

Effects of predation risk across a latitudinal temperature gradient

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Abstract The nonconsumptive effects (NCEs) of predators on prey behavior and physiology can influence the structure and function of ecological communities. However, the strength of NCEs should depend on the physiological and environmental contexts in which prey must choose between food and safety. For ectotherms, temperature effects on metabolism and foraging rates may shape these choices, thereby altering NCE strength. We examined NCEs in a rocky intertidal food chain across a latitudinal sea surface temperature gradient within the Gulf of Maine. The NCEs of green crabs (*Carcinus maenas*) on the foraging, growth, and growth efficiency of prey snails (*Nucella lapillus*) were consistent across a broad (~8.5 °C) temperature range, even though snails that were transplanted south consumed twice as many mussels (*Mytilus edulis*) and grew twice as much as snails that were transplanted north. The positive effects of warmer temperatures in the south allowed snails under high risk to perform similarly to or better than snails under low risk at cooler temperatures. Our results suggest that for prey populations residing at temperatures below their thermal optimum, the positive effects of future warming may offset the negative effects of predation risk. Such effects may be favorable to prey populations facing increased predation rates due to warmer temperatures associated with climate change. Attention to the

direct and indirect effects of temperature on species interactions should improve our ability to predict the effects of climate change on ecological communities.

Keywords Growth efficiency · Nonconsumptive effect · *Nucella lapillus* · Thermal performance · Trait-mediated interactions

Introduction

Predators often have strong effects on their prey without consuming them (i.e., the “ecology of fear”), and such nonconsumptive effects (NCEs) can influence the structure and dynamics of ecological communities (Werner and Peacor 2003; Ripple and Beschta 2004). For example, predation risk can drive trophic cascades by causing prey to reduce foraging activity or move to safer habitats (Schmitz et al. 2004). In addition, the physiological stress that predation risk imposes on prey can compound the negative effects of reduced foraging rates on prey growth and fitness (Boonstra et al. 1998; Trussell et al. 2006a; Creel et al. 2007). By causing prey to divert energy and nutrients away from growth, NCEs on prey physiology can affect important ecosystem functions such as nutrient cycling and the efficiency of energy transfer between trophic levels (Trussell et al. 2006a; Schmitz et al. 2010).

NCEs on prey and emergent indirect effects (i.e., trait-mediated indirect interactions or TMIIIs; Abrams et al. 1996) on basal resources or ecological processes arise, in part, because prey must balance conflicting demands for food and safety (Sih 1980; Werner and Anholt 1993). When predation risk is high, prey may trade energy gains from food for safety from predators by reducing their foraging activity or increasing the use of refuge habitats, but

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the cost of these behaviors is often reduced growth (i.e., the growth/predation risk trade-off). Environmental or physiological conditions that alter the relative costs and benefits of foraging likely shape how prey balance this trade-off and thus the strength of NCEs. For example, theory and empirical work suggests that the effects of predation risk may be more important in resource-rich systems (McNamara and Houston 1987; Houston et al. 1993; Luttbeg et al. 2003). In such cases, prey are able to establish greater energy reserves and lower their risk of starvation, which affords them an enhanced capacity to respond to predation risk.

For ectotherms, energetic demands and foraging rates are often dictated by the physiological effects of temperature (Cossins and Bowler 1987; Hochachka and Somero 2002). Differences in temperature can influence predator-prey interactions by altering individual metabolism and foraging rates, with strong consequences for community structure and dynamics (Pincebourde et al. 2008; O'Connor 2009; Vucic-Pestic et al. 2011; Rall et al. 2012; Dell et al. 2013). On rocky shores, for example, small decreases in sea surface temperature (~2–3 °C) due to seasonal upwelling cause keystone predatory seastars (*Pisaster ochraceus*) to reduce foraging rates on mussels (*Mytilus* spp.) by 29 % (Sanford 1999).

The positive effects of warmer temperatures on metabolism and foraging pose two challenges for prey trying to balance growth/predation risk trade-offs. First, increased activity and foraging rates of prey under warmer temperatures can make them more conspicuous to potential predators, and warmer temperatures can also enhance predator foraging rates (Lima and Dill 1990; Angilletta et al. 2003; Dell et al. 2013). Second, higher resting metabolic rates under warmer temperatures can increase the amount of energy required by prey for maintenance or survival and increase the depletion rate of energy reserves (Cossins and Bowler 1987; Hochachka and Somero 2002). Elevated energetic demands due to temperature may thus limit prey growth and the capacity of prey to trade food for safety. For example, reductions in seastar foraging rates at cooler temperatures are not accompanied by reductions in growth, presumably because reduced metabolic demands at cooler temperatures improve seastar growth efficiency (Sanford 2002a, b). Cooler temperatures may therefore reduce the growth costs associated with risk-induced reductions in foraging, while warmer temperatures may exacerbate such costs. Hence, temperature may be an important but underappreciated component of prey foraging decisions under predation risk, acting to shape the growth/predation risk trade-off and its influence on community structure.

