Journal of Experimental Marine Biology and Ecology 530–531 (2020) 151416

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

The legacy of predators: persistence of trait-mediated indirect effects in an intertidal food chain

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ARTICLE INFO

Keywords:
Predator-prey interactions
Trait-mediated interactions
Anti-predatory behavior
Intertidal ecology

ABSTRACT

Trait mediated indirect effects are integral to many multiple-level predator-prey interactions. They arise routinely when, in response to predators, prey decrease their foraging on a basal resource, often due to fear. Less examined is a common assumption about trait-mediated indirect effects: that reductions in prey foraging track the instantaneous presence or absence of predators. In particular, although it is recognized that behavioral, physiological, and morphological changes in prey can persist after a predator departs, whether those changes ultimately affect trophic levels below remains an open question. Here, we tested whether legacy effects of predators lead to trait-mediated indirect effects that persist beyond when predators are present, using a model intertidal system that included a crab predator (*Cancer productus*), a carnivorous snail prey (*Nucella ostrina*), and a basal suspension feeder (the mussel, *Mytilus californianus*). We found that previous conditioning of snails to predator cue instilled a sustained behavioral fear response that depressed foraging by snails for at least two weeks beyond when the predator cue was present. Indeed, snails conditioned previously to predator cue consumed similar numbers of mussels as snails currently subjected to cue. Because such durations are long enough to allow new mobile predators to enter prey detection domains previously vacated by other predators, these findings suggest that neglecting the time course of persistence of trait-mediated indirect effects could appreciably underestimate their strengths. Our study supports the notion that prey use prior experience in addition to their body state to inform their anti-predatory decision making, which results in a persistent trophic cascade.

1. Introduction

Ever since the Green World Hypothesis was introduced by Hairston et al. (1960), top-down control has been recognized as a fundamental process structuring communities (see, e.g., Carpenter et al., 1985; Wootton, 1994; Pace et al., 1999; Jackson et al., 2001; Werner and Peacor, 2003; Estes et al., 2011; Vieira et al., 2012). Across a range of habitats, predators set the abundance levels of prey (Peterson, 1999; Albins and Hixon, 2008), induce population cycles (Krebs et al., 2001; Fauteux et al., 2015), mediate competitive interactions between prey species (Purcell, 1991; Wootton, 1994; González-Rivero et al., 2012; Ripple and Beschta, 2012) and dictate local levels of biodiversity (Paine, 1966; Lubchenco and Menge, 1978; Shears and Babcock, 2003). Moreover, the influence of predators extends not only to their prey, but also indirectly down the food chain. In particular, a predator's consumption of prey often releases a basal resource – the food for prey – from foraging pressure, defined as a trophic cascade. Trophic cascades have been observed in many systems and are recognized as one of the dominant factors governing the abundance of a variety of basal species, such as giant kelp (Estes and Palmisano, 1974; Estes and Duggins, 1995), riparian vegetation (Ripple and Beschta, 2004, 2012), and phytoplankton (Carpenter et al., 1985; Daskalov, 2002).

Cascading effects of predators, however, do not arise only from their consumption of prey. Studies over recent decades have highlighted the importance of predator-induced fear in prey and how it can impact the latter's foraging on basal resources (Schmitz et al., 1997; Trussell et al., 2003; Grabowski, 2004; Davidson et al., 2015; Madin et al., 2016; Morgan et al., 2016). In particular, a predator can – simply through its presence in the vicinity of prey – induce shifts in prey traits including behavior, thereby reducing the intensity with which the prey forages on a basal resource. Such trait-mediated indirect interactions (TMIIs) have been shown to be at least as significant as density-mediated indirect interactions (DMIIs; i.e., the indirect effects predators have through actual consumption of prey; Schmitz et al., 2004; Preisser et al., 2005; Peckarsky et al., 2008).

An implicit, yet often underemphasized detail in conceptualizations

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https://doi.org/10.1016/j.jembe.2020.151416
Received 30 December 2019; Received in revised form 29 April 2020; Accepted 5 June 2020

of trait-mediated trophic cascades is that trait-driven interactions are governed by the *current* presence or absence of predators. That is, the possibility that the *history* of predator exposure might influence indirect effects is often neglected. However, studies suggest that effects of fear on prey do not always track the instantaneous presence or absence of predators. After sustained exposure to risk cues, prey may become desensitized to those cues and resume normal behavior (Magurran and Girling, 1986; Rodriguez-Prieto et al., 2009, 2011; Magnhagen et al., 2017). Similarly, prey may forgo fear responses as their hunger state increases, and they are compelled to forage (Lima and Bednekoff, 1999; Matassa and Trussell, 2014; Gravem and Morgan, 2016; Kimbro et al., 2017). Such findings suggest that a history of prey exposure to predators can weaken fear effects and TMIIs.

Less explored is the contradictory, yet equally plausible, scenario where previous predator exposure can instead strengthen trait-based interactions. Such a scenario might arise, for example, if predator-induced traits persisted beyond the period when the predator is present. This possibility relaxes the common expectation that prey will resume feeding as soon as a predator leaves (Lima and Bednekoff, 1999). Indeed, it is known that certain prey species maintain elevated vigilance even after a predator departs (Adamec and Shallow, 1993; Masini et al., 2006). That said, it remains unclear whether such persistence in anti-predatory behavior tends to drive cascading impacts on the basal resource. If it does, it would join other pathways by which trait-driven trophic cascades can become decoupled from a predators' presence. A possible pathway common to the marine realm, for instance, involves changes in prey morphology (i.e., “inducible defenses”) (Harvell, 1990). Such responses include shifts in size as well as the production of mechanical defenses like spines or thicker shells in the presence of predators (Appleton and Palmer, 1988; Harvell, 1990; Freeman, 2007; Miner et al., 2013). Morphological changes of this kind can clearly remain after a predator is gone, and could in turn cause lasting changes to how prey interact with a basal resource. For example, if a thicker, heavier shell or an awkwardly protruding spine of a prey species also hinders its feeding (Grünbaum, 1997), then positive indirect effects of the predator on the basal resource could continue to manifest even after departure of that predator. Similarly, predator-induced reductions in growth and/or body size (Relyea, 2002; Trussell et al., 2011) could have long-term implications for prey metabolic rates, strengthening trait-driven trophic cascades by decreasing food requirements of smaller prey individuals.

