

Resource levels and prey state influence antipredator behavior and the strength of nonconsumptive predator effects

Catherine M. Matassa, Sarah C. Donelan, Barney Luttbeg and Geoffrey C. Trussell

C. M. Matassa (<http://orcid.org/0000-0003-2632-6191>)(matassa.c@gmail.com), S. C. Donelan and G. C. Trussell, Marine Science Center, Northeastern University, 430 Nahant Road, Nahant, MA 01908, USA. – B. Luttbeg, Dept of Integrative Biology, Oklahoma State University, Stillwater, OK, USA.

The risk of predation can drive trophic cascades by causing prey to engage in antipredator behavior (e.g. reduced feeding), but these behaviors can be energetically costly for prey. The effects of predation risk on prey (nonconsumptive effects, NCEs) and emergent indirect effects on basal resources should therefore depend on the ecological context (e.g. resource abundance, prey state) in which prey manage growth/predation risk tradeoffs. Despite an abundance of behavioral research and theory examining state-dependent responses to risk, there is a lack of empirical data on state-dependent NCEs and their impact on community-level processes. We used a rocky intertidal food chain to test model predictions for how resources levels and prey state (age/size) shape the magnitude of NCEs. Risk cues from predatory crabs *Carcinus maenas* caused juvenile and sub-adult snails *Nucella lapillus* to increase their use of refuge habitats and decrease their growth and per capita foraging rates on barnacles *Semibalanus balanoides*. Increasing resource levels (high barnacle density) and prey state (sub-adults) enhanced the strength of NCEs.

Our results support predictions that NCEs will be stronger in resource-rich systems that enhance prey state and suggest that the demographic composition of prey populations will influence the role of NCEs in trophic cascades. Contrary to theory, however, we found that resources and prey state had little to no effect on snails in the presence of predation risk. Rather, increases in NCE strength arose because of the strong positive effects of resources and prey state on prey foraging rates in the absence of risk. Hence, a common approach to estimating NCE strength – integrating measurements of prey traits with and without predation risk into a single metric – may mask the underlying mechanisms driving variation in the strength and relative importance of NCEs in ecological communities.

Predation risk can initiate trophic cascades by causing changes in prey foraging behavior or habitat use that weaken the strength of interactions between prey and basal resources (reviewed by Werner and Peacor 2003, Schmitz et al. 2004). Antipredator behaviors, such as increased refuge use or reduced foraging activity, can result in reduced energy intake, indicating that prey trade off foraging and growth for safety from predators (Sih 1980, Lima and Dill 1990). The nature and magnitude of prey responses to predation risk, or nonconsumptive predator effects (hereafter, NCEs), and emergent indirect effects on basal resources should therefore be sensitive to conditions that limit or enhance the ability of prey to engage in antipredator behaviors.

Theoretical models have greatly advanced our understanding of how prey foraging decisions balance the relative costs (increased vulnerability) and benefits (increased energy gain) of foraging (Mangel and Clark 1986, McNamara and Houston 1987, Houston et al. 1993) and suggest that the effects of predation risk are context-dependent. It is predicted that when, where, and how much prey forage in the face of predation risk will depend on their energetic state (e.g. due to reserve levels, body mass, resource availability;

for review, Lima and Dill 1990, Lima 1998). Examples from theoretical and empirical research show that a lower energetic state can cause prey to forage more during riskier time periods, increase their use of risky but high reward habitats, and increase overall foraging effort (Gilliam and Fraser 1987, McNamara and Houston 1987, Brown 1988, Werner and Anholt 1993, Kotler et al. 2004, Ovadia and Schmitz 2004). For instance, increases in shark density cause sea turtles with good body condition to shift their grazing effort into safer habitats, but low condition turtles graze in riskier habitats regardless of shark density, presumably because these riskier habitats have higher quality seagrass (Heithaus et al. 2007).

Models incorporating state-dependent foraging theory show that resource abundance and prey state can influence prey responses to predation risk and the strength of NCEs (Luttbeg et al. 2003). Luttbeg et al. (2003) compared the foraging and growth of prey in the presence of a low number of predators (control) to preys receiving additional cues of predation risk (risk manipulation) and estimated NCE strength as the proportional reduction in resources consumed in the risk manipulation compared to the control. In their model, optimal prey foraging efforts are shaped by

the tradeoff of the expected benefit of resources consumed and the associated predation risk caused by the foraging effort. Because of the risk of starvation, additional consumed resources often have the greatest effect on expected prey fitness when resource consumption is low. Thus, when resources are scarce, the benefit of increasing foraging effort, and thereby gaining more resources, is expected to outweigh the associated increase in predation risk. This dynamic leads to the prediction that NCEs should increase in magnitude as resource levels increase (Luttbeg et al. 2003). Essentially, when resources are abundant, prey can afford to lower their foraging effort when perceived predation risk increases, and this causes a larger NCE. However, when resources are scarce, prey must keep foraging to avoid the risk of starvation; thus they respond less to increases in perceived predation risk, and NCEs are smaller.

Despite advances in theory, empirical studies that examine community-level impacts of state-dependent responses to predation risk are still limited (but see Olsson et al. 2002, Ovadia and Schmitz 2002, Danner and Joern 2003, Heithaus et al. 2007, Matassa and Trussell 2014). This study empirically examined the prediction that NCEs will be stronger in resource-rich systems that enhance prey state (Luttbeg et al. 2003) using a simple but ecologically important rocky intertidal food chain. On rocky shores in New England, USA, waterborne risk cues from predatory green crabs *Carcinus maenas* cause prey snails *Nucella lapillus* (hereafter *Nucella*) to increase their use of refuge habitats and decrease their foraging rates on barnacles *Semibalanus balanoides*, leading to reduced *Nucella* growth (Trussell et al. 2003, 2006, Matassa and Trussell 2011). The resulting positive indirect effects of green crabs on barnacles can influence the structure and dynamics of rocky shore communities because of the key role that barnacles play in intertidal community succession (reviewed by Benedetti-Cecchi and Trussell 2013). Barnacle larvae settle on rocky shores annually during a discrete time period each spring and are one of the first species to colonize bare spaces that arise after disturbance from winter storms. The subsequent recruitment of other species, such as canopy-forming seaweeds (e.g. *Ascophyllum nodosum*, *Fucus* spp.) and competitively dominant mussels (*Mytilus edulis*), is positively influenced by barnacle density (Menge 1976, Lubchenco 1983, Navarrete and Castilla 1990, Bertness et al. 2004).

