

## Temperature-induced mismatches between consumption and metabolism reduce consumer fitness

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**Abstract.** As physiological processes of ectotherms are coupled to environmental temperature, climate change will likely alter their fundamental biological rates, including metabolism, consumption, growth, and reproduction. Here we combine the metabolic theory of ecology (MTE) with metabolism and consumption measurements of a model organism, the urchin *Lytechinus variegatus*, to test how climate change will affect consumer fitness. Unexpectedly, we found that metabolism and consumption exhibit different scaling relationships with temperature and are mismatched at high temperatures. This led to a dramatic reduction in ingestion efficiency and potentially in consumer fitness. Using meta-analysis, we showed that such temperature-driven mismatches between consumption and metabolism are common across taxa and frequently lead to reduced consumer fitness. Our empirical and synthetic analyses identify a mechanism by which climate change reduces the fitness of ectotherm consumers that may be applied to a broad array of taxonomic groups. Moreover, we showed that the assumptions of MTE do not hold at temperatures near the upper range of species' thermal tolerances for a wide array of taxa. Models using MTE to predict the effects of climate change on consumer–resource dynamics may therefore be underestimating the consequences of rising temperatures on population and community dynamics.

**Key words:** *ecophysiology; fitness; growth; ingestion; reproduction; temperature; thermal response curve.*

### INTRODUCTION

Increases in metabolism at high temperatures may have profound effects on all levels of the biological hierarchy (Gillooly et al. 2001, Brown et al. 2004). For example, increased metabolic rate can increase resource uptake by primary producers (Enquist et al. 2003) and consumption by species at higher trophic levels (Rall et al. 2010). Such changes may be responsible for restructuring competitive dominance hierarchies and increasing predation rates at moderate levels of warming (de Valpine and Harte 2001, Rall et al. 2010). Therefore, predicting how temperature-driven changes in physiology influence population dynamics and community structure is key to understanding the impacts of climate change.

The metabolic theory of ecology (MTE; Brown et al. 2004) proposes that metabolic rates are constrained by thermodynamics and exhibit Arrhenius relationships with temperature, resulting in an exponential increase in metabolic rate with temperature (Gillooly et al. 2001).

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There is good evidence that metabolic rates increase exponentially with temperature within a species, supporting MTE (Gillooly et al. 2001, Clarke 2004). MTE further predicts that metabolic demand drives other vital biological rates, such as consumption, growth, and reproduction and that temperature scaling of these biological rates should match that of metabolism (Brown et al. 2004). Accordingly, MTE is a promising avenue for incorporating temperature dependence in dynamic population models to predict the effects of climate change (Vassuer and McCann 2005, O'Connor et al. 2011).

However, equivalent scaling of metabolic rates and other vital biological rates used in these population models lacks empirical support (O'Connor et al. 2007), suggesting that these models may not be sufficient for predicting population responses to climate change. For example, simultaneous measurements of metabolism and consumption along temperature gradients have shown a mismatch between the temperature scaling of metabolism and consumption. Metabolism frequently increases more quickly with temperature than does consumption (Rall et al. 2010). Such temperature-driven

mismatches may reduce ingestion efficiency, defined as the amount of carbon assimilated per unit of carbon respired (Vassuer and McCann 2005). Reduced ingestion efficiencies may decrease individual fitness, as there is less energy available for growth and reproduction after basic cell maintenance costs have been considered. Thus, mismatches of metabolism and consumption at high temperatures suggest that climate change can decrease consumer fitness and lead to unstable population dynamics and possible consumer extinction (Vassuer and McCann 2005). By using published studies based on interspecific comparisons of metabolism and consumption, Vassuer and McCann (2005) concluded that consumption usually increases more rapidly than metabolism, thus unstable population dynamics are rare under climate change scenarios. However, if metabolism increases faster than consumption, as intraspecific patterns suggest, the likelihood of consumer extinction under climate change increases substantially.

Here, we evaluated the effects of temperature on the performance of a common marine herbivore, the sea urchin *Lytechinus variegatus*. We asked three specific questions: (1) How does metabolism scale with temperature? (2) Does consumption scale with temperature in the same manner as metabolism? and (3) Does temperature affect the ingestion efficiency of *L. variegatus*? We also used meta-analysis to address two additional questions: (4) Are mismatches between metabolism and consumption common across taxa? and (5) What are the fitness consequences of such mismatches? In testing basic assumptions of MTE, we provide a mechanism for declines in fitness at high temperatures across a range of species.

