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A FLEXIBLE MULTIVARIABLE MODEL FOR PHYTOPLANKTON GROWTH

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Abstract. We introduce a new multivariable model to be used to study the growth dynamics of phytoplankton as a function of both time and the concentration of nutrients. This model is applied to a set of experimental data which describes the rate of growth as a function of these two variables. The form of the model allows easy extension to additional variables. Thus, the model can be used to analyze experimental data regarding the effects of various factors on phytoplankton growth rate. Such a model will also be useful in analysis of the role of concentration of various nutrients or trace elements, temperature, and light intensity, or other important explanatory variables, or combinations of such variables, in analyzing phytoplankton growth dynamics.

1. Introduction.

In order to better understand the growth dynamics of phytoplankton, this paper presents a mathematical model which allows for the analysis of the dynamics of phytoplankton growth in the presence of one or more explanatory variables affecting the growth rate. Phytoplankton are microscopic plants living in the upper levels of the oceans and other bodies of water. While many phytoplankton are single-cellular, there are cases of multicellular organisms as well as colonies built of single-cellular units. The photosynthesis of phytoplankton is extremely important and is a primary reason for their study, with a significant percentage of the Earth's oxygen originating from photosynthesis of phytoplankton. This process furthermore makes them a significant player in the carbon cycle, fixing carbon dioxide from the atmosphere and making it biologically available to the food chains of the oceans and fresh waters. Through their role in the carbon cycle, phytoplankton has a role in climate patterns, and they are furthermore directly affected by climate patterns. Phytoplankton also attracts interest because they are the source of undersea oil deposits. For these reasons phytoplankton has been the subject of ongoing study, and one primary area of interest is the understanding of the growth of phytoplankton populations. A more thorough understanding of the growth of phytoplankton thus has many important applications. Sobczak et al. (2002) describe the need for understanding and even stimulating the growth of phytoplankton in the Sao Joaquin River delta to amplify these populations as a primary aspect of the

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management plan for this region. Based on "projected trends in worldwide land use", Sobczak also predicts the increasing importance of bioavailability of organic matter produced within the ecosystem.

A number of mathematical models have been presented to describe the rate of growth and amount of photosynthesis of phytoplankton. Note that the rate of growth and rate of photosynthesis are influenced by a wide variety of factors, including levels of available nutrients, temperature, amount of light, as well as numerous others. In Section 2 we present a flexible mathematical model representing the growth of phytoplankton as a function of time and one or more additional variables. The variety of factors influencing the growth rate will be discussed further in Section 3.

In Section 4, the proposed mathematical model is used to analyze a data set regarding growth of phytoplankton as a function of both time and the level of nutrients. One representative example is given to demonstrate the model's accuracy and computational simplicity and to present some uses of its closed form solution. In this example, time and nutrient level, as well as the interaction between these variables, all turn out to be significant factors affecting growth. This example further demonstrates how the significance of model parameters may be tested using Wald, Maximum Likelihood or Score tests.

2. **A multivariable model for phytoplankton growth.** Particularly in the case of the growth of phytoplankton, evidence has demonstrated that the growth dynamics of the population size P depends not only on time as a variable, but also on intensity of light, the amount of nutrients available, and a number of additional explanatory variables.

A more complete understanding of the growth dynamics of phytoplankton and the influence of various factors on this growth remains an area of ongoing investigation. This section presents a model for phytoplankton growth dynamics that is capable of describing the influence of one or more explanatory variables on the growth dynamics. One point of strength of this model is its accuracy in representing experimental data by an explicitly defined function. This resulting function can be used to investigate the growth dynamics as rate of growth with respect to time, or with respect to level of nutrients. Growth dynamics are determined by the rate of growth, and a good multivariable growth model must reflect numerous factors influencing this rate. In our growth model, define X as the vector of covariates including the interaction between or among variables and M, $\delta, \gamma, \theta, \lambda$ be the model parameters and P(X;M, $\delta, \gamma, \theta, \lambda$)be the population size. We consider how the partial derivatives describing growth with respect to each variable changes as a function of time and all other explanatory variables. This growth rate is represented by partial differential equations of the following form.

$$\begin{aligned}&\frac{\partial P(X;M,\delta,\gamma,\theta,\lambda)}{\partial X_i}\\&=(M-P(X;M,\delta,\gamma,\theta,\lambda))\left(\partial\gamma g(X;\lambda)^{\gamma-1}+\frac{\theta}{\sqrt{1+\theta^2 g(X;\lambda)^2}}\right)\frac{\partial g(X;\lambda)}{\partial X_i}\end{aligned} \tag{1}$$

and i=1,2,...,k with the initial condition $P_0 = P(X_0;M, \delta, \gamma, \theta, \lambda)$.

