Habitat effects on the relative importance of trait- and density-mediated indirect interactions

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Abstract
Classical views of trophic cascades emphasize the primacy of consumptive predator effects on prey populations to the transmission of indirect effects [density-mediated indirect interactions (DMIIs)]. However, trophic cascades can also emerge without changes in the density of interacting species because of non-consumptive predator effects on prey traits such as foraging behaviour [trait-mediated indirect interactions (TMIIs)]. Although ecologists appreciate this point, measurements of the relative importance of each indirect predator effect are rare. Experiments with a three-level, rocky shore food chain containing an invasive predatory crab (Carcinus maenas), an intermediate consumer (the snail, Nucella lapillus) and a basal resource (the barnacle, Semibalanus balanoides) revealed that the strength of TMIIs is comparable with, or exceeds, that of DMIIs. Moreover, the sign and strength of each indirect predator effect depends on whether it is measured in risky or refuge habitats. Because habitat shifts are often responsible for the emergence of TMIIs, attention to the sign and strength of these interactions in both habitats will improve our understanding of the link between individual behaviour and community dynamics.

Keywords
Behaviour, food chain, predation risk, trait-mediated, indirect interactions, trophic cascade.

INTRODUCTION
Top-down trophic cascades are a classic example of the positive indirect effect that predators can have on basal resources in a variety of aquatic and terrestrial systems (Paine 1980; Carpenter et al. 1985; Menge 1995; Pace et al. 1999; Post et al. 1999; Schmitz et al. 2000; Shurin et al. 2002). Traditional views of trophic cascades emphasize the consumptive effects of predators on prey populations and emergent indirect effects [i.e. density-mediated indirect interactions (DMIIs), Abrams et al. 1996]. However, growing evidence indicates that many cascades are either partly or entirely driven by trait-mediated indirect interactions (TMIIs) that emerge because of the effect of predation risk on prey traits (for review see Schmitz et al. 2004).

Predator-induced habitat shifts by prey are perhaps the most common mechanism underlying trait-mediated cascades (Werner et al. 1983; Power et al. 1985; Fraser & Gilliam 1987; Turner & Mittlebach 1990; Kotler et al. 1991; Peckarsky & McIntosh 1998; Bernot & Turner 2001; Trussell et al. 2004). Such shifts are likely governed by tradeoffs between foraging and predation risk, where prey trade reduced foraging success for reduced predation risk (Lima & Dill 1990; Lima 1988). For example, in old-field communities (Beckerman et al. 1997; Schmitz et al. 1997; Schmitz 1998) grasshoppers confronted with predation risk by spiders shift their habitat use from risky but nutritious grasses, where spiders are effective predators, to less nutritious but structurally complex herbs where spiders are less effective. This change in grasshopper behaviour results in a positive indirect predator effect on grasses (a trophic cascade) and a negative indirect predator effect on herbs (an inverse cascade).

Theory predicts that prey foraging decisions under predation risk are influenced by resource levels (McNamara & Houston 1987; Mangel & Clark 1988; Luttbeg et al. 2003), which likely change as prey shift habitats. Hence, attention to the sign and strength of indirect predator effects on resources in both risky and refuge habitats will improve our understanding of how prey solve foraging/predation risk tradeoffs and the importance of individual behaviour to community dynamics. Although there is evidence that the
sign of indirect predator effects can differ between risky and refuge habitats (Beckerman et al. 1997; Schmitz et al. 1997; Schmitz 1998) there have been, as far as we know, no measures of how habitat type influences both the sign and relative magnitude of TMIIs and DMIIs. Several recent reviews (Bolker et al. 2003; Luttbeg et al. 2003; Werner & Peacor 2001; Griffin & Thaler 2006 for empirical estimates and Bolnick & Preisser 2005; Preisser et al. 2005 for meta-analyses).

Here, we examine how consumptive and non-consumptive predator effects influence prey foraging rates and the occurrence of trait- and density-mediated trophic cascades in a three-level, rocky shore food chain. We found that trait-mediated cascades were either as strong or stronger than density-mediated cascades. Moreover, the sign and size of indirect predator effects depended strongly on whether they were measured in risky or refuge habitat.

MATERIALS AND METHODS

We examined the relative importance of non-consumptive and consumptive predator effects and resulting indirect interactions (i.e. TMIIs and DMIIs) in a three-level food chain consisting of a predator (the green crab, Carcinus maenas), an intermediate consumer (the carnivorous snail, Nucella lapillus), and a basal resource (the barnacle, Semibalanus balanoides). We created experimental basal resource communities by anchoring granite tiles (15 cm × 15 cm) in the rocky intertidal zone during the recruitment season (late March to mid-April). All tiles were recovered in early May and returned to the laboratory. Barnacle abundance on tiles was determined by counting the number of barnacles in digital images of each tile with Adobe Photoshop (version 7.0; Adobe Systems 2002) and NIH Image J (version 1.34s).

We randomly assigned pairs of tiles that were sandwiched together (back-to-back) to 30 replicate containers. The top tiles (risky habitat) had significantly higher initial barnacle abundance (2985.4 ± 68.14 individuals; ANOVA $F_{1,58} = 220.73, P < 0.0001$) than the bottom (refuge habitat) tiles (1588.8 ± 64.8 individuals). We intentionally manipulated resource abundance in this way because resources are often higher or of better quality in risky vs. refuge habitats (e.g. Schmitz 1998). Each container (27 × 15 × 5 cm) was divided into two sections separated by a perforated barrier. One section (tile section, 16 × 15 × 5 cm) housed the tiles containing barnacles and had a plastic mesh (3.75 × 2.90 mm) roof to permit water flow. This section also had four plastic spacers (1 cm H) that elevated tiles above the bottom of each container to create a refuge to which Nucella could retreat in response to predation risk. Hence, foraging Nucella had access to barnacles in both the risky and refuge habitat. The other section (risk cue section, 11 × 15 × 5 cm) had a clear plastic roof and contained either a single green crab and 10 Nucella (‘crab’ treatment) or just 10 Nucella (‘no crab’ treatment). Flowing seawater was delivered to the risk cue section of each container via plastic tubing. Water then passed through the perforated barrier, into the experimental section housing the barnacle community, and exited through the mesh above the tile. This design ensured that experimental snails feeding on the tiles were exposed to water with or without risk cues originating from the upstream section of the container. Each container was housed in a larger (35 × 15 × 15 cm) plastic container to prevent water exchange among individual replicates.

We randomly applied two treatments (predation risk and snail removal) to containers in a fully factorial design with five replicates per experimental combination. Predation risk (crab and no crab) was manipulated by placing either a single green crab or no crab into the upstream section of appropriate containers. In the crab treatment, crabs were provided with a weekly supply of Nucella ($n = 10$) as food; Nucella in the no crab treatment were also replaced weekly. To simulate consumptive predator effects (snail removal) without the confounding effect of green crab risk cues, we manually removed snails from appropriate replicates following an exponential removal schedule (see Peacor & Werner 2001). This was achieved by removing 0%, 8% or 16% of the snails residing in a given container at a given time period and led to an exponential decline in snail density in the 8% and 16% treatments. Each container was initially stocked with 20 juvenile Nucella [mean ± SE shell length (mm), 9.44 ± 0.11], so the application of snail removals every 6 days resulted in an average snail density of 20 (0%), 13.58 (8%) or 9.08 (16%) snails per container over the duration of the experiment. These levels (8%, 16%) also produced average removal rates of 0.47 (16%) or 0.33 (8%) snails per day, which are considerably higher than field estimates of daily predation rates on Nucella (0.002 snails per day, Etter 1988). By using these high removal rates, our results comparing the relative importance of consumptive and non-consumptive predator effects on Nucella foraging and emerging indirect effects are quite conservative.

This experiment ran for 36 days. Every 3 days, we recorded the position of snails within each container. Snails underneath or directly on the bottom tile were scored as in refuge habitat whereas those foraging on the top tile (risky habitat) or in other areas above the top tile were scored as out of refuge habitat. The number of snails in refuge divided by the total number of snails present in each container at a given time yielded the proportion of snails in refuge habitat. We recorded the total number of barnacles consumed (initial – final abundance) in each replicate by re-photographing tiles at the end of the experiment and counting them as described above. We calculated per capita rates of
barnacle consumption by dividing the total number of barnacles consumed for a given replicate by its average snail density over the course of the experiment.

**Effect sizes and statistical analyses**

We calculated the proportional effect of predation risk (non-consumptive effect, \( \Delta_{NCE} \)) and snail removals (consumptive effect, \( \Delta_{CE} \)) on \( Nucella \) per capita foraging rates (\( F \)). Our approach is quantitatively identical to that of Peacor & Werner’s (2004) \( \Delta_{BG} \), which estimates the proportional reduction in foraging rate caused by predation risk alone. However, because we wanted to make similar estimates of the effect of snail removal, we chose different symbols to reflect each type of predator effect on \( Nucella \) foraging rate. The reduction in per capita \( Nucella \) foraging rate caused solely by predation risk (i.e. 0% removal) was calculated as

\[
\Delta_{NCE} = 1 - \left( \frac{F_{\text{crab}}}{F_{\text{no crab}}} \right),
\]

and that caused solely by snail removal (i.e. no cues present) was calculated as

\[
\Delta_{CE} = 1 - F_{\text{no crab}} / F_{\text{no crab}}, 0\%.
\]

A value of 0.5 for either \( \Delta_{NCE} \) or \( \Delta_{CE} \) means that foraging rates were reduced by 50% by predation risk or snail removal respectively. Note that negative values for \( \Delta_{NCE} \) or \( \Delta_{CE} \) indicate that foraging rates were enhanced by predation risk or snail removal.

We also calculated the strength of TMIIs, DMIIs and the total indirect predator interaction (TII) effect, which incorporates both consumptive and non-consumptive predator effects. The size of each effect in terms of barnacle abundance (\( A \)) at the end of the experiment was calculated as follows:

\[
\text{TMII} = (A_{\text{crab}}, 0\% / A_{\text{no crab}}, 0\%) - 1,
\]

\[
\text{DMII} = (A_{\text{no crab}}, 16\% or 8\% / A_{\text{no crab}}, 0\%) - 1,
\]

\[
\text{TII} = (A_{\text{crab}}, 16\% / A_{\text{no crab}}, 0\%) - 1.
\]

The numerators for the proportions above were provided by each replicate for a given treatment combination whereas the denominator was always the average amount of barnacles remaining at the end of the experiment across all replicates of the ‘no crab’, 0% removal treatment combination (see Wojdak & Luttbeg 2005 for a similar approach). These estimates of indirect effect magnitude use the same quantities as those for \( \Delta_{NCE} \) and \( \Delta_{CE} \) except that their calculation is reversed to reflect the proportional increase in resources due to each indirect predator effect.

Data on the proportion of snails using refuge habitat were analysed with a two-way, repeated measures ANOVA that considered ‘predation risk’ and ‘snail removal’ treatments as fixed effects and sampling time as a random effect. Per capita foraging rate and final barnacle abundance in the ‘risky’ and ‘refuge’ habitats were analysed with a two-way MANOVA that considered ‘predation risk’ and ‘snail removal’ as fixed effects. We used MANOVA because snail foraging rates and final barnacle abundance in each habitat are not independent from one another. MANOVA with effect type (TMI and DMII) as a fixed effect was also used to analyse variation in effect sizes in each habitat. TIs were not included in this analysis because we wanted to determine the relative importance of TMIIs and DMIIs. Because the sign of indirect effects sometimes differed between habitats, we did not analyse the raw effect size estimates (Preisser et al. 2005). For example, a TII of −0.85 and a DMII of +0.85 may end up being significantly different simply because of their differences in sign when in reality their magnitudes are identical. Hence, we analysed the absolute values of each effect type but plotted both their magnitude and sign (Fig. 3) so readers could appreciate both properties of each indirect effect. All MANOVAs were followed up with univariate ANOVAs (Scheiner 1993) on each response variable and linear contrasts when necessary. All analyses were performed on JMP software (SAS Institute, Cary, NC, USA).

