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Trophic cascades in rocky shore tide pools: distinguishing lethal and nonlethal effects

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Abstract The effects of predators on the density of their prey can have positive indirect effects on the abundance of the prey's resource via a trophic cascade. This concept has strongly influenced contemporary views of how communities are structured. However, predators also can transmit indirect effects by inducing changes in prey traits. We show that the mere presence of predator risk cues can initiate a trophic cascade in rocky shore tide pools. In large (mean surface area = 9 m²), natural tide pools, we manipulated crab density and their foraging ability to examine the relative importance of lethal (density-mediated) and non-lethal (trait-mediated) predator effects to algal community development. We found that perceived predation risk reduced snail density as much as the direct predation treatment, showing that green crab predation was not an important factor regulating local snail density. Instead, snail emigration away from resident crabs appears to be the most important factor regulating local snail density. As a result, the abundance of ephemeral green algae was similar in the predation risk and direct predation treatments, suggesting that the consumption of snails by crabs plays a minimal role in mediating the trophic cascade. Increased attention to trait-mediated effects that are transmitted by predator-induced changes in prey behavior may change our view of how predators exert their strong influence on community structure.

Keywords Trophic cascade · Green crab · Green alga · Snails

Introduction

Trophic cascades can drive community dynamics in numerous systems (Brooks and Dodson 1965; Estes and Palmisano 1974; Paine 1980; Power 1990; Carpenter and Kitchell 1993; McClaren and Peterson 1994; Estes et al. 1998; Pace et al. 1999; Terborgh et al. 2001) and the consumptive (or density-mediated) effects of predators are commonly viewed as the principal mechanism regulating herbivore density and transmitting indirect predator effects (for review see Schmitz et al. 2004). A growing body of work suggests, however, that the non-lethal effects of predators (trait-mediated effects) on prey populations, such as changes in prey behavior (Dill 1987; Lima 1988a, 1988b) in response to predator risk cues, can also drive trophic cascades (McIntosh and Townsend 1996; Beckerman et al. 1997; Schmitz et al. 1997, 2004; Turner et al. 2000) and other ecological processes such as competition (Werner 1992; Peacor and Werner 1997, 2000, 2001).

Ecologists are increasingly aware of the potential importance of trait-mediated interactions between predators and their prey to community dynamics, but this issue has received relatively little attention in marine environments (but see Wootton 1992; Raimondi et al. 2000; Trussell et al. 2003, 2003; Dill et al. 2003). This is surprising because many important consumer species in marine environments exhibit behavioral and morphological plasticity in response to predators (Hadlock 1980; Appleton and Palmer 1988; Trussell and Smith 2000; Heithaus and Dill 2002; Trussell and Nicklin 2002; for review see Dill et al. 2003).

One of the more influential and classical examples of top-down control via density-mediated trophic cascades emerged from early studies on New England rocky shores (Lubchenco 1978). In this study, Lubchenco experimentally showed that herbivorous snail (*Littorina littorea*) grazing exerted strong control on the diversity and succession of tide pool algal communities (also see Lubchenco 1980, 1983). A widely accepted hypothesis (Little and Kitching 1996; Bertness 1999; Menge and Branch 2001; Steneck and Carlton 2001; Castro and

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Huber 2003), which emerged from this work, is that predation by the green crab (*Carcinus maenas*) indirectly influences rocky shore algal community structure and diversity by controlling *L. littorea* density. Correlation evidence (Lubchenco 1978) suggested that when abundant in tide pools, green crabs consume resident snails, thereby releasing palatable ephemeral green algae [e.g. *Enteromorpha intestinalis* (hereafter, *Enteromorpha*), *Ulva lactuca* (hereafter, *Ulva*)] from grazing pressure and allowing them to outcompete less palatable perennial species (e.g. *Chondrus crispus*, *Fucus vesiculosus*). In the absence of green crabs, preferential snail grazing on ephemeral species is largely unchecked and the algal community becomes dominated by tougher, less palatable, perennial species.

