Temperature triggers a non-linear response in resource–consumer interaction strength

GUSTAVO S. BETINI1,†, TAL AVGAR1,2, KEVIN S. MCCANN1, AND JOHN M. FRYXELL1

1Department of Integrative Biology, University of Guelph, Guelph, Ontario N1G 2W1 Canada
2Department of Wildland Resources, Utah State University, Logan, Utah 84322 USA


Abstract. Although temperature is recognized as a major determinant of many ecological processes, it is still not clear whether temperature increase caused by climate change will strengthen or weaken species interactions. One hypothesis is that interactions will respond non-monotonically to temperature because thermal performance curves, which determine the strength of these interactions, are also non-monotonic. To evaluate this hypothesis, we developed a temperature-dependent consumer–resource model and tested predictions from this model in large freshwater mesocosms populated with green algae (Chlorella vulgaris) and herbivorous zooplankton (Daphnia magna). We found both in the model simulations and empirical investigations that the suppressive effect of the consumer depended non-monotonically on the temperature. As predicted by the model, Daphnia suppressed the algal maximum per capita growth rate at the temperature that maximized algal growth rate but had little effect on resource growth at either lower or higher temperatures. This finding could help explain why effects of temperature variation on species interaction are variable in the literature and suggests that predicting the effects of temperature on the strength of food web interactions requires knowledge of the thermal performance curves for multiple traits, for multiple species and over a range of temperatures.

Key words: aquatic ecology; Chlorella vulgaris; Daphnia magna; density dependence; paradox of enrichment; predation; trophic control.

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† E-mail: gabetini@gmail.com

INTRODUCTION

Temperature is perhaps the most widely recognized environmental factor driving ecological processes today. Change in temperature experienced by organisms because of climate change has been documented to trigger behavioral responses, shifts in geographic distribution and phenological mismatches between consumers and resources (Hughes 2000, Parmesan 2006, Hansen et al. 2010). In addition, temperature is expected to affect the way species interact via changes in organismal physiology (Dell et al. 2011, 2014, Schaum 2017). For example, the feeding rate of two species of Daphnia under controlled conditions increased with initial changes in temperature, making Daphnia a more effective grazer (West and Post 2016). However, at higher levels of temperature, Daphnia feeding rate dropped sharply, compromising grazing capacity, whereas algal growth rate remained high. These differences in response to temperature variation between resource and consumer could have cascading effects on food web structure, ecosystem function, and biodiversity given that consumer–resource dynamics control the flow of energy between trophic levels (O’Connor et al. 2009, Gilbert 2014, Osmond et al. 2017). Thus, it is essential
that we gain a better understanding of how temperature affects key physiological traits that could mediate species interaction (Vasseur and McCann 2005, Dell et al. 2011, 2014, Gilbert 2014).

Recent theoretical work suggests that the unimodal response to temperature of physiological traits could scale up to affect higher order processes, such as species interaction, leading to a similar unimodal change in interaction strength (Amarasekare 2015, Uszko et al. 2017, Bideault et al. 2019). This could happen because thermal performance curves, which are determined by metabolic rate, are often a dome-shaped function of ambient temperature (Brown et al. 2004, Savage et al. 2004, Sibly et al. 2012). This dome-shaped form has been empirically demonstrated for several key traits that mediate species interactions, including resource growth rates and feeding rates of many consumers in aquatic and terrestrial system (Savage et al. 2004, Knies and Kingsolver 2010, Dell et al. 2011, Englund et al. 2011, Fey and Cottingham 2012, West and Post 2016, Jarvis et al. 2016). In addition, the position and shape of such curves vary across species (Dell et al. 2011, Schulte et al. 2011), and changes in temperature might have different effects for consumers than it does for their resources (Savage et al. 2004, Ohlberger 2013, Dell et al. 2014). As a consequence, species can differ in the magnitude, rate, and/or peak of changes in thermal response with important effects on species interactions (Porter and Farrell 2008, Kordas et al. 2011, Dell et al. 2014, Bideault et al. 2019). Although this link between the unimodal response of physiological traits and species interaction has been suggested theoretically, we still lack empirical evidence under realistic environmental conditions.