In addition to these effect size estimates, we also calculated Hedges’ \( d \) (see Rosenberg et al. 2000) to allow comparison of our results (Table 1) to those from a recent meta-analysis on TMIIs and DMIIs (Preisser et al. 2005). However, it is important to note that we restrict all statistical analyses to our effect size estimates as described above.

**Table 1** Effect sizes due to trait-mediated indirect interactions (TMI), density-mediated indirect interactions (DMII) and total indirect interactions (TII) on final barnacle abundance

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Effect size, mean (SE)</th>
<th>Hedges’ ( d ), mean (variance)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Risky habitat</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TMII</td>
<td>5.82 (0.71)</td>
<td>4.22 (1.29)</td>
</tr>
<tr>
<td>DMII (16%)</td>
<td>4.31 (1.06)</td>
<td>2.21 (0.64)</td>
</tr>
<tr>
<td>TII</td>
<td>6.77 (1.01)</td>
<td>3.62 (1.06)</td>
</tr>
<tr>
<td><strong>Refuge habitat</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TMII</td>
<td>−0.84 (0.06)</td>
<td>−1.25 (0.48)</td>
</tr>
<tr>
<td>DMII (16%)</td>
<td>1.02 (0.53)</td>
<td>0.89 (0.44)</td>
</tr>
<tr>
<td>TII</td>
<td>−0.53 (0.18)</td>
<td>−0.72 (0.43)</td>
</tr>
</tbody>
</table>

For both metrics, estimates of DMII strength are based on the most intense snail removal treatment (16%) in the absence of risk cues (no crab) and TII strength on 16% snail removal in the presence of risk cues (crab). Mean (± SE) effect sizes in the left-hand column were calculated as described in the Materials and methods and mean (variance) Hedges’ \( d \) was calculated following Rosenberg et al. (2000). There is strong agreement between the two approaches and Hedges’ \( d \) is provided to allow comparison with recent meta-analyses (Bolnick & Preisser 2005; Preisser et al. 2005) on the relative importance of trait- and density-mediated effects.
RESULTS

Snail habitat use

Repeated measures ANOVA revealed that predation risk caused a higher proportion of snails to utilize the spatial refuge \( (F_{1,24} = 60.16, P < 0.0001) \) whereas snail removal \( (F_{2,24} = 0.06, P = 0.94) \) and the interaction \( (F_{2,24} = 1.89, P = 0.17) \) were unimportant (Fig. 1). The effect of predation risk on refuge use varied through time and was strongest \( (F_{6,142} = 2.47, P = 0.0275) \) from days 12 to 36. All other within-subject interactions were not significant (all \( P \geq 0.29) \).

Snail foraging

Predation risk \( (F_{1,24} = 13.51, P = 0.0012) \) and snail removal \( (F_{2,24} = 24.06, P < 0.0001) \) significantly influenced snail per capita foraging rate and their effects were additive (interaction, \( F_{2,24} = 0.23, P = 0.7960) \). Analysis of within-subject effects revealed that the effects of predation risk \( (F_{1,24} = 36.07, P < 0.0001) \) and snail removal \( (F_{2,24} = 4.15, P = 0.0284) \) on snail per capita foraging rate differed in each habitat. In the risky habitat, predation risk strongly suppressed snail foraging \( (\Delta_{\text{CE}} = 0.56, \text{univariate ANOVA}, F_{1,24} = 103.77, P < 0.0001) \) but had no significant effect in the refuge habitat \( (\Delta_{\text{CE}} = -0.17, \text{univariate ANOVA}, F_{1,24} = 2.08, P = 0.1621) \). In addition, the positive effect of snail removal (16% vs. 0%) on foraging rate was much stronger in the refuge habitat \( (\Delta_{\text{CE}} = -1.12, \text{univariate ANOVA}, F_{1,24} = 14.57, P < 0.0001) \) than in the risky habitat \( (\Delta_{\text{CE}} = -0.24, \text{univariate ANOVA}, F_{1,24} = 10.67, P = 0.0005) \). Finally, the combined effects of predation risk and snail removal on foraging rate was the same in each habitat \( (F_{2,24} = 0.01, P = 0.9879) \).