Here, we conducted laboratory experiments to test whether previous predator exposure has a sustained effect on prey foraging and in turn on a basal resource, even after the predator is removed. We tested for both behavioral and morphological legacies of prior predation. Our study system consisted of a tri-trophic food chain, using the red rock crab, *Cancer productus*, as the predator, the carnivorous dogwinkle, *Nucella ostrina*, as the prey species, and the California mussel, *Mytilus californianus*, as the basal resource. The *Nucella* genus is especially appropriate for such a study because it can display both a behavioral and morphological shift in the presence of predatory crabs (Appleton and Palmer, 1988; Bourdeau, 2010; Large and Smee, 2010; Bourdeau, 2011), allowing us to evaluate which aspects of anti-predatory responses have a persistent effect on prey foraging and thus on a basal resource.

Two core hypotheses can be envisioned regarding how previous exposure to a predator might alter foraging of *Nucella* snails on mussels. First, snails conditioned in advance to predator cues might consume more mussels than naïve snails during subsequent exposure to predator cue. Such a decrease in trait-driven trophic cascades could arise as a consequence of habituation to predator cues, or due to an increase in hunger state of the snails that causes them to increasingly ignore predators over time. We term this scenario the ‘TMII attenuation model,’ and have provided a figure of the predicted outcome under this model in Fig. 1. Second, snails conditioned previously to predator cues might feed on fewer mussels than naive *Nucella* after the predator cue is removed. Such persistence of the TMII could manifest through a morphological change hindering the foraging of *Nucella*, including a smaller body size that decreases per capita food needs, or a lasting effect of previously instilled fear (Fig. 1c). We identify this second scenario as the ‘TMII persistence model.’

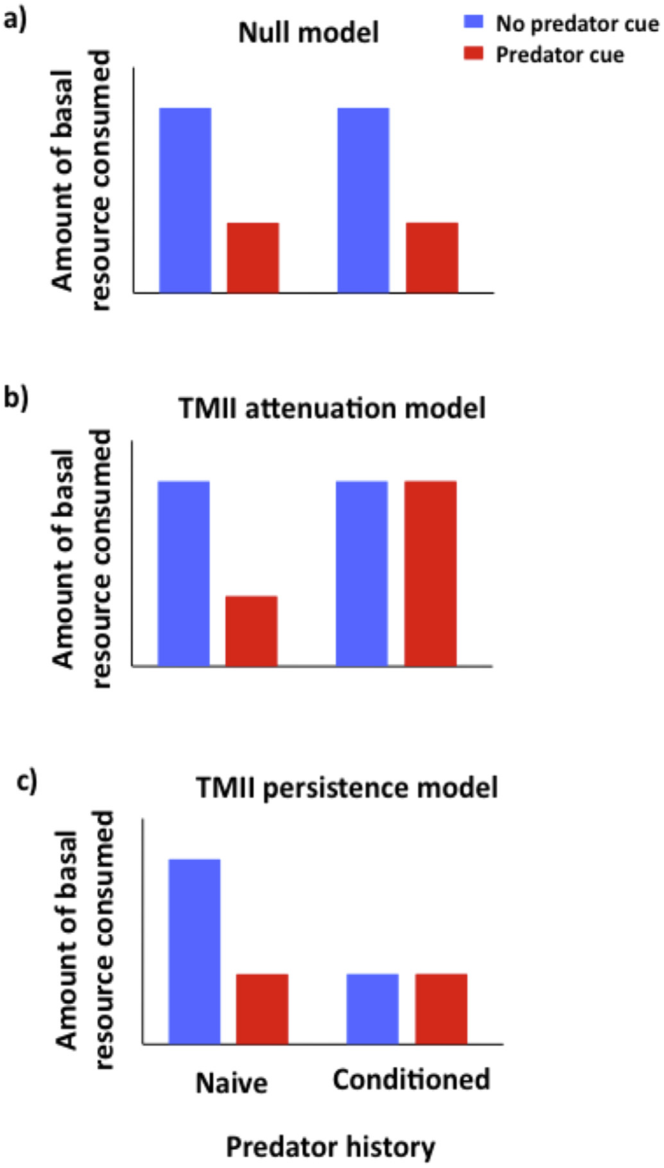

Fig. 1. A schematic displaying various predictions for how the feeding activities of prey might change after exposure to a predator. a) In the null model, prey foraging depends only on the current presence or absence of a predator, with no legacy effects of prior predator exposure. In this situation, prey respond in the same way to predators regardless of whether they have been previously conditioned to predators or are naïve to them. b) In the TMII attenuation model, naïve prey respond to predators by decreasing their foraging, whereas prey that have a history of predator exposure do so to a lesser degree or not at all. This latter pattern can arise from either habituation to predators or an increase in hunger state over time. c) In the TMII persistence model, prey that have previously encountered predators continue to forage less, and consume less of a basal resource, regardless of whether predators are present or absent currently.

