVA, all $P > 0.63$). A priori, we included two tiles per chamber because we wanted to ensure that there was an adequate barnacle supply for feeding snails. Pairs of tiles are not independent from one another and were therefore treated as a single experimental unit when making final counts to assess the impact of snail feeding on barnacle density.

Two treatments (Risk Cue and Snail Density) each having two levels (Crab and No Crab; High and Low, respectively) were randomly applied to the experimental units. Twenty-four replicates contained three individually marked juvenile (shell length = 6.54 ± 0.06 mm, mean ± 1 SE) Nucella lapillus (Low Density) and the remaining 24 contained six juvenile (shell length = 6.58 ± 0.05 mm) N. lapillus (High Density), three of which were individually marked. Marked snails in both treatments were used to assess the effect of risk cues and snail density on snail growth. Our density treatments (Low Density = 108 snails/m², High Density = 216 snails/m²) are within natural densities of N. lapillus in the field (311.5 ± 54.2 snails/m², range = 0–460 snails/m²).

Both snail density treatments were exposed to either the presence (Crab) or absence (No Crab) of waterborne risk cues released by the green crab (Carcinus maenas). Hence, there were 12 replicates for each Snail Density × Risk Cue treatment combination. The Crab treatment was created by placing a perforated plastic tub (15 cm diameter) containing a single male green crab and 15 N. lapillus (conspecific stimulus snails) inside 12 replicate experimental chambers for each density treatment. This design has been used in other experiments examining predator-induced morphological plasticity in L. obtusata (Trussell 1996, 2000, Trussell and Smith 2000, Trussell and Nicklin 2002), and it exposes free-ranging snails within each experimental chamber to risk cues released by crabs and the conspecifics they are feeding on. We should point out that while both cue types are important, the available data indicate that risk cues from green crabs are responsible for the majority of the induced morphological plasticity in snails (Appleton and Palmer 1988, Trussell and Nicklin 2002). The No Crab controls had similar plastic tubs placed within the remaining 12 replicate chambers for each snail-density treatment, but these contained only live conspecific snails. Every week for the duration of the experiment, a fresh batch of conspecific snails was added to each Crab and No Crab chamber. This experiment ran for 60 d, at which time all barnacles remaining on experimental tiles were counted and morphological measurements on experimental snails were made (see Materials and Methods: Snail morphometrics).

Trait-mediated effects on fucoid density: experimental design

In early June, all experimental fucoid tiles ($N = 120$) were returned from the field to the laboratory for as-

sessment of fucoid recruitment density. Precise counts of initial fucoid density, which require a microscope, were simply not possible given the extremely high recruitment densities (often in excess of 300 individuals/cm²). Hence, tiles were scanned underneath a microscope and recruitment density was qualitatively characterized. Only those tiles deemed as having uniformly high recruitment were used in the experiment. From this pool of suitable tiles ($N = 48$), we randomly allocated individual tiles to experimental treatments.

Two treatments, each having two levels, were replicated twelve times: Grazing (Snail, No Snail) and Risk Cues (Crab, No Crab). For the Grazing treatment, 24 replicates received four individually marked juvenile (shell length = 5.39 ± 0.02 mm, mean ± 1 SE) *Littorina littorea*, and the remaining 24 replicates received no snails. These densities (144 snails/m²) are within densities of *L. littorea* in the field for juveniles (229 ± 54.02 snails/m², range = 48–484 snails/m²) and adults (207 ± 24.68 snails/m², range = 124–324 snails/m²).

Twelve replicates of each Grazing treatment were subjected to either the presence or absence of risk cues (Crab or No Crab). We included a No Snail/Crab and a No Snail/No Crab experimental combination because we wanted to determine whether the presence of green crabs and associated risk cues and excretory products had a fertilization effect on the fucoid community.

Single tiles were randomly assigned to 48 replicate chambers, each having an independent supply of flowing seawater. Each chamber (27 × 15 × 5 cm) was divided into two sections by a perforated barrier. One section (16 × 15 × 5 cm, Tile Section) housed the tile and had a plastic mesh (3.75 × 2.90 mm) roof to permit water flow and light penetration. The other section (11 × 15 × 5 cm, Risk Cue Section) had a solid, clear plastic roof and contained either a single male green crab and 15 conspecific *Littorina littorea* (Crab) or just 15 conspecific *L. littorea* (No Crab). Flowing seawater was delivered to the Risk Cue section of each chamber via plastic tubing. Water then passed through the perforated barrier, into the experimental section housing the granite tile, and exited through the mesh opening above the tile. This design also ensured that experimental snails grazing on the tiles were exposed to risk cues originating from the upstream section of the chamber. Each of these chambers was placed within a larger (35 × 15 × 15 cm) plastic tub (the same size as those used in the *Nucella lapillus* experiment). Hence, green crab risk cue concentrations (on a volumetric basis) were probably similar in both experiments.

This experiment ran for 150 d, at which time the number of fucoid germlings remaining on each tile was counted. A grid composed of 1-cm² squares was placed over each tile, and the number of fucoids in 25 randomly chosen 1-cm² squares was counted. All counts were performed using a dissecting microscope. We chose to randomly subsample each tile because count-

ing all the fucoid germlings on each tile (particularly in the Crab and No Snail treatments) was not feasible. All of the morphological measurements made on snails at the beginning of the experiment were repeated (see *Materials and Methods: Snail morphometrics*).

Snail morphometrics

Because we wanted to determine whether predator-induced suppression of snail feeding influenced snail growth, we made morphological measurements on both *Nucella lapillus* and *Littorina littorea* at the beginning and end of each experiment. Measurements of shell length and shell thickness of *N. lapillus* and *L. littorea* were made following Palmer (1990) and Trussell (1996), respectively. However, we were unable to measure initial shell thickness for *N. lapillus* because their fragile, thin shells often broke when we attempted to do so.

To assess treatment-specific differences in tissue growth, we used the nondestructive, buoyant weighing technique of Palmer (1982). Briefly, snails were weighed while submerged in seawater to obtain an estimate of shell mass. Estimates of actual shell mass were then calculated from previously determined regressions of actual shell mass (Y) as a function of submerged mass (X). Snails were then allowed to dry in air for ~30 min and extravisceral water was removed from the aperture with absorbent tissue before weighing the snail in air. Estimates of wet tissue mass were calculated by subtracting the estimate of actual shell mass from the mass of the snail obtained when weighed in air. These measurements at the beginning and end of the experiment allowed us to calculate tissue growth. More detailed descriptions of this method are provided elsewhere (Palmer 1982, Trussell 2000, Trussell and Smith 2000, Trussell and Nicklin 2002).

