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The Temperature-Size Rule in Ectotherms: Simple Evolutionary Explanations May Not Be General

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ABSTRACT: In many organisms, individuals in colder environments grow more slowly but are larger as adults. This widespread pattern is embodied by two well-established rules: Bergmann's rule, which describes the association between temperature and body size in natural environments, and the temperature-size rule, which describes reaction norms relating temperature to body size in laboratory experiments. Theory predicts that organisms should grow to be larger in colder environments when growth efficiency decreases with increasing environmental temperature. Using data from 97 laboratory experiments, including 58 species of ectotherms, we found little evidence that growth efficiency is negatively related to environmental temperature within the thermal range that is relevant to the temperature-size rule. Instead, growth efficiency was either positively related or insensitive to environmental temperature in the majority of cases (73 of 89 cases for gross growth efficiency and 18 of 24 cases for net growth efficiency). Two possibilities merit consideration. First, high temperatures may impose constraints on growth that only arise late during ontogeny; this simple and potentially general explanation is supported by the fact that thermal optima for growth efficiency and growth rate decrease as individuals grow. Alternatively, the general explanation for relationships between temperature and body size may not be simple. If the latter view is correct, the best approach might be to generate and test theories that are tailored specifically to organisms with similar behavior and physiology.

Keywords: body size, ectotherms, growth efficiency, growth rate, life history, temperature.

On-line enhancements: appendix table, literature cited.

Biologists are fascinated by variation in body size (for recent reviews, see Peters 1983 or Bonner 1988). This fascination is hardly surprising, considering that the range of body sizes spans six orders of magnitude, from bacteria to blue whales. Even within species, body sizes of adults can vary dramatically. Intraspecific variation in body size is particularly intriguing because it suggests strong associations between an organism's size and its environment. For example, Bergmann (1847; translation by James [1970]) noticed that mammals tend to be larger in colder environments, a phenomenon now referred to as Bergmann's rule. Recently, phylogenetic comparative analyses confirmed the existence of Bergmann's rule in mammals (Ashton et al. 2000), and similar relationships between environmental temperature and body size were established for birds and some ectotherms (reviewed by Ashton 2001; also see Ashton 2002*a*, 2002*b*; Ashton and Feldman, 2003). In general, animals found in colder climates tend to be larger as adults than their conspecifics in warmer climates. This pattern even holds when altitude or latitude is used as a proxy for environmental temperature (James 1970; Ashton et al. 2000; Ashton 2002*a*, 2002*b*; Ashton and Feldman 2003).

Laboratory studies support the notion that animals reared at lower temperatures grow to a larger body size. In fact, recent reviews indicate that this pattern is observed in a diverse group of organisms, including animals, plants, protozoans, and bacteria. Atkinson (1994, 1995) estimated that >80% of ectothermic species studied in laboratories exhibited faster growth but smaller adult body size at higher rearing temperatures. This trend, dubbed the temperature-size rule (Atkinson 1996), is a special case of Bergmann's rule in which the relationship between environmental temperature and body size is the product of phenotypic plasticity (von Bertalanffy 1960). Recognition of the temperature-size rule has caused a resurgence of efforts to understand how temperature influences the growth and body size of organisms (reviewed by Atkinson and Sibly [1997]). If one can demonstrate that natural selection favors a reaction norm in which organisms at low temperatures delay maturity until reaching a relatively

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large body size, then a single explanation might account for much of the variation in body size observed in laboratories and natural populations.

Though the temperature-size rule applies to many ectotherms, Berrigan and Charnov (1994) noted that the phenomenon is a puzzle for life historians. Other environmental variables that affect growth rate (e.g., food availability) have a parallel effect on adult body size, such that better conditions result in faster growth to a larger final size. However, temperature has contradictory effects on growth rate and body size; higher temperatures result in faster growth to a smaller final size. Until recently, few models of life-history evolution were capable of explaining such a reaction norm, and none seemed to be applicable to so many different groups of ectotherms (Berrigan and Charnov 1994). Indeed, the quest for generality has had a major influence on both theoretical and empirical efforts to solve the puzzle. Atkinson (1996) aptly summarized the frame of mind that has predominated efforts to understand the effects of temperature on body size: "The discovery of a widespread relationship such as a temperature-size rule tends to direct research towards general explanations which apply throughout the ectotherms, and away from those specific to particular populations, species or groups of species. Simple, rather than complex explanations are also usually sought" (p. 188).

Several simple explanations have been proposed for the temperature-size rule (reviewed by Atkinson and Sibly 1997). All but one, however, have failed the test of generality. In this article, we evaluate the generality of a promising mechanism for the relationship between temperature and body size that was first proposed by von Bertalanffy (1960). Despite recent attempts to reinterpret and modify von Bertalanffy's original idea, we show that the mechanism is not valid for a large sample of ectotherms, including fish, mollusks, and arthropods. We discuss alternative mechanisms that are capable of producing the patterns of growth and body size observed in ectotherms. Finally, we argue that a general explanation for the relationship between temperature and life history may not be simple and might only be attained by carefully considering the mechanisms operating in each of many special cases.

The Berrigan-Charnov Model: A General Explanation for the Temperature-Size Rule?

Berrigan and Charnov (1994) not only recognized that the temperature-size rule was puzzling, but they also offered a promising solution to the puzzle. They proposed that a trade-off between the growth rate and the asymptotic body size could produce life histories that conform to the temperature-size rule. To illustrate their point, they modeled the optimal age and size at maturity for organisms that exhibit asymptotic growth, described by the function

$$s(t) = A(1 - Be^{-kt}), \tag{1}$$

where t is time, $s(t)$ is body size at time t, A is asymptotic body size, k is a coefficient of growth, and $B = (1 - s(0)/A)$, where $s(0)$ is the size at the beginning of the growth interval. Additionally, they assumed that fecundity increases with increasing body size and that the rate of juvenile mortality is constant. Based on these assumptions, relatively rapid growth would favor early maturity at a small body size if the coefficient of growth k and the asymptotic size A are negatively related. Thus, Berrigan and Charnov provided a plausible explanation for the temperature-size rule, assuming that increasing environmental temperature does, in fact, decrease A while increasing k. In support of their model, Berrigan and Charnov noted that negative correlations between k and A are found in some fish. However, using parameters estimated from empirical studies of growth to test the model is tautological because the asymptotic sizes are probably a consequence of diverting resources from growth to reproduction and are not an actual constraint on growth (Czarnoleski and Kozlowski 1998). In other words, empirical estimates of k and A are determined by the life-history strategy, so they cannot be used to explain that strategy. Berrigan and Charnov (1994) realized the need for a better validation of their model and suggested studying the growth of organisms that have been experimentally manipulated to prevent reproduction. Strong support for the model requires the discovery of a proximate mechanism for a negative relationship between k and A. In particular, why would increasing environmental temperature increase k but decrease A (Sevenster 1995)?

Perrin (1995) was quick to offer a proximate mechanism for the negative relationship between k and A. Perrin based his argument on the ideas of von Bertalanffy (1960), who outlined a simple equation to describe the growth rates of organisms:

$$d\omega/dt = \eta\omega^{\mathrm{m}} - \kappa\omega^{\mathrm{n}}, \tag{2}$$

where ω is the body mass of an organism, η and κ are coefficients of anabolism and catabolism, respectively, and m and n are constants. Von Bertalanffy surmised that faster growth but smaller final sizes at higher temperatures is caused by the differential effects of temperature on anabolism and catabolism; catabolism relies mainly on chemical processes that are highly sensitive to temperature, but anabolism relies on physical processes that are relatively insensitive to temperature (von Bertalanffy 1960). Perrin (1995) formalized von Bertalanffy's argument by proposing the following relationship between the thermal sensitivities of anabolism and catabolism:

$$\frac{1}{\kappa}\frac{d\kappa}{dT} > \frac{1}{\eta}\frac{d\eta}{dT}, \tag{3}$$

where T is the environmental temperature (a simplified formulation from Atkinson and Sibly 1997). If this expression is valid, the Q_{10} of catabolism must be greater than the Q_{10} of anabolism. The von Bertalanffy-Perrin model provides a proximate mechanism for the temperature-size rule because it predicts that increased temperature would result in faster growth but a smaller asymptotic size, even though increased food availability would speed growth and increase asymptotic size (Perrin 1995). Therefore, support for this model would also be considered support for Berrigan and Charnov's ultimate explanation for the temperature-size rule. Although there is anecdotal support for the von Bertalanffy-Perrin model (reviewed by Atkinson and Sibly 1997), a thorough evaluation has not been undertaken.

Evaluating the von Bertalanffy-Perrin Model

The validity of the von Bertalanffy-Perrin model rests on two critical assumptions (see Perrin 1995). The first assumption is that the rate of catabolism increases more rapidly with body mass than does the rate of anabolism. This assumption takes the following form:

$$d\omega/dt = \eta\omega^{2/3} - \kappa\omega^{1}. \tag{4}$$

Note that m and n have been assigned values of 2/3 and 1, respectively (Perrin 1995). The second assumption is that the coefficient of catabolism, κ, is more sensitive to temperature than is the coefficient of anabolism, η (see eq. [3]). Both assumptions are necessary to generate a result that is consistent with the temperature-size rule. If the first assumption is violated, an organism will grow indefinitely and no asymptotic body mass will be attained (von Bertalanffy 1960, p. 180). If the second assumption is violated, the von Bertalanffy-Perrin model would not produce the result of a negative relationship between the growth coefficient and the asymptotic size, which is the mechanism for the temperature-size rule that was proposed by Berrigan and Charnov (1994).