We focus our study on two potentially interacting factors that might influence the strength of NCEs: basal resource abundance and prey body size. We tested whether the initial abundance of barnacles altered the effects of green crab predation risk on the refuge use, per capita foraging rates (number of barnacles consumed), and growth of relatively small (juvenile) and large (sub-adult) *Nucella*. We also estimated NCE strength across the resource gradient. The positive effects of resource levels on prey state and foraging efficiency should increase the strength of NCEs (Luttbeg et al. 2003). However, for prey under constant high risk (relative to those under constant safety), as we examine here, the increased foraging efficiency afforded by high resource levels may allow prey to gather more resources despite risk-induced reductions in foraging effort or increases in refuge use, potentially weakening the positive effects of resources on NCEs as predicted by Luttbeg

et al. (2003). Foraging efficiency may also vary with body size due to its effects on resource handling times (Peters 1986). Because the handling times for barnacles decrease with *Nucella* size (Dunkin and Hughes 1984, Burrows and Hughes 1991), increased body size may have an impact on NCE strength that is qualitatively similar to that produced by increased barnacle abundance.

In addition to foraging efficiency, body size can affect both an individual's actual risk of predation and how it balances growth/predation risk tradeoffs (Paine 1976, Werner and Gilliam 1984, Embar et al. 2014). Larger prey may respond less to increased predation risk (weaker NCEs) if size refuges make them less vulnerable to predators (negative size-dependent predation risk). Alternatively, because body size often correlates with energetic state or age/development stage, as for *Nucella* (Etter 1989), larger prey may respond more strongly to risk (stronger NCEs) because larger body mass or energy reserves increase their ability to forego foraging under increased predation risk (McNamara and Houston 1987, Houston et al. 1993) and/or because their greater investments in reproductive tissues increase the relative cost of a potential predator attack (i.e. the asset protection principle; Ludwig and Rowe 1990, Clark 1994). Because the two *Nucella* size classes used in our experiment are at different stages of development, our study cannot fully isolate the effects of size and age/developmental stage. We therefore refer to our size class treatment using the aggregate term 'prey state.' Within a population, *Nucella* foraging rates and fitness are tightly linked (Burrows and Hughes 1990), and individuals forage and grow continuously as they develop and for several years after reaching sexual maturity (Crothers 1985, Etter 1989, 1996). Given the life history of *Nucella*, the size classes used, and the timing of our experiment (details in Methods), state-dependent foraging decisions that rely on reproductive time constraints or step-functions to describe the relationship between foraging and fitness are likely not relevant to our study (Abrams 1991, Houston et al. 1993; see Matassa and Trussell 2014 for more on the role fitness functions on NCEs in this system).

Methods

To examine how resource abundance and prey state interact to shape responses to predation risk and the strength of NCEs, we fully crossed two levels of predation risk (crab or no crab) with four levels of resource abundance (none, low, moderate, or high density of barnacles) and two levels of prey state. The 16 resulting treatment combinations were randomly assigned to 96 independent, flow-through mesocosms in the outdoor seawater lab at Northeastern University's Marine Science Center in Nahant, Massachusetts, USA ($n = 6$). Each mesocosm consisted of a modified plastic utility box ($27 \times 15 \times 5$ cm, $l \times w \times h$) with a perforated interior barrier that divided the box into upstream and downstream chambers. Continuously flowing seawater was delivered to the upstream chamber through a vinyl hose, flowed through the perforated barrier, and exited the downstream chamber through a mesh roof. Each mesocosm was placed in a separate 6-l container to prevent water exchange among units.

To manipulate predation risk, the upstream chamber of the mesocosm either remained empty (no crab treatment) or contained a single male green crab (crab treatment) that was fed three *Nucella* per week. The downstream chamber held an experimental barnacle community (granite settlement tile, 15 × 15 × 1 cm; barnacle size range approximately 1.5–4.0 mm opercular diameter). To manipulate prey state, either eight small (shell length range 9–12 mm) or eight larger *Nucella* (16–20 mm) were added the downstream chamber of each mesocosm. Both size classes of *Nucella* are susceptible to predation by green crabs, but successful attack rates decline as shell lengths exceed 14 mm, with individuals > 27 mm reaching a size refuge (Hughes and Elner 1979).

The experiment ran for 21 days beginning 27 July 2009. All *Nucella* were collected on 23 July 2009 from a wave-exposed shore with high barnacle density (75–100% cover in collection areas) in mid-coast Maine, USA. *Nucella* breed during the spring, and juveniles hatch from deposited egg cases 3–4 months later in the middle of the growing season, which lasts from spring through fall (Crothers 1985). In the western Atlantic, juvenile *Nucella* reach sexual maturity 1–2 years after hatching, reproduce for the first time during the following spring, and continue to grow for several years, with maximum sizes > 35 mm (Crothers 1985, Etter 1989, Fisher et al. 2009). Growth rates, size at maturity, maximum size and population size structure are correlated with one another and depend on environmental factors such as wave disturbance and food availability (Crothers 1985, Etter 1989, 1996, Fisher et al. 2009). At a wave-exposed shore, Etter (1989) found that 0% of snails < 15 mm were mature, while 72% of individuals 16–18 mm and 100% of individuals ≥ 19 mm were sexually mature, and these sizes were greater on a nearby wave-protected shore (i.e. no individuals < 20 mm were mature). We did not directly examine individuals for sexual maturity because this can be challenging outside of the breeding season (Etter 1989). But, given their life history and the timing of our collections, we are confident that the smaller (9–12 mm) *Nucella* in our experiment had not reached sexual maturity and are probably ≤ 1 year old. Hence, we refer to this as the juvenile size class. The larger *Nucella* (16–20 mm) in our experiment were likely between one and two years old and had either reached sexual maturity recently or were in the process of achieving sexual maturity during our experiment. We therefore refer to the larger size class as sub-adults, which are sexually mature but have not yet reproduced.

Prior to the experiment, three of the eight *Nucella* in each mesocosm were individually marked with plastic bee tags and measured for initial shell length and initial tissue mass using Palmer's (1982) non-destructive buoyant weighing technique (details in Matassa and Trussell 2014). Initial shell length and tissue mass estimates for tagged individuals were (mean ± SD) 10.97 ± 0.42 mm and 56.75 ± 8.82 mg for juveniles (n = 144 tagged individuals) and 17.51 ± 0.51 mm and 200.72 ± 34.90 mg for sub-adults (n = 144 tagged individuals). Tissue mass measurements were repeated at the end of the experiment. Tissue growth (mg) was calculated as final – initial tissue mass for each tagged individual.