On rocky shores of the Gulf of Maine, predatory green crabs (*Carcinus maenas*) exert strong indirect effects on ephemeral (*Ulva* spp.) and canopy-forming seaweeds (*Fucus* spp., *Ascophyllum nodosum*) and sessile

invertebrates (mussels, *Mytilus edulis*, and barnacles, *Semibalanus balanoides*) by influencing the behavior and foraging rates of herbivorous (*Littorina* spp.) and carnivorous (*Nucella lapillus*) snails, respectively (Trussell et al. 2002, 2003, 2006b). The indirect effects resulting from green crab predation risk (TMIs) can be stronger than those caused by the numerical effects of crabs eating snails (i.e., density-mediated indirect interactions, DMIs) (Trussell et al. 2006b; Matassa and Trussell 2011) and can vary with environmental factors such as wave exposure (Freeman and Hamer 2009). The cascading effects of risk in this system are likely sensitive to the large seasonal and latitudinal variation in sea surface temperatures within the Gulf of Maine. For example, laboratory studies show that the respiration, foraging, and growth rates of *Nucella* spp. increase with increasing water temperatures from ~5 to 22 °C; however, thermal stress associated with water temperatures that exceed 25 °C, or high temperatures during aerial exposure at low tide, can have the opposite effect, reducing the foraging and growth of *Nucella* spp. (Largen 1967; Stickle and Bayne 1982, 1987; Dahlhoff et al. 2001; Sanford 2002a; Yamane and Gilman 2009).

Using the natural latitudinal gradient in summer sea surface temperature within the Gulf of Maine (see Online Resource 1, Appendix A, Fig. A1 in the Electronic Supplementary Material), we examined the influence of temperature on the response of *N. lapillus* snails to green crab predation risk. We found that NCEs of the green crab on *N. lapillus* foraging, growth, and growth efficiency were consistent across a broad (~8.5 °C) range of sea surface temperatures despite two-fold variation in *N. lapillus* foraging and growth rates. Our results indicate that the effects of warmer temperatures on prey foraging and growth may alter the indirect effects of predation risk on prey populations and community structure.

Materials and methods

We examined the influence of green crab (*Carcinus maenas*) risk cues on the foraging and growth rates of Atlantic dogwhelks (*Nucella lapillus*; hereafter, “*Nucella*”) across a broad range of summer sea surface temperatures within the Gulf of Maine. *Nucella* can strongly shape the structure of rocky shore communities by consuming and limiting the abundance of species that play important roles in community succession (i.e., acorn barnacles *Semibalanus balanoides* and blue mussels *Mytilus edulis*) (Menge 1978a, b; Bertness et al. 2004). Here, we focus on the influence of green crab predation risk on the interaction between *Nucella* and *M. edulis*. We collected *Nucella* and *M. edulis* from a semi-exposed shore at a central site within the Gulf of Maine (New Harbor, ME, USA) and transplanted them

Table 1 Mean water, daily maximum, daily minimum, and overall temperatures (°C) and the number of days that the temperature exceeded 25 °C for at least 1 h at the southern (Manchester, MA), central (New Harbor, ME), and northern (Lubec, ME) field sites

	South	Central	North
Water (°C)	17.4 (2.0, 0.12)	14.4 (1.2, 0.08)	8.9 (0.4, 0.04)
Daily maximum (°C)	21.5 (2.5, 0.12)	20.1 (3.3, 0.16)	14.6 (2.1, 0.14)
Daily minimum (°C)	15.8 (1.7, 0.11)	13.0 (1.2, 0.09)	8.7 (0.5, 0.06)
Overall mean (°C)	18.1 (2.3, 0.13)	15.6 (2.4, 0.15)	10.1 (1.8, 0.18)
No. days >25 °C	4	3	0
Start date	17 June 2011	15 June 2011	14 June 2011
End date	15 July 2011	13 July 2011	12 July 2011
Latitude (°N)	42°33'47"	43°53'9"	44°49'10"
Longitude (°W)	70°46'11"	69°28'31"	66°57'36"

Standard deviations, SD, and coefficients of variation, CV, are given in parentheses (SD, CV). Exact start and end dates and geographic coordinates are given for each field site

to a warmer southern site in Massachusetts (Manchester, MA) and a cooler northern site in Maine (Lubec, ME; see Table 1 for GPS coordinates or Online Resource 1, Fig. A1 for a map of field sites). As a control, we also maintained these species at the central site in mid-coast Maine. All three field sites were within the eastern North American ranges of *M. edulis* (North Carolina to the Arctic; Bayne 1976; Jones et al. 2010), *Nucella* (Long Island Sound to Greenland; Hughes 1972), and *C. maenas* (Virginia to Newfoundland; Klassen and Locke 2007).