Although the critical assumptions of the von Bertalanffy-Perrin model are easily identified, evaluating the model is not a simple matter. Both von Bertalanffy (1960) and Perrin (1995) used the terms "anabolism" and "catabolism" synonymously with the increase and decrease in body mass, respectively. As such, the coefficients of anabolism and catabolism in von Bertalanffy's model comprise physiological processes that proceed at different rates (e.g., digestion, metabolism, and excretion), and these rates are difficult to estimate independently over comparable time periods. Consequently, a goal of estimating the effects of temperature on η and κ for a large number of species is unreasonable. Fortunately, the model does make a testable prediction about the effect of temperature on growth efficiency, as it is commonly defined by physiologists (Wieser 1994). Growth efficiency includes both anabolic and catabolic processes, and these processes are typically measured in a common currency (e.g., mass or energy) for an identical duration. Moreover, the thermal sensitivity of growth efficiency has been measured in a broad set of ectothermic taxa in controlled laboratory settings, enabling one to use existing data to conduct a rigorous test of the von Bertalanffy-Perrin model.

Using equation (4), we generated a testable prediction about the relationship between environmental temperature and growth efficiency. Assuming that body composition is relatively homogeneous (i.e., we can use the terms "change in mass" and "change in energy content" interchangeably), the terms $\eta\omega^{2/3}$ and $\kappa\omega^{1}$ are equal to the rates at which energy is anabolized and catabolized, respectively. In fact, von Bertalanffy's equation is functionally equivalent to the balanced energy equation of Winberg (1956), in which the growth of an nonreproductive individual is described as follows:

$$P = [C(AE)] - R, \tag{5}$$

where P is the production of somatic tissue (i.e., growth), C is the consumption of energy, AE is the efficiency with which consumed energy is absorbed, and R is the sum of all metabolic expenditures. From Winberg's model, the equation for net growth efficiency (K_2) can be derived (Wieser 1994):

$$K_2 = \frac{P}{P+R} = \frac{[C(AE)] - R}{C(AE)}. \tag{6}$$

If we consider K_2 to be instantaneous, $C(AE)$ and R are equivalent to $\eta\omega^{2/3}$ and $\kappa\omega^{1}$, respectively. By substituting the arguments of Winberg's model for those of the von Bertalanffy-Perrin model and by simplifying the equation, we can define K_2 as follows:

$$K_2 = \frac{[C(AE)] - R}{C(AE)} = \frac{\eta\omega^{2/3} - \kappa\omega^{1}}{\eta\omega^{2/3}} = 1 - \frac{\kappa}{\eta}\omega^{1/3}. \tag{7}$$

To explore the influence of temperature on the K_2 of an organism, we make κ and η functions of temperature as assumed by the von Bertalanffy-Perrin model:

$$K_2 = 1 - \frac{\kappa(T)}{\eta(T)}\omega^{1/3}. \tag{8}$$

Taking the derivative of K_2 with respect to temperature yields the following:

$$\frac{dK_2}{dT} = -\omega^{1/3}\left[\frac{\kappa'(T)\eta(T) - \kappa(T)\eta'(T)}{\eta(T)^2}\right]. \tag{9}$$

Note that the derivative of K_2 with respect to T is negative when the following condition is met:

$$\frac{\eta'(T)}{\kappa'(T)} < \frac{\eta(T)}{\kappa(T)}. \tag{10}$$

The von Bertalanffy-Perrin model requires that this condition be met because it assumes that $\eta'(T)$ is positive and less than $\kappa'(T)$ (eq. [3]) and that $\eta(T)$ is greater than $\kappa(T)$ for an organism that is growing (eq. [4]). Therefore, K_2 must decrease with increasing temperature if the von Bertalanffy-Perrin model is an accurate description of the growth of an organism. Gross growth efficiency ($K_1 = P/C$) is also predicted to decrease with increasing temperature, unless *AE* increases appreciably (Malloy and Targett 1991).

