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## Climate Change Enhances the Negative Effects of Predation Risk on an Intermediate Consumer

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

3  
4 **Running Head: Climate change and predation risk**

5  
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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.

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## INTRODUCTION

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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; Tylianakis *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 versus 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; Trussell & Schmitz, 2012; Hawlena

63 & Schmitz, 2010a,b). Mounting evidence reveals that predation risk can elevate prey metabolic  
64 rates (Rovero *et al.*, 1999; Beckerman *et al.*, 2007; Slos & Stoks, 2008), and increase the  
65 production of stress hormones (Boonstra *et al.*, 1998; Creel *et al.*, 2007, 2009), heat-shock  
66 proteins (Kagawa *et al.*, 1999; Pauwels *et al.*, 2005), and antioxidant enzymes (Slos & Stoks,  
67 2008). These risk effects on prey physiology, and thus energy budgets, may reduce the capacity  
68 of prey to cope with the additional physiological stress imposed by warming, particularly if risk  
69 and warming effects are synergistic.

70 Globally, intertidal communities will be subject to shifting environmental temperatures  
71 both during high tide as the seas warm, and during low tide when the confluence of weather and  
72 calm seas can drive temperatures to extremes (Denny *et al.*, 2009). Hence, simultaneous changes  
73 in both ocean and air temperatures may strongly affect marine intertidal communities in complex  
74 ways. In temperate ocean systems, warming temperatures often lead to increased metabolic rates  
75 in marine organisms when temperatures remain within those species' physiological tolerance  
76 limits. Such changes in metabolic rate can drive increases in productivity rates and consumption  
77 at all trophic levels (O'Connor, 2009; O'Connor *et al.*, 2009; Carr & Bruno, 2013). For example,  
78 important rocky intertidal consumers such as seastars (Sanford, 1999, 2002; Gooding *et al.*,  
79 2009) and carnivorous snails (Bayne & Scullard, 1978; Yamane & Gilman, 2009; Miller, 2013)  
80 increase feeding rates as water temperature rises to peak summer temperatures. However, when  
81 water temperatures continue to rise to stressful levels, or when low tide temperatures hit peak  
82 temperatures, these species often seek refuge, curtail feeding, and exhibit lower growth rates  
83 (Largen, 1967; Burrows & Hughes, 1989; Pincebourde *et al.*, 2008, 2012; Yamane & Gilman,  
84 2009; Vaughn *et al.*, 2014).

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

95           We used snails from Nahant, MA, which is near the southern end of the range for *N.*  
96 *lapillus* in North America. Current summer temperatures, particularly during aerial emersion at  
97 low tide, may induce sublethal stress and occasionally approach the thermal limits for this  
98 species (Sandison, 1967; Etter, 1988; Leonard, 2000). If temperature projections remain within  
99 the range where sublethal stress is minimal, then one might expect snail foraging on mussels to  
100 increase in order to support increasing metabolic demands. However, such increases in snail  
101 foraging may not yield increased snail growth because metabolic demands can rise faster than  
102 energy intake (Rall *et al.*, 2010; Lemoine & Burkepile, 2012). In contrast, if water and air  
103 temperatures become high enough to either increase the frequency and intensity of physiological  
104 stress or threaten survival, then one might expect decreases in snail foraging because they forgo  
105 feeding to seek refuge from high temperature. Moreover, increases in metabolic costs may cause  
106 further declines in growth as has been observed in other species (Yamane & Gilman, 2009;  
107 Vaughn *et al.*, 2014). We hypothesized that the stress imposed by risk and warming would

108 combine additively to reduce snail performance and alter their community impacts by reducing  
109 foraging on basal resources.

## 110 MATERIALS AND METHODS

### 111 *Mesocosms and Experimental Design*

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

119 We initially stocked each cage enclosure with four tagged and measured experimental  
120 snails (juvenile *Nucella lapillus*; shell length 8-14 mm) and 30 mussels (*Mytilus edulis*; shell  
121 length 9-16mm) that served as food for the snails. In the predator cue treatments (+ Risk), we  
122 placed a single male green crab (*Carcinus maenas*; carapace width 60-90 mm) and 3 *N. lapillus*  
123 in the lower crab chamber of the mesocosm. These *N. lapillus* served as food for the crab and  
124 were replaced every 6 days. Although this approach subjected prey to risk cues for the full  
125 duration of high tides, which was the most logistically feasible approach for this experiment, we  
126 should note that previous work has shown that reduced exposure to risk cues also can produce  
127 strong responses in prey (Trussell *et al.*, 2011). For replicates of the no-predator cue treatments (-  
128 Risk) only 3 *N. lapillus*, also replaced every 6 days, were placed in the lower chamber as  
129 controls. We fully crossed these predator cue treatments (- Risk, + Risk) with the temperature  
130 warming treatment (Ambient, Warming); there were 14 replicates of each treatment

131 combination. In order to evaluate natural mussel mortality rates, we included 8 additional  
132 mesocosms (2 per treatment combination) that were manipulated as above but contained no *N.*  
133 *lapillus* in the upper cage enclosure. The risk cue and warming treatments were randomly  
134 assigned among the 64 mesocosms in the array, and the experiment ran 30 days from July 5 to  
135 August 4, 2010.

