A nutrient-induced seasonal algal bloom model

Wichuta Sae-jie, Kornkanok Bunwong, and Elvin J. Moore

***Abstract*—**A model for nutrient-phytoplankton dynamics is constructed and analyzed. We contribute theoretical analyses for a constant nutrient input and a time-varying nutrient input in terms of steady state, local and global stabilities, and limit cycle behavior. Numerical simulations of the model are carried out to examine the dynamics of the model for four types of nutrient input: 1) constant input, 2) sinusoidal input, 3) periodic step function input with fixed upper and lower amplitudes, 4) periodic step function input with time-varying upper and lower amplitudes. The numerical solutions confirm the non-oscillatory and oscillatory behaviors predicted from the theoretical analysis. It is shown that periodic nutrient inputs of types 2) and 3) cause phytoplankton blooms with periodic behavior and that changes in the frequency of the input produce blooms with a wide range of different dynamical behavior. It is found that nutrient inputs of type 4) give the best agreement between the model and the observed data.

***Keywords*—**Seasonal algal blooms, Nutrient-phytoplankton interaction, Oscillatory behavior, Seasonal nutrient input.

I. INTRODUCTION

PHYTOPLANKTON plays an important role for marine organisms as they are a fundamental food source at the bottom of the marine food chain. They are, for example, a food source for zooplankton [1]-[3], which are also a food source for higher marine animals. Like plants, phytoplankton absorb carbon dioxide in the presence of sunlight and produce oxygen by photosynthesis. Eventhough phytoplankton are essential as a fundamental food source for marine life, they can also severely damage marine life if their populations become excessively large. Some examples of these damaging effects are reduction of water quality and oxygen levels, release of toxic substances or creation of dead zones. Excessive phytoplankton levels in lakes, rivers or the ocean are often visible and are called algal blooms.

In addition to the damaging effects mentioned above, blooms of some algae are directly toxic to marine organisms. These blooms are called harmful algal blooms (HABs) and caused by toxic plankton species such as *chrysochrochomulina* spp [4]. These blooms can kill a wide range of wild organisms as well as farmed fish [5].

Although the growth of a phytoplankton population depends on many factors, the availability of nutrient, especially nitrate and phosphate, is often a key factor [6]-[7]. Excessive concentrations of these nutrients can be a major cause of algal bloom [4], [6]-[8]. This excess can be due to both natural and human causes. Human causes include uncontrolled run-off of nutrient-rich water from agricultural fields or disposal of untreated sewage into rivers, lakes and coastal seas. Other major environmental causes of algal blooms have been discussed in [8]

In 2002, Huppert, Blasius, and Stone [8] proposed that eutrophication can often be understood using a model that includes only nutrient and phytoplankton. Their main purpose was to determine how the nutrient input affected the phytoplankton population. Their model showed that an algal bloom was triggered whenever nutrient input reached a threshold level. In 2005, Huppert *et al.* [4] studied the dynamical behavior of a model for seasonal algal blooms with environmental forcing. Their forcing term was assumed to explicitly affect phytoplankton growth. They considered periodic forcing with a one year period of either sinusoidal or step function type.

A variety of mathematical models of phytoplankton dynamics have been proposed in the literature. These models can be nutrient-phytoplankton models [1]-[2], [8] or nutrient-phytoplankton-zooplankton (NPZ) models [1]-[3]. Various functional forms have been assumed for the interactions in these models [1]-[3]. Common functions used for nutrient uptake by phytoplankton are Lotka-Volterra interaction [9], Monod type or Michaelis-Menten kinetics or Holling type II [10]-[12].

In this paper, we consider a model for seasonal algal blooms in which the seasonal effects are due to changes in the nutrient input. The structure of this paper is as follows. In section II, we summarize field information on the occurrence of algal blooms and the seasonal pattern of coastal nutrient concentrations. Models of nutrient-phytoplankton interaction are proposed and their properties are analyzed theoretically in section III,. Moreover, four different functional forms of nutrient input are considered, namely, constant nutrient input, sinusoidal input, periodic step function input with constant upper and lower amplitudes in each period, and step function

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input with time-varying upper and lower amplitudes in each period. In section IV the results of numerical simulations are shown that reveal the wide variety of different types of asymptotic behavior of algal blooms that can occur as the type and frequency of the nutrient input is changed. The final section is discussion and conclusions.

