

A method to transform a variable thermal regime to a physiologically equivalent effective temperature

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ABSTRACT

We present a method to characterize variable thermal regimes in terms of an equivalent or effective temperature. Our method is based on a first order exponential transformation of a time series of temperatures to yield an exponentially-weighted mean temperature characteristic of the regime and independent of any particular species or end point. The resulting effective temperature or exponential mean, \bar{T}_e , offers an improved method for summarizing mean temperature where biological response scales exponentially to temperature. The exponential mean allows growth under varying thermal regimes to be predicted using constant temperature models and offers a compact descriptor communicating the growth capacity of variable thermal regimes. The method combines mathematical simplicity with translatability to different Q_{10} values without recourse to the underlining time series data. It also provides a quantitative baseline that improves on mean temperature by incorporating the effect of Jensen's inequality and it remains applicable at near zero temperatures where thermal sums lack accuracy.

1. Introduction

Numerous models have been proposed to describe the temperature dependence of biological growth under different constant temperature conditions. However, the ecological application of such models is hindered by the fact that most real-world thermal regimes are variable and intrinsically more complex owing to non-linearity in thermal scaling. The ability to accurately predict growth and development under conditions of varying temperatures is especially important when assessing subtle, ecosystem-level effects such as competitive equilibria and phenological mismatch (Visser and Holleman, 2001; Genner et al., 2009) that may occur at temperatures below recognizable stress response thresholds. The ability to characterize temperature variations in natural thermal regimes is also desirable when considering the effects of climate change where increases in temperature variation may cause a greater impact than the changes in mean temperature (Vasseur et al., 2014).

One of the earliest approaches to predicting growth under varying thermal regimes involved the method of thermal sums, widely known

as the degree-day method. This method dates to the eighteenth century and has continued in use, with various modifications, to present (Neuheimer and Taggart, 2007). The degree day is the sum of the product of temperature and time and may be applied to predict growth (the gain in mass with time) or development (progress toward recognizable morphological stages). Commonly, complete development occurs for an approximately constant number of degree days Blaxter (1988).

The degree day method results in a relationship between temperature and growth that follows a power function whose slope is asymptotic to the Y-axis at zero degrees. A biological zero parameter (representing the temperature below which development ceases) is therefore required to partially overcome this mathematical limitation, or to accommodate growth with a lower thermal bound at temperatures greater than zero. Fig. 1 illustrates limitations of the degree day method compared to an exponential model when applied to a cold-developing species such as the lake whitefish (*Coregonus clupeaformis*). In addition to the problem of a biological zero, only a fraction of the thermal performance curve occurs at a near-constant number of degree

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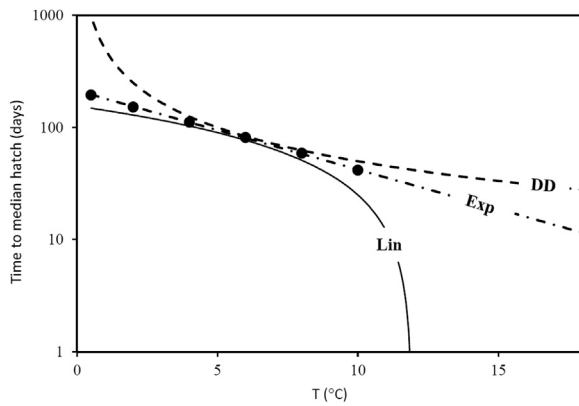


Fig. 1. Observed days to median hatch for lake whitefish under constant incubation temperature (circles, from Brooke, 1975) compared to predicted curves based on DD: 500 degree days, exp: an exponential relationship given by $h_{50}=213e^{-0.16T}$ (regression using data from Brooke, 1975), and Lin: a linear relationship given by $h_{50}=-13T+155$. Application of a negative biological zero parameter would effectively shift curve DD to the right but still result in a flatter slope than the observed temperature dependence of hatching.

days.

An alternative approach is the use of incremental growth-at-temperature (IGT) to predict total growth either as a continuous function of time steps (e.g. Alderdice and Velsen, 1978; Katsanevakis and Verriopoulos, 2006; Thome et al., 2016) or through stage-wise growth models (e.g. Brooke, 1975; Berlin et al., 1977) that apply different thermal scaling relationships to different development stages. In contrast to thermal sums, IGT adds increments of growth over discrete time steps $\Delta t_1, \Delta t_2, \Delta t_3, \dots$ at temperatures T_1, T_2, T_3, \dots and thus allows for non-linear temperature dependence of biological growth. Known as Jensen's inequality (Ruel and Ayres, 1999; Martin and Huey, 2008; Ragland and Kingsolver, 2008), an accelerating thermal dependence causes growth rates under varying temperatures to exceed those that would be predicted by simply using the mean temperature. IGT is, to the best of our knowledge, the only existing method for modeling growth under varying thermal regimes that accounts for Jensen's inequality. Unfortunately IGT yields a summation of species-specific growth increments ill-suited for statistical analysis and unwieldy for the description of the thermal regime being considered.