136 A natural tidal cycle was recreated in each mesocosm by fitting two drains, one below the  
137 tile in the upper cage, and one above the top of the upper cage. The lower drain could be closed  
138 off by an electric-actuated ball valve (Aquatic Ecosystems, Apopka, Florida) to raise the water  
139 level in the mesocosm to simulate high tide, or opened to drain water away from the mussel and  
140 snail enclosure, simulating low tide. The drains in each mesocosm were isolated from  
141 neighboring mesocosms by one-way valves. We created a natural tidal cycle in the mesocosms  
142 using LabVIEW software (National Instruments Corporation, Austin, Texas) to cycle the valves  
143 using the natural predicted tides for the nearby Boston Harbor NOAA tide gauge. Mesocosms  
144 were exposed to low tide conditions whenever the tide dropped below 1.5 m above zero tide  
145 level, with a 15-minute period of high-low water level cycling at the beginning and end of each  
146 low-tide period to simulate the wave-swash that accompanies the transition between tide heights  
147 in the field.

#### 148 *Temperature settings*

149 The low and high tide temperature increases in the warming treatments were based on  
150 projected air temperature and sea surface temperature changes for the Nahant, MA area.  
151 Projections were based on data available as part of the World Climate Research Program's  
152 Coupled Model Intercomparison Project 3 (Meehl *et al.*, 2007). Monthly average surface air  
153 temperature and sea surface temperatures from an ensemble of ten models from the CMIP3



154 database were extracted for 1961-1990 as a baseline, and 2090-2099 under the IPCC SRES B1  
155 emissions scenario (IPCC, 2000) for the future projections. For each model in the ensemble, we  
156 extracted temperature data for the grid cell enclosing Nahant (air temperature) or adjacent to  
157 Nahant (sea surface temperature) for May through September, representing the primary growth  
158 season for *Nucella* in this region. The temperature difference between the baseline period and the  
159 end of the 21<sup>st</sup> century was calculated for each month in each model, and the results averaged  
160 across all ten models. The mean projected air temperature increase was 3.01 °C, and the mean  
161 projected sea surface temperature increase was 2.46 °C.

### 162 *Temperature manipulation*

163 The water and air temperature warming projections from the CMIP3 dataset were used as  
164 target increases for replicate mesocosms of the warming treatment in the array. During high tide,  
165 seawater from the MSC flow-through system was heated using 500 W electric submersible  
166 heaters (TSH-500, JEHM Co. Inc., NJ, USA) and distributed to the warming replicates.

167 Thermistor temperature sensors (01T1002FF Vishay/Dale, CT, USA) were used to monitor  
168 incoming ambient water temperature and outgoing warmed water temperatures, with LabVIEW  
169 software monitoring the temperature change and adjusting power to the submersible heaters as  
170 necessary. Ambient seawater temperatures within the mesocosms were within 1°C of seawater  
171 temperatures at the field intake of the MSC seawater system.

172 During low tide periods, the temperature in mesocosms was monitored using thermistors  
173 mounted at the base of the upper cage containing *N. lapillus* and mussels. The mussels formed  
174 aggregations in the cages that covered the thermistors, and *N. lapillus* tended to occupy that same  
175 microhabitat as they fed on mussels within the matrix. Heated mesocosms had a 500 W infrared  
176 lamp mounted 20 cm above the substratum. Ambient temperatures were measured concurrently

177 in control mesocosms, and the LabVIEW software controlled power to the heat lamps in order to  
178 maintain the heated mesocosms at 3 °C above ambient. All temperatures were measured at 2-  
179 second intervals to provide fine control over temperature conditions. We assume that the long-  
180 term projected average air temperature increases calculated from the CMIP3 models will be  
181 accompanied by a similar warming of substratum temperatures and organism temperatures  
182 during low tide.

183 To assess the realism of the low tide temperature conditions in our ambient mesocosms,  
184 we made temperature measurements of model snails in the field at the MSC. On two mid-day  
185 low tides in August and September 2010, while the mesocosm array was operating for a separate  
186 experiment, we deployed a set of 8 silicone-filled *N. lapillus* shells in the intertidal zone. The  
187 model snails had a thermocouple mounted inside them, and the measured temperature was  
188 assumed to approximate live snail body temperatures (Vaughn *et al.*, 2014). The model snails  
189 were set out in three types of southeast-facing microhabitats: sun-exposed barnacle beds,  
190 underneath a *Fucus vesiculosus* algal canopy, or in shallow crevices. The model snail  
191 temperatures were measured every 5 minutes for two hours during low tide, and compared to the  
192 low tide temperatures measured in the ambient mesocosms over the same time period.

