

The temperature-size rule is predicted to stabilize the
response of consumer-resource dynamics under warming

or

Temperature-dependent body size alters the effects of
temperature on consumer resource dynamics

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Abstract

Body size influences the dynamical relationship between consumers and their resources. Mount-
3 ing evidence suggests that body size declines with increasing temperature, a pattern called the
temperature-size rule (TSR). The growing theory on temperature-dependent consumer resource
interactions has yet to integrate the TSR into a general framework for how temperature af-
6 fects consumer resource dynamics. We expanded an existing temperature-dependent consumer-
resource model to include the indirect effects of warming, through changes in body size, and
parameterized the model with values drawn from data syntheses. We analyzed this model to
9 answer the following questions: 1) How does including the TSR affect predictions for how tem-
perature affects consumer-resource stability and biomass ratios? 2) Under what circumstances
are the effects of the TSR most substantial? We found that including the TSR led to two qualita-
12 tively different predictions: under warming i) consumer-resource biomass is no longer expected
to decline and ii) the dynamics are expected to become more stable, as opposed to the decline in
stability predicted without the TSR. These qualitatively different predictions were strengthened
15 by asymmetric temperature-size responses and type-II functional responses. Our analyses sug-
gest that the effect of temperature on body size likely plays an important role in the response of
consumer-resource systems to changing temperatures.

18 Introduction

Populations of consumers and their resources are joined across time by the fact that energy to the consumer comes from the resource, and the consumer determines mortality rates of the resource. In these systems, temperature-dependent consumption, growth and mortality rates can change dynamics and their outcomes. Through the temperature-dependence of metabolism (Gillooly et al., 2001; West et al., 1997) and hence temperature-dependent demographic vital rates, small changes in temperature that are not necessarily physiologically stressful for organisms can translate to changes in the stability and coexistence of consumers and their resources, producing predictable but non-intuitive effects of warming on simple food webs (Gilbert et al., 2014; O'Connor et al., 2011; Rall et al., 2010; Vasseur and McCann, 2005).

Demographic rates and consumer-resource interactions also depend on body size (DeLong et al., 2015; Yodzis and Innes, 1992). Not only do rates of growth, mortality and consumption scale predictably with individual body sizes, but the consumption rates of consumer-resource systems can also depend on the ratio of body masses between consumers and prey (Kalinkat et al., 2013). Changes in body size or body size ratios can therefore change demographic and interaction rates. Given the importance of body size to the dynamics and outcomes of consumer-resource interactions, frameworks for understanding how temperature affects consumer-resource dynamics have not considered the importance of changes in body size with temperature.

The frequently-observed negative relationship between temperature and body size, the temperature-size rule (TSR), has been called the third universal response to warming (Gardner et al., 2011). For comparisons within populations, among species and across biogeographic gradients, body size of ectotherms tends to decline with increasing temperature (Atkinson, 1994; Daufresne et al., 2009; DeLong, 2012; Forster et al., 2012). Although the mechanism for declining body size with warming varies among examples, including physiological plasticity, selection for smaller individuals, and turnover in species composition, the pattern is similar across levels of organization (Forster et al., 2012). Forster et al. (2012) reported a mean slope of $-3.65\%/^{\circ}\text{C}$ for aquatic organ-

isms, ranging from $-1.80\%/^{\circ}\text{C}$ for unicells, and becoming stronger (more negative) in increasingly
 45 large aquatic multicelled organisms.

Because body size is so central to consumer-resource dynamics, such a systematic pattern of
 changing body size with temperature could alter predictions for how temperature affects stability,
 48 persistence and coexistence in consumer-resource systems. We therefore integrated the TSR into
 a general framework for temperature-dependent consumer-resource interactions to answer the
 following questions: 1) How does the TSR affect stability and consumer:resource biomass ratios
 51 over a temperature gradient?, 2) Does the effect of the TSR depend on whether consumer and
 resource body sizes respond similarly to temperature?, 3) Does the effect of the TSR depend on
 the form of the functional response?, And finally, 4) does the TSR itself induce a change in the
 54 functional response?