2. Materials & methods

2.1. Predator conditioning

The first step of the experiment consisted of conditioning the

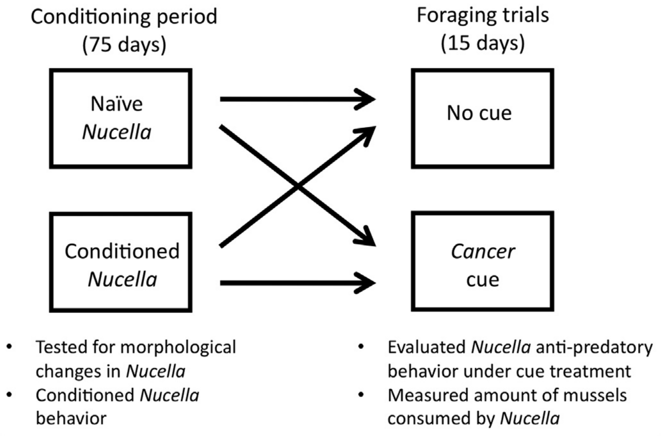

Fig. 2. Conceptual diagram of the methods used. During the conditioning period, *Nucella* snails were separated into two treatments where they were either held in control seawater or conditioned with predator cues. Snails were also measured before and after this period to test for induced morphological changes. *Nucella* were then further separated into two treatments where they were exposed to predatory cues from *Cancer* crabs or not, creating four distinct treatment combinations of conditioning treatment and predator cue treatment. The numbers of mussels consumed by *Nucella* during this period were quantified to examine how the strength of trait-mediated indirect effects was affected by the previous conditioning period. The anti-predatory behavior of *Nucella* was also assayed to determine if behavior or morphology was the mechanism behind the persistence or attenuation of the indirect effects.

intermediate consumer (*Nucella ostrina*) in our tri-trophic food web to the presence of predators or not (Fig. 2). This step was necessary to initiate any induced morphologies that might contribute to outcomes consistent with the TMII persistence model. We collected *Nucella* ($N = 250$) during May and June 2017 along the shores of Campbell Cove near Bodega Bay, California (38° 17′ 60″ N, 123° 3′ 10.8″ W) where rock crabs commonly co-occur with these snails (Byrnes et al., 2006). We measured the length from the apex to the siphonal notch (12.1 mm +/− 0.2 s.d.) and total weight (0.37 g +/− 0.02 s.d.) of the snails prior to placing them in flowing seawater in the laboratory. We chose *Nucella* from smaller size classes, which exhibit higher size-specific growth rates, to maximize the chance of detecting any induced morphological changes that might arise subsequently. Each of the snails was randomly assigned to one of 10 plastic containers (33 mm × 20 mm × 11.5 mm), and these containers were supplied with seawater from one of five randomly selected supply sumps (∼60 L) with a flow rate of ∼150 L/h. Three of the sumps contained two *Cancer productus* crabs each (108 mm +/− 10.6 s.d in carapace width), and two of the sumps held no predators. The seawater flowing through the sumps and into the snail containers had an average temperature of 10.5 °C and salinity of 34.1 ppt. The *Nucella* snails and *Cancer* crabs were fed weekly with juvenile mussels (*Mytilus californianus*) and other *Nucella* respectively, through August 2017. At this point we ended the conditioning period of predator or no-predator exposure (Fig. 2).

2.2. Morphology

The above conditioning period lasted 75 days, a duration that has been documented in previous studies to cause a morphological change in *Nucella* (Bourdeau, 2010; Bourdeau, 2011). Therefore, we tested for proportional changes in the length and weight of our snails that may have occurred during the conditioning phase and the weight:length ratio by repeating the measurements we had made at the outset of our experiments. We specifically examined these two morphological traits as previous studies on *Nucella ostrina* shown that shell length grew less in the presence of predator cues while the ratio of shell mass to tissue mass remained relatively constant in the presence of predator cues (Bourdeau, 2011; Barclay et al., 2019).

2.3. Prey behavior and foraging

Using a subset of the conditioned and naïve snails ($n = 80$ each), we next tested how predator conditioning affected their behavior and foraging when they were subsequently exposed to predator cue or not (Fig. 2). If predator conditioning altered *Nucella* morphology and their foraging, we also wanted to examine whether a snail's size might alter its response to predator cue and its foraging on mussels. We therefore first grouped the *Nucella* into five size classes of 16 *Nucella* each, from smallest to largest, creating a size gradient. We created this array of multiple size classes for both predator-conditioned and naïve snails.

We then divided each set of 16 snails into two containers (33 mm × 20 mm × 11.5 mm) with eight *Nucella* individuals per container; half of the containers received outflow from sumps containing crabs and half received seawater free of predator cue (this overall protocol thus yielded 2 conditioning exposures x 5 size classes x 2 cue treatments = 20 containers total). All 20 containers were then supplied with 20 juvenile mussel individuals each, as a basal food source for the carnivorous snails. This configuration created a 2 × 2 design stratified by size with conditioning history as one treatment and predator cue as the second treatment. We then measured the number of mussels consumed by the snails daily over the course of the next 15 days, without replacement of consumed mussels, along with the number of snails above or below the water line within each container as a metric of anti-predatory escape behavior. This latter metric has been used as an indicator of anti-predatory behavior for multiple gastropod species (Fawcett, 1984; Klose, 2011; Jellison et al., 2016), because a variety of intertidal prey taxa leave the water during flight responses. Individuals of *Nucella ostrina*, in particular, have been shown to not only withdraw into their shells in the presence of predator cue, but also actively avoid predator cues (Mach and Bourdeau, 2011). This behavior is particularly relevant to snails interacting with *Cancer* crabs because the latter do not forage out of the water (Robles et al., 1989).

Because multiple *Nucella* individuals were conditioned together in containers, the experiment technically employed a split-plot design where the *Nucella* were subsamples of ‘container’ as the experimental unit. However, in order to create size classes of snails to test the effect of snail size on mussels consumed, we had to cross snails from various containers for the behavioral experiments (e.g. the smallest snails from each container were combined into one new container). This requirement meant that the containers for the behavioral experiment were not fully independent units. We emphasize, however, that in testing the morphology of *Nucella* we observed that containers as a random effect accounted for only 0.09 and 0.04 of the standard deviation of length and weight, respectively, across morphology. Furthermore, a comparison of AIC scores of models with and without the random effects showed a 12 and 17 increase in AIC scores, respectively for length and weight, in the more complex models, suggesting that container was not a strong predictor. Therefore, since the morphology of *Nucella* was only marginally influenced by container, we treated individual snails as independent units for the behavioral trials.

