

Climate change enhances the negative effects of predation risk on an intermediate consumer

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Abstract

Predators are a major source of stress in natural systems because their prey must balance the benefits of feeding with the risk of being eaten. Although this 'fear' of being eaten often drives the organization and dynamics of many natural systems, we know little about how such risk effects will be altered by climate change. Here, we examined the interactive consequences of predator avoidance and projected climate warming in a three-level rocky intertidal food chain. We found that both predation risk and increased air and sea temperatures suppressed the foraging of prey in the middle trophic level, suggesting that warming may further enhance the top-down control of predators on communities. Prey growth efficiency, which measures the efficiency of energy transfer between trophic levels, became negative when prey were subjected to predation risk and warming. Thus, the combined effects of these stressors may represent an important tipping point for individual fitness and the efficiency of energy transfer in natural food chains. In contrast, we detected no adverse effects of warming on the top predator and the basal resources. Hence, the consequences of projected warming may be particularly challenging for intermediate consumers residing in food chains where risk dominates predator-prey interactions.

Keywords: *Carcinus maenas*, climate change, foraging, *Nucella lapillus*, predation risk, predator-prey, species interactions, temperature

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Introduction

Physiological studies examining variation in species' thermal tolerances and where organisms live relative to their thermal optima (Stillman, 2003; Pörtner & Knust, 2007; Deutsch *et al.*, 2008; Tewksbury *et al.*, 2008) have provided a valuable mechanistic basis for identifying the potential 'winners' and 'losers' in the face of continued climate change (Somero, 2010). However, because climate change is expected to significantly alter the nature and strength of species interactions (Sanford, 1999; Tyljanakis *et al.*, 2008; Gilman *et al.*, 2010; Harley, 2011), temperature studies that focus on species in isolation are not likely to reveal the full suite of climate change impacts that are possible in a multi-species context. Recent work has begun to reveal the diverse consequences of warming for interacting species and the communities they inhabit. For example, experimental warming has been shown to strengthen herbivore-plant interactions (O'Connor, 2009), increase the relative importance of top-down vs. bottom-up effects (Hoekman, 2010; Kratina *et al.*, 2012; Carr & Bruno, 2013), and

increase the strength of indirect interactions (Barton *et al.*, 2009; Marquis *et al.*, 2014) in natural food webs.

Here, we focus on the interaction between climate change and predator effects because predators frequently exert top-down control on ecosystems (Estes *et al.*, 2011) either by consuming their prey or via risk effects that induce changes in prey foraging behavior. Indeed, in many ecosystems, the effect of the 'fear' of being eaten can rival or exceed that produced by predators consuming prey (Schmitz *et al.*, 2004). Moreover, the stress that predation risk imposes on prey (Creel *et al.*, 2007; Boonstra, 2013) may be particularly sensitive to climate change because predation risk and temperature can influence the same aspects of an organism's biology such as foraging, growth and development, and metabolic rate (Cossins & Bowler, 1987; Rovero *et al.*, 1999; Sanford, 1999; Trussell & Smith, 2000; Hawlena & Schmitz, 2010a,b; Trussell & Schmitz, 2012). Mounting evidence reveals that predation risk can elevate prey metabolic rates (Rovero *et al.*, 1999; Beckerman *et al.*, 2007; Slos & Stoks, 2008), and increase the production of stress hormones (Boonstra *et al.*, 1998; Creel *et al.*, 2007, 2009), heat shock proteins (Kagawa & Mugiya, 2002; Pauwels *et al.*, 2005), and antioxidant enzymes (Slos & Stoks, 2008). These risk effects on prey physiology, and thus energy budgets, may reduce the capacity of prey to cope with the

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additional physiological stress imposed by warming, particularly if risk and warming effects are synergistic.

Globally, intertidal communities will be subject to shifting environmental temperatures both during high tide as the seas warm, and during low tide when the confluence of weather and calm seas can drive temperatures to extremes (Denny *et al.*, 2009). Hence, simultaneous changes in both ocean and air temperatures may strongly affect marine intertidal communities in complex ways. In temperate ocean systems, warming temperatures often lead to increased metabolic rates in marine organisms when temperatures remain within those species' physiological tolerance limits. Such changes in metabolic rate can drive increases in productivity rates and consumption at all trophic levels (O'Connor, 2009; O'Connor *et al.*, 2009; Carr & Bruno, 2013). For example, important rocky intertidal consumers such as seastars (Sanford, 1999, 2002; Gooding *et al.*, 2009) and carnivorous snails (Bayne & Scullard, 1978; Yamane & Gilman, 2009; Miller, 2013) increase feeding rates as water temperature rises to peak summer temperatures. However, when water temperatures continue to rise to stressful levels, or when low tide temperatures hit peak temperatures, these species often seek refuge, curtail feeding, and exhibit lower growth rates (Largen, 1967; Burrows & Hughes, 1989; Pincebourde *et al.*, 2008, 2012; Yamane & Gilman, 2009; Vaughn *et al.*, 2014).