We manipulated resource abundance by thinning barnacles on settlement tiles to one of four levels: high (no barnacles removed), moderate (50% removed), low (75%

removed), or none (all barnacles removed), resulting in (mean ± 1 SD) 867 ± 95, 473 ± 50, 182 ± 29, or 0 barnacles per tile, respectively. These levels were determined based on previous work (Matassa and Trussell 2011) so that both juvenile and sub-adult *Nucella* could deplete the barnacle supply in the low resource treatment prior to the end of the experiment but would not become resource-limited in the high abundance treatment, allowing us to determine whether differences in foraging efficiency contributed to any effects of prey state on per capita foraging rates (i.e. different functional responses of juveniles versus sub-adults). Barnacles were thinned haphazardly so that the spatial distribution of resources was not altered. Prior to thinning, we cleared a 4 × 14 cm area along one edge of each tile to allow placement of a refuge 'hut,' which provided ample refuge habitat within the mesocosm for *Nucella* of all sizes. Refuge huts were half-pipe sections of 1" schedule 40 PVC pipe (10.5 cm length × 2.6 cm inside diameter, 3.3 cm outside diameter,) with an additional 2.0 × 1.3 cm central opening. In addition to the huts, the vertical walls, roof and corners of the mesocosm were considered refuge microhabitats, as these spaces mimic the natural cracks, overhangs and crevices where *Nucella* shelter in the field (Gosselin and Bourget 1989, Burrows and Hughes 1991, Matassa and Trussell 2011). We observed *Nucella* behavior every three to four days and recorded the number of individuals using refuge versus risky (non-refuge) microhabitats. We calculated refuge use for each week of the experiment as the mean proportion of *Nucella* found in refuge habitats.

We digitally photographed barnacle communities at the beginning of the experiment and every seven days thereafter to identify and count consumed barnacles (details in Matassa and Trussell 2011), which were evident by empty or missing tests. We calculated the per capita number of barnacles consumed each week as the number of barnacles consumed divided by the mean *Nucella* density in the mesocosm during that week. Due to mortality, which remained low throughout the experiment (14 of 768 total *Nucella* died, five of which were tagged), mean densities ranged from seven to eight *Nucella* per mesocosm. We then calculated the cumulative per capita number of barnacles consumed over time (one, two, and three weeks) as the sum of all previous weekly foraging rates (i.e. days 0–7, 0–14 and 0–21, respectively). We used these values to estimate the strength of NCEs, or the proportional reduction in prey foraging rates due to predation risk, over time. For each prey state × resource abundance treatment combination, replicate estimates of NCE strength were obtained using the formula $1 - (Y_{r,crab} / \bar{Y}_{t,no\ crab})$, where $Y_{r,crab}$ is the cumulative per capita number of barnacles consumed (Y) at time t in replicate r of the crab treatment, and $\bar{Y}_{t,no\ crab}$ is the mean cumulative per capita number of barnacles consumed (\bar{Y}) across all six replicates in the corresponding no crab treatment at the same time, t (see Luttbegg et al. 2003, Wojdak and Luttbegg 2005 and Matassa and Trussell 2011 for similar approaches). We did not calculate mass-specific per capita foraging rates because the body mass of *Nucella* changed throughout the experiment. Furthermore, accurate interpretation of mass-specific foraging rates would be difficult because we do not know the scaling relationship between metabolism and body mass for *Nucella* or how behavior, resource levels, or

predation risk (Trussell et al. 2006, Steiner and Van Buskirk 2009) may quantitatively affect *Nucella's* metabolic rates. However, we do discuss ways that our results can be interpreted after taking size/biomass differences into account.

Statistical analyses were performed in R ver. 3.2.2 (<www.r-project.org>). We analyzed *Nucella* refuge use with a factorial mixed model ANOVA that included crab cues, prey state, resource abundance, and time as fixed effects. Mesocosm (nested within the crab cues, prey state and resource abundance treatments) was included in the model as a random effect. Cumulative per capita foraging rates at the end of each week and individual tissue growth were analyzed with three-way ANOVAs. Crab cues, prey state, and resource abundance were fixed effects. Our analysis of tissue growth included mesocosm as a nested random effect to account for the multiple *Nucella* measured within each mesocosm. We tested the effects of prey state and resource abundance on the size of green crab NCEs through weeks one, two, and three using a mixed effects model that included a random slope (time) and intercept (mesocosm). Prey state, resource abundance, time, and all interactions were included in the model as fixed effects. We fit mixed models using the R package nlme (Pinheiro et al. 2015). We included REML-estimated weighted variance structures in statistical models as necessary to account for unequal variances among treatment combinations according to procedures outlined by Zuur et al. (2009). We verified assumptions of normality with visual inspection of histograms, residual plots and normal-quantile plots. We used orthogonal polynomial contrasts to test for linear and quadratic trends in per capita foraging rates, growth and final NCE strength across non-zero resource abundances. We weighted the contrast coefficients to account for the uneven spacing between resource levels. Significant interactions were explored using least-squares (ls) contrasts to compare group means (R package lsmeans, Lenth 2015).

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.7sr33>> (Matassa et al. 2016).

Results

Patterns of prey refuge use over time and across resource levels

The temporal patterns of *Nucella* refuge use depended on the interaction between predation risk and barnacle density (time \times crab cues \times resource abundance: $p = 0.0113$; Table 1, Fig. 1). In the complete absence of food (Fig. 1a), refuge use remained relatively high ($> 75\%$) throughout the experiment regardless of risk, although risk further increased refuge use (to 98%) during the first week (ls contrast: $F_{1,160} = 16.78$, $p = 0.0001$). When food was available (barnacle density > 0), refuge use increased over time and was greater under predation risk (Fig. 1b–d). In the presence of risk and food, *Nucella* increased their refuge use, on average, from 45% during week one to 86% during week three (ls contrast: $F_{1,160} = 140.07$, $p < 0.0001$; Fig. 1b–d, filled symbols). In the absence of risk, *Nucella* also increased

Table 1. Results from a mixed model factorial ANOVA testing the fixed effects of crab cues [c] (crab or no crab), prey state [p] (juvenile or sub-adult *Nucella*), and resource abundance [r] (none, low, moderate, or high) on the proportion of *Nucella* using refuge habitats over time [t] (weeks one, two, or three). Mesocosm was nested within the crab cues, prey state, and resource abundance treatments and included in the model as a random effect. Numerator and denominator degrees of freedom are given as DF_n and DF_d , respectively. * $p < 0.05$.