At each site, we exposed *Nucella* to the presence (“Crab”) or absence (“No Crab”) of green crab predation risk using modified plastic boxes that held a pair of smaller containers (see Online Resource 1, Fig. A2). The upper container was stocked with four “food” *Nucella* (replaced or replenished weekly) plus either a single male green crab or no crab to manipulate predation risk (Crab or No Crab, respectively). Green crabs (carapace width 45–60 mm) were collected from the Damariscotta River estuary, ~15 km from the central field site, and typically consumed all food *Nucella*. The lower container held four tagged and measured juvenile *Nucella* (initial shell length, mean \pm SD, 10.15 \pm 0.69 mm, $N = 240$ *Nucella*) and a supply of 120 small mussels as food (initial shell length range 8–15 mm).

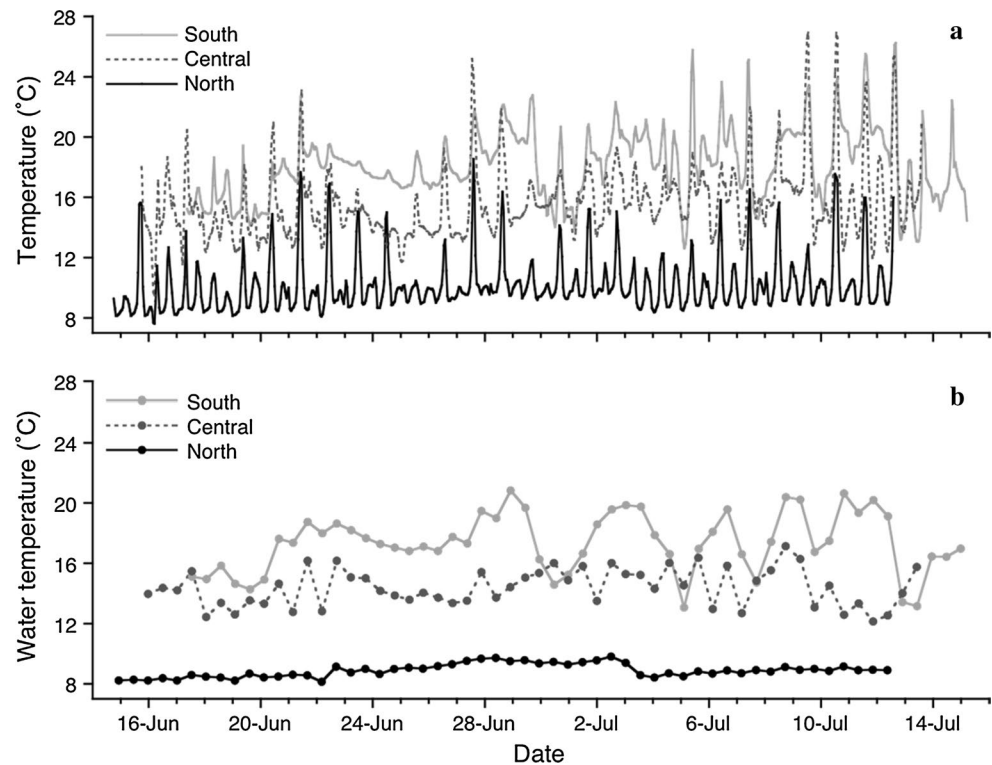
Twenty boxes (10 Crab + 10 No Crab) were deployed in wave-protected habitats at each site to avoid damage from crashing waves. Boxes were anchored in the lower intertidal zone (submerged 60–80 % of the time) adjacent to rock walls or large boulders so that they would remain covered by the rockweed (*Ascophyllum nodosum*) canopy

during low tide (Online Resource 1, Fig. A2). All boxes were separated by at least 1 m, with Crab and No Crab treatments interspersed randomly throughout the site. Temperatures were continuously monitored (every 6 min) with TidbiT v2 temperature data loggers (model UTBI-001, Onset Computer Corp.) that were placed inside 2–3 boxes at each site. We measured local water temperature as the mean of all recorded temperatures during the hour before and hour after each local high tide ($n = 54$ high tides per site). Hourly averages were used to estimate the daily maximum, daily minimum, and overall mean temperature at each site (Table 1; Fig. 1).