We should note that analysis of initial trait values for *Nucella lapillus* revealed no significant differences in shell length among experimental groups (all $P \geq$ 0.14). There were subtle, but significant differences among experimental groups for *N. lapillus* tissue mass ($P = 0.005$), with snails in the Crab treatment having slightly greater tissue mass (21.38 ± 0.44 mg, mean ± 1 SE) than those in the No Crab treatments (19.57 ± 0.42 mg). However, these differences are much smaller than, and opposite to, our final result of less tissue mass for snails raised in the Crab (32.92 ± 5.39 mg) compared to those raised in the No Crab (75.08 ± 5.16 mg) treatments ($P < 0.0001$). We detected no significant differences among risk treatments for initial shell length ($P = 0.51$), tissue mass ($P = 0.59$), and shell thickness ($P = 0.75$) of *Littorina littorea*.

Statistical analyses

All statistical analyses were performed using JMP software for the Macintosh (JMP 1995). Data were transformed when necessary (to meet assumptions of parametric tests) using the square-root transformation
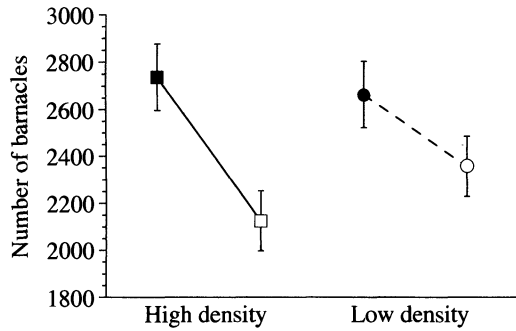
FIG. 1. Barnacle (*Semibalanus balanoides*) density (mean ± 1 SE, from ANOVA) for experimental tiles subjected to high-density and low-density *Nucella lapillus* feeding in the presence (solid square, solid circle) and absence (open square, open circle) of risk cues from *Carcinus maenas*. Values for each treatment were obtained by counting all barnacles on each pair of tiles for each replicate at the end of the experiment (see *Methods*).

for counts and the logarithmic transformation for morphological data. We analyzed final barnacle density with a two-way ANOVA that considered Snail Density and Risk Cue treatments as fixed effects. Final fucoid density was analyzed with a two-way nested ANOVA that considered Grazer treatment and Risk Cue treatment as fixed effects. Because multiple counts on each tile were used to estimate fucoid density, replicate chambers were considered a random effect nested within each experimental combination. This nested term was used by JMP to construct error mean squares, F ratios, and degrees of freedom for main effects and their interaction (SAS 1995).

Morphological data on experimental snails were analyzed with two-way ANCOVAs with the same main

effects used in our models evaluating community responses. Because there were multiple, and thus nonindependent, snails in each replicate, replicates were again treated as a random effect nested within each experimental combination. For growth analyses, the difference between initial and final measurements was the response variable and the initial value of the trait in question was used as the covariate. For analysis of shell thickness data, shell length was used as the covariate. Although slopes in all cases were homogeneous (all $P > 0.34$), thus satisfying the parallel slopes assumption of ANCOVA, these terms were not pooled.

RESULTS

Treatment differences in barnacle density, and N. lapillus growth and induced defense

The two-way ANOVA on final barnacle density revealed a strong Risk Cue effect ($F_{1,40} = 11.65$, $P = 0.0015$) with *Nucella lapillus* feeding in the absence of risk cues consuming 28.8% more barnacles (High Density treatment) and 13% more barnacles (Low Density treatment) compared to snails feeding in the presence of risk cues (Fig. 1). Our analyses detected no significant Snail Density effect ($F_{1,40} = 0.34$, $P = 0.56$) and no significant Risk Cue × Snail Density interaction ($F_{1,40} = 1.30$, $P = 0.26$).

Patterns of snail growth were consistent with predator-induced reductions in snail feeding rates. *N. lapillus* feeding in the presence of risk cues grew 118.0–133.7% less in terms of shell length (Table 1, Fig. 2) and 524–1151% less in terms of tissue mass (Table 1, Fig. 3) compared to those feeding in the absence of risk cues. There were no significant Snail Density effects on snail growth (Table 1). Inducible defenses (i.e.,

TABLE 1. Summary of two-way nested ANCOVAs on the effect of *Nucella lapillus* density (High, Low) and risk cues (Crab, No Crab) on *N. lapillus* growth and shell thickness.

Source	df	MS	F	P
Shell length growth (Y) vs. initial shell length (X)				
Risk cues (R)	1	143.86	24.51	<0.0001
Snail density (S)	1	5.28	0.90	0.3480
Risk cues × Snail density	1	1.42	0.26	0.6120
Replicate(R,S)	41	5.89	1.08	0.3846
Slope	1	1.62	0.30	0.5883
Error	71	5.47		
Tissue mass growth (Y) vs. initial tissue mass (X)				
Risk cues (R)	1	6.67×10^4	40.65	<0.0001
Snail density (S)	1	3.37×10^3	2.05	0.1583
Risk cues × Snail density	1	298.93	0.20	0.6599
Replicate(R,S)	41	1.66×10^3	1.08	0.3775
Slope	1	460.91	0.30	0.5847
Error	71	1.53×10^3		
Final shell thickness (Y) vs. final shell length (X)				
Risk cues (R)	1	0.19	37.88	<0.0001
Snail density (S)	1	0.01	2.77	0.1006
Risk cues × Snail density	1	8.1×10^{-4}	0.14	0.7132
Replicate(R,S)	41	4.82×10^{-3}	0.80	0.7796
Slope	1	1.48×10^{-3}	0.24	0.6222
Error	71	6.03×10^{-3}		

GEOFFREY C. TRUSSELL ET AL.

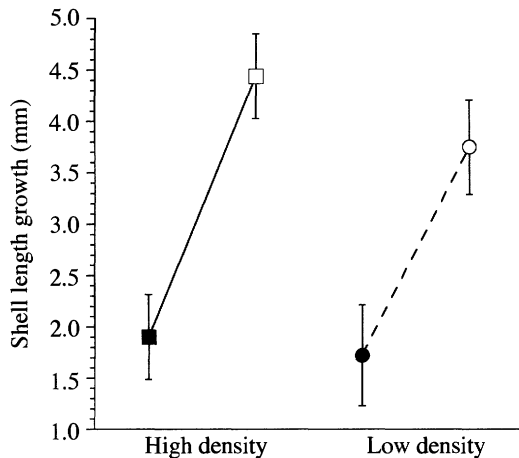FIG. 2. Change in shell length (mean ± 1 SE) of *Nucella lapillus* raised at high and low snail densities and in the presence (solid square, solid circle) and absence (open square, open circle) of risk cues from *Carcinus maenas*. Results are least-squares means from ANCOVA (see Table 1).