The solution to the equation (1) is

$$P(X;M,\delta,\gamma,\theta,\lambda) = M - \alpha\exp\left(-\delta g(X;\lambda)^{\gamma} - \operatorname{arcsin}h(\theta g(X;\lambda))\right) \tag{2}$$

where $\alpha = (M - P_0)\exp\left(\delta g(X_0;\lambda)^{\gamma} + \operatorname{arcsin} h(\theta g(X;\lambda))\right)$

We call the function P(X;M, $\delta, \gamma, \theta, \lambda$) of equation (2) a multivariable growth model for phytoplankton growth. The positive parameter M represents the limiting value of the population in the environment. The overall growth rate is determined jointly among the parameters M, δ, γ, θ and λ. The parameter δ plays the role of the intrinsic growth rate. The parameter γ is an allometric constant, which modulates growth through its action on the inputs $(X;\lambda)$ in the term g$(X;\lambda)^{\gamma}$. The modulus of θ reflects the distance from the symmetric form of a sigmoidal curve and finally, is the vector of parameters associated with the model variables. The choice of g$(X;\lambda)$ depends on the nature of the study. In general a link function of the form g(X;λ) = exp $\left(\sum_{i=1}^{k}\lambda_i X_i\right)$ may often prove to be effective. The parameter vector $\lambda = (\lambda_1, \ldots, \lambda_k)$ is directly associated to the covariates and the interaction variables included in the model.

In Section 4, we use a link function of the form

$$g(X;\lambda) = \exp\left(\lambda_1 X_1 + \lambda_2 X_2 + \lambda_3 X_1 X_2\right) \tag{3}$$

and analyze the phytoplankton growth with respect to vector of variables X = (X_1,X_2, X_3), where the interaction variable X_3 is the product of the two variables X_1(time) and X_2 (level of available nutrients.) Here the vector of parameters $\lambda = (\lambda_1, \lambda_2, \lambda_3)$ describes the effect of time (λ_1), concentration (λ_2), and their interaction (λ_3).

Note that when the only covariate in the model is time t, then replacing the link function g(X;λ) in the equation (2) by t results in the hyperbolastic growth model of type III of Tabatabai et al. (2005). Thus one may consider model (1) as a generalization for the hyperbolastic growth rate of type III. See also Eby et al. (2010), Tabatabai et al. (2010), Tabatabai et al. (2011) for other applications of H3 to biological growth. Note that it is also possible to make similar multivariable growth models by incorporating a similar link function into the other hyperbolastic growth models of type I and II.

3. **Variables affecting phytoplankton growth.** In modeling the growth of phytoplankton, a primary concern is to accurately represent the influence of variables such as light and available nutrients on the growth rate. The entire range of variables which impact growth are not yet fully known, and work to describe the mathematical relationship between the variables and the growth rate also continues. Research to elucidate many of these variables and their means of influencing the growth of phytoplantkton has been ongoing, and here we point out some of the important variables as described in recent articles. We begin with a few remarkable models.

Evans and Paranjape (1992) consider non-linear growth models that may be used to represent experimental data for phytoplankton growth in the presence of grazing by microzooplankton. These authors argue for the importance of considering nonlinear models when representing experimental data. Mailleret et al. (2005) consider models for algae in a chemostat, under variable yield growth assumptions, and provide a nonlinear control design. Flynn (2001) developed a model of phytoplankton growth by simulating the growth as a function of ammonium, silicon, nitrate, iron, temperature and light. Kmeť et al. (1993) present mechanistic model of adaptation of phytoplankton photosynthesis, based on transition of photosynthetic between resting, activated, or inhibited states. This model is used to study optimal levels of photosynthetic production.