Methods and results

The underlying consumer-resource dynamics

We begin, like Gilbert et al. (2014), with the Rosenzweig-MacArthur equations (Rosenzweig and
 MacArthur, 1963)

$$\begin{aligned}\frac{dR}{dt} &= rR \left(1 - \frac{R}{K}\right) - f(R)RC \\ \frac{dC}{dt} &= ef(R)RC - mC,\end{aligned}\tag{1}$$

57 which describe the rates of change in total resource $R \in [0, K]$ and consumer $C \geq 0$ biomass with
 time t .

In the absence of consumers, $C = 0$, the resource grows logistically, with intrinsic growth
 60 rate $r \geq 0$ and carrying capacity $K > 0$. The intrinsic growth rate describes the rate at which
 resource biomass increases (per unit biomass) in the absence of consumers when the resource is
 rare, $R \approx 0$. The carrying capacity is the equilibrium biomass of the resource without consumers.

63 Resource biomass is consumed by consumers at a rate $f(R)RC$, where $f(R) \geq 0$ is called
 the functional response. Of the biomass consumed, the unitless conversion efficiency parameter

$e \in [0, 1]$ determines the proportion of resource biomass that is directly converted into consumer

biomass. Consumers biomass dies at a constant per unit biomass mortality rate $m \geq 0$.

An equilibrium is reached when the two rates of change in Equation (1) are zero, and solving the system at this point gives equilibrium resource \hat{R} and consumer \hat{C} biomass. There are three equilibria for this system: total extinction $(R, C) = (0, 0)$, consumer extinction $(R, C) = (K, 0)$, and coexistence $(R, C) = (\hat{R}, \hat{C})$, with $\hat{R} > 0$ and $\hat{C} > 0$. We are primarily concerned with the latter equilibrium, as that is presumably the equilibrium current consumer-resource systems are near (we would not consider them consumer-resource systems if either the consumer or resource were absent). At this coexistence equilibrium one can calculate the ratio of consumer to resource biomass, $\hat{C} : \hat{R}$, and also perform a linear stability analysis to derive the leading (largest in absolute value) eigenvalue λ , which determines if (and how readily) the system, when perturbed a small amount from this equilibrium, will return to it (see the supplementary Mathematica file for details). Our measure of stability will be the negative of the real part of the leading eigenvalue. The system is stable if and only if this value is positive, and the system will return to equilibrium faster when this value is larger (i.e., larger positive values imply “more stable” systems). Together these two measures tell us how biomass is partitioned and how stable this partitioning is.

As explained in Gilbert et al. (2014), two aggregates well describe the dynamics of this system. The first is $m/(ef(\hat{R}))$, which describes (the inverse of) consumer growth at equilibrium, is the slope of the consumer zero-net growth isocline, and is the abundance of the resource at the coexistence equilibrium. The second aggregate is K , the equilibrium resource biomass in the absence of consumers. Dividing the second aggregate by the first gives a measure that defines the biomass potential of the resource that is converted into consumer biomass

$$B_{CR} = \frac{ef(\hat{R})K}{m}.$$

In what follows we will examine how our three measures, B_{CR} , $\hat{C} : \hat{R}$, and stability, change with temperature. We start by assuming a type-I functional response, $f(R) = a$, where a is called

84 the attack rate, which describes the rate of resource consumption per resource biomass. We later
 explore the effect of a type-II functional response and the potential for the functional response to
 change with changes in temperature.