### 193 *Snail feeding, growth, and growth efficiency*

194 During the course of the 30-day experiment, we counted and removed dead mussels at 6-  
195 day intervals during low tide, and replaced mussels to keep the density at 30 mussels per  
196 enclosure. In each mesocosm, we calculated the per capita number of mussels consumed by  
197 snails,  $M_t$ , during each time period,  $t$ , as  $(D + N_c)/S_t$  where  $S_t$  is the mean number of snails  
198 present during time  $t$  in a given mesocosm (to account for snails that died during a 6 day interval  
199 and did not contribute to mussel consumption),  $D$  is the number of drilled, empty mussels, and

200  $N_c$  is the corrected (for background mortality) value of  $N$ , the number of empty, non-drilled  
201 mussels. For  $N > 0$ ,  $N_c = N - N_a$ , where  $N_a$  is the mean number of empty, undrilled mussels in the  
202 autogenic control mesocosms (mesocosms without *N. lapillus*). We used mean values of  $N_a$  ( $N_a$   
203 = 0.625, 1.000, 0.250, 0.125, and 0.625 for days 6, 12, 18, 24, and 30, respectively) because we  
204 found no significant differences in background mortality among any of the treatment  
205 combinations. For  $N = 0$ ,  $N_c = 0$ . The total per capita number of mussels consumed was  
206 calculated as  $\sum(M_t)$ . We measured the shell length of each empty mussel to estimate its tissue  
207 mass (Burrows & Hughes, 1990) and caloric value (19.5 J mg<sup>-1</sup>; Elner & Hughes, 1978). The  
208 per capita amount of energy acquired was calculated as above, but where  $D$ ,  $N$ , and  $N_a$  are the  
209 sum of energy from mussels rather than the number of mussels.

210 While measuring *N. lapillus* foraging was straightforward, the proximal physiological  
211 effects of predator risk cues and changing temperatures is likely complex. For example,  
212 respiration and metabolic rate of *N. lapillus* will increase with increasing temperatures  
213 (Sandison, 1967), and stressful temperatures may be accompanied by additional energetic costs  
214 stemming from the heat shock response as demonstrated in related *Nucella* species (Dahlhoff *et*  
215 *al.*, 2001; Sorte & Hofmann, 2005). Although we recognize this complexity, we use growth and  
216 growth efficiency to measure the integrated outcome of the myriad physiological changes that  
217 may occur when *N. lapillus* is subjected to predation risk and temperature stress because  
218 individual fitness is ultimately determined by these long-term measures of performance.

219 At the beginning of the experiment, each experimental *N. lapillus* ( $n = 4$  per mesocosm)  
220 was labeled with a plastic bee tag and measured non-destructively (Trussell & Smith, 2000) to  
221 obtain initial tissue mass. We measured each snail again at the end of the experiment and  
222 calculated individual wet tissue growth as final - initial wet tissue mass. Wet tissue mass was

223 calculated by subtracting the dry shell mass from the total mass of the snail. Dry shell mass was  
224 calculated from a linear regression equation obtained by destructively sampling snails from the  
225 same source population as those in our experiment (Dry Shell Mass =  $1.5455 \times \text{Submerged Mass}$   
226  $+ 3.5055 \text{ mg}$ ;  $R^2 = 0.9997$ ,  $n = 50$ ). Mean wet tissue growth was then calculated for each  
227 replicate mesocosm. Tissue production was calculated by converting initial and final wet tissue  
228 mass into dry tissue mass using a linear regression equation obtained by destructively sampling  
229 snails from the same source population as those in our experiment (Dry Tissue Mass =  
230  $0.2874 \times \text{Wet Tissue Mass} - 2.8393 \text{ mg}$ ,  $R^2 = 0.9816$ ,  $n = 50$ ). Dry tissue growth (final-initial dry  
231 tissue mass) was converted into tissue production using a conversion factor of  $22.7 \text{ J mg}^{-1}$   
232 (Hughes, 1972). We estimated growth efficiency for each replicate by dividing the mean *Nucella*  
233 tissue production (J) by the per capita amount of energy acquired (J). *N. lapillus* that died during  
234 the experiment were removed and excluded from our analyses. Data from mesocosms with more  
235 than two dead *N. lapillus* ( $n = 4$  mesocosms in total) were discarded from all analyses. This  
236 approach left 13 replicate mesocosms in the - Risk/Warming treatment, 11 mesocosms in the +  
237 Risk/Warming, and 14 mesocosms in the + Risk/Ambient and - Risk/Ambient treatments.

### 238 *Statistical Analyses*

239 All analyses were carried out in R 2.15.2 (R Core Team, 2012). Data on the per capita  
240 number of mussels consumed, *N. lapillus* tissue growth and *N. lapillus* growth efficiency were  
241 analyzed with separate two-way ANOVAs (Type III SS) with predator cue treatment (+ Risk, -  
242 Risk) and temperature treatment (Ambient, Warming) as fixed effects. In the case of *N. lapillus*  
243 growth, we used a generalized least-squares model with a weighted variance structure for the  
244 Risk factor to account for greater variance in the - Risk treatment (varIdent in R package nlme,  
245 Pinheiro & Bates, 2000). We calculated  $\omega^2$  and its 95% confidence limits using a non-central F-

246 distribution (Sokal & Rohlf, 2012) to evaluate the relative magnitude of risk and warming effects  
247 in each analysis.