The direct link between phytoplankton growth and photosynthesis has received much attention, and Sakshang et al. (1989) and Greider (1990) discuss the role on phytoplankton growth of length of exposure to daylight and more generally of the role of the photosynthesis-light curve in determining this rate. Kiefer and Cullen (1991) studied the interaction of environmental variables such as light intensity, photoperiod, temperature, and nutrient supply on the growth rate of phytoplankton. Gao et al. (2007) studied the effect of ultraviolet radiation on photosynthesis and growth of tropical phytoplankton, finding that photosynthetic production can be enhanced by ultraviolet radiation so that an accurate estimate must take ultraviolet radiation into account. Pahl-Wost and Imboden (1990) presented a mathematical model for dynamic change of photosynthesis with light intensity, where it is necessary to consider not only instantaneous light intensity, but also response time within the algae.

Wofsy (1983) examined the environmental effects on the phytoplankton growth rate using data from nutrient-saturated, light-limited marine systems. Baird et al. (2001) developed a model of phytoplankton growth and compared its behavior with chemostat cultures using different temperature settings, nutrient inputs, and a variety of dilution rates. Duarte et al. (2006) studied rates of phytoplankton growth in relation to biodiversity, climate change, and ecosystem function. These authors consider many variables, including salinity, temperature, nutrients, species composition of the phytoplankton, and chlorophyll A concentration, and they studied increased photosynthetic efficiency found under certain conditions.

Other more subtle variables studied by researchers include stoichiometry of the nutrients and within the phytoplankton, the role of certain important trace elements, upwellng of nutrients within the ocean, and the size composition of the phytoplankton communities. Takahashi et al. (1986) modeled phytoplankton growth and nutrient disappearance together with the upwelling of nutrients to the surface. Ho et al. (2003) state the important role of iron in phytoplankton growth, as well as the more general influence of metals in growth, demonstrating a differential effect across species. Mei et al. (2009) describe the role of size and cell volume on nutrient uptake, light absorption, and cellular metabolism, all directly affecting the growth rate of the phytoplankton colony. These authors expect the next generation of models to include the size structure of communities, and they want to better understand the relationship between size, light and nutrient use, and growth.

Beardall et al. (2009) are also concerned with investigating biovolume and specific growth of phytoplankton, and the factors that determine the growth. These authors state that much research remains to be done in determining which factors are the most important in influencing growth.

Such studies are important both for the purposes of modeling the growth of phytoplankton, and also from the evolutionary perspective, in order to better understand the selection of slow-growing species.

4. **Modeling phytoplankton growth.** Phytoplankton is a plant-type microscopic organism, often single–cellular that live and grow on or near the surface of the water such as the world's seas or oceans where there is plenty of light. Phytoplankton are responsible for making up a major proportion of the Earth's oxygen. They are the main source of food for other species in and out of the water. For instance, phytoplankton is the primary food supply for cultured mussels, Safi and Gibbs (2003). As mentioned above, the significance of studying the growth of

phytoplankton relates directly to climate and to a number of other important issues in ecology.

The multivariable model we presented above can be used to model the growth dynamics of phytoplankton as a function of time and any number of other explanatory variables. Such a model should be important to bioscientists, environmentalists, and policy makers in order to predict phytoplankton growth more accurately and to better understand possible interactions between explanatory variables involved in the growth dynamics. For instance, if an increased temperature is seen to slow phytoplankton growth, this is an important consideration to include when assessing climate change. The role of phytoplankton in oxygen production and carbon fixations makes these considerations essential, especially in regard to climate change.

In this section the multivariable growth model for phytoplankton growth, presented in Section 2, is used as a model to predict the growth of the phytoplankton biovolume. This model estimates the biomass of phytoplankton, in mm^3 of cells per liter of solution as a function of time, in days. The data is found in Nagle and Saff (1996). This data was originally obtained from Oliver Bernard, Station Zoologique de Villefranche-Sur-Mer France. The nutrients may be used as a management tool in managing phytoplankton community composition, as observed in Roelke et al. (1999). The following system of differential equations represent a classical model from the article of Monod (1950), to represent the change in S, concentration of the nutrient and B, biovolume of phytoplankton

$$\frac{dB}{dt} = \rho \frac{SB}{S+k} - \alpha B$$
$$\frac{dS}{dt} = \alpha \left(s_i - S\right) - \frac{\rho}{y} \frac{SB}{S+K}$$

α is dilution rate, ρ is growth rate, s_i is input concentration, and k, y are model constants. This model is the classical model for growth in the chemostat, assuming constant yield, although more modern models have introduced the concept of variable yield, starting with Droop (1974). For the phytoplankton data, we assume a model of the form

$$B_i = P(S_i, t_i; M, \delta, \gamma, \theta, \lambda) + \epsilon_i$$

where for i=1,...,n, the conditional mean of the random error terms are given as

$$E(\epsilon_i | S_i, t_i; M, \delta, \gamma, \theta, \lambda) = 0$$

and the conditional variance of the error term are

$$variance(\epsilon_i | S_i, t_i; M, \delta, \gamma, \theta, \lambda) = \sigma^2$$