During the summer, which is the primary growing season for rocky intertidal species in the North Atlantic, we used a novel outdoor climate change array to examine how predicted warming scenarios (Fig. 1) may modify the effects of predation risk on the foraging and performance of an intermediate consumer in a 3-level rocky shore food chain. Our experimental food chain consisted of the presence and absence of waterborne risk cues from an invasive predatory crab (the green crab, *Carcinus maenas*), an intermediate consumer (the snail, *Nucella lapillus*) that is a common prey item for *Carcinus*, and mussels (*Mytilus edulis*) serving as a basal resource for *N. lapillus*. Top-down interactions driven by risk effects from this predatory crab on snail foraging can strongly influence the organization and dynamics of rocky intertidal communities in New England, USA (Trussell *et al.*, 2002, 2003, 2006a).

We used snails from Nahant, MA, which is near the southern end of the range for *N. lapillus* in North America. Current summer temperatures, particularly during aerial emersion at low tide, may induce sublethal stress and occasionally approach the thermal limits for this species (Sandison, 1967; Etter, 1988; Leonard, 2000). If temperature projections remain within the range where sublethal stress is minimal, then one might expect snail foraging on mussels to increase to support increasing

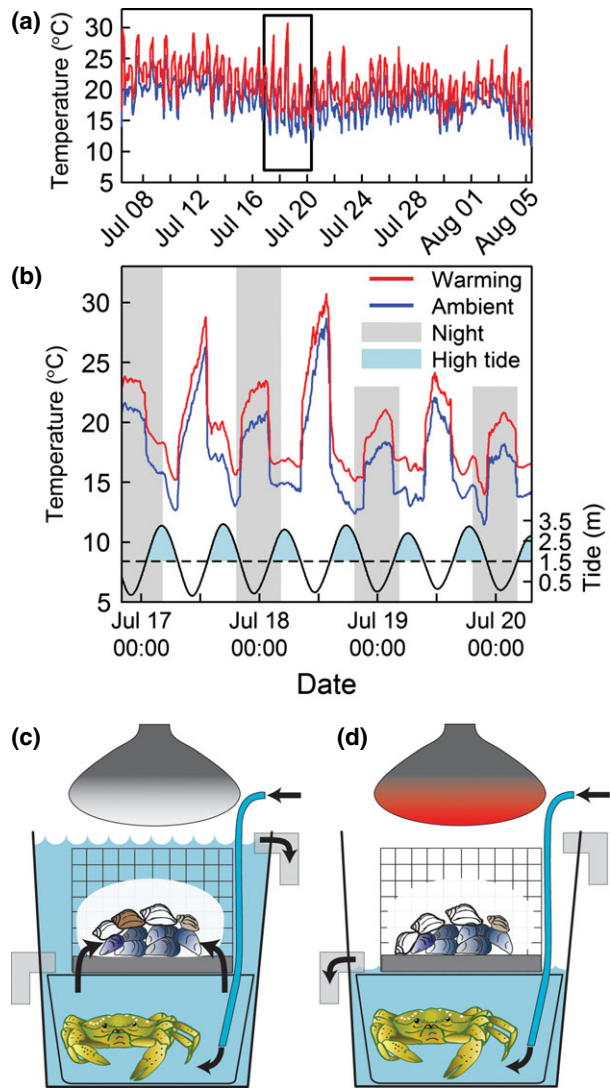


Fig. 1 Temperature records for ambient and warming mesocosms for (a) the duration of the 30-day experiment and (b) a close-up of temperatures and tide cycles for a subset of days [from the boxed region in (a)]. Ambient mesocosms were allowed to follow natural variation in air and seawater temperatures while temperatures in warming mesocosms were continuously monitored and raised to meet projected temperature increases for Nahant, MA under the IPCC Working Group III (2000) B1 emissions scenario (Meehl *et al.*, 2007). Mesocosms were flooded with ambient or warmed seawater (c) when the natural tide exceeded 1.5 m; during low tide heat lamps were used to warm the upper chamber of the mesocosm (d).

metabolic demands. However, such increases in snail foraging may not yield increased snail growth because metabolic demands can rise faster than energy intake (Rall *et al.*, 2010; Lemoine & Burkepile, 2012). In contrast, if water and air temperatures become high enough to either increase the frequency and intensity of

physiological stress or threaten survival, then one might expect decreases in snail foraging because they forgo feeding to seek refuge from high temperature. Moreover, increases in metabolic costs may cause further declines in growth as has been observed in other species (Yamane & Gilman, 2009; Vaughn *et al.*, 2014). We hypothesized that the stress imposed by risk and warming would combine additively to reduce snail performance and alter their community impacts by reducing foraging on basal resources.

Materials and methods

Mesocosms and experimental design

Our outdoor climate change array contained 64 mesocosms (plastic tubs, 2.6 l volume) and was based at Northeastern University's Marine Science Center (MSC) in Nahant, MA. Each mesocosm contained a lower crab chamber (perforated 500 ml plastic container) above which we placed a square granite tile (7.5 × 7.5 cm) that formed the base of a 7.5 × 7.5 × 7.5 cm mesh (mesh size 3 mm) cage enclosure. Water was supplied from the MSC flow-through seawater system, first to the interior crab container, and then flowed out into the main plastic tub to wash over the upper cage and out the drains (Fig. 1c, d).