Effect	DF_n	DF_d	F	p
Crab cues [c]	1	80	301.72	$< 0.0001^*$
Resource abundance [r]	3	80	234.43	$< 0.0001^*$
Prey state [p]	1	80	1.04	0.3113
c \times r	3	80	24.53	$< 0.0001^*$
c \times p	1	80	11.52	0.0011*
p \times r	3	80	0.20	0.8995
c \times p \times r	3	80	4.62	0.0050*
Time [t]	2	160	149.29	$< 0.0001^*$
t \times c	2	160	0.11	0.8999
t \times r	6	160	20.11	$< 0.0001^*$
t \times p	2	160	1.42	0.2449
t \times c \times r	6	160	2.86	0.0113*
t \times c \times p	2	160	2.14	0.1214
t \times p \times r	6	160	1.37	0.2297
t \times c \times p \times r	6	160	0.73	0.6258

their use of refuge habitats over time, but refuge use reached greater maximum levels when resources were scarce (70%; Fig. 1b, open symbols) than when resources were abundant (35%; Fig. 1d, open symbols; ls contrast of low versus high resource treatments during week three: $F_{1,160} = 36.74$, $p < 0.0001$).

When averaged over the three-week experiment, the magnitude of risk effects on refuge use was more pronounced for sub-adult *Nucella* than for juveniles (crab cues \times prey state: $p = 0.0011$), but this effect depended on the presence of barnacle resources (crab cues \times prey state \times resource abundance: $p = 0.0050$; Table 1). When no barnacles were available (Fig. 1a), sub-adults and juveniles used refuge habitats at similarly high rates regardless of risk (ls contrasts: $F_{1,160} = 0.01$, $p = 0.94$ and $F_{1,160} = 2.52$, $p = 0.12$ in the presence and absence of risk, respectively; Fig. 1a). When barnacles were available (Fig. 1b–d), sub-adult *Nucella* used refuges more than juveniles in the presence of risk (ls contrast: $F_{1,160} = 9.64$, $p = 0.0026$), but juvenile *Nucella* used refuges more than sub-adults in the absence of risk (ls contrast: $F_{1,160} = 7.97$, $p = 0.0060$).

Per capita foraging rates and growth

During the first week of the experiment, sub-adult *Nucella* consumed more barnacles than juveniles, but this difference decreased under predation risk (crab cues \times prey state: $p = 0.0005$; Table 2a, Fig. 2a). Sub-adult *Nucella* consumed 64% more barnacles than juveniles in the absence of risk (ls contrast: $F_{1,60} = 119.31$, $p < 0.0001$), but only 45% more barnacles in the presence of risk ($F_{1,60} = 7.88$, $p = 0.0067$). The effects of resource levels on *Nucella* foraging rates also depended on prey state (prey state \times resource abundance: $p = 0.012$). Analysis of polynomial trends revealed that the foraging rates of sub-adults ($p = 0.0067$), but not juveniles

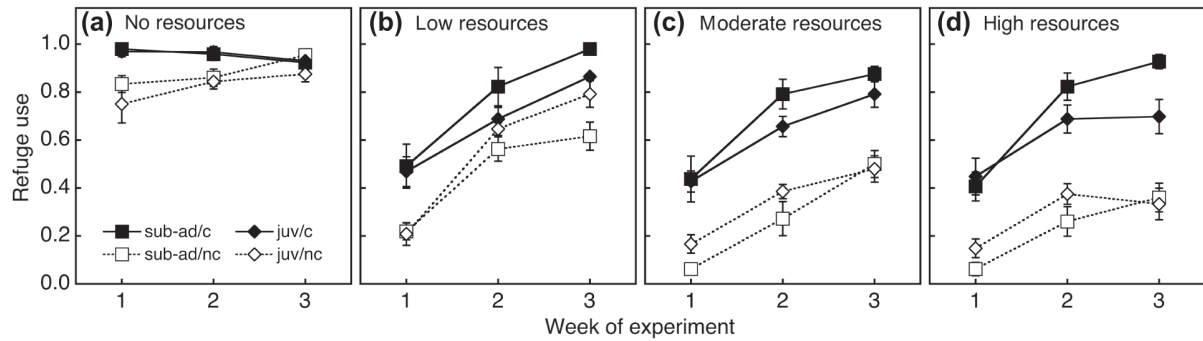


Figure 1. Weekly refuge use of juvenile (diamonds, juv) and sub-adult (squares, sub-ad) *Nucella* in the presence (filled symbols, c) or absence (open symbols, nc) of green crab risk cues in mesocosms with either (a) no food or a (b) low, (c) moderate, or (d) high abundance of barnacle resources. Values are the mean proportion of *Nucella* in refuge habitats, \pm SE ($n = 6$). Error bars are sometimes smaller than symbols.

($p = 0.66$), tended to increase linearly with increasing resource levels (Table 2a, Fig. 2a).

Nucella continued to forage throughout the experiment or until resources were depleted (Fig. 2). By the end of the three-week experiment, the effects of predation risk depended strongly on prey state and resource abundance (crab cues \times prey state \times resource abundance: $p = 0.0002$; Table 2c, Fig. 2c). In the presence of risk, the foraging rates of sub-adult ($p = 0.014$), but not juvenile ($p > 0.1$), *Nucella* increased with increasing resource levels, although there were no significant differences between the foraging rates of sub-adult and juvenile *Nucella* at each specific resource level (pairwise ls contrasts: all $p > 0.15$). Sub-adults under risk consumed 8.4 more barnacles per capita at high versus low resource abundance. In the absence of risk, foraging rates of sub-adults increased linearly with increasing resources (linear $p < 0.0001$, quadratic $p > 0.05$), while juvenile foraging rates also increased (linear $p = 0.0001$), but at a decelerating rate (quadratic $p = 0.0001$;

Table 2c). Juveniles and sub-adults foraged at similar rates when resources were low (ls contrast: $F_{1,60} = 0.26$, $p = 0.61$), consuming 97–100% of all available barnacles. At moderate resource levels, sub-adult *Nucella* consumed 31% more barnacles than juveniles (ls contrast: $F_{1,60} = 16.13$, $p = 0.0002$) and effectively depleted their resource supply (91–98% and 57–83% of barnacles consumed by sub-adults and juveniles, respectively). Increasing barnacle density from moderate to high levels caused an increase in the foraging rates of sub-adult *Nucella* (ls contrast: $F_{1,60} = 22.64$, $p < 0.0001$) but not juveniles (ls contrast: $F_{1,60} = 2.13$, $p = 0.15$). At high resource abundance, sub-adults consumed 89% more barnacles than juveniles (ls contrast: $F_{1,60} = 104.70$, $p < 0.0001$). Neither sub-adults nor juveniles depleted their barnacle supply at high resource levels (56–67% and 29–53% of barnacles consumed, respectively; Fig. 2c).