#### METHODS

*Lytechinus variegatus* is an herbivorous urchin found in seagrass beds throughout the Caribbean and Gulf of Mexico and can exert strong top-down control on seagrass biomass (Valentine et al. 2000). Thus, *L. variegatus* is an important study organism regarding herbivory research in marine systems (e.g., Prado and Heck 2011). Moreover, the physiology of tropical and subtropical species such as *L. variegatus* will likely be most affected by climate change (Dillon et al. 2010). Individuals were collected from Virginia Key, Florida, USA (25.736° N, 80.156° W) from June through August 2011 and held in a flow-through tank at ambient temperatures ( $26.7^{\circ} \pm 1.1^{\circ}\text{C}$  [mean  $\pm$  SE]). Wet masses of urchins used in this study ranged from 30.59–256.46 g. Urchins were provided fresh *Thalassia testudinum* seagrass, their preferred food source, ad libitum.

For our metabolism measurements, one randomly chosen urchin was placed into each of five independent, recirculating seawater baths held at 26°C. Temperatures were adjusted to 20°, 23°, 26°, 29°, or 31°C gradually over 24 hours (<1°C change per hour), and respiration

measured following Siikavuopio et al. (2008) (Appendix B). These temperatures were within the range of temperatures normally experienced by *L. variegatus* (Appendix A: Fig. A1). The upper limit of temperatures at our collection site is 31°C and this temperature will likely become more frequent under current climate change projections. All temperatures were run simultaneously, with one replicate of each temperature run per day for five days ( $n = 5$  replicates per temperature). Preliminary experiments showed that 24 hours allowed for sufficient metabolic adjustment (Appendix A: Fig. A2).

To measure consumption rates across the temperature gradient, urchins were randomly assigned to 1.6-L closed feeding arenas that were placed into water baths held at 26°C and were assigned the same temperatures used in the metabolism trials ( $n = 12$  trials per temperature). Three replicates of each temperature were run per day. Grazing rates did not differ among days for each temperature, so data were pooled across days for analysis. Urchins were starved for 24 hours while acclimating to the new temperatures (Prado and Heck 2011). Fresh *T. testudinum* was blotted dry then weighed to obtain a pre-assay wet mass. Urchins were fed  $2.00 \pm 0.10$  g. After 24 hours, any remaining seagrass was removed, blotted dry, and reweighed to get a post-assay wet mass. Consumption was estimated as the difference between pre-mass and post-mass. We excluded observations where <5% of seagrass mass was consumed. *T. testudinum* wet masses were converted to dry masses using linear regression (dry mass =  $0.228[\text{wet mass}]$ ;  $P < 0.001$ ,  $R^2 = 0.998$ ). Dry masses were converted to mg carbon consumed using estimates of carbon content in *T. testudinum* as 40% of dry mass (Prado and Heck 2011).

We measured the assimilation efficiency of *L. variegatus* at the same temperatures used in the respiration and consumption assays. Randomly chosen urchins were placed in feeding arenas held at ambient seawater temperatures and starved for five days, clearing the digestive tract of all fecal material (e.g., Prado and Heck 2011). Experimental arenas were then placed in water baths randomly assigned one of the five temperature treatments listed above ( $n = 3$  baths per temperature). Seagrass consumption was estimated as described. Fecal material was siphoned from each feeding arena daily for five days after the feeding assay and dried to a constant mass at 60°C. Assimilation efficiency was estimated as  $1 - (\text{fecal mass}/\text{consumption})$  (Watts et al. 2011). Decreasing values indicate lower assimilation efficiency of food for maintenance, growth, or reproduction. Consumption was converted to mg C as described in the previous paragraph.