We initially stocked each cage enclosure with four tagged and measured experimental snails (juvenile *Nucella lapillus*; shell length 8–14 mm) and 30 mussels (*Mytilus edulis*; shell length 9–16 mm) that served as food for the snails. In the predator cue treatments (+ Risk), we placed a single male green crab (*Carcinus maenas*; carapace width 60–90 mm) and 3 *N. lapillus* in the lower crab chamber of the mesocosm. These *N. lapillus* served as food for the crab and were replaced every 6 days. Although this approach subjected prey to risk cues for the full duration of high tides, which was the most logistically feasible approach for this experiment, we should note that previous work has shown that reduced exposure to risk cues also can produce strong responses in prey (Trussell *et al.*, 2011). For replicates of the no-predator cue treatments (–Risk) only 3 *N. lapillus*, also replaced every 6 days, were placed in the lower chamber as controls. We fully crossed these predator cue treatments (–Risk, + Risk) with the temperature warming treatment (Ambient, Warming); there were 14 replicates of each treatment combination. To evaluate natural mussel mortality rates, we included eight additional mesocosms (two per treatment combination) that were manipulated as above but contained no *N. lapillus* in the upper cage enclosure. The risk cue and warming treatments were randomly assigned among the 64 mesocosms in the array, and the experiment ran 30 days from July 5 to August 4, 2010.

A natural tidal cycle was recreated in each mesocosm by fitting two drains, one below the tile in the upper cage, and one above the top of the upper cage. The lower drain could be closed off by an electric-actuated ball valve (Aquatic Ecosystems, Apopka, FL, USA) to raise the water level in the mesocosm to simulate high tide, or opened to drain water away

from the mussel and snail enclosure, simulating low tide. The drains in each mesocosm were isolated from neighboring mesocosms by one-way valves. We created a natural tidal cycle in the mesocosms using LABVIEW software (National Instruments Corporation, Austin, TX, USA) to cycle the valves using the natural predicted tides for the nearby Boston Harbor NOAA tide gauge. Mesocosms were exposed to low tide conditions whenever the tide dropped below 1.5 m above zero tide level, with a 15-min period of high-low water level cycling at the beginning and end of each low tide period to simulate the wave-swash that accompanies the transition between tide heights in the field.

Temperature settings

The low and high tide temperature increases in the warming treatments were based on projected air temperature and sea surface temperature changes for the Nahant, MA area. Projections were based on data available as part of the World Climate Research Program's Coupled Model Intercomparison Project 3 (Meehl *et al.*, 2007). Monthly average surface air temperature and sea surface temperatures from an ensemble of ten models from the CMIP3 database were extracted for 1961–1990 as a baseline, and 2090–2099 under the IPCC SRES B1 emissions scenario (IPCC Working Group III, 2000) for the future projections. For each model in the ensemble, we extracted temperature data for the grid cell enclosing Nahant (air temperature) or adjacent to Nahant (sea surface temperature) for May through September, representing the primary growth season for *Nucella* in this region. The temperature difference between the baseline period and the end of the 21st century was calculated for each month in each model, and the results averaged across all ten models. The mean projected air temperature increase was 3.01 °C, and the mean projected sea surface temperature increase was 2.46 °C.

Temperature manipulation

The water and air temperature warming projections from the CMIP3 dataset were used as target increases for replicate mesocosms of the warming treatment in the array. During high tide, seawater from the MSC flow-through system was heated using 500 W electric submersible heaters (TSH-500, JEHM Co. Inc., Lambertville, NJ, USA) and distributed to the warming replicates. Thermistor temperature sensors (01T1002FF Vishay/Dale, Shelton, CT, USA) were used to monitor incoming ambient water temperature and outgoing warmed water temperatures, with LABVIEW software monitoring the temperature change and adjusting power to the submersible heaters as necessary. Ambient seawater temperatures within the mesocosms were within 1 °C of seawater temperatures at the field intake of the MSC seawater system.

During low tide periods, the temperature in mesocosms was monitored using thermistors mounted at the base of the upper cage containing *N. lapillus* and mussels. The mussels formed aggregations in the cages that covered the thermistors, and *N. lapillus* tended to occupy that same microhabitat as they fed on mussels within the matrix. Heated mesocosms

had a 500 W infrared lamp mounted 20 cm above the substratum. Ambient temperatures were measured concurrently in control mesocosms, and the LABVIEW software controlled power to the heat lamps to maintain the heated mesocosms at 3 °C above ambient. All temperatures were measured at 2-sec intervals to provide fine control over temperature conditions. We assume that the long-term projected average air temperature increases calculated from the CMIP3 models will be accompanied by a similar warming of substratum temperatures and organism temperatures during low tide.

To assess the realism of the low tide temperature conditions in our ambient mesocosms, we made temperature measurements of model snails in the field at the MSC. On two mid-day low tides in August and September 2010, while the mesocosm array was operating for a separate experiment, we deployed a set of eight silicone-filled *N. lapillus* shells in the intertidal zone. The model snails had a thermocouple mounted inside them, and the measured temperature was assumed to approximate live snail body temperatures (Vaughn *et al.*, 2014). The model snails were set out in three types of southeast-facing microhabitats: sun-exposed barnacle beds, underneath a *Fucus vesiculosus* algal canopy, or in shallow crevices. The model snail temperatures were measured every 5 min for 2 h during low tide, and compared to the low tide temperatures measured in the ambient mesocosms over the same time period.

