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Thermal time: body size, food quality and the 10°C rule

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ABSTRACT

Developmental rates of ectotherms (y) are often linearly related to temperature (T_c in °C) within some biologically relevant range of temperatures as $y = (1/S)(T_c - T_b)$, where T_b is the estimated temperature at zero development, and the thermal constant S is the development time multiplied by the temperature above T_b (i.e. degree days above T_b). Among similar species, it has been widely shown that S and T_b are negatively related across environments, that S is positively related to body size, and that T_b is independent of body size but increases with mean environmental temperature. Here we present a model that predicts quantitatively each of these relationships by showing that the developmental rate equation (y) is a linear approximation to a universal exponential function (in Kelvin) reflecting the underlying biochemical kinetics of metabolism. The model combines the effects of body size and temperature on individual growth to explain the majority of variation in development rates among a broad assortment of aquatic ectotherms (fish, amphibians, zooplankton) at different life stages. Specifically, the model predicts that body size enters as $(\text{mass})^{1/4}$, and that T_b is about 10°C below the mean developmental temperature for ectotherms in nature ('the 10°C rule'). We conclude by explaining how differences in food type would affect the model.

Keywords: degree days, growth, temperature, threshold temperature.

INTRODUCTION

For ectotherms, thermal time refers to a linear relationship between development rate (y), measured as $1/(\text{time to complete some phase of development})$, and temperature in °C (T_c) (Honek and Kocourek, 1990; Trudgill, 1994; Trudgill and Perry, 1994; Gilbert and Raworth, 1996; Honek, 1996a,b, 1999; Bonhomme, 2000). As an example, the larval development period is measured for an insect reared at four temperatures within the normal range experienced by the larvae such that the fitted line is $y = (1/S)(T_c - T_b)$, where $1/S$ is the slope and $y = 0$ when $T_c = T_b$, the estimated lowest temperature for development (Fig. 1). S is called the 'thermal constant for development', because the development period at every temperature takes $S = (T_c - T_b)/y$ degree days accumulated above the developmental threshold (T_b). Thermal time is widely used to understand development time in both plants and animals, and T_b and S have been estimated under a wide variety of conditions (Honek and Kocourek, 1990; Trudgill, 1994; Trudgill and Perry, 1994; Gilbert and Raworth, 1996; Honek,

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1996a,b, 1999; Bonhomme, 2000). Among similar organisms, S and T_b are often negatively correlated with each other across various environments (Honek and Kocourek, 1990; Trudgill, 1994; Trudgill and Perry, 1994; Honek, 1996a,b, 1999; Bonhomme, 2000), and S is positively related to body size (Trudgill, 1994; Trudgill and Perry, 1994; Honek, 1999). T_b is often correlated with the typical environmental temperature (Gilbert and Raworth, 1996; Honek, 1996a, 1999; Bonhomme, 2000), but apparently not with body size (Honek, 1996a); for example, T_b is higher for tropical species than temperate species (Honek, 1996a). Finally, some evidence suggests that food type may influence S (Honek, 1999).

This paper develops an approach to thermal time by combining temperature and body mass into a general production or growth function for ectotherms. The resulting differential equation may then be solved to yield the time for development through any life-history phase. The linear regression of (development time)⁻¹ versus rearing temperature then yields a general equation for S and T_b (Fig. 1).

THE GROWTH FUNCTION

Most models for growth of individual body mass (m) ignore temperature, but include body mass itself (Reiss, 1989), and yield a bowed-upward trajectory of mass versus time (Reiss, 1989). The simplest model (Gillooly *et al.*, 2002) for pre-reproductive growth that includes body size *and* temperature has a growth rate proportional to whole body metabolism ($\propto m^{0.75}$),

$$\frac{dm}{dt} \approx am^{0.75} \quad (1)$$

with the temperature dependence of growth contained in a , via an approximation of the (°K) Boltzmann's factor; the °C (T_c) approximation is $a(T_c) \propto e^{a \cdot T_c}$ (Gillooly *et al.*, 2002), where a can be predicted from the basic biochemical kinetics of metabolism and the transformation from °K to °C (Gillooly *et al.*, 2002). We use this $a(T_c) \propto e^{a \cdot T_c}$. This addition of temperature yields