We not only can confirm whether the von Bertalanffy-Perrin model offers a viable mechanism for the temperature-size rule, but we also can define the exact range of temperatures over which the model applies. The temperature-size rule is based partly on the observation that animals grow faster at higher temperatures. In fact, Atkinson (1994, 1995) confined his reviews of the effect of temperature on body size to the range of temperatures in which growth rate increased with increasing temperature. The thermal sensitivity of growth rate in ectotherms is well described by a unimodal function, such that growth rate is maximal at an intermediate temperature and is significantly reduced at lower and higher temperatures (Warren and Davis 1967; Brett 1979). Because growth efficiency is 0 when growth rate is 0, the function describing the thermal sensitivity of growth efficiency must also have a particular form: growth efficiency must equal 0 at the critical thermal limits for growth rate (i.e., the lower and upper temperatures at which growth rate is 0), and the maximal growth efficiency must occur at an intermediate temperature. The von Bertalanffy-Perrin model can only apply to the range of temperatures in which growth rate increases but net growth efficiency decreases with increasing temperature. Such a thermal range can only exist if the temperature that maximizes growth efficiency is lower than the temperature that maximizes growth rate (fig. 1). The exact magnitude of this thermal range for a given ectotherm can be quantified by comparing the thermal optima for growth rate and growth efficiency.

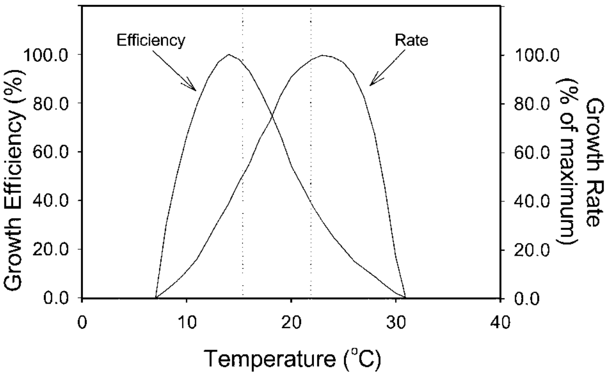

Figure 1: Hypothetical thermal sensitivities of growth rate and growth efficiency. The dotted lines define the range of temperatures over which the von Bertalanffy-Perrin model can apply. Within this range, theory predicts that individuals reared at higher temperatures should grow faster but reach a smaller final size. Note that this condition exists only when the thermal optimum for growth efficiency is lower than the thermal optimum for growth rate.

A comparison of growth efficiencies among individuals reared at different temperatures is only an appropriate test of the von Bertalanffy-Perrin model if all individuals are of the same body mass because growth efficiency is assumed to be mass dependent (eq. [9]). Otherwise, we must consider how differences in body mass might alter the prediction that growth efficiency is negatively related to environmental temperature. As it turns out, this consideration does not affect the prediction that the von Bertalanffy-Perrin model makes about the thermal sensitivity of growth efficiency. Even though long time intervals would enable individuals reared at different temperatures to diverge significantly in body mass, the net effect of this divergence would be that individuals at higher temperatures should still grow less efficiently. The reason is that, in the model, body mass has a greater impact on catabolism than it does on anabolism (eq. [4]). Thus, as long as individuals assigned to different temperatures are of the same initial mass and are reared for the same duration, the von Bertalanffy-Perrin model predicts that individuals at higher temperatures will have lower growth efficiencies.

Recent analyses of the relationship between environmental temperature and growth efficiency have yielded mixed results. Straile (1997) used published data to determine the effect of temperature on gross growth efficiency in several groups of protozoans and metazoans. He concluded that growth efficiency was negatively related to temperature in flagellate protozoans, was positively related to temperature in ciliate protozoans and copepods, and was not affected by temperature in rotifers and cladocerans. In contrast to Straile's conclusion, Ikeda et al. (2001) reported a negative relationship between temperature and net growth efficiency for marine copepods. Finally, Houde (1989) concluded that the gross growth efficiency of fish was insensitive to temperature. Nevertheless, all of these conclusions were based on interspecific relationships, which do not necessarily reflect intraspecific relationships between temperature and growth efficiency. Given that the von Bertalanffy-Perrin model is intended to explain phenotypic plasticity in response to environmental temperature, a rigorous test of its prediction requires examination of the thermal sensitivity of growth efficiency within species. More importantly, one must demonstrate not only that growth efficiency is negatively related to environmental temperature but also that the initial rate of growth is positively related to temperature. If these criteria were met in the majority of species, Berrigan and Charnov's hypothetical trade-off between the growth rate and the asymptotic body size would be supported as a general mechanism for the temperature-size rule.

Methods

To assess the validity of the von Bertalanffy-Perrin model, we examined the literature for laboratory studies that reported controlled observations of growth rate and growth efficiency at different temperatures. Most studies were focused on fish, but a smaller number of studies of mollusks and arthropods were also acquired. Although the taxonomic focus was based on the availability of data, it is relevant to our goal. Berrigan and Charnov (1994) used negative relationships between k and A in fish to support their model. Therefore, it is logical to focus our investigation on fish so that we might conclude that the von Bertalanffy-Perrin model is a potential cause of these relationships.