Predation risk caused reductions in *Nucella* growth that became larger with increasing resource levels and more

Table 2. Results from three-way ANOVAs testing the effects of crab risk cues [c] (crab or no crab), prey state [p] (juvenile or sub-adult), and resource abundance [r] (low, moderate, or high) on the cumulative per capita number of barnacles consumed by *Nucella* after (a) one, (b) two, and (c) three weeks. Denominator DF = 60 for each effect test and polynomial contrast. * $p < 0.05$.

Effect	(a) 1 week			(b) 2 weeks			(c) 3 weeks		
	DF	F	p	DF	F	p	DF	F	p
Crab cues [c]	1	145.20	<0.0001*	1	301.10	<0.0001*	1	358.80	<0.0001*
Prey state [p]	1	70.13	<0.0001*	1	79.18	<0.0001*	1	48.93	<0.0001*
Resource abundance [r]	2	5.03	0.0096*	2	38.30	<0.0001*	2	78.07	<0.0001*
c \times p	1	13.66	0.0005*	1	29.83	<0.0001*	1	25.53	<0.0001*
c \times r	2	0.42	0.6607	2	15.10	<0.0001*	2	32.41	<0.0001*
p \times r	2	4.76	0.0121*	2	13.52	<0.0001*	2	14.82	<0.0001*
c \times p \times r	2	0.58	0.5640	2	6.97	0.0019*	2	9.74	0.0002*
Polynomial trends across resource levels									
Linear: juveniles	1	0.19	0.6625	1	0.12	0.7279	1	2.39	0.1273
crab	1			1	1.72	0.1949	1	18.87	0.0001*
no crab	1			1			1		
Quadratic: juveniles	1	0.72	0.3993	1	1.35	0.2504	1	0.77	0.3847
crab	1			1	6.76	0.0117*	1	16.94	0.0001*
no crab	1			1			1		
Linear: sub-adults	1	7.89	0.0067*	1	4.86	0.0313*	1	6.48	0.0135*
crab	1			1	85.71	<0.0001*	1	200.71	<0.0001*
no crab	1			1			1		
Quadratic: sub-adults	1	2.39	0.1276	1	0.22	0.6422	1	0.06	0.8089
crab	1			1	27.80	<0.0001*	1	3.79	0.0562
no crab	1			1			1		

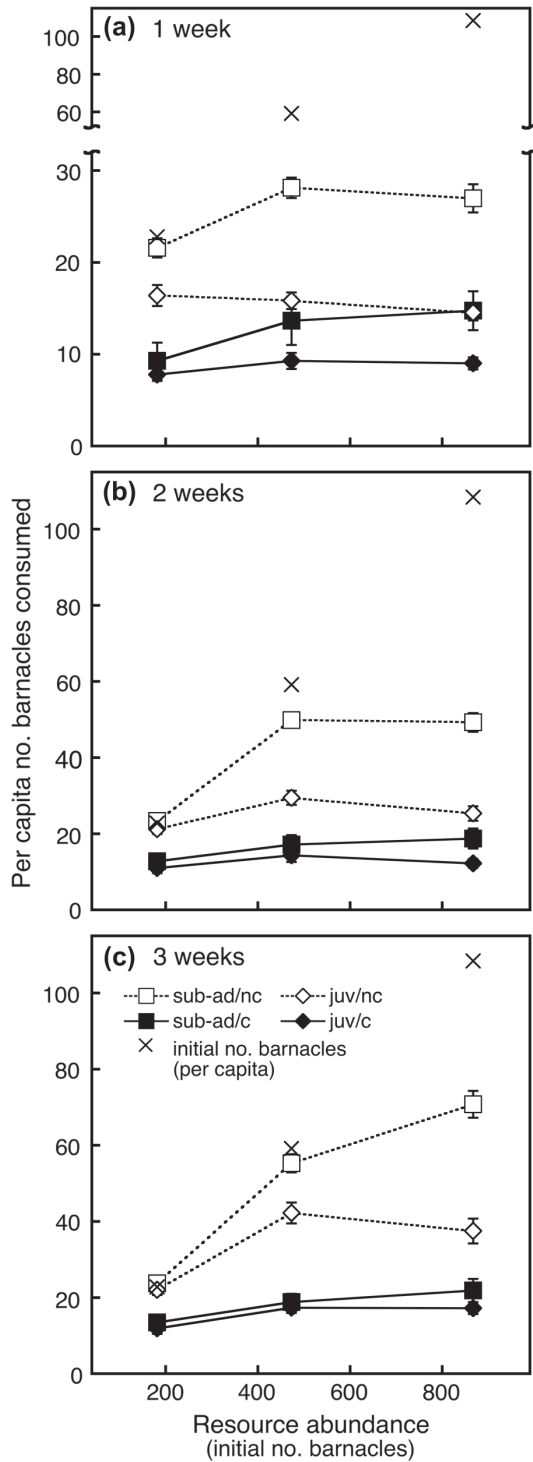


Figure 2. Cumulative per capita number of barnacles consumed after (a) one, (b) two, and (c) three weeks by juvenile (diamonds, juv) and sub-adult (squares, sub-ad) *Nucella* in the presence (filled symbols, c) or absence (open symbols, nc) of green crab risk cues across three fixed levels of initial resource abundance. X's indicate the mean number of barnacles initially available (per capita) for each level of the resource abundance treatment. Note the axis break and unique scale in (a). Values and error bars (sometimes smaller than symbols) are means \pm SE ($n = 6$).

pronounced in sub-adult *Nucella* (crab cues \times prey state \times resource abundance: $p = 0.0016$; Table 3, Fig. 3). With no food available, *Nucella* lost an average 6.4 mg of body

Table 3. Results from a nested three-way ANOVA testing the effects of crab cues [c] (crab or no crab), prey state [p] (juvenile or sub-adult), and resource abundance [r] (none, low, moderate, or high) on *Nucella* tissue growth (mg). Mesocosm was nested within the crab cues, prey state, and resource abundance treatments and included in the model as a random effect to avoid pseudoreplication. Denominator DF = 80 for each effect test and polynomial trend. Polynomial trends were across non-zero resource levels. * $p < 0.05$.

Effect	DF	F	p
Crab cues [c]	1	196.22	<0.0001*
Prey state [p]	1	12.18	0.0008*
Resource abundance [r]	3	110.49	<0.0001*
c \times p	1	9.44	0.0029*
c \times r	3	47.60	<0.0001*
p \times r	3	7.61	0.0002*
c \times p \times r	3	5.59	0.0016*
Polynomial trends across non-zero resource levels			
Linear: juveniles, crab	1	1.35	0.2491
Linear: juveniles, no crab	1	32.62	<0.0001*
Quadratic: juveniles, crab	1	1.21	0.2752
Quadratic: juveniles, no crab	1	1.39	0.2412
Linear: sub-adults, crab	1	0.99	0.3226
Linear: sub-adults, no crab	1	65.81	<0.0001*
Quadratic: sub-adults, crab	1	2.27	0.1354
Quadratic: sub-adults, no crab	1	0.28	0.5979

mass over the course of the experiment regardless of risk treatment (ls contrast of crab versus no crab: $F_{1,80} = 0.26$, $p = 0.61$) or prey state (ls contrast of sub-adults versus juveniles: $F_{1,80} = 1.17$, $p = 0.28$). In the presence of risk, prey state had no significant effects on the amount of new tissue growth at any level of initial resource abundance (pairwise ls contrasts: all $p > 0.38$), and, excluding treatments with no food, neither sub-adult nor juvenile growth increased with resource levels (all polynomial trends $p > 0.13$; Table 3).

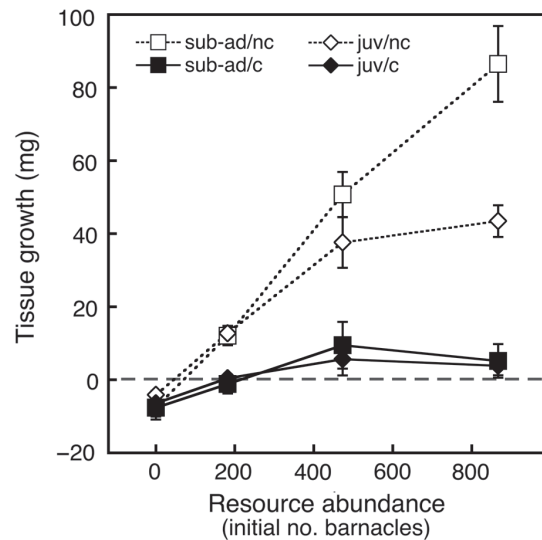


Figure 3. Tissue growth of juvenile (diamonds, juv) and sub-adult (squares, sub-ad) *Nucella* in the presence (filled symbols, c) or absence (open symbols, nc) of green crab risk cues at four fixed levels of initial resource abundance. Dashed gray line indicates tissue growth = 0. Values are means \pm SE (error bars sometimes smaller than symbols) calculated from pooled replicate means ($n = 6$).

Table 4. Results from a mixed model ANOVA testing the effects of prey state [p] (juvenile or sub-adult *Nucella*) and resource abundance [r] (low, moderate, or high) on the strength of green crab NCEs over time. The model included a random intercept (mesocosm) and slope (time). Numerator and denominator degrees of freedom are given as DF_n and DF_d , respectively. Polynomial trends were used to test for the effects of resource abundance on NCE strength after three weeks. * $p < 0.05$.

Effect	DF_n	DF_d	F	p
Prey state [p]	1	30	2.37	0.1338
Resource abundance [r]	2	30	0.84	0.4397
Time [t]	2	60	8.43	0.0006*
$p \times r$	2	30	0.66	0.5225
$t \times p$	2	60	0.20	0.8201
$t \times r$	4	60	10.38	$< 0.0001^*$
$t \times p \times r$	4	60	3.36	0.0152*
Polynomial trends across resources (after three weeks)				
Linear: juveniles	1	30	0.94	0.3393
Quadratic: juveniles	1	30	1.71	0.2013
Linear: sub-adults	1	30	11.89	0.0017*
Quadratic: sub-adults	1	30	1.84	0.1855

By contrast, in the absence of risk, sub-adult and juvenile *Nucella* growth increased linearly with increasing resource levels (both $p < 0.0001$, Table 3), but this increase was more pronounced for sub-adult *Nucella* (Fig. 3). Juveniles and sub-adults produced similar amounts of new tissue mass at both low (ls contrast: $F_{1,80} = 0.03$, $p = 0.86$) and moderate resource levels (ls contrast: $F_{1,80} = 2.42$, $p = 0.12$), and both juveniles and sub-adults grew 3.5 times more when resource levels were moderate than when resources were low (ls contrast: $F_{1,80} = 49.93$, $p < 0.0001$). As with foraging rates, juveniles grew similarly at moderate and high resource abundances (ls contrast: $F_{1,80} = 0.61$, $p = 0.44$), while sub-adults grew more as resources increased from moderate to high levels (ls contrast: $F_{1,80} = 14.59$, $p = 0.0003$).

Strength of NCEs

Differences in the foraging rates of *Nucella* across resource levels and over time led to differences in the absolute effects of predation risk (i.e. the difference between no crab and crab treatments) but also in the strength of green crab NCEs, which measure the proportional reduction in foraging rates due to risk. The strength of NCEs varied over time, but

the direction of these changes depended on initial resource abundance (time \times resource abundance: $p < 0.0001$) and its interaction with prey state (time \times resource abundance \times prey state: $p = 0.015$; Table 4, Fig. 4). The strength of NCEs decreased over time when resource levels were low (ls contrast of week 1 versus week 3: $F_{1,60} = 7.33$, $p = 0.009$; Fig. 4a) but increased over time when resource levels were high (ls contrast: $F_{1,60} = 27.17$, $p < 0.0001$; Fig. 4c). By the end of the experiment, the strength of NCEs on sub-adult *Nucella* increased with increasing resource levels ($p = 0.0017$), but resource levels did not significantly affect NCEs on juvenile *Nucella* ($p \geq 0.20$; Table 4).

