

Refuge quality impacts the strength of nonconsumptive effects on prey

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Abstract. Prey often retreat into the safety of refuges for protection from predators. This shift into refuge can reduce foraging opportunities, escalating the costs of risk and the strength of nonconsumptive effects. Such costs, however, may be shaped by the variation in resources that refuges harbor for prey foraging (i.e., refuge quality), and change dynamically via impacts on prey state. Despite its potential importance, we lack an explicit understanding of how refuge quality impacts prey performance under risk. Using a rocky intertidal food chain, we examined the interaction between predation risk and the amount of resources available for prey in refuge. We found that refuges with more resources greatly reduce the costs of refuge use, and that nonconsumptive effects are thereby weakened by as much as one-half, with especially strong impacts on prey growth and growth efficiency. These results suggest that failure to consider refuge quality could result in overestimation of the negative effects associated with prey refuge use.

Key words: *antipredator; barnacles; Carcinus maenas; foraging/predation risk trade-off; growth efficiency; habitat use; Nucella lapillus; prey state; resource availability.*

INTRODUCTION

The nonconsumptive effects of predation risk, where predators impact prey traits rather than consume them, operate in many natural systems (see Lima 1998, Schmitz et al. 2004, Peckarsky et al. 2008 for reviews), and can be of equal or greater importance than the effects of direct consumption (e.g., Lima and Dill 1990, Anholt and Werner 1995, Werner and Peacor 2003, Ohgushi et al. 2012). In the presence of predation risk, prey often shift from foraging in risky habitats where they are more vulnerable to refuge habitats that provide protection from predation (Sih 1980, Werner et al. 1983, Mangel and Clark 1986, McNamara and Houston 1986, Turner and Mittelbach 1990). The increased safety, and thus reduced mortality, afforded by shifts into refuge is frequently traded for reduced foraging opportunities by prey (e.g., Werner and Hall 1988, Kotler et al. 1991, Kats and Dill 1998, Lima 1998). This foraging/predation risk trade-off may emerge because (1) resource competition can be particularly intense within refuges due to high conspecific density, resulting in reduced per capita resource availability (Mittelbach 1988, Persson and Eklöv 1995) and (2) the quality of resources within a refuge may be low compared to riskier habitats (Schmitz et al. 2004, Hernández and Laundré 2005). Hence, the use of refuge habitats by prey can result in substantial costs such as decreased growth (Martín and López 1999), fecundity (Fraser and Gilliam 1992), and metabolic efficiency (Trussell et al.

2006b), as well as affect important ecosystem characteristics and processes such as productivity, diversity, and nutrient mineralization (Ripple and Beschta 2003, Schmitz 2009). Because of the potentially high costs of refuge use, refuges can counterintuitively strengthen the negative effects of predators on prey (Orrock et al. 2013).

Although refuge habitats can vary in the degree of protection they afford (Hixon and Beets 1993, Persson and Eklöv 1995, Krivan 1998), they generally benefit prey by reducing the instantaneous mortality rate imposed by predators. In the presence of predation risk, prey should initially move into refuge because the cost of doing so for a brief time is low (Lima and Bednekoff 1999, Sih and McCarthy 2002). If risk persists, however, resources within the refuge will become increasingly limited such that prey state (i.e., energy reserves) will also decline until it becomes optimal for prey to leave the refuge in order to gain access to greater foraging opportunities (Dill and Fraser 1984, Mangel and Clark 1986, McNamara and Houston 1986, Lima and Bednekoff 1999). The propensity of prey to utilize refuge, therefore, should be shaped by variation in the quality and quantity of resources available for prey within the refuge (refuge carrying capacity; Krivan 1998). Indeed, adaptive foraging behavior predicts that prey are more likely to utilize a habitat where their risk of mortality is low relative to their foraging/growth rate (“death per unit energy” rule; Werner and Gilliam 1984, Gilliam and Fraser 1987), and this ratio should decrease with increasing refuge quality. Hence, prey that occupy refuges with greater or more beneficial foraging opportunities should remain in refuge longer (Krivan 1998) while simultaneously performing better than prey with access to lower quality foraging

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opportunities in refuge. The strength of nonconsumptive effects is therefore likely to vary across landscapes of resource availability. Despite advances in theory and the ecological implications of refuge quality on prey behavior and performance, it has received little experimental attention. Notably, it has been difficult to precisely evaluate the cost of refuges because their costs and benefits are often confounded, such as when shifts into refuge necessitate changes in prey diet. For example, green sea turtles exposed to tiger shark predation risk seek safety on the edge of shallow seagrass meadows that allow for easy escape, but also suffer energetic costs because seagrasses on the edge of these meadows are less nutritious (Heithaus et al. 2007).