Ingestion efficiency ( $I$ ) is a unitless metric that provides an estimate of the excess carbon available after cellular maintenance costs have been considered. When  $I > 1$ , excess carbon is available for growth and

reproduction; when  $I < 1$ , consumption is insufficient to meet metabolic demand. We calculated the predicted metabolic rate,  $R$ , of each urchin used in the consumption trials as  $R = 1.61 \times 10^6 \exp(0.46)^{-1/kT} M^{0.33}$  (see *Results*). We then estimated ingestion efficiency as  $I = wC/\lambda R$ , where  $w$  is assimilation efficiency (0.70, see *Results*),  $C$  is mg C consumed in 24 hours,  $R$  is mg C respired in 24 hours, and  $\lambda$  is a scaling coefficient relating basal metabolic rate (i.e., metabolic rate of inactive, fasting animals) to field metabolic rate (i.e., average metabolic rate in natural conditions) (Rall et al. 2010). Savage et al. (2004) determined that field metabolic rates are approximately three times higher than basal metabolic rates ( $\lambda = 3$ ) for vertebrates. However, the concept of basal metabolic rate as used by many physiologists is not appropriate for invertebrates (Clarke and Fraser 2004). We therefore set  $\lambda = 1$ , indicating that field metabolic rates equal lab metabolic rates, providing a conservative estimate of  $I$ .

#### Data analysis

MTE predicts exponential temperature relationships for respiration and consumption within species (Gillooly et al. 2001), but performance curves for many species show unimodal trends with temperature (Angilletta 2009). Therefore, we used Akaike information criteria corrected for small sample size ( $AIC_c$ ) to evaluate five a priori chosen temperature-scaling models for each response variable (respiration, consumption, assimilation efficiency, and ingestion efficiency): (1) exponential (MTE prediction), (2) Gaussian, (3) Brière1, (4) a linear relationship, and (5) a null model of no temperature effect. A Gaussian model is commonly used to evaluate thermal performance curves (Angilletta 2006). The Brière1 model (Brière et al. 1999) is an asymmetrical, unimodal curve that often provides the best description of thermal performance curves by allowing for a rapid drop-off beyond the thermal optimum (Shi and Ge 2010). A linear model was used to contrast the thermal response curves to a simple linear increase in biological rates with temperature. Finally, a null model of no temperature effect was included to evaluate how well the other models compare to a model of no temperature effect (Hilborn and Mangel 1997). For exponential and Gaussian models, temperature was first converted to Kelvins to model the Arrhenius exponential function (Gillooly et al. 2001), whereas for linear and Brière1 models, temperature was left in °C.

Each model initially included urchin mass as a potential covariate, but mass was removed if the 95% confidence interval of the parameter included 0 and the model re-evaluated. Models with  $\Delta AIC_c > 2$  were considered to have poor support. We also calculated the posterior probability of each model to provide a plurality of model-choice criteria following Hilborn and Mangel (1997). We assumed that all models were equally probable a priori

(i.e., flat priors). Posterior probabilities represent the probability that each model is the “true” model, given the data. All results are reported as mean  $\pm$  1 SE.

#### Meta-analysis

We examined whether fitness reductions due to mismatches between consumption and metabolism were common across taxa. We therefore conducted a literature search on ISI Web of Science using combinations of the key words *metab\**, *resp\**, *consumption*, *ingestion*, and *temperature*. We selected only manipulative lab experiments that (1) simultaneously measured consumption and metabolism across three or more temperatures to allow for possible curvilinear effects, (2) used ectothermic species, and (3) only manipulated temperature within the range of temperatures naturally experienced by the study species. We found nine studies encompassing 19 experiments, including the current one, that met these criteria. Additionally, six studies and 13 experiments also measured growth rates, allowing us to link mismatches between consumption and metabolism to growth (Appendix C).

As units and magnitudes of each parameter varied widely among experiments and taxa, we calculated the  $z$  scores of metabolism, consumption, and growth rates within each study. Within each study, we added a constant to growth rates to ensure that only observations with negative growth had negative  $z$  values so that standardized growth rates less than 0 indicate loss of mass. It did not affect the rank order of observations within a study. We calculated the ratio of metabolism to consumption (M:C) after adding the same constant to every metabolism and consumption  $z$  score to make all values positive across all studies. This preserved the rank order of observations within and among studies while preventing complications due to differing positive and negative signs (Appendix A: Fig. A3). Increasing M:C indicates higher metabolic demand relative to consumption. This ratio does not indicate ingestion efficiency, as the units are in standard deviations, but expresses the relative strengths of metabolism and consumption. We regressed M:C against temperature and also regressed growth rates against M:C using linear mixed-effects models with species as a random factor. We chose the best model among null, linear, and quadratic models using AIC. All statistical analyses were conducted in R version 2.13 (R Development Core Team 2011).