2.4. Statistical analysis

We analyzed the proportional change in both length and weight of *Nucella* over the course of the conditioning phase by dividing the final length and weight of each individual by the average initial length and weight of the individuals in each container and subtracting 1. Differences in the degree of any such change between the cue and no-cue conditioning exposures would indicate an induced morphological response. We analyzed the morphometrics using a two-way mixed effects model with predator exposure as a fixed effect and container as a random effect (Bates et al., 2015). Similarly, we analyzed the weight to length ratio of individual snails both before and after the conditioning

Table 1

The various candidate models tested when analyzing *Nucella* behavioral data. Models are ranked from lowest to highest AIC scores, and a backwards stepwise regression was used to select the final model. *CH* is conditioning history, *PC* is predator cue, and *T* is duration over the course of the behavioral assay.

Model	AIC score
$CH + PC + T + CH:T + PC:T$	779.74
$CH + PC + T + CH:PC + CH:T + PC:T$	780.06
$CH + PC + T + CH:T$	780.37
$CH + PC + T + CH:PC + CH:T$	780.82
$CH + PC + T + CH:PC + CH:T + PC:T + CH:PC:T$	782.06
$CH + PC + T + PC:T$	783.35
$CH + PC + T + CH:PC + PC:T$	783.87

phase with predator exposure and time as fixed effects and containers as a random effect.

For the foraging assay portion of the experiment, we analyzed the change in *Nucella* predator-avoidance behavior over time, which involved a binary outcome of whether a snail was in or out of water, using a three-way mixed effects logistic regression model with a logit link and binomial error distribution. We treated conditioning history, predator cue, and time as fixed factors and included the latter as a continuous variable because if predator conditioning altered prey behavior, we wanted to test how long the conditioning effect persisted. We incorporated container as a random factor for both the intercepts and slopes with respect to time to account for variations among containers. We chose our final model based on AIC scores (Akaike 1974) using backward elimination stepwise regression. Our initial model contained the three fixed factors along with all two-way and three-way interactions. We then compared the full model with a model without the three-way interaction. If the less complex model had a lower AIC score, we repeated the process by comparing that model with another candidate model of lower complexity until a lower complexity model had a higher AIC score. Table 1 summarizes the various models tested along with their AIC scores.

We analyzed total mussel consumption by *Nucella* snails using a three-way linear regression with conditioning history and predator cue as the two categorical predictors and the average size of snail per container as a continuous predictor. Since each container produced only one estimate of the total number of mussels consumed, no random effects were included. To avoid issues of over-fitting, we compared various models with different two-way and three-way interaction terms removed and settled upon the model with the lowest AIC score (Akaike, 1974).

We checked the assumptions of our models by visually evaluating the residuals of each model, using a quantile-quantile plot. We also plotted the residuals of the behavioral model over time to ensure that *Nucella* behavior could be approximated by a linear function under a logit link over time. When we found a significant interaction in our models, we conducted pair-wise comparisons between different treatments, using the 'emmeans' package in the computer software package, *R* (Length, 2018) and employing a Tukey correction. We also used the 'emmeans' package to compare whether slopes of different treatments differed from each other.

3. Results

We detected little evidence of induced morphological change in *Nucella* due to predator exposure during the predator conditioning phase of the experiment. In particular, although we observed a slight increase in *Nucella* length and weight overall there was not a significant difference in either length ($t = -0.79$, df = 2.96, $p = .49$) or weight ($t = -0.472$, df = 2.88, $p = .67$) between *Nucella* exposed to *Cancer* cues or not (Fig. 3A, B). In addition, although there was a difference in the weight to length ratio between the two conditioning treatments ($t = -2.02$, df = 499, $p = .04$), that difference was observed both at the start and at the end of the experiment, suggesting that it was not predator conditioning that caused this difference (Fig. 3C, $t = 0.57$, df = 499, $p = .57$).

In contrast, anti-predatory escape behavior in the snails during the foraging phase of the experiment was strongly influenced by conditioning history (Fig. 4, Table 2a). In particular, the proportion of *Nucella* above the water line changed over time, depending on its past exposure to *Cancer* cue. This pattern was evident in our results as a significant interaction of time with previous predator exposure (Exposure history*Time: z = −2.6, $p = .01$). There was also a significant effect of current predator cue (Predator cue: z = 2.39, $p = .02$) with marginally nonsignificant interaction with time (Predator cue*Time: z = 1.8, $p = .08$; Predator cue*Exposure history was excluded from the final model based on AIC scores). This latter trend suggests that the effect of contemporaneous predator cue did not substantially change throughout the duration of the experiment. Taken together, these interaction terms suggest that conditioned *Nucella* initially spent significantly more time out of the water than their naïve counterparts in the absence of current predator cues. Over the course of the two-week assay, conditioned *Nucella* reentered the water at a significantly faster rate than naïve *Nucella* both in the absence of predator cue and in the presence of predator cue (z = −2.6, $p = .047$, z = 3.0, $p = .013$, respectively). In other words, there was a 0.17 decrease in log odds per day for conditioned snails that were held in predator-free water to be out of the water, compared to a decrease of just 0.06 log odds per day for naïve snails in predator-free water and an increase of 0.03 log odds per day for naïve snails in cue water (Table 2b). Both conditioned and naïve *Nucella* spent similar amount of time out of water when exposed to predator cues (Fig. 4). Although we also saw a difference in how naïve and previously exposed *Nucella* reacted to predator cue over time (z = −2.6, $p = .046$), this difference may be marginal since the interaction between predator cue and time was not significant.