Lubchenco's study is considered a textbook example of a density-mediated trophic cascade (Little and Kitching 1996; Bertness 1999; Castro and Huber 2003), but the relative importance of direct consumption of snails by crabs versus predator-induced changes in snail feeding behavior in causing this cascade has not been experimentally tested. Rocky shore tide pool communities provide an excellent opportunity to examine the relative importance of density and trait-mediated effects to algal community dynamics. More generally, although ecologists are beginning to address the relative importance of each type of predator effect (Beckerman et al. 1997; Schmitz et al. 1997; Gastreich 1999), our understanding of their ecological significance remains incomplete.

Most studies on trait-mediated effects to date have been conducted in closed systems such as mesocosms (e.g., Peacor and Werner 2001; Trussell et al. 2003). These studies have been very informative in identifying trait-mediated effects that are transmitted by changes in the per capita feeding rates of prey or small-scale changes in refuge seeking behavior. However, work in closed systems does not allow one to evaluate the importance of emigration behavior in transmitting trait-mediated effects because prey densities are experimentally held constant. In open systems like rocky intertidal shores, emigration behavior may allow prey to avoid locations having high predator concentrations (Turner and Mittlebach 1990; Turner 1997; Rochette and Dill 2000; Bernot and Turner 2001; Heithaus and Dill 2002, Heithaus et al. 2002; Dill et al. 2003) and may be more important to the transmission of trait-mediated effects compared to closed systems.

In this study, we tested Lubchenco's trophic cascade hypothesis with a large-scale experiment in natural tide pools. By manipulating both the density and trait-mediated effects of green crabs (*Carcinus maenas*) on herbivorous snails (*Littorina littorea*) we examined the relative importance of lethal and non-lethal predator effects to this trophic cascade. Finally, our design permitted snail emigration to occur thus providing insight into the importance of this behavior in transmitting trait-mediated effects.

Materials and methods

We manipulated nine large tide pools located on East Point (Nahant, Massachusetts) that had similar physical characteristics [mean (\pm SE) pool surface area = 9.00 ± 1.03 m², mean pool depth = 0.26 m ± 0.02 , mean pool volume = 2.44 m³ ± 0.56]. Fortunately, before our experiment began, wave surge and scour from a large winter storm removed virtually all plants and animals.

In early spring, we stocked all pools with *Littorina littorea* (shell length range, 15–10 mm) at a density of 100 snails m⁻² and then applied three treatments (Lethal, Non-Lethal, Control) to each of three pools. We created the Lethal treatment by stocking pools with green crabs at a density of 2 crabs m⁻², which is representative of that previously reported for Nahant tide pools (0–5 crabs m⁻², Lubchenco 1978). Crabs in this treatment were thus able to forage naturally within these pools, and their indirect effects on the algal community were expected to occur because of their consumptive control of snail density. We also stocked Non-lethal pools with the same density of green crabs, except that they were placed inside perforated plastic tubs anchored within each pool. Hence, crabs in this treatment were not able to consume snails within tide pools, but their release of risk cues into each pool was hypothesized to alter snail-feeding behavior (see Trussell et al. 2002, 2003). Every 7–10 days, crabs were fed with mussels (*Mytilus edulis*) and conspecific snails placed within each tub. In Control pools, crabs were excluded to prevent their impact on snail density, snail behavior, and the algal community.

We covered all pools with vinyl-coated wire mesh (3.5 cm \times 3.5 cm) that was anchored to the substratum around each pool with galvanized bolts and strapping to prevent crab movement into or out of the pools. These covers prevented most crabs from entering or escaping from our experimental pools, but permitted adequate light penetration for algal growth. In addition, crab traps were placed in each pool and checked weekly to remove smaller crabs (<35 mm carapace width) that were able to enter pools through mesh openings. Every week we counted crabs within Lethal pools and added crabs, if necessary, to maintain desired densities.