The strength of TMIIs and DMIIs

Both predation risk \( (F_{1,24} = 28.61, P < 0.0001) \) and snail removal \( (F_{2,24} = 6.69, P = 0.0049) \) significantly influenced barnacle abundance and their interaction exhibited a non-additive trend \( (F_{2,24} = 2.62, P = 0.0934) \). Within-subject tests revealed that final barnacle abundance was greatest in the risky habitat \( (F_{1,24} = 286.32, P < 0.0001) \) and that the effects of predation risk \( (F_{1,24} = 67.83, P < 0.0001) \) and snail removal \( (F_{2,24} = 5.85, P = 0.0085) \) on final barnacle abundance differed in each habitat (Fig. 2b). In the risky habitat, predation risk led to higher barnacle abundance regardless of the level of snail removal (univariate ANOVA, \( F_{1,24} = 46.24, P < 0.0001) \) whereas the opposite trend
emerged in the refuge habitat (univariate ANOVA, $F_{1,24} = 15.10, P = 0.0007$). Snail removal had a strong positive effect on barnacle abundance in the absence (linear contrast, $P = 0.0003$) but not the presence (linear contrast, $P = 0.3709$) of predation risk in the risky habitat but a negligible effect in the refuge habitat regardless of predation risk (univariate ANOVA, $F_{2,24} = 2.04, P = 0.1520$).

Analysis of TMII and DMII strength (Fig. 3, also see Table 1) revealed a significant difference in the size of indirect predator effect types ($F_{2,12} = 4.39, P = 0.0371$). Within-subject analysis indicated that the strength of indirect predator effects differed in each habitat type ($F_{1,12} = 70.92, P < 0.0001$) and were non-additive ($F_{2,12} = 4.39, P = 0.0151$). Predation risk caused a trophic cascade in the risky habitat and the strength and sign of this indirect effect was the same as the most intense (16%) snail removal treatment (linear contrast, $P = 0.2061$). Predation risk led to communities with 580% more barnacles in the risky habitat whereas snail removal (16%) led to communities with 431% more barnacles. Compared with intermediate levels of snail removal (8%), the effect of TMII was 2.4 times stronger (linear contrast, $P = 0.0062$).

In contrast, in the refuge habitat there were no significant differences in indirect predator effect size (univariate ANOVA, $F_{2,12} = 0.90, P = 0.4329$) but important differences in the sign of each indirect predator effect (Fig. 3). In the refuge habitat, TMII drove an inverse cascade reducing barnacle abundance by 85% whereas the effect of both levels of snail removal was positive, resulting in communities with 43–101% more barnacles. Hence, the positive indirect effect produced by the most intense snail removal (16%) was comparable with the negative effect of TMII on barnacle resources. However, our results suggest that the change in sign of TMII in the refuge habitat was more important because the sign of the TII effect (Fig. 3) was also negative. Finally, TMII and the most intense DMII (16% removal) were considerably weaker in the refuge vs. the risky habitat (Fig. 3, Table 1) but there was no habitat-specific difference in the strength of indirect effects produced by intermediate levels of snail removal (8%).

**DISCUSSION**

Our results clearly show that predation risk induced snails to spend more time in refuge habitat (Fig. 1) and altered their per capita foraging rates accordingly (Fig. 2a). Predation risk reduced per capita barnacle consumption by 56% in the risky habitat, but increased it by 18% in the refuge habitat. Hence, the direct effect of predation risk on both the magnitude and sign of snail foraging rate was strongly dictated by habitat type, with snails responding less to risk cues when residing in the refuge habitat. In contrast, whereas snail removal had a relatively small but significant effect (24% increase) on snail per capita foraging rate in the risky habitat, it strongly increased (112%) foraging rates in the refuge habitat.