The experiment ran for 28 days beginning in mid-June (Table 1). We terminated the experiment at 28 days to avoid confounding effects of resource limitation on *Nucella* foraging behavior or growth. At the end of the experiment, we counted and measured the shell lengths (mm) of all consumed mussels, which were evident by the presence of a drill hole in a pair of empty valves. We used shell length (measured to the nearest 0.01 mm with digital calipers) to estimate the mass of mussel tissue consumed and energy acquired by *Nucella*. To estimate mussel tissue mass, we randomly selected three live mussels from each experimental box at the end of the experiment ($N = 177$ mussels because one replicate was lost) and measured their shell lengths. We then dried the live mussels at 60 °C to constant weight, separated shell and tissue, and measured shell and tissue mass to the nearest 0.1 mg on a digital balance. We analyzed ln-transformed dry mussel tissue mass with a two-way nested ANCOVA that considered Risk and Site as fully crossed fixed effects. Replicates were a random effect, and ln-transformed shell length was the covariate. Neither Risk nor Site had a significant effect on mussel tissue mass, and none of the interactions/slope terms were statistically significant (all $P > 0.29$). Only shell length had a significant effect on tissue mass ($P < 0.0001$). Therefore, we pooled the data to derive a single regression equation that we used to estimate dry tissue mass (mg) from the shell length (mm) of empty, consumed mussels: $\ln(\text{dry tissue mass}) = 2.388 \times \ln(\text{shell length}) - 4.010$ ($F_{1,175} = 700.1$, $P < 0.0001$, $r^2 = 0.80$). We then multiplied dry tissue mass by an energetic conversion factor of 19.5 J mg⁻¹ (Elner and Hughes 1978). The sum of energy from consumed mussels and the total number of mussels consumed in each box were each divided by the average *Nucella* density in the given box during the experiment to estimate the per capita energy acquired (J *Nucella*⁻¹) and per capita number of mussels consumed (no. mussels *Nucella*⁻¹), respectively.

Tagged *Nucella* were measured for shell and tissue mass at the beginning and end of the experiment using a non-destructive buoyant weight technique (Palmer 1982; Trussell et al. 2006a). We estimated *Nucella* tissue production (J) by converting wet tissue growth (final mass – initial mass,

Fig. 1 Mean **a** hourly temperatures (air and water, °C) and **b** high tide water temperatures (°C) at southern (*solid grey lines*), central (*dashed grey lines*), and northern (*solid black lines*) experimental sites within the Gulf of Maine (see corresponding Table 1)



mg) into dry tissue equivalents (dry tissue = $0.288 \times$ wet tissue; Matassa 2014) and multiplying by an energetic conversion factor of 22.7 J mg^{-1} (Hughes 1972). We then calculated the mean per capita tissue production (J Nucella^{-1}) and growth efficiency (per capita tissue produced/per capita energy acquired) in each replicate box. The energetic cost of shell deposition for *Nucella* spp. ranges from 1 to 2 J mg^{-1} (Palmer 1992) and is thus considerably less costly than tissue production. We therefore focus our analyses on body tissue but include a figure of shell growth data in the supplementary material (Online Resource 1, Fig. A3).

Data from replicate boxes with more than two dead tagged *Nucella* ($n = 3$ boxes in total), plus an additional box that was lost during the experiment, were excluded from all analyses. The resulting number of replicates at the southern site was 9 Crab + 9 No Crab, and there were 9 Crab + 10 No Crab at both the central and northern sites ($N = 56$). We analyzed the per capita amount of energy acquired (J Nucella^{-1}), tissue produced (J Nucella^{-1}), and growth efficiency of *Nucella* with separate two-way ANOVAs (Type III sums of squares) that included Risk (2 levels: Crab, No Crab) and Site (3 levels: South, Central, North) as fully crossed fixed effects. Our analyses of foraging rates and tissue production included weighted variance structures (REML-estimated) to account for unequal variances among sites (Zuur et al. 2009). The per capita number of mussels consumed was analyzed with a quasi-Poisson GLM (log-link function) that included the same fixed effects, which

were then tested with ANODEV F tests. For each effect, we calculated ω^2 effect sizes and 95 % confidence limits using a noncentral F -distribution according to Sokal and Rohlf (2012).

To compare risk effects across prey traits, we first estimated NCE sizes at each site as the proportional reduction in each of three prey traits (per capita energy acquired, tissue produced, and growth efficiency) due to risk using the formula $NCE_{tsr} = 1 - (Y_{tsrCrab}/Y_{tsNoCrab})$, where $Y_{tsrCrab}$ is the value of trait t in replicate r of the Crab treatment at site s , and $Y_{tsNoCrab}$ is the mean value of trait t at site s in the No Crab treatment (see Matassa and Trussell 2011 for a similar approach). We analyzed NCE sizes using a repeated-measures ANOVA that included Site as a between-subjects fixed effect and prey trait as a within-subjects fixed effect because multiple traits were measured within each replicate box. To correct for correlated errors across prey traits, we used the Greenhouse-Geisser estimate of Box's ϵ to correct the degrees of freedom when testing for the effects of prey trait and the site \times prey trait interaction (corrected P values indicated as P_{G-G}). All statistical analyses were conducted in R v3.0.2 (R Core Team 2013).