We define a refuge as a habitat where prey are completely protected from predators (total refuge), and refuge quality by the amount of resources available for prey to consume while in refuge. While refuge quality can have direct implications for prey foraging activity and energetic state, it may further influence prey by impacting the stress associated with their foraging decisions under risk, and thereby affect the ability of prey to convert ingested energy into body mass (i.e., growth efficiency; Trussell et al. 2006b). Such energetic inefficiencies can emerge because elevated stress caused by predation risk can influence a number of physiological pathways (Slos and Stoks 2008, Janssens and Stoks 2013), and divert energy away from growth and/or reproduction (Trussell et al. 2006b, Matassa and Trussell 2014a). While the presence of risk itself can increase prey stress, this stress is likely intensified if the costs of antipredator behavior are especially high, as would be the case in a low-quality refuge. Prey in low-quality refuges are more likely to reach a lower energetic state while in refuge, itself a high cost, and as a result, leave the refuge to forage in a riskier habitat, which may further compound the stress associated with predation risk. In contrast, prey in high-quality refuges do not experience heightened costs of refuge use and can avoid such stressful, risky behavior. Thus, both the amount of resources available for prey in refuge and the resulting effects on prey energetic efficiency may ultimately define refuge quality and the costs of refuge use to prey.

Here, we build upon the important work of others who have examined how resource depletion within a refuge over time (Turner 1997) and resource partitioning between two competing species foraging in a refuge (Persson 1993) affect prey behavior and foraging activity. By manipulating initial refuge quality, our study allows us to directly compare how variation in refuge resource availability impacts prey behavior via its effects on prey state (i.e., energy reserves). This is especially important because changes in prey growth and growth efficiency in response to predation risk can be more accurate indicators of the fitness costs incurred by prey under risk (Matassa and Trussell 2014b), and hence have important implications for prey populations.

On rocky intertidal shores in New England, predation risk from the green crab (*Carcinus maenas*) can strongly

influence interactions between their prey, the carnivorous snail *Nucella lapillus*, and barnacles (*Semibalanus balanoides*), a dominant space occupier whose abundance can shape community organization and dynamics (Menge 1976, Bryson et al. 2014). In the field, *Nucella* typically seek refuge in narrow rock crevices and beneath ledges (Feare 1971, Burrows and Hughes 1989) that are inaccessible to larger predators, but can vary appreciably in the amount of resources they contain (Chabot and Bourget 1988, MacPherson et al. 2008). In addition, predator cues from the green crab cause *Nucella* to preferentially choose refuge habitats even at the cost of reduced foraging opportunities (Vadas et al. 1994, Trussell et al. 2003). Thus, this is a model system to examine the importance of refuge quality because (1) *Nucella* often choose refuges when confronted with risk and (2) we can manipulate resource abundance without affecting other aspects (e.g., protection level) of the refuge habitat, which, as highlighted above, can confound efforts to elucidate the driver of prey refuge use in other systems. We experimentally examined how green crab predation risk and refuge quality (amount of barnacles available for *Nucella* to consume while in total refuge) interact to influence *Nucella* decision-making and performance. We found that high-quality refuges reduce the costs of refuge use for prey, and can therefore substantially reduce the strength of nonconsumptive effects, particularly those on prey growth and growth efficiency. Hence, investigating refuge quality and its effects on prey performance is essential to enhancing our theoretical and empirical understanding of the different mechanisms by which predators mediate prey populations.

MATERIALS AND METHODS

Experimental design and study organisms

This study examined the effects of refuge quality (amount of resources, the barnacle *S. balanoides*, available in a total refuge habitat) and predation risk by the green crab (*C. maenas*) on the risk-avoidance behavior, foraging rate, growth, and growth efficiency of prey, the carnivorous snail *N. lapillus* (hereafter, *Nucella*). Exposure to predation risk (present, absent) was fully crossed with refuge quality; refuges contained 0%, 12%, 25%, 50%, or 100% of the number of barnacles compared to the risky, non-refuge habitat. We created barnacle communities by anchoring granite tiles (15 × 15 × 1 cm) in the field in March in mid-coast Maine to capture annual barnacle settlement. Tiles were retrieved and returned to the running seawater system at the Marine Science Center in Nahant, Massachusetts, in May. We counted the number of barnacles on tiles with the highest settlement in order to establish the barnacle density on full resource tiles (100% cover, 2748.0 ± 22.9 [mean number of barnacles ± SE]), which were used for all non-refuge, risky habitats. We then used this density to establish five levels of refuge quality (0% compared to a

risky tile, 0 barnacles; 12%, 325.0 ± 10.9 ; 25%, 715.9 ± 20.83 ; 50%, 1443.9 ± 27.4 ; 100%, 2697.4 ± 19.3 [mean number of barnacles \pm SE] by randomly removing barnacles throughout the remaining tiles as appropriate.