In our analysis, we only included the results of experiments in which the following conditions were met: growth rate and growth efficiency (K_1 or K_2) were measured at a minimum of three temperatures, the initial size of individuals did not differ significantly among treatment groups, growth was measured for the same duration at all temperatures, and food was supplied at a rate that enabled animals to achieve satiation. When growth was examined at multiple diets or salinities, we used data for the treatment that maximized growth rate because this criterion was used by Atkinson (1994) when he established the temperature-size rule. Based on our criteria, we obtained estimates of the thermal sensitivities of K_1 and K_2 for 89 populations of 53 species and 24 populations of 20 species, respectively (see appendix in the online edition of the *American Naturalist*). For eight of these species, we used data presented by the authors to calculate growth efficiencies according to equation (6).

For each study, we examined growth efficiency over the range of temperatures at which growth rate increased with increasing temperature (see fig. 1) and determined whether the relationship between temperature and growth efficiency was positive, negative, unimodal, or constant (i.e., no relationship). Whenever possible, we used the results of statistical analyses performed by the authors (i.e., ANOVA and post hoc tests) to determine the temperatures that maximized growth rate and growth efficiency. If statistical analyses were not presented, we used 95% confidence intervals to assess differences in growth rate and growth efficiency among groups reared at different temperatures. In many cases, the maximal growth rate or maximal growth efficiency occurred at two or more temperatures (e.g., see data for *Abudefduf abdominalis* in online appendix), indicating the existence of an optimal temperature range (sensu Huey and Stevenson 1979). When estimating the thermal optimum for growth rate, we used the lowest temperature in the optimal temperature range because the temperature-size rule does not apply to temperatures within or above the optimal temperature range. When there was an optimal temperature range for growth efficiency, we used the temperature that was closest to the optimal temperature for growth rate. Our procedures for estimating thermal optima were chosen to ensure the most accurate description of the thermal range over which the von Bertalanffy-Perrin model could be valid.

When testing the hypothesis that individuals reared at higher temperatures have lower growth efficiencies, we noted that growth measured as change in wet body mass might not accurately reflect the change in dry body mass or energy content. Both von Bertalanffy and Atkinson used the term "growth" synonymously with change in body mass (von Bertalanffy 1960, p. 178; Atkinson 1994, p. 7), and the temperature-size rule is based partially on studies of reporting only wet body masses of organisms (Atkinson 1994, 1995). Still, environmental temperature can affect the body composition of an organism. Therefore, we distinguished between studies that only accounted for growth in terms of wet body mass and those that estimated growth in terms of dry body mass or energy. This approach enabled us to identify any bias caused by the effect of environmental temperature on body composition, without arbitrarily dismissing studies that did not account for this effect.

Results

The prediction that growth efficiency would be negatively related to temperature in the majority of cases was not well supported (table 1). Of the 24 populations for which

Table 1: Relationships between temperature and growth efficiency vary greatly among ectotherms

Taxon	Positive	Negative	Unimodal	Constant	Total
Gross (K_1):					
Fish	44	4	8	18	74
Mollusks	5	1	0	2	8
Arthropods	4	1	2	0	7
Total	53	6	10	20	89
Net (K_2):					
Fish	3	0	1	2	6
Mollusks	6	1	1	0	8
Arthropods	4	1	2	3	10
Total	13	2	4	5	24

Note: Data are the number of studies for which the relationship between temperature and growth efficiency (gross or net) was positive, negative, unimodal, or constant (i.e., no relationship).

the effect of temperature on K_2 was quantified, negative or unimodal relationships between temperature and growth efficiency were reported in only six cases. A positive relationship between temperature and K_2 was observed about twice as often (13 of 24 cases). Of the 89 populations for which K_1 was quantified, negative or unimodal relationships were reported in 16 cases, but positive relationships were reported in 53 cases. The proportion of the populations in each category did not differ significantly between studies of K_1 and studies of K_2 (likelihood ratio $\chi^2 = 0.60$, df = 3, $P = .90$). When both K_1 and K_2 were measured, the thermal sensitivities were usually similar (12 of 16 cases; see online appendix).

The critical test of the von Bertalanffy-Perrin model is whether the thermal optimum for growth efficiency is lower than the thermal optimum for growth rate. Our analysis shows very clearly that this is not the case (fig. 2). This prediction was supported in only 16 of 54 populations for K_1 and six of 16 populations for K_2. Contrary to the prediction, the optimum temperature for growth efficiency and that for growth rate were equivalent in the majority of cases (36 of 54 populations for K_1 and eight of 16 populations for K_2). Of the 29 species of fish, six species of mollusks, and nine species of arthropods that are represented, the von Bertalanffy-Perrin model can only be valid for 14 species. Even for those species in which the optimum temperature for growth efficiency was lower than the optimum temperature for growth rate, the difference between the two thermal optima averaged only 4.5°C (range = 1°–12.5°C). Thus, we conclude that the von Bertalanffy-Perrin model applies to a very narrow range of temperatures in the minority of ectotherms studied to date.