II. FIELD OBSERVATIONS

Monitoring of *Peridinium gatunense* population was carried out from 1970 to 1999 in Lake Kinneret (Sea of Galilee), Israel. Fig. 1 illustrates the time series of phytoplankton biomass showing the mostly annual bloom dynamics [8]. The bloom usually occurs in spring and often in the same month. Each bloom looks like a spike with a different amplitude each year.

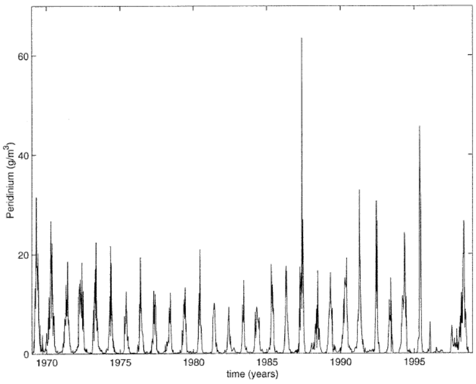

Fig. 1 Phytoplankton blooms from 1970-1999 [8].

Fig. 2 shows time series of monthly average concentrations of nutrients measured off southern Norway from 1990 to 2002 [5]. The time series data was obtained by sampling nutrient levels every second to third week at depths between 0-30 m. The pattern of nutrient concentrations shows annual fluctuations with a different amplitude each year. This data gives good guidance for developing a bottom-up model for algal blooms induced by seasonal changes in nutrient level.

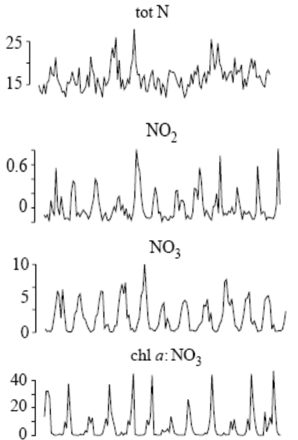

Fig. 2 Sampled nutrient data from 1990-2002 [5].

We will consider four different types of nutrient input, namely, a constant input, a sinusoidal input, a step function input with fixed upper and lower amplitudes, and a step function input with time-varying upper and low amplitudes.

III. THEORETICAL RESULTS

A. A General Nutrient-Phytoplankton Interaction Model

We consider a general forced dynamical model of nutrient-phytoplankton interaction of the following form:

$$\frac{dN}{dt} = \lambda(t)Q - f(N,P) - \phi N \quad (1)$$

$$\frac{dP}{dt} = g(N,P) - \sigma P, \quad (2)$$

where the following assumptions are made. The system is composed of homogenous compartments of nutrient and phytoplankton. Units are calculated in terms of nutrient concentration and biomass (phytoplankton) density. (1) describes the changing rate of nutrient concentration (N). The term $\lambda(t)Q$ represents an external nutrient input, where Q is a constant amplitude and $\lambda(t)$ gives the time dependence of the input. The term $f(N,P)$ represents a decreasing rate of N due to phytoplankton uptake, and the term ϕN is a rate of nutrient loss due to sinking to depths below the phytoplankton. (2) describes the changing rate of phytoplankton density (P). The term $g(N,P)$ is the growth rate of phytoplankton due to nutrient uptake and the term σP gives the decreasing rate of phytoplankton due to death. The parameters Q,σ,ϕ and the functions $f(N,P)$ and $g(N,P)$ are all nonnegative.

There are a variety of assumptions that have been made in the literature for the functional forms for nutrient input, phytoplankton growth, and phytoplankton uptake [3]. Commonly used phytoplankton growth functions are Malthus exponential growth, κP , logistic growth or growth limited by carrying capacity $\left(1-P/\kappa\right)P$, and Gompertz growth, $P\log(\kappa/P)$, where κ is a positive constant. Obviously, these growth functions do not explicitly show the effect of nutrient on phytoplankton population. Phytoplankton growth functions that explicitly include the effect of nutrient are: Lotka-Volterra interaction, γNP [9], Monod type or Michaelis-Menten kinetics or Holling type II, $\gamma\frac{NP}{\kappa+N}$ [10]-[11], and Holling type III, $\gamma\frac{N^2P}{\kappa+N^2}$ where γ is a positive coefficient that represents the conversion efficiency from food consumed into newborn plankton

In a chemostat environment [13], the nutrient input can be easily controlled. However, in the real-world, the nutrient input must be considered as a function of time. This nutrient input is often seasonal with an annual period, but with amplitude variations from year to year. In this paper, we examine the algal bloom behavior for three types of time-dependent nutrient input function.