One full resource tile (i.e., risky habitat) was randomly paired with one refuge tile (of varying quality), placed back to back, and set upon four, raised PVC spacers (1 cm tall) with the refuge tile oriented down in experimental mesocosms (sensu Trussell et al. 2006a). The narrow space between the refuge tile and the bottom of the mesocosm created by the PVC spacers provided a total refuge habitat, such that *Nucella* in refuge would have complete protection from green crab predators if crabs were allowed to forage freely. *Nucella* could move freely between the top, risky habitat and bottom, refuge habitat via a narrow space between the edge of the tiles and the outer wall of the mesocosm. On emergent rocky shores, *Nucella* are often found in narrow rock crevices or under rocky outcroppings (Feare 1971, Burrows and Hughes 1989) that provide protection from larger predators, and our refuge design mimics these enclosed spaces. In addition, previous experiments in this (Trussell et al. 2006a) and other (Bernot and Turner 2001) systems demonstrate that snails spend more time in covered habitats in the presence of predation risk, and thus appear to perceive these spaces as refuge habitat. Mesocosms ($27 \times 15 \times 5$ cm) consisted of two compartments divided by a perforated wall: an upstream chamber with a plastic roof for the manipulation of predation risk and a downstream chamber with a mesh roof that housed experimental *Nucella* and barnacle tiles. Predation risk was manipulated by the presence (risk) or absence (no risk) of one adult male green crab. Ten juvenile *Nucella* (shell length 9.98 ± 0.06 mm [mean \pm SE]) collected from a wave-exposed shore in mid-coast Maine were randomly assigned to replicates, and placed in the downstream compartment with the barnacle tiles. Each mesocosm was placed in a larger plastic container ($33 \times 19 \times 12$ cm) in order to maintain independence, and received its own supply of flowing seawater. There were eight replicates of each treatment combination ($N = 80$). The experiment ran for 54 days in June and July, when intertidal organisms are most active, in the sea tables at the Marine Science Center, and ended before any total resource depletion occurred.

We monitored *Nucella* behavior (i.e., proportion in refuge) every three days by opening each mesocosm and noting the position of each snail. *Nucella* found anywhere on or underneath the bottom tile were considered in refuge habitat, and those anywhere above the bottom tile were considered in risky habitat. We determined average refuge use by calculating the average proportion of *Nucella* found in refuge in each mesocosm across all behavioral observations ($n = 18$).

All barnacle tiles were photographed at the beginning and end of the experiment to examine per capita *Nucella* foraging rates. Barnacles were scored as alive or dead (identified by an empty shell) at both time points using

Photoshop (v. CS4, Adobe Systems Inc., San Jose, California, USA) and counted in ImageJ (v. 1.41, NIH, Bethesda, Maryland, USA). To determine the per capita foraging rate, we divided the total number of barnacles consumed (initial – final abundance) by the average number of *Nucella* in each replicate over the duration of the experiment. We also monitored *Nucella* tissue growth (final – initial tissue mass) by marking four of the 10 snails in each replicate with a plastic bee tag and weighing them at the beginning and end of the experiment using a nondestructive buoyant weighing technique (Palmer 1982). We then converted tissue growth and per capita foraging rate into their energetic equivalents (Joules, J), using empirically derived conversions (see Miller et al. [2014] for detailed description).

We calculated *Nucella* growth efficiency to examine the effect of predation risk on *Nucella* physiology by dividing individual *Nucella* tissue growth (J) by the average per capita foraging rate in that replicate (J). We focused only on tissue growth because tissue requires substantially more energy to produce than shell (Palmer 1992), and is thus a strong indicator of *Nucella* energetic requirements.

To calculate the magnitude of the nonconsumptive effect (NCE) of green crab predation risk on *Nucella* foraging rate, growth, and growth efficiency, we used the formula

$$\text{NCE} = 1 - (T_{r \text{ risk}} / \bar{T}_{\text{no risk}})$$

where $T_{r \text{ risk}}$ is the value of trait T in the presence of risk in replicate r of a given refuge quality and $\bar{T}_{\text{no risk}}$ is the mean of all no risk replicates at that same refuge quality.

Statistical analyses

We used a model-selection approach to explore how *Nucella* behavior and performance changed with refuge quality in the presence and absence of risk. We defined refuge quality using the actual number of barnacles initially available in refuge rather than the five predetermined treatment levels. We expected *Nucella* performance to improve with refuge quality, which was confirmed by visual inspection of the data. In several cases, we observed a plateaued response at higher levels of refuge quality and therefore fit either a modified (to accommodate negative values) Michaelis-Menten saturation curve or a linear model, and used Akaike information criterion (AIC) model selection to determine the best fit (Burnham and Anderson 2002). When the best fit models were linear in both risk treatments, we conducted a one-way ANCOVA with predation risk as the fixed factor and refuge quality as the covariate to determine if the positive effects of refuge quality were similar in the presence and absence of risk. ANCOVA could not be performed for growth and growth efficiency because the linearity assumption was violated in the presence of risk.