At first glance, the small positive indirect effect of snail removal on per capita foraging rate in the risky habitat seems counterintuitive because such removals should relax the intensity of intraspecific competition. However, recent models suggest that prey may use conspecific density to assess predation risk (Peacor 2003) with low conspecific density indicating high risk and vice versa. If this is the case, then the positive effect of snail removal in reducing the intensity of intraspecific competition may have been diminished by an increase in the per capita predation risk perceived by prey (Bolnick & Preisser 2005). In contrast, the positive effects of snail removal in reducing the intensity of competition were more likely important in the refuge habitat because of relatively (compared with the risky habitat) low resource availability. Furthermore, because snails clearly perceived the refuge as safe, the positive effects of snail removal were not diluted by potential risk signalled by reduced conspecific density.

The effects of predation risk and snail removal on snail foraging rate transmitted strong indirect effects that
influenced barnacle abundance in each habitat. The presence of predation risk and resulting TMIIs led to communities with 580% more barnacles in the risky habitat but 85% fewer barnacles in the refuge habitat (Fig. 2b). Thus, consistent with non-consumptive predator effects on foraging rate, both the sign and magnitude of TMIIs depended on habitat type. Our results are generally consistent with previous studies (e.g. Werner et al. 1983; Beckerman et al. 1997; Schmitz 1998) because predation risk led to positive indirect effects on resources in the risky habitat but negative indirect effects on resources in the refuge habitat. These differences in the sign of the indirect effect arose because snails traded abundant resources and higher predation risk for comparatively fewer resources and lower predation risk in the refuge habitat.

This dynamic should change as resources are depleted in the refuge habitat. Theory predicts that once resources are in short supply prey become more willing to accept higher predation risk so as to acquire the resources necessary to avoid starvation (McNamara & Houston 1987, 1996; Mangel & Clark 1988; Werner & Anholt 1993). Had our experiment run longer, resource depletion in the refuge habitat should eventually induce snails to begin foraging in the risky habitat, thus diminishing the strength of TMIIs. Recent theory and models show that prey state and resource levels should affect the relative importance of TMIIs (Luttbeg et al. 2003) and we suggest that attention to resource dynamics in refuge habitats may further advance our understanding of this issue. This focus is needed because the influence of refuge habitat quality on the strength and nature of indirect predator effects may not be uniform across different systems. For example, research on experimental oyster reefs (Grabowski & Kimbro 2005) shows that while an intermediate predator (mud crab) seeks refuge inside oyster reefs in the presence of a top predator (toadfish), this behavioral shift does not enhance the impact of mud crabs on clams residing inside the reef despite their being closer to one another. Increased mud crab foraging on refuge resources did not occur because: (i) habitat complexity within the refuge made it more difficult for mud crabs to locate their prey; and (ii) toadfish risk cues suppress the foraging of mud crabs even when crabs are hiding in the refuge habitat (Grabowski 2004; Grabowski & Kimbro 2005). Hence, refuge resource depletion is unlikely to occur suggesting that temporal dynamics in TMII strength are not influenced by refuge resources when habitat characteristics impede the foraging of top and intermediate predators in a similar manner.

Trait-mediated indirect interactions are predicted to be as strong, if not stronger, than DMIIs because non-consumptive predator effects can simultaneously affect an entire prey population whereas consumptive predator effects require time to accumulate (Schmitz et al. 1997; Peccor & Werner 2001). This prediction is supported by recent meta-analyses showing that 85% of the TII effect on prey resources is trait-mediated (Preisser et al. 2005). Moreover, our results also clearly show that the strength of TMIIs was either similar to or exceeded that of DMIIs, and that relative differences in each indirect predator effect depended on habitat type (Fig. 3). The greater barnacle abundance (580%) caused by TMIIs in the risky habitat was similar to that (431%) caused by high (16%) snail removal and substantially greater than that (207%) caused by low (8%) snail removal. In contrast, in the refuge habitat only the sign of indirect effects (negative for TMIIs, positive for DMIIs) differed. Using our measure of effect size, TMIIs represented 86% of the TII effect (Fig. 3) in the risky habitat. This result is consistent with meta-analyses where TMIIs represented 97% of the TII effect in three-level, marine food chains (Preisser et al. 2005). Moreover, another estimate (Hedges’ $d$) of TMIIs effect size in the risky habitat ($d = 4.22$, variance = 1.29) exceeds the values reported in Preisser et al. (2005).