B. Nutrient Input

Without loss of generality, we assume $\lambda(t)=1$. In plankton dynamics models it is often assumed that the growth of plankton depends on the quantities of its food consumed so that the functional forms of growth rate and uptake rate are the same. We will make this assumption here. We also assume that the functional forms of the growth rate and uptake functions are separable and linear in *P*, i.e., we assume $f(N,P)=\gamma h(N)P$ and $g(N,P)=\beta h(N)P$, where $h(N)$ is a strictly increasing function of *N* with $h(0)=0$. These assumptions are satisfied for the Lotka-Volterra, Monod type, and Holling type III growth functions mentioned above. Therefore, (1) and (2) become:

$$\frac{dN}{dt}=Q-\gamma h(N)P-\phi N\,, \tag{3}$$

$$\frac{dP}{dt}=(\beta h(N)-\sigma)P. \tag{4}$$

An equilibrium solution (N^*,P^*) must satisfy $dN/dt=0$ and $dP/dt=0$. Obviously, the trivial equilibrium state $(Q/\phi,0)$ always exists. From (4), it can be seen that P will decrease to 0 if $\beta h(N^*)-\sigma<0$. Therefore the trivial equilibrium state will be asymptotically stable in this case. On the other hand, if $\beta h(N^*)-\sigma>0$ then the trivial equilibrium state will be unstable.

The conditions for the existence of a second nontrivial equilibrium point (N^*,P^*) of (3) and (4) are that:

$$h(N^*)=\frac{\sigma}{\beta} \text{ and } P^*=\frac{Q-\phi N^*}{\gamma h(N^*)}=\frac{\beta(Q-\phi N^*)}{\gamma\sigma}>0. \tag{5}$$

Positive solutions for (5) exist iff $\underset{N}{Max}\,\beta h(N)\geq\sigma$ and $Q>\phi N^*$. To check the asymptotic stability of the nontrivial equilibrium point, we use the linearization method (Liapunov's first method [9]) and obtain the Jacobian as:

$$J(N^*,P^*)=\begin{bmatrix}-\gamma h'(N^*)P^*-\phi & -\gamma h(N^*)\\ \beta h'(N^*)P^* & 0\end{bmatrix} \tag{6}$$

We have assumed that $h(N)$ is a strictly increasing function and therefore the derivative $h'(N^*)>0$. Then, the real parts of the eigenvalues λ_1,λ_2 of (6) must be negative because

$\text{trace}(J)=\lambda_1+\lambda_2=-\gamma h'(N^*)P^*-\phi<0$ and

$\det(J)=\lambda_1\lambda_2=\beta\gamma h(N^*)h'(N^*)P^*>0$.

Therefore, if the nontrivial equilibrium point exists it must be locally asymptotically stable. We now consider the equilibrium states for the.Lotka-Volterra and Monod type interactions.

Case 1 Lotka-Volterra type interactions [19]

$f(N,P)=\gamma NP$, $g(N,P)=\beta NP$, $\sigma\neq\phi$.

The two equilibrium points are $(N_1^*,P_1^*)=(Q/\phi,0)$ and

$$N_2^*=\frac{\sigma}{\beta},\qquad P_2^*=\frac{\beta(Q-\phi N_2^*)}{\gamma\sigma} \tag{7}$$

The trivial equilibrium point is asymptotically stable if $\beta Q<\phi\sigma$, whereas the second equilibrium point exists and is locally asymptotically stable if $\beta Q>\phi\sigma$. In this case, it can also be proved that (N_2^*,P_2^*) is globally stable. A commonly used global stability test is Liapunov's second method and involves finding a Liapunov function $V(N,P)$ [14]. Then, if the properties in the following two lemmas are satisfied in some region *O*, the system must be globally stable.

Lemma 1 $V(N,P)$ is positive definite in *O*.

Lemma 2 $\dot V(N,P)$ is negative definite in *O*.

For the Lotka-Volterra uptake function a suitable Liapunov function is [13],[15]

$$V(N,P)=(N-N_2^*)+N_2^*\ln\left(\frac{N_2^*}{N}\right)+(P-P_2^*)+P_2^*\ln\left(\frac{P_2^*}{P}\right). \tag{8}$$

Case 2. Monod type interactions [16]-[17]

$f(N,P)=\gamma h(N)P$, $g(N,P)=\beta h(N)P$, $\sigma\neq\phi$, where $h(N)=N/(\kappa+N)$.