#### RESULTS

Respiration rates increased from  $0.02 \pm 0.003$  mg C per day (mean  $\pm$  SE) to  $0.04 \pm 0.005$  mg C per day as temperature increased from 20° to 31°C (Fig. 1A). This relationship was best described by the exponential function predicted by MTE (Appendix A: Table A1). The temperature exponent of respiration was estimated

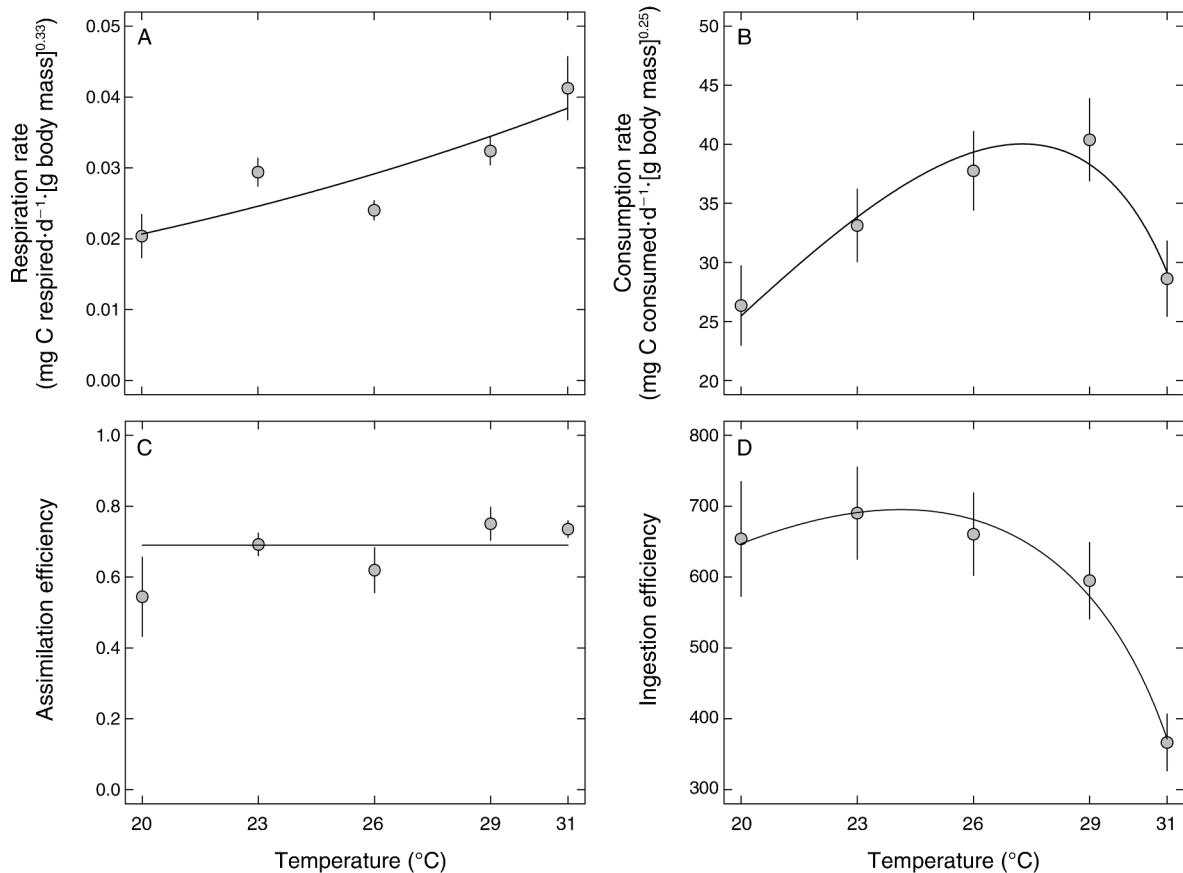


FIG. 1. (A) Relationship between whole-organism metabolic rates and temperature. The fitted line shows the exponential model. Respiration rates were mass-corrected using the scaling parameter estimated by nonlinear regression. (B) Relationship between daily consumption rates and temperature. The fitted line shows the Briere1 model. Consumption rates have been mass-corrected using the mass-scaling parameter estimated by nonlinear regression. (C) Relationship between assimilation efficiency and temperature. The fitted line shows the null model. (D) Relationship between ingestion efficiency and temperature. The fitted line shows the Briere1 model. For all panels, data points represent means  $\pm$  SE.