248 To compare the effects of each treatment on different prey traits (foraging, growth, and  
249 growth efficiency), we calculated replicate estimates of the proportional reduction in each prey  
250 trait due to the different treatment types (+ Risk/Ambient, - Risk/ Warming, and +  
251 Risk/Warming) relative to the control group (- Risk/Ambient) as  $\Delta_{pi} = 1 - (V_{pi} / C_p)$ , where  $C_p$  is  
252 the mean value of prey trait  $p$  for the control group and  $V_{pi}$  is the value of prey trait  $p$  in replicate  
253  $i$  of the treatment group (see Trussell *et al.*, 2008 for a similar approach). For each of the 3  
254 treatment groups, we analyzed replicate estimates of  $\Delta$  using a mixed-model ANOVA that  
255 included “Prey Trait” as a fixed effect and replicate mesocosms as a random effect. To correct  
256 for potentially correlated errors among prey traits within each mesocosm, we adjusted the  
257 degrees of freedom for fixed effects tests (indicated as  $P_{G-G}$ ) using Greenhouse-Geisser estimates  
258 of Box’s epsilon ( $\epsilon$ ) when data failed to satisfy the assumption of sphericity. Values of  $\Delta$  for the  
259 + Risk/Warming treatment group and its corresponding analysis were log-transformed to satisfy  
260 parametric assumptions. Pairwise comparisons among prey traits within each treatment type  
261 were examined using Tukey HSD post-hoc tests (Fig. 3).

262 We isolated the effects of risk and warming on mussels from those due to snail foraging  
263 (autogenic loss) with two methods. First, in mesocosms that contained *N. lapillus*, we counted  
264 the total number of dead mussels that were not drilled and had no tissue consumed, which  
265 indicated that they had likely died due to causes other than consumption by *N. lapillus*. Because  
266 these counts were dominated by zeros, we fit a zero-inflated Poisson model to the count data  
267 with Risk and Warming as fixed factors, and used likelihood ratio tests to assess the importance  
268 of these main effects and their interaction (R package *pscl*, Zeileis *et al.*, 2008; Zuur *et al.*,

269 2009). To test for potential differences in the quality of mussels, we measured the shell length  
270 and dry tissue mass of live mussels in each pair of autogenic control mesocosms (those that  
271 contained no *N. lapillus*) at the conclusion of the experiment. We then fit an ANCOVA model to  
272 log-transformed tissue mass as a function of log-transformed shell length, with Risk and  
273 Warming as fixed factors, and individual mesocosms as a random, nested factor to account for  
274 the non-independence of mussels within each mesocosm.

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

## 278 RESULTS

### 279 *Temperature manipulation*

280 Temperature manipulation in mesocosms resulted in an average warming of 2.4°C ( $\pm$   
281 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  
282 and 3.0°C for high and low tide, respectively. Compared to field conditions on two sunny, mid-  
283 day low tides in August and September, our ambient mesocosms produced conditions ( $24.4 \pm 2.6$   
284 °C, 1SD) similar to those found in mussel beds under *Fucus* algal canopies or in shallow crevices  
285 ( $24.3 \pm 4.5$  °C), both of which were cooler than model snails placed on sun-exposed barnacles  
286 ( $29.1 \pm 2.9$  °C). The range of temperatures in the warming treatment (Fig. S1) remained well  
287 below the mortality limits for *N. lapillus* from Nahant (40°C for 60 min, Etter, 1988) and  
288 predominantly below sublethal heat coma limits for *N. lapillus* from colder habitats in the United  
289 Kingdom (30°C for 90 min, Sandison, 1967). Low tide temperatures inside the mussel matrix  
290 where *N. lapillus* resided exceeded 30°C for less than one hour during the 30 day experiment,  
291 and maximum temperatures in the ambient mesocosms only exceeded 28°C for one hour.

292 *Impacts on prey foraging rate, tissue growth and growth efficiency*

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

297 We observed significant reductions in *N. lapillus* growth (Fig. 2b) in response to  
298 predation risk ( $F_{1,48} = 61.24, P < 0.0001, 77\%$  reduction) and warming ( $F_{1,48} = 28.97, < 0.0001,$   
299  $59\%$  reduction), and the combined effects of risk and warming had a significant interaction ( $F_{1,48}$   
300  $= 5.74, P < 0.05$ ) that suppressed growth by 99%, to near zero (Fig. 2b; Table 1). Growth  
301 efficiency was strongly reduced by both risk ( $F_{1,48} = 45.20, P < 0.0001, 60\%$  reduction) and  
302 warming ( $F_{1,48} = 34.85, P < 0.0001, 53\%$  reduction). There was no significant interaction  
303 between the stressors, but their combined effects reduced growth efficiency to below zero (Fig.  
304 2c; Table 1).

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

311 *Impacts on the top predator and basal resources*

312 Green crab survivorship was high throughout the experiment. Of the crabs that died and  
313 had to be replaced, five were from ambient temperature mesocosms and two were from warmed  
314 mesocosms. We detected no difference in the number of *N. lapillus* consumed by crabs in the

315 ambient and warming treatments ( $X^2 = 0.03$ ,  $df = 1$ ,  $P = 0.86$ ). Among dead mussels in the  
316 mesocosms with *N. lapillus* that were not drilled or consumed, and thus likely died via other  
317 causes, there were no significant effects of predation risk ( $X^2 = 3.89$ ,  $d.f. = 2$ ,  $P = 0.14$ ), warming  
318 ( $X^2 = 1.62$ ,  $d.f. = 2$ ,  $P = 0.45$ ), or their interaction ( $X^2 = 1.01$ ,  $d.f. = 2$ ,  $P = 0.60$ ). In assessing  
319 mussel quality, ANCOVA revealed no significant effects of predation risk, temperature, or their  
320 interaction on either the elevations ( $F_{1,4} = 0.06$ ,  $P = 0.82$ ;  $F_{1,4} = 0.25$ ,  $P = 0.64$ ; and  $F_{1,4} = 0.48$ ,  $P$   
321  $= 0.53$ , respectively) or slopes ( $F_{1,247} = 0.02$ ,  $P = 0.88$ ;  $F_{1,247} = 0.11$ ,  $P = 0.74$ ; and  $F_{1,247} = 0.22$ ,  
322  $P = 0.64$ , respectively) of regressions of log-transformed tissue mass vs. log-transformed shell  
323 length of live mussels in autogenic control mesocosms at the end of the experiment. Mussel  
324 tissue mass varied only with mussel shell length ( $F_{1,247} = 124.85$ ,  $P < 0.0001$ ), and shell length  
325 did not vary with predation risk ( $F_{1,4} = 0.09$ ,  $P = 0.79$ ), temperature ( $F_{1,4} = 0.04$ ,  $P = 0.85$ ), or  
326 their interaction ( $F_{1,4} = 0.03$ ,  $P = 0.87$ ).