Snail feeding, growth, and growth efficiency

During the course of the 30-day experiment, we counted and removed dead mussels at 6-day intervals during low tide, and replaced mussels to keep the density at 30 mussels per enclosure. In each mesocosm, we calculated the per capita number of mussels consumed by snails, M_t , during each time period, t , as $(D + N_c)/S_t$, where S_t is the mean number of snails present during time t in a given mesocosm (to account for snails that died during a 6 day interval and did not contribute to mussel consumption), D is the number of drilled, empty mussels, and N_c is the corrected (for background mortality) value of N , the number of empty, nondrilled mussels. For $N > 0$, $N_c = N - N_a$, where N_a is the mean number of empty, undrilled mussels in the autogenic control mesocosms (mesocosms without *N. lapillus*). We used mean values of N_a ($N_a = 0.625, 1.000, 0.250, 0.125, \text{ and } 0.625$ for days 6, 12, 18, 24, and 30, respectively) because we found no significant differences in background mortality among any of the treatment combinations. For $N = 0$, $N_c = 0$. The total per capita number of mussels consumed was calculated as $\sum(M_t)$. We measured the shell length of each empty mussel to estimate its tissue mass (Burrrows & Hughes, 1990) and caloric value (19.5 J mg^{-1} ; Elner & Hughes, 1978). The per capita amount of energy acquired was calculated as above, but where D , N , and N_a are the sum of energy from mussels rather than the number of mussels.

While measuring *N. lapillus* foraging was straightforward, the proximal physiological effects of predator risk cues and changing temperatures is likely complex. For example, respiration and metabolic rate of *N. lapillus* will increase with increasing temperatures (Sandison, 1967), and stressful

temperatures may be accompanied by additional energetic costs stemming from the heat shock response as demonstrated in related *Nucella* species (Dahlhoff *et al.*, 2001; Sorte & Hofmann, 2005). Although we recognize this complexity, we use growth and growth efficiency to measure the integrated outcome of the myriad physiological changes that may occur when *N. lapillus* is subjected to predation risk and temperature stress because individual fitness is ultimately determined by these long-term measures of performance.

At the beginning of the experiment, each experimental *N. lapillus* ($n = 4$ per mesocosm) was labeled with a plastic bee tag and measured nondestructively (Trussell & Smith, 2000) to obtain initial tissue mass. We measured each snail again at the end of the experiment and calculated individual wet tissue growth as final – initial wet tissue mass. Wet tissue mass was calculated by subtracting the dry shell mass from the total mass of the snail. Dry shell mass was calculated from a linear regression equation obtained by destructively sampling snails from the same source population as those in our experiment (Dry Shell Mass = $1.5455 \times \text{Submerged Mass} + 3.5055 \text{ mg}$; $R^2 = 0.9997$, $n = 50$). Mean wet tissue growth was then calculated for each replicate mesocosm. Tissue production was calculated by converting initial and final wet tissue mass into dry tissue mass using a linear regression equation obtained by destructively sampling snails from the same source population as those in our experiment (Dry Tissue Mass = $0.2874 \times \text{Wet Tissue Mass} - 2.8393 \text{ mg}$, $R^2 = 0.9816$, $n = 50$). Dry tissue growth (final-initial dry tissue mass) was converted into tissue production using a conversion factor of 22.7 J mg^{-1} (Hughes, 1972). We estimated growth efficiency for each replicate by dividing the mean *Nucella* tissue production (J) by the per capita amount of energy acquired (J). *N. lapillus* that died during the experiment were removed and excluded from our analyses. Data from mesocosms with more than two dead *N. lapillus* ($n = 4$ mesocosms in total) were discarded from all analyses. This approach left 13 replicate mesocosms in the –Risk/Warming treatment, 11 mesocosms in the + Risk/Warming, and 14 mesocosms in the + Risk/Ambient and –Risk/Ambient treatments.

Statistical analyses

All analyses were carried out in R 2.15.2 (R Development Core Team, 2012). Data on the per capita number of mussels consumed, *N. lapillus* tissue growth and *N. lapillus* growth efficiency were analyzed with separate two-way ANOVAS (Type III SS) with predator cue treatment (+ Risk, – Risk) and temperature treatment (Ambient, Warming) as fixed effects. In the case of *N. lapillus* growth, we used a generalized least-squares model with a weighted variance structure for the Risk factor to account for greater variance in the –Risk treatment (varIdent in R package nlme, Pinheiro & Bates, 2000). We calculated ω^2 and its 95% confidence limits using a noncentral F-distribution (Sokal & Rohlf, 2012) to evaluate the relative magnitude of risk and warming effects in each analysis.

To compare the effects of each treatment on different prey traits (foraging, growth, and growth efficiency), we calculated replicate estimates of the proportional reduction in each

prey trait due to the different treatment types (+ Risk/Ambient, – Risk/Warming, and + Risk/Warming) relative to the control group (– Risk/Ambient) as $\Delta_{pi} = 1 - (V_{pi}/C_p)$, where C_p is the mean value of prey trait p for the control group and V_{pi} is the value of prey trait p in replicate i of the treatment group (see Trussell *et al.*, 2008 for a similar approach). For each of the three treatment groups, we analyzed replicate estimates of Δ using a mixed-model ANOVA that included 'Prey Trait' as a fixed effect and replicate mesocosms as a random effect. To correct for potentially correlated errors among prey traits within each mesocosm, we adjusted the degrees of freedom for fixed effects tests (indicated as P_{G-G}) using Greenhouse-Geisser estimates of Box's epsilon (ϵ) when data failed to satisfy the assumption of sphericity. Values of Δ for the + Risk/Warming treatment group and its corresponding analysis were log-transformed to satisfy parametric assumptions. Pairwise comparisons among prey traits within each treatment type were examined using Tukey HSD *post hoc* tests (Fig. 3).

We isolated the effects of risk and warming on mussels (autogenic loss) from those due to snail foraging with two methods. First, in mesocosms that contained *N. lapillus*, we counted the total number of dead mussels that were not drilled and had no tissue consumed, which indicated that they had likely died due to causes other than consumption by *N. lapillus*. Because these counts were dominated by zeros, we fit a zero-inflated Poisson model to the count data with Risk and Warming as fixed factors, and used likelihood ratio tests to assess the importance of these main effects and their interaction (R package *pscl*, Zeileis *et al.*, 2008; Zuur *et al.*, 2009). To test for potential differences in the quality of mussels, we measured the shell length and dry tissue mass of live mussels in each pair of autogenic control mesocosms (those that contained no *N. lapillus*) at the conclusion of the experiment. We then fit an ANCOVA model to log-transformed tissue mass as a function of log-transformed shell length, with Risk and Warming as fixed factors, and individual mesocosms as a random, nested factor to account for the nonindependence of mussels within each mesocosm.

We tracked the number of *N. lapillus* consumed by green crabs when provided as food in the lower chambers of mesocosms, and compared the proportion of available snails that were eaten using a generalized linear model with a binomial distribution.

Results

Temperature manipulation

Temperature manipulation in mesocosms resulted in an average warming of 2.4 °C (\pm 0.45 1SD) at high tide and 3.2 °C (\pm 0.65) at low tide, compared to our target increases of 2.4 °C and 3.0 °C for high and low tide, respectively. Compared to field conditions on two sunny, mid-day low tides in August and September, our ambient mesocosms produced conditions (24.4 ± 2.6 °C, 1SD) similar to those found in mussel beds under *Fucus* algal canopies or in shallow

crevices (24.3 ± 4.5 °C), both of which were cooler than model snails placed on sun-exposed barnacles (29.1 ± 2.9 °C). The range of temperatures in the warming treatment (Fig. S1) remained well below the mortality limits for *N. lapillus* from Nahant (40 °C for 60 min, Etter, 1988) and predominantly below sublethal heat coma limits for *N. lapillus* from colder habitats in the United Kingdom (30 °C for 90 min, Sandison, 1967). Low tide temperatures inside the mussel matrix where *N. lapillus* resided exceeded 30 °C for less than one hour during the 30 day experiment, and maximum temperatures in the ambient mesocosms only exceeded 28 °C for one hour.

Impacts on prey foraging rate, tissue growth and growth efficiency

Predation risk ($F_{1,48} = 84.48$, $P < 0.0001$) and warming ($F_{1,48} = 7.69$, $P < 0.01$) significantly suppressed snail foraging (Fig. 2a) by 42% and 14% respectively, although the interaction was not significant (Table 1). The additive effects of predation risk and warming reduced *N. lapillus* foraging by 52% compared to the control conditions.

We observed significant reductions in *N. lapillus* growth (Fig. 2b) in response to predation risk ($F_{1,48} = 61.24$, $P < 0.0001$, 77% reduction) and warming ($F_{1,48} = 28.97$, $P < 0.0001$, 59% reduction), and the combined effects of risk and warming had a significant interaction ($F_{1,48} = 5.74$, $P < 0.05$) that suppressed growth by 99%, to near zero (Fig. 2b; Table 1). Growth efficiency was strongly reduced by both risk ($F_{1,48} = 45.20$, $P < 0.0001$, 60% reduction) and warming ($F_{1,48} = 34.85$, $P < 0.0001$, 53% reduction). There was no significant interaction between the stressors, but their combined effects reduced growth efficiency to below zero (Fig. 2c; Table 1).

The effect size, Δ , of warming differed significantly between foraging, growth, and growth efficiency traits ($F_{2,24} = 19.0$, $P < 0.0001$), due to much larger effects on growth and growth efficiency compared to the relatively small effect on foraging. Predation risk had significantly different effect sizes on all three traits ($F_{2,26} = 42.7$, $P < 0.0001$), while the combined effects of risk and warming ($F_{2,20} = 52.7$, $P < 0.0001$) resulted in significantly larger effect sizes for growth and growth efficiency than for foraging (Fig 3, Table 2).

Impacts on the top predator and basal resources

Green crab survivorship was high throughout the experiment. Of the crabs that died and had to be replaced, five were from ambient temperature mesocosms and two were from warmed mesocosms. We