We also used AIC to determine whether refuge quality affected the strength of NCEs. We hypothesized that NCEs would weaken as refuge quality improved and

based on visual trends in the data, we compared a one-phase exponential decay against a linear model. To determine whether the magnitude of NCEs differed among the three traits measured (foraging rate, growth, and growth efficiency), we conducted a repeated measures MANOVA that considered refuge quality as a between-subjects fixed effect and trait as a within-subjects fixed effect to account for non-independence among traits. We used the Greenhouse-Geisser correction when analyzing the prey trait \times refuge quality interaction to estimate Box's ϵ adjustment of degrees of freedom (indicated as P_{G-G}). One replicate was excluded from all analyses because of high (40%) *Nucella* mortality. AIC analyses were conducted in R (v. 3.2.3) using the package *bbmle* (Bolker 2014), and ANCOVA and MANOVA analyses were conducted in JMP 11.1 (SAS Institute, Cary, North Carolina, USA) using Type III Sums of Squares.

RESULTS

More *Nucella* were found in refuge as refuge quality improved in both the presence ($R^2 = 0.71$) and absence ($R^2 = 0.56$) of predation risk. This effect was strongest at lower levels of refuge quality, and began to plateau once refuge quality reached 50% (Appendix S1: Table S1; Fig. 1). The positive effects of improvements between relatively low-quality refuges (0–25%) increased the proportion of *Nucella* in refuge in both risk treatments, though more *Nucella* were generally found in refuge in the presence of predation risk. We also found that *Nucella* foraging (per capita energy consumed) increased linearly at the same rate with increased refuge quality (Appendix S1: Table S1, ANCOVA slope term, $F_{1,75} = 1.80$, $P = 0.18$) in the presence ($R^2 = 0.65$, $F_{1,38} = 71.6$, $P < 0.0001$) and absence ($R^2 = 0.85$, $F_{1,37} = 208.8$, $P < 0.0001$) of risk (Fig. 2a); however, at any given refuge quality, *Nucella* foraged more in the absence of risk (ANCOVA elevation term, $F_{1,75} = 155.25$, $P < 0.0001$).

We observed different functional responses to enhanced refuge quality for *Nucella* growth and growth efficiency. Growth increased linearly in the absence of risk ($R^2 = 0.11$, $F_{1,37} = 4.38$, $P = 0.043$), but was nonlinear in the presence of predation risk and was best described by a Michaelis-Menten saturation curve ($R^2 = 0.39$, Appendix S1: Table S1; Fig. 2b). For growth efficiency, refuge quality had no effect in the absence of risk ($F_{1,37} = 0.50$, $P = 0.48$), but was nonlinear (Michaelis-Menten) in the presence of risk ($R^2 = 0.41$, Appendix S1: Table S1; Fig. 2c). Hence in the presence of risk, both growth and growth efficiency increased with the addition of relatively few resources to the refuge (0–25%) until they reached an asymptote at intermediate levels (50%) of refuge quality.

Nonconsumptive effects (NCEs) on snail foraging decreased linearly with increasing refuge quality ($R^2 = 0.21$, $F_{1,38} = 10.03$, $P = 0.003$, Appendix S1: Table S1; Fig. 3). In contrast, NCEs on growth ($R^2 = 0.42$, $F_{1,38} = 27.85$, $P < 0.0001$) and growth efficiency ($R^2 = 0.41$, $F_{1,38} = 26.66$, $P < 0.0001$) decayed exponentially as refuge