87 **Adding temperature dependence**

Gilbert et al. (2014) discuss what is known about the temperature dependencies of the population
 dynamic parameters r , K , a , m , and e , and give equations and parameter estimates in their Table
 1. Briefly, resource growth rate r is expected to scale with metabolism as a Boltzmann-Arrhenius
 factor,

$$r(T) = r_0 \exp(-E_B/(kT))$$

where E_B is the activation energy of metabolism B (in units of eV), k is Boltzmann's constant
 ($\approx 8.62 \times 10^{-5}$ eV/Kelvin), and T is the temperature (in Kelvins). Resource carrying capacity
 K is determined by the ratio of the supply rate of nutrients into the system, S , and the rate of
 uptake of nutrients by the resource, r . With supply rate also scaling as a Boltzmann-Arrhenius
 factor with activation energy E_S , the prediction for carrying capacity becomes

$$K(T) = K_0 \exp(-(E_S - E_B)/(kT)).$$

Attack rate a depends on the temperature dependence of the body velocities v in both species,
 both of which scale as Boltzmann-Arrhenius factors with activation energies $E_{v,i}$, for $i = \{R, C\}$.
 Attack rate is then

$$a(T) = a_0 \sqrt{\sum_i [\nu_{0,i} \exp(-E_{v,i}/(kT))]^2}$$

where $\nu_{0,i}$ are rate-constants. Consumer mortality is also expected to scale as a Boltzmann-
 Arrhenius factor,

$$m(T) = m_0 \exp(-E_m/(kT)).$$

Conversion efficiency is assumed to be independent of temperature such that $e(T) = e_0$.

The black curves in Figure 1 show B_{CR} , equilibrium consumer to resource biomass ratio $\hat{C} : \hat{R}$,
 90 and stability of the coexistence equilibrium as functions of temperature T (plotted in Celsius).

In these plots r , K , a , and m all depend on temperature, unlike Figure 3 in Gilbert et al. (2014) where only K depends on temperature and the rest of the parameters are held constant. Comparing with Figure 3 in Gilbert et al. (2014), we see that adding temperature dependence in r , a , and m causes equilibrium consumer:resource biomass to decline with temperature (instead of increasing) and stability to decrease at a slower rate with increasing temperature. These changes are largely driven by the temperature dependence of consumer mortality (see supplementary Mathematica file): increasing temperature increases consumer mortality, lowering equilibrium consumer biomass and increasing stability at high temperatures (relative to the case where mortality m does not depend on temperature).

Adding mass dependence and the temperature size-rule

We next allow the population dynamic parameters to depend on the body size of the interacting species. Following DeLong et al. (2015), each parameter can be written as a power law function of the body mass of resource M_R or consumer M_C . Here we combine DeLong et al. (2015) and Gilbert et al. (2014) by letting the parameters depend on both temperature and mass: $r(T, M_R) = r(T)M_R^\rho$, $K(T, M_R) = K(T)M_R^K$, $a(T, M_C) = a(T)M_C^\alpha$, $e(T, M_C) = e(T)M_C^\epsilon$, and $m(T, M_C) = m(T)M_C^\mu$.

If mass does not change with temperature then adding these mass dependencies does not change the response of the consumer-resource dynamics to temperature. However, mass is expected to change with temperature, according to the temperature-size rule (Atkinson (1994)). We incorporate a simple form of the temperature-size rule here for illustrative purposes. In particular, we assume body mass declines linearly with temperature,

$$M_i(T) = M_i(T_{ref})(1 - \beta_i(T - T_{ref}))$$

, where β_i is the fraction that mass is reduced as temperature is increased by one degree and T_{ref} is a reference temperature, which we set to 15°C throughout. This linear decline best approximates the response of organisms with a dry mass of less than 10^{-3} mg, whereas larger organisms

experience a faster than linear decline (Forster et al., 2012).