Here, we investigate how changes in ambient temperature modify thermal performance responses and species interaction strength through a combination of theory and controlled experimentation. We first developed a consumer–resource model in which the maximum rate of resource growth, handling time, and attack rate by the consumer were temperature-dependent (Amarasekare 2015, Uszko et al. 2017, Bideault et al. 2019). This model allowed us to make predictions about the potential effect of shifts in temperature on species interaction via their thermal performance peak. We hypothesized that when the peak of trait performance is different between consumer and resource, changes in temperature that approach one of the peaks should benefit resources differently than consumers. For example, if the thermal optimum of the density-independent growth rate (r_{max}) of the resource is at higher temperature than the feeding rate parameters for the consumer, increases in temperature should weaken the demographic effect of consumption because the resource would perform better at higher temperature. We investigated this hypothesis on the non-motile green algae Chlorella vulgaris (resource) and the freshwater water flea Daphnia magna (consumer) living in 26,000 L freshwater mesocosms. Previous work with the same algae strain showed that the maximum exponential rate of increase (r_{max}) by C. vulgaris peaks at 20°C (Jarvis et al. 2016). Daphnia has been shown to exhibit a type II functional response (Rigler 1961, Porter et al. 1983), meaning that Daphnia should have their greatest impact on per capita rates of algal growth rate at low levels of resource density (Fryxell et al. 2014). The maximum feeding rate by D. magna should also be around 20°C, because the thermal performance curve of most freshwater invertebrates peaks at around 21°C (Dell et al. 2011). In addition, both the algae and Daphnia strains used in this study have been kept under laboratory conditions for many years at 20°C. We estimated the standardized effect of consumer on the resource by comparing algal realized r_{max} with or without consumers.

Model development

To evaluate the potential effects of temperature-dependent traits on consumer–resource dynamics, we developed a model in which the intrinsic growth rate of the resource r (T), the attack rate a (T), and the handling time h (T) by the consumer were all independent parabolic functions of ambient temperature, with potentially different thermal optima. Studying species interaction strength with temperature-dependent traits models has been done previously (Amarasekare 2015, Uszko et al. 2017, Bideault et al. 2019). We elected to use a simpler version of these models to capture the essence of consumer–resource interaction with the minimum number of parameters possible. We used this model to demonstrate the wide variety of
outcomes with respect to interaction strength that could occur, depending on the degree to which thermal optima for different traits coincide. We operationally defined consumer interaction strength as the difference in realized maximum per capita growth rates experienced by a resource population with and without consumers.

Let the temperature-dependent rates of resource growth, attack rate, and handling time take a quadratic form, such that

\[
\begin{align*}
    r_{\text{max}}(T) &= \varphi_1 T - \varphi_2 T^2 - \varphi_3 \\
    a(T) &= \varphi_4 T - \varphi_5 T^2 - \varphi_6 \\
    h(T) &= -\varphi_7 T + \varphi_8 T^2 + \varphi_9 
\end{align*}
\]

where \(\varphi_1-9\) are constants specific to each physiological trait. Note that \(r_{\text{max}}(T)\) and \(a(T)\) are dome-shaped, but \(h(T)\) takes the opposite shape. Assume that the type II functional response of the consumer is given by the following equation

\[
f(N) = \frac{a * N}{1 + a * h * N}
\]

where \(f\) is the intake rate and \(N\) is prey density (Holling 1959). The temperature-dependent type II functional response is obtained by replacing \(a\) and \(h\) for \(a(T)\) (Eq. 2) and \(h(T)\) (Eq. 3) in Eq. 4 (Appendix S1: Fig. S1):

\[
f(T,N) = \frac{(\varphi_1 T - \varphi_2 T^2 - \varphi_3) * N}{1 + (\varphi_4 T - \varphi_5 T^2 - \varphi_6) * (-\varphi_7 T + \varphi_8 T^2 + \varphi_9) * N}
\]

We then calculate the per capita mortality risk to the resource \((g)\) by dividing the functional response by resource density (Appendix S1: Fig. S2):

\[
g(T,N) = \frac{f(T,N)}{N}
\]

The temperature-dependent interaction effect of the consumer on the resource can be accordingly calculated by the following relationship

\[
\Psi(T,N) = r_{\text{max}}(T) - g(T,N)
\]