With the conditional mean of the product of different random errors given by

$$E(\epsilon_i \epsilon_j | S_i, t_i, S_j, t_j; M, \delta, \gamma, \theta, \lambda) = 0, i \neq j.$$

For testing hypothesis regarding model parameters, we use asymptotic normality property of the estimate vector of the parameters. We use the multivariable model introduced in Section 2 to analyze the growth dynamics of biovolume which is considered as an estimation of biomass of phytoplankton and is measured in cubic millimeter of cells per liter of solution. Our explanatory variables are time and concentration of nutrient. The nutrient concentration is measured in μmol per liter. A link function of the form (3) from Section 2 was used in the analysis of this data.

Table 1. Parameter estimates for the phytoplankton data

Parameter	Estimate	Std Error	95% CI Lower Bound	95%CI Upper Bound
M	18.672	0.051	18.569	18.775
δ	0.098	0.016	0.066	0.130
γ	0.588	0.009	0.570	0.606
θ	-0.013	0.004	-0.022	-0.005
λ_1	1.230	0.068	1.094	1.367
λ_2	-0.102	0.008	-0.117	-0.086
λ_3	0.027	0.001	0.024	0.029

Table 1 presents the parameter estimates for the phytoplankton growth model (2), with link function (3). Using these parameters with the functions determined by (2) and (3), it is possible to estimate the biovolume at each time and nutrient concentration. Figure 1 shows a scatter plot of the growth dynamic of phytoplankton biovolume. There is hardly any visual significant difference between the observed and the estimated values. Statistical analysis of this data shows the mean Absolute Relative Error is 0.0649 with a standard deviation of 0.05556.

The Residual Mean Squared Error for this model is 0.024 with an R-Squared value of 1.00. This Residual Mean Squared Error is an estimate for σ^2. The plot of residuals against time showed no visible violation regarding the assumption of uncorrelated errors. Figure 2 presents a three dimensional graph of phytoplankton biovolume as a function of time and nutrient concentration. Figure 3 shows the velocity and acceleration for phytoplankton biomass as a function of time, at the fixed median concentration of 17.6 μmol/L and Figure 4 gives the time course of the growth of biovolume velocity as a function of time at three fixed concentrations. The concentrations used are the median concentration of 17.6 μmol/L, together with high and low concentrations of 43.81 μmol/L and 0.015 μmol/L, respectively.

In general, the link function g(X, λ) used in the model can be tailored to fit the variables of importance. Or it may also be used to test whether individual variables, or their interactions, significantly affect the growth dynamics. Testing of parameters for statistical significance using the Wald test gives a test statistic of χ^2= 327.184 for the time variable, χ^2 = 162.583 for the concentration variable, and χ^2 = 729 for the time-concentration interaction. These have two-sided p-values of 7.89E-73, 6.235E-37, and 2.956E-160, respectively. Thus these variables are all highly significant in determining phytoplankton growth dynamics, and this time-concentration interaction is the most highly significant. These results confirm our expectations, as concentration and time are both important factors in phytoplankton growth, and their effect is greatest with both acting together. The Likelihood Ratio and the Score Tests also give similar results, with the same conclusion from the data.

The model ability to produce explicit functions for velocity and acceleration is one of the strengths of this model that is not found in other models. We expect the velocity and acceleration functions to assist scientists in understanding phytoplankton growth dynamics. From the graphs in Figure 3 we can observe a large bump in the velocity, or a large burst in the growth rate of the phytoplankton, between days 4 and 5.5. On the graph of the experimental data and estimates in Figure 1 this corresponds to the period after the plateau where the growth takes off again. The dip in growth rate that we observe in this graph from days 3 to 4