The above changes in behavior also resulted in differences among treatments in the number of total mussels consumed (Fig. 5), indicating that prior predator exposure did affect the trait-mediated indirect interactions (TMII) of this system. We detected a significant interaction between predator conditioning and predator cue on number of mussels consumed ($t = 3.3$, df = 16, $p = .005$). A subsequent Tukey pair-wise test shows that *Nucella* exposed to contemporaneous *Cancer* cues fed on similar numbers of mussels regardless of their previous predator exposure ($t = 0.78$, df = 16 $p = .86$). In contrast, when *Nucella* were not exposed to contemporaneous *Cancer* cues, snails that had previously experienced crab cue consumed significantly fewer mussels than naive *Nucella* ($t = 5.4$, df = 16, $p = .0003$). In fact, *Nucella* that had previously been conditioned to predator cue consumed similar amounts of mussels compared to *Nucella* that were currently experiencing predator cue (*Nucella* with previous exposure versus *Nucella* with previous exposure plus current predator cue: $t = 2.6$, df = 16, $p = .08$; *Nucella* with previous exposure versus *Nucella* without previous exposure plus current predator cue: $t = -1.8$, df = 16, $p = .3$).

Even though there was not a significant difference in overall average size among snail individuals that experienced one or the other of the two conditioning regimes, we were still able to test whether *Nucella* size had an effect on the number of mussels consumed. Surprisingly, the size of *Nucella* did not have a significant effect on number of mussels consumed. We included *Nucella* length in a model with both predator conditioning and predator cue as further predictors of mussel consumption, and neither *Nucella* length nor its interaction with the other predictors came out as significant ($p > .05$ for all terms) (Fig. 6).

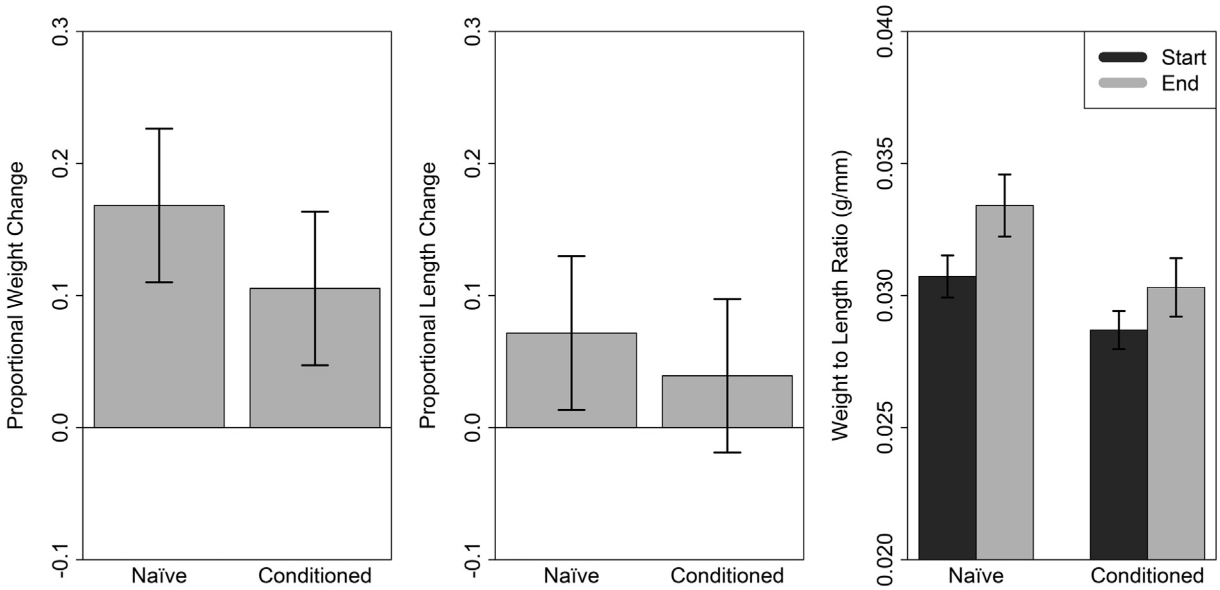

Fig. 3. Proportional changes (final measurement/initial measurement-1) in weight (panel a) and length (panel b) of *Nucella* (mean ± SE) after being conditioned in predator cue or seawater without cue for approximately 2.5 months during the conditioning period. No significant differences between naïve and conditioned snails were detected. Panel c depicts the change in weight:length ratio over the course of the conditioning period both for naïve *Nucella* and *Nucella* exposed to *Cancer* cues. Dark gray bars represent the ratios at the start of the conditioning period before conditioned *Nucella* were exposed to predator cues, and light gray bars represent ratios at the end. Although there was a difference in the ratios between the start and end of the conditioning period, both naïve and conditioned *Nucella* had similar increases in ratios.

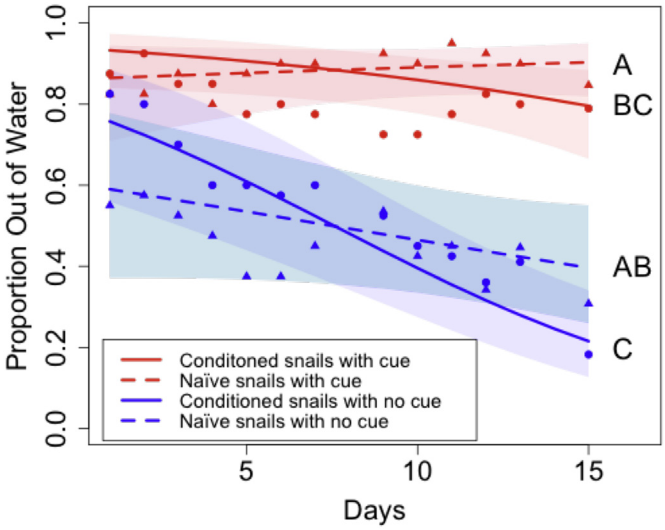

Fig. 4. Effects of prior conditioning with predator cue (or not) and current exposure to predator cue (or not) on the proportion of snails out of water over the duration of the experiment. This latter quantity characterizes a known anti-predatory behavior in *Nucella*. Letters denote if there is a significant difference between the slopes of the four treatments. Lines represent the best-fit curves from the most parsimonious logistic regression model, and the shading indicates the 95% confidence intervals. Triangular points represent naïve *Nucella*, and circular points represent conditioned *Nucella*.