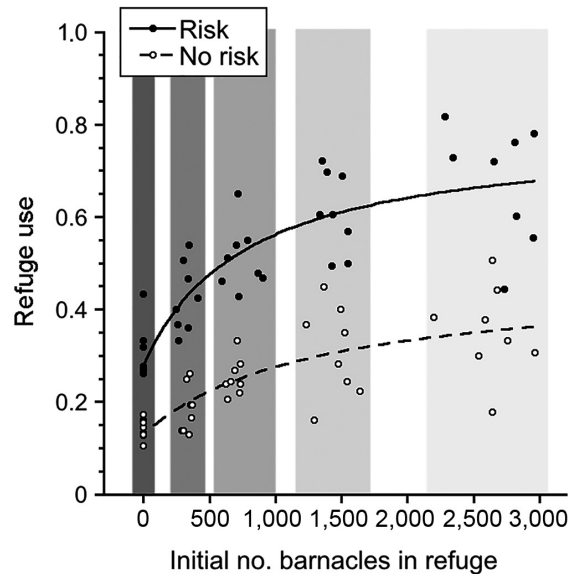


FIG. 1. Mean replicate values of refuge use (proportion in refuge) by prey (*Nucella lapillus*) exposed to the presence (filled circles) and absence (open circles) of predation risk from the green crab *Carcinus maenas* at varying levels of refuge quality (percentage of resources [the barnacle, *Semibalanus balanoides*] available in the refuge habitat relative to risky habitat, RQ). Initial number of barnacles in refuge corresponds to the five predetermined levels (gray blocks) of refuge quality in order from least to most valuable refuge (0%, 12%, 25%, 50%, 100%). Lines represent best fit model as determined by AIC (Appendix S1: Table S1). A modified Michaelis-Menten curve best described variation in proportion of time spent in refuge across refuge qualities in both the presence ($y = (-388.6 / [770.4 + RQ]) + 0.78$) and absence ($y = (-429.2 / [1291.3 + RQ]) + 0.46$) of risk.

quality improved (Appendix S1: Table S1; Fig. 3); NCE strength declined substantially between relatively low-quality refuges (12% and 25%) before plateauing at the two highest quality refuges (50% and 100%). NCEs were significantly stronger on growth and growth efficiency than on foraging (MANOVA, $P_{G-G} = 0.006$, Fig. 3). Predation risk decreased *Nucella* foraging by $27\% \pm 0.02\%$ (mean \pm SE), whereas it decreased *Nucella* growth by $104\% \pm 0.08\%$ and growth efficiency by $108\% \pm 0.06\%$ (linear contrasts, $P_{G-G} < 0.0001$).

DISCUSSION

The use of refuge habitats by prey in response to predation risk is ubiquitous (Sih et al. 1988, Lima and Dill 1990, Lima 1998). Refuge habitats can reduce instantaneous predation rates but their other effects on prey, such as reduced foraging rates or resource quality (Werner et al. 1983, Lima 1998) can also impose costs (e.g., decreased growth and fecundity) that adversely affect prey fitness (Mangel and Clark 1986, Fraser and Gilliam 1992, Houston et al. 1993). The cost of refuge use by prey can therefore strengthen these nonconsumptive predator effects, as concluded by a recent meta-analysis (Orrock et al. 2013). However, robust tests of this hypothesis have been elusive