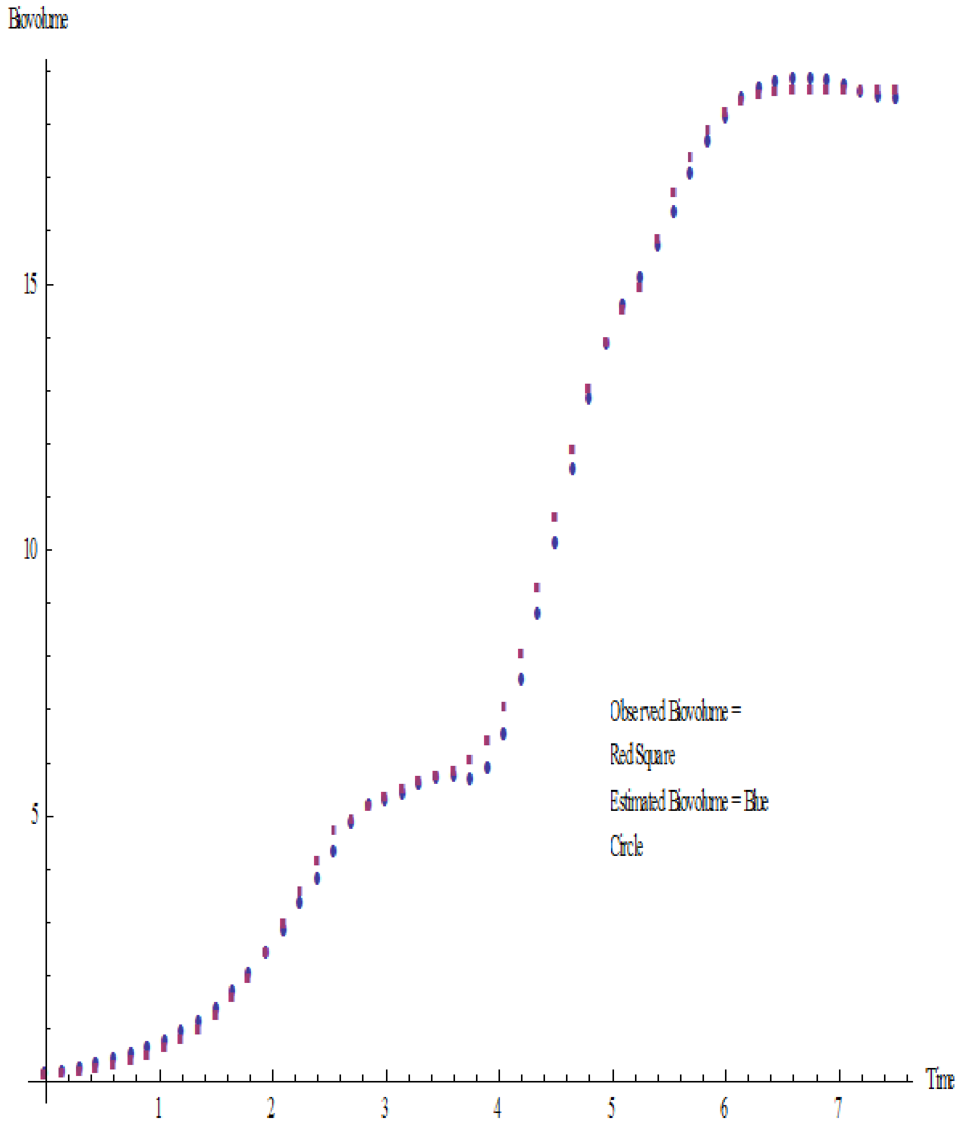

Figure 1. Experimental and Predicted Values for Phytoplankton Biomass.

corresponds to the plateau in phytoplankton growth, as seen in Figures 1 and 2. The maximum velocity is 11.8038 mm^3/L-day, and it occurs on day 4.6283. To better understand the growth dynamics and the role of nutrient concentration, we also explore variation in the concentration variable. In Figure 4, we can see how the time course of velocity is affected by concentration. There we consider the low and high concentrations of 0.015 μmol/L and 43.18 μmol/L, respectively, in addition to the median concentration of 17.6 μmol/L.