We used three approaches to evaluate the effects of these treatments on the amount of unoccupied bare space and ephemeral green algal cover. First, we photographed four quadrats (0.25 m²) randomly placed within each pool. Resulting photographs were projected to natural size on a horizontal surface, and percent cover of ephemeral green algae and bare space was estimated by counting the presence of each category for 50 random points. We focused on ephemeral green algae because these species respond quickly to *L. littorea* grazing and are important in dictating algal succession in tide pools (Lubchenco 1978). Second, we estimated the percent cover of *Enteromorpha*, *Ulva*, and bare space on the tops of stainless steel snail exclusion cages (20 cm \times 20 cm) randomly anchored to the substratum within each pool ($n = 8$ per pool). These cages were originally intended to evaluate algal community development in the complete absence of *L. littorea* grazing, but we were unable to do so because colonizing ephemerals quickly fouled the cages, thus shading the substratum beneath. In addition to estimating percent cover, we harvested all green algal biomass on each cage and weighed it after drying at 60°C for 72 h. *L. littorea* density was estimated at the end of the experiment by counting the total number of snails in five quadrats (0.25 m²) randomly placed within each pool.

All percent cover and density data were examined to ensure that they conformed to the assumptions of ANOVA. In a few instances it was necessary to log₍₁₀₎ transform data to conform to the homogeneity of variance assumption. Data were analyzed with a one-way ANOVA that considered treatment (Control, Non-lethal, Lethal) as a fixed effect. All analyses were conducted using JMP software for Macintosh (Version 3.2.2, SAS, Cary, N.C., USA). Because sampling quadrats and cages within each pool were not independent, they were declared a random effect nested within each experimental treatment. Because three post hoc contrasts were performed for each response variable, we used a Bonferroni adjusted alpha of 0.017 to evaluate significance. Post hoc tests were performed using the linear contrast feature of JMP.

Results

After 6 months, mean (\pm SE) *Littorina littorea* density (Fig. 1) was significantly different among experimental treatments (ANOVA, $F_{2,12}=38.74$, $P<0.0001$). Both Lethal (70.7 snails $m^{-2} \pm 7.7$) and Non-Lethal (65.9 snails $m^{-2} \pm 6.8$) pools had significantly fewer snails than control pools (linear contrasts, both $P<0.0001$). Snail density was reduced 29–34% from the initial stocking density of 100 snails m^{-2} in Lethal and Non-Lethal pools, respectively, but increased 59% in control pools (158.9 snails $m^{-2} \pm 14.8$). These large differences in snail density had dramatic consequences for the developing algal community.

Analysis of photographed quadrats revealed that experimental treatment significantly influenced the amount of green algae within pools (Treatment effect: $F_{2,9}=15.6$, $P=0.0006$; Replicate effect: $F_{9,21}=0.59$, $P=0.7941$). Pools with Lethal and Non-Lethal predator effects had at least 3 times more ephemeral green algae than control pools (linear contrasts, both $P<0.001$; Fig. 1). The amount of unoccupied bare space also differed significantly among treatments (Treatment effect: $F_{2,9}=14.01$, $P=0.0012$; Replicate effect: $F_{9,21}=1.14$, $P=0.3768$). Unoccupied bare space was 2 times greater in control pools compared to Lethal and Non-lethal pools (linear contrasts, both $P<0.005$) and similar between the two predator effect treatments (linear contrast, $P=0.97$).

Estimates of percent cover of *Enteromorpha*, *Ulva* and unoccupied bare space on cage tops produced similar results (Table 1, Fig. 2A). Linear contrasts revealed that Lethal and Non-lethal pools had significantly more *Enteromorpha* (both $P<0.005$) and *Ulva* (both $P<0.0001$) and less bare space (both $P<0.001$) than control pools. Comparison of Lethal and Non-lethal pools revealed no difference in *Enteromorpha* cover ($P=0.088$), *Ulva* cover ($P=0.0351$), or unoccupied bare space ($P=0.0171$). Total biomass of *Enteromorpha* and *Ulva* was generally consistent with that for percent cover on cages (Table 1, Fig. 2B). Lethal and Non-Lethal pools had significantly