FIG. 3. Tissue growth (mean ± 1 SE) of *Nucella lapillus* raised at high and low snail densities and in the presence (solid square, solid circle) and absence (open square, open circle) of risk cues from *Carcinus maenas*. Results are least-squares means from ANCOVA (see Table 1).
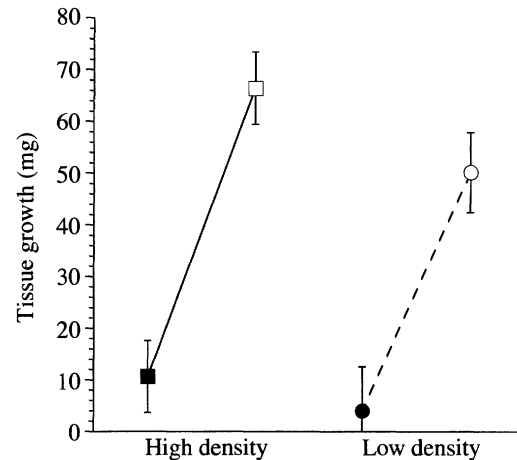
increased shell lip thickness) also were evident. Snails exposed to risk cues produced shells that were 27.3–33.3% thicker compared to those that were not exposed to risk cues (Table 1, Fig. 4).

Treatment differences in fucoid density, and L. littorea growth and induced defense

We detected similar effects in our experiment examining how risk cues mediate the impact of *Littorina littorea* grazing on fucoid germlings (Table 2, Fig. 5). Tiles subjected to snail grazing in the presence of risk cues had 460% more fucoids than those subjected to snail grazing in the absence of risk cues (linear contrast, $P < 0.0001$; Fig. 5). A strong Risk Cue × Grazer interaction indicated that the effects of risk cues on fucoid density differed among Grazer treatments. There was no significant difference (linear contrast, $P = 0.7192$; Fig. 5) in fucoid density between the Crab/No Snail and the No Crab/No Snail treatments indicating that the presence of green crab risk cues and excretory products alone did not affect fucoid density. There also was no significant difference in fucoid density between the Crab/Snail and the Crab/No Snail treatments (linear contrast, $P = 0.5216$; Fig. 5). This similarity in fucoid density suggests that the suppressive effect of risk cues on snail feeding was so large that it was essentially equivalent to having no snails grazing on the tile. The strong effect of snail grazing on fucoid density in the absence of risk cues was evident after comparing the No Crab/Snail and the No Crab/No Snail treatments. In the absence of risk cues, tiles subjected to snail grazing had 603.7% fewer fucoids than tiles experiencing no snail grazing (linear contrast, $P < 0.0001$; Fig. 5).

Reduced snail feeding as evidenced by morphological plasticity in response to risk cues also was detected,

but the results were a little more complex for *Littorina littorea*. In terms of tissue growth, snails grazing in the absence of risk cues grew 45.6% more than snails grazing in the presence of risk cues (Table 3, Fig. 6). Repeated-measures ANCOVA (Table 4, Fig. 7a) revealed that total overall change in shell length of snails raised without risk cues was significantly greater than that for snails raised with risk cues. However, when changes in shell length were analyzed separately for each time period, it became clear that this treatment effect was primarily caused by growth differences during the first half of the experiment (Fig. 7b). During the first half of the experiment, snails raised without risk cues grew 45.8% more than snails raised with risk cues (ANCOVA: $F_{1,22} = 45.85$, $P < 0.0001$). However, during
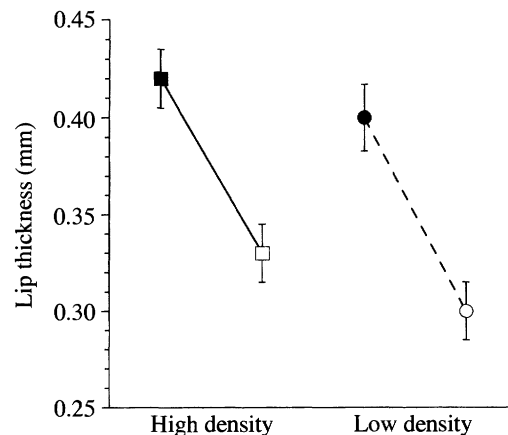

FIG. 4. Final apertural lip thickness (mean ± 1 SE) of *Nucella lapillus* raised at high and low snail densities and in the presence (solid square, solid circle) and absence (open square, open circle) of risk cues from *Carcinus maenas*. Results are least-squares means from ANCOVA (see Table 1).

TABLE 2. Summary of two-way ANOVA on the effect of *Littorina littorea* grazing (Present, Absent) and risk cues (Crab, No Crab) on fucoid density after 150 d.

Source	df	MS	F	P
Risk cues (R)	1, 44	518.44	9.88	0.0030
Grazing (G)	1, 44	1095.35	20.87	<0.0001
Risk cues × Grazer	1, 44	701.02	13.36	0.0007
Replicate(R, G)	44, 1152	52.48	13.96	<0.0001
Error	1152	3.76		

the second half of the experiment, there was no statistically significant difference in the growth rate of snails from both treatments (ANCOVA: $F_{1,22} = 0.13$, $P = 0.7172$).

Inducible defenses in the form of plastic increases in shell thickness also depended on the measurement period. Halfway through the experiment, snails from the Crab treatment had shells that were 13.4% thicker compared to those from the No Crab treatment (ANCOVA: $F_{1,22} = 12.05$, $P = 0.001$; Fig. 8). However, by the end of the experiment, there was no statistical difference in shell thickness among the two treatments (ANCOVA: $F_{1,22} = 0.65$, $P = 0.4259$; Fig. 8).

DISCUSSION

Our experiments suggest that predator effects on prey traits in addition to prey density may importantly influence species interactions and community structure in the rocky intertidal zone of New England. In the presence of green crab risk cues, *Nucella lapillus* consumed 13–29% fewer barnacles (Fig. 1) and *Littorina littorea* consumed 459% fewer fucoids (Fig. 5) compared to conspecifics not exposed to risk cues. These risk-specific differences in the impact of both snail species on their respective food resources likely reflect predator-induced changes in snail behavior and feeding rates.
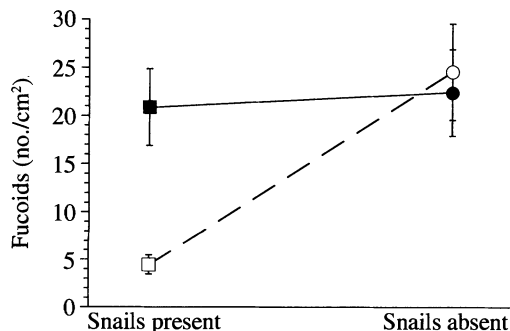

FIG. 5. Final fucoid density (cm⁻²; mean ± 1 SE) on experimental tiles with and without *Littorina littorea* grazing in the presence (solid square, solid circle) and absence (open square, open circle) of risk cues from *Carcinus maenas*. Values (from ANOVA, see Table 2) for each treatment were obtained at the end of the experiment by counting all the fucoids in 25 1-cm² quadrats randomly placed on each tile.

Risk cues induce differences in snail behavior and growth

Although not quantitatively characterized, there were clear differences in snail behavior among risk treatments. In the barnacle experiment, we often observed *N. lapillus* drilling the sides of barnacle tests ("test drilling") instead of the more common method of sitting on top of the barnacle and drilling between the opercular plates (Barnett 1979). Test drilling is certainly more inconspicuous because it allows the snail to remain snugly against the granite substratum among the interstices of barnacle tests. However, this tactic may be more time consuming and energetically expensive because it does not exploit what is presumably the most vulnerable region (sutures between the opercular plates) of the barnacle (Barnett 1979). We never observed test drilling in the absence of risk cues. In addition, both *N. lapillus* and *L. littorea* exposed to risk cues often remained on the underside of experimental tiles (also see Palmer 1990), whereas in the absence of risk cues the snails were consistently on top of tiles consuming barnacles and fucoids. The greater refuge use by both snail species in the presence of risk cues is certainly consistent with their diminished impact on their respective food resource.

This reduced impact is clearly evident from the reduced growth rates and increased levels of inducible defense for snails in the presence of risk cues. When exposed to risk cues, both snail species grew significantly less in terms of shell length (Figs. 2 and 7a, b) and tissue mass (Figs. 3 and 6) compared to conspecifics that were not exposed to risk cues. Moreover, exposure to risk cues induced increased shell thickening in both snail species (Figs. 4 and 8), which also is consistent with reduced snail feeding rates. Because there is a limit to the maximum rate of shell calcification (Palmer 1981, 1992), snails devoting shell ma-

TABLE 3. Summary of one-way ANCOVA on the effect of risk cues (Crab, No Crab) on *Littorina littorea* tissue growth after 150 d.

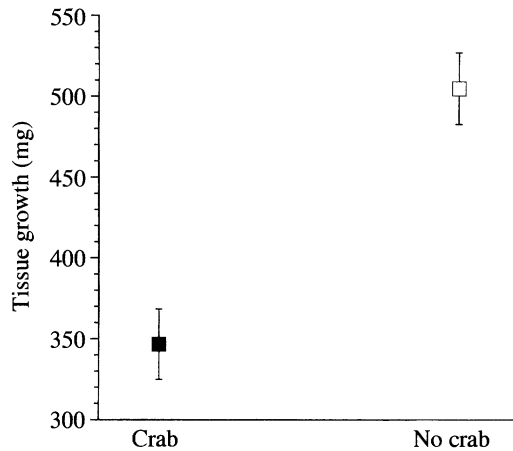| Source	df	MS	F	P
Risk cues	1, 22	5.15×10^5	23.02	<0.0001
Replicate(Risk cues)	22, 67	2.52×10^4	3.95	<0.0001
Slope	1, 67	2.52×10^3	0.39	0.5327
Error	67	6.39×10^3		

FIG. 6. Tissue growth (mean ± 1 SE) of *Littorina littorea* raised in the presence (solid square) and absence (open square) of risk cues from *Carcinus maenas*. Results are least-squares means from ANCOVA (see Table 3).

terial to increased shell thickening must do so at the expense of linear shell growth. Thus, snails with slower growing shells are typically thicker and have less tissue mass than fast growing ones (Kemp and Bertness 1984). In our experiments, thicker shells in both snail species were accompanied by reduced linear growth (also see Trussell and Nicklin 2002).

Our *Littorina littorea* data, in particular, illustrate the relationship between the amount of shell thickening and linear shell growth. Just over halfway through the experiment, *L. littorea* raised with risk cues grew 45.8% less compared to snails raised without risk cues (Fig. 7a). However, during the second half of the experiment, snails raised without risk cues slowed their growth considerably, to the point that there was no difference in shell growth among risk treatments (Fig. 7b). This change in *L. littorea* growth rate may explain why there was a convergence in shell thickness by the end of the experiment (Fig. 8). These data also suggest that, in the absence of risk cues, snails delay shell thickening until they reach a certain size. Doing so delays the onset of tissue mass trade-offs that typically accompany the production of thicker shells. Such trade-

TABLE 4. Summary of two-way repeated-measures AN-COVA on the effect of risk cues (Crab, No Crab) on change in shell length of *Littorina littorea* after 88 and 150 d.

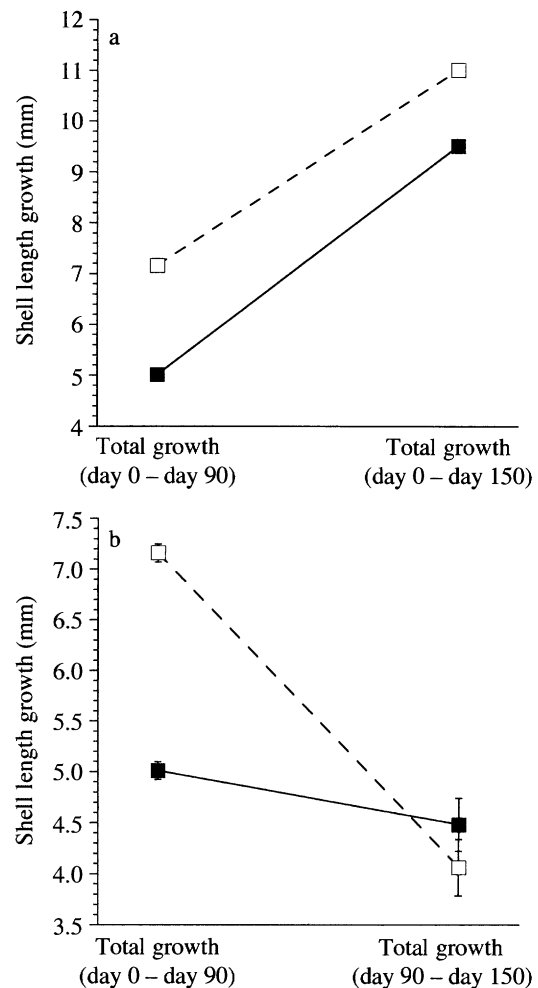| Source	df	Wilks' lambda	F	P
Between subjects				
Risk cues	1, 68	0.94	4.62	0.0351
Replicate(Risk cues)	22, 68	0.44	3.97	<0.0001
Within subjects				
Time	1, 68	0.93	5.45	0.0225
Time × Treatment	1, 68	0.98	1.18	0.2806
Slope	1, 68	0.99	0.92	0.3399