Our conclusions were not altered by excluding those cases in which growth efficiencies were calculated from measures of wet mass, rather than dry mass or its energetic equivalent. In fact, K_2 was calculated from measures of wet mass for only one of 24 populations (Malloy and Targett 1991), and no significant relationship between temperature and growth efficiency was observed in this case. Of the 47 populations for which K_1 was estimated from dry mass or its energetic equivalent, a negative or a unimodal relationship between temperature and growth efficiency was observed in only eight cases. A positive relationship was observed in 26 cases, and no significant relationship was observed in 13 cases. The proportion of the populations in each category did not differ significantly between studies measuring wet mass and those measuring

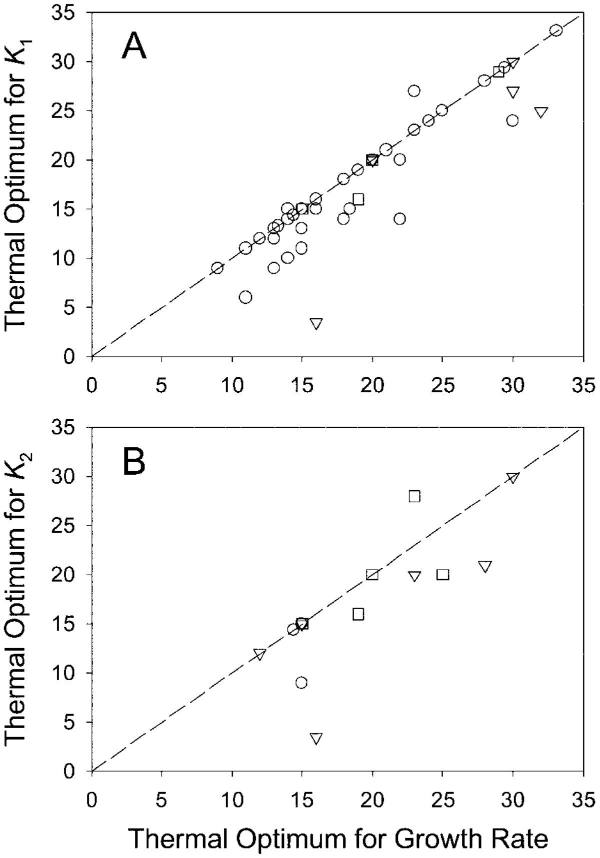

Figure 2: The thermal optimum for growth efficiency was usually less than or equal to the thermal optimum for growth rate. Plots *A* and *B* show data for gross growth efficiency ($n = 54$) and net growth efficiency ($n = 16$), respectively. Eleven points overlap in *A*; two points overlap in *B*. In each plot, the dashed line is a reference at which the two thermal optima are equivalent. Twenty-nine species of fish (*circles*), six species of mollusks (*squares*), and nine species of arthropods (*triangles*) are represented. The von Bertalanffy-Perrin model can only account for the temperature-size rule within a narrow range of temperatures in 14 of the 44 species.

dry mass or energy (likelihood ratio $\chi^2 = 6.12$, df = 3, $P = .11$).

Discussion

The model of Berrigan and Charnov (1994) provides a relatively simple yet potentially general explanation for the temperature-size rule. If higher environmental temperatures enhance the growth rate but reduce the asymptotic body size, one might expect the optimal reaction norm to be a negative relationship between temperature and adult body size. The von Bertalanffy-Perrin model offers a proximate mechanism by which the hypothetical trade-off between the growth rate and the asymptotic body size could arise (Perrin 1995); unfortunately, this model is not general to ectotherms. The required condition that net growth efficiency decreases with increasing temperature was observed in only six of 20 species for which data are currently available (online appendix). More often than not, growth rate and growth efficiency were maximized at the same temperature (fig. 2), indicating the von Bertalanffy-Perrin model does not apply to the majority of species. Even when the thermal optimum for growth rate was higher than the thermal optimum for growth efficiency, the difference between the two averaged only 4.5°C. In each case, the actual difference between thermal optima might have been larger than estimated because measures of growth were made at intervals of 1°–6°C (average = 3.4°C). However, the temperature-size rule describes reaction norms that typically span ranges ≥10°C (see Atkinson 1994 and references therein). Therefore, there is little evidence that the von Bertalanffy-Perrin model can provide a proximate mechanism for the trade-off between k and A that is assumed in Berrigan and Charnov's optimization model.

Why do available data fail to support the von Bertalanffy-Perrin model? One possibility is that many of the species included in our analysis are exceptions to the temperature-size rule. If that is so, broadening the taxonomic scope of future analyses might lead to the realization that many ectotherms do not follow the temperature-size rule and that the von Bertalanffy-Perrin model applies to those species that do follow the rule. Two observations indicate that additional data will not generate better support for the von Bertalanffy-Perrin model. The first observation is that two of the species that are known to follow the temperature-size rule, *Paralichthys olivaceus* and *Drosophila melanogaster*, did not suffer reduced growth efficiency when reared at temperatures that resulted in faster growth (online appendix). Second, within each of the major clades (i.e., Pisces, Mollusca, and Arthropoda), the number of cases in which growth efficiency decreased with increasing temperature was exceeded by the number of cases in which growth efficiency increased with increasing temperature (table 1). Unless the majority of species represented in each clade happen to be exceptions to the temperature-size rule, additional data will not alter our conclusion.

A more likely reason for the failure of the von Bertalanffy-Perrin model is that it includes some critical assumptions about thermal physiology that are invalid for most ectotherms. One of these assumptions is that the effects of temperature on anabolism and catabolism remain constant through time. However, acclimation can alter the acute effects of temperature on the rates of anabolism and catabolism (i.e., Q_{10} effects). Chronic exposures to different temperatures alter rates of anabolism and catabolism via modifications of cellular activities (Vezina and Guderley 1991; Foster et al. 1992; Koch et al. 1992), reducing variation in the scope for growth during fluctuations in environmental temperature (Evans 1990; Requena et al. 1997). Thus, thermal sensitivities of anabolism and catabolism measured over short durations are not necessarily accurate predictors of thermal sensitivities of growth rates and growth efficiencies over longer durations. The von Bertalanffy-Perrin model does not account for the possibility of acclimation, which might eliminate or reverse the anticipated relationship between environmental temperature and growth efficiency. Acclimation of growth efficiency undoubtedly involves costs, but these costs can be outweighed by the benefits of relatively rapid growth in certain environments (see review by Gotthard [2001]).

The von Bertalanffy-Perrin model also includes a critical assumption about the allometries of anabolism and catabolism. Specifically, von Bertalanffy (1960) and Perrin (1995) assumed that anabolism scales allometrically with body mass ($m = 2/3$) and that catabolism scales isometrically with body mass ($n = 1$; see eq. [4]). Actually, resting metabolic rate, which is a large component of catabolism, scales allometrically with body mass ($n < 1$) in most fish (Clarke and Johnston 1999). This fact alone does not refute the von Bertalanffy-Perrin model; as long as the scaling exponent for catabolism is greater than the scaling exponent for anabolism ($n > m$), the von Bertalanffy growth equation predicts an asymptotic growth trajectory. Therefore, even if catabolism scales allometrically, the model could predict asymptotic growth and thus could still provide a proximate explanation for the temperature-size rule. However, other investigators have argued convincingly that asymptotic growth functions, such as the one used in the von Bertalanffy-Perrin model, are inappropriate for modeling the evolution of age and size at maturity because such functions place unrealistic restrictions on the growth trajectories of individuals (Day and Taylor 1997; Czarnoleski and Kozlowski 1998). Asymptotic growth would result from the optimal allocation of energy to growth and reproduction even if no restrictions on body size were imposed (Kozlowski 1992, 1996; Kozlowski and Teriokhin 1999). If asymptotic growth is a consequence of optimal energy allocation, the scaling exponents estimated from empirical studies are not parameters that constrain adult body size; rather, they are a by-product of the ontogenetic shift in the allocation of energy from growth to reproduction. In this case, one should not expect the scaling exponents to conform to the strict assumptions of the von Bertalanffy-Perrin model. In support of this idea, there is empirical evidence that the scaling exponents that relate anabolism and catabolism to body mass are not constants but depend on environmental temperature. Not surprisingly, the condition necessary to force an asymptotic growth trajectory, $n > m$, is not always met (Strong and Daborn 1980; Sharma and Pant 1984; Fonds et al. 1992; Ikeda et al. 2001).