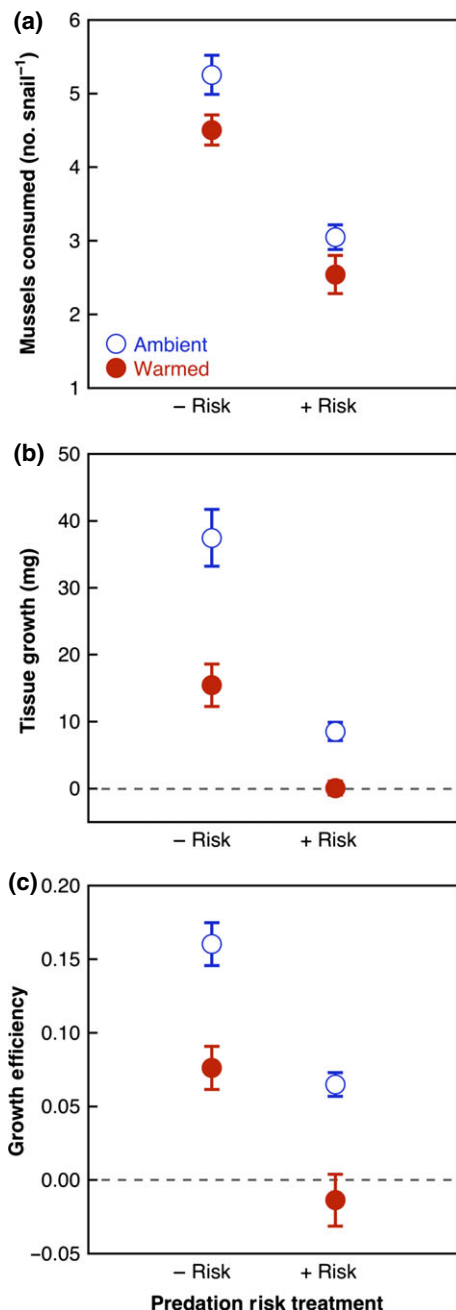


Fig. 2 The mean (\pm SE) per-capita number of mussels (*Mytilus edulis*) consumed (a), growth (b) and growth efficiency (c) for *Nucella lapillus* raised in the absence (–Risk) or presence (+ Risk) of risk cues from an invasive predatory crab (*Carcinus maenas*) under air and water temperatures that were ambient (open blue circles) or increased according to projected warming (filled red circles; see Fig. 1). For corresponding statistical analyses, see Table 1.

detected no difference in the number of *N. lapillus* consumed by crabs in the ambient and warming treatments ($X^2 = 0.03$, d.f. = 1, $P = 0.86$). Among dead

Table 1 Results of ANOVAs on *N. lapillus* (a) foraging, (b) growth, and (c) growth efficiency. Risk and Warming were fully crossed fixed effects. See corresponding Fig. 2

Response	Effect	$F_{1,48}$	P	ω^2 (95% CL's)
(a) Foraging	Risk	84.48	< 0.0001	0.76 (0.62, 0.85)
	Warming	7.69	0.008	0.21 (0.02, 0.47)
	Risk \times Warming	0.29	0.59	0.00 (0.00, 0.19)
(b) Growth	Risk	61.24	< 0.0001	0.70 (0.52, 0.81)
	Warming	28.97	< 0.0001	0.52 (0.28, 0.69)
	Risk \times Warming	5.74	0.021	0.27 (0.003, 0.43)
(c) Efficiency	Risk	45.20	< 0.0001	0.63 (0.42, 0.76)
	Warming	34.85	< 0.0001	0.57 (0.33, 0.72)
	Risk \times Warming	0.04	0.84	0.00 (0.00, 0.13)

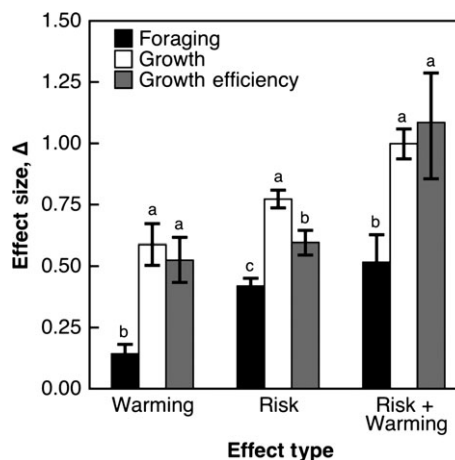


Fig. 3 The mean proportional reduction (Δ) in *N. lapillus* foraging (black bars), growth (white bars) and growth efficiency (gray bars) caused by the effects of Warming, Risk, or Risk + Warming. For each effect type, repeated measures ANOVA revealed that effect sizes (Δ) varied among prey traits and were strongest for growth and growth efficiency (see Table 2). Letters denote significant differences (Tukey HSD tests, $P < 0.05$) among prey traits within each effect type. Error bars are 95% confidence limits for warming and risk effects and back-transformed 95% confidence limits for risk + warming effects.

Table 2 Results of ANOVAs testing the effects of prey trait identity on the size of Risk, Warming, and Risk + Warming effects (Δ). The effects of Prey Trait (foraging, growth, or growth efficiency) were tested separately for each effect type, and replicate mesocosms were included in each model as a random effect. See corresponding Fig. 3

Effect Type	d.f.	F	P	P_{G-G} (ϵ)
Risk	2, 26	42.74	< 0.0001	< 0.0001 (0.595)
Warming	2, 24	19.00	< 0.0001	< 0.001 (0.526)
Risk + Warming	2, 20	52.74	< 0.0001	

mussels in the mesocosms with *N. lapillus* that were not drilled or consumed, and thus likely died via other causes, there were no significant effects of predation risk ($\chi^2 = 3.89$, d.f. = 2, $P = 0.14$), warming ($\chi^2 = 1.62$, d.f. = 2, $P = 0.45$), or their interaction ($\chi^2 = 1.01$, d.f. = 2, $P = 0.60$). In assessing mussel quality, ANCOVA revealed no significant effects of predation risk, temperature, or their interaction on either the elevations ($F_{1,4} = 0.06$, $P = 0.82$; $F_{1,4} = 0.25$, $P = 0.64$; and $F_{1,4} = 0.48$, $P = 0.53$, respectively) or slopes ($F_{1,247} = 0.02$, $P = 0.88$; $F_{1,247} = 0.11$, $P = 0.74$; and $F_{1,247} = 0.22$, $P = 0.64$, respectively) of regressions of log-transformed tissue mass vs. log-transformed shell length of live mussels in autogenic control mesocosms at the end of the experiment. Mussel tissue mass varied only with mussel shell length ($F_{1,247} = 124.85$, $P < 0.0001$), and shell length did not vary with predation risk ($F_{1,4} = 0.09$, $P = 0.79$), temperature ($F_{1,4} = 0.04$, $P = 0.85$), or their interaction ($F_{1,4} = 0.03$, $P = 0.87$).

