REPORT

Field evidence of trait-mediated indirect interactions in a rocky intertidal food web

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Abstract

Studies on the implications of food web interactions to community structure have often focused on density-mediated interactions between predators and their prey. This approach emphasizes the importance of predator regulation of prey density via consumption (i.e. lethal effects), which, in turn, leads to cascading effects on the prey's resources. A more recent and contrasting view emphasizes the importance of non-lethal predator effects on prey traits (e.g. behaviour, morphology), or trait-mediated interactions. On rocky intertidal shores in New England, green crab (*Carcinus maenas*) predation is thought to be important to patterns of algal abundance and diversity by regulating the density of herbivorous snails (*Littorina littorea*). We found, however, that risk cues from green crabs can dramatically suppress snail grazing, with large effects on fucoid algal communities. Our results suggest that predator-induced changes in prey behaviour may be an important and under-appreciated component of food web interactions and community dynamics on rocky intertidal shores.

INTRODUCTION

The trophic cascade concept has greatly improved our understanding of the importance of food web interactions to community dynamics (Brooks & Dodson 1965; Paine 1966; Carpenter *et al.* 1985, 1987; McQueen *et al.* 1989; Vanni *et al.* 1997). Most work in this area has focused on how predators regulate the density of their prey (via consumption) and the cascading effects this has on the abundance of the prey's resources (Sih *et al.* 1985; Peacor & Werner 2001). For example, by directly controlling the abundance of herbivores, predators can have a positive indirect effect on the abundance of primary producers (Carpenter & Kitchell 1993).

Predators also have non-lethal indirect effects on prey by inducing changes in prey traits such as behaviour (Phillips 1976; Fishlyn & Phillips 1980; Garrity & Levings 1981; Turner & Mittlebach 1990; Werner 1992; Turner 1997; Turner *et al.* 1999, 2000) and morphology (Raimondi *et al.* 2000) instead of prey density (also see Wootton 1992, 1993). Such trait-mediated interactions (Abrams *et al.* 1996) can have important implications to intra- and interspecific competition (Werner & Anholt 1996; Peacor & Werner

1997, 2000, 2001), but our understanding of their role in community dynamics is still limited despite the elegant work of Schmitz and colleagues (Beckerman *et al.* 1997; Schmitz *et al.* 1997; Schmitz 1998; Schmitz & Suttle 2001) on spider–grasshopper interactions in old fields.

The density-mediated indirect effects of predators are widely recognized as important to the structure of rocky intertidal communities (Menge 1995, 1997; Menge & Branch 2001), but relatively little attention has been paid to the role of trait-mediated indirect effects (but see Garrity & Levings 1981; Wootton 1992, 1993). However, many intertidal predators are known to induce behavioural (Phillips 1976; Fishlyn & Phillips 1980; Hadlock 1980; Marko & Palmer 1991) and morphological (Lively 1986; Appleton & Palmer 1988; Palmer 1990; Trussell 1996, 2000; Leonard *et al.* 1999; Smith & Jennings 2000; Trussell & Smith 2000; Trussell & Nicklin 2002) changes in their prey, suggesting that trait-mediated effects of predators may be particularly important to the structure of these communities.

In this study, we examined the importance of trait-mediated interactions between green crabs (*Carcinus maenas*) and a herbivorous snail (*Littorina littorea*) to intertidal algal

communities in a tidal estuary in Maine. Previous work hypothesized that density-mediated interactions between green crabs and *L. littorea* can influence the composition of algal communities on rocky shores (Lubchenco 1978, 1980, 1983). However, the importance of trait-mediated interactions in this system has not been considered. We addressed this issue by experimentally subjecting fucoid algal communities to snail grazing in the presence and absence of risk cues from green crabs. In addition to dramatically suppressing the impact of juvenile snail grazing on fucoid germlings, the presence of risk cues from crabs also reduced ambient adult snail densities within experimental plots.

MATERIALS AND METHODS

To establish experimental fucoid algal communities (*Ascophyllum nodosum, Fucus vesiculosus*), we anchored granite tiles (15 cm × 15 cm) on a granite outcropping in the Damariscotta River estuary (Lowes Cove) having dense *Ascophyllum nodosum* cover (90–100% of the available surface area). We anchored four tiles in each of 12 replicate plots (~1 m² in area, each plot separated by at least 3 m). Each tile within each plot was individually enclosed by a stainless steel cage (15 cm × 15 cm; mesh size = 4 mm × 4 mm) to prevent snail grazing before applying experimental treatments. By late spring, all tiles had dense fucoid germling cover.

In early May, two risk-cue treatments (Crab & No Crab) and two snail-grazing treatments (Snail & No Snail) were randomly applied to our replicate plots. There were six Crab plots and six No Crab plots. We surrounded Crab plots with nine perforated plastic tubs (20 cm diameter) that were bolted to the substratum and spaced evenly around the perimeter of each experimental plot. Within each tub, we placed a single male green crab (*C. maenas*) and 25 *L. littorea* to serve as food for the crab. This design exposed juvenile snails on our experimental tiles (see below) to risk cues released from crabs inside the tubs. A fresh batch of 25 *L. littorea* was added to each tub every two weeks and any dead crabs were replaced. The No Crab plots were surrounded in similar fashion except that the tubs contained no crabs or *L. littorea*.

Two of the four individually caged tiles within each experimental plot received four juvenile (mean (± SE) shell length = 6.34 mm (± 0.04)) *L. littorea* to serve as grazers on the developing fucoid community (Snail); the remaining two tiles within each plot received no snails (No Snail). We included the No Snail treatment because we were interested in determining whether risk cues and excretory products from crabs would have a fertilization effect on the developing algal community.

Tiles remained in the field under these conditions for 6 months, at which time all tiles were returned to the laboratory. Using a dissecting microscope, we counted the total number of fucoids contained within 10 1 cm² quadrats randomly placed on each tile. Most of the fucoid germlings were less than 1 mm long, making it impossible to distinguish between *Ascophyllum nodosum* and *Fucus vesiculosus*. The data were analysed with a two way nested ANOVA that considered risk-cue and snail-grazing treatments as fixed effects. Plots were considered our experimental units and were a random effect nested within risk-cue and snail-grazing treatment. Because there were two tiles within each plot, they were considered a random factor nested within each plot × risk-cue × snail-grazing treatment combination. By using this nested design and considering plot as our experimental unit, our analysis is not confounded by the lack of independence of samples within tiles and tiles within plots.

We also measured the final shell length of juvenile snails from our cages to assess risk-specific differences in snail growth. We did so because we hypothesized that the presence of risk cues would suppress snail grazing, thus reducing snail growth and their impact on the fucoid community. Because shell length was statistically similar among risk treatments at the beginning of the experiment (ANOVA, $F_{1,10} = 0.07$; $P = 0.8037$), final shell length was used as our growth estimate. A nested ANOVA similar to that described above was used to analyse growth data.

During the course of the experiment, we also counted (every 2–4 weeks) the total number of adult snails naturally present within each experimental plot. Although adult snails were not able to graze on our experimental tiles, we made these counts to evaluate the broader spatial effects of risk cues on snail behaviour. A final count of each experimental plot also was made 1 month after termination of the experiment because we wanted to determine whether the removal of risk cues would alter differences in snail density among experimental plots. These data were analysed with a repeated-measure ANOVA that considered risk-cue treatment as a fixed effect and sampling time as a random, repeated effect.

The square root transformation was used on fucoid counts to meet the assumptions of ANOVA (Sokal & Rohlf 1981) and all analyses were conducted using the JMP statistical package version 3.2 (JMP 1995). A priori post hoc comparisons were performed using the linear contrast feature in JMP.

RESULTS

Our experiment examining how risk cues influence the impact of *L. littorea* grazing on fucoid germlings produced large effects (Fig. 1). Both snail-grazing (ANOVA, $F_{1,24} = 6.2$; $P = 0.0214$) and risk-cue treatment (ANOVA, $F_{1,24} = 5.8$; $P = 0.0259$) significantly influenced fucoid density. However, a strong risk cue by grazing treatment interaction indicated that the effect of risk cues depended on the level of grazing treatment (ANOVA, $F_{1,24} = 21.5$, $P = 0.0002$).
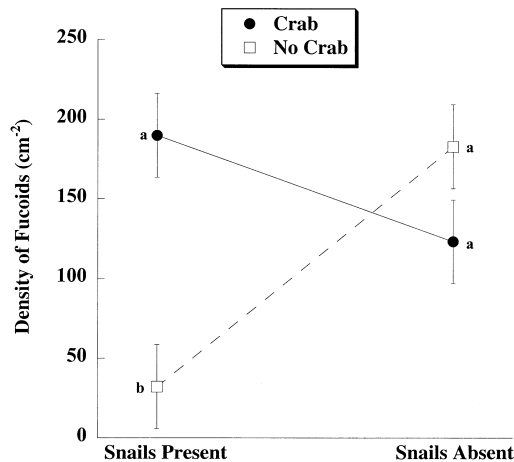
Figure 1 Mean (± SE) fucoid density (cm^{-2}) on experimental tiles with and without *Littorina littorea* grazing in the presence and absence of risk cues from *Carcinus maenas*. Values for each treatment were obtained by counting all of the fucoids in 10 1 cm^{-2} quadrats randomly placed on each tile.

Snails grazing in the presence of risk cues consumed 490% fewer fucoid germlings compared to those grazing in the absence of risk cues (linear contrast, $P < 0.0001$). That juvenile snails grew 20% less (ANOVA, $F_{1,10} = 25.24$; $P = 0.0004$) in the presence of risk cues is consistent with risk-specific differences in snail grazing.

There was no significant difference (linear contrast, $P = 0.15$) in fucoid density between the Crab/No Snail and No Crab/No Snail treatments indicating that the presence of risk cues alone did not affect fucoid density. There also was no significant difference (linear contrast, $P = 0.13$) in fucoid density between the Crab/Snail and the Crab/No Snail treatments, indicating that the suppressive effect of risk cues was equivalent to having no snails present at all. The 468% difference in fucoid density between the No Crab/Snail and the No Crab/No Snail treatments illustrates the strong effect (linear contrast, $P < 0.0001$) of snail grazing on fucoid density in the absence of risk cues.

Our analysis of *L. littorea* density within Crab and No Crab plots also yielded highly significant results (Fig. 2). During the course of the experiment, *L. littorea* density was on average 89% (range 41–160%) greater in No Crab plots compared to Crab plots (Wilk's $\Lambda = 0.40$, d.f. = 1, 10; $P = 0.0030$). Although average *L. littorea* density varied significantly through time (Wilk's $\Lambda = 0.11$, d.f. = 5, 6; $P = 0.0078$), treatment effects were consistent throughout the experimental period as evidenced by a non-significant treatment–time interaction (Wilk's $\Lambda = 0.40$, d.f. = 5, 6; $P = 0.2356$). However, 1 month (mid October) after crabs were removed from Crab plots, snail density was virtually identical among the Crab and No Crab plots.
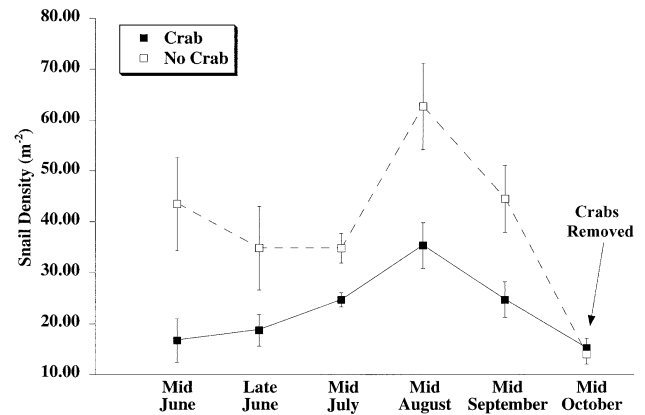

Figure 2 Mean (± SE) adult *Littorina littorea* density in experimental Crab (*Carcinus maenas*) and No Crab plots during the course of, and 1 month after, the experiment. Note that after removal of crabs from experimental tubs in September, adult snail density was no longer different among the two risk-cue treatments.

DISCUSSION

On the rocky intertidal shores of New England, interactions between the green crab (*Carcinus maenas*) and the herbivorous snail *Littorina littorea* appear to strongly influence algal community succession and dynamics. Although other factors are operating, classic work (Lubchenco 1978) clearly demonstrated that algal abundance and diversity were highly correlated with *L. littorea* density. In tide pools, algal diversity is highest at intermediate *L. littorea* densities, whereas on emergent substrata algal diversity and *L. littorea* density are negatively correlated. Moreover, Lubchenco (1978) suggested that direct predation by the green grab can modulate *L. littorea* density, thereby exerting a positive indirect influence on algal abundance and diversity. This hypothesis has not been tested experimentally, but data from New England tide pools are highly suggestive. Lubchenco (1978) found a negative correlation between *L. littorea* density and green crab density and a positive correlation between percentage cover of algae and green crab density.

Our results suggest that trait-mediated interactions may significantly contribute to the strong association between algal community dynamics and *L. littorea* density documented by Lubchenco (1978) for algal communities on emergent substrata and in tide pools. Tiles subjected to snail grazing in the presence of risk cues had 490% more fucoid germlings compared to those experiencing snail grazing in the absence of risk cues (Fig. 1). These differences in fucoid density probably reflect predator-induced reductions in snail grazing, as evidenced by the reduced growth of juvenile snails caged on tiles within our Crab plots. Moreover, our results showing reduced adult snail density within Crab plots

(Fig. 2) suggest that the influence of risk cues can operate across a broad spatial scale. Indeed, differences in adult *L. littorea* density between Crab and No Crab plots disappeared within 1 month after we removed crabs from their experimental plots.

By altering snail feeding rates and/or behaviour, the presence of risk cues may be sufficient to reduce the impact of *L. littorea* grazing on the algal community. In addition, the presence of trait-mediated interactions between green crabs and *L. littorea* on rocky intertidal shores may produce patterns of algal diversity and succession that are contrary to predictions based solely on snail density. For example, the suppression of *L. littorea* feeding by risk cues could create grazing pressure that is effectively typical of intermediate snail densities even though snail density may be numerically high.

Our work was performed on an emergent community in a tidal estuary where snails are exposed to risk cues only during high tide and ambient crab densities are naturally quite high (Leonard *et al.* 1998). Hence, despite the relatively shorter exposure time to risk cues (about half of each tidal cycle) and the fact that the effect of our experimental presentation of risk cues could have been diluted by naturally occurring background cues, we were able to detect a striking effect on the community. We suspect that the importance of predator-induced alterations in snail behaviour to snail–algal interactions may be even more pronounced in tide pools, because green crabs readily colonize these habitats (Lubchenco 1978) and low tides would permit substantial accumulation of risk cues.

Future work in this system must determine (1) the relative importance of trait-mediated vs. density-mediated indirect effects (see Schmitz *et al.* 1997) and (2) whether the within-season effects observed in this study influence long-term community dynamics. Peacor & Werner (2001) make a strong argument that the impact of trait-mediated indirect effects may be greater than one might expect. This is especially true for predator-induced changes in prey behaviour, because prey responses are often immediate and can occur throughout the local population. In contrast, 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 & Werner 2001). Our results suggest a new perspective on the nature of trophic interactions in New England rocky intertidal food webs. Moreover, these results and those of a study (Trussell, Ewanchuk & Bertness unpublished) examining interactions between the green crab, a carnivorous snail (*Nucella lapillus*), and barnacles (*Semibalanus balanoides*) suggest that trait-mediated interactions may be a general feature of food web interactions and community dynamics on rocky intertidal shores (Garrity & Levings 1981; Raimondi *et al.* 2000).

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