Toward predicting community-level effects of climate: relative temperature scaling of metabolic and ingestion rates

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Abstract. Predicting the effects of climate change on ecological communities requires an understanding of how environmental factors influence both physiological processes and species interactions. Specifically, the net impact of temperature on community structure depends on the relative response of physiological energetic costs (metabolism) and energetic gains (ingestion of resources) that mediate the flow of energy throughout a food web. However, the relative temperature scaling of metabolic and ingestion rates have rarely been measured for multiple species within an ecological assemblage and it is not known how, and to what extent, these relative scaling differences vary among species. To investigate the relative influence of these processes, I measured the temperature scaling of metabolic and ingestion rates for a suite of rocky intertidal species using a multiple regression experimental design. I compared oxygen consumption rates (as a proxy for metabolic rate) and ingestion rates by estimating the temperature scaling parameter of the universal temperature dependence (UTD) model, a theoretical model derived from first principles of biochemical kinetics and allometry. The results show that consumer metabolic rates (energetic costs) tend to be more sensitive to temperature than ingestion rates (energetic gains). Thus, as temperature increases, metabolic rates tend to increase faster relative to ingestion rates, causing the overall energetic efficiencies of these rocky intertidal invertebrates to decline. Metabolic and ingestion rates largely scaled in accordance with the UTD model; however, nonlinearity was evident in several cases, particularly at higher temperatures, in which alternative models were more appropriate. There are few studies where multiple rate dependencies are measured on multiple species from the same ecological community. These results indicate that there may be general patterns across species in the temperature scaling of biological rates, with important implications for forecasting temperature effects on ecological communities.

Key words: body mass; body temperature; climate change; food webs; herbivory; ingestion rate; metabolic rate; predation; rocky intertidal; species interaction strength.

Introduction

With mounting evidence of climate change, ecologists face the challenge of forecasting the impacts of changing environmental temperatures on entire ecological communities (Helmuth et al. 2006). Microcosm experiments show that temperature has strong effects at the community level with altered population dynamics affecting community composition and ecosystem functioning (Petchey et al. 1999, Beveridge et al. 2010a, b). These community-level temperature effects are thought to result, in part, from changes to the strength of species interactions (Petchey et al. 1999, 2010, Vasseur and McCann 2005, Rall et al. 2009). All species interact with other species in food webs through which they must acquire resources for survival and reproduction. The strength of these fundamentally important feeding interactions is directly related to ingestion rates (Berlow

et al. 2004, Vasseur and McCann 2005, Wootton and Emmerson 2005, Rall et al. 2009), which in turn depend on temperature (e.g., Sanford 1999, 2002a, b, Pince-bourde et al. 2008, Rall et al. 2009, 2012, Yamane and Gilman 2009, Vucic-Pestic et al. 2010). However, the flow of energy through food webs depends not only on energetic gains from ingestion but also on physiological energetic costs, which depend similarly on temperature (Gillooly et al. 2001, Rall et al. 2009, Vucic-Pestic et al. 2010). Thus, the net impact of temperature on community structure and dynamics depends on the relative response of physiological energetic costs (metabolism) and interspecific energetic gains (ingestion). A mismatch between the rates at which ingestion and metabolism scale with temperature would change an organisms' ingestion efficiency, or the ratio of carbon assimilated per carbon respired (Vasseur and McCann 2005, Lemoine and Burkepile 2012). Because species are embedded within food webs, the direct effects of temperature on a species ingestion efficiency will not only affect its own population growth, but also that of

its prey, its predators, and potentially all the other species in the community (Brose et al. 2012).

Several general theoretical models have explored the effects of a mismatch in temperature scaling between related biological processes on community structure and dynamics. For example, the relative temperature scaling of consumer metabolism and ingestion rates (Vasseur and McCann 2005, Rall et al. 2009), herbivore metabolism and autotroph production rates (Vasseur and McCann 2005, O'Connor et al. 2011), and consumer attack rates and handling times (Petchey et al. 2010). These modeling exercises confirm that the rate at which these processes scale relative to one another is extremely important for predicting ecosystem responses to temperature change. For instance, theoretical analyses indicate that if metabolic rates increase faster than ingestion rates with warming, then population stability increases but also the risk of starvation and extinction of top predators (Vasseur and McCann 2005, Rall et al. 2009). Alternatively, if ingestion outpaces metabolism in response to warming, then consumers have a larger impact on their resources and system stability declines (Vasseur and McCann 2005, Rall et al. 2009). Thus, to understand temperature effects at the ecosystem level, we need to determine if there are systematic differences in how complementary physiological responses scale with temperature.

The temperature scaling of metabolic and ingestion rates for several species from the same community have only been published for a group of spider and beetle species from a terrestrial forest floor community. In this community, metabolic rates were more sensitive to temperature than ingestion rates (Rall et al. 2009, Vucic-Pestic et al. 2010). Here, I measure these responses to temperature on a suite of invertebrate species from a rocky intertidal community. My main objective is to investigate the relative temperature scaling of metabolic and ingestion rates to identify general patterns among species from the same community. Because theoretical analyses indicate that cold-adapted communities are more stable when metabolic rates are more sensitive to temperature than ingestion rates (Vasseur and McCann 2005), and the measurements on species from the forest floor community corroborate this (Rall et al. 2009, Vucic-Pestic et al. 2010), I hypothesized that for rocky intertidal species, metabolic rates would also be more sensitive to temperature than ingestion rates. The results support this hypothesis and I discuss possible causes of this trend and consequences in the face of climate change.

Identifying such general patterns in the effects of temperature on the flow of energy though food webs would significantly increase our ability to predict how food web structure and functioning may shift under climate change using community models. My secondary objective was to use these empirical temperature scaling data to parameterize a theoretical temperature scaling model that is increasingly being used in allometric and temperature-scaled community models (Vasseur and McCann 2005, Petchey et al. 2010, Binzer et al. 2012, Rall et al. 2012). The universal temperature dependence (UTD) model characterizes the joint effects of temperature and body mass on metabolic rate and is derived from first principles of biochemical kinetics and allometry (Gillooly et al. 2001, Brown et al. 2004, Allen and Gillooly 2007). The UTD model has also been extended to other biological rates, including ingestion rate (Rall et al. 2009, Vucic-Pestic et al. 2010). The results indicate broad support for the temperature term of the UTD model under typical water temperatures with some evidence of curvature at higher temperatures.

METHODS

All measurements of metabolic and ingestion rates took place at the Hatfield Marine Science Center (HMSC; Newport, Oregon, USA). The animals and algae were collected from two rocky intertidal field sites along the Oregon coast, Fogarty Creek (44°50′24″ N, 124°3′36″ W) and Yachats Beach (44°19′12″ N, 124°7′12″ W). During collection, I ensured that the individuals selected for experimentation were evenly distributed along the range of body sizes encountered at the field sites, since body size is the primary determinant of physiological rates (Brown et al. 2004). The species included a classic keystone predator, the sea star *Pisaster ochraceus* Brant and its main prey *Mytilus californianus* Conrad, a mussel that is a dominant competitor for space and a foundation species in the mid-intertidal zone; two secondary predators, the whelks *Nucella ostrina* (Gould) and *Nucella canaliculata* (Duclos); and two of their preferred prey, the mussel *Mytilus trossulus* Gould and the barnacle *Balanus glandula* Darwin; and two common grazers of the kelp *Saccharina sessilis* (C.Agardh), the urchin *Strongylocentrotus purpuratus* (Stimpson) and the chiton *Katharina tunicata* (Wood). For more details on how these species are connected in this rocky intertidal food web, see Appendix A. Because *B. glandula* could not be collected nondestructively, I bolted 10 × 10 cm PVC plates covered in Safetywalk antislip tape (3M Company, Saint Paul, Minnesota, USA) to intertidal rocks, to which barnacles readily settled on and grew (Farrell et al. 1991, Menge et al. 2011). Animals were held in the laboratory for 1 week prior to the start of the experimental trials in tanks with flow through seawater pumped directly from the ocean. Thus, the experimental animals were subject to natural variation in water temperature.

Metabolic rate trials

I used an experimental regression study design to measure how oxygen consumption rates (as a proxy for metabolic rate) scale with body mass and temperature for *P. ochraceus*, *M. californianus*, *M. trossulus*, *S. purpuratus*, *K. tunicata*, *N. ostrina*, and *N. canaliculata*. Oxygen measurements were made using a Fibox 3 fiberoptic oxygen meter (PreSens; Precision Sensing GmbH,

TABLE 1. Details of the consumer ingestion rate experimental trials including the resource used for the trial, the amount of resource made available to consumers at the beginning of the trial, and the duration of the trial (days).

Consumer	Resource	Resource amount	Trial duration (d)
Nucella canaliculata	*Mytilus trossulus*	30 individuals	10
Nucella canaliculata	*Balanus glandula*	34.7 ± 3.2 individuals	8
Nucella ostrina	*Mytilus trossulus*	20 individuals	15
Nucella ostrina	*Balanus glandula*	46.5 ± 21.5 individuals	8
Pisaster ochraceus	*Mytilus californianus*	30 individuals	9
Katharina tunicata	*Saccharina sessilis*	23.1 ± 0.7 g	7
Strongylocentrotus purpuratus	*Saccharina sessilis*	23.0 ± 0.7 g	6

Note: Values in resource amount are means ± SD.

Regensburg, Germany) and oxygen sensitive spots. The oxygen sensitive spots were mounted inside clear, airtight containers (respirometers) of various sizes to accommodate different body sizes. The water was aerated, filtered, and sterilized with a UV filter for at least 18 hours prior to each trial. Individual organisms were sealed underwater into a respirometer and both the organism and chamber were checked to ensure there were no trapped air bubbles. For each trial, I took three to five oxygen measurements from each respirometer over a 3–4 hour period. I repeated these oxygen consumption trials at different water temperatures ranging from ~7.5–20°C. I maintained stable water temperatures by keeping the respirometers in water baths of the same temperature, removing them briefly to make oxygen concentration measurements.

Measurements were made using the default setting of the oxygen meter (air saturation [%]) and were converted to μmol/L with atmospheric pressure readings from the HMSC weather station and the average summertime salinity of HMSC seawater (34 ppt). Due to the low solubility of O_2 in water, aquatic animals come to hypoxic conditions relatively faster than air breathing animals in traditional respirometers, which can considerably change their metabolism (Lamprecht et al. 1999, Petchey et al. 1999). Thus, I calculated the rate of change of O_2 concentration ($\mu mol\ O_2 \cdot L^{-1} \cdot s^{-1}$) only over the period of time in which the animals were experiencing normoxia (>110 μmol O_2/L). I converted the oxygen consumption rate into energetic equivalents of metabolism (J/s) by assuming an oxycaloric equivalent of 0.44 ($J \cdot \mu mol \cdot O_2^{-1}$), which represents the catabolism of a mixed metabolic substrate dominated by proteins but also containing carbohydrates and lipids (Lauff and Wood 1996, Hand and Kemp 1999). These measurements reflect metabolic responses to acute temperature change and don't reflect the ability of animals to acclimate over time.

Ingestion rate trials

I used an experimental regression study design to measure how ingestion rates scale with body mass and temperature. The details of each ingestion rate experimental trial can be found in Table 1. The experimental system consisted of 65, 19-L buckets, each with an air hose and air stone, insulated with reflective bubble insulation (Reflectix, Markleville, Indiana, USA) and plumbed with flow-through seawater. The individual animals used for the ingestion rate trials were different than those used for the metabolic rate trails. To help prevent escape, the experimental animals and algae were confined to smaller plastic containers with mesh sides within the buckets, except for the *P. ochraceus* trial, in which the animals were placed directly in the buckets. The system was housed within a cold room with the thermostat set to 5°C. To vary the water temperatures among the buckets, I used 7.5- and 15-W aquarium heaters (Hydor Mini Heaters, Hydor USA, Sacramento, California, USA) to randomly assign a heating rate of 0, 7.5, 15.0, 22.5, or 30.0 W to each bucket. Although the variation in water temperature was created with distinct levels, as in an ANOVA design, I instead used temperature as a continuous variable, measured every other day with a digital handheld thermometer (Model HH-22A, Omega Engineering, Stamford, Connecticut, USA) and averaged over the course of each experiment. This is because there were many factors affecting the final water temperature of each bucket, including variation in air temperature around the room and the randomly assigned temperatures of neighboring buckets, despite the insulation. However, the variability of water temperatures within the buckets was low, with a pooled standard deviation of 0.62°C, as measured every 30 minutes by iButton temperature loggers (Maxim Integrated Products, Sunnyvale, California, USA) placed in 12 haphazardly chosen buckets for the duration of each experimental trial.

The ingestion rate experimental trials were run consecutively from June through September 2010. The duration of each trial depended on the fastest rate at which the resources were being consumed so that no individual consumer exhausted its resource (Table 1). For the trials using *B. glandula* as the resource, I randomly assigned one barnacle plate per container, as the number of barnacles that settled on each plate varied. Each experimental trial included five consumer-free controls, one for each wattage level, which showed that resource mortality was negligible. For the trials using *S. sessilis* as the resource, the percentage of biomass lost from the controls was taken into account when calculating urchin and chiton consumption rates.

Other than the controls, each container held one consumer, which was weighed at the start of each trial.

For each consumer j and resource i, I calculated ingestion rate J_{ij} (J/s) as

$$J_{ij} = (N_e M_i \varepsilon)/t \qquad (1)$$

where N_e is the number of prey eaten (1 for *S. sessilis*), M_i is the estimated shell-free wet mass (g) of an averaged length prey item based on length–mass relationships for each prey species i (A. C. Iles, *unpublished data*) or the wet mass (g) of *S. sessilis* eaten, and t is time in seconds. The energy content of the resources, ε, was set to 6173 and 5751 J/g of ash free wet mass for *Mytilus* spp. and *B. glandula*, respectively (B. A. Menge, *unpublished data*), and 3122 J/g for *S. sessilis* (Paine and Vadas 1969).

Statistical analyses

The data were first analyzed using the universal temperature dependence (UTD) model. Under the UTD, per capita rates of metabolism, I_j (J/s), and ingestion, J_{ij} (J/s), of ectothermic organisms depend jointly on body mass, M (g), and environmental temperature, T (K) as

$$I_j = i_0 M_j^{b_I} e^{-E_I/kT} \qquad (2)$$

$$J_{ij} = j_0 M_j^{b_J} e^{-E_J/kT} \qquad (3)$$

where b is an allometric exponent, E (eV) is the activation energy, k is Boltzmann's constant (8.62×10^{-5} eV/K) and i_0 and j_0 are normalization constants. Taking the natural logarithm of both sides of Eqs. 2 and 3, results in the form of the multiple linear regression UTD models used to estimate the scaling coefficients of the continuous variables (1) body mass [$\ln(M)$], and (2) water temperature ($1/kT$) and the normalization constants for each species

$$\ln(I_j) = b_I \ln(M_j) - E_I \left(\frac{1}{kT}\right) + \ln(i_0) \qquad (4)$$

$$\ln(J_{ij}) = b_J \ln(M_j) - E_J \left(\frac{1}{kT}\right) + \ln(j_0). \qquad (5)$$

Zero values in the ingestion rate data set were omitted because this is often an indication of injury or stress for these rocky intertidal invertebrates due to removal and transport from the field site, which can induce a state of torpor. Thus, including zero values in the ingestion rate data may bias the results. The highest water temperatures were observed as being physiologically stressful, as animals would move away from their food to the air/water interface where the cold air would lower their body temperatures. Thus, data for water temperatures >17°C were excluded, a cutoff point chosen to match the highest water temperatures experienced by these

rocky intertidal invertebrate populations from Oregon. No behavioral stress response was noted at the extreme cold temperatures and these data points remained in the models. Regression diagnostics were performed on all models including tests for normality and constant variance of residuals. The residuals of several models were non-normally distributed due to influential outliers and curvature in the relationship. Because linear least squares is not robust to influential outliers and the estimation of regression parameters was my secondary objective, I also estimated the UTD model parameters using the Huber method for robust linear regression (see Appendix B).

I investigated possible curvature in the metabolic and ingestion rate data in a separate analysis in which I compared the fit of the theoretical UTD model to alternative models. The alternative models included possible interaction and quadratic terms for body mass and temperature. I tested the level of empirical support for the alternative models by assessing the change in Akaike's information criteria adjusted for small sample sizes (ΔAIC_c) relative to the UTD model.

The difference between the slopes of the temperature dependencies of ingestion and metabolic rates ($E_J - E_I$) in the UTD models, is termed consumer thermal impact (CTI). CTI describes how the net impact of a consumer on its resource changes with temperature (Vasseur and McCann 2005). A negative (positive) CTI means that the top-down strength of a consumer's impact on its resource, or the strength of the species interaction, decreases (increases) with temperature. From an organismal-level perspective, consumers with a negative (positive) CTI would have lower (higher) ingestion efficiencies at higher temperatures. Thus, consumers with a negative (positive) CTI would do better at cooler (warmer) temperatures and could be considered cold (warm) adapted. For species of the rocky intertidal, I hypothesized that they would be cold adapted and exhibit negative CTI. Although rocky intertidal invertebrates can tolerate very warm aerial temperatures at low tide, they are only active and foraging at high tide. Thus, their physiological performance at water temperatures of about 8°–16°C determines their success. For each species, I calculated its CTI and used a t test to determine if it was significantly different from zero.

I used MATLAB 7.13 (MathWorks, Natick, Massachusetts, USA) for data processing and R 2.13.2 (R Development Core Team 2011) for all statistical analyses.

Results

Metabolic rates and ingestion rates tended to increase with temperature and body mass in accordance with the UTD model (Table 2, Figs. 1 and 2). However, ingestion rate decreased with body size for *N. canaliculata* when feeding on *B. glandula* and convex curvature was evident in several models, indicating that the UTD model is inappropriate in some cases.

TABLE 2. Linear least-squares regression coefficients and statistics for the universal temperature difference (UTD) models of the effect of body mass and water temperature on metabolic and ingestion rates in rocky intertidal invertebrate species.

Species or interaction	b	E (eV)	$\ln(c)$	R^2	P	n
ln(metabolic rate)						
M. californianus	0.61 (0.04)***	0.76 (0.21)**	22.11 (8.38)*	0.90	8.12×10^{-13}	27
M. trossulus	0.47 (0.05)***	0.77 (0.13)***	22.29 (5.19)***	0.86	2.84×10^{-10}	25
N. canaliculata	0.55 (0.09)***	0.59 (0.16)**	14.93 (6.56)*	0.71	1.09×10^{-6}	25
N. ostrina	0.56 (0.11)***	1.02 (0.21)***	32.60 (8.52)***	0.69	2.45×10^{-6}	25
P. ochraceus	0.42 (0.08)***	0.77 (0.25)**	23.22 (10.30)*	0.60	1.17×10^{-5}	28
K. tunicata	0.82 (0.06)***	0.66 (0.16)***	17.83 (6.36)**	0.89	2.22×10^{-13}	29
S. purpuratus	0.43 (0.10)***	0.63 (0.27)*	17.27 (10.98)	0.46	2.69×10^{-4}	30
ln(ingestion rate)						
N. canaliculata–B. glandula	−0.28 (0.10)**	0.09 (0.24)	−8.31 (9.92)	0.17	0.02	44
N. canaliculata–M. trossulus	0.35 (0.08)***	0.82 (0.12)***	27.42 (5.01)***	0.54	2.38×10^{-9}	54
N. ostrina–B. glandula	0.13 (0.10)	0.54 (0.14)***	11.26 (5.70)†	0.26	9.62×10^{-4}	49
N. ostrina–M. trossulus	0.55 (0.07)***	0.80 (0.10)***	26.61 (4.25)***	0.69	9.00×10^{-13}	51
P. ochraceus–M. californianus	0.62 (0.13)***	0.50 (0.21)*	15.99 (8.57)†	0.50	9.05×10^{-5}	30
K. tunicata–S. sessilis	0.16 (0.27)	1.04 (0.58)†	36.76 (23.32)	0.17	0.22	19
S. purpuratus–S. sessilis	0.52 (0.33)	0.74 (0.67)	24.59 (27.35)	0.19	0.23	17

Notes: All the models are of the form $y = b \ln(M) - E(1/kT) + \ln(c)$, where M is body mass (g), T is water temperature (K), and k is Boltzmann's constant (8.62×10^{-5} eV/K). The coefficients (with SE in parentheses) include b, the allometric exponent; E, the activation energy (eV); and c, the normalization constant. Other variables are R^2 for coefficient of determination, and n for sample size.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$, † $P < 0.1$.

Although body mass explained much more of the variation in the data than temperature, temperature was a significant factor for all the UTD models of metabolic rate and four out of seven UTD models for ingestion rate (Table 2, Figs. 1 and 2). The range of each statistically significant activation energy estimate overlapped with the theoretical range of 0.6–0.7 eV (Allen and Gillooly 2007). The robust regression analysis yielded similar results with slightly different estimates for the model coefficients (Appendix B).

Convex curvature occurred most often in models involving whelk predators (Table 3). A squared temperature term produced a better fit to the metabolic rate data over the UTD model for *N. canaliculata* and a marginally better fit for *N. ostrina*. By restricting the range of temperatures to the increasing, linear portion of *N. canaliculata*'s metabolic response (water temperatures <14°C), the squared term becomes insignificant, and the estimate of the activation energy is much higher ($E_I = 1.40 \pm 0.23$ [mean $\pm$ SD], $P < 0.001$). Adding a squared body mass term improved the fit of the ingestion rate data for *N. canaliculata* when feeding on *B. glandula* and was suggestive of a curved relationship for the *N. ostrina–B. glandula* interaction.

In both the least-squares and robust regression analyses, consumer metabolic rates tended to be more sensitive to temperature than ingestion rates (i.e., a negative CTI; Table 4). There were two exceptions, *K. tunicata* and *S. purpuratus*, both grazers on *S. sessilis*, which exhibited a positive CTI, although neither was significantly greater than zero.

DISCUSSION

Metabolic rates tended to be more sensitive to temperature than ingestion rates (i.e., a negative CTI) for several species of rocky intertidal invertebrate

consumers. This result is consistent with temperature-scaling measurements for beetle and spider taxa from forest-floor communities (Rall et al. 2009, Vucic-Pestic et al. 2010). Although no other studies have looked at temperature scaling between ingestion and metabolic rates for a suite of species from the same community, a recent meta-analysis pooled across species from many different communities also found that metabolic rates increased faster than ingestion (Lemoine and Burkepile 2012). In a meta-analysis of the thermal responses of a variety of traits from many species across habitats, traits that act below the level of consciousness, like basal metabolism, tended to be more sensitive to temperature than traits representative of positive, conscious motivations, such as ingestion (Dell et al. 2011). Finally, in a study that slowly warmed freshwater microcosm communities, both consumer extinction rates and producer biomass increased (Petchey et al. 1999), which is consistent with model predictions only when consumers exhibit negative CTIs (Vasseur and McCann 2005, Rall et al. 2009).