It is important to note that our snail removals mimicked predation rates on snails that averaged 0.33 (8% removal) to 0.47 (16% removal) snails consumed per day, which is comparable with or considerably higher than available field estimates of predation rates on Nucella and other intertidal snails. The detected difference between TMIIs and DMIIs is thus conservative because DMIIs are likely less important in a natural setting. For example, based on previous tethering experiments (Etter 1988) on shores in and around Nahant, Massachusetts, we estimate Nucella mortality due to predation to be 0.002 snails per day. In addition, experiments examining the consumptive and non-consumptive effects of green crabs on tidepools stocked with Littorina littorea at a density of 150 snails per m$^2$ indicate that an individual crab consumes on average only 0.22 (± 0.04) snails per day (G.C. Trussell and P.J. Ewanchuk, unpublished data). Instead, crabs focused on mussels available within tidepools, which is consistent with other field observations showing that mussels rather than snails are by far the biggest component of the green crab diet (Etter 1988). We suggest that both predator diet breadth and the abundance and diversity of available prey, in addition to predator identity (Turner et al. 1999; Bernot & Turner 2001; Schmitz et al. 2004), may be key determinants of the relative importance of TMIIs and DMIIs. Hence, TMIIs may be more important in trophic cascades that are driven by generalist predators having access to a variety of prey, whereas DMIIs may be more important in food webs containing specialist predators.

The indirect effects of predation risk on barnacle populations observed here likely influence the dynamics of other species on rocky intertidal shores (see Trussell et al. 2002, 2004). Lubchenco (1983) found that barnacles increase the pace of community succession through their
facilitation of fucoid algae (Aposthylum nodosum, Fucus vesiculosus). This facilitation occurs because the crevices created by barnacle tests (shells) interfere with herbivorous snail (e.g. L. littorea) grazing that slows the rate of rocky shore succession (Lubchenco 1983; Bertness 1984; Bertness et al. 2002, 2004). The strength of facilitation between barnacles and fucoids will be partly dictated by barnacle abundance. Hence, the intensity of Nucella foraging on barnacles, which is influenced by predation risk, may strongly influence this dynamic. For example, Nucella using refuges (cracks and crevices) in response to predation risk will consume fewer barnacles in riskier, open habitat, resulting in stronger facilitative interactions between barnacles and fucoids. Thus, the effects of predation risk on Nucella foraging should hasten the pace of succession in risky habitats and this positive interaction will be strongest when refuges have high resource levels that require more time to deplete. In contrast, if refuge resources are low and depleted quickly, the exploitation of riskier habitats by Nucella should weaken the facilitation of fucoids by barnacles. The effects of predation risk and resulting TMIIs on community succession are likely stronger than DMIIs because, as discussed above, consumptive predator effects appear to be particularly weak in this system.

It is clear that TMIIs exert a strong influence in this and other rocky shore food chains. For example, other intermediate consumers (L. littorea, Littorina obtusata) and basal resources such as mussels (Mytilus edulis) modify their behaviour or morphology in response to green crab predation risk (Smith & Jennings 2000; Trussell et al. 2002, 2003, 2004). Given that the green crab is an invasive species that arrived on New England shores from Europe in the early 1900s (Trussell & Smith 2000), it is remarkable that so much of its influence on these food webs is through non-consumptive rather than consumptive effects. Hence, the intuitive prediction that invasive predators will have large, primarily consumptive impacts on native prey populations does not always hold true.

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