Jensen's inequality may also be incorporated by transforming a variable thermal regime to an equivalent or effective temperature provided that the thermal dependence of growth follows an exponential relationship. The resulting method has advantages over thermal sums as a quantitative baseline and it may simultaneously facilitate the modeling of multiple species interactions while providing a compact, mathematically convenient, form that facilitates communication and statistical analysis of temperature-dependent phenomena.

2. Method description and development

Our approach may be summarized as follows:

- 1) Where biological growth to a consistent and definable end point (e.g. hatching) under varying temperatures may be described as the incremental sum of a continuous monotonic function of time-at-temperature $f(T)$, there exists an equivalent constant temperature, T_{eq} , such that $\sum_0^t f(T) = f(T_{eq})$
- 2) Where $f(T)$ is selected to be independent of species-specific parameters, it may be used to transform a varying thermal regime to an equivalent constant temperature, T_{eq} suitable for application across a range of taxa, biological processes, and end points

Although $f(T)$ could be any continuous monotonically increasing equation, we have used a first order exponential relationship because of

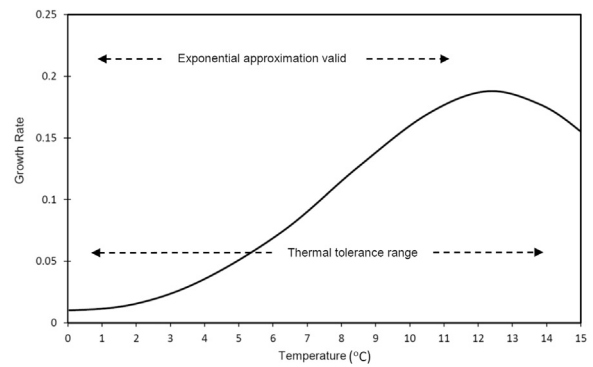


Fig. 2. General shape of the growth-temperature relationship described by the Sharpe-Schoolfield equation (Sharpe and DeMichele, 1977). For much of the thermal tolerance range (0–15 °C in the example shown), growth follows an exponential relationship as described in the Eyring equation.

its mathematical simplicity and well-established mechanistic basis. Both the Eyring and Sharpe-Schoolfield equations are based on an exponential relationship between growth and temperature for all (Eyring) or a portion (Sharpe-Schoolfield) of the thermal domain (Fig. 2). Where $f(T)$ is an exponential function of T , we show that T_{eq} takes the form of an exponentially transformed mean \bar{T}_e .

Clarke and Johnston (1999) analyzed thermal dependence of resting metabolism for 69 species of teleost fish and found similar slopes despite significantly different rates of absolute growth. Similar conclusions were drawn by Gillooly et al. (2001) and Brown et al. (2004) who proposed a general model relating biological growth to size and temperature lending support to the hypothesis that the observed temperature dependency of growth in fish reflects biological processes common to life in general (Huey and Kingsolver, 2011; Clarke, 2004). Thus, the exponential scaling of growth to temperature is well supported by observations across different species and life stages. However, natural temperature variability may include temperatures corresponding to a negative slope in the Sharpe-Schoolfield domain, particularly for insects (Wagner et al., 1984; Régnière et al., 2012).

When considering the time to grow to a definable end point, the simplest exponential relationship is:

$$t_h = \alpha e^{-\beta T} \quad (1)$$

where the time, t_h , required to attain a biological end point (for example hatching), at constant temperature T , is inversely proportional to an exponential function defined by the exponent $-\beta$, and where α is a species-specific parameter defining the time to reach the specified end point at a temperature of zero degrees.

We may restate Eq. (1) t_h to eliminate the negative sign on β such that:

$$f(T) = \frac{1}{t_h} = \frac{1}{\alpha} e^{\beta T} \quad (2)$$

The relationship between the equivalent constant temperature \bar{T}_e and the variable values for T may be approximated numerically by:

$$\frac{1}{\alpha} e^{\beta \bar{T}_e t} = \sum_0^n \frac{1}{\alpha} e^{\beta T} \Delta t \quad (3)$$

where t is the sum of the time increments. Dividing each side by $\frac{1}{\alpha}$ removes the species-specific temporal parameter α and allows for generalization in the form:

$$e^{\beta \bar{T}_e t} = \sum_0^n e^{\beta T} = (e^{\beta T_0} \Delta t_0 + e^{\beta T_1} \Delta t_1 + \dots e^{\beta T_n} \Delta t_n) \quad (4)$$

This can be solved numerically by varying the value for \bar{T}_e until the left and right sides of the equation are equal. Alternatively, we may solve for temperature dependent growth to determine the time, t_h , required to attain a hypothetical reference endpoint. Since we have assumed that the fractional growth rate, $F(t)$, with variable tempera-

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