

Short note

Theoretical effects of monotonically changing and fluctuating temperature on oscillating biological systems

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ABSTRACT

A phenomenological model of non-isothermal evolution of naturally oscillating biological systems was constructed on the assumption that the momentary growth or decline rate is the isothermal rate at the momentary temperature, at the time that corresponds to the system's momentary state. Simulations using this model show that monotonic temperature rise or fall only affects the oscillations amplitude and frequency. In contrast, fluctuating temperature can induce irregular periodicity, aperiodic outbursts of varying magnitude and duration and/or extinction, depending on the temperature fluctuations' complexity, and frequency relative to that of the biological system's own. This suggests that coupling of the regular oscillations of a population or biological process, with temperature or other fluctuations in its environment could be a cause of irregular and apparently chaotic patterns, at least in principle. For lack of suitable data, the described model is yet to be validated. However, it is a testable model that could be confirmed experimentally by future research.

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1. Introduction

The kinetics of oscillating biological systems has been extensively studied and described by a variety of mathematical models (Alvarez-Ramirez et al., 2009; Blomberg, 2006; Novak and Tyson, 2008; Petrovskii and Malchow, 2001; Petrovskii et al., 2004; Rai et al., 2007; Zhang et al., 2002). The large majority of them are population balance models, continuous or discrete, whose output is a periodic function; regular, complicated or chaotic (Baurmann and Feudel, 2004; Hosseini, 2006; Vandermeer, 2006). Almost invariably, the investigated or simulated process is assumed to take place in an "isothermal" environment, in which case the observed changes are in the quantities involved but not in the coefficients of the differential equations themselves. The same can be said on the many models that describe the oscillation patterns of macro-organisms or microbial populations. The oscillations that they describe are primarily in the population's size, not in the coefficients of the differential or difference equations that regulate their relationship with the environment or other populations. It would therefore be interesting to investigate what might happen when the parameters, which govern the oscillations amplitude and frequency, either drift monotonically or fluctuate themselves. A good example would be the effect of changing temperature on the

progress of an oscillatory biological process or the size of aquatic or terrestrial microbial or insect populations.

The effect of temperature fluctuations on biological systems has been primarily studied as the oscillations' cause (e.g., Rinaldi et al., 1993; Ruoff and Rensing, 2004; Upadhyay et al., 1998). Our starting point is that the system in question is known to be oscillatory even under isothermal conditions and that the temperature only affects the oscillations' amplitude and frequency. The mechanisms that produce and regulate the oscillations, can be complex and in many cases not fully known in detail. Hence we will resort to a phenomenological model in the search of potential patterns. The same can be said on monotonic growth too. With few exceptions, information concerning the exact state of the individual elements or members of the populations is either incomplete or lacking altogether. Similarly, in many monotonic decay processes or mortality, the exact chain of events at the fundamental level is also rarely fully known and hence population models are almost universally used to describe and predict them. The above should not be construed as a suggestion to abandon the mechanistic approach to kinetics. On the contrary, we fully subscribe to the notion that effective control of a biological system rather than merely its description will always require an insight into the underlying mechanisms and their dynamics.

In this work, we will only address hypothetical abstract systems that can be described by a continuous deterministic model. The goal is to demonstrate that exposing an oscillating biological system to temperature fluctuations can by itself produce

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oscillatory patterns that cannot be intuitively deduced from the isothermal ones.

2. Theoretical background

Most of the standard models of population growth, notably the logistic (Verhulst) model and its various modifications, were originally developed for an isothermal habitat, and the same can be said on mortality or survival kinetics. However, the isothermal growth and mortality models can both be adapted for a dynamic environment if one assumes that the system's momentary rise or fall rate is the isothermal rate at the momentary temperature, at the time, t^* , which corresponds to the momentary state of the system (Peleg, 2003, 2006). The validity of this assumption has been demonstrated with published experimental results on microbial growth (e.g., Corradini and Peleg, 2005), microbial mortality (e.g., Corradini and Peleg, 2004a; Pardey et al., 2005) and chemical degradation (e.g., Corradini and Peleg, 2006, 2004b). Validation came from the resulting dynamic models' ability to predict correctly the growth, mortality or chemical degradation curves under non-isothermal conditions, including under fluctuating temperature, from experimental isothermal data. The concept was further strengthened by the models' ability to predict correctly non-isothermal microbial growth and mortality curves from other non-isothermal data too (e.g., Smith-Simpson et al., 2007; Peleg and Normand, 2004). All these demonstrations, however, were in systems where under isothermal conditions the population size or process's product rose or fell monotonically. The concept has also been applied to peaked processes governed by competing mechanisms of growth-mortality or synthesis-degradation (e.g., Peleg et al., 2009). In that case, however, experimental validation of the models will have to wait until suitable published data become available. Finding suitable joint isothermal and non-isothermal data on peaking biological processes and populations has been proven extremely difficult, and the same can be said about oscillating biological systems. But, since the objective of the present work is only to investigate potential theoretical implica-

tions of the hypothesis concerning the momentary rate of change under dynamic conditions, we will proceed without the backing of an experimental database.

2.1. Simple oscillating systems

Consider an ideal simple oscillatory system that under isothermal conditions follows the equation:

$$Y(t) = Y_0 \{1 + a(T) \sin[\omega(T)t + d]\}, \quad a(T) < 1 \quad (1)$$

or

$$\log Y(t) = \log Y_0 + \log\{1 + a(T) \sin[\omega(T)t + d]\}, \quad a(T) < 1 \quad (2)$$

where $Y(t)$ is an organismic population size or density, a resource concentration, etc., $a(T)$ and $\omega(T)$ are its oscillations' temperature dependent amplitude and frequency, respectively, and d a phase angle ($0 \leq d \leq 1$).

We assume that in the pertinent temperature range, $a(T)$ and $\omega(T)$ are monotonic functions of temperature. For simplicity we will also assume that both $a(T)$ and $\omega(T)$ rise with temperature in this range, although this is not essential for what follows. Examples of hypothetical $a(T)$ and $\omega(T)$ relationships and the corresponding isothermal $Y(t)$ curves produced with Eq. (1) as a model are shown in Fig. 1.

As in peaked processes (Peleg et al., 2009), formulating the rate equation in terms of $dY(t)/dt$ can result in negative solutions that have no physical meaning, a problem that does not exist when $d \log Y(t)/dt$ is used instead.

The momentary isothermal logarithmic rate of a system described by Eqs. (1) and (2) is:

$$\frac{d \log Y(t)}{dt} = \frac{a(T)\omega(T)\cos[d + \omega(T)t^*]}{1 + a(T)\sin[d + \omega(T)t^*]} \quad (3)$$

where t^* is the time that corresponds to the system's momentary state, $Y(t)$.

Under dynamic conditions, the momentary value of $t^*(t)$ at any given momentary temperature, $T(t)$, is the inverse of Eq. (1) at that

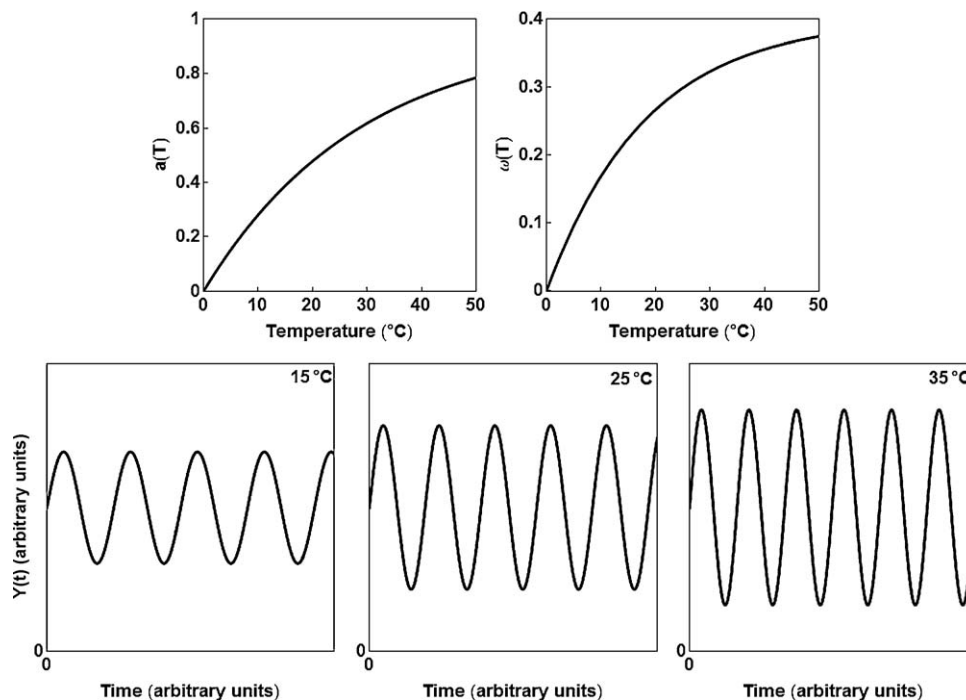


Fig. 1. A hypothetical example of how temperature can affect a biological system's regular oscillations amplitude and frequency (top), and corresponding oscillation patterns at three fixed temperatures are shown at the bottom. They were produced with Eq. (1) as a model with $d = 0$.

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