## 327 DISCUSSION

328 Marine ectotherms (Sanford, 1999; Pincebourde *et al.*, 2008; Gooding *et al.*, 2009),  
329 including *Nucella* species (Bayne & Scullard, 1978; Sanford, 2002; Yamane & Gilman, 2009),  
330 are known to increase their foraging rate under moderate temperature increases, presumably  
331 because such increases moved them to a more favorable portion of their thermal performance  
332 curve (Huey & Kingsolver, 1989; Angilleta, 2009; Monaco & Helmuth, 2011). Hence, projected  
333 warming scenarios could enhance the foraging rates of ectotherms in the middle of food chains  
334 (O'Connor, 2009) thus offsetting the positive indirect effects of predation risk on basal resources.  
335 However, although temperatures in our warming treatment were predominantly below those that  
336 cause acute trauma such as heat coma or death in *N. lapillus* (Sandison, 1967), we saw  
337 significant reductions in snail foraging under warming. Many intertidal species live near their



338 thermal thresholds (Somero, 2002; Stillman, 2003) and this appears to be the case for our study  
339 populations from Nahant, MA, which are close to the southern limit of *Nucella*'s range in the  
340 western Atlantic. As a result, their ability to acclimate to or benefit from the temperature  
341 increases in our warming treatments may have been limited. Moreover, the effects of risk and  
342 elevated temperature were additive and together reduced snail foraging by 52%, further  
343 strengthening the positive indirect effect on mussels. This result suggests that top down control  
344 caused by changes in prey foraging behavior may be enhanced under projected climate change  
345 scenarios (Barton *et al.*, 2009; Hoekman, 2010; Kratina *et al.*, 2012), particularly in the many  
346 systems where risk effects play a strong role in the ecology of predator-prey interactions.

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

357         The conversion of ingested energy into trophic biomass (i.e., growth efficiency) provides  
358 a measure of both the stress experienced by an individual as well as ecosystem function in the  
359 form of energy transfer between trophic levels (Trussell *et al.*, 2006b, 2008). Predation risk and  
360 warming strongly reduced growth efficiency in our experiment (60% and 53% reductions,

361 respectively), and their combined effects led to negative growth efficiency and no tissue  
362 production in *N. lapillus*. These reductions in growth efficiency likely explain the mismatch  
363 between foraging effects and growth effects resulting from the risk and warming treatments.  
364 Warming alone reduced foraging by only 14%, but snail growth in those treatments was reduced  
365 by 59%, presumably due to increased metabolic demand created by warming temperatures  
366 thereby magnifying the effects of reduced foraging. Although debate continues over whether  
367 growth efficiency should decline with increasing temperature as predicted by theory (Angilletta  
368 & Dunham, 2003), the negative relationship between temperature and growth efficiency revealed  
369 by our experiment suggests that warming had strong adverse effects on individual physiology  
370 that ultimately may impact ecosystem function.

371         Our experiment created simultaneous increases in high and low tide temperatures that  
372 intertidal animals are predicted to experience, but this approach prevented us from partitioning  
373 the effects of warming air and water temperatures. It is likely that we observed a mixture of non-  
374 stressful metabolic rate increases and energetically costly stress effects, with the negative effects  
375 of temperature stress shifting the balance towards reduced foraging and growth. Previous work  
376 with related *Nucella* species from the northeastern Pacific found that moderate warming of water  
377 temperatures within the normal seasonal range without warming low tide temperatures tended to  
378 increase snail foraging (Sanford, 2002) and growth rates (Yamane & Gilman, 2009), suggesting  
379 a positive effect of metabolic rate increases. Our increased water temperatures exceeded the  
380 current day summer maxima for Nahant during portions of the experiment, so it remains an open  
381 question as to whether the water temperature manipulation caused only positive rate effects. For  
382 northeastern Pacific *Nucella*, adding stressful low tide temperatures removed the positive effects  
383 of warming water temperatures, indicating that the additional energetic costs of dealing with

384 stress at low tide could cancel out the positive rate effects of warming water (Yamane & Gilman,  
385 2009). Although warm low tide temperatures might be expected to increase metabolic rates,  
386 there is evidence that some intertidal molluscs down-regulate metabolic rates during hot low  
387 tides (Shick *et al.*, 1988; Marshall & McQuaid, 1991; Marshall *et al.*, 2011). This response may  
388 mitigate some of the negative effects of warm temperatures at low tide, but when low tide  
389 temperatures approach the thermal tolerance limits of a species, such down-regulation typically  
390 ceases and energetically costly heat shock responses are employed (Dahlhoff *et al.*, 2001). Our  
391 combined high and low tide warming treatment, which included natural day-to-day variation in  
392 environmental conditions that occasionally pushed snails near their thermal tolerance limits,  
393 clearly had cumulative negative effects on both the behavior and physiology of *N. lapillus*  
394 despite any potential beneficial rate effects caused by experimental warming.