Results

Nucella foraging (mussels consumed and energy acquired, both $P < 0.0001$; Table 2a, b; Fig. 2a, b) and

Table 2 Summary of results from analyses of the per capita (a) number of mussels consumed, (b) energy acquired, and (c) tissue produced by *Nucella lapillus*, and (d) growth efficiency of *N. lapillus*

Response	Effect	df	F	P	ω^2 (95 % CLs)
(a) Mussels consumed	Site	2	70.38	<0.0001	0.788 (0.733–0.887)
	Risk	1	36.67	<0.0001	0.561 (0.429–0.788)
	Site \times risk	2	1.24	0.30	0.026 (0.000–0.544)
(b) Energy acquired	Site	2	60.40	<0.0001	0.761 (0.696–0.873)
	Risk	1	28.60	<0.0001	0.497 (0.341–0.754)
	Site \times risk	2	1.86	0.17	0.085 (0.000–0.599)
(c) Tissue produced	Site	2	22.76	<0.0001	0.539 (0.394–0.745)
	Risk	1	46.20	<0.0001	0.618 (0.510–0.818)
	Site \times risk	2	2.14	0.13	0.109 (0.000–0.619)
(d) Growth efficiency	Site	2	0.87	0.43	0.000 (0.000–0.248)
	Risk	1	29.36	<0.0001	0.504 (0.350–0.757)
	Site \times risk	2	0.01	0.99	0.000 (0.000–0.000)

Site and risk were fully crossed fixed effects. Denominator degrees of freedom = 50 for all tests. Estimates of effect sizes (ω^2) and 95 % confidence limits are given for each effect

growth ($P < 0.0001$; Table 2c; Fig. 2c) varied significantly among field sites. Compared to *Nucella* at the central site, those transplanted to the warmer site in the south consumed 53 % more mussels (LS contrast: $F_{1,50} = 55.14$, $P < 0.0001$), acquired 59 % more energy (LS contrast: $F_{1,50} = 51.13$, $P < 0.0001$), and produced 68 % more body tissue (LS contrast: $F_{1,50} = 24.18$, $P < 0.0001$). In contrast, *Nucella* transplanted to the cooler site in the north consumed 24 % fewer mussels (LS contrast: $F_{1,50} = 18.39$, $P < 0.0001$), acquired 24 % less energy (LS contrast: $F_{1,50} = 20.24$, $P < 0.0001$), and produced 17 % less tissue than those at the central site (LS contrast: $F_{1,50} = 4.02$, $P = 0.051$). The efficiency with which *Nucella* converted energy from consumed mussels into new tissue production (growth efficiency) did not vary significantly among sites ($P = 0.43$; Table 2d; Fig. 2d), indicating that differences in tissue production among sites were due to site-specific differences in energy acquisition.

At all three field sites, the presence of green crab risk cues suppressed *Nucella* foraging (both $P < 0.0001$; Table 2a, b; Fig. 2a, b), growth ($P < 0.0001$; Table 2c; Fig. 2c), and growth efficiency ($P < 0.0001$; Table 2d; Fig. 2d). For each trait, the effects of site and risk were additive (site \times risk: all $P > 0.1$; Table 2). NCE size, which estimates the proportional reduction in a given prey trait due to predation risk, did not vary among sites ($P = 0.96$; Table 3). However, the size of NCEs varied among prey traits ($P_{G-G} < 0.0001$; Table 3; Fig. 3), and trait effects did not differ among sites ($P_{G-G} = 0.72$; Table 3). NCEs caused a 24.1 ± 3.5 % (mean \pm SE) reduction in *Nucella* foraging rates (per capita energy acquired) and 26.4 ± 3.4 % reduction in growth efficiency. NCEs on tissue production (43.8 ± 3.7 % reduction) were larger than those on foraging and growth efficiency (LS contrasts: both $P_{G-G} < 0.001$; Fig. 3).

Discussion

At three locations in the Gulf of Maine, spanning ~400 km and an 8.5 °C temperature range, green crabs had strong nonconsumptive effects (NCEs) on the foraging, growth, and growth efficiency of *Nucella*. On average, predation risk reduced *Nucella* foraging rates on mussels (24–27 %) and *Nucella* growth efficiency (26 %), resulting in even stronger NCEs on *Nucella* growth (~44 % reduction in tissue production). These risk effects were similar at all sites (Fig. 3) despite twofold variation in *Nucella* foraging rates and growth rates (Fig. 2).

When transplanted south to the warmer site in Massachusetts, *Nucella* from the central Maine site acquired 2.1 times more energy from mussels and produced 2.0 times more body tissue than those transplanted to the cooler site in the north (Fig. 2b, c). Increased foraging and growth rates of southern transplants likely arose because these individuals were shifted closer to the optimal temperatures of their thermal performance curves (i.e., thermal reaction norms; Angilletta et al. 2003; Monaco and Helmuth 2011). Laboratory studies with *N. lapillus* suggest that peak foraging rates on mussels (*M. edulis*) occur within 15–23 °C (Largen 1967; Stickle et al. 1985), and water temperatures at our southern site fell within this range (Table 1; Fig. 1). In addition, estimates of Q_{10} for feeding ($Q_{10} = 2.4$) and growth ($Q_{10} = 2.2$) rates of *Nucella* at northern vs. southern sites (using mean water temperatures in Table 1) fall within the range of values for most biological processes ($Q_{10} = 2$ –3, or a 200–300 % increase per 10 °C increase in temperature) occurring below their thermal optima (Hochachka and Somero 2002).