The red curves in Figure 1 depict our main results: adding mass dependencies and the temperature-size rule modifies our prediction of how consumer-resource dynamics respond to changes in temperature. While there is little change in B_{CR} , the equilibrium consumer to resource biomass ratio is no longer expected to decline with increasing temperature and stability is now expected to increase. These changes are brought on by the indirect effect of temperature, through body mass, on the population dynamic parameters, which are acting in opposition to its direct effects. In particular, the lack of decline in the consumer to resource biomass ratio with the temperature-size rule, relative to the case without it, is primarily driven by changes in consumer conversion efficiency and the intrinsic growth rate of the resource (see supplementary Mathematica file). Both of these rates increase with declining body mass, supporting a relatively larger consumer biomass. The increase in stability at high temperatures with the temperature-size rule is caused by the increase in the resource's intrinsic growth rate along with a decrease in attack rate with decreasing consumer body size. So we see that, in the case of stability, the indirect effects of temperature are strong enough to override its direct effects, producing a qualitatively different prediction of how consumer-resource systems will respond to temperature.

In the supplementary Mathematica file we explore how the strength of the temperature-size response $\beta_C = \beta_R = \beta$ affects our predictions (see also Figure 2, green). We find that predictions for biomass ratio and stability at higher temperatures differ qualitatively from those of Gilbert et al. (2014) for $\beta \geq 0.02$. The biomass ratio begins to increase with temperature around $\beta \sim 0.03$. Larger temperature-size responses cause both the biomass ratio and stability to increase faster with temperature.

Exploring asymmetric temperature-size responses

In Figure 1 we assumed both resource and consumer body mass declined with temperature at the same rate, $\beta_C = \beta_R = 0.02$, i.e., both decline 2% per degree increase. However, larger organisms often experience larger declines in body size with temperature (Forster et al. (2012)). In Figure

2 (blue) we let consumer body size decline twice as fast as the resource, $2\beta_R = \beta_C = 0.04$.

The main effect of the asymmetric temperature-size response is that i) the B_{CR} with $E_S > E_B$

138 now asymptotes at higher temperatures (compare with the dark solid curves in Figure 1) and ii) stability now increases even faster with increasing temperature. These effects are driven by the now larger decline in attack rate. Thus, expected asymmetries in the temperature-size response
141 cause our predictions to deviate even further from those of without the temperature-size rule (Gilbert et al., 2014).

Type-II functional response

The consumption of resources in some systems may be better described by a type-II functional response,

$$f(R) = b/(1 + bhR)$$

144 where b is sometimes called the capture rate (the per resource biomass per consumer biomass rate of resource biomass consumption) and h is the handling time. This collapses to a type-I functional response at low resource biomass, $f(R) \approx b$ for $R \ll 1/(bh)$. At high resource
147 biomass a type-II functional response implies that the rate of resource consumption per consumer biomass asymptotes at $\lim_{R \rightarrow \infty} f(R)R = 1/h$, describing satiation of the consumer.

Both capture rate and handling time are known to depend on temperature and body mass. In particular, Rall et al. (2012) argue that capture rate scales like

$$b(T, M_R, M_C) = b_0 M_R^{b_R} M_C^{b_C} \exp(-E_b/(kT))$$

and handling time like

$$h(T, M_R, M_C) = h_0 M_R^{h_R} M_C^{h_C} \exp(-E_h/(kT))$$

. With these scaling the type-II functional response increases faster with temperature than the
150 type-I functional response (see supplementary Mathematica file) Much of the difference in the response of the functional responses to temperature is due to the differing temperature- and

mass- dependencies of attack rate a and capture rate b (see supplementary `Mathematica` file), and
 153 not due to the form of the functional responses (i.e., setting $h = 0$ has little effect on the response
 of the type-II functional response to temperature). When capture rate has the same temperature-
 and mass- dependencies as attack rate (Gilbert et al. (2014)), there is little difference between
 156 the response of the type-I and type-II functional responses to temperature (see supplementary
`Mathematica` file).

With the parameter values given in Rall et al. (2012), we can plot B_{CR} , $\hat{C} : \hat{R}$, and stability
 159 as functions of temperature when there is a type-II functional response (Figure 3). The main
 conclusions are: in comparison to a type-I functional response, a type-II functional response
 i) makes B_{CR} increase faster with temperature, ii) makes equilibrium biomass ratios increase
 162 with temperature, and iii) makes stability increase more quickly with temperature, despite the
 fact that a type-II functional response decreases stability at our reference temperature (15°C,
 i.e., without a direct or indirect temperature response). Thus, a type-II functional response,
 165 like asymmetric temperature-size responses, causes our predictions to vary further from those
 without the temperature-size rule (Gilbert et al., 2014).

