



# Temperature-dependent models of *Zannichellia palustris* seed germination for application in aquatic systems



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## ABSTRACT

The temperature-dependent germination rates of *Zannichellia palustris*, a native submersed aquatic plant from the spring-fed Fall River in Northern California, were examined with linear models and with the non-linear Logan Type III biophysical model. The Logan Type III model, which previously had not been applied to predicting seed germination, provided superior fit for estimating germination rates across eight constant temperatures (5–40 °C) and across a range of subpopulations representing the entire examined seed population. The Logan model was particularly successful at estimating seed germination rates at sub-optimal temperatures (5–25 °C) that occur under field conditions and at temperatures near the base and maximum germination temperatures. Based on the Logan Type III model, a computer simulation was developed using Time Varying Distributed Delays as implemented in the USDA-ARS Hermes (Hierarchical Environment for Research Modeling of Ecological Systems) simulation modeling system, tested across fluctuating temperatures in the laboratory, and applied to predict seed germination of *Z. palustris* under actual field conditions over an entire year in differing sections of the Fall River. The Logan Type III biophysical model and the Hermes simulation system are shown to be useful for predicting germination under fluctuating temperature conditions in the field and in seed populations that do not exhibit a linear germination response.

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## 1. Introduction

Assessment and prediction of key biological processes can be of extreme importance to land and waterway managers as they work to restore natural systems (Frissell and Bayles, 1996; Palmer et al., 1997). Such is the case with the on-going restoration of the Fall River, California's largest spring-fed wild trout fishery (see <http://fallriverconservancy.org/programs/restoration/>). Threats to the river include a combination of sedimentation events (Spencer and Ksander, 2002) and invasion by *Myriophyllum spicatum* (Eurasian watermilfoil) (Spencer and Carruthers, 2012). Central to the restoration effort is *Zannichellia palustris* (horned pondweed), a globally distributed species (van Vierssen, 1982; Lombardi et al., 1996; Greenwood and DuBow, 2005) and the most abundant

native submersed macrophyte in the Fall River (Spencer and Ksander, 1998; USDA, NRCS, 2013).

Understanding the germination dynamics of *Z. palustris* is particularly important, as this annual plant regenerates each season from newly produced seeds and from those within the seed-bank (van Vierssen, 1982). To aid waterway managers, it is important to understand seed production and the timing of germination in specific waterways, such as the Fall River. Bytnerowicz and Carruthers (in review) conducted germination studies for *Z. palustris* from the Fall River under variable light and temperature conditions. Results denote a primarily temperature-dependent germination response, an extensive variability of the population response within and between test temperatures, and an absence of a dormancy period in the tested seed population. These results are supported by the observation that temperature is the most important environmental factor controlling the rate and overall germination percentage of non-dormant seeds across plant species (Bewley and Black, 1982; Garcia-Huidobro et al., 1982a; Steinmaus et al., 2000). The work presented here, was designed to further address the impact of temperature on *Z. palustris* seed germination and to develop dynamic means of assessing and forecasting seed germination timing in the natural environment.

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Germination response across temperatures has most frequently been described with thermal-time models that rely on linear relationships between germination rate and temperature (Garcia-Huidobro et al., 1982a; Scott et al., 1984; Washitani, 1985; Covell et al., 1986; Ellis et al., 1986; Ellis and Butcher, 1988). Thermal-time models assume that germination rate increases linearly from a base temperature ( $T_b$ ) to an optimal temperature ( $T_o$ ) and decreases linearly from  $T_o$  to a maximum temperature ( $T_m$ ). They have been widely used to compare seeds from different species and climates (Garcia-Huidobro et al., 1982a; Covell et al., 1986; Ellis et al., 1986; Ellis and Butcher, 1988; Hardegree, 2006) and to make predictions on the timing of seed germination in nature (Alvarado and Bradford, 2002).

The use of thermal-time models for describing temperature-dependent germination rates is a powerful tool for germination response that is linear. However, other modeling schemes may be equally or more appropriate for seed populations that do not fit the linear shape constraints (McDonald, 2002; Hardegree, 2006; Bytnerowicz and Carruthers, in review). In such seed populations, linear regression can be especially ill-suited for fitting lower and upper developmental thresholds that are typically determined by extrapolating a straight line through the temperature axis. It is in these extreme regions of these response curves where development is often underestimated at lower temperatures and overestimated at higher temperatures (Hilbert and Logan, 1983; Wagner et al., 1984). We suggest the use of the Logan Type III biophysical model as an alternative for such seed populations. Logan models have been frequently used to estimate temperature-dependent developmental rates, and lower and upper thresholds of development in the discipline of entomology (Logan et al., 1976; Sharpe and DeMichele, 1977; Hilbert and Logan, 1983; Wagner et al., 1984; Wermelinger and Seifert, 1988; López et al., 2001; Roy et al., 2002; Herrera et al., 2005). The model, originally developed by Logan et al. (1976), and improved by Hilbert and Logan (1983), is a hybrid function composed of two subcomponents, each describing different phases of a temperature-dependent developmental rate curve. The ascending phase of the curve is represented by a sigmoid function, while the descending phase is represented by an exponential decay function. Combined, the two processes form the non-linear Logan Type III equation, as follows:

$$r(T) = \psi \left\{ \left( \frac{(T - T_b)^2}{(T - T_b)^2 + D^2} \right) - \exp \left( \frac{-(T_m' - (T - T_b))}{\Delta T} \right) \right\}, \quad (1)$$

where  $r(T)$  is the germination rate ( $1/d$ ) at  $T$ ,  $T$  is temperature ( $^{\circ}\text{C}$ ),  $T_b$  is the arbitrary base temperature,  $T_m'$  is the arbitrary lethal maximum temperature,  $\Delta T$  is the width of high temperature breakdown, and  $\psi$  and  $D$  are estimated constants that alter the shape of their fitted “biophysical” function.

Independent of the method used to estimate the temperature-dependent developmental curves in the laboratory, relating such functions to actual event prediction in the field may be more complicated due to the non-linearity of the relationship and the time varying nature of temperature patterns in the environment. That is, temperatures are rarely constant, fluctuating both diurnally and seasonally in most habitats and their combined effects on development are not necessary additive as suggested in simple linear models. Thus more dynamic methods of prediction such as non-linear thermal accumulations and/or event simulations are often required to estimate complex temperature-dependent processes where the stimulus variable changes continuously with time (Legaspi et al., 1997).

Here we propose to test aggregate simulation methods (Forrester, 1961; Manetsch, 1976) that are especially appropriate for linking dynamic and non-linear environmental variables, such as temperature, with functional response equations (such as the

Logan Type III biophysical model). We propose to simulate these rate processes using “Time Varying Distributed Delays”, TVDDs (Manetsch, 1976; Carruthers et al., 1986, 1992; Larkin et al., 2000). TVDDs are commonly used simulation components that allow complex biological processes such as phenological development and overall population response levels to be predicted accurately under changing environmental conditions, using well known and highly tested simulation routines developed by system scientists and engineers. By altering just two parameters, DEL (the mean delay time) and  $k$  (a distribution shape parameter), TVDDs can simulate a wide range of delay processes like seed germination or age-specific organism development with realistic means and variances, as those observed under both constant and cycling temperature conditions (Abkin and Wolf, 1976). The temperature-dependent maturation times (DEL, duration of germination period for *Z. palustris* seeds) were calculated as:

$$DEL = \frac{1.0}{\psi \{ (T - T_b)^2 / [(T - T_b)^2 + D^2] - \exp[-(T_m' - (T - T_b)) / \Delta T] \}}, \quad (2)$$

that is, the inverse of the Logan Type III biophysical model. The second parameter value ( $k$ ) is a characterization of the variance of the seed germination response at each experimental temperature (converting developmental rate to germination time).

In a TVDD, the simulation of the full population response is achieved by calculating output that follows the Erlang family of probability density functions using  $k$ th-order differential equations (see Larkin et al., 2000 for an in-depth discussion of TVDDs and their application in simulating biological processes). This approach produces distributed output according to the Erlang law, which is used to calculate a series of response curves that range from an exponential decay curve ( $k=1$ ), to highly skewed distributions ( $k=2-15$ ), to near to normal distributions ( $k>20$ ), on to a discrete spike or pulse as  $k$  approaches infinity. In each situation the value of  $k$  describes the distribution of the response data that can be controlled through changing the order of the differential equation involved in the simulation (Manetsch, 1976; Larkin et al., 2000). Values of  $k$  are directly calculable from observed data using the following relationship:

$$k = \frac{DEL^2}{\text{variance}} \quad (3)$$

Values of  $k$  tend to be fairly constant for a population, as plants (as well as insects and fungi) often have a relatively stable relationship between the mean developmental time and the variance observed across treatment conditions, as reported by Garcia-Huidobro et al. (1982a) specifically for seed germination.

In this study, we were interested in using and comparing a variety of statistical seed germination models for our experimental system (*Z. palustris* in the Fall River of California), based on laboratory implemented constant temperature experiments (Bytnerowicz and Carruthers, in review). First we examine the most appropriate means to describe temperature-dependent seed germination rates for *Z. palustris*, and then we apply appropriate statistical models as the bases for constructing a computer simulation to estimate germination times under highly controlled fluctuating temperature conditions and then under actual field conditions where temperature changes dynamically within individual days and across the entire growth season. We are further interested in assessing changes in germination response through time and at different geographical locations along the course of the river.

## 2. Materials and methods

### 2.1. Seed collection

Mature *Z. palustris* plants, from which newly produced seeds were harvested, were collected from the Fall River in the autumn

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