Increased temperatures are known to increase crawling speed (Largen 1967), decrease handling and ingestion times (Miller 2013), and reduce the duration of the post-ingestion (digestive) phase of the feeding cycle (Bayne

Fig. 2 Mean **a** per capita number of mussels (*Mytilus edulis*) consumed (no. *Nucella*⁻¹), **b** per capita energy acquired (J *Nucella*⁻¹), **c** tissue produced (J *Nucella*⁻¹) by *Nucella lapillus*, and **d** growth efficiency of *N. lapillus* in the presence (Crab, filled circles) or absence (No crab, open circles) of risk cues from *Carcinus maenas* at a southern, central, and northern site within the Gulf of Maine. Error bars represent 1 SE ($n = 9$ for all Crab treatments; $n = 9, 10,$ and 10 for the No crab treatments at the southern, central, and northern sites, respectively) (see corresponding Table 2)

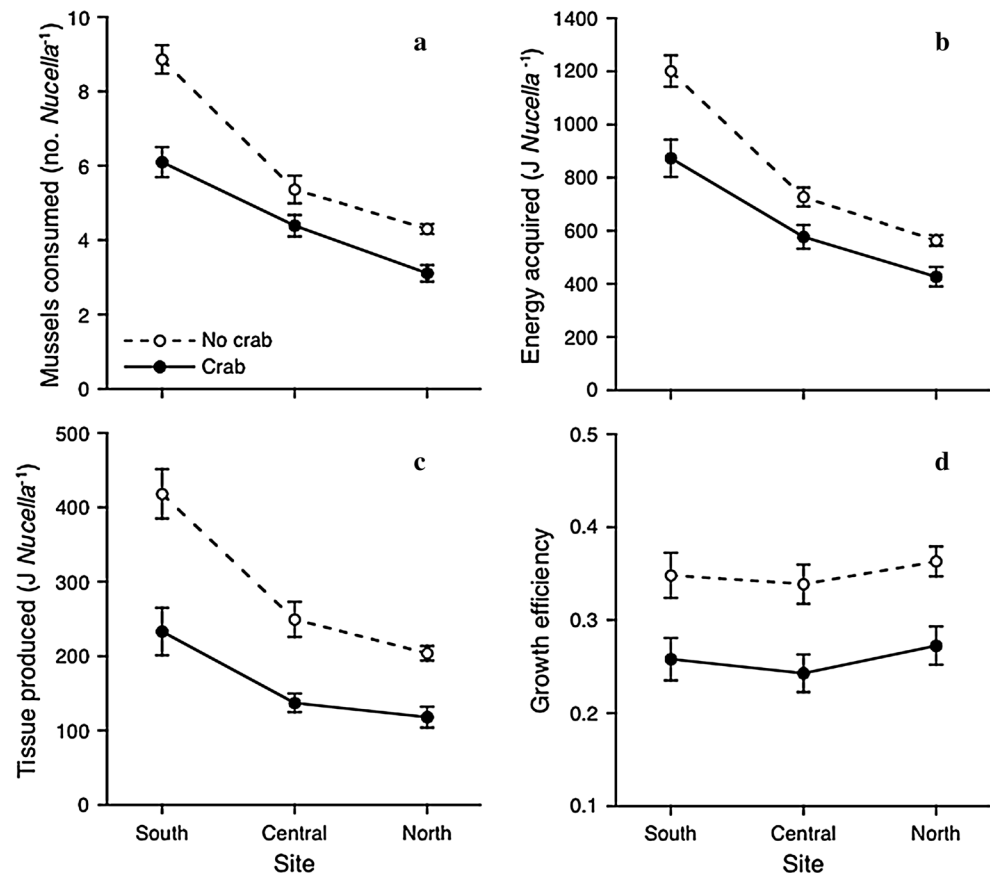


Table 3 Summary of results from repeated-measures ANOVA on the size of green crab NCEs

Effect	df_n	df_d	F	P	ϵ_{G-G}	P_{G-G}
Site	2	24	0.04	0.96		
Prey trait	2	48	20.17	<0.0001	0.59	<0.0001
Site \times prey trait	4	48	0.38	0.82	0.59	0.72

Site (between-subjects effect) and prey trait (within-subjects effect) were fixed effects. Prey trait and the site \times prey trait interaction were also tested with Greenhouse-Geisser (P_{G-G}) adjusted values of epsilon (ϵ_{G-G}) to account for lack of sphericity and possible autocorrelations among traits. Numerator and denominator degrees of freedom for each effect test are given as DF_n and DF_d , respectively

and Scullard 1978) in *Nucella*, all of which may contribute to the increase in foraging rates in our experiment. Importantly, increased crawling speed and reduced handling or ingestion times may also reduce the vulnerability of *Nucella* to predators by allowing individuals to acquire the same amount of energy in less time. This reduction in “vulnerability per Joule” may explain why *Nucella* exhibited increased foraging rates (and growth) in the south even when exposed to green crab risk cues and why we did not observe greater NCE sizes at the southern site. Alternatively, increased metabolic demands associated with warmer temperatures (Cossins and Bowler 1987) may have led to increased *Nucella* foraging rates despite predation risk in order to reduce the risk of starvation (McNamara

and Houston 1987; Werner and Anholt 1993). However, it is unlikely that *Nucella* at the southern site had a high risk of starvation given their high growth rates.