395         It is now well established that predation risk can alter aspects of prey physiology, such as  
396 metabolism, that will have substantial impacts on the energy budget available for growth (for  
397 review see Hawlena & Schmitz, 2010a). Our results provide further evidence that the combined  
398 effects of risk and warming are particularly taxing for prey. Thus the impact of projected  
399 warming may be more pronounced in food chains where risk is an important component of  
400 predator-prey interactions. It has been hypothesized that the adverse effects of predation risk on  
401 prey physiology, and thus energy transfer between trophic levels, may explain the general  
402 shortness of food chains (Trussell *et al.*, 2006b, 2008). Because of these physiological costs, the  
403 ability of prey to convert ingested resources into secondary production (i.e., growth efficiency)  
404 that is available to other trophic levels is reduced. Thus, predation risk causes “trophic heat”,  
405 which is energy loss from the system that otherwise would be available for other species to  
406 consume (Trussell & Schmitz, 2012). As a result, trophic heat can strongly limit the important

407 ecosystem function of energy transfer to higher trophic levels. We suggest that further  
408 inefficiencies caused by warming may exacerbate this effect with important consequences for  
409 food chain length, which can determine ecosystem productivity (Carpenter & Kitchell, 1993) and  
410 nutrient cycling and stability (DeAngelis *et al.*, 1989).

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

420         In contrast, we saw no evidence that warming and risk created similar challenges for  
421 basal resources. Mussels can produce morphological defenses (thicker shells) in response to  
422 green crab risk cues (Leonard *et al.*, 2000; Freeman *et al.*, 2009), but these defenses were not  
423 accompanied by trade-offs in body mass. We did not detect risk or temperature effects on mussel  
424 quality, so differences in snail performance cannot be attributed to differences in the amount of  
425 energy available from mussels. *M. edulis* from Nahant are capable of surviving single 6 h  
426 exposures to air or water temperatures above 35°C, and up to 5 consecutive days of 6 h  
427 exposures to air or water temperatures near 30°C (Jones *et al.* 2009; Sorte *et al.* 2011) and it is  
428 clear that lethal limits for this species were not reached in our experiment because mussel  
429 survivorship and relative tissue mass were similar in both warmed and ambient treatments.

430 Finally, we observed no adverse effect of warming on green crab survivorship or feeding. Green  
431 crabs exhibit substantial ability to acclimate to warming temperatures and robust tolerance to  
432 water temperatures near 35°C (Tepolt & Somero, 2014). The broad thermal tolerance of green  
433 crabs is a common characteristic of many successful marine invaders (Sorte *et al.*, 2013), which  
434 may explain their invasion success around the globe. The contrasting responses of three trophic  
435 levels to warming in our experiment highlights the need for more research that examines whether  
436 general patterns emerge regarding the impact of warming on different trophic levels (see Voigt *et*  
437 *al.*, 2003; Freitas *et al.*, 2007; Gauthier *et al.*, 2013).

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

448 Because species interactions are fundamental to the organization and dynamics of natural  
449 communities, ecologists have recently emphasized the importance of examining how such  
450 interactions may be altered by climate change (Tylianakis *et al.*, 2008; Gilman *et al.*, 2010;  
451 Harley, 2011). Predator-prey interactions are ubiquitous in nature, and prey foraging under risk  
452 must balance the benefits of feeding with the costs of increased vulnerability to predators.

453 Theory predicts that the calculus of feeding versus hiding by prey can be strongly shaped by their  
454 energetic status, which can be dictated by other factors such as competition, resource availability  
455 and abiotic stress (Luttbeg *et al.*, 2003). As we have shown here, attention to the impacts of  
456 warming on the energetic status of individuals, in addition to species interaction strengths, will  
457 be essential to a more complete understanding of the impacts of climate change on natural  
458 systems.

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### **Supporting Information Legends**

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

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

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690	<b>Response</b>	<b>Effect</b>	$F_{1,48}$	$P$	$\omega^2$ (95% CL's)
691	(a) Foraging	Risk	84.48	< 0.0001	0.76 (0.62, 0.85)
692		Warming	7.69	0.008	0.21 (0.02, 0.47)
693		Risk X Warming	0.29	0.59	0.00 (0.00, 0.19)
694					
695	(b) Growth	Risk	61.24	< 0.0001	0.70 (0.52, 0.81)
696		Warming	28.97	< 0.0001	0.52 (0.28, 0.69)
697		Risk X Warming	5.74	0.021	0.27 (0.003, 0.43)
698					
699	(c) Efficiency	Risk	45.20	< 0.0001	0.63 (0.42, 0.76)
700		Warming	34.85	< 0.0001	0.57 (0.33, 0.72)
		Risk X Warming	0.04	0.84	0.00 (0.00, 0.13)