As an aside, in this analysis we set b_0 to give $f(R) = 0.1$ at 15°C, to remain consistent
 168 with Gilbert et al. (2014). This leaves h_0 as a free parameter. However, this free parameter
 only influences the results in the case of stability. When h_0 is small enough to allow a stable
 coexistence equilibrium (roughly $h_0 < 10^{-12}$) we find that stability increases exponentially with
 171 temperature (blue curve in Figure 3). Thus, even though a type-II functional response decreases
 stability at the reference temperature (because of the lags induced by handling time), stability
 is increased at higher temperatures. The increased stability at higher temperatures with a type-
 174 II functional response is caused by the temperature dependence of the capture rate (Rall et al.
 (2012)), which differs from the temperature dependence of the type-I attack rate (Gilbert et al.,
 2014). Giving capture rate the same temperature dependence as attack rate (Gilbert et al., 2014),
 177 with a small enough handling time at the reference temperature ($h_0 < \sim 10^{-13}$) stability still
 increases exponentially with temperature, from the reference temperature, but the square root in

the expression now allows the temperature dependence of other parameters to slow and revert
this increase at higher temperatures. Larger handling times prevent the exponential increase in
stability with temperature, and the increase in handling time with temperature can even cause
stability to decrease with temperature (see supplementary Mathematica file for details).

Rall et al. (2012) compiled a large database on capture rates and handling times and compared the data to their theoretical predictions. They found that capture rate and handling time responded less strongly to temperature than expected (see their Figure 2a,d). Interestingly, we find that the temperature-size rule reduces the sensitivity of both capture rate and handling time to temperature (see supplementary Mathematica file) and hence may help explain the discrepancies observed.

A functional response that depends on the body size ratio

Functional responses tend to be roughly type-II when consumers and resources have similar body sizes, but become more sigmoidal and hence more type-III when consumers are much bigger than their resource, as resources are then better able to hide when rare (Kalinkat et al., 2013). Without the temperature-size rule, the body mass ratio remains constant with temperature, and therefore the form of the functional response is not expected to change. However, with the temperature-size rule, body sizes change. When the temperature-size responses are asymmetric, the ratio of body sizes will change and influence the form of the functional response. Because consumers are often larger than their resource, and because larger organisms are expected to have greater reductions in body size with temperature (Forster et al., 2012), the ratio of consumer to resource body size will often decrease with temperature. As stated above, lower consumer to resource body size ratios produce functional responses more like type-II, which are less stable than type-III functional responses. Hence the temperature-size rule can be said to destabilize the consumer-resource dynamics at high temperatures by promoting type-II functional responses (it can also be said that the temperature-size rule stabilizes the dynamics at lower temperatures by promoting type-III functional responses). However, the amount by which the shape of the functional response is

adjusted by the temperature-size rule does not appear to be large and therefore the stabilizing effects discussed in previous sections will likely prevail (see supplementary Mathematica file for details).

Discussion

Our results suggest changes in body size with warming have important dynamical consequences for food webs in changing thermal environments. In our temperature- and mass-dependent consumer-resource model, declining body size with warming changes the predicted outcome of consumer-resource dynamics in response to temperature. When body size declines with warming at a rate consistent with empirical observations (Forster et al. (2012)), consumer-resource biomass ratios remain stable under warming. Further, a TSR response facilitates a slight increase in system stability with warming, relative to a decrease in stability without shifts in body size. At the same time, the bioenergetic interaction strength metric (BCR) is relatively unaffected by the TSR.