From these graphs it is clear that at higher concentrations of nutrients, the bump in velocity, or burst in growth of the phytoplankton occurs sooner and has a higher maximum velocity. The time course has the same form in all three cases, with

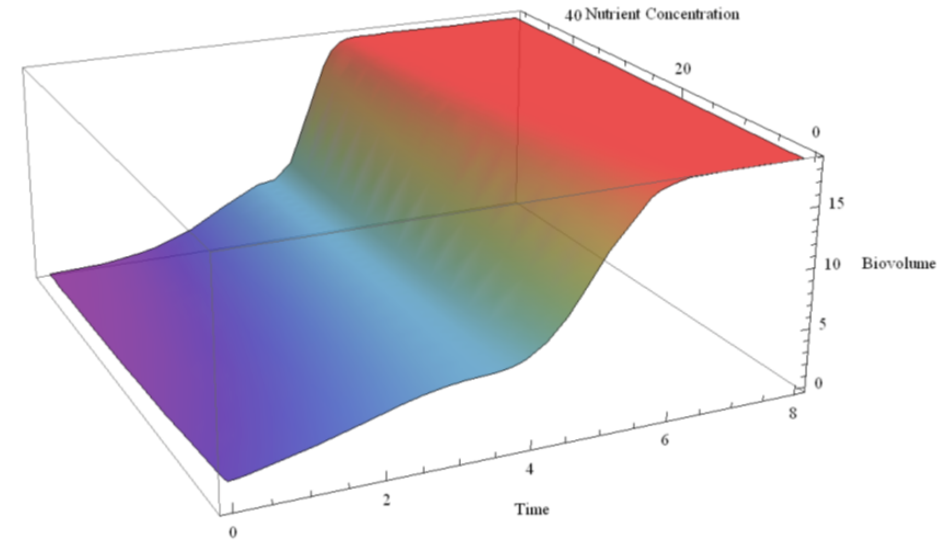

FIGURE 2. Phytoplankton Biomass as a Function of Time and Nutrient Concentration

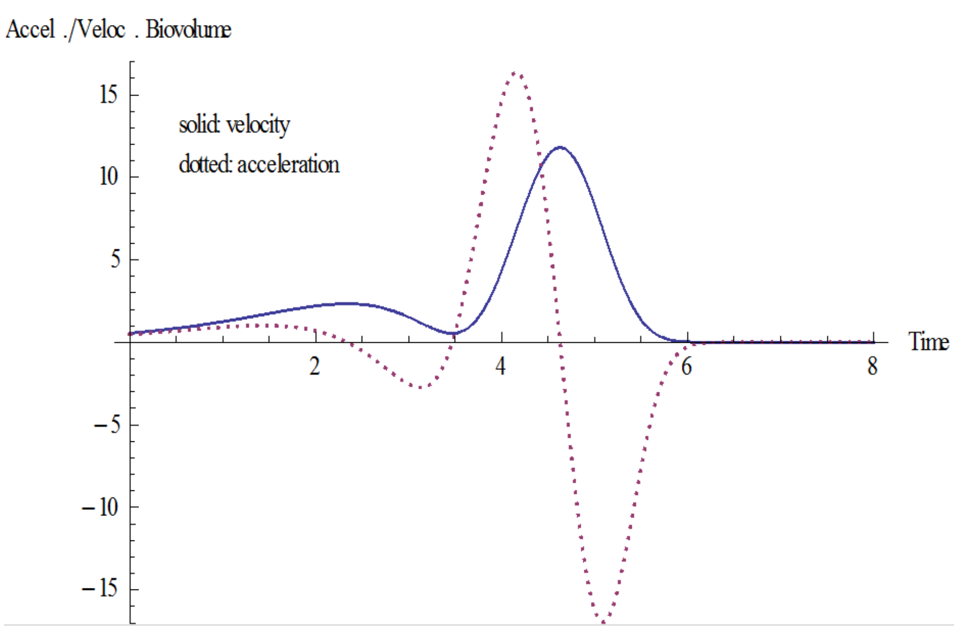

FIGURE 3. Velocity and Acceleration of Increase in Biovolume at Fixed Median Concentration

initially slow growth ending in a local minimum of velocity in the neighborhood of 3.5 days. This slowing in growth corresponds to the plateau in Figures 1 and 2, and it is followed by a burst in growth with an absolute maximum velocity somewhere between days 4.5 and 5.5. We now give the precise location of these local extrema of the velocity at the different concentrations. At the low concentration of 0.015