Despite the failure of the von Bertalanffy-Perrin model, there may be still be a relatively simple explanation for the temperature-size rule. Atkinson (1996) proposed that early maturity at a small body size in warm environments could be caused by a constraint on growth that arises late in ontogeny. Our review of the literature leads us to believe that such a constraint might result from thermal effects on the allometries of anabolism and catabolism. Strong and Daborn (1980) used power functions to describe the allometries of ingestion and metabolism in isopod *Idotea baltica* at temperatures ranging from 4° to 14°C. The rate of ingestion was proportional to $\omega^{0.94}$ at 4°C, but it was proportional to $\omega^{0.71}$ at 14°C. In contrast, metabolic rate was proportional to $\omega^{0.68}$ at 9°C but was proportional to $\omega^{1.00}$ at 14°C. A direct consequence of these thermal shifts in allometries is that the thermal optimum for growth decreases throughout ontogeny. Strong and Daborn argued that this ontogenetic shift in the thermal optimum for growth determined the relationship between environmental temperature and adult body size in isopods. This hypothetical mechanism is independent of that proposed by von Bertalanffy (1960) and Perrin (1995) because it deals with thermal sensitivities of the exponents in von Bertalanffy's equation (m and n of eq. [2]), not the coefficients (η and κ of eq. [2]). Whereas the von Bertalanffy-Perrin model assumes that the coefficients of anabolism and catabolism increase with increasing temperature, in *I. baltica*, the coefficient in the relationship between body mass and metabolic rate actually decreased with increasing temperature (Strong and Daborn 1980).

If Strong and Daborn's data (1980) are indicative of a widespread relationship between body size and the thermal sensitivity of growth, Atkinson's hypothetical constraint on growth at large sizes might be a general explanation for the temperature-size rule. The data assembled for our analysis lend preliminary support to the generality of Strong and Daborn's observations. In all six species for which the thermal sensitivities of growth rate and growth efficiency were estimated for individuals of different sizes, the thermal optimum for growth efficiency decreased with increasing body size. In addition to *I. baltica*, the thermal optimum for growth efficiency decreased with increasing body size in three species of fish (*Gadus morhua*, *Hippoglossus hippoglossus*, and *P. olivaceus*) and two species of amphipods (*Asellus aquaticus* and *Hyalella azteca*). In *P. olivaceus*, the thermal optimum for K_1 dropped from 20°C at 4–16 g to 10°C at 176 g. A similar phenomenon was observed in mollusks: the thermal optimum for K_2 was 26°C in small oysters, *Ostea edulis* (Beiras et al. 1995), but was 10°–15°C in larger oysters (Buxton et al. 1981). Consequently, the thermal optimum for growth rate tended to decrease with increasing body size in these species (Boehlert and Yoklavich 1983; Degani et al. 1988; Björnsson and Tryggvadóttir 1996; Panov and McQueen 1998; Björnsson et al. 2001). Additional empirical studies are needed to assess the generality of these observations, and a quantitative theory is needed to link these empirical relationships to the evolution of reaction norms for age and size at maturity.

The fact that the temperature-size rule applies to the majority of ectotherms studied to date does not guarantee that there is a simple, general explanation for the relationship between environmental temperature and life history. Because all ectotherms do not exhibit the same behavior and physiology, one should not expect the same proximate mechanisms to underlie temperature-size relationships in all ectotherms even if most ectotherms do exhibit similar reaction norms for growth rate and body size. Studies of geographic variation in body size illustrate the complex mechanisms that can underlie intraspecific variation in body size. Bergmann size clines, although consistent with the reaction norms described by the temperature-size rule, have a genetic basis in some species because differences in body size among populations are preserved when all are reared for several generations in a common environment (Partridge and Coyne 1997). Moreover, the same pattern of variation in body size can be generated via different proximate mechanisms (Partridge and French 1996). For example, Huey et al. (2000) found that convergent evolution of a Bergmann size cline in *Drosophila subobscura* was based on two different means of lengthening the wing. If the general explanation for geographic variation in body size seems to be complicated, one should not expect that the general explanation for the temperature-size rule is any less complicated.

Given the diversity of proximate mechanisms that underlie intraspecific variation in body size, a more productive approach might be to focus attempts to explain temperature-size relationships on sets of closely related organisms. That way, the number of oversimplifying assumptions made by a theory can be minimized, and the behavior and physiology of the organisms in question can be incorporated. There are plausible explanations for the effect of temperature on body size that apply to specific groups of ectotherms. For example, oxygen availability is a potential limit to body size at high temperatures, particularly for aquatic organisms and those terrestrial organisms that rely primarily on diffusion for gas exchange (Atkinson 1996; Woods 1999). Frazier et al. (2001) noted that temperature influenced the effect of hypoxia on body size in *D. melanogaster*; at high temperatures, flies reared in a hypoxic environment were smaller than those reared in a normoxic environment, but hypoxia had no effect on body size at low temperatures. Although the thermal effect on oxygen transport is a potential mechanism for the temperature-size rule in aquatic organisms and some terrestrial insects, this mechanism is not likely to limit the body size of terrestrial ectotherms that use forced convection in gas exchange. A truly general explanation for the temperature-size rule must incorporate the causal mechanisms for the relationships between environmental temperature and body size in all ectotherms, including those mechanisms by which certain species violate the rule (Dunham and Beaupre 1998). Therefore, even the simplest form of general explanation is bound to be far more complex than those that have been considered to date.

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