as 0.46 and the 95% confidence interval included 0.65 ( $CI_{95\%} = 0.25\text{--}0.67$ ), the activation energy predicted by MTE (Allen et al. 2005). The  $Q_{10}$  of respiration for other urchin species ranged from 1.72–3.01, corresponding to activation energies of 0.37–0.76 (Gillooly et al. 2001, Siikavuopio et al. 2008). Our estimate of activation energy is therefore within the range of activation energies measured for other urchin species. Whole-organism respiration rates increased with body mass, although the confidence interval of the scaling parameter narrowly excluded zero ( $CI_{95\%} = 0.01\text{--}0.63$ ; Appendix A: Table A1, Fig. A4).

Consumption rates increased from  $26.35 \pm 3.37$  mg C per day to  $40.38 \pm 3.50$  mg C per day between 20° and 29°C. At 31°C, consumption rates dropped rapidly to  $28.62 \pm 3.19$  mg C per day (Fig. 1B). The Briere1 model best described this relationship (Table A1). The predicted maximum consumption rates were at 27.19°C.

Consumption rates also increased with body mass ( $CI_{95\%} = 0.07\text{--}0.43$ , Table A1, Fig. A5).

Assimilation efficiency was relatively constant at 0.70 over all temperatures (Fig. 1C). Although the null model provided a slightly worse fit than the exponential or linear models (Table A1), the 95% confidence intervals of the temperature coefficient for both linear and exponential models included zero (linear  $CI_{95\%} = -0.002\text{--}0.018$ , exponential  $CI_{95\%} = -0.02\text{--}0.20$ ), reducing these models to the null model. As confidence intervals narrowly included zero, assimilation efficiency may increase with temperature but the rate of change is negligible over the temperatures measured in this study. Also, assimilation efficiency did not scale with mass in either the linear ( $CI_{95\%} = -0.003\text{--}0.009$ ) or exponential ( $CI_{95\%} = -0.04\text{--}0.14$ ) models.

Consumption scaled equivalently with metabolism from 20–26°C, leading to relatively constant ingestion efficiency in these temperature ranges. Beyond 26°C,