Table 2

2a provides the summary output for the model on the analysis of *Nucella* behavior over time as a function of exposure history and presence of predator cue. The intercept for this regression describes the proportion of snails out of water (in log odds) for naïve snails in the absence of predator cues at the start of the experiment. 2b summarizes the change in proportion of *Nucella* out of water over time (in log odds) for the four different treatment combinations along with their standard error.

	Estimate	Z value	*P* value
a)			
Intercept	0.42	0.87	0.39
Exposure history	0.89	1.55	0.12
Time	−0.06	−1.51	0.13
Predator cue	1.41	2.39	0.02
Time:Exposure history	−0.12	−2.60	0.01
Time:Predator cue	0.08	1.77	0.08
b)			
Intercept	0.42	0.87	0.39
Exposure history	0.89	1.55	0.12
Time	−0.06	−1.51	0.13
Predator cue	1.41	2.39	0.02
Time:Exposure history	−0.12	−2.60	0.01
Time:Predator cue	0.08	1.77	0.08

4. Discussion

4.1. Implications for predator-prey dynamics

Our data support a growing awareness that previous exposure of prey to predators can result in cascading effects that persist well beyond the period of predator exposure, with implications for the time-aggregate strength of trait-mediated indirect interactions. In particular, our findings substantiate the second of our two core hypotheses, where we anticipated that conditioned snails would decrease foraging on mussels even in the absence of further predator cues (Fig. 1). Not only did we demonstrate that trait-driven interactions can persist in the absence of predators, but we also showed the mechanism by which the persistence arose. In our system the reduction in foraging by *Nucella* arises not from a permanent change in morphology or size engendered through a pathway associated with inducible defense (Figs. 3, 6), but rather through a lag in *Nucella's* response to the absence of predator cue during which they continue to remain out of the water (Fig. 4). Additionally, it is likely that conditioned *Nucella* are displaying some form of passive avoidance even when underwater (Mach and Bourdeau, 2011), which can also result in a decrease in foraging on mussels. Within the 15-day span of the experiment, this legacy of fear results in a behavioral trophic cascade that is comparable to the indirect effects

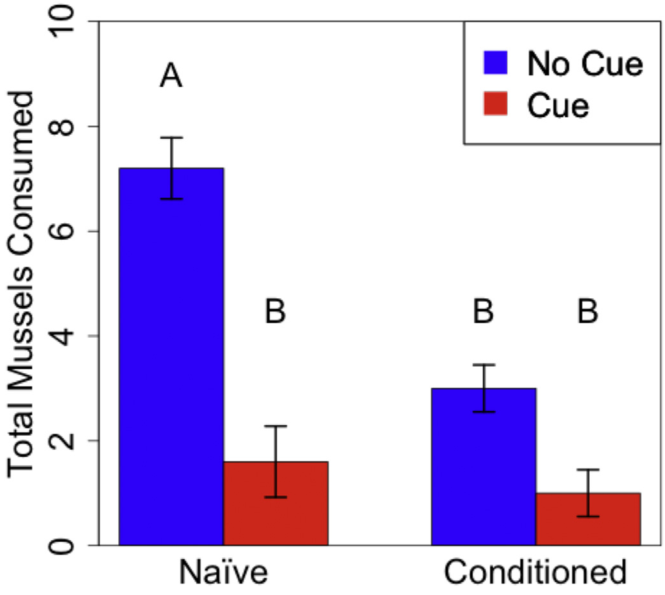

Fig. 5. Snails previously conditioned with predator cue, but not currently experiencing such cue, consumed a similar number of mussels as snails that were contemporaneously encountering the cue (mean number of mussels consumed over 15-day experiment ± SE). This pattern indicates that TMIIs can persist for up to 15 days after the removal of a predator. Letters denote a significant difference in number of mussels consumed.

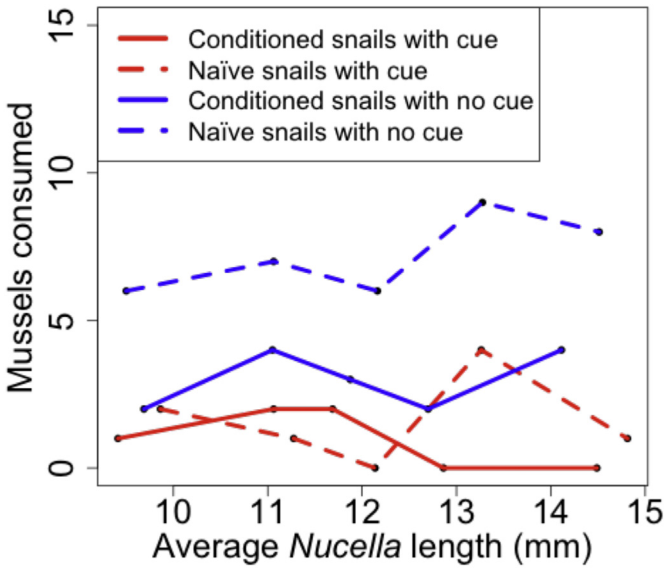

Fig. 6. The size of *Nucella* did not affect the number of mussels consumed regardless of the previous or current exposure of *Nucella* to predator cues. In all four of the treatments, no significant relationship exists between the length of *Nucella* and mussels consumed. However, as in Fig. 5, predator cue and conditioning treatment affect predict mussel consumption.

produced in the presence of predators (Fig. 5).