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

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<b>Effect Type</b>	<b><i>df</i></b>	<b><i>F</i></b>	<b><i>P</i></b>	<b><i>P<sub>G-G</sub></i> (<math>\epsilon</math>)</b>
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	

709

**FIGURE LEGENDS**

710 Figure 1. Temperature records for ambient and warming mesocosms for **(a)** the duration of the  
711 30-day experiment and **(b)** a close-up of temperatures and tide cycles for a subset of days (from  
712 the boxed region in **(a)**). Ambient mesocosms were allowed to follow natural variation in air and  
713 seawater temperatures while temperatures in warming mesocosms were continuously monitored  
714 and raised to meet projected temperature increases for Nahant, MA under the IPCC (2000) B1  
715 emissions scenario (Meehl et al. 2007). Mesocosms were flooded with ambient or warmed  
716 seawater **(c)** when the natural tide exceeded 1.5 m; during low tide heat lamps were used to  
717 warm the upper chamber of the mesocosm **(d)**.

718

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

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725 Figure 3. The mean proportional reduction ( $\Delta$ ) in *N. lapillus* foraging (black bars), growth  
726 (white bars) and growth efficiency (gray bars) caused by the effects of Warming, Risk, or Risk +  
727 Warming. For each effect type, repeated measures ANOVA revealed that effect sizes ( $\Delta$ ) varied  
728 among prey traits and were strongest for growth and growth efficiency (see Table 2). Letters  
729 denote significant differences (Tukey HSD tests,  $P < 0.05$ ) among prey traits within each effect  
730 type. Error bars are 95% confidence limits for warming and risk effects and back-transformed  
731 95% confidence limits for risk + warming effects.

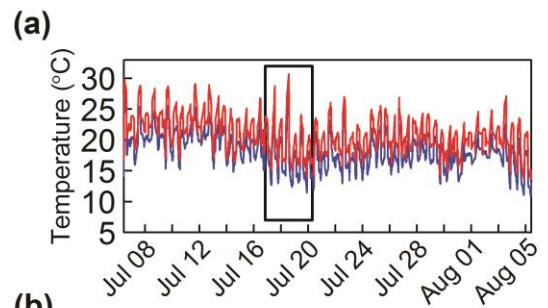
732 Figure 1.

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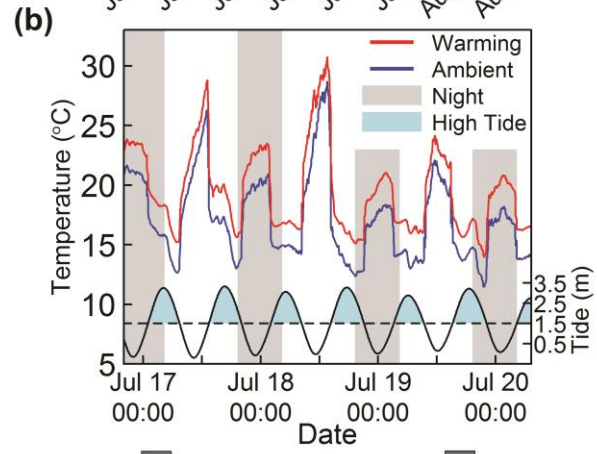
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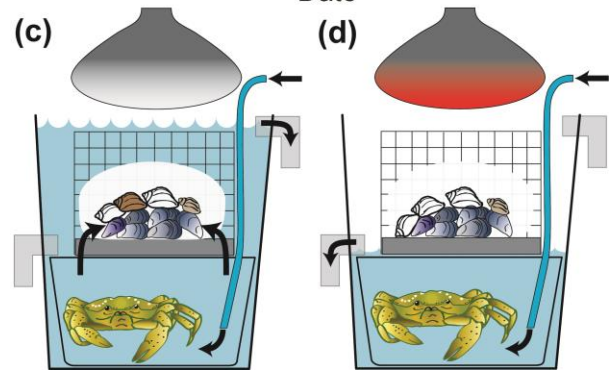
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755 Figure 2.