Although it has yet to be shown for an entire community assemblage, it is possible for species to exhibit positive CTIs, at least up to some optimal temperature (Sentis et al. 2012). Here, possible exceptions to the negative CTI trend were the herbivores, the chiton *K. tunicata* and the urchin *S. purpuratus*. Unfortunately, low sample sizes resulted in poor estimates of the temperature scaling coefficients and although the CTI estimates were positive, they were not significantly different from zero. Thus, it is unlikely that this indicates a general, systematic difference for grazers and others have previously measured decreasing energetic efficiencies (i.e., negative CTIs) in another urchin species (Lemoine and Burkepile 2012). The *N. canaliculata–M. trossulus* interaction also had a positive CTI,
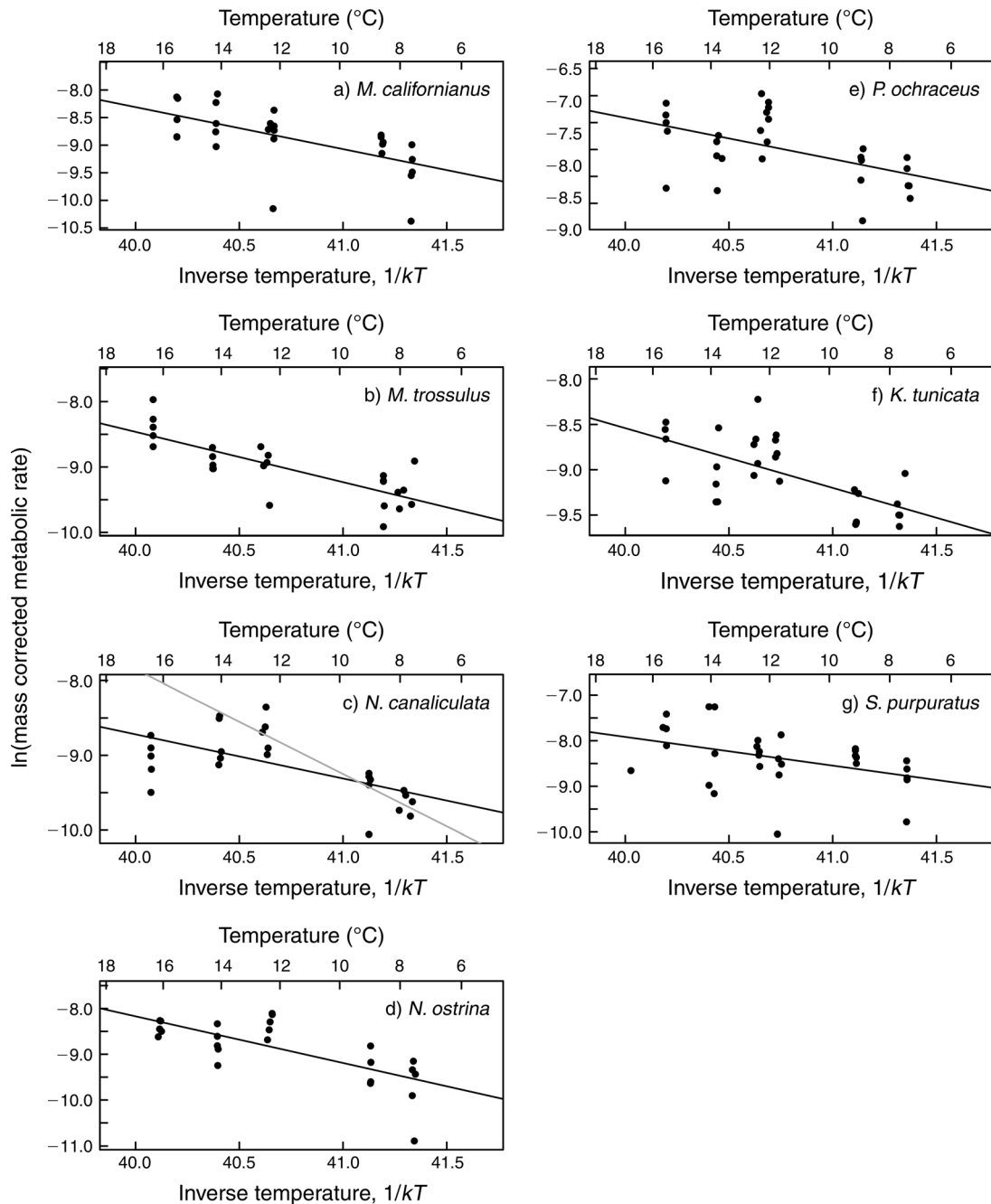
Fig. 1. Metabolic rates as a function of (a–g) water temperature and (h–n) body mass (measured in grams) for seven species of rocky intertidal invertebrates: *Mytilus californianus* (a, h), *M. trossulus* (b, i), *Nucella canaliculata* (c, j), *N. ostrina* (d, k), *Pisaster ochraceus* (e, l), *Katharina tunicata* (f, m), and *Strongylocentrotus purpuratus* (g, n). Variables were ln-transformed and metabolic rates were normalized by body mass (a–g) or temperature (h–n). Statistically significant universal temperature difference (UTD) regression models ($\alpha \leq 0.05$) are plotted in black. The gray regression line in subplot c represents a regression on the increasing linear subset of data (temperatures $\leq 14°C$). The temperature axes scale inversely as $1/kT$ (1/eV), where T is temperature (K) and k is Boltzmann's constant (8.62×10^{-5} eV/K). A transformed temperature scale in °C is on the top axis in panels (a–g).

however, *N. canaliculata* exhibited convex curvature in the scaling of metabolic rate with temperature, which means the UTD model is inappropriate as it violates a basic assumption of regression analyses. Reducing the temperature range to where the relationship was linear,

and the UTD model was appropriate, resulted in a much higher estimate of the activation energy for metabolic rate and a negative CTI. Previous research has also shown that the UTD model breaks down at extreme temperatures (Lemoine and Burkepile 2012, Sentis et al.
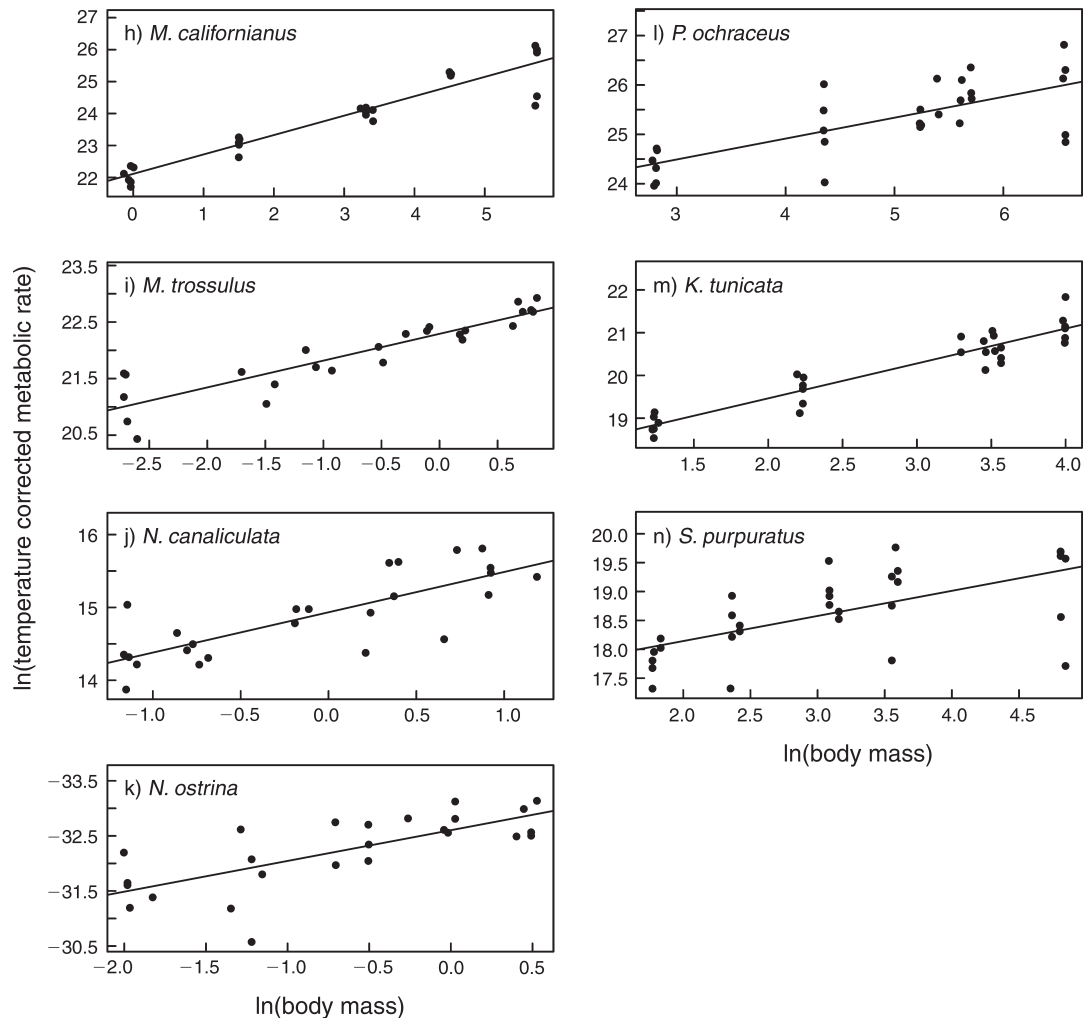
Fig. 1. Continued.