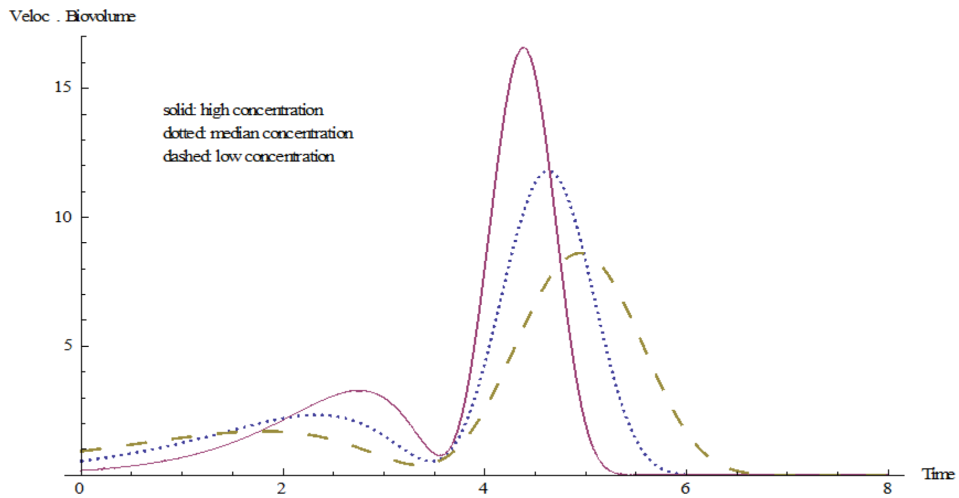

FIGURE 4. Velocity of Increase in Biovolume at Several Concentrations

μmol/L, the first local max of 1.68727 mm^3/L-day occurs at time 1.78585 days, the local min of 0.393078 mm^3/L-day occurs at time 3.3483 days, and the absolute max of 8.51719 mm^3/L-day occurs at time 4.9565 days. For the median concentration of 17.6 μmol/L, the first local max of 2.33837 mm^3/L-day occurs at time 2.34048 days, the local min of 0.544761 mm^3/L-day occurs at time 3.46788 days, and the absolute max of 11.8038 mm^3/L-day occurs at time 4.6283 days. For the high concentration of 43.18 μmol/L, the first local max of 3.28548 mm^3/L-day occurs at time 2.75481 days, the local min of 0.765406 mm^3/L-day occurs at time 3.55722 days, and the absolute max of 16.5848mm^3/L-day occurs at time 4.38312 days. Thus, we see how this multivariable model can help us to estimate the time and rate for the maximum and minimum rates of increase of phytoplankton biovolume for varying levels of nutrient concentration.

In addition to representing the data of phytoplankton growth as a function of time and concentration variables, the model allows us to test the significance of all variables, as well as their interactions. In obtaining an explicit function representing growth dynamics as a function of each explanatory variable, we then can apply derivatives to analyze further the velocity and the time course of the growth.

5. **Discussion.**

Recent work has demonstrated the effectiveness of hyperbolastic growth models in describing the growth rate of individual cells in a living system, such as tumor cells (Tabatabai et al. 2005) or stem cells (Bursac et al. 2006 and Tabatabai et al. 2010). As single-celled organisms growing within a larger living environment, phytoplankton may also be expected to follow growth dynamics that can be approximated well by similar models. However, growth of phytoplankton has an increased level of complexity, bringing in the issues of photosynthesis, light availability, and concentration of available nutrients which directly affect the growth rate. In the case of phytoplankton, much of the interest in modeling the growth dynamics relates to better understanding how these additional environmental factors affect the growth rate. The multivariable model for phytoplankton growth introduced in this paper can be a useful tool for scientists investigating the roles of these different variables in the dynamics of phytoplankton growth.

This new model for the growth of phytoplankton proves its accuracy and yields a closed form solution which closely approximates the experimental data set. It is thus possible to represent the partial derivative of the phytoplankton biovolume with respect to either time or nutrient concentration. Thus the explicit function produced by the model contains information about the phytoplankton growth rate, both as a function of time and as a function of level of nutrient concentration. In particular, the explicit velocity and acceleration curves that can be produced from the explicitly defined function produced by this model are novel features. Because of the excellent fit to the data, the information from the partial derivatives of this function gives highly accurate approximations to the actual growth rates. Thus it is also possible to use this model to determine the growth rate of phytoplankton under certain conditions for a given set of data points representing biovolume as a function of time.

In general the growth rate of phytoplankton is highly complicated and is dependent upon many variables. Given the appropriate experimental data, this model can be used to represent the impact on any one of these variables on the phytoplankton growth. Furthermore the model is capable of including the effects of multiple variables, such as temperature, light intensity, and nutrient concentration. As the growth dynamics of phytoplankton is not completely understood but still an area of investigation, this model is recommended to researchers in the field for use in modeling the dynamics of phytoplankton growth and describing the influence of explanatory variables.

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