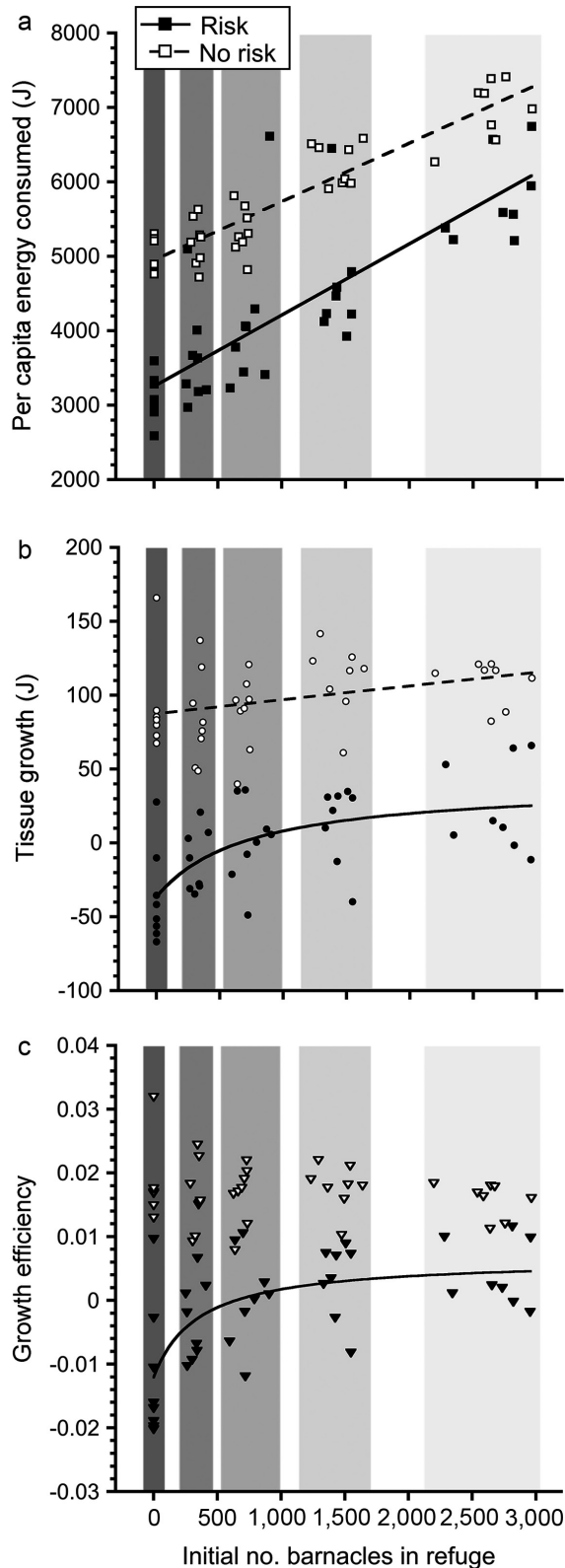


FIG. 2. (a) Per capita energy consumed (foraging rate, J), (b) tissue growth (J), and (c) growth efficiency of *Nucella lapillus* exposed to the presence (filled shapes) and absence (open shapes) of predation risk from the green crab *Carcinus maenas* at varying levels of refuge quality (percent of resources [the barnacle, *Semibalanus balanoides*] available in the refuge habitat relative to risky habitat, RQ). Negative growth efficiencies in panel c emerged due to loss of tissue. Initial number of barnacles in refuge corresponds to the five predetermined levels (gray blocks) of refuge quality in order from least to most valuable refuge (0%, 12%, 25%, 50%, 100%). Lines represent best fit model as determined by AIC (Appendix S1: Table S1). A modified Michaelis-Menten curve best described the variation in growth ($y = (-55439 / [719.8 + RQ]) + 40.4$) and growth efficiency ($y = (-6.49 / ([349.5 + RQ]) + 0.006)$) across refuge qualities in the presence of risk.

because studies often do not fully consider the impact of refuge quality (e.g., the amount of resources they provide) on prey behavior and state, thereby potentially leading to overestimates of the costs of refuge use for prey. This inattention is somewhat understandable because the costs and benefits of refuge use are often confounded; for instance, refuges that afford the highest protection may also have the poorest resources (Beckerman et al. 1997, Heithaus et al. 2007). Our experiment explicitly tests whether high-quality refuges (as measured by the amount of initial resources available to prey while in total refuge) diminish the costs of refuge use and affect prey state and physiology. Consequently, our study can inform how refuge quality fundamentally modifies the strength of nonconsumptive effects of predators on prey behavior and performance.

The foraging/predation risk trade-off posits that prey experience costs while in refuge because resources become scarce and/or prey state (e.g., energetic level) declines through time as competition for resources intensifies (Werner and Hall 1988, Lima and Dill 1990, Sih 1992, Houston et al. 1993). Prey are predicted to modify their foraging behavior over time in order to attain their maximum possible fitness (Abrams 1984, 1991), and therefore should utilize a refuge only as long as the benefits of safety outweigh the costs of lost foraging opportunities (Brown 1992, Sih 1992, Turner 1997, Sih and McCarthy 2002). Refuges with greater or higher quality resources should minimize the costs of refuge use because they enhance prey foraging and performance compared to low-quality refuges. We found that prey foraging decisions and performance were influenced by refuge quality. The proportion of *Nucella* in refuge increased nonlinearly with refuge quality in both the presence and absence of risk (Fig. 1). In both cases (i.e., with and without risk present), increases in resource availability in relatively low-quality refuges (e.g., 12% and 25% refuge quality treatments) enhanced refuge use before plateauing at the highest levels of quality, but this effect was generally stronger for *Nucella* in the presence of risk. Therefore, our study suggests that even refuges with relatively few resources can greatly reduce risk-taking behavior by prey.

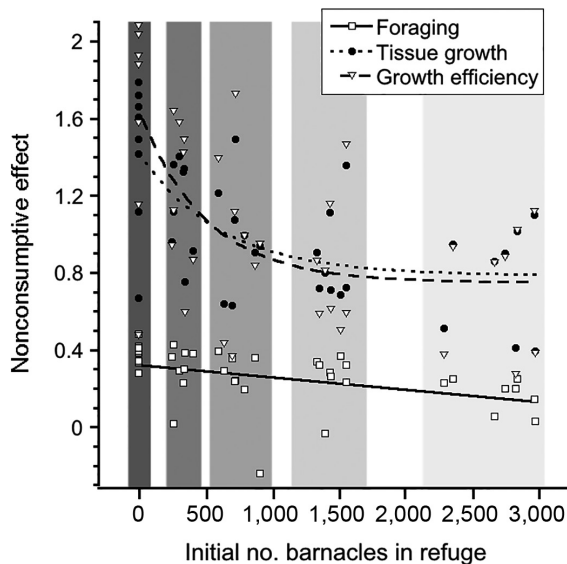


FIG. 3. Strength of nonconsumptive effects (NCEs) on *Nucella lapillus* foraging (open squares), tissue growth (filled circles), and growth efficiency (open triangles) at varying levels of refuge quality (percentage of resources [the barnacle, *Semibalanus balanoides*] available in the refuge habitat relative to risky habitat, RQ). Values >1 indicate that *Nucella* lost tissue in the presence of risk. Initial number of barnacles in refuge corresponds to the five predetermined levels (gray blocks) of refuge quality in order from least to most valuable refuge (0%, 12%, 25%, 50%, 100%). Lines represent best fit model as determined by AIC (Appendix S1: Table S1). A one-phase exponential decay model best described the variation in NCEs on growth ($y = 0.79 + 0.64e^{-0.0016RQ}$) and growth efficiency ($y = 0.75 + 0.90e^{-0.002RQ}$) across refuge qualities.