The trivial equilibrium point is again $(N_1^*,P_1^*)=(Q/\phi,0)$. Using (5) and the formula $h(N)=N/(\kappa+N)$, we find that the nontrivial equilibrium point is given by:

$$N_2^*=\frac{\sigma\kappa}{\beta-\sigma},\qquad P_2^*=\frac{\beta(Q-\phi N_2^*)}{\gamma\sigma} \tag{9}$$

A comparison of this second equilibrium point with the equilibrium point for the Lotka-Volterra interaction in (7) shows that the equilibrium nutrient level for the Monod interaction will be lower than that for the Lotka-Volterra if and only if $0<\sigma<\beta(1-\kappa)$ and then the equilibrium phytoplankton population for the Monod will be greater than for the Lotka-Volterra. Alternatively, if $\sigma>\beta(1-\kappa)$ then the equilibrium nutrient level for the Monod will be greater than that for the Lotka-Volterra and the phytoplankton population for the Monod will be less than for the Lotka-Volterra. From the theory given above, the nontrivial Monod equilibrium will be locally asymptotically stable if it exists. We will now prove that the function in (8) is a Liapunov function for the Monod interaction and therefore that the nontrivial Monod equilibrium is globally stable.

Proof. The function in (8) is positive definite. We now show that $\dot V(N,P)=\frac{\partial V}{\partial N}\dot N+\frac{\partial V}{\partial P}\dot P$ is negative definite relative to $E^*=(N^*,P^*)$.

$\dot V(N^*,P^*)=0$, when $N_2^*=\frac{\sigma\kappa}{\beta-\sigma}$ and $P_2^*=\frac{\beta(Q-\phi N_2^*)}{\gamma\sigma}$

$$\dot{V}(N,P) = \left(1-\frac{N_2^*}{N}\right)\left(Q-\frac{\gamma NP}{\kappa+N}-\phi N\right) + \left(P-P^*\right)\left(\frac{\beta N}{\kappa+\mathrm{N}}-\sigma\right)$$

Let $H = \begin{bmatrix} \dot{V}_{NN} & \dot{V}_{NP} \\ \dot{V}_{PN} & \dot{V}_{PP} \end{bmatrix}_{\left[N_2^*,P_2^*\right]}$

Since $\dot{V}_{PP}=0$, the determinant is $-\dot{V}_{PN}\dot{V}_{NP}<0$.

Thus, $\dot{V}(N,P)$ is negative definite.

C. Sinusoidal Nutrient Input

We summarize the results for two special cases where analytic solutions can be found for periodic nutrient input. Further details can be found in [9].

Case 3. $f(N,P)=g(N,P)$, $\sigma=\phi$. [15]

In this case a simple solution for $s(t)=N(t)+P(t)$ can be found from (3) and (4). Summing (3) and (4), we obtain a linear equation for $N(t)+P(t)$ which can be solved using the integrating-factor method. The solution for this special case is

$$s(t)=(N+P)(t)=e^{-\sigma t}\left[\int_0^t \lambda(\tau)Qe^{\sigma\tau}d\tau+C\right]$$

where C is an arbitrary constant.

For a sinusoidal input, $\lambda(t)=(1+\cos\omega t)/2$, the solution is

$$s(t)=e^{-\sigma t}\left[\Phi(t)+C\right]$$

where $C=s(0)$ and $\Phi(t)=\frac{1}{2}Q\int_0^t e^{\sigma\tau}(1+\cos\omega t)d\tau$.

A straightforward integration then gives the result

$$s(t)=\frac{1-e^{-\sigma t}}{\sigma}+\frac{(\sigma\cos\omega t+\omega\sin\omega t)-\sigma e^{-\sigma t}}{\sigma^2+\omega^2}+s(0)e^{-\sigma t}.$$

For a sufficiently large t, the exponential terms tend to zero and the solution becomes

$$s(t)=\frac{1}{\sigma}+\frac{(\sigma\cos\omega t+\omega\sin\omega t)}{\sigma^2+\omega^2}$$

which is a periodic solution with the same frequency as the input. Therefore, nutrient and phytoplankton have the same periodic behavior. For the next case, we consider the system when growth and uptake functions as well as loss of nutrient and phytoplankton are not identical. The Monod form has already been considered by Jang *et al.* [18]. We consider the Lotka-Volterra interaction.

Case 4 $f(N,P)=\gamma NP$, $g(N,P)=\beta NP$, $\sigma\neq\phi$:

The system when $P=0$ is considered first.

$$\frac{dN}{dt}=\lambda(t)Q-\phi N. \tag{10}$$

(9) has a trivial ω-periodic solution $(\bar{N}(t),0)$ where $\bar{N}(t)$ is a unique ω-period solution of the form [9]

$$\bar{N}(t)=\frac{\phi e^{-\phi t}}{e^{\phi\omega}-1}\int_t^{t+\omega}\frac{e^{\phi s}\lambda(s)Q}{\phi}ds \tag{11}$$

and a general solution $N(t)$ can be written as

$$N(t)=\bar{N}(t)+(N(0)-\bar{N}(0))e^{-\phi t}.$$

Therefore $N(t)\to\bar{N}(t)$ as $t\to\infty$. Some properties of the solutions are summarized in the following lemma and theorem.

Lemma 3 Solutions of (10) are nonnegative and the system is dissipative.

Proof. See [9].

Theorem If $\mu_0=\int_0^\omega(\beta\bar{N}(t)-\sigma)dt<0$, the solution $(N(t),P(t))$ of (10) satisfies $\lim_{t\to\infty}(N(t)-\bar{N}(t))=\lim_{t\to\infty}P(t)=0$

Proof. See [9].

Therefore, if $\mu_0<0$ the nutrient input is insufficient to support the phytoplankton population and the population becomes extinct. As shown in [9], the trivial solution is stable if $\mu_0<0$ and unstable if $\mu_0>0$. In order to show that (10) has a nontrivial ω-periodic solution $(\tilde{N}(t),\tilde{P}(t))$, similarly to Jang *et al.* [18], more lemmas and theorems are required.

D. StepFunction Nutrient Input

We consider two types of step function for the time-dependent nutrient input factor $\lambda(t)$ in (1).

Type 1) Constant upper and lower amplitudes. We assume that the input has a period T divided into a high amplitude interval τ with amplitude α_1 and a low amplitude interval $T-\tau$ with amplitude α_2. That is,

$$\lambda(t_m)=\begin{cases}\alpha_1, & t_m\in[mT,mT+\tau)\\ \alpha_2, & t_m\in[mT+\tau,(m+1)T)\end{cases} \quad m=0,1,2,\ldots$$

In this case, for sufficiently long values of T and τ, the solutions of (1) and (2) would converge to steady states corresponding to constant nutrient input $Q\alpha_1$ in each interval of length τ and constant nutrient input $Q\alpha_2$ in each interval of length $T-\tau$. For shorter time intervals, the behavior has to be determined by integration of (1) and (2). Some numerical examples are given in section IV.

Type 2) Periodically varying upper and lower amplitudes. We assume that the input has a period T divided into a high amplitude interval τ with sinusoidally varying function of amplitude α_1 and frequency ω_1 and a low amplitude interval $T-\tau$ with a sinusoidally varying function of amplitude α_2 and frequency ω_2 That is,

$$\lambda(t_m)=\begin{cases}\alpha_1(1+\cos(\omega_1 t_m))/2, & t_m\in[mT,mT+\tau)\\ \alpha_2(1+\cos(\omega_2 t_m))/2, & t_m\in[mT+\tau,(m+1)T)\end{cases}$$

In this case, for sufficiently long values of T and τ, the solutions of (1) and (2) would converge in each interval to the periodically varying solutions discussed in section III. For shorter time intervals, the behavior has to be determined by integration of (1) and (2). Some numerical examples are given in section IV.

IV. NUMERICAL RESULTS

In this section we investigate the dynamical behavior of the system for typical values of the parameters for four types of nutrient input. We first show the behavior for constant nutrient input and then show the behavior for three types of time-dependent input. We assume parameter values similar to those given in Huppert *et al* [8] for algal blooms in Lake Kinneret in Israel, i.e., $Q = 0.0075$, $\gamma = \beta = 1$, $\phi = 0.001$, $\sigma = 0.1$, and with the initial condition $(N, P) = (0.0005, 0.05)$. The ODE solver *ode45* in Matlab has been used to solve (3) and (4).

A. Constant Nutrient Input

Fig. 3 shows the solution to the system in Case 1, i.e., for the Lotka-Volterra nutrient uptake function. The phytoplankton density and nutrient concentration initially oscillate but eventually tend to the stable nontrivial equilibrium solutions of (9). For the parameter values used, the analytic solution gives

$$(N_2^*, P_2^*) = \left(\sigma/\beta, \left(\beta Q/\sigma - \phi\right)/\gamma\right) = \left(0.1, 0.0740\right).$$

in agreement with the numerical solution shown in Fig. 1. It can be seen that the maxima and minima of the phytoplankton densities occur with a short delay after the maxima and minima of the nutrient concentrations. The behavior looks like a damped oscillation with a period of approximately 90 days and a decay time of approximately 200 days.

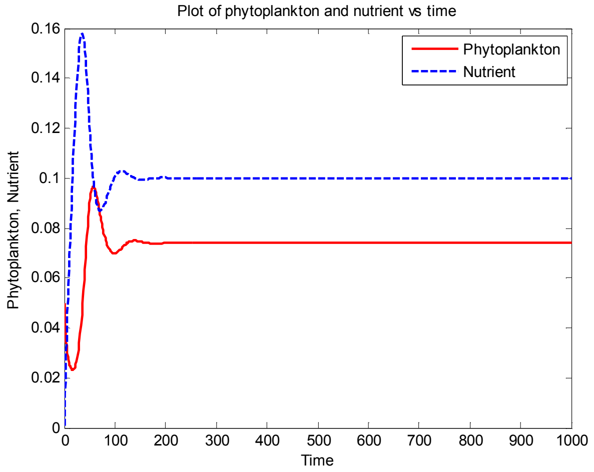

Fig. 3 The time series of the solution to the system for Lotka-Volterra uptake function and constant input with $Q = 0.0075$, $\gamma = \beta = 1$, $\phi = 0.001$, $\sigma = 0.1$.

Fig. 4 shows the solution to the system in Case 2, i.e., for Monod-type nutrient uptake function. The qualitative behavior of the solution is similar to that for the Lotka-Volterra uptake function, but there are differences in detail. For the value of $\kappa = 0.5$ used, the nutrient equilibrium values from (9) are $(N_2^*, P_2^*) = (0.0556, 0.0744)$ in agreement with the results shown in Fig. 4. Further, the nutrient equilibrium value is lower than for the Lotka-Volterra and the phytoplankton equilibrium is higher, in agreement with the theoretical results in section 3.

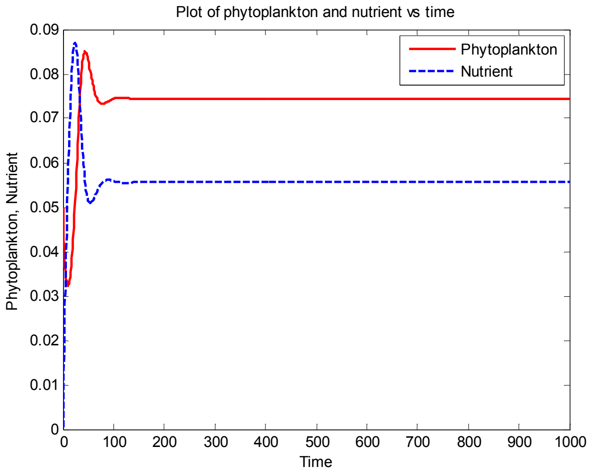

Fig. 4 The time series of the solution to the system for the Monod uptake function and constant input with $\kappa = 0.5$, $Q = 0.0075$, $\gamma = \beta = 1$, $\phi = 0.001$, $\sigma = 0.1$

B. Sinusoidal Nutrient Input

We consider three cases. We first show the behavior for input periods close to the natural transient periods in Fig. 3 and 4, then we show behavior for input periods much greater than the natural periods and finally we show behavior for nutrient periods much less than the natural periods.

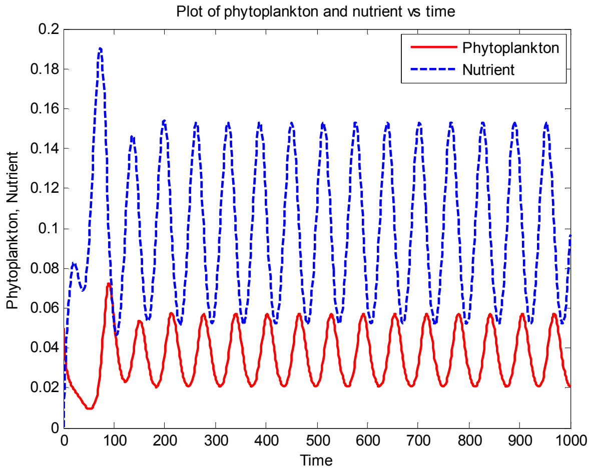

Fig. 5 The time series of the solution to the system for Lotka-Volterra uptake function and sinusoidal input with $Q = 0.0075$, $\gamma = \beta = 1$, $\phi = 0.001$, $\sigma = 0.1$, $\omega = 0.1$.

Fig. 5 displays the oscillatory behavior that occurs for sinusoidal input when the forcing frequency of the Lotka-Volterra nutrient input is $\omega = 0.1$. This forcing frequency corresponds to a period that is approximately 63 days, which is approximately two-thirds of the period of approximately 90 days shown in Fig. 3 for constant Lotka-Volterra nutrient input. After initial transient fluctuations, it can be seen that the solution tends to an oscillating solution with a period approximately the same as that of the periodic nutrient input. As in Fig. 3, maxima and minima in phytoplankton density occur shortly after maxima and minima of nutrient concentration

Fig. 6 shows the oscillatory behavior that occurs for sinusoidal input when the forcing frequency of the Monod nutrient input is $\omega = 0.1$. The qualitative behavior of the solutions are similar to that for the Lotka-Volterra nutrient uptake function, but there are again differences in detail.

In the remainder of this paper, we will only show results for the Lotka-Volterra nutrient uptake function. As in the examples shown above, we have found that the qualitative behavior of the Monod nutrient uptake function is similar to that of the Lotka-Volterra function in all cases considered.

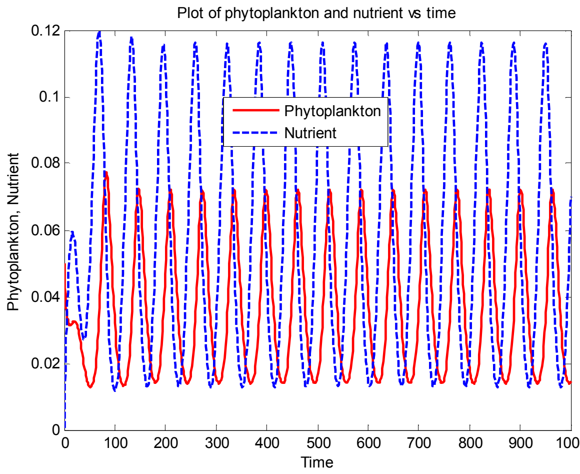

Fig. 6 The time series of the solution to the system for Monod uptake function and sinusoidal input with $\kappa = 0.5$, $Q = 0.0075$, $\gamma = \beta = 1$, $\phi = 0.001$, $\sigma = 0.1$, $\omega = 0.1$

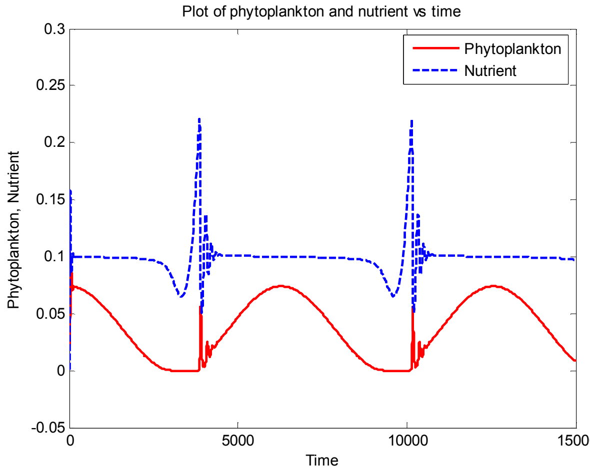

Fig. 7 The time series of the solution to the system for Lotka-Volterra uptake function and sinusoidal input with $Q = 0.0075$, $\gamma = \beta = 1$, $\phi = 0.001$, $\sigma = 0.1$, $\omega = 0.001$.

Fig. 7 shows the oscillatory behavior that occurs for sinusoidal input when the input frequency is $\omega = 0.001$. This frequency corresponds to a period much greater than the period of approximately 90 days in Fig. 3. The observed behavior in Fig. 7 looks like a set of separated damped oscillating solutions similar to the damped oscillating solution for constant input of Fig. 3. In this case, the phytoplankton response looks like a response to a set of constant inputs of two distinct amplitudes. If time between amplitude changes is long compared with the natural decay time of the phytoplankton, then a set of separated constant input solutions of the type shown in Fig. 7 would be expected to occur. This interpretation can be seen more clearly for the step wave input function behavior shown in the next section. As before, maxima and minima in phytoplankton density occur shortly after maxima and minima in nutrient concentration.

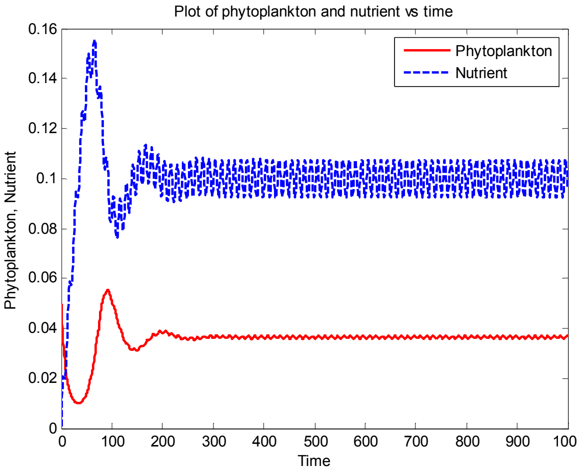

Fig. 8 The time series of the solution to the system for Lotka-Volterra uptake function and sinusoidal input with $Q = 0.0075$, $\gamma = \beta = 1$, $\phi = 0.001$, $\sigma = 0.1$, $\omega = 0.5$.

Fig. 8 shows the dynamical behavior that occurs when $\omega = 0.5$. This frequency corresponds to a period which is much less than the period of the constant input solutions. In this case, the nutrient input is oscillating much faster than the phytoplankton density can respond. Therefore, the phytoplankton responds to a time-averaged input which appears approximately constant. Therefore the solution looks like a constant input solution, but with small superimposed rapid fluctuations. As usual, maxima and minima in phytoplankton density follow maxima and minima in nutrient concentration.

C. *Periodic Step Function Nutrient Input*

We use the time varying input shown as case 1 in section IIID, i.e.,

$$\lambda(t_m) = \begin{cases} \alpha_1, & t_m \in [mT, mT+\tau) \\ \alpha_2, & t_m \in [mT+\tau, (m+1)T) \end{cases} \qquad m = 0, 1, 2, \ldots$$

In figure captions, the value of α_1 is "Q", the value of α_2 is "Nutrient factor times Q", the value of τ is "odd interval" and the value of $T - \tau$ is "even interval".

Fig. 9 shows the time series solution for the case where the total time interval T is 360 days or 1 year, which is four times the natural transient period of 90 days for the same value of *Q*. It can be seen that the behavior is periodic with a period equal to 360 days.

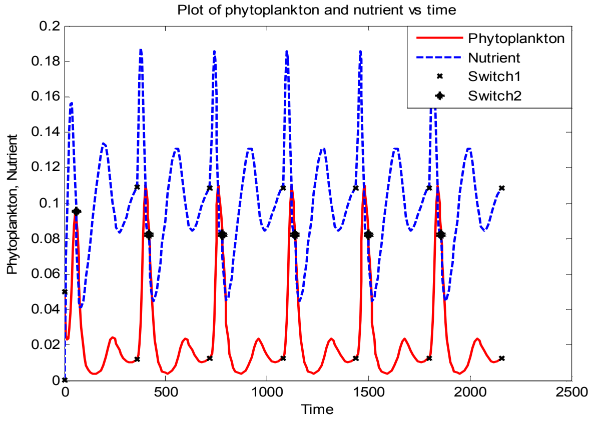

Fig. 9 The time series of the solution to the system for Lotka-Volterra uptake function and step function with $Q = 0.0075$, $\gamma = \beta = 1$, $\phi = 0.001$, $\sigma = 0.1$, Nutrient factor = 0.2, odd interval = 60, even interval = 300, $\omega_1 = 0$, $\omega_2 = 0$.

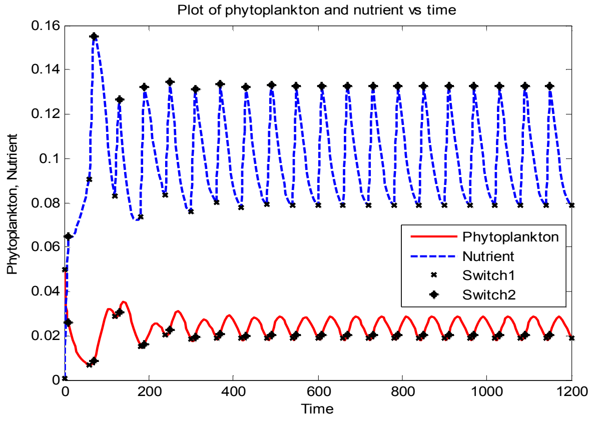

Fig. 10 The time series of the solution to the system for Lotka-Volterra uptake function and step function with $Q = 0.0075$, $\gamma = \beta = 1$, $\phi = 0.001$, $\sigