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Partitioning mechanisms of Predator Interference in different Habitats

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Abstract Prey are often consumed by multiple predator species. Predation rates on shared prey species measured in isolation often do not combine additively due to interference or facilitation among the predator species. Furthermore, the strength of predator interactions and resulting prey mortality may change with habitat type. We experimentally examined predation on amphipods in rock and algal habitats by two species of intertidal crabs, *Hemigrapsus sanguineus* (top predators) and *Carcinus maenas* (intermediate predators). Algae provided a safer habitat for amphipods when they were exposed to only a single predator species. When both predator species were present, mortality of amphipods was less than additive in both habitats. However, amphipod mortality was reduced more in rock than algal habitat because intermediate predators were less protected in rock habitat and were increasingly targeted by omnivorous top predators. We found that prey mortality in general was reduced by (1) altered foraging behavior of intermediate predators in the presence of top predators, (2) top predators switching to foraging on intermediate predators rather than shared prey, and (3) density reduction of intermediate predators. The relative importance of these three mechanisms was the same in both habitats; however, the magnitude of each was greater in rock habitat. Our study demonstrates that the strength of specific mechanisms of interference between top and intermediate predators can be quantified but cautions that these results may be habitat specific.

Keywords Density-mediated indirect effects · Intraguild predation · Multiple predator effects · Risk reduction · Trait-mediated indirect effects

Introduction

With few exceptions, prey are consumed by multiple predator species. The combined effect of multiple predators on shared prey is therefore an important component of community dynamics. Predation by multiple predators may be greater, or more frequently, less than predicted based on predation by each species separately (Sih et al. 1998). Shared prey consumption that is less than predicted, or risk reduction, often occurs when predators interfere with each other's foraging ability through processes such as intraguild predation (Crumrine and Crowley 2003; Lang 2003).

When intraguild predation occurs, interactions between top and intermediate predators (i.e., intraguild predators and intraguild prey, respectively) may reduce consumption of shared prey via three mechanisms: (1) decreased foraging by intermediate predators in the presence of top predators (behavioral effect); (2) decreased consumption of shared prey by top predators because they switch to foraging on intermediate predators (prey switching); and (3) decreased consumption of shared prey by intermediate predators because they themselves are consumed by top predators (density effect) (Crumrine and Crowley 2003). While these mechanisms are biologically distinct, they are closely associated and should often occur together.

The strength of these mechanisms may be habitat specific. For instance, prey refuges within habitats can decrease the efficiency of predator foraging (Gause 1934; Huffaker 1958; Jackson et al. 2001; Byers 2002; Grabowski 2004), thus altering the intensity of interactions between predator and prey (Sietz et al. 2001; Woodley and Peterson 2003). Differential refuge value between habitats may therefore result in habitat specific foraging efficiency (e.g., Lipcius and Hines 1986). Additionally, habitat structures can reduce encounters between predators (Marshall and Rypstra 1999; Roda et al. 2000; Norton et al. 2001) and may therefore decrease interactions between predators (Grabowski and Powers

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2004). Thus, changes in predator–prey and predator–predator interactions with habitat may lead to variable strengths of each of the mechanisms between habitats, resulting in habitat specific strengths of risk reduction. In fact, previous work has demonstrated that risk reduction can both increase (Warfe and Barmuta 2004) and decrease (Finke and Denno 2002) with changes in habitat complexity.

Differences in risk reduction for shared prey between habitats may be explained by differences in the strength of intraguild predation (i.e., differential risk of predation for intermediate predators between habitats). When intermediate predators are more vulnerable to predation, each of the mechanisms of risk reduction listed above may be stronger. For example, intermediate predators may alter foraging behavior in proportion to the threat of predation that they experience (Lima 1998). Thus the behavioral effect may be stronger when intermediate predators are more vulnerable to predation. Additionally, top predators may switch more readily from foraging on shared prey to foraging on intermediate predators in habitats where intermediate predators are more vulnerable to predation. This may lead to less shared prey consumption by both top predators and intermediate predators (i.e., stronger prey switching and density effect, respectively).

In a controlled laboratory experiment, we compared risk reduction for shared prey in two different habitat types that provided different levels of predation refuge to intermediate predators. We test the hypothesis that habitat specific changes in the strength of the mechanisms of risk reduction lead to stronger risk reduction in habitats where intermediate predators are more vulnerable. We show that risk reduction was greater in rock habitat where the risk of predation to intermediate predators was greater. Additionally, the strengths of each of the mechanisms responsible for reducing shared prey consumption were habitat specific, and were stronger in rock habitat.

Natural history

The relatively low species diversity found on marine rocky intertidal shores of New England provides an excellent opportunity to isolate interactions between a limited number of focal species. One such shore is found at Odiorne Point, a relatively sheltered site on the outer coast of New Hampshire, USA. Two species of shore crabs are the dominant predators at Odiorne Point, the European green crab (*Carcinus maenas*) and the Asian shore crab (*Hemigrapsus sanguineus*). These two species have similar diets and potentially compete for food (Tyrrell and Harris 1999; Jensen et al. 2002). Additionally, predation occurs between these crabs, with the larger individuals of each species consuming smaller heterospecifics (Lohrer and Whitlatch 2002). Low tide sampling at the site revealed that various sized individuals of the two species inhabited the same areas and

were frequently found under the same rocks (Fig. 1). While various sized individuals of both species were present, juvenile *C. maenas* and adult *H. sanguineus* were most frequently observed (Fig. 1).

The few potential prey sources found at the site include mussels (*Mytilus edulis*), snails (*Littorina littorea*), and amphipods (*Gammarus* spp.). Small *C. maenas* that predominate at Odiorne Point are inefficient at penetrating calcium carbonate shells of mussels and snails, but readily consume amphipods. Amphipods are also an important prey source for *H. sanguineus* (McDermott 1998; Lohrer et al. 2000),

The predominant refuge habitat for both crabs and amphipods at Odiorne Point is cobble, covering approximately 30% of the sandy substrate (Tyrrell and Harris 1999). Though spatially and temporally variable, drift algae is also common at Odiorne Point (Tyrrell and Harris 1999) and provides another important type of refuge habitat. *Ceramium rubrum* is a red alga that is a major component of the drift algae at Odiorne. We conducted mesocosms experiment in which we provided both rock and drift algae habitat to investigate the effects of these habitats on risk reduction.

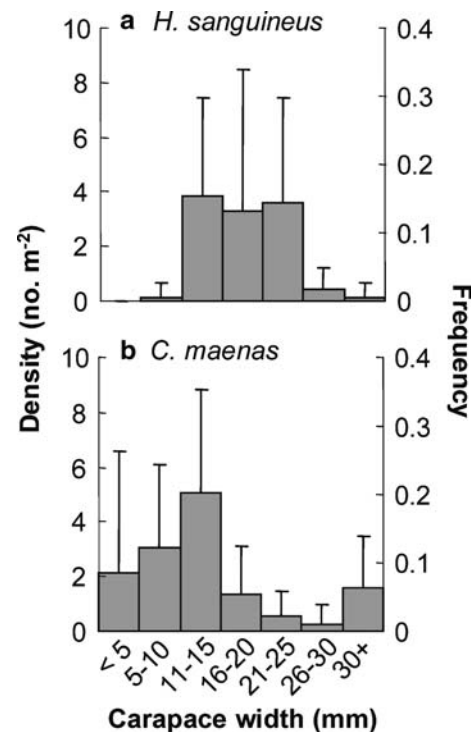


Fig. 1 Density and frequency distribution (avg. + 1 SD) of carapace size classes for **a** *H. sanguineus* and **b** *C. maenas* at Odiorne Point, New Hampshire. Average was determined by sampling 0.5 m² quadrats ($n=15$) at approximately 1 m above mean low water during low tide. The average density (± 1 SD) of all *C. maenas* and *H. sanguineus* at the site was 14 (± 8.9) and 11.4 (± 7.9) ind. m⁻², respectively

Methods

Refuge value of habitats

We first determined the relative refuge from predation for intermediate predators provided by cobble and drift algae. Experimental mesocosms consisted of polypropylene containers (78×31.5×30 cm³ deep), containing 1 cm of beach sand and 18 l (approximately 8 cm depth) of unfiltered seawater. We provided refuge habitat using either 12 rocks (mean diameter approx. 10 cm) or 50 g wet weight of drift algae (*C. rubrum*) so that approximately 30% of the surface area of the mesocosms was covered by refuge habitat, thus facilitating comparison between habitat types with equivalent percent cover. Sand, rock, algae, and water were obtained from the outer coast of New Hampshire, USA.

We collected *H. sanguineus* and *C. maenas* by hand from Odiorne Point, NH, and placed them in separate aquaria without food for 24 h prior to experimentation to standardize hunger level. We used large *H. sanguineus* [carapace width (CW) = 2.16 ± 0.24 cm, mean ± SD] and small *C. maenas* (CW = 1.37 ± 0.10 cm) in the experiments because these sizes were the modal sizes for each species found at Odiorne Point, NH (Fig. 1), and the size differential was sufficient to elicit intraguild predation by the larger *H. sanguineus* on smaller *C. maenas* (Lohrer and Whitlatch 2002). We conducted experiments in a controlled temperature/light room in aerated seawater tanks at 20°C on a 16:8 light:dark cycle (lux = 957). Individual crabs were used only a single time.

We conducted five replicates in each habitat. We placed ten *C. maenas* in mesocosms containing either rocks or algae, followed by two large *H. sanguineus*. This *C. maenas* density is higher than the mean natural density (Fig. 1); however, it is within the range of natural densities observed in the field, and was necessary to give sufficient resolution for quantifying mortality due to *H. sanguineus* predation. Mortality of *C. maenas* was assessed after 24 h and was compared between the two habitats using a two-tailed *t*-test.

Risk reduction in different habitats

We examined the relative strength of risk reduction in algal and rock habitats by conducting multiple predator experiments in each habitat type. We established experimental mesocosms and refuge habitats as described above for the habitat refuge experiment. Fifty amphipods (0.5–1 cm total length) were added to each mesocosm 1 h before the addition of one *H. sanguineus*, three *C. maenas*, or no predators (control). These crab densities fall within the natural densities observed at Odiorne Point, NH (Fig. 1). Amphipod densities at Odiorne Point are extremely variable, ranging from none to thousands m⁻². We therefore chose the experimental

amphipod density to ensure that amphipods were not completely depleted during the course of the trials.

The experiment included seven predator treatments in each of the two habitat types (Table 1) to quantify their effect on shared prey (amphipod) mortality. In three of these treatments, predators were rendered nonlethal by removing chelipeds and gluing the maxillipeds with cyanoacrylate. Based on extensive preliminary studies, both procedures were necessary to prevent crabs from killing or consuming amphipods. Neither of these procedures appeared to affect crab foraging behavior, as nonlethal crabs still attempted to capture prey. We conducted six 48-h trials with a complete treatment combination replicated once during each trial. For each trial, we randomized treatments among mesocosms and changed the water in experimental mesocosms.

The presence of risk reduction within each habitat type was determined by comparing observed amphipod mortality when predators foraged together (i.e., when predator interference potentially occurred) to predicted prey consumption if predators had additive effects. Predicted prey consumption when the predators were combined was derived from predation by each species separately using the multiplicative risk model (Soluk 1993). Specifically, predicted prey consumption (C_{HC}) was calculated as follows:

$$C_{HC} = N(P_H + P_C - P_H P_C), \quad (1)$$

where N is the number of prey at the start of the experiment, and P_H and P_C are the probabilities of prey consumption by *H. sanguineus* and *C. maenas* alone, respectively. The $P_H P_C$ term accounts for the fact that as prey are consumed they are no longer available to other predators. C_{HC} was calculated independently for both habitat types in each trial. Differences between the model predictions and observed predation when both predator species were combined indicate either risk reduction or risk enhancement. Risk reduction resulting from predator interference was anticipated because of antagonistic interactions between *H. sanguineus* and *C. maenas* (Lohrer and Whitlatch 2002). Therefore, observed and predicted (C_{HC}) amphipod mortality were compared within each habitat type using one-tailed, paired *t*-tests to determine whether predators had additive effects (Swisher et al. 1998; Warfe and Barmuta 2004).

Partitioning risk reduction

The importance of each of the three mechanisms that reduce shared prey mortality was determined by using the nonlethal predator treatments (Table 1) and was calculated for each trial separately, as follows (adapted from Crumrine and Crowley 2003):

Behavioral effect

Shared prey mortality is reduced as intermediate predators alter their foraging behavior in the presence of

Table 1 Experimental treatments used to test for the presence of risk reduction when multiple predators foraged together and to determine the strength of the behavioral effect and prey switching

Treatment	<i>H. sanguineus</i>	<i>C. maenas</i>	Effect tested
1	1	–	Predation rate of <i>H. sanguineus</i>
2	–	3	Predation rate of <i>C. maenas</i>
3	1	3	Presence and magnitude of risk reduction for shared prey when both predators forage together (treatment 3 compared to the model combination of treatments 1 and 2)
4	1 Nonlethal	3	Changes in foraging behavior of <i>C. maenas</i> when <i>H. sanguineus</i> is present (behavioral effect, treatment 2–treatment 4)
5	1	3 Nonlethal	Reductions in foraging on amphipods by <i>H. sanguineus</i> due to prey switching to <i>C. maenas</i> (prey switching, treatment 1–treatment 5)
6	1 Nonlethal	3 Nonlethal	Effectiveness of methods for rendering predators nonlethal
7	–	–	Background amphipod mortality

The strength of the density effect was calculated using additional data from a supplemental experiment as explained in the text. Each of these treatments was replicated six times in both rock and algal habitats. Numbers are individuals per mesocosm.

top predators. We quantified this reduction in amphipod mortality by subtracting shared prey consumption when intermediate predators foraged in the presence of a nonlethal top predator (Table 1, Treatment 4) from prey consumption when intermediate predators foraged alone (Table 1, Treatment 2).

Prey switching

Shared prey mortality is reduced as top predators forage on intermediate predators rather than on amphipods. We quantified this reduction in amphipod mortality by subtracting shared prey consumption when top predators forage in the presence of nonlethal intermediate predators (Table 1, Treatment 5) from prey consumption when top predators foraged alone (Table 1, Treatment 1).

Density effect

To calculate the density effect, one must know the number of intermediate predators that die and thus how many shared prey survive as a direct result of having fewer predators. Treatment 3 (Table 1) determined the number of intermediate predators (*C. maenas*) that died as a result of combining lethal top and intermediate predators. To address the second component of the density effect, we conducted a second, separate experiment in which we measured the number of amphipods consumed by one, two, and three *C. maenas* in the presence of nonlethal *H. sanguineus*. This complete suite of densities allows us to account for potential nonlinearities in our calculation of the density effect if conspecific interference among intermediate predators occurs. We included nonlethal *H. sanguineus* to account for reduced foraging by *C. maenas* due to the presence of *H. sanguineus* (i.e., the behavioral effect) and thus avoid overestimating predation by *C. maenas* in our calculation of the density effect. The difference between amphipod consumption by three and two

C. maenas, and by three and one *C. maenas*, indicates the impact of decreasing the intermediate predator density by one and by two, respectively. The reduction of live *C. maenas* quantified in each replicate of Treatment 3 could thus be translated into the number of amphipods that would have been consumed if *C. maenas* had not died.

As described, the calculation to this point yields a maximum density effect estimate that would occur if the death of intermediate predator *C. maenas* occurred immediately. However, the exact time that intermediate predators were consumed during the trials was unknown, and some may have eaten amphipods before dying. We therefore assumed that *C. maenas* died at the midpoint of each trial, and thus, divided this maximum reduction in amphipod mortality in each trial by two. Other assumptions regarding the timing of *C. maenas* mortality did not change the conclusions drawn about the influence of the density effect.

We compared the strength of risk reduction and the contribution of each of the mechanisms in each habitat using a two-way ANOVA with reduction in amphipod consumption (i.e., risk reduction) as the response variable and mechanism (three levels) and habitat (two levels) as fixed factors. We transformed the data [$\ln(x+1)$] prior to analysis to meet the assumptions of ANOVA.

Results

Refuge value of habitats

The experiment that compared the relative refuge from predation for intermediate predator *C. maenas* between habitats indicated that rock was the riskier habitat, as *C. maenas* mortality in the rock habitat was 2.5 times that in the algal habitat (two-tailed *t*-test, $t = 2.27$, $df = 8$, $P = 0.028$, Fig. 2). Based on this result, if risk reduction for amphipods occurs, it is expected to be stronger in rock than in algal habitats.

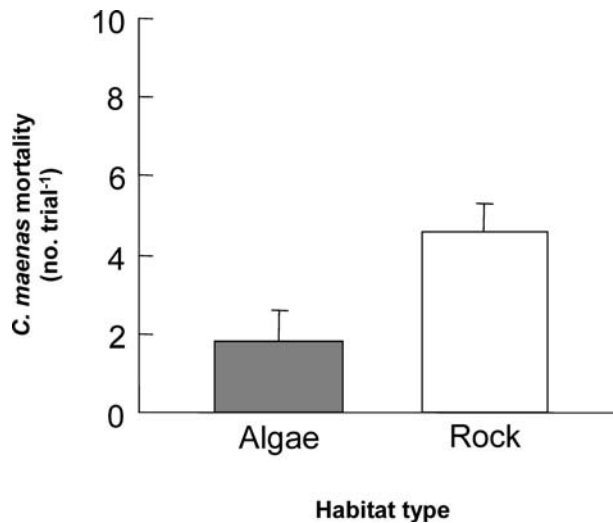


Fig. 2 *Carcinus maenas* mortality (avg. + SE, $n = 5$) due to predation by *H. sanguineus* in algal (*C. rubrum*) and rock refuge habitats

Risk reduction in each habitat

Each predator consumed amphipods when foraging separately in both habitats, and *C. maenas* consumed more amphipods than *H. sanguineus* did (Fig. 3). When both predators foraged together, amphipod mortality was lower than predicted based on predation by each species separately, indicating that risk reduction occurred in both rock and algal habitats. Specifically, the proportional reduction in amphipod mortality was 0.38 ± 0.06 (avg. \pm SE) in rock and 0.20 ± 0.05 in algae (one-tailed, t -tests, $t = 3.77$, $df = 5$, $P = 0.006$ and $t = 6.75$, $df = 5$, $P = 0.0005$, respectively; Fig. 3).

Partitioning risk reduction

The behavioral effect, prey switching, and density effect all contributed to risk reduction in both of the habitat

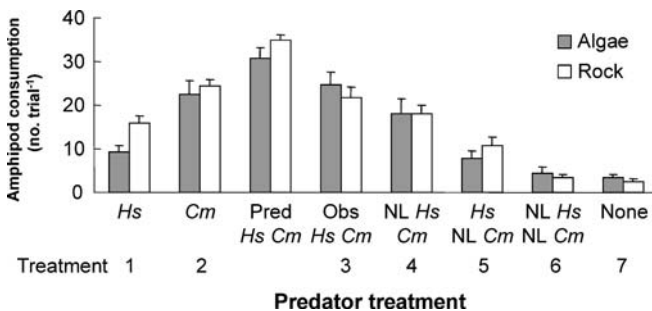


Fig. 3 Consumption of shared prey (amphipods) (mean + SE, $n = 6$) in algal (*C. rubrum*) and rock habitats in predator treatments: top predator *H. sanguineus* (Hs), intermediate predator *C. maenas* (Cm), predicted consumption by both predators together based on single predator treatments (Pred Hs Cm), observed consumption by both predators together (Obs Hs Cm), combinations with nonlethal predators (NL) and no predators (None). Numbers on x-axis correspond to the treatment number shown in Table 1

types (Fig. 4). Each was stronger in rock than in algae, leading to stronger risk reduction in rock than in the algal habitat (ANOVA habitat effect: $F_{1,35} = 5.83$, $p = 0.022$; Fig. 4). The mechanisms of predator interference differed in their effects on risk reduction (ANOVA mechanism effect: $F_{2,35} = 7.48$, $p = 0.002$; Fig. 4). However, the relative effects of the mechanisms did not vary significantly between habitats (ANOVA habitat \times mechanism interaction: $F_{2,35} = 0.40$, $p = 0.67$; Fig. 4). The behavioral effect (reduced foraging by *C. maenas* in the presence of *H. sanguineus*) was the largest; it was responsible for 67% of the reduction in amphipod mortality in the algal habitat and 48% in the rock habitat. Prey switching (reduced consumption of amphipods by *H. sanguineus* as it forages instead on *C. maenas*) decreased amphipod mortality more in rock (38%) than in algal habitats (21%). The density effect (decreased number of intermediate predators available to consume shared prey) was similar in both habitats at 14% in rock and 12% in algae.

Discussion

We have shown that the strength of interference between predator species is habitat specific (Fig. 4) and that the relative magnitude of risk reduction in different habitats can be readily quantified and partitioned into its underlying mechanisms. While prey switching and density effect occurred in both habitats, the behavioral effect accounted for most risk reduction in both habitats, indicating that *C. maenas* reduced its feeding when *H. sanguineus* was present, regardless of the habitat. Even though the chance of predation was greatly reduced for *C. maenas* in algae compared to rock (Fig. 2), the behavioral effect was still strong in this habitat. Strong behavioral effects can still occur in habitats where intermediate predators are relatively more protected from top predators, if intermediate predators are

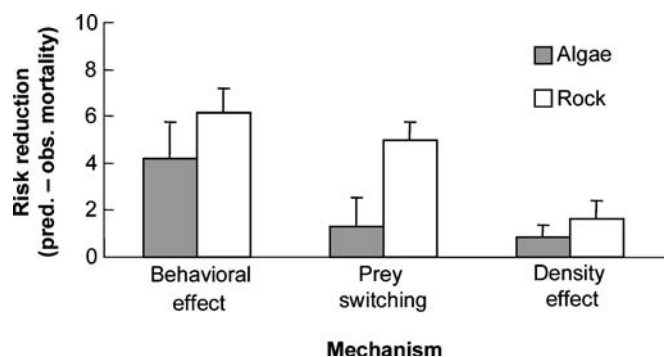


Fig. 4 Magnitude of risk reduction (mean + SE, $n = 6$) for shared amphipod prey attributable to behavioral effect, prey switching, or density effect mechanisms in algal (*C. rubrum*) and rock habitats. Magnitude of risk reduction was determined by the difference between predicted and observed prey mortality in each habitat type, respectively

incapable of discerning predation risk from top predators (Grabowski 2004).

The behavioral and prey switching effects examined here are examples of trait-mediated indirect interactions. Specifically, the behavioral effect is mediated by changes in intermediate predator foraging behavior, and prey switching is mediated by changes in top predator foraging behavior. In contrast, the density effect is a density-mediated indirect interaction. Few studies have attempted to partition the relative importance of these two components of indirect effects (reviewed in Werner and Peacor 2003), and their relative importance across different habitat types remains uncertain. While we found that the total indirect effect (i.e., risk reduction) was stronger in the rock than in the algal habitat, there was little difference in the relative importance of trait- and density-mediated effects across habitat types. Trait-mediated effects were responsible for 88% and 86% of the total risk reduction in algal and rock habitats, respectively, with the density effect accounting for the remainder (Fig. 4). These findings are consistent with previous arguments that behavioral or trait-mediated indirect interactions of predators may be stronger than density-mediated indirect interactions (Werner and Peacor 2003).

Our results are also consistent with previous studies that have shown the strength of risk reduction to be habitat specific (Finke and Denno 2002; Warfe and Barmuta 2004). Differences in risk reduction between the habitats in our study resulted from the increased strength of each of the mechanisms in rock as compared to algae (Fig. 4). This was anticipated because *C. maenas* was more vulnerable in rock than in algae (Fig. 2). Thus, the difference in vulnerability of *C. maenas* between the two habitats was directly responsible for the difference in risk reduction. Our study therefore shows that when top and intermediate predators are present, the difference in risk reduction between habitats may be explained by the differential refuge value of each habitat for intermediate predators. The riskiness of rock habitat for *C. maenas* is consistent with patterns of habitat use by *C. maenas* in the presence of *H. sanguineus* (Jensen et al. 2002). Jensen et al. (2002) demonstrated that the number of juvenile *C. maenas* found under rocks is drastically reduced in the presence of *H. sanguineus*, as compared to areas where the two species do not overlap, i.e. the coast of central/northern Maine.

Changes in shared prey behavior in response to predator presence can also cause multiple predators to have nonadditive predation (Losey and Denno 1998; Eklov and VanKooten 2001; Harvey et al. 2004). Thus, habitats that cause or allow prey species to behave differently could also be responsible for differences in nonadditive effects of predators between habitats. However, preliminary observations in our system indicate that while amphipods increased refuge use in the presence of predators, this did not depend on predator identity or refuge type (Griffen, unpublished data). Differences in risk reduction between rock and algal

habitats were thus most strongly affected by changes in predator foraging behavior. Other factors, such as prey density, may also influence the magnitude of risk reduction. Amphipod density in the field is highly variable, and previous work has shown that the magnitude of risk reduction or risk enhancement may (Soluk 1993; Losey and Denno 1998) or may not (Vance-Chalcraft and Soluk 2005) change with prey density.

Nonlethal predators in our experiments were rendered nonlethal by the only method that proved to successfully reduce predation, removal of their chelipeds. However, this manipulation may have simultaneously decreased the defensive capabilities of intermediate *C. maenas* predators, as more nonlethal than lethal *C. maenas* predators were consumed by *H. sanguineus* in each habitat type during our experiment. The treatment where lethal top predators and nonlethal intermediate predators were combined (Treatment 5, Table 1) may therefore overestimate the magnitude of prey switching observed in this experiment. Because overall risk reduction is the total of the behavioral, prey switching, and density effects, we could independently calculate the prey switching effect by subtracting the density and behavioral effects from the overall risk reduction in each habitat (Treatment 3, Table 1). This calculation produced a virtually identical estimate of prey switching to our experimental estimate and therefore did not change the relative importance of the various mechanisms in each habitat.

Most natural environments are not homogeneous, but rather are a mosaic of habitat types that provide varying levels of refuge for prey species. We have shown that differences in refuge value between habitats can lead to behaviorally-mediated changes in trophic interaction in multiple predator systems. Habitat specific changes in behavior can potentially link environmental heterogeneity to population and community dynamics through changes in refuge use and encounter rates among predators and between predators and prey (Chesson and Rosenzweig 1991). Understanding interactions between habitat use and behaviors that underlie complex trophic interactions may therefore lead to better predictions of population and community consequences of anthropogenic habitat change.

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