Discussion

In the absence of predation risk, juvenile and sub-adult *Nucella* delayed and reduced their use of refuge habitats, consumed more barnacles, and produced more body tissue as resource levels (barnacle density) increased. In addition, the positive effects of resource levels on foraging and growth were more pronounced for sub-adult *Nucella* than for juveniles. By contrast, in the presence of risk, barnacle density had little to no effect on the refuge use, foraging, or growth of juvenile or sub-adult *Nucella*. Hence, the negative effects of green crab predation risk on *Nucella* foraging and growth rates increased with resource levels and prey state.

Prey refuge use: the importance of risky habitat quality and prey state

Patterns of refuge use by *Nucella* were strongly shaped by predation risk and the amount of barnacle resources available in riskier habitats. Refuge use increased with risk and as resource levels decreased (Fig. 1). Similar patterns of refuge use have been observed in other taxa (Cerri and Fraser 1983, Werner et al. 1983, Gilliam and Fraser 1987, Brown 1988, Holbrook and Schmitt 1988, Heithaus and Dill 2002). In headwater streams, for example, juvenile creek chubs spend less time in refuge habitats as resource density in riskier habitats increases (Gilliam and Fraser 1987). This foraging strategy allows creek chubs to minimize their relative risk of mortality per unit of energy gain because high resource density improves foraging efficiency, thereby reducing the

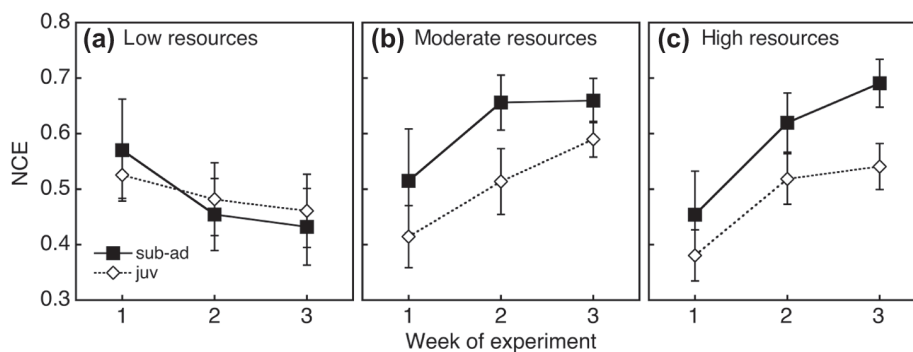


Figure 4. Strength of green crab nonconsumptive effects (NCE) on the cumulative per capita foraging rates of juvenile (open diamonds, juv) and sub-adult (filled squares, sub-ad) *Nucella* after one, two, and three weeks with either (a) low, (b) moderate, or (c) high levels of initial resource abundance.

amount of time a forager is exposed to predators while acquiring a given amount of energy. Our results are also consistent with previous work showing that *Nucella* generally prefer to forage near refuges, but risk effects shape foraging behavior as resources near refuges are depleted. In the absence of risk, *Nucella* expand their foraging activity away from refuge habitats, but, in the presence of risk, *Nucella* remain near refuge habitats despite declining resources (Matassa and Trussell 2011).

Clearly, the decision to use refuge habitats depends not only on the degree of predation risk perceived by prey, but also on the relative costs and benefits of avoiding riskier habitats (Sih 1980, Holbrook and Schmitt 1988, Brown and Kotler 2004). Prey may use refuges at high rates even when perceived predation risk is low if the refuge provides adequate resources or if the missed opportunity costs of staying in the refuge are also low, as was the case for *Nucella* in our study when no food was available (Fig. 1a). The use of refuge habitats by *Nucella* to such a high degree in the combined absence of risk and food has important implications for assays of risk effects that are based on prey behavior. Experiments that measure refuge use by prey in the presence and absence of predation risk may fail to detect risk effects if the quality of alternative, non-refuge habitats is poor (i.e. no food), or if the quality of refuge habitats is sufficiently high.

Risk caused a larger increase in refuge use by sub-adults compared to juveniles, even though *Nucella* in our sub-adult size range should be somewhat less vulnerable to crab attack (Hughes and Elner 1979). This result is consistent with state-dependent models of antipredator behavior: small or juvenile prey with lower energy reserves should be more willing to accept the predation risk associated with foraging (Mangel and Clark 1986, McNamara and Houston 1987). The state-dependent anti-predator behaviors of *Nucella* are also consistent with the asset protection principle, which predicts that larger or more mature prey should be more protective of the reproductive assets they have accrued (Ludwig and Rowe 1990, Clark 1994). Therefore, larger prey, or those approaching reproduction, should exhibit stronger antipredator behaviors despite the potential energetic costs of doing so. Our results indicate that such costs may be minimal for sub-adult *Nucella* because they consumed at least as many barnacles and produced as much new tissue mass as juveniles despite their increased refuge use under predation risk (Fig. 2, 3). We suspect that greater foraging efficiency influenced the foraging and growth of sub-adults. Handling times decline with increasing body size, age, or experience in many organisms (Werner and Gilliam 1984, Peters 1986, Woodward et al. 2005), including *Nucella* (Dunkin and Hughes 1984, Hughes and Drewett 1985, Burrows and Hughes 1991, Hughes et al. 1992, Miller 2013). It is likely that lower handling times increased sub-adult foraging efficiency and reduced the costs associated with spending more time in refuge habitats and less time foraging. Hence, larger body size may reduce the degree to which prey must trade off food for safety by allowing larger individuals to acquire the same amount of resources in less time, thereby reducing their relative risk of predation per unit energy gain (Gilliam and Fraser 1987).

Prey foraging rates, growth, and the strength of NCEs

The per capita foraging rates and growth of *Nucella* remained relatively low in the presence of risk but increased with resource levels and body size in the absence of risk (Fig. 2, 3). In the absence of risk cues, both juvenile and sub-adult *Nucella* fully depleted their supply of barnacles in the low resource treatment within the first two weeks (Fig. 2b), while those in the presence of risk were able to continue foraging, albeit at low rates. The strength of resulting NCEs therefore decreased over time when resource abundance was low (Fig. 4a).

By contrast, the strength of NCEs increased over time when resources were high (Fig. 4c). This pattern emerged, in part, because, even in the absence of risk, *Nucella* never depleted their resource supply when given a high abundance of barnacles (Fig. 2c). Thus, unlike those with low resource levels, *Nucella* at high resource levels were able to forage at high rates throughout the experiment, increasing the cumulative number of barnacles consumed over time. Meanwhile, because *Nucella* in the presence of risk maintained relatively low foraging rates, both the absolute (no crab – crab) and proportional (NCE strength) effects of predation risk increased over time (Fig. 2, 4c). This effect was enhanced by the greater per capita foraging rates of sub-adult *Nucella* in the absence of risk such that, by the end of the experiment, the strength of NCEs was greatest for sub-adult *Nucella* with high barnacle density (Fig. 4).

The relatively unlimited supply of barnacles in the high resource treatment also revealed differences in the foraging functions of sub-adults and juveniles that contributed to patterns of NCE strength. With high resource levels, juvenile *Nucella* foraged and grew at similar rates to those with moderate resources (Fig. 2c, 3), indicating that, in the absence of risk, foraging rates at high resource levels were limited by physical constraints such as longer handling times (Burrows and Hughes 1991), similar to Holling's type II functional response (Holling 1959). However, the foraging and growth of sub-adults increased with each increase in resource abundance (i.e. type I functional response). Compared to the low resource treatment, *Nucella* with high barnacle abundance were able to consume an additional 47 barnacles per capita, but this increase was much smaller (eight additional barnacles) in the presence of risk (Fig. 2c). Hence, the stronger positive effect of resource levels on sub-adults in the absence of risk caused the strength of NCEs to increase with increasing resource abundance.

These results have important implications for the study of NCEs and how the effects of predation risk may vary across ecological contexts. Because prey foraging rates remained relatively low under predation risk, changes in the absolute (no crab – crab) and proportional (NCE strength) effects of risk over time and across resource levels are likely a direct result of the how sub-adult and juvenile *Nucella* foraged in the absence of risk. The impact of NCEs in natural systems therefore depends just as much on what happens when predators are absent (i.e. whether prey–resource interactions are strong or weak or the shape of prey foraging functions) as when they are present (i.e. growth/predation risk tradeoffs). Thus, studies evaluating NCEs across ecological contexts should not rely solely on metrics of NCE 'strength' because

this approach may mask the underlying mechanisms driving variation in the magnitude of NCEs.

Resource depletion also affected NCEs in our experiment. Weaker NCEs at low resource levels were due in part to resource depletion, which limited both juvenile and sub-adult foraging rates in the absence of risk. How patterns of NCEs observed in our experiment translate into other systems or play out over longer time periods likely depends on the relative time scale of resource renewal and prey growing seasons (Peacor and Werner 2004, Werner and Peacor 2006). Barnacle populations renew relatively slowly, with recruitment occurring once per year just before the start of *Nucella*'s growing season. Barnacle density declines over time due to a variety of biotic and abiotic factors including consumption by *Nucella* (Menge 1976, Bertness et al. 2004, Benedetti-Cecchi and Trussell 2013), which may weaken NCEs as the growing season draws to a close. Resources that renew more rapidly, such as algae or periphyton, may allow for the persistence of strong NCEs because they are better able to maintain high densities over longer time scales. Unlike slowly-renewing resources (e.g. barnacles or detritus), rapidly-renewing resources can allow predators to have positive effects on prey growth (Peacor and Werner 2004, Werner and Peacor 2006, Preisser et al. 2009). For example, predator-induced reductions in tadpole grazing activity enhance the productivity of algae (Peacor 2002). The resulting increase in tadpole grazing efficiency, which is not afforded to tadpoles in the absence of predators, increases tadpole growth and leads to a positive NCE on tadpole growth despite a negative NCE on tadpole foraging activity (Peacor 2002). Slowly-renewing resources yield different results because the cumulative foraging and growth of prey in the presence and absence of predation risk are predicted to converge over time as resources become depleted or prey satisfy their energetic requirements, leading to initially strong negative NCEs on foraging and growth that weaken over time (Luttbeg et al. 2003, Peacor and Werner 2004), as we observed in our low resource treatment (Fig. 4a).

Our results suggest that the impacts of predation risk on natural systems will be greatest in resource-rich communities with strong prey–resource interactions. The different functional responses of sub-adult and juvenile *Nucella* and resulting influence on NCEs highlight the importance of considering functional traits to better understand direct and indirect predator effects in food webs (Bolker et al. 2003). As a functional trait, body size varies among and within species as well as within an individual as it matures, with important community-level consequences (Werner and Gilliam 1984, Bolnick et al. 2003, Woodward et al. 2005). The strong influence of predation risk in natural systems often emerges because predators can simultaneously scare many prey (Peacor and Werner 2001, Werner and Peacor 2003, Preisser et al. 2005), and this effect will likely be shaped by the age or size structure of prey populations. Because of their larger per capita impact on resources in the absence of risk, prey populations dominated by a greater proportion of large individuals may transmit stronger trait-mediated indirect effects to their resources than those dominated by smaller or juvenile prey. For example, on rocky shores, the positive indirect effects of green crab predation risk on barnacle abundance may be more pronounced on wave-protected shores where

Nucella foraging and growth rates and size at maturity are often greater and populations consist of mostly large individuals (Burrows and Hughes 1990, 1991, Hughes and Burrows 1993, Etter 1989, 1996), especially if these effects operate early in the season when barnacle density is greatest following annual recruitment. However, interpretation of the effects of demography on a prey population's potential to transmit trait-mediated indirect effects depends on whether one characterizes that population's structure in terms of individuals, as above, or in terms of biomass. For example, in the absence of risk, juveniles in our experiment consumed about half as many barnacles as sub-adults on a per capita basis (Fig. 2c, high resource treatment), but they consumed nearly twice as many barnacles as sub-adults on a per mg (initial body mass) basis. This is because juveniles were about one-quarter the size of sub-adults. Hence, for two populations of the same total biomass, the population with a greater proportion of biomass contributed by juveniles or smaller size classes should have a greater total impact on resources and potentially transmit stronger trait-mediated indirect effects. In cases where predators are size selective, prey demography may be particularly important for how consumptive and nonconsumptive predator effects interact to shape the total indirect effects of predators. We suggest that the demographics of prey populations will influence the relative importance of predation risk in driving trophic cascades, and these effects will be most pronounced in productive systems with abundant resources.

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