Deviations in the response of consumer-resource dynamics to temperature, compared to a system with no TSR, reflects the body mass-dependence of demographic parameters. In this way, temperature acts on the system first by directly altering demographic rates, and then by indirectly altering demographic rates through allometric scaling relationships. For instance, the indirect response of the resource to warming - increased intrinsic growth rates at smaller body sizes - allows the resource to support a relatively greater consumer biomass at higher temperatures if body sizes decline. When we allowed larger (consumer) organisms to experience a greater decline in body size with warming, and thus a temperature-dependent consumer-resource body size ratio, effects of the TSR were further amplified relative to a model with symmetric declines in body size.

The body size decline rates used here were drawn from a comprehensive synthesis of experimentally observed temperature-body size responses in organisms ranging from fish to mi-

crobes (Forster et al. (2012)). Although there are a number of theoretical explanations for the
231 TSR (Angilletta and Dunham (2003); Berrigan and Charnov (1994); DeLong (2012); Perrin (1995);
van der Have and de Jong (1996)), much of its support is empirical, and rates of decline are not yet
predictable a priori. Drawing on this empirical evidence, we considered effects of instantaneous
234 body size shifts within species.

This model does not consider shifts in species composition that could further compound
the dynamical effects of shifts in body size. Our model also assumes that body size responds to
237 temperature independently of any effects of the changing consumer-resource interaction on body
size. In other words, consumer-resource interactions can select for optimal body sizes (Abrams
and Rowe (1996)), and this selection may vary over a thermal gradient. We have extended a
240 general model for how temperature affects consumer-resource interactions by including a major
empirical pattern, the TSR. Further extensions could include integrating multiple trophic levels
to determine how temperature and the TSR affect trophic cascade strength. Our model suggests
243 it would weaken it.

Our main predictions are: equilibrium consumer to resource biomass ratio is expected to
increase with temperature (due to increases in consumer conversion efficiency and the growth
246 rate of the resource associated with declining body sizes). Could test this by comparing two
systems: one where body size is allowed to decrease with temperature, and another where the
smallest individuals are removed (or the opposite).