It is somewhat unexpected that we did not observe a change in shell size in *Nucella ostrina* as has been previously documented (Bourdeau, 2011; Barclay et al., 2019). However, given that our predator exposure period was shorter in duration than some of these studies (Barclay et al., 2019) and that *N. ostrina* shows a weaker response to predator cues compared to its congeners (Bourdeau, 2011), it is possible that the conditioning period was not long enough to detect a significant change between growth rates. Like other studies, we also did not see a change in the ratio of mass to length due to exposure to predator cue (Bourdeau, 2011; Barclay et al., 2019). In addition, from our size-structured design in the foraging trials, we did not find evidence that smaller size affects *Nucella* feeding. That said, although we have strong evidence that differences in mussel consumption arose via changes in behavior, it remains possible that some other change in *Nucella* morphology (i.e., one unmeasured in our experiment) may have contributed to the differences in mussels consumed.

Behaviorally driven trophic cascades (TMIIs) have been shown to be as important if not more important than predation-driven trophic cascades (DMIIs) in most predator-prey systems (reviewed in Preisser et al., 2005). If fear persistence is a common phenomenon in other predator-prey systems, this outcome would suggest that the behavioral component within a trophic cascade may have a more pronounced effect on the basal resource than is often estimated. The greater indirect impact of anti-predatory behavior would arise not because their intensity has been miscalculated but because their duration has been underappreciated. Take for instance, the *Cancer* and *Nucella* predator-prey pair. As a mobile predator, a single *Cancer* crab can induce fear in a number of *Nucella* individuals encountered along its path, influencing the foraging activities of those snails. Based on our findings, we can also anticipate that even after the above crab leaves the area, the affected cohort of *Nucella* individuals would still exhibit anti-predatory responses. Although the persistence is not permanent, another crab could enter the area before the response decays, thereby reigniting the fear effects in *Nucella* before those effects have a chance to dissipate. In this regard, the persistence of fear effects in *Nucella* could operate to “fill in” times when predators may be absent, extending the effective total duration over which predators drive a trophic cascade. In fact, our study could explain why in certain cases, temporal variability of predators does not appear to affect the strength of TMIIs (Trussell et al., 2011). Additional experiments should explore the physiological basis for the persistence of fear, as well as the influence of predator identity and the length of the conditioning period on the persistence attributes of the TMII.

4.2. *Study limitations*

We also acknowledge several limitations of this study. For one, the conditioning period to predator cues we used for the experiment can be considered substantial for a behavioral trial (Weissburg et al., 2014). Our chosen conditioning period was based on the length of previous studies that have induced morphological changes in gastropods (Appleton and Palmer, 1988; Palmer, 1990; Bourdeau, 2011). It is possible that the duration of fear persistence could be correlated with the duration of previous predator exposure. Nevertheless, although the exact 15-day period of fear persistence observed in our study might not be replicated in the field, the overall phenomenon likely retains ecological relevance. The containers during the conditioning period of our experiment were held in a flow-through system with a 23-min turnover rate, limiting the concentrations of *Cancer* cues. Furthermore, other studies suggest that the phenomenon of behavioral persistence can manifest even following quite brief exposure periods (e.g., Masini et al., 2006; Chivers et al., 2016). In addition, a prior study on *Nucella lapillus* showed that the fear response in *Nucella* was relatively insensitive to the length of predator exposure, suggesting that behavioral patterns in prey might not linearly correlate with the temporal duration of predator's presence (Matassa and Trussell, 2014). A persistence of even just 12 h could be enough for *Nucella* to be in a near-constant state of vigilance since *Cancer* crabs are known to move into and out of the intertidal zone to forage according to the fluctuating tides (Robles et al., 1989).

Second, because the *Nucella* used in this study were collected from a single field site, traits of that site could have imposed a specific pattern of prior exposure history on predators, and that history could in turn have interacted with our conditioning treatments. Though we are unable to explicitly rule out this possibility, the size distribution of *Nucella* we collected (~12.1 mm) suggests that they were juveniles (Etter, 1989; Donelan and Trussell, 2018) whose lifespan in the natural environment was likely not appreciably longer than the 75 days exposure regime of this study. Furthermore, any such effects would presumably be observed in all of our treatments. It is also the case that our findings could in theory apply only to the population we examined, given that *Nucella ostrina* broods its young and so has low dispersal capacity, which could facilitate local adaptation. Indeed, other species of *Nucella* have been shown to exhibit geographic variation in prey foraging capabilities (Sanford et al., 2003). Further studies are needed to document the prevalence of, and any variation in, this fear persistence.

4.3. Relevance to the risk allocation hypothesis

Findings of our work can also be considered in the context of existing theory regarding foraging behaviors of animals. The risk allocation hypothesis (Lima and Bednekoff, 1999) posits that in an environment where risks of predation fluctuate through time, foraging rates of prey should increase during periods of reduced risk, to compensate for depressed feeding during high-risk intervals. Furthermore, under sustained exposure to predators, prey should eventually forgo their anti-predator behaviors in favor of meeting their energetic requirements. This latter prediction contributes to our TMII attenuation model (Fig. 1b), which receives partial support in our study because conditioned *Nucella* re-entered the water despite the continuous presence of predator cue (Fig. 4). However, this slight damping of the fear response did not translate down to the basal resource since both conditioned and naïve *Nucella* fed on similar numbers of mussels. Moreover, even in the absence of predator cues, conditioned *Nucella* fed on similar numbers of mussels compared to *Nucella* currently exposed to predator cues. These latter results are thus more consistent with our TMII persistence model (Fig. 1c) and suggest that even though we expect prey with a higher hunger state to exhibit weakened anti-predatory responses in favor of foraging (Morton et al., 1995; Matassa and Trussell, 2014; Gravem and Morgan, 2016), the legacy effects of fear in our system seem to overwhelm such tendencies. Other studies have similarly demonstrated variation in the degree of adherence to the risk allocation hypothesis (reviewed in Ferrari et al., 2009). One potential cause for variable results is the extent to which prey may or may not be approaching starvation (Ferrari et al., 2009). *Nucella* species have been observed to forage infrequently, suggesting that they do not have a high metabolic rate (Hughes and Drewett, 1985), and fearful *Nucella* that decrease their activity levels may experience even lower metabolic demands (Barry, 2014; but see Trussell et al., 2006). Modest metabolic requirements in *Nucella* might therefore reconcile this species' behavior with predictions of the risk allocation hypothesis, since *Nucella* would then tend to consistently maintain an adequate energy budget to enact an anti-predatory response.