Discussion

Marine ectotherms (Sanford, 1999; Pincebourde *et al.*, 2008; Gooding *et al.*, 2009), including *Nucella* species (Bayne & Scullard, 1978; Sanford, 2002; Yamane & Gilman, 2009), are known to increase their foraging rate under moderate temperature increases, presumably because such increases moved them to a more favorable portion of their thermal performance curve (Huey & Kingsolver, 1989; Angilletta, 2009; Monaco & Helmuth, 2011). Hence, projected warming scenarios could enhance the foraging rates of ectotherms in the middle of food chains (O'Connor, 2009) thus offsetting the positive indirect effects of predation risk on basal resources. However, although temperatures in our warming treatment were predominantly below those that cause acute trauma such as heat coma or death in *N. lapillus* (Sandison, 1967), we saw significant reductions in snail foraging under warming. Many intertidal species live near their thermal thresholds (Somero, 2002; Stillman, 2003) and this appears to be the case for our study populations from Nahant, MA, which are close to the southern limit of *Nucella*'s range in the western Atlantic. As a result, their ability to acclimate to or benefit from the temperature increases in our warming treatments may have been limited. Moreover, the effects of risk and elevated temperature were additive and together reduced snail foraging by 52%, further strengthening the positive indirect effect on mussels. This result suggests that top-down control caused by changes in prey foraging behavior may be enhanced under projected climate change scenarios (Barton *et al.*, 2009; Hoekman, 2010;

Kratina *et al.*, 2012), particularly in the many systems where risk effects play a strong role in the ecology of predator-prey interactions.

When confronted with both stressors, *N. lapillus* had negligible scope for growth during the summer season when snail growth is typically fastest. The juvenile life stages of many species grow more rapidly under slightly warmer conditions, but such rapid growth is often accompanied by maturation at smaller sizes (Atkinson, 1994; Kingsolver & Huey, 2008), which can have strong effects on population growth because of the positive relationship between body size and fitness in nearly all organisms (Peters, 1986). The reduced growth we observed under warming further suggests that our experimental *N. lapillus* populations were close to their thermal tolerance limits and therefore had limited capacity to benefit from increased temperature. Hence, to predict the consequences of climate change we must have a better understanding of where populations reside on their thermal performance curves (Stillman, 2003).

The conversion of ingested energy into trophic biomass (i.e. growth efficiency) provides a measure of both the stress experienced by an individual as well as ecosystem function in the form of energy transfer between trophic levels (Trussell *et al.*, 2006b, 2008). Predation risk and warming strongly reduced growth efficiency in our experiment (60% and 53% reductions, respectively), and their combined effects led to negative growth efficiency and no tissue production in *N. lapillus*. These reductions in growth efficiency likely explain the mismatch between foraging effects and growth effects resulting from the risk and warming treatments. For example, warming alone reduced foraging by only 14%, but snail growth in this treatment was reduced by 59%, presumably due to the increased metabolic demand created by warmer temperatures, thereby magnifying the effects of reduced foraging. Although debate continues over whether growth efficiency should decline with increasing temperature as predicted by theory (Angilletta & Dunham, 2003), the negative relationship between temperature and growth efficiency revealed by our experiment suggests that warming had strong adverse effects on individual physiology that ultimately may impact ecosystem function.

Our experiment created simultaneous increases in high and low tide temperatures that intertidal animals are predicted to experience, but this approach prevented us from partitioning the effects of warming air and water temperatures. It is likely that we observed a mixture of nonstressful metabolic rate increases and energetically costly stress effects, with the negative effects of temperature stress shifting the balance toward reduced foraging and growth. Previous research with

related *Nucella* species from the northeastern Pacific found that moderate warming of water temperatures within the normal seasonal range without warming low tide temperatures tended to increase snail foraging (Sanford, 2002) and growth rates (Yamane & Gilman, 2009), suggesting a positive effect of metabolic rate increases. Our increased water temperatures exceeded the current day summer maxima for Nahant during portions of the experiment, so it remains an open question as to whether the water temperature manipulation caused only positive rate effects. For northeastern Pacific *Nucella*, adding stressful low tide temperatures removed the positive effects of warming water temperatures, indicating that the additional energetic costs of dealing with stress at low tide could cancel out the positive rate effects of warming water (Yamane & Gilman, 2009). Although warm low tide temperatures might be expected to increase metabolic rates, there is evidence that some intertidal molluscs down-regulate metabolic rates during hot low tides (Shick *et al.*, 1988; Marshall & McQuaid, 1991; Marshall *et al.*, 2011). This response may mitigate some of the negative effects of warm temperatures at low tide, but when low tide temperatures approach the thermal tolerance limits of a species, such down-regulation typically ceases and energetically costly heat shock responses are employed (Dahlhoff *et al.*, 2001). Our combined high and low tide warming treatment, which included natural day-to-day variation in environmental conditions that occasionally pushed snails near their thermal tolerance limits, clearly had cumulative negative effects on both the behavior and physiology of *N. lapillus* despite any potential beneficial rate effects caused by experimental warming.