$$\frac{dm}{dt} \approx H \cdot e^{a \cdot T_c} \cdot m^{0.75} \quad (2)$$

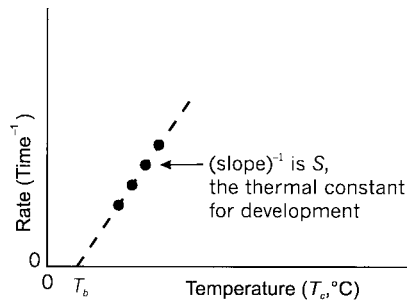


Fig. 1. In this hypothetical case, the time to grow from egg to pupa ($1/y$) is studied for an insect at four temperatures (T_c) and the development rate (y) is approximately linear with temperature. The fitted line is $y = (1/S)(T_c - T_b)$, where S is called the 'thermal constant for development' and T_b is the (estimated) lower threshold temperature for development (i.e. $y = 0$ when $T_c = T_b$).

(H is discussed in Gillooly *et al.*, 2002), which may be integrated from time zero to time t_d , size m_0 to size m_d . Setting the initial size (m_0) ≈ 0 , we get:

$$\frac{t_d}{m_d^{0.25}} = \frac{4}{H \cdot e^{\alpha \cdot T_c}} \quad (3)$$

t_d is the development time to reach mass m_d at a fixed temperature T_c ; if T_c varies during the development period, growth equation (2) must be integrated to reflect the time dependence of $e^{\alpha \cdot T_c}$. Then, one must rewrite equation (3) as $1/t_d$ to get at ‘thermal time’:

$$\frac{1}{t_d} = \frac{H}{4 \cdot m_d^{0.25}} e^{\alpha \cdot T_c} \quad (4)$$

So, a plot of $1/t_d$ versus T_c will be exponential for a species reared at different temperatures, provided the temperatures do not alter m_d [actually, since m_d enters equation (4) as $m_d^{0.25}$, m_d can vary with T_c by up to $\approx \pm 50\%$ without distorting the exponential very much].

THE LINEAR APPROXIMATION (S AND T_b)

Various authors have noted that a developmental rate ought to be approximately exponential in temperature, and that thermal time is a linear approximation to the exponential (e.g. Bonhomme, 2000). This section develops the linear approximation to equation (4), and then predicts several unusual features of S and T_b that are not discussed elsewhere.

Suppose the rearing temperatures represent a relatively small range in T_c , so the exponential looks rather linear. If we fit a line to this, what will the line look like? If the T_c range is not too big, the line will be approximately tangent to the exponential at \bar{T}_c , the average rearing temperature. We illustrate this in Fig. 2. Of course, a fitted line will be a little above the tangent, but we ignore this detail here. Now the slope of an exponential at \bar{T}_c is $h\alpha e^{\alpha \bar{T}_c}$ [where $h = (H/4m^{0.25})$ from equation 4], so a line through the point y_0, x_0 ($y_0 = h e^{\alpha \bar{T}_c}$, $x_0 = \bar{T}_c$) with this slope has the equation:

$$y - y_0 = \text{slope} \cdot (x - x_0)$$

Or, using equation (4):

$$y - h e^{\alpha \bar{T}_c} = h \alpha e^{\alpha \bar{T}_c} [T_c - \bar{T}_c] \quad (5)$$

T_b is where $y = 0$, so equation (5) yields:

$$T_b = \bar{T}_c - \frac{1}{\alpha} \quad (6)$$

which is independent of h and thus independent of body mass.

S , the thermal constant for development, is $1/\text{slope}$; since the slope of the line is $h\alpha e^{\alpha \bar{T}_c}$, $S = (1/h\alpha) e^{-\alpha \bar{T}_c}$. From equation (6) we may write:

$$S = \left(\frac{1}{h\alpha}\right) \left(\frac{1}{e}\right) e^{-\alpha \cdot T_b} \quad (7a)$$

or

$$S = \left(\frac{4}{H \cdot \alpha \cdot e} \right) m_d^{0.25} \cdot e^{-\alpha \cdot T_b} \quad (7b)$$

To summarize, under our body-size growth model (equation 2), where the rate of development ($1/t_d$) is a linear approximation of the exponential temperature function (Fig. 2):

1. Across environments with different \bar{T}_c 's, S is a negative exponential function of T_b for species with similar body sizes and the same α (equation 7b). Indeed, the 'size-corrected S^* ' ($= S/m_d^{0.25}$) is a negative exponential function of T_b (equation 7b). Below we show that α is expected to be very similar among otherwise diverse species (Gillooly *et al.*, 2002).
2. The 'temperature-corrected S^* ' ($= S \cdot e^{\alpha \cdot T_b}$) should scale with body mass to the 0.25 power (equation 7b).
3. T_b is expected to be about $1/\alpha$ degrees below the mean temperature, \bar{T}_c (equation 6).

We test these three predictions below.

WHAT SETS α ?

The term α is set by the temperature dependence of the biochemical reactions of cellular metabolism that govern the rate of growth and development in organisms. We argue elsewhere (Gillooly *et al.*, 2001, 2002) that this temperature dependence ought to be described by a Boltzmann's factor in $T = K$ ($\propto e^{-E/kT}$), which can be well approximated (Box 1 in Gillooly *et al.*, 2002) in $^{\circ}\text{C}$ as $e^{(E/kT_0^2)(T)}$, where $\alpha = (\bar{E}/kT_0^2)$. In this formulation, \bar{E} is the average activation energy of metabolic reactions (~ 0.62 eV), k is Boltzmann's constant (8.62×10^{-5} eV K^{-1}), $T_0 = 273$ K, and T_c is the development temperature in $^{\circ}\text{C}$ (Gillooly *et al.*, 2002). Thus, $\alpha \approx 0.1$ for all organisms across the biological temperature range (~ 0 – 40°C).

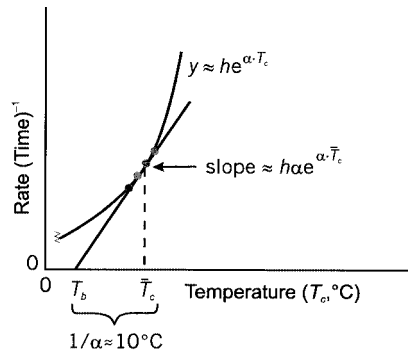


Fig. 2. Thermal time. Suppose the rate (y) is approximately an exponential in $^{\circ}\text{C}$; then, 'thermal time' is a linear approximation to the exponential over some temperature range centred at a mean temperature of \bar{T}_c . The linear threshold for zero development (T_b) is α^{-1} $^{\circ}\text{C}$ below the average temperature, \bar{T}_c . The thermal constant for development (S) is $1/\text{slope}$ at \bar{T} , or $S = (1/(h \cdot \alpha \cdot e))e^{-\alpha \cdot T_b}$, since $\bar{T}_c = T_b + (1/\alpha)$. The parameter h is probably $\propto m^{-0.25}$ (m = body mass, or final body mass at the end of development). The parameter α is theoretically predicted to equal about 0.10 (Gillooly *et al.*, 2002), so $1/\alpha \approx 10^{\circ}\text{C}$; thus, T_b is predicted to be about 10°C below \bar{T} . We call this the '10 $^{\circ}\text{C}$ rule.'

S AND T_b FOR AQUATIC ECTOTHERMS

We have studied development time for aquatic ectotherms (fish, amphibians and zooplankton) (Gillooly *et al.*, 2002): time for eggs to hatch into free-living larval forms and, for zooplankton, time to grow to adulthood. The thermal time study reported here used a subset of the species for which each species was studied at three (or more) temperatures, so a line could be fit to the data; we regressed y on $^{\circ}\text{C}$. Figure 3 for hatching time (1/days) in fish eggs (21 species) shows typical results when the species are uncorrected for egg size. Thus, each species gives us S and T_b , as well as body mass (egg mass).

Each of the three predictions was supported using growth rates for the diverse assortment of aquatic ectotherms (fish, amphibians and zooplankton) grown at different constant temperatures in the laboratory. First (equation 7b), plots of the natural logarithm of body mass-corrected development rate (i.e. $S/m^{0.25}$) versus T_b for each taxon yielded straight lines with slopes (range 0.08–0.14) close to the predicted value of $\alpha \approx 0.1$ (Fig. 4). In the case of the zooplankton, this includes the growth rates of two different life-history stages, both embryonic and post-embryonic. Data for amphibian eggs (Fig. 4b) are the least convincing and have the smallest sample size. Second, when these same data are temperature-corrected (i.e. $\ln(S \cdot e^{aT_b})$) and plotted versus the natural logarithm of body mass, the slopes are close to the predicted value of 0.25 (Fig. 5). Together, these results strongly support the second prediction. Finally, when these data are combined ($n = 75$ species), plots of T_b versus \bar{T}_c yield a straight line with a slope of 1.0 and an intercept of -10.3 (Fig. 6). This final result lends strong support to ‘the 10°C rule’; T_b is about 10°C below \bar{T}_c .

DISCUSSION

A multitude of data in the literature *qualitatively* support these three predictions (Honek and Kocourek, 1990; Trudgill, 1994; Trudgill and Perry, 1994; Gilbert and Raworth, 1996; Honek, 1996a,b, 1999; Bonhomme, 2000), although body size is an uncontrolled variable in many data sets and \bar{T}_c is rarely reported. As a result, differences among species are

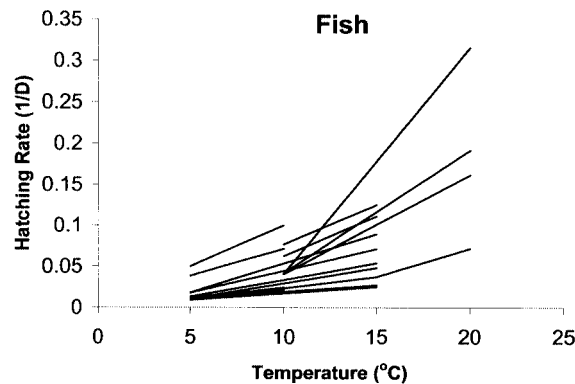


Fig. 3. Hatching rate ($D =$ days) versus temperature for the eggs of fish grown at different constant temperatures. Each line represents a different species (21 species). Hatching rates are not corrected for the effects of egg size. Data sources in Gillooly *et al.* (2002).

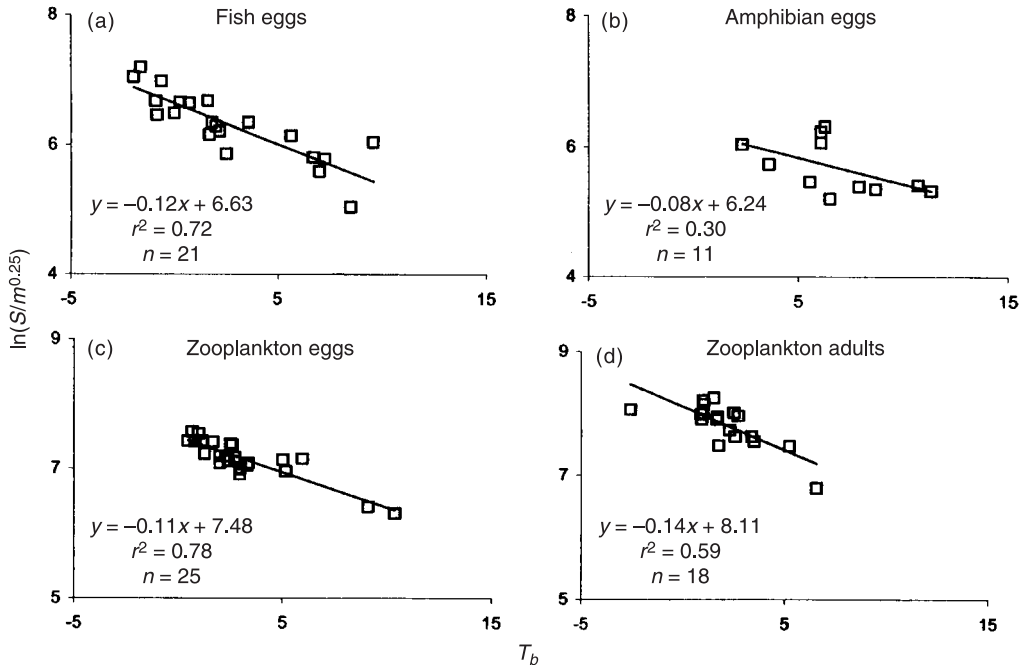


Fig. 4. The natural logarithm of body mass-corrected developmental rate ($S/m^{0.25}$) versus the lower developmental threshold temperature (T_b in °C) for eggs of assorted fish (a), amphibians (b) and freshwater zooplankton (c), and for adults of zooplankton (i.e. generation time⁻¹; for rotifers, copepods and cladocerans) (d). Rates were determined for species grown at different constant temperatures, and then mass-corrected according to the model presented in equation (7b). Data sources in Gillooly *et al.* (2002).

often exaggerated and misinterpreted. Although it is well known that T_b increases with the ‘typical’ environmental temperature (Gilbert and Raworth, 1996; Honek, 1996a, 1999), this has been interpreted (for example) as an adaptation *in* T_b to match the lowest temperatures experienced (Gilbert and Raworth, 1996). Our approach (Fig. 2) suggests that the exponential temperature function itself causes the estimated T_b to increase with \bar{T}_c (see also Bonhomme, 2000).

The concept of ‘thermal time’ has been useful [i.e. development takes xx degree days above T_b (Honek and Kocourek, 1990; Trudgill, 1994; Trudgill and Perry, 1994; Gilbert and Raworth, 1996; Honek, 1996a,b, 1999; Bonhomme, 2000)], even if it is an approximation of a more fundamental exponential relation. But, across broad temperature ranges, the exponential function [either °C approximation or the Boltzmann in K (Gillooly *et al.*, 2002)] is better, and it is simple to integrate equation (2) to reflect, for example, varying temperatures. In one sense, the linear approximation obscures the more universal features ($\alpha \approx 0.10$) of the exponential. Our approach extends the concept by *beginning* with a size/temperature-dependent growth function (equation 2) and then integrating over time – and temperature if it varies – to get the development interval, $1/t_d$, as a function of size *and* temperature. Our growth model (equation 2) is very simple, and more complex formulations in terms of how body size affects growth are clearly