Since per capita mortality risk becomes infinitely large as \(N\to 0\), we standardized the interaction term at an arbitrarily low level of prey density \(N = 1\). The final model is obtained by substituting the full temperature-dependent terms for \(r(T)\) and \(g(T,N)\) into Eq. 7:

\[
\Psi(T,N) = (\varphi_1 T - \varphi_2 T^2 - \varphi_3) \\
- \left[ \frac{(\varphi_4 T - \varphi_5 T^2 - \varphi_6)}{1 + (\varphi_4 T - \varphi_5 T^2 - \varphi_6) * (-\varphi_7 T + \varphi_8 T^2 + \varphi_9)} \right]
\]

To illustrate the model and for simplicity, we held the resource thermal response constant, while varying the thermal response curve of the consumer. Our goal was to investigate how temperature might influence interaction strength when the thermal performance curve for the consumer peaks at a lower, identical, or higher temperature than that of its resource, which were determined based on previous publications (Dell et al. 2011, Jarvis et al. 2016; see also Introduction). To displace the thermal optimum of a given physiological trait, we either subtracted or added 5°C from the temperature \(T\) in Eq. 8. Positive values displace the curve to the right, increasing the thermal optimum, and negative values have the opposite effect. Parameter values used in the model simulations are given in Table 1.

**Table 1.** Parameter values used in Eqs. 1–8 to investigate the effects of consumer on the maximum per capita growth rate \(r_{\text{max}}\) of the resource when both the \(r_{\text{max}}\) and the functional response parameters of the consumer are temperature-dependent.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\varphi_1)</td>
<td>(r_{\text{max}}) constant, Eq. 1</td>
<td>0.28</td>
</tr>
<tr>
<td>(\varphi_2)</td>
<td>(r_{\text{max}}) constant, Eq. 1</td>
<td>0.007</td>
</tr>
<tr>
<td>(\varphi_3)</td>
<td>(r_{\text{max}}) constant, Eq. 1</td>
<td>1.8</td>
</tr>
<tr>
<td>(\varphi_4,7)</td>
<td>Attack rate and handling time constant, Eqs. 2 and 3</td>
<td>0.14</td>
</tr>
<tr>
<td>(\varphi_5,8)</td>
<td>Attack rate and handling time constant, Eqs. 2 and 3</td>
<td>0.0035</td>
</tr>
<tr>
<td>(\varphi_6)</td>
<td>Attack rate and handling time constant, Eqs. 2 and 3</td>
<td>0.9</td>
</tr>
<tr>
<td>(\varphi_9)</td>
<td>Handling time constant, Eq. 3</td>
<td>1.9</td>
</tr>
<tr>
<td>(T)</td>
<td>Temperature</td>
<td>(T) varies from 10 to 30</td>
</tr>
<tr>
<td>(N)</td>
<td>Density</td>
<td>(N) varies from 0 to 100</td>
</tr>
</tbody>
</table>
Our model predicts that the strongest demographic effect of the consumer on the algae should occur at the temperature at which the attack rate is highest, and the handling time is lowest, regardless of whether these optima occur at 15°C, 20°C, or 25°C (Fig. 1). Away from these optima, the impact of the consumer on the resource depends on whether the thermal optimum of the consumer is higher or lower than that of its resource. For example, when the thermal performance curve of the consumer peaks at a lower temperature than that of its resource, the demographic impact of the consumer on the resource should decline monotonically with temperature (Fig. 1a, b). Conversely, when the thermal performance curve of the consumer peaks at a higher temperature than that of its resource, the demographic impact of the consumer on the resource should increase monotonically with temperature (Fig. 1e, f). When the thermal optima of the consumer and its resource coincide, the demographic impact of the consumer on resource growth rates should be highest at the resource thermal optimum (Fig. 1c, d).

**EXPERIMENT**

We tested the predictions from our temperature-dependent consumer–resource model with data from large-scale aquatic experiments with the green algae *Chlorella vulgaris* and the freshwater water flea *Daphnia magna*. The study was conducted in the Guelph Limnotron facility, which consists of six double-walled stainless-steel cylinders, each filled with 26,000 L of filtered raw well water. Details of this system and animals used in the experiment are described elsewhere (Betini et al. 2017). Briefly, each tank is...