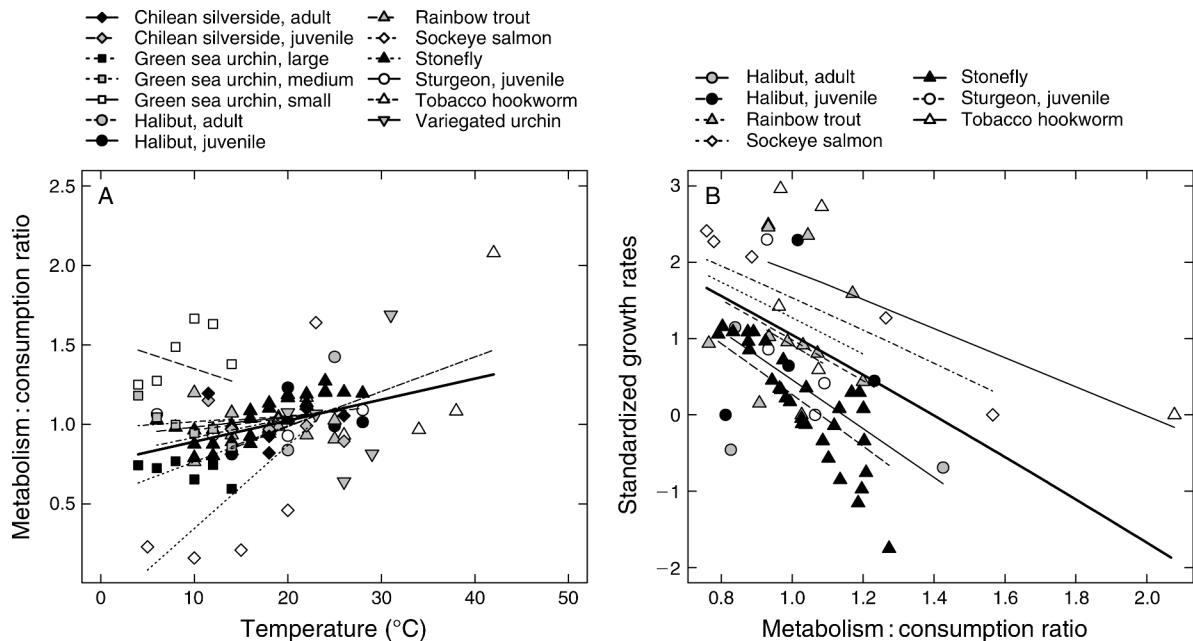


FIG. 2. (A) Relationship between the metabolism:consumption ratio and temperature. (B) Relationship between growth rates and the metabolism:consumption ratio. For simplicity, we show the quadratic model, though the linear model fit the data equally well (Appendix A: Table A2). In each panel, the solid black line is the overall trend, and the other lines are the species-level trends.

metabolism increased much more rapidly with temperature than did consumption, leading to a rapid decrease in ingestion efficiency (Fig. 1D). A Brière1 model best described this pattern (Table A1). Ingestion efficiency did not vary with body mass (mass scaling parameter  $CI_{95\%} = -0.12-0.16$ ). Though ingestion efficiency was still relatively high at 31°C ( $\sim 366.55 \pm 40.13$ ), the rate of decrease was so severe that, when the curve is extrapolated, ingestion efficiency drops to  $\sim 72$  at 32°C and becomes zero at  $\sim 32.62^\circ\text{C}$ , temperatures well within climate change predictions.

#### Meta-analysis

MTE predicts the metabolism:consumption ratio (M:C) to be temperature invariant or to decrease with increasing temperature. However, when pooled across species, M:C increased linearly with temperature (Fig. 2A, Appendix A: Table A2;  $R^2 = 0.57$ ). Despite interspecific variation in the temperature ranges, metabolism increased more quickly with temperature than did consumption for all species except small *Strongylocentrotus droebachiensis* urchins, which showed a negative relationship (Fig. 2A). Importantly, increasing disparity between metabolism and consumption led to lower growth rates in all species for which data were available (Table A2, Fig. 2B,  $R^2 = 0.58$ ). All but one observation of negative growth occurred at or above M:C = 1, indicating that organisms can lose mass if metabolism outpaces consumption (Fig. 2B).

#### DISCUSSION

Rising temperatures will likely increase metabolic demand of individuals, especially ectotherms (Gillooly et al. 2001). In turn, rising metabolic costs may alter many vital biological rates, such as mortality, reproduction, and growth, thereby having profound impacts on community structure and ecosystem function (Allen et al. 2005). Our data support the prediction that temperature-driven changes in metabolic demand alter individual biological rates, but the relationships are more complex than exponential relationships proposed by MTE. A temperature-induced mismatch of metabolism and consumption dramatically reduced the ingestion efficiency of the urchin *L. variegatus*. Moreover, warming frequently led to higher metabolic rates relative to consumption across several species, resulting in reductions in fitness. Modest temperature increases predicted by climate change may therefore have severe consequences for an organism's fitness and population dynamics and potentially alter consumer-resource interactions.

One potential concern is that our short-term warming experiments do not allow for acclimatization of organisms and their metabolism that may happen over time. This would mean that we overestimated the mismatch between metabolism and consumption. However, it is unlikely that the unimodal consumption curve exhibited by *L. variegatus* in this study is a product of acute temperature stress. Consumption by *L. variegatus*

exposed to temperatures ranging from 16–28°C for eight weeks showed a similar unimodal curve with a slow increase from 16–22°C (~2.2–2.5 g/d, respectively) and then a decrease in consumption at 28°C (~1.8 g/d; Watts et al. 2011), suggesting that a decrease in consumption rates is sustained over long time periods. Further, a recent meta-analysis found that 66% of species examined exhibited unimodal consumption curves with respect to temperature (Dell et al. 2011), suggesting that unimodal patterns of consumption may be the most common relationship with temperature.

Ingestion efficiency of *L. variegatus* declined by ~50% between 27–31°C due to the mismatch between metabolism and consumption at high temperatures (Fig. 1D). This decline in ingestion efficiency likely leads to lowered fitness as growth rates, gonad production, and gonad production efficiency of *L. variegatus* show a similar unimodal trend with temperature (Watts et al. 2011). If temperature increases to 32°C, ingestion efficiency drops to 72 and becomes zero at ~32.6°C; both temperatures are well within the 2° warming expected from climate change. While this pattern extrapolates slightly beyond our available data, the qualitative pattern is that slight warming at high temperatures drastically reduces energy for growth and reproduction. This could be especially important during summer spawning periods of *L. variegatus*, during which water temperatures already average 30–31°C. Further, *L. variegatus* currently spends, on average, 50% of the year at or above 26°C when ingestion efficiency starts to decline and energy available to growth and reproduction becomes less available. Under a conservative estimate of 2°C warming with climate change, *L. variegatus* would spend 66% of the year above 26°C, severely reducing the amount of time available for energy accumulation.

The negative effects of high temperatures on growth efficiency have long been known. For example, sockeye salmon, *Oncorhynchus nerka*, have slower growth rates at high temperatures that are likely driven by mismatches between consumption and metabolism nearly identical to those reported here (Brett 1971). That all but one size class of one species in our analyses exhibited mismatches between metabolism and consumption, and subsequently reduced growth rates, under experimental warming suggests that this is likely a general pattern among ectotherms. More recently, this mismatch between consumption and metabolism has been linked to declining fitness at high temperatures across a taxonomically diverse set of species, including reptiles, fishes, crustaceans, and arthropods (Angilletta 2009, Donelson et al. 2010). However, the physiological mechanism behind such fitness reductions has rarely been quantified.

One mechanism responsible for fitness reductions at high temperatures is a mismatch between the costs of cellular maintenance and energy supply. Determinant

growth of many organisms arises from more rapid increases in the cost of cellular maintenance than available energy supply with increasing body mass (West et al. 2001). Thus, a greater fraction of energy is devoted to maintenance rather than growth at large body sizes. Similarly, rising temperatures increase both the cellular demand for ATP and the fraction of ATP devoted to cellular maintenance needed to repair damaged DNA and denatured proteins (Somero 2011). Moreover, ectotherms experience reduced aerobic scope (i.e., excess oxygen available for processes other than basal metabolism) at high temperatures (Pörtner and Knust 2007). Thus, the majority of assimilated energy at high temperatures is devoted to cellular maintenance and repair, leaving little excess energy for work (i.e., consumption, reproduction) or growth.

Models using MTE to predict the effects of climate change on consumer–resource interactions generally show that herbivore biomass declines at increased temperatures. Such models assume that consumption scales equivalently with metabolism (O'Connor et al. 2011) or use comparative studies among species to confirm that consumption increases more rapidly than metabolism as temperature increases (Vassuer and McCann 2005). However, comparative studies are based on interspecific comparisons at species' average body temperatures and may not represent intraspecific patterns. We show that, within a species, more rapid increases in consumption than metabolism may be the exception rather than the rule. Thus, previous models likely underestimated the consequences of climate change on consumer biomass if metabolism–consumption mismatches do induce unstable population cycles (Vassuer and McCann 2005).

MTE provides a promising avenue for predicting the effects of climate change on populations and communities, yet few studies evaluate its underlying assumptions regarding temperature-dependence of biological rates. If physiology-based population models such as MTE are used to predict the effects of climate change, we must define the conditions under which their assumptions are not met and their predictions incorrect (O'Connor et al. 2006). We demonstrated that some assumptions of MTE are not valid at the upper range of species' thermal tolerances, the range critical to predicting climate change effects. Specifically, mismatches between consumption and metabolism are widespread and frequently lead to reduced fitness in a variety of taxa. Such reductions in fitness may severely impact population dynamics and ecosystem function. Thus, thermal mismatches between metabolism and consumption should be explicitly considered when modeling the effects of climate change on populations and communities.

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## SUPPLEMENTAL MATERIAL

## Appendix A

Parameter and AIC estimates for all analyzed models and all supplementary figures (*Ecological Archives* E093-233-A1).

## Appendix B

Respiration methods and conversion from oxygen consumption to carbon respired (*Ecological Archives* E093-233-A2).

## Appendix C

List of sources used in the meta-analysis (*Ecological Archives* E093-233-A3).