It is now well established that predation risk can alter aspects of prey physiology, such as metabolism, that will have substantial impacts on the energy budget available for growth (for review see Hawlena & Schmitz, 2010a). Our results provide further evidence that the combined effects of risk and warming are particularly taxing for prey. Thus the impact of projected warming may be more pronounced in food chains where risk is an important component of predator-prey interactions. It has been hypothesized that the adverse effects of predation risk on prey physiology, and thus energy transfer between trophic levels, may explain the general shortness of food chains (Trussell *et al.*, 2006b, 2008). Because of these physiological costs, the ability of prey to convert ingested resources into secondary production (i.e. growth efficiency) that is available to other trophic levels is reduced. Thus, predation risk causes 'trophic heat', which is energy loss from the system that otherwise would be available for other species to consume

(Trussell & Schmitz, 2012). As a result, trophic heat can strongly limit the important ecosystem function of energy transfer to higher trophic levels. We suggest that further inefficiencies caused by warming may exacerbate this effect with important consequences for food chain length, which can determine ecosystem productivity (Carpenter & Kitchell, 1993) and nutrient cycling and stability (DeAngelis *et al.*, 1989).

Elsewhere (Trussell & Schmitz, 2012) we have argued that that species residing in the middle of food chains may play a paramount role in community organization and ecosystem processes because they must balance the trade-off between eating and being eaten (also see Lawton & McNeill, 1979; Abrams, 1984). Indeed, predation risk exerts a strong influence on intermediate consumers in many systems (see Werner & Peacor, 2003; Schmitz *et al.*, 2004; Long & Hay, 2012) and diversity in food webs is dominated (~60% of the total species) by species occupying middle trophic levels (Williams & Martinez, 2000). Our results suggest that the additional stress imposed by warming may represent an important tipping point for prey balancing the foraging-predation risk trade-off.

In contrast, we saw no evidence that warming and risk created similar challenges for basal resources. Mussels can produce morphological defenses (thicker shells) in response to green crab risk cues (Leonard *et al.*, 1999; Freeman *et al.*, 2009), but these defenses were not accompanied by trade-offs in body mass. We did not detect risk or temperature effects on mussel quality, so differences in snail performance cannot be attributed to differences in the amount of energy available from mussels. *M. edulis* from Nahant are capable of surviving single 6 h exposures to air or water temperatures above 35 °C, and up to five consecutive days of 6 h exposures to air or water temperatures near 30 °C (Jones *et al.*, 2009; Sorte *et al.*, 2011) and it is clear that lethal limits for this species were not reached in our experiment because mussel survivorship and relative tissue mass were similar in both warmed and ambient treatments. Finally, we observed no adverse effect of warming on green crab survivorship or feeding. Green crabs exhibit substantial ability to acclimate to warming temperatures and robust tolerance to water temperatures near 35 °C (Tepolt & Somero, 2014). The broad thermal tolerance of green crabs is a common characteristic of many successful marine invaders (Sorte *et al.*, 2013), which may explain their invasion success around the globe. The contrasting responses of three trophic levels to warming in our experiment highlights the need for more research that examines whether general patterns emerge regarding the impact of warming on different trophic levels (see Voigt *et al.*, 2003; Freitas *et al.*, 2007; Gauthier *et al.*, 2013).

Our experiment allowed us to assess the impacts of risk and warming on species interactions (prey foraging rates), individual performance (growth) and ecosystem function (growth efficiency). The independent effect of warming ($\omega^2 = 0.21$) on foraging was substantially less than that of risk ($\omega^2 = 0.76$), suggesting that, relative to predation risk, warming alone may have a comparatively minor role in driving predator-prey interactions. We also found that the negative effects of risk and warming on prey are trait-dependent (Fig. 3). For example, warming and risk caused reductions in growth and growth efficiency that exceeded their respective effects on foraging rates, suggesting that prey fitness and ecosystem function may be more sensitive than foraging to the combined effects of these stressors. Thus, the trait being considered will clearly shape our predictions on the impact of climate change.

Because species interactions are fundamental to the organization and dynamics of natural communities, ecologists have recently emphasized the importance of examining how such interactions may be altered by climate change (Tylianakis *et al.*, 2008; Gilman *et al.*, 2010; Harley, 2011). Predator-prey interactions are ubiquitous in nature, and prey foraging under risk must balance the benefits of feeding with the costs of increased vulnerability to predators. Theory predicts that the calculus of feeding vs. hiding by prey can be strongly shaped by their energetic status, which can be dictated by other factors such as competition, resource availability and abiotic stress (Luttbeg *et al.*, 2003). As we have shown here, attention to the impacts of warming on the energetic status of individuals, in addition to species interaction strengths, will be essential to a more complete understanding of the impacts of climate change on natural systems.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Distributions of average temperatures in the ambient (blue) and warming (red) mesocosms.

SUPPLEMENTARY FIGURES

1

2

3 Figure S1. Distributions of average temperatures in the ambient (blue) and warming (red)

4 mesocosms.

5

6

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