FIG. 7. Change in shell length (mean ± 1 SE) of *Littorina littorea* raised in the presence (solid squares) and absence (open squares) of risk cues from *Carcinus maenas*. (a) Results are least-square means from a repeated-measure ANCOVA (see Table 4) that examined the total change in shell length at two time intervals: after 88 d and after 150 d. Note that, overall, snails in the risk-cue treatment grew less than those raised without risk cues. (b) Results are least-squares means from separate ANCOVAs (see *Results*) examining the total change in shell length for each time period. Hence, this analysis is different from that presented in (a) because it examines the total amount of growth that occurred during each time period. Note that during the 0–88 d time interval snails in the risk treatment grew less than those raised without risk cues. In contrast, during the 88–150 d time interval, there was no significant difference in snail growth among the risk treatments. Snails in the risk treatment actually grew 10.8% more than those raised without risk cues. Error bars are sometimes smaller than symbols.

offs are architecturally driven and appear to be universal in studies examining inducible defenses in rocky shore snails (Appleton and Palmer 1988, Palmer 1990, Trussell 1996, 2000, Trussell and Smith 2000, Trussell and Nicklin 2002). Future work on this issue is necessary because our data also suggest that inducible defenses (i.e., increased shell thickening) in marine snails
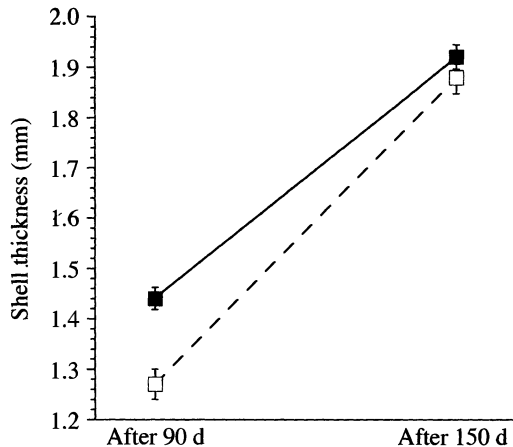
FIG. 8. Shell thickness (mean ± 1 SE) of *Littorina littorea* raised in the presence (solid squares) and absence (open squares) of risk cues from *Carcinus maenas*. Results are least-squares means from separate ANCOVAs examining mean shell thickness for each time period. Note that after 88 d, snails in the risk treatment were significantly thicker than those raised without risk cues. In contrast, after 150 d there was no significant difference in shell thickness among the risk treatments.

may be a simple by-product of reduced growth caused by predator-induced changes in behavior rather than a direct response to the presence of predator risk cues.

TMIIs and rocky intertidal community structure

Although freshwater (Turner and Mittlebach 1990, McIntosh and Townsend 1996, Peacor and Werner 1997, 2000, 2001, Peckarsky and McIntosh 1998, McIntosh et al. 1999, Turner et al. 1999, Peckarsky et al. 2002) and terrestrial (Beckerman et al. 1997, Schmitz et al. 1997, Schmitz and Suttle 2001) ecologists are increasingly appreciative of the potential role of TMIIs in their systems, marine ecologists are just beginning to explore this issue. Recent work by Raimondi et al. (2000) nicely illustrated the influence of predator-induced polymorphisms on rocky intertidal community structure in the Gulf of California. Contact with the predatory snail *Acanthina angelica* induces juvenile barnacles to form a "bent" morph, which reduces their vulnerability to *A. angelica* predation (see Lively 1986*a*, *b*, *c*). In contrast, the noninduced "conic" morph is more vulnerable to *A. angelica* predation. They found that mussels (*Brachidontes semivaelis*) dominate the community when conic morphs are more common, whereas algae (*Ralfsia* sp.) dominate when bent morphs are more common. Hence, *A. angelica* abundance and the degree to which it induces bent morphs in the local population will strongly influence subsequent community development. The dominance of mussels when conic morphs are more common is attributed to more successful *A. angelica* predation because mussels readily settle within the empty tests of conic morphs (also see Lively and Raimondi 1987).

Our study focused on barnacles and fucoids because these foundation species (see Bruno and Bertness 2001) can strongly influence the dynamics of communities on rocky intertidal shores in New England. For example, barnacles facilitate the establishment of mussels in high flow environments, such as constrictions in tidal estuaries (Leonard et al. 1998, Bertness et al. 2002) or on wave-exposed shores on the open coast (Menge 1976, 1978*a*, *b*, Menge and Branch 2001). Similarly, substratum heterogeneity created by barnacles in low flow environments is thought to facilitate the establishment of fucoid algae by providing a spatial refuge from *L. littorea* grazing (Lubchenco 1983; G. C. Trussell and P. J. Ewanchuk, *unpublished data*). Recent work suggests that such heterogeneity, whether biogenically created by barnacles or naturally occurring in rock crevices, is critical to the establishment of fucoid canopies in the presence of intense grazing pressure by *L. littorea* (Bertness et al. 2002). Knowing the factors influencing the establishment or maintenance of fucoid canopies is critical to understanding community structure on rocky shores because they can enhance species diversity by providing considerable thermal buffering, particularly on wave sheltered shores (Bertness and Leonard 1997, Bertness et al. 1999, Menge 2000*b*).

It is clear that by regulating the abundance of their food resources, consumers such as *N. lapillus* and *L. littorea* can strongly influence community dynamics on rocky shores (Connell 1961, Lubchenco 1978, Lubchenco and Menge 1978, Menge 1978*a*, *b*, 1983, Leonard et al. 1998, Menge and Branch 2001). Hence, factors controlling either the density or feeding rates of these snail consumers are expected to have positive indirect effects on barnacles and fucoids. Although several factors are likely operating (for review see Menge and Branch 2001), several studies suggest that green crab (*Carcinus maenas*) predation may significantly influence snail abundance on wave-sheltered rocky shores (Kitching et al. 1959, 1966, Ebling et al. 1964, Lubchenco 1978, Lubchenco and Menge 1978, Hadlock 1980, Menge 1983, Seeley 1986, Leonard et al. 1998, 1999, Menge 2000*a*, Menge and Branch 2001), thereby exerting a positive indirect influence on snail food resources. For example, Lubchenco's (1978) classic work invoked this hypothesis to explain the negative correlation between *L. littorea* density and green crab density and the positive correlation between percent cover of algae and green crab density in rocky shore tide pools. Of course, these interactions are probably both direct (e.g., green crabs also consume barnacles; Leonard et al. 1999) and indirect, and future work is needed to determine the relative importance of each form of interaction.

Because green crabs are more common on wave-sheltered shores (Kitching et al. 1959, 1966, Kitching and Lockwood 1974, Menge 1978*b*, 2000*a*, Reimchen 1982, Palmer 1985, Seeley 1986, Trussell 1996, 1997),

interactions involving green crabs, snails, and their food resources are likely strongest in these habitats. Our results suggest that the trait-mediated effects of green crabs may be an important part of these interactions. By suppressing snail-feeding rates via changes in snail behavior, the presence of green crab risk cues may significantly reduce the impact of snails on their food resources. Indeed, TMIIs may be particularly important in less turbulent habitats (e.g., tidal pools and wave-sheltered shores) because the detection of green crab risk cues by snails is presumably not hindered by increased turbulence (see Weissburg and Zimmer-Faust 1993) from breaking waves.

Although some may question the relevance of laboratory experiments to natural systems, the large effect of predator risk cues observed in both food chains suggests that a better understanding of the role TMIIs play on rocky intertidal shores is worth pursuing. This view is supported by experiments demonstrating the strong influence of green crab risk cues in the field, such as induced plasticity in snail morphology (Trussell and Smith 2000) and habitat use (Trussell et al. 2002), and trait-mediated effects on community structure (Trussell et al. 2002). For example, trait-mediated interactions between green crabs and *L. littorea* on a wave-sheltered shore had remarkably similar effects on fucoid density to those reported here; snails consumed 490% fewer fucoids in the presence of green crab risk cues than in the absence of risk cues (Trussell et al. 2002). Moreover, preliminary experiments in rocky shore tide pools (G. C. Trussell et al., *unpublished data*) suggest a strong influence of trait-mediated interactions between green crabs and *L. littorea* on the abundance of ephemeral green algae (*Ulva* sp., *Enteromorpha* sp.). Compared to control pools where snails grazed in the absence of green crab risk cues, trait-mediated pools had ~200% more ephemeral green algae and 150% less bare space.

Density-based thinking has been central to how ecologists evaluate the importance of direct and indirect effects in rocky intertidal communities (but see Wootton 1992, 1993, 1994). However, strong arguments suggest that the impact of TMIIs may be greater than one would initially predict, and this is especially true for behaviorally mediated indirect interactions. Predator-induced reductions in prey feeding rates are often immediate and can affect the entire population, whereas density reduction of prey by predators can take considerably more time and the effect is manifested solely by the proportion of prey removed from the system (Peacor and Werner 2001). Hence, community models based on density mediated interactions may be misleading in environments where predators are common because they may overestimate the numerical importance of consumer species. Moreover, a better understanding of how predator risk cues modify prey traits will improve our knowledge of the role species interactions play in intertidal community structure and dy-

namics. Future efforts must determine whether the role of TMIIs in marine communities is comparable to that of DMIIs, as is the case in spider–grasshopper interactions in old field food webs (Schmitz et al. 1997).

LITERATURE CITED

Abrams, P. A. 1983. Arguments in favor of higher-order interactions. American Naturalist **121**:887–891.

Abrams, P. A., B. A. Menge, G. G. Mittlebach, D. Spiller, and P. Yodzis. 1996. The role of indirect effects in food webs. Pages 371–395 *in* G. Polis and K. Winemiller, editors. Food webs: dynamics and structure. Chapman and Hall, New York, New York, USA.

Adler, F. R., and W. F. Morris. 1994. A general test for interaction modification. Ecology **75**:1552–1559.

Appleton, R. D., and A. R. Palmer. 1988. Water-borne stimuli released by crabs and damaged prey induce more predator-resistant shells in a marine gastropod. Proceedings of the National Academy of Sciences (USA) **85**:4387–4391.

Barnett, B. E. 1979. A laboratory study of predation by the dog-whelk *Nucella lapillus* on the barnacles *Elminius modestus* and *Balanus balanoides*. Journal of the Marine Biological Association of the United Kingdom **59**:299–306.

Beckerman, A. P., M. Uriarte, and O. J. Schmitz. 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. Proceedings of the National Academy of Sciences (USA) **94**:10735–10738.

Belovsky, G. E., and J. B. Slade. 1993. The role of vertebrate and invertebrate predators in a grasshopper community. Oikos **68**:193–201.

Bertness, M. D., and G. H. Leonard. 1997. The role of positive interactions in communities: lessons from intertidal habitats. Ecology **78**:1976–1989.

Bertness, M. D., G. H. Leonard, J. M. Levine, P. R. Schmidt, and A. O. Ingraham. 1999. Testing the relative contribution of positive and negative interactions in rocky intertidal communities. Ecology **80**:2711–2726.

Bertness, M. D., G. C. Trussell, P. J. Ewanchuk, and B. R. Silliman. 2002. Do alternate stable community states exist in the Gulf of Maine rocky intertidal zone? Ecology **83**: 3434–3448.

Billick, I., and T. J. Case. 1994. Higher order interactions in ecological communities: what are they and how can they be detected? Ecology **75**:1529–1543.

Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and the composition of plankton. Science **150**:28–35.

Bruno, J. F., and M. D. Bertness. 2001. Habitat modification and facilitation in benthic marine communities. Pages 201–218 *in* M. D. Bertness, S. D. Gaines, and M. E. Hay, editors. Marine community ecology. Sinauer Associates, Sunderland, Massachusetts, USA.

Carpenter, S. R., and J. F. Kitchell. 1993. The trophic cascade in lakes. Cambridge University Press, London, UK.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading tropic interactions and lake productivity. BioScience **35**:634–639.