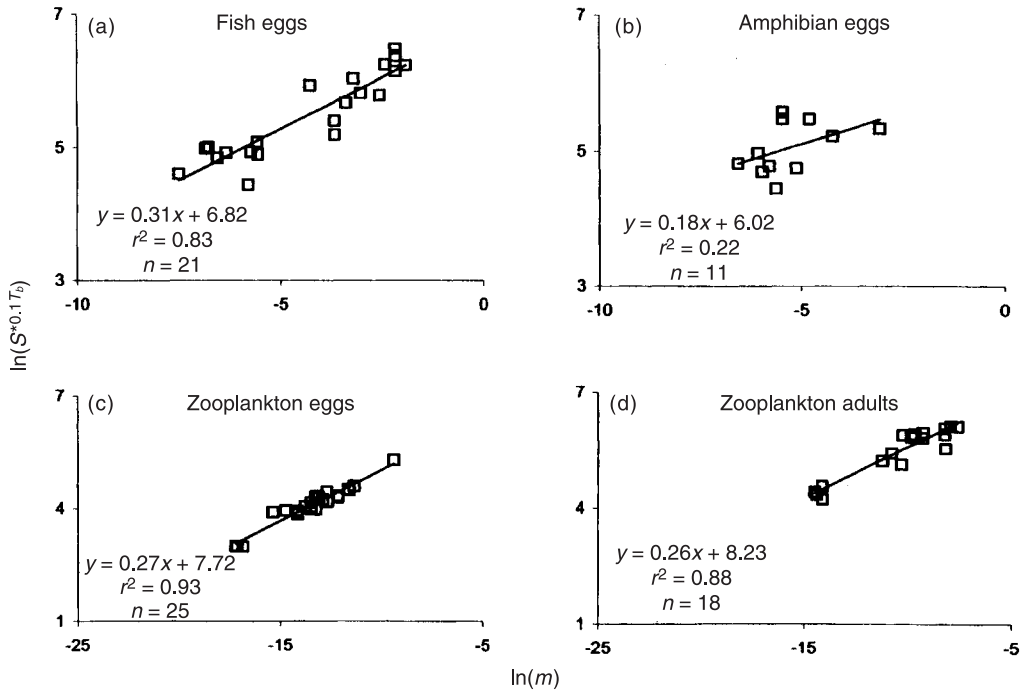


Fig. 5. The natural log of temperature-corrected development rate ($S \cdot e^{0.17T_b}$) versus the natural log of body mass (m , in grams) for the eggs of assorted fish (a), amphibians (b) and freshwater zooplankton (c), and for the adults of zooplankton species (i.e. generation time⁻¹; for rotifers, copepods and cladocerans) (d). Rates were determined for species grown at different constant temperatures, and then temperature-corrected using T_b according to the model presented in equation (7b). Data sources in Gillooly *et al.* (2002).

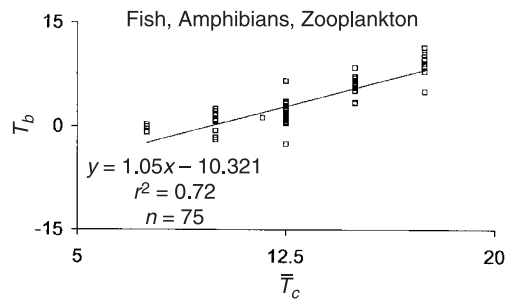


Fig. 6. The lower developmental threshold temperature, T_b , versus the mean temperature of development, T_c , for the fish, amphibian and zooplankton data presented in Figs 4 and 5. Data include both embryonic and post-embryonic development rates. Note that T_b is about 10°C below T_c (the '10°C rule').

possible; yet time intervals often increase with $m^{0.25}$, the integral form of something like $dm/dt \propto m^{0.75}$.

Although body size and temperature explain the majority of variation, residual variation

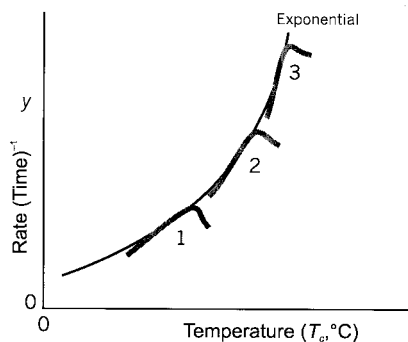


Fig. 7. When corrected for body size and food quality, the exponential curve describing development rate is expected to be similar for all animals. A given species (populations) occupies only a certain interval along the curve (three species shown here), resulting in an approximately linear relation for each.

in developmental intervals for free-feeding zooplankton are strongly correlated with whole-body stoichiometry, specifically the whole-body carbon-to-phosphorus ratio (Gillooly *et al.*, 2002). Zooplankton individuals with more phosphorus are growing faster, having invested in the phosphorus-rich molecular machinery needed for fast growth (Elser *et al.*, 1996); they clearly do this because of the availability of phosphorus-rich (and nitrogen-rich) food sources. Food quality may be expected to affect growth rates similarly in other species. Of course, anti-herbivore factors (e.g. toxins, toughness) may also play a role here. Interestingly, the ‘10°C rule’ for T_b may well be independent of food type, just as it is for body size, because food type is expected to affect the height, but not the exponent, of the exponential in Fig. 2.

Figure 7 is a schematic representation of our hypothesis. This exponential is body size and food-quality corrected, and so it is expected to look the same for all species. Populations (species) 1, 2 and 3 live in different thermal environments and their development (time) rates are approximately linear. Temperature impairs development at the upper temperature for each population as biochemical adaptations allow each to develop in only a restricted temperature range. What determines that range is perhaps as interesting as our suggestion that the successive lines approximate the *same* underlying exponential function.

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