Because refuge use can dramatically affect prey survival (Persson and Eklöv 1995), the ability to spend more time in refuge without incurring high costs can have important consequences for prey populations, particularly in systems where predators are central to community organization (e.g., demersal aquatic systems; Shurin et al. 2002). Moreover, even improvements between relatively low-quality refuges appeared to greatly reduce the costs of refuge use and promote refuge use by *Nucella*. For example, in the presence of predation risk, *Nucella* in the 25% refuge quality treatment were found in refuge 22% more often than those in the 12% refuge quality treatment (Fig. 1). Thus, even though foraging opportunities were relatively poor in both refuges compared to the risky habitat, *Nucella* clearly preferred the higher quality refuge (25%) more. This occurred despite the fact that these refuges, which differed in their initial resource abundance, were of similar quality (i.e., contained the same number of barnacles) by the end of the experiment.

Work by Brown (1988, 1992) and others (Charnov 1976, Gilliam and Fraser 1987, Jacob and Brown 2000) predicts that prey giving up densities (GUDs) should be lower in safe habitats if they provide similar foraging opportunities to risky habitats, but should also be influenced by prey state (i.e., energy level) if they differ in their

energetic value. Refuge quality impacted prey state in our experiment, with *Nucella* in higher quality refuges gaining more tissue. Prey with greater energetic reserves should be less willing to leave a safe habitat in search of greater foraging opportunities (Dill and Fraser 1984, McNamara and Houston 1986, Lima 1988), and hence will remain in refuge even if their foraging rates are low. Higher quality refuges, in contrast, not only allow prey to forage at higher rates while remaining in relative safety, but further benefit prey by improving their energetic state such that they can delay the decision to leave the refuge. The effect of refuge quality on *Nucella* refuge use was generally weaker in the absence of risk, supporting theoretical expectations that prey should relinquish higher quality habitats despite advantageous foraging rates in the presence vs. absence of predation risk (Gilliam and Fraser 1987, Brown 1988, 1992). The substantial behavioral changes we observed in response to improvements in refuge quality can therefore have important consequences for prey fitness and likely operate in the field, where refuge quality is often highly variable, as well as create differences in prey behavior on small spatial scales, depending on the mosaic of refuge qualities available.

Increased time spent in higher quality refuges also improved *Nucella* performance, though the effects were mediated by risk exposure. Although *Nucella* foraging increased linearly with enhanced refuge quality in both the presence and absence of risk (Fig. 2a), we observed different patterns for growth (Fig. 2b). In the absence of risk, *Nucella* growth was linear, whereas in the presence of risk, it was nonlinear because growth was more strongly affected by improvements between relatively low levels of refuge quality (Fig. 2b). For example, between the 12% and 25% refuge quality treatments, *Nucella* added four times as much tissue in the presence of risk (13.2 J on average) vs. absence of risk (3.4 J on average).

The mechanistic basis of improvements in *Nucella* tissue growth at higher quality refuges in the presence of risk is twofold. Clearly, *Nucella* in higher quality refuges had access to greater foraging opportunities. This enhanced their energetic state via increased growth, which in turn increased their refuge use. However, increased growth at higher quality refuges was also mediated by changes in prey growth efficiency (Fig. 2c). Growing evidence (McPeck 2004, Trussell et al. 2006b) has revealed that the stress imposed by predation risk can reduce the physiological efficiency of prey, including growth efficiency (the ability to convert ingested energy into body mass). Such inefficiencies likely emerge because the stress of predation risk enhances the production of costly molecules associated with the prey stress response (Slos and Stoks 2008, Hawlena and Schmitz 2010), reducing the amount of energy available for growth and reproduction. Remarkably, we found that refuge quality strongly influenced *Nucella* growth efficiency in the presence, but not absence, of risk (Fig. 2c). This result may explain the mismatch between *Nucella* foraging and

growth in the presence of risk. Moreover, the positive effect of refuge quality on *Nucella* growth efficiency under risk was nonlinear, and revealed that growth efficiency improved even with the addition of relatively few resources to the refuge (e.g., from the 0% to the 12% or 25% refuge qualities).