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![Fig. 1. The effect of the consumer on the resource $r_{max}$.](image)

In (a), (c), and (e), the algal $r_{max}$ was calculated in the absence (solid lines) and in the presence (dotted lines) of the consumer. Plots (b), (d), and (f) show the difference between algal $r_{max}$ calculated in the presence and absence of the consumer. In (a) and (b), the thermal optima of the physiological traits of the consumer attack rate $a$ and handling time $h$ are lower than the resource $r_{max}$. The opposite is shown in plots (e) and (f). Plots (c) and (d) present the effect of the consumer on the algal $r_{max}$ when the thermal optima of the physiological traits of the consumer and resource were the same. Vertical lines represent the thermal optimum of $a$ and $h$. $r_{max}$ was kept constant at 20°C.
equipped with 18 different sampling ports that allow samples to be taken vertically and horizontally. Tanks were initially inoculated with 650 mL of algal solution (density ~5 × 10^6 algae cells/mL). Three weeks after algal inoculation, we added 2 L of clonal Daphnia culture in three tanks (initial population size ~250 Daphnia composed of ~20 adults and ~230 juveniles). There was no forced circulation in the tanks.

To mimic optimal and suboptimal growing conditions for both the resource and the consumers, tanks were maintained at an average temperature of 15°C, 20°C, and 25°C. Temperature in the tanks ranged at different depths between 15°C and 18°C (14.93°C, 1.95; mean and SD), 19°C and 23°C (20.16°C, 1.71), or from 23°C to 31°C (24.84°C, 3.10) in the tanks kept at a mean temperature of 15°C, 20°C, and 25°C, respectively (Betini et al. 2017). This setting mimics the vertical gradient of thermocline and light conditions commonly found in many natural lakes in northern North America (Hondzo and Stefan 1993, Dobiesz and Lester 2009, Betini et al. 2017).

Population densities of both algae and D. magna were estimated by sampling 1 L of water from each of 18 different ports from each tank twice a week for up to 288 d. For the purpose of the current paper, we were not interested in the effects of spatial variation within tanks, and we simply averaged daily rate of algal growth (estimated by \( r_t = \ln(N_{t+\tau}/N_t)/\tau \), where \( \tau \) is the time elapsed between two consecutive sampling occasions, either three or four days) over 18 spatial replicates within each tank. This results in a sample size of \( n = 306 \) algal daily growth rate estimates (Appendix S1: Table S1). Algal density was estimated with a handheld fluorometer cued to the concentration of chlorophyll a (excitation: 460 ± 20 nm/emission: >665 nm). Fluorometer readings were transformed into algal density (cells/mL) using a calibration curve obtained by counting number of cells in samples collected from the tanks (\( y = 31,170 + 7332 \times \)Fluorometer Reading, \( R^2 = 0.82, n = 89 \)). The density of D. magna (number of individuals/L) was estimated visually by counting the number of individuals present in each 1-L sample after pouring the sample into a flat, transparent jar. All samples were collected during the dark phase, with tanks maintained on a 12 h light:12 h dark schedule.

We assessed resource performance by regressing \( r_t \) against the algal density at time \( t \) in each tank, with and without D. magna at three different tank temperatures (15°C, 20°C, and 25°C). We interpreted the intercept of each of the resulting six regressions as the maximum daily growth rate and the interaction strength as the difference in the intercept in tanks with and without consumers.

In our mesocosm experiment, algal \( r_{\text{max}} \) in the tank kept at 20°C was 65% and 80% higher than algal \( r_{\text{max}} \) in the tanks kept at 15°C and 25°C, respectively (Appendix S1: Table S2). These results corroborate previous laboratory studies on the thermal optimum of the C. vulgaris strain used in this study (Jarvis et al. 2016). In the presence of the consumer, there was a decline in algal \( r_{\text{max}} \) in all treatments (Fig. 2b); however, in the 15°C and 25°C treatments, the standard error bars overlapped between the treatment with and without D. magna. This was not the case in the 20°C treatment, meaning that decline in \( r_{\text{max}} \) caused by the presence of D. magna was only significant in the 20°C treatment (Fig. 3).