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Figure legends

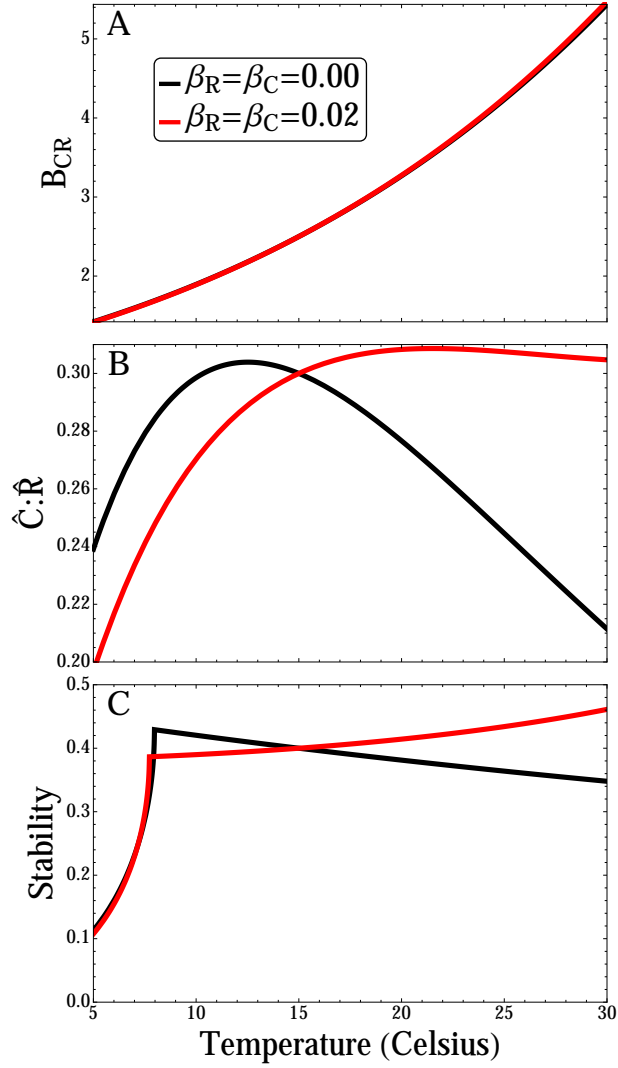


Figure 1: B_{CR} , equilibrium consumer to resource biomass ratio $\hat{C} : \hat{R}$, and stability of the coexistence equilibrium as functions of temperature T (plotted in Celsius) with (red) and without (black) mass dependencies and the temperature-size rule. Rate-constants were chosen to make $r = 2$, $K = 100$, $a = 0.1$, $m = 0.6$, and $e = 0.15$ at 15°C (as in Figure 3 of Gilbert et al., 2014). Other parameters as in Gilbert et al. (2014) and DeLong et al. (2015): $E_B = 0.32$, $E_S = 0.9$, $E_m = 0.65$, $E_{v,i} = 0.46$, $v_{0,i} = 1$, $\kappa = -0.81$, $\alpha = 1$, $\epsilon = -0.5$, $\mu = -0.29$, $\rho = -0.81$, $\beta_i = 0$ (black), $\beta_i = 0.02$ (red). Note that we allow all population dynamic parameters to depend on temperature and mass, unlike Figure 3 in Gilbert et al. (2014), where only K varies.