The positive effects of refuge quality on *Nucella* growth efficiency likely emerged not only because prey in high-quality refuges maintained a higher energetic state than those in low-quality refuges, but also because they achieved this state in relative safety. Growing more in a relatively safe environment should diminish the perceived likelihood of mortality from predation, and thereby weaken the physiological stress and costs associated with risk. In contrast, *Nucella* in the lowest quality refuges struggled to maintain tissue mass (Fig. 2b), thereby making it advantageous to leave the refuge to forage in a risky habitat, which exacerbates the negative effects of risk. The physiological stress due to increased competition (Glennemeier and Denver 2002) or resource limitation (Clinchy et al. 2004) has been found to negatively affect prey state, and is likely operating here for prey in low-quality refuges. This striking result emphasizes the substantial impact of refuge quality in reducing the costs associated with refuge use by prey.

Finally, we found that the strength of nonconsumptive effects (NCEs) on prey foraging rate, growth, and growth efficiency decreased as refuge quality improved (Fig. 3). Between the lowest and highest quality refuges, NCEs were nearly half as strong for all three prey traits (Fig. 3). Moreover, the decline in NCE strength was nonlinear for growth and growth efficiency, revealing that even refuges of moderate quality (i.e., 25%) reduced NCE strength by 31–41%. Our results question the prevailing view that, because of limited resources, total refuge use *necessarily* increases NCE strength (Orrock et al. 2013); rather, the impact of predation risk will depend upon the relative foraging opportunities available for prey in vs. out of refuge as well as the consequences of prey foraging decisions mediated by prey state and physiological stress.

Although many studies have acknowledged the influence of resource abundance on prey refuge use under risk, most have focused on the availability of food *outside* of the refuge habitat (e.g., Werner et al. 1983, Gilliam and Fraser 1987, Holbrook and Schmitt 1988) while either preventing prey from foraging in refuge or failing to explicitly measure relative resource differences between risky and refuge habitats. Exceptions to this include Persson (1993), who manipulated refuge quality haphazardly by allowing basal resource communities in the risky and refuge habitats different amounts of time to establish, and Turner (1997), where initial resource abundances were similar between risky and refuge habitats, but varied through time as prey depleted refuge resources. Our study provides important advancements beyond this work by precisely determining the energetic costs of refuge use and evaluating how relative differences in refuge quality impact prey behavior via impacts on prey state. In

addition, by utilizing a static (over the time scale of this experiment) and energetically uniform basal resource, we were able to more accurately measure prey energy consumption and its impact on refuge use. Assessing the role of prey state is also vital because it more accurately conveys the fitness consequences of changes in foraging (Matassa and Trussell 2014b). Finally, by isolating one component of refuge quality (resource availability) and offering prey variable habitats similar to what they may face in the field, our experimental approach more explicitly partitions the mechanistic basis of how refuge quality influences prey behavior and performance.

Resource availability and structural complexity are key factors shaping prey assessment of refuge quality, but evaluating their independent contributions can be challenging in many systems because the physical structure of the refuge either is the food source for prey (e.g., herbs in old fields [Schmitz 1998], conifer forests [Fortin et al. 2005], etc.) or directly influences the resources available for prey (e.g., zooplankton/macroinvertebrates in submerged aquatic vegetation [Persson 1993]). For example, in old field systems, grasshoppers shift from foraging in structurally simple grasses to complex herb canopies to reduce their vulnerability to predatory spiders. This habitat shift requires grasshoppers to forage predominantly on less nutritious herbs (Beckerman et al. 1997, Rothley et al. 1997), which alters grasshopper metabolic efficiency and nutrient demands (Hawlena and Schmitz 2010), and has cascading consequences for plant diversity and nutrient mineralization rates in the surrounding soil (Schmitz 2009). We suggest that the costs and benefits of refuge use and their emergent ecological consequences are often unclear, and that more nuanced attention to refuge quality and its effects on prey foraging decisions may provide better insight into how predation risk influences organismal performance and the structure and function of natural communities.

Our results also suggest that prey assessment of refuge quality will vary through time as resources within the refuge change via consumption or replenishment, as suggested by Turner (1997). Refuge use by prey should be less costly in systems where resource renewal within the refuge remains dynamic and rapid (e.g., periphyton in streams), and thus refuge quality is more stable relative to the time scale over which predation risk and prey starvation thresholds operate. In contrast, in systems like rocky intertidal shores where some resources (i.e., barnacles) recruit only once a year, the cost of refuge use will be particularly sensitive to spatial and temporal resource dynamics that set initial refuge quality. For example, one would expect stronger NCEs in refuge habitats in years or areas with low levels of barnacle recruitment. In general, the effects of predation risk and the costs of refuge may be stronger in systems where resources recruit infrequently and/or grow slowly. Overall, any mechanism that shapes the relative availability of resources between safe and dangerous habitats is likely a central factor influencing prey responses to predation risk and ultimately community structure.

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