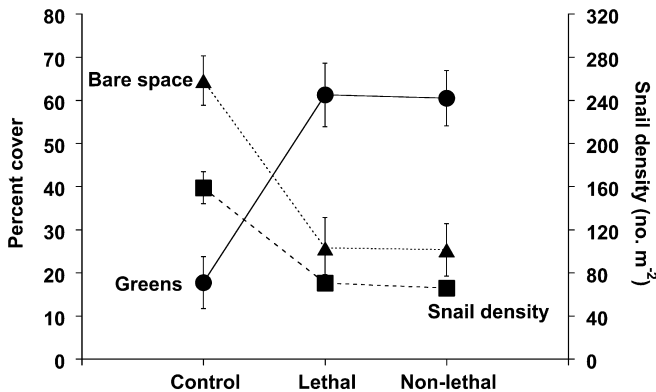


Fig. 1 Mean (\pm SE) percent cover of ephemeral green algae (circles) and unoccupied bare space (triangles) and *Littorina littorea* density (squares) in tide pools subjected to either green crab (*Carcinus maenas*) predation (Lethal), green crab risk cues (Non-lethal), or a Control having no green crab predation or risk cues. In some cases the SE bars are smaller than the symbols

more *Enteromorpha* (linear contrasts, both $P<0.0001$) and *Ulva* (both $P<0.0001$) biomass than control pools. Although there was no difference in total biomass of *Enteromorpha* ($P=0.0432$) between Lethal and Non-Lethal pools, Non-lethal pools had significantly more *Ulva* ($P=0.0006$) than Lethal pools.

Discussion

Species interactions are the foundation of ecological processes such as competition, facilitation, and succession. Although these phenomena have been typically approached from a density-mediated perspective, growing evidence of trait-mediated interactions in diverse habitat types (Schmitz et al. 2004) indicates that our view of species interactions must be context dependent (Werner and Peacor 2003). For example, those species that exhibit some form of plasticity in response to predator cues may have different per-capita impacts on their resources depending on whether predators are present or absent in the system. Theory suggests that trait-mediated (or non-lethal) predator effects may indeed be stronger than the more familiar density-mediated (or lethal) predator effects because predator-induced changes in traits like behavior are often immediate, rapid, and can affect the entire local population throughout the lifetime of its individuals

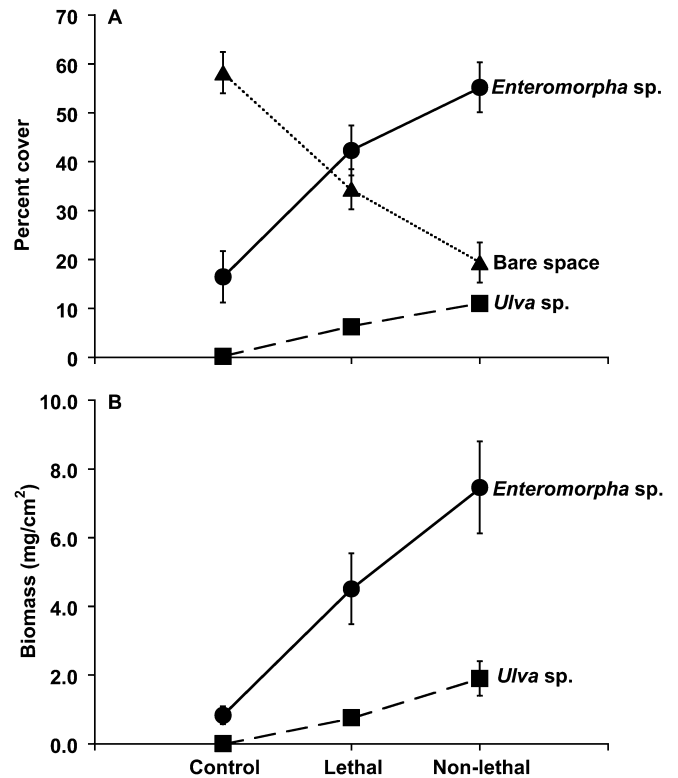


Fig. 2 a Mean (\pm SE) percent cover of *Enteromorpha* sp. (circles), *Ulva* sp. (squares), and unoccupied bare space (triangles) on experimental cages. b Mean (\pm SE) biomass of *Enteromorpha* sp. (circles) and *Ulva* sp. (squares) on experimental cages. See Table 1 for statistical analyses. In some cases the SE bars are smaller than the symbols

Table 1 ANOVA on the effect of experimental treatment (Lethal, Non-lethal, Control) on percent cover of *Enteromorpha*, *Ulva* and unoccupied bare space and biomass of both algal species on 20 cm × 20 cm cage tops

% Cover		<i>Enteromorpha</i>			<i>Ulva</i>		
Source	<i>df</i>	MS ($\times 10^2$)	<i>F</i>	<i>P</i>	MS ($\times 10^2$)	<i>F</i>	<i>P</i>
Treat	2	90.09	14.41	0.0001	0.0353	32.82	<0.0001
Rep (Treat)	21	6.24	0.79	0.7081	0.0011	0.40	0.9881
Error	47	7.83	0.0027				
Biomass		<i>Enteromorpha</i>			<i>Ulva</i>		
Treat	2	0.58	27.93	<0.0001	0.054	66.31	<0.0001
Rep (Treat)	21	0.0021	0.81	0.6979	0.00082	0.27	0.9991
Error	48	0.0026	0.0031				
% Cover		Unoccupied bare space					
Source	<i>df</i>	MS ($\times 10^2$)	<i>F</i>	<i>P</i>			
Treat	2	88.80	22.07	<0.0001			
Rep (Treat)	21	4.00	0.54	0.9387			
Error	47	7.46					

(Peacor and Werner 2001). In contrast, the lethal effects of predators on prey density likely require more time and are manifested solely by the rate at which predators consume prey. Of course, in most natural situations predators are likely to have both lethal and non-lethal effects, which is why it is important that we identify the relative importance of each in shaping community structure and dynamics.

Few studies have examined the relative importance of density and trait-mediated effects (Schmitz et al. 2004), but it is becoming increasingly clear that trait-mediated effects can be just as, if not more, important to community dynamics (Beckerman et al. 1997; Schmitz et al. 1997; Gastreich 1999) and competitive interactions (Peacor and Werner 2001). Interactions between crabs, snails and algae in rocky shore tide pools have been viewed as a classical example of density-mediated trophic cascade (Lubchenco 1978; Steneck and Carlton 2001; Castro and Huber 2003). This study suggests an alternative view that emphasizes the importance of trait-mediated effects to community dynamics in this system. We found that the abundance of ephemeral green algae was equally high in the predation risk (non-lethal) and direct predation (lethal) treatments, suggesting that the consumption of snails by crabs plays a minimal role in mediating the trophic cascade. This similarity in algal community response likely occurred because both predator effect treatments caused similar reductions (from initial stocking densities) in snail density. Because crabs in the predation risk treatment were incapable of consuming stocked snails, reductions in the snail density of these pools was clearly caused by emigration. Emigration behavior probably occurred in our direct predation pools as well, so this treatment actually reflects a combination of density and trait-mediated effects. Thus our experiment probably overestimates the importance of direct predation in our Lethal pools, which prevents a precise determination of the relative importance of each type of predator effect. Nevertheless, our results suggest that changes in snail

density caused by emigration behavior rather than mortality due to direct predation may be the principal means of transmitting the indirect effects of green crabs on algal abundance.

Because the transmission of trait-mediated effects in this system ultimately involves snail density, some may wonder whether we have raised a semantic point. We do not think so for a couple of reasons. First, green crabs are generalist predators that consume other prey in addition to Littorine snails, including predatory snails (*Nucella lapillus*), sea urchins (*Strongylocentrotus droebachiensis*) and mussels (*Mytilus edulis*), all of which are commonly found in tide pools. Mussels are a particularly large component of the green crab diet, and when offered a choice of mussels and Littorine snails, crabs preferentially consume mussels (Trussell et al., unpublished data), presumably because they are easier to subdue. Thus, the impact of green crabs on resident Littorine snail density may largely depend on the availability of other prey.