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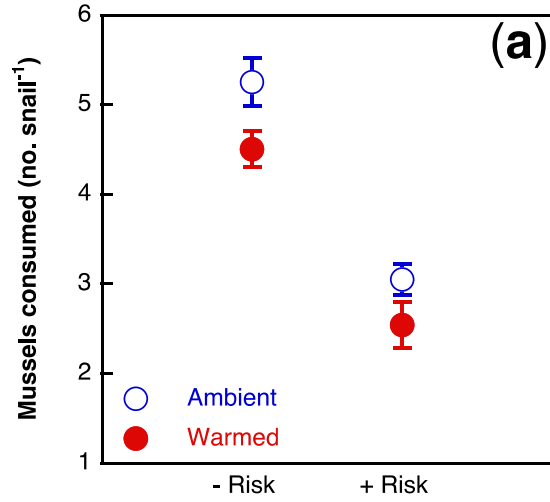
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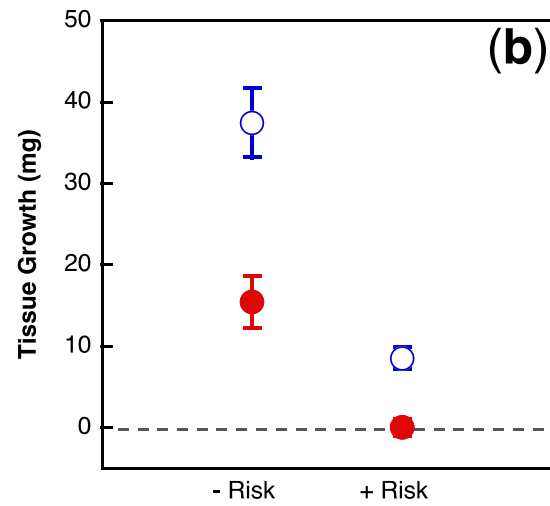
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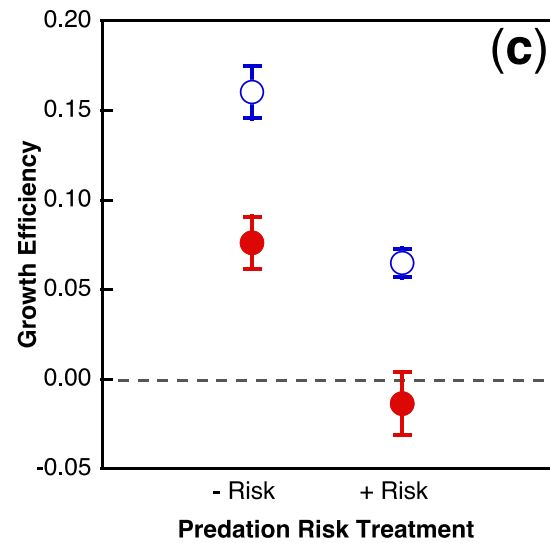
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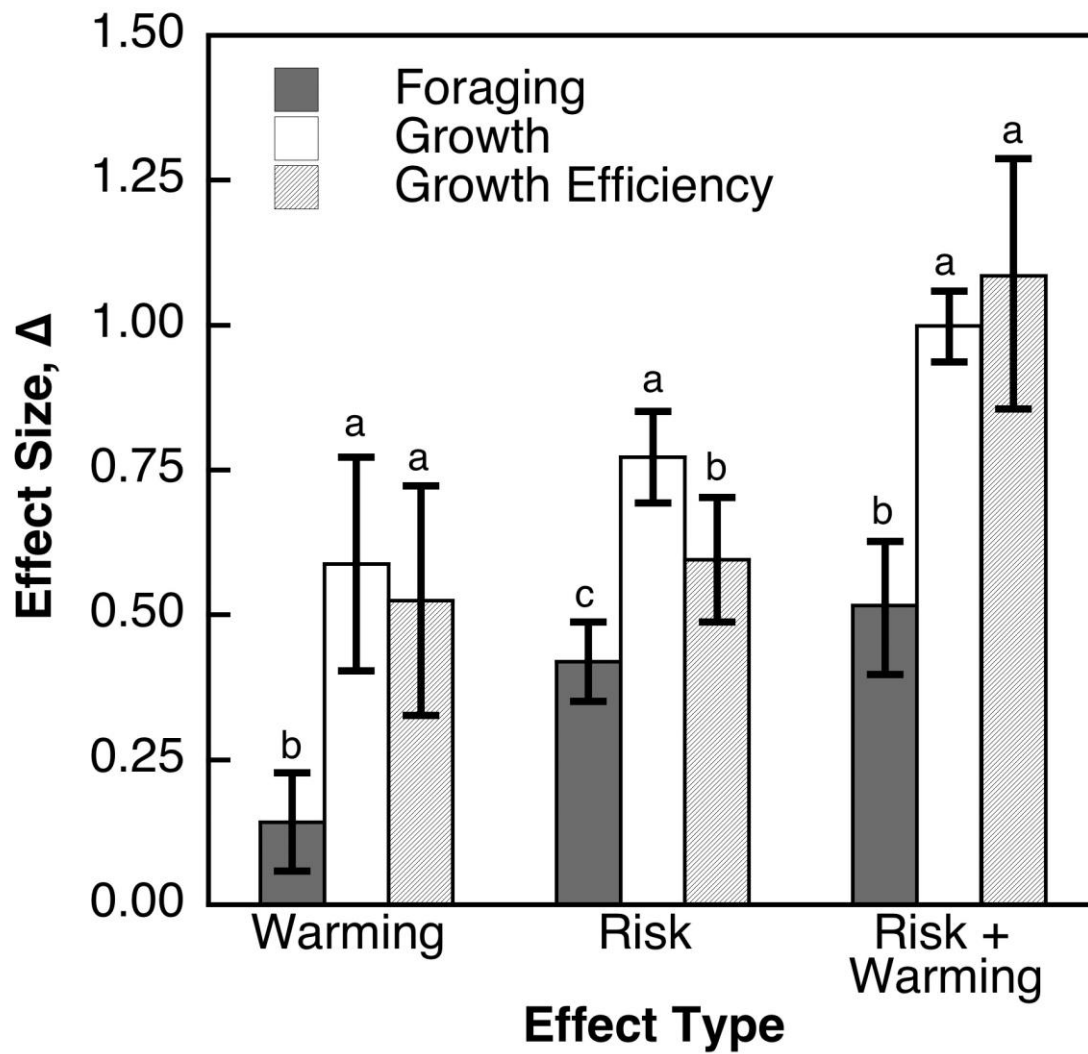
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778 Figure 3.



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## SUPPLEMENTARY FIGURES

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

803 mesocosms.

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