2012). This curvature at extreme temperatures may have been particularly evident for *N. canaliculata* because it is less tolerant of warmer temperatures than the congeneric species, *N. ostrina* (Sorte and Hofmann 2005). Including the higher, physiologically stressful temperatures for the other species would have resulted in similar effects.

The differences in temperature scaling between metabolic and ingestion rates may reflect evolutionary pressures to optimize energetic efficiencies of different kinds of physiological performances under variable thermal conditions. In a quantitative model of the evolution of thermal physiology, a wider performance breadth was favored under variable environmental temperatures (Huey and Kingsolver 1993). For rocky intertidal invertebrates, metabolic costs are incurred over a much wider range of temperatures than the ingestion of prey. This is because the foraging, handling, and attacking of prey typically only occurs under water during high tide, when temperatures are cool and much more stable. In Oregon, rocky intertidal water temper-

atures fluctuate from ~8°C to 16°C due to the intermittent upwelling of cold water along the coast from depth, whereas low tide aerial temperatures range from ~0°C to 35°C, depending on the season and the daily timing of the low tide. Although most intertidal invertebrates are unable to forage during low tide and often take refuge from warm temperatures in cracks and crevices in the rock, some species may take advantage of warmer body temperatures to speed up digestion before the next high tide when they can again forage. Many species behaviorally regulate to a higher body temperature when digesting a meal (Dorcas et al. 1997, Coggan et al. 2011) and thermoregulatory behavior in intertidal invertebrates may also be co-adapted to optimize digestion rates and/or feeding rates. For instance, during a warm low tide, *P. ochraceus* could take advantage of higher body temperatures to speed digestion and enhance foraging when the tide returns. Indeed, experimental evidence shows that feeding rates following a warm low tide tend to be higher (Pincebourde et al.
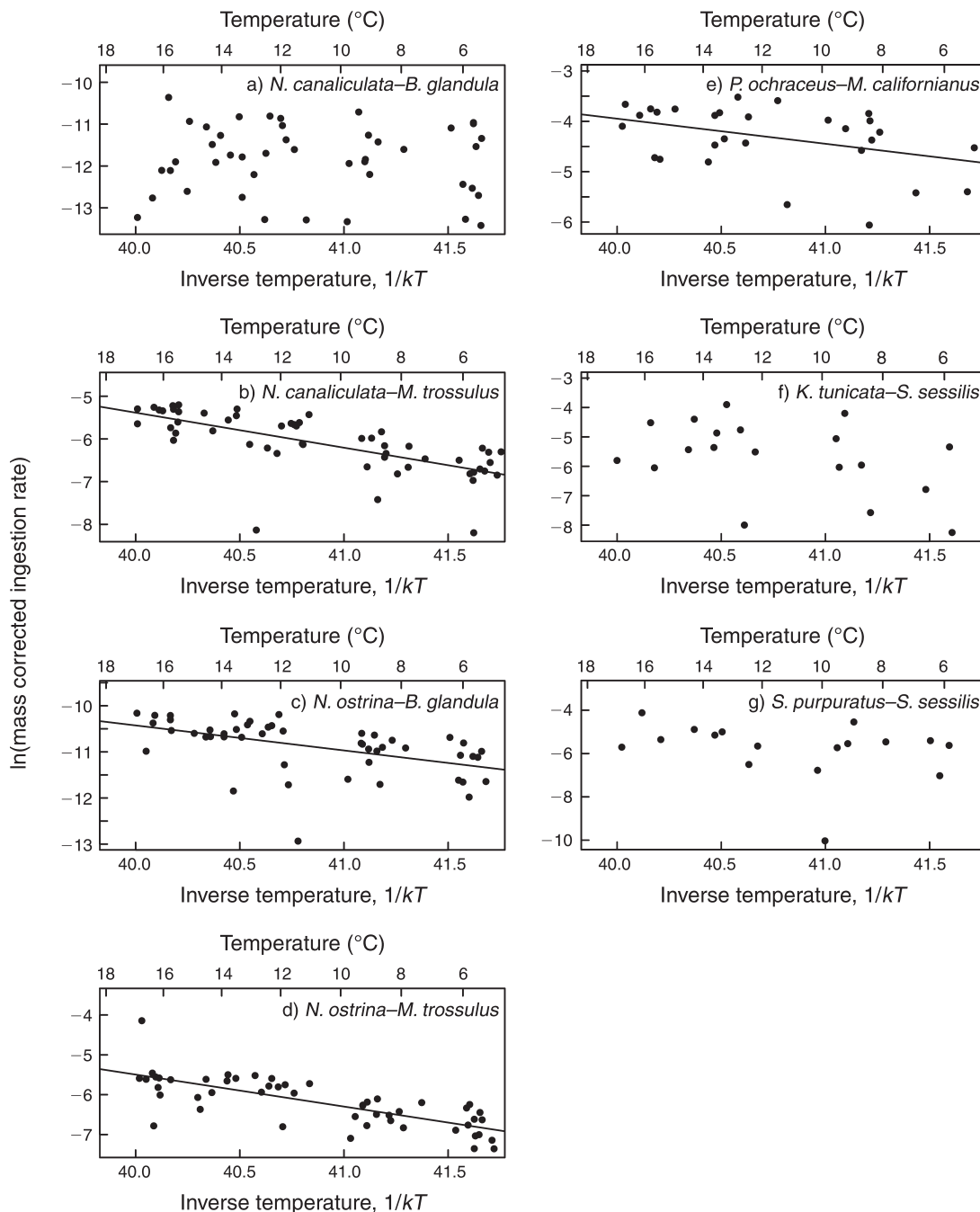
FIG. 2.   Ingestion rates as a function of (a–g) water temperature and (h–n) body mass (measured in grams) for seven rocky intertidal species interactions: *N. canaliculata–B. glandula* (a, h), *N. canaliculata–M. trossulus* (b, i), *N. ostrina–B. glandula* (c, j), *N. ostrina–M. trossulus* (d, k), *P. ochraceus–M. californianus* (e, l), *K. tunicata–S. sessilis* (f, m), and *S. purpuratus–S. sessilis* (g, n). Variables were ln-transformed and ingestion rates were normalized by body mass in panels (a–g) or temperature in panels (h–n). Statistically significant UTD regression models ($\alpha \leq 0.05$) are plotted in black. The temperature axes scale inversely as $1/kT$ (1/eV), where T is temperature (K) and k is Boltzmann's constant (8.62×10^{-5} eV/K). A transformed temperature scale in °C is on the top axis in panels (a–g).