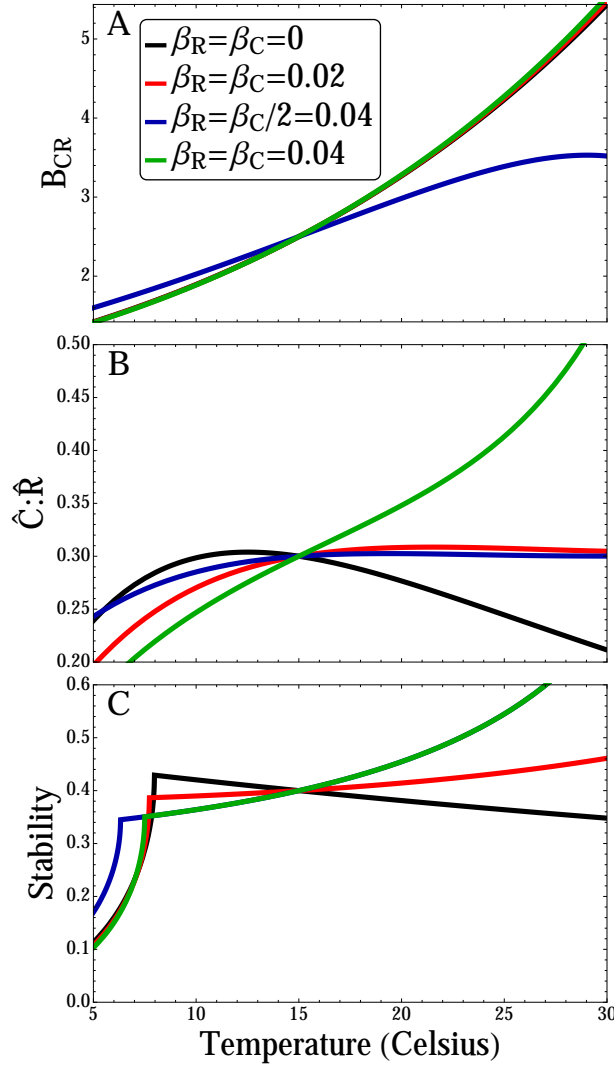


Figure 2: B_{CR} , equilibrium consumer to resource biomass ratio $\hat{C} : \hat{R}$, and stability of the coexistence equilibrium as functions of temperature T (plotted in Celsius) without the temperature-size rule (black), with a relatively weak, symmetric temperature size rule (red), with an asymmetric temperature-size rule (green), and with a relatively strong, symmetric temperature-size rule (blue). Rate-constants were chosen to make $r = 2$, $K = 100$, $a = 0.1$, $m = 0.6$, and $e = 0.15$ at 15°C (as in Figure 3 of Gilbert et al., 2014). Other parameters as in Gilbert et al. (2014) and DeLong et al. (2015): $E_B = 0.32$, $E_S = 0.9$, $E_m = 0.65$, $E_{v,i} = 0.46$, $v_{0,i} = 1$, $\kappa = -0.81$, $\alpha = 1$, $\epsilon = -0.5$, $\mu = -0.29$, $\rho = -0.81$.

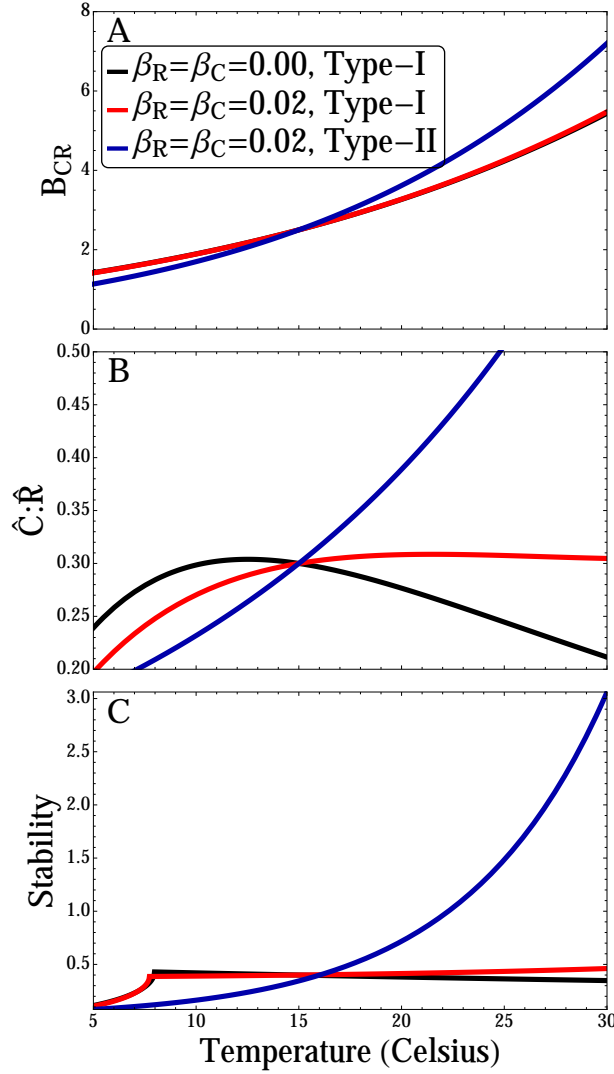


Figure 3: B_{CR} , equilibrium consumer to resource biomass ratio $\hat{C} : \hat{R}$, and stability of the coexistence equilibrium as functions of temperature T (plotted in Celsius) with (red and blue) and without (black) mass dependencies and the temperature-size rule. Type-II functional response in blue. Rate-constants were chosen to make $r = 2$, $K = 100$, $f(R) = 0.1$, $m = 0.6$, and $e = 0.15$ at 15°C (as in Figure 3 of Gilbert et al. (2014)). Other parameters as in Gilbert et al. (2014), DeLong et al. (2015), and Rall et al. (2012): $E_B = 0.32$, $E_S = 0.9$, $E_m = 0.65$, $E_{v,i} = 0.46$, $v_{0,i} = 1$, $\kappa = -0.81$, $\alpha = 1$, $\epsilon = -0.5$, $\mu = -0.29$, $\rho = -0.81$, $a_C = 1/4 + 2/3$, $a_R = 1/3$, $h_C = -2/3$, $h_R = 0.5$, $E_a = 0.65$, $E_h = -0.65$, $h_0 = 10^{-13}$.