Regardless of whether energetic factors modulate the extent to which *Nucella* exhibits a persistent fear response, our results suggest that this species errs on the side of caution after experiencing predator cues. Even though the no-cue treatment represents a risk-free environment, snails appear to forgo foraging – therefore eliminating their chance to acquire food – based on their prior experiences. Further studies are needed to test whether this approach would ultimately benefit the organisms in nature, but one potential explanation for why snails might follow the TMII persistence model is that in environments where sensory cues are unreliable, such as the turbulent, wave-swept rocky shores inhabited by *Nucella*, prey species may distrust a lack of predator cue. In such instances, a prey species might maintain a fear response longer than in an environment where the presence or absence of cues is a reliable indicator of predators' presence (Kotler et al., 1991; Leahy et al., 2011). Indeed, there are many examples of environments where disruption of the sensory pathway occurs, degrading the ability of prey to acquire sensory information (Ferner et al., 2009; Smee et al., 2010; Weissburg et al., 2014). Organisms inhabiting such environments may therefore rely on repeated sampling of predator-free conditions to determine that the environment is truly safe. Other aquatic gastropods have the capability to form memories (Kobayashi et al., 1998; Lechner et al., 2000; Orr and Lukowiak, 2008) and associatively learn (Ito et al., 1999), so the potential use of past experiences to inform present decisions may apply also to *Nucella*.

4.4. Relevance to other systems

While yet unknown, it is plausible that persistent fear responses, as observed here, could represent a relatively widespread phenomenon. For one reason, even though we did not observe a change in morphology with our *Nucella*, there are many prey species that do display strong morphological changes when predators are present (Harvell, 1990; Sherker et al., 2017; Valley and Emlet, 2018), including induced defenses that potentially interfere with prey foraging. For example, filtration of phytoplankton by the bryozoan, *Membranipora membranacea*, is impaired by defensive spines in the presence of a predatory nudibranch (Harvell, 1986; Grünbaum, 1997; Iyengar and Harvell, 2002). Since these spines will remain even if the predator subsequently departs, the reduction in filtration rate can generate persistent trait-driven indirect effects. Future studies examining the role of induced morphology on prey feeding may reveal more examples of persistent trait-mediated indirect interactions (TMIIs).

On the other hand, it is also possible for induced morphologies to attenuate trait-mediated trophic cascades. If individuals have a fixed energy budget for anti-predatory traits, allocating resources for morphological changes may result in reduced allocation for behavioral changes. For instance, the common goldfish, *Carassius auratus*, will grow a deeper body and also reduce activity levels in the presence of predators (Chivers et al., 2007). However, deeper bodied *C. auratus* show higher levels of activity than shallow bodied *C. auratus* during further exposure to predators (Chivers et al., 2007). If activity levels correspond to foraging, past experiences with predators may weaken trophic cascades by increasing feeding rates of prey on the basal resource.

Additional fear-related behavioral responses in consumers might also translate into persistent TMIIs. Neophobia, the fear of novel cues, has been demonstrated in various prey species (Chivers et al., 2016; Mitchell et al., 2016). In these studies, prey that have been previously exposed to injured conspecific cues act more afraid to novel predator cues than prey that were not exposed to injured conspecific cues (Chivers et al., 2016). Neophobia can be adaptive because it allows prey from risky environments to learn to avoid predators more efficiently. If prey are using their previous experiences with predator cues or injured conspecific cues to inform their future behavior, persistent TMIIs may arise from neophobia. One key difference in our system is that *Nucella* displayed a fear response in the absence of any cues, while examples of neophobia involve novel cues (Mitchell et al., 2016).

Perhaps the simplest interpretation of our results is that they reveal a trait-driven trophic interaction consistent with studies showing that prey sometimes increase their vigilance after exposure to predator cues. For example, rats exposed to predatory cat and ferret cues become warier, reduce exploration, and display increased levels of anxiety even after the predatory cues have been removed (Adamec and Shallow, 1993; Masini et al., 2006). This heightened vigilance dissipates over time, similar to what we observed with *Nucella*, but early after predator exposure, foraging behavior could be impacted, which may sustain a behaviorally-driven trophic cascade. Therefore, although a sizeable subset of prior studies has been couched in the field of post-traumatic stress disorder (Zoladz et al., 2015; Pitman et al., 2012; Schöner et al., 2017), and have not explored consequences for a basal resource in a multi-level trophic web, there may be ecological implications of persistent anxiety and vigilance that apply to the broader feeding networks present within natural communities.

5. Conclusions

Persistent fear behaviors that translate to altered foraging activities of an intermediate consumer have important implications for quantifying the time-averaged strength of trait-mediated indirect interactions (TMIIs). TMIIs may have a more enduring effect on a community than is often realized, given that such indirect effects may last appreciably after a predator departs. Furthermore, this persistent TMII originates from a temporary continuation of anti-predatory behavior. Additional research is needed to determine if TMII persistence is prevalent in other systems, including ones involving prey species that exhibit induced morphologies and behaviors involving sustained vigilance.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This work was supported by National Science Foundation (NSF) grant OCE-1636191, and GN received additional funding from an NSF Graduate Research Fellowship. No funding sources had a role in the design, writing, or submission of this manuscript. We thank K. Elsmore, A. Ninokawa, S. Merolla, A. Ricart, A. Saley, and A. Smart for invaluable input on the manuscript, and we would also like to thank K. Barclay for helping with field collections.

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