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology **42**:710–723.

Dayton, P. K. 1971. Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41:351–389.

Dill, L. M. 1987. Animal decision making and its ecological consequences: the future of aquatic ecology and behavior. Canadian Journal of Zoology 65:803–811.

Ebling, F. J., J. A. Kitching, L. Muntz, and C. M. Taylor. 1964. The ecology of Lough Ine XIII. Experimental observations of the destruction of *Mytilus edulis* and *Nucella lapillus* by crabs. Journal of Animal Ecology 33:73–82.

Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. Science 185:1058–1060.

Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science 282:473–476.

Gaines, S. D., and J. Roughgarden. 1985. Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. Proceedings of the National Academy of Sciences (USA) 82:3707–3711.

Hadlock, R. P. 1980. Alarm response of the intertidal snail *Littorina littorea* (L.) to predation by the crab *Carcinus maenas* (L.). Biological Bulletin 159:269–279.

JMP. 1995. Statistics and graphics guide, version 3. 1. SAS Institute, Cary, North Carolina, USA.

Kareiva, P. 1994. Higher order interactions as a foil to reductionist ecology. Ecology 75:1527–1528.

Kemp, P., and M. D. Bertness. 1984. Snail shape and growth rates: evidence for plastic shell allometry in *Littorina littorea*. Proceedings of the National Academy of Sciences (USA) 81:811–813.

Kitching, J. A., and J. Lockwood. 1974. Observations on shell form and its ecological significance in thaisid gastropods of the genus *Lepsiella* in New Zealand. Marine Biology 28:131–144.

Kitching, J. A., L. Muntz, and F. J. Ebling. 1966. The ecology of Lough Ine XV. The ecological significance of shell and body forms in *Nucella*. Journal of Animal Ecology 35:113–126.

Kitching, J. A., J. F. Sloan, and F. J. Ebling. 1959. The ecology of Lough Ine VIII. Mussels and their predators. Journal of Animal Ecology 28:331–341.

Leonard, G. H., P. J. Ewanchuk, and M. D. Bertness. 1999. How recruitment, intraspecific interactions, and predation control species borders in a tidal estuary. Oecologia 118:492–502.

Leonard, G. H., J. M. Levine, P. R. Schmidt, and M. D. Bertness. 1998. Flow-driven variation in intertidal community structure in a Maine estuary. Ecology 79:1395–1411.

Lima, S. L. 1988a. Nonlethal effects in the ecology of predator–prey interactions—what are the ecological effects of anti-predator decision making? BioScience 48:25–34.

Lima, S. L. 1988b. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Advances in the Study of Behavior 27:215–290.

Lively, C. M. 1986a. Predator-induced shell dimorphism in the acorn barnacle *Chthamalus anisopoma*. Evolution 40:232–242.

Lively, C. M. 1986b. Competition, comparative life histories and the maintenance of shell dimorphism in a barnacle. Ecology 67:858–864.

Lively, C. M. 1986c. Canalization versus developmental conversion in a spatially variable environment. American Naturalist 128:561–572.

Lively, C. M., and P. T. Raimondi. 1987. Desiccation, predation, and mussel–barnacle interactions in the northern Gulf of California. Oecologia 74:304–309.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. American Naturalist 112:23–39.

Lubchenco, J. 1983. *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. Ecology 64:1116–1123.

Lubchenco, J., and B. A. Menge. 1978. Community development and persistence in a low rocky intertidal zone. Ecological Monographs 48:67–94.

Marko, P. B., and A. R. Palmer. 1991. Responses of a rocky shore gastropod to the effluents of predatory and non-predatory crabs: avoidance and attraction. Biological Bulletin 181:363–370.

McIntosh, A. R., B. L. Peckarsky, and B. W. Taylor. 1999. Rapid size-specific changes in the drift of *Baetis bicaudatus* (Ephemeroptera) caused by alterations in fish odour concentration. Oecologia 118:256–264.

McIntosh, A. R., and C. R. Townsend. 1996. Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish-induced changes in grazer behavior? Oecologia 108:174–181.

McQueen, D. J., M. R. S. Johannes, J. R. Post, T. J. Stewart, and D. R. S. Lean. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. Ecological Monographs 59:289–309.

Menge, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. Ecological Monographs 46:355–393.

Menge, B. A. 1978a. Predation intensity in a rocky intertidal community: relation between predator foraging activity and environmental harshness. Oecologia 34:1–16.

Menge, B. A. 1978b. Predation intensity in a rocky intertidal community: effect of an algal canopy, wave action and desiccation on predator feeding rates. Oecologia 34:17–35.

Menge, B. A. 1983. Components of predation intensity in the low zone of the New England rocky intertidal region. Oecologia 58:141–155.

Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. Ecological Monographs 65:21–74.

Menge, B. A. 2000a. Top-down and bottom-up community regulation in marine rocky intertidal habitats. Journal of Experimental Marine Biology and Ecology 250:257–289.

Menge, B. A. 2000b. Testing the relative importance of positive and negative effects on community structure. Trends in Ecology and Evolution 15:46–47.

Menge, B. A., and G. M. Branch. 2001. Rocky intertidal communities. Pages 221–252 *in* M. D. Bertness, S. D. Gaines, and M. E. Hay, editors. Marine community ecology. Sinauer Associates, Sunderland, Massachusetts, USA.

Miller, T. E., and W. C. Kerfoot. 1987. Redefining indirect effects. Pages 33–37 *in* W. C. Kerfoot and A. Sih, editors. Predation: direct and indirect impacts on aquatic communities. University of New England Press, Hanover, New Hampshire, USA.

Mills, E. L., J. L. Forney, and K. Wagner. 1987. Fish predation and its cascading effect on the Oneida Lake food chain. Pages 118–131 *in* W. C. Kerfoot and A. Sih, editors. Predation: direct and indirect impacts on aquatic communities. New England University Press, Hanover, New Hampshire, USA.

Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology and Evolution 14:483–488.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist 100:65–75.

Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. Journal of Animal Ecology 49:667–685.

Palmer, A. R. 1981. Do carbonate skeletons limit the rate of body growth? Nature 292:150–152.

Palmer, A. R. 1982. Growth in marine gastropods: a nondestructive technique for independently measuring shell and body weight. Malacologia 23:63–73.

Palmer, A. R. 1985. Adaptive value of shell variation in *Thais lamellosa*: effect of thick shells on vulnerability to and preference by crabs. Veliger 27:349–356.

Palmer, A. R. 1990. Effect of crab effluent and scent of damaged conspecifics on feeding, growth, and shell morphology of the Atlantic dogwhelk *Nucella lapillus* (L.). Hydrobiologia 193:155–182.

Palmer, A. R. 1992. Calcification in marine molluscs: how costly is it? Proceedings of the National Academy of Sciences (USA) 89:1379–1382.

Peacor, S. P., and E. E. Werner. 1997. Trait-mediated indirect interactions in a simple aquatic food web. Ecology 78:1146–1156.

Peacor, S. P., and E. E. Werner. 2000. Predator effects on an assemblage of consumers through induced changes in consumer foraging behavior. Ecology 81:1998–2010.

Peacor, S. P., and E. E. Werner. 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. Proceedings of the National Academy of Sciences (USA) 98:3904–3908.

Peckarsky, B. L., and A. R. McIntosh. 1998. Fitness and community consequences of avoiding multiple predators. Oecologia 113:565–576.

Peckarsky, B. L., A. R. McIntosh, B. W. Taylor, and J. Dahl. 2002. Predator chemicals induce changes in mayfly life history traits: a whole-stream manipulation. Ecology 83:612–618.

Raimondi, P. T., S. E. Forde, L. F. Delph, and C. M. Lively. 2000. Processes structuring communities: evidence for trait-mediated indirect effects through induced polymorphisms. Oikos 91:353–361.

Reimchen, T. E. 1982. Shell size divergence in *Littorina mariae* and *L. obtusata* and predation by crabs. Canadian Journal of Zoology 60:687–695.

SAS. 1995. JMP user's guide. SAS Institute, Cary, North Carolina, USA.

Schmitz, O. J. 1992. Exploitation in model food webs with mechanistic consumer-resource dynamics. Theoretical Population Biology 41:161–183.

Schmitz, O. J. 1993. Trophic exploitation in grassland food webs: simple models and a field experiment. Oecologia 93:327–335.

Schmitz, O. J. 1994. Resource edibility and trophic exploitation in an old-field food web. Proceedings of the National Academy of Sciences (USA) 91:5364–5367.

Schmitz, O. J. 1998. Direct and indirect effects of predation and predation risk in old-field interaction webs. American Naturalist 151:327–342.

Schmitz, O. J., A. P. Beckerman, and K. M. O'Brien. 1997. Behaviorally-mediated trophic cascades: effects of predation risk on food web interactions. Ecology 78:1388–1399.

Schmitz, O. J., and K. B. Suttle. 2001. Effects of top predator species on direct and indirect interactions in a food web. Ecology 82:2072–2081.

Seeley, R. H. 1986. Intense natural selection caused a rapid morphological transition in a living marine snail. Proceedings of the National Academy of Sciences (USA) 83:6897–6901.

Sih, A., P. Crowley, M. McPeek, J. Petranka, and K. Strothmeier. 1985. Predation, competition, and prey communities: a review of field experiments. Annual Review of Ecology and Systematics 16:269–312.

Sousa, W. P. 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecological Monographs 49:227–254.

Threlkeld, S. T. 1988. Planktivory and planktivore biomass effects on zooplankton, phytoplankton, and the trophic cascade. Limnology and Oceanography 33:1362–1375.

Tollrian, R. I., and C. D. Harvell. 1999. The ecology and evolution of inducible defenses. Princeton University Press, Princeton, New Jersey, USA.

Trussell, G. C. 1996. Phenotypic plasticity in an intertidal snail: the effects of a common crab predator. Evolution 50:448–454.

Trussell, G. C. 1997. Phenotypic plasticity in the foot size of an intertidal snail. Ecology 78:1033–1048.

Trussell, G. C. 2000. Predator-induced plasticity and morphological trade-offs in latitudinally separated populations of *Littorina obtusata*. Evolutionary Ecology Research 2:803–822.

Trussell, G. C., P. J. Ewanchuk, and M. D. Bertness. 2002. Field evidence of trait-mediated indirect interactions in a rocky intertidal food web. Ecology Letters 5:241–245.

Trussell, G. C., and M. O. Nicklin. 2002. Cue sensitivity, inducible defense, and trade-offs: the influence of contrasting invasion histories between a crab predator and a marine snail. Ecology 83:1635–1647.

Trussell, G. C., and L. D. Smith. 2000. Induced defenses in response to an invading crab predator: an explanation of historical and geographic phenotypic change. Proceedings of the National Academy of Sciences (USA) 97:2123–2127.

Turner, A. M. 1996. Freshwater snails alter habitat use in response to predation. Animal Behavior 51:747–756.

Turner, A. M. 1997. Contrasting short-term and long-term effects of predation risk on consumer habitat use and resources. Behavioral Ecology 8:120–125.

Turner, A. M., R. J. Bernot, and C. M. Boes. 2000. Chemical cues modify species interactions: the ecological consequences of predator avoidance by freshwater snails. Oikos 88:148–158.

Turner, A. M., S. A. Fetterolf, and R. J. Bernot. 1999. Predator identity and consumer behavior: differential effects of fish and crayfish on the habitat use of a freshwater snail. Oecologia 118:242–247.

Turner, A. M., and G. G. Mittlebach. 1990. Predation avoidance and community structure: interactions among piscivores, planktivores, and plankton. Ecology 71:2241–2254.

Vanni, M. J., C. D. Layne, and S. E. Arnott. 1997. "Topdown" trophic interactions in lakes. Ecology 78:1–20.

Weissburg, M. J., and R. K. Zimmer-Faust. 1993. Life and death in moving fluids: hydrodynamic effects on chemosensory-mediated predation. Ecology 74:1428–1443.

Werner, E. E. 1991. Nonlethal effects of a predator on competitive interactions between two anuran larvae. Ecology 72:1709–1720.

Werner, E. E. 1992. Individual behavior and higher-order species interactions. American Naturalist 140:s5–s32.

Werner, E. E., and B. R. Anholt. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. American Naturalist 142:242–272.

Werner, E. E., and B. R. Anholt. 1996. Predator-induced behavioral indirect effects: consequences to competitive interactions in anuran larvae. Ecology 77:157–169.

Wootton, J. T. 1992. Indirect effects, prey susceptibility, and habitat selection: impact of birds on limpets and algae. Ecology 73:981–991.

Wootton, J. T. 1993. Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. American Naturalist 141:71–98.

Wootton, J. T. 1994. Putting the pieces together: testing the independence of interactions among organisms. Ecology 75:1544–1551.