Although snails appear to be able to differentiate between risk cues associated with crabs feeding on conspecifics or heterospecifics when producing induced morphological defenses (thicker shells), the effect of green crab risk cues alone dominates these responses (see Trussell and Nicklin 2002). It is likely that this dominance also applies to behavioral responses like emigration because they are relatively cheap and provide immediate benefits compared to morphological responses, which are costly and require time to produce (Trussell and Smith 2000; Trussell and Nicklin 2002). Other tide pool inhabitants in addition to *Littorina littorea*, including *Mytilus edulis* (Smith and Jennings 2000), *Nucella lapillus* (Palmer 1990; Trussell et al. 2003), and *Littorina obtusata* (Trussell 1996; Trussell and Smith 2000; Trussell and Nicklin 2002) have clearly evolved sensitivity to green crab risk cues and we think it unlikely that responses like flight behavior are strongly determined by whether crabs are feeding on conspecifics or other prey. In the case

where other prey are abundant, trait-mediated effects may therefore exert a much stronger influence on snail density, and thus algal community structure, than density mediated effects. In contrast, if snails are the only available prey, then density-mediated effects may assume a larger role depending on how quickly snails are able to exit the system.

Recent advances in trait-mediated theory (Schmitz et al. 2004) have yielded interesting predictions regarding predator identity (in terms of their hunting mode) to the relative importance of trait-mediated effects in natural communities. We suggest that predator diet (generalist versus specialist) may also provide valuable insight into how diet breadth may magnify or diminish the strength of trait-mediated effects.

Second, as mentioned above, trait-mediated effects on snail density are likely to manifest their influence on local snail density much more rapidly than the consumptive effects of predators (Peacor and Werner 2001). Consumption of prey by predators takes time, whereas emigration behavior can occur simultaneously for all snails inhabiting the pool. Although density and trait-mediated effects on prey density may ultimately have the same effects over the long term, their impact on community dynamics may differ considerably simply because trait-mediated effects can occur rapidly. Hence, the pace of community dynamics and succession may be strongly influenced by the relative importance of the trait-mediated and density-mediated effects that are operating on important consumer species.

Our design allowed immigration and emigration to occur in our experimental pools, whereas previous designs (e.g. Trussell et al. 2002, 2003) have prevented these processes from occurring. Emigration behaviors may be more common in open systems and the transmission of trait-mediated effects may thus not depend on how predators modulate the per capita rate of resource consumption by prey. In contrast, in closed systems the transmission of trait-mediated predator effects requires changes in the per capita rate that prey consume their resources. Changes in per capita rates can clearly produce strong effects (Beckerman et al. 1997; Schmitz et al. 1997; Trussell et al. 2002, 2003), but we think processes like emigration may magnify the importance of trait-mediated effects in ecological communities (also see Post et al. 1999; Rochette and Dill 2000; Heithaus and Dill 2002; Dill et al. 2003). This may be particularly true in open systems where prey fleeing patches having high predator densities will surely have an impact on the new and presumably low predator density habitats they colonize (McIntosh and Peckarsky 1999; Bernot and Turner 2001). Thus, depending on the identity (Schmitz et al. 2004) and abundance of predators on a landscape scale, trait-mediated effects may operate on scales greater than those represented by the “local” community.

The consumptive or lethal effects of predators on their prey has been central to our understanding of the importance of direct and indirect effects to the dynamics of rocky intertidal and other communities (Sih et al. 1985;

Menge 1995; Abrams et al. 1996). Our results indicate that the non-lethal effects of green crabs on herbivorous snails are all that is required to drive trophic cascades in rocky shore tide pools. Recent calls have been made for a stronger integration of phenotypic plasticity into community ecology theory and empiricism (Tollrian and Harvell 1999; Agrawal 2001). Indeed, if community level effects arising from plastic interactions between predators and prey are widespread in nature, they may change our view of how predators exert their strong influence on ecological communities. For example, a better knowledge of the interactions between predators and prey may improve our understanding of how consumers affect important measures of ecosystem function, such as productivity (Duffy 2002; Paine 2002).

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