The natural change in sea surface temperature experienced by *Nucella* transplanted south (3 °C increase compared to the central site) is remarkably similar to the increase in sea surface temperature projected to occur in the western Gulf of Maine (2–4 °C) due to climate change within the twenty-first century (Frumhoff et al. 2007; Miller et al. 2014). The positive effects of warmer temperatures on *Nucella* foraging rates suggest that future climate change may increase their impact on competitively dominant mussels (*M. edulis*), with important consequences for community structure (Menge 1976, 1978b). Indeed, *Nucella*

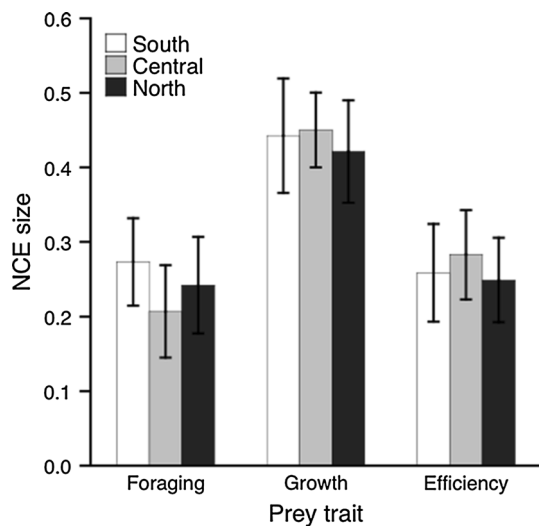


Fig. 3 Mean size of green crab NCEs on different prey traits (foraging = per capita energy acquired ($J Nucella^{-1}$), growth = tissue produced ($J Nucella^{-1}$), efficiency = growth efficiency) of *Nucella lapillus* at southern (white bars), central (grey bars), and northern (black bars) field sites within the Gulf of Maine. Error bars represent 1 SE ($n = 9$) (see corresponding Table 3)

under predation risk at warmer temperatures consumed more mussels than those foraging in the absence of risk at the cooler temperatures of the central and northern sites. Although prey foraging rates and the strength of NCEs can depend on resource density (Luttbeg et al. 2003; Bolnick and Preisser 2005; Matassa 2014), which is variable in the Gulf of Maine (Bryson et al. 2014), our results indicate that the positive effects of warmer temperatures can offset the negative effects of predation risk on prey foraging rates and thus indirect predator control of basal resource abundance.

The scenarios hypothesized above suggest that the ecological impacts of climate change will likely be influenced by the shape of a given population's thermal performance curve and how temperature changes shift the position of organisms on these curves (Somero 2002; Stillman 2003; Tewksbury et al. 2008; Matzelle et al. 2014). We observed positive effects of increased temperature on the foraging of *Nucella* from the central Gulf of Maine, suggesting that warmer temperatures in the south shifted these snails to a more favorable portion of their performance curve. However, other work in our system indicates that this is not always the case because warmer temperatures simulating IPCC projections (2000) in the southern Gulf of Maine can combine synergistically with the negative effects of predation risk on multiple *Nucella* traits. For example, Miller et al. (2014) worked with *Nucella* from populations in Nahant, MA, USA ($42^{\circ}25'00''N$, $70^{\circ}54'20''W$), which is close to the southern edge of this species' biogeographic range (Hughes 1972) and where these populations are likely approaching their thermal limits. Miller et al.

(2014) suggest that the temperature changes ($2\text{--}3^{\circ}C$) used in their study, despite being quite similar in magnitude to the natural temperature changes in our field experiment, likely pushed *Nucella* from this southern population close to their thermal limits and into a more stressful temperature range. Thus, in contrast to our study, both elevated temperature and predation risk strongly suppressed *Nucella* foraging. Hence, the effects of climate change on trait-mediated trophic cascades should depend on where prey are located along their thermal performance curves. By modifying the strength of consumer-resource interactions, warmer temperatures will likely alter the relative importance of trait- versus density-mediated indirect effects, especially when predator foraging rates and thermal tolerance are also affected by temperature (Dell et al. 2013). Although our experiment focused on the effects of temperature, the impacts of future climate change on marine predator-prey interactions may also depend on ocean acidification, which can negatively impact the calcification, growth, and survival of a wide variety of taxa and possibly interact with warming effects (Kroeker et al. 2013). For *Nucella lapillus*, experimental ocean acidification can cause shell damage and reduced shell density (Queirós et al. 2014), increasing its susceptibility to shell-crushing predators such as *C. maenas*. However, ocean acidification can also reduce the claw strength of *C. maenas* (Landes and Zimmer 2012). Hence, how the interactions among *C. maenas*, *N. lapillus*, and *M. edulis* (which does not appear to respond strongly to ocean acidification; Hiebenthal et al. 2013) will change under future climate scenarios will likely depend on species-specific responses to the combined effects of warming and ocean acidification (Kroeker et al. 2013).