**DISCUSSION**

In our experimental system, D. magna had its strongest demographic effect on algal growth rates at the intermediate temperature that optimized algal growth but had little detectable effect at lower or higher temperatures. Our theoretical model suggests that this would be expected if the thermal optima for both consumers and resources were similar. Indeed, previous laboratory trials suggest that D. magna have a thermal optimum around 20°C (Giebelhausen and Lampert 2001), similar to that for the green algal species used in this study (Jarvis et al. 2016). This correspondence between our empirical results and previous studies on thermal optima of the species we used in the experiment suggests that our model approach, which incorporates unimodal thermal dependencies with very few parameters, could be useful when trying to predict the impacts of temperature on species interaction strength.

Our empirical results corroborate predictions from our model and other previous mathematical investigations (Amarasekare 2015, Uszko et al. 2017, Bideault et al. 2019), but we still have...
little information about the physiological mechanisms driving non-monotonic responses. It is likely that different species have their specific biochemistry that would alter the peak and shape of the thermal response. For example, peaks of metabolic rate have been shown to vary with taxa, habitat, and even body size (DeLong et al. 2018) and temperature can have opposite effects on species interaction strength at different latitude (Marino et al. 2018) and different levels of food availability (Sentis et al. 2014). Solid physiological understanding of how different taxa and environmental conditions affect the shape and peak of the temperature response of physiological traits would increase our ability to predict changes in species interaction strength caused by global warming.

Empirical work in the recently published literature has yielded widely varying conclusions about the potential effects of global warming on trophic control: Increases in temperature can either strengthen or weaken species interactions.
Frank et al. 2006, Sommer et al. 2007, O'Connor et al. 2009, Gilbert 2014, Marino et al. 2018). Our work suggests that disparity in findings among past studies could be potentially explained by differences in thermal optima between resources and consumers and the unimodal shape of the physiological traits. Other theoretical studies have also emphasized that the shape of physiological traits can scale up to affect species interaction (Amarasekare 2015, Uszko et al. 2017, Bideault et al. 2019), and our unique empirical approach that mimics more realistic environmental conditions suggests that this might be the case in many field populations. Few field studies on natural populations can detect these optima or sample individuals over temperatures that span the thermal performance curves needed to detect the kinds of non-linear effects we have demonstrated here. A critical lack of controlled experimental studies might help to explain why the published literature shows such variable outcomes regarding the effect of increasing temperature on the strength of trophic interactions.

The metabolic theory of ecology predicts that metabolism and mortality rate (i.e., mortality scaling to the cost of living) of the consumer ought to also scale with temperature (Yodzis and Innes 1992, Savage et al. 2004, Gilbert 2014). For example, Gilbert (2014) noted that if warming drove mortality rates to increase more rapidly than attack rates, then this would reduce relative growth rates more than expected strictly based on changes in attack rate. In our framework, mortality rate could be incorporated as a consumer loss function in Eq. 8 in a manner that reduces consumer $r_{\text{max}}$ but has no effect on the symmetry between $r_{\text{max}}$ of the consumer and the resource (it would only lower the dotted lines in Fig. 1). In natural populations, it would be important to understand how consumption (attack rate) or mortality contributes to changes in relative growth rate under different warming scenarios.

Understanding the effects of human-induced environmental stressors has been considered one of the most critical problems facing modern society (Ehrlich and Ehrlich 2013). Directional and unpredictable variation in temperature caused by climate change has the potential to alter survival and reproduction of many species, affecting how they interact with each other and the resilience of their populations and communities (Hughes 2003, Parmesan 2006, Hansen et al. 2010). Theoretical and empirical studies suggest that thermal performance curves of physiological traits can drive organismal responses to changes in temperature and are key to understand the effects of climate change on the native biota (Brown et al. 2004, Savage et al. 2004, Bowler and Terblanche 2008, Hansen et al. 2010, Schulte et al. 2011). Our theoretical and empirical results suggest that species interactions should respond in a complex manner to variation in temperature, depending in part on whether thermal optima are similar in both consumers and their resources and the shape of the temperature responses of physiological traits. Thus, understanding the effects of temperature on the dynamics of food webs requires knowledge of the thermal performance curves for multiple species and multiple traits over a wide range of temperatures.

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LITERATURE CITED


Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual


Supporting Information

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