2008). Furthermore, *P. ochraceus* has the capacity to store energy from periods of intensive feeding as lipids, proteins and glycogen reserves in their pyloric caeca (Lawrence and Lane 1982). When water temperatures are very cold and foraging is inefficient, *P. ochraceus* could take advantage of depressed metabolic rates to efficiently convert stored energy in their pyloric caeca into gonadal or somatic growth (Sanford 2002*a*).
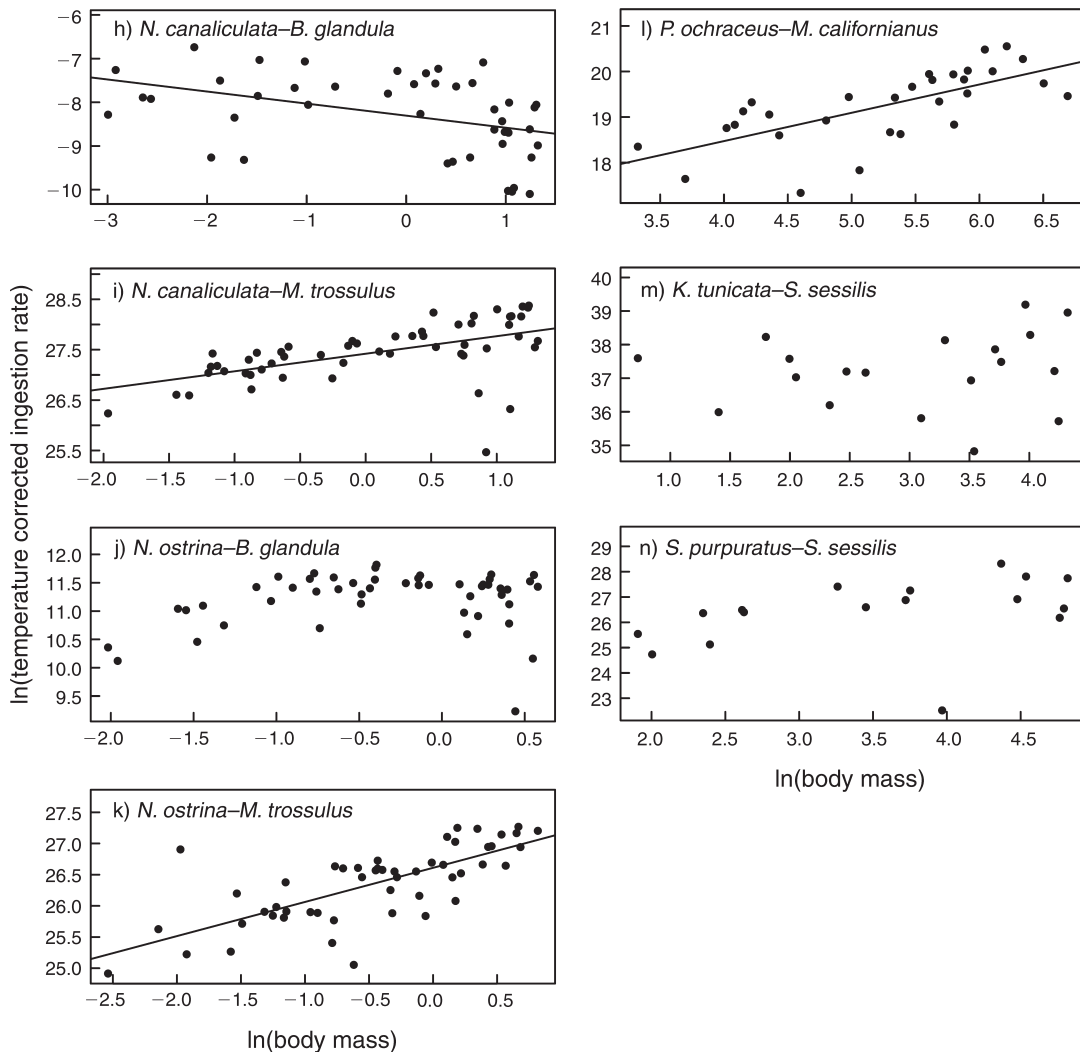
FIG. 2. Continued.

Indeed, there is field evidence that the predation rate of *P. ochraceus* is much lower during cold upwelling conditions (Sanford 1999). Thus, having a metabolic scope that is highly sensitive to temperature may be advantageous to consumers capable of thermoregulation under extremely variable aerial and aquatic temperatures.

Asymmetrical thermal responses between consumers and their resources would also affect how temperature changes consumer energetic efficiency (Dell et al. 2013). For example, an increase in ingestion rate at warmer temperatures due to greater consumer mobility may not be apparent in another consumer–resource interaction where the mobility of the resource also increased. In this study, all of the consumers have body velocities much greater than their resources. Even the filter-feeding mussels siphon phytoplankton at a rate that is much faster than the rate at which phytoplankton can swim. Thus, the effects of temperature on encounter rates can arise only through the mobility (or siphoning rate) of the consumer. In other situations where the resources are relatively more mobile with respect to the mobility of their consumers, potential asymmetry between species thermal responses must be addressed (Dell et al. 2013).

Understanding the community-level effects of environmental temperature is of great concern in a changing climate. Along the west coast of the United States, climate-induced trends indicate that upwelling is becoming stronger and more persistent (Bakun 1990, Bakun et al. 2010, García-Reyes and Largier 2010, Iles et al. 2012). With negative CTIs and long periods of cold upwelled water, consumer energetic efficiency would increase in this system. Theoretical simulation work indicates that this would cause stronger top-down effects of consumers, which would reduce the risk of starvation for top trophic levels but compromise population stability (Vasseur and McCann 2005, Rall et al. 2009). In other ecosystems where the environment is likely to

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TABLE 3. Coefficients for the alternative models of the effects of body size and temperature on metabolic and ingestion rates in rocky intertidal species.

Species or interaction	β_0	β_1	β_2	β_3	β_4	R^2	ΔAIC_c
ln(metabolic rate)							
N. canaliculata	−2419 (613.2)	0.55 (0.07)		119 (30.13)	−17040 (4294)	0.84	−10.83
N. ostrina	−2153 (1000)	0.57 (0.10)		106.3 (49.1)	−15280 (6992)	0.75	−1.97
ln(ingestion rate)							
N. canaliculata–B. glandula	−5.39 (9.57)	−0.52 (0.14)	−0.19 (0.09)	−0.15 (0.23)		0.26	−2.59
N. ostrina–B. glandula	12.77 (4.87)	−0.45 (0.16)	−0.51 (0.12)	−0.58 (0.12)		0.47	−14.21

Notes: Values in parentheses are SE. The change in the Akaike information criterion adjusted for small sample sizes (ΔAIC_c) values indicate the improvement in fit over the UTD models presented in Table 2. The models are of the form $y = \beta_0 + \beta_1(\ln M) + \beta_2(\ln M^2) + \beta_3(1/kT) + \beta_4(1/kT^2)$, where M is body mass (g), T is water temperature (K), and k is Boltzmann's constant (8.62×10^{-5} eV/K). Note that not all terms are present in each model. R^2 is the coefficient of determination.

become warmer, negative CTIs would mean that consumer energetic efficiencies would decline, leading to a weaker top-down effect of consumers on resource species. Simulations of long-term dynamics indicate that such a scenario would stabilize population dynamics but also increase the risk of starvation and extinction of top trophic-level species (Vasseur and McCann 2005, Rall et al. 2009). However, because I measured responses to acute temperature changes, it is unclear how acclimation to long-term climate change may mitigate these effects.

Scaling up climate change predictions to the entire food web is difficult without knowing how primary production will respond to temperature. Although I did not measure the relative temperature scaling of algal productivity, upwelled waters in these coastal systems are not only cold but are also rich in nutrients. Consequently, upwelling is associated with colder temperatures, higher nutrient concentrations, and higher chlorophyll levels in rocky intertidal waters (Iles et al. 2012). More persistent upwelling due to climate change may thus increase algal productivity, in spite of the colder temperatures. A recent model of food-chain dynamics indicates that this combination of low

temperatures and enrichment is highly destabilizing, causing oscillatory dynamics until consumers are driven to extinction and only the basal species survive, growing up to the carrying capacity (Binzer et al. 2012). Indeed, upwelling systems are showing symptoms of such runaway productivity. Extremely high phytoplankton productivity from periods of unusually persistent upwelling has led to severe oxygen depletion and mass die-offs of fish and invertebrates (Grantham et al. 2004, Chan et al. 2008).

This study did not attempt to examine the effects of extreme, physiologically stressful, aerial (or water) temperatures on metabolic or ingestion rates. Yamane and Gilman (2009) found that although there was no change in the ingestion rates of *N. ostrina* after experiencing aerial body temperatures of 12°–20°C, exposure to extremely high aerial temperatures (>28°C) caused decreased consumption rates during the subsequent high tide. In lab experiments with *P. ochraceus*, acute exposure to high aerial temperatures positively affected feeding rates, although chronic exposure caused reductions in feeding (Pincebourde et al. 2008). Although aerial heat stress at low tide can

TABLE 4. Estimates of consumer thermal impact (CTI) with t tests of the hypothesis that metabolic rates increase faster with temperature than ingestion rates.

Consumer	Resource	CTI	df	P
M. californianus	*Rhodomonas* spp.	−0.43 (0.21)[†]	55	0.02
M. trossulus	*Rhodomonas* spp.	−0.44 (0.14)[†]	53	0.001
N. canaliculata	*M. trossulus*	−0.58 (0.26)[‡]	67	0.015
N. ostrina	*B. glandula*	−0.49 (0.25)	72	0.031
N. ostrina	*M. trossulus*	−0.22 (0.22)	74	0.18
P. ochraceus	*M. californianus*	−0.27 (0.27)	56	0.21
K. tunicata	*S. sessilis*	0.38 (0.60)	46	0.27
S. purpuratus	*S. sessilis*	0.11 (0.72)	45	0.44
Beetles (five species)[§]	*Lucilia caesar*	−0.63 (0.09)	261	<0.001
Spiders (four species)[§]	*Gryllus sigillatus*	−0.50 (0.10)	227	<0.001

Notes: For comparison, results from a previous study on terrestrial forest floor beetles and spider consumers are also listed. $CTI = E_J − E_I$, where I (J/s) is the per capita rate of metabolism and J (J/s) is the per capita rate of ingestion. CTI values are means with SE in parentheses.

[†] Using a weighted average of ingestion rate estimates from the literature (Jorgensen et al. 1990, Kittner and Riisgard 2005); the standard error is equivalent to the standard deviation of this sampling distribution.

[‡] Using the estimate for activation energy of metabolic rate with water temperatures <14°C, where the relationship is linear and the UTD model is appropriate.

[§] Values for these taxa are from Rall et al. (2009).

affect intertidal predation rates, such high temperatures only occur occasionally (Sanford 2002b) and field surveys indicate that *P. ochraceus* seek refuge from chronic exposure (Pincebourde et al. 2008). Sedentary organisms, such as mussels and barnacles that cannot take refuge from chronic exposure, often reach much higher body temperatures than their mobile predators (Broitman et al. 2009) and their upper distribution limits are often thermally constrained at warm sites (Harley and Helmuth 2003). When scaling up to community-level dynamics over ecological time scales, for mobile species at least, the physiological rate effects of typical environmental temperatures are likely to be relatively more important than the physiological effects of occasional exposures to extreme temperatures.

Conclusions

In conjunction with previous measurements on terrestrial invertebrates, this study of a rocky intertidal invertebrate community advances our understanding of community-level effects by providing compelling evidence for possible systematic differences in the temperature scaling of basal metabolic and ingestion rates. Incorporating such general, systematic differences into a framework linking variation in environmental temperature to complex systems of species interactions will enable us to test hypotheses on how climate change will affect community structure and dynamics. However, ecological communities are inherently complex and in order to predict temperature effects on community structure and dynamics, much more work must be done to establish such generalities in the temperature scaling of biological rates and to identify where exceptions are likely to occur.

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SUPPLEMENTAL MATERIAL

Appendix A

U.S. West Coast rocky intertidal food web and species natural history (*Ecological Archives* E095-231-A1).

Appendix B

Robust linear regression analysis for the estimation of the coefficients of the UTD model (*Ecological Archives* E095-231-A2).