At each field site, predation risk suppressed *Nucella* growth substantially more than foraging because of its strong negative effects on growth efficiency. In contrast, the effect of temperature on growth was proportional to that on foraging; thus, growth efficiency did not vary among field sites (Fig. 2d). Theory predicts that growth efficiency should decline with increasing temperature, but empirical support for a general temperature effect on ectotherm growth efficiency varies widely among species (Perrin 1995; Angilletta and Dunham 2003; Angilletta et al. 2004) and even among closely related *Nucella* species. For example, laboratory studies of Pacific congeners of *Nucella lapillus* found that the effects of warming temperatures on the foraging and growth of *N. ostrina* were similar (Yamane and Gilman 2009), but effects on foraging were stronger than those on growth for *N. canaliculata* (Sanford 2002a, b). A recent study of several rocky intertidal species suggests that increases in metabolic demands due to temperature outpace increases in foraging rates, thereby causing reduced growth efficiency (Iles 2014). Given these findings, and that higher temperatures are often stressful for intertidal organisms

(Dahlhoff et al. 2001; Hochachka and Somero 2002; Somero 2002), we were surprised that growth efficiency was similar at all our field sites. Although it is possible that thermal stress influenced *Nucella* at the southern and central site (temperatures exceeded 25 °C on a few occasions; Table 1; Fig. 1a), it is clear that the net positive effects of warmer temperatures on foraging and growth trumped any potential negative effects on growth efficiency. If growth efficiency does indeed decline with warmer temperatures as predicted by theory (Perrin 1995; Angilletta et al. 2004), then the growth efficiency we observed for *Nucella* at our southern and central site is greater than expected. A possible explanation for these results is that growth rates at the southern site were enhanced by the greater variability in water temperature (e.g., coefficient of variation = 0.12 and 0.05 for southern and northern sites, respectively) as opposed to the increase in mean water temperature (Table 1). Fluctuations in water temperature (e.g., 29 June vs. 1 July; Fig. 1b) may provide alternating periods of high foraging gains during warmer periods and reduced metabolic costs (or increased growth efficiency) during colder periods, resulting in a net positive effect on growth efficiency. For example, *Pisaster* exhibits higher conversion efficiencies at colder water temperatures (9 °C) and with simulated periodic upwelling (9–12 °C) than at constant warmer temperatures (12 °C), and growth trends suggest the same is true for *N. canaliculata* (Sanford 2002a).

Although growth efficiency did not differ between cooler and warmer field sites, predation risk consistently reduced *Nucella* growth efficiency by 26 %. The stress of predation risk can thus exacerbate the energetic consequences of reduced foraging gains and limit the amount of energy available for prey growth and reproduction. Physiological stress responses to predation risk, such as elevated metabolic rates (Rovero et al. 1999) and the expression of heat shock proteins (Pauwels et al. 2005; Slos and Stoks 2008), can divert energy away from growth. For *Nucella*, growth and fitness are tightly coupled (Burrows and Hughes 1990), and the combined effects of reduced foraging and physiological stress on growth may slow development or reduce fecundity with important population consequences. For example, chronic stress induced by predation risk fuels the declines of snowshoe hare populations during predator-prey population cycles (Boonstra et al. 1998) and may have also contributed to the positive indirect effects of wolf reintroductions in the greater Yellowstone ecosystem by reducing the reproductive success of female elk (Creel et al. 2007).

It is well established that temperature can strongly shape the strength and outcome of species interactions within intertidal communities (Menge 1978b; Bertness and Leonard 1997). Although the effects of temperature stress have received considerable attention (Menge 1978a; Burrows

and Hughes 1989; Dahlhoff et al. 2001; Pincebourde et al. 2008; Yamane and Gilman 2009), our results support a growing body of work (Sanford 1999, 2002b; O'Connor 2009; Yamane and Gilman 2009; Kordas et al. 2011; Rall et al. 2012) showing that warming temperatures within the normal, non-stressful temperature ranges experienced by organisms can enhance the strength of consumer-resource interactions in the field. For prey populations residing at temperatures below their thermal optimum, the positive effects of future warming may offset the negative effects of predation risk, weakening the positive trait-mediated indirect effects of top predators on basal resources. However, it is likely that warmer temperatures will also increase the feeding rates of prey and their predators and thus the relative importance of density-mediated indirect effects. This scenario may be especially true for invasive predators such as *Carcinus maenas*, whose invasion success appears to be enhanced by warmer water temperatures (Grosholz and Ruiz 1996; Trussell and Smith 2000; Tepolt and Somero 2014). Thus, increased attention to how temperature influences direct and indirect species interactions should improve our ability to predict the effects of climate change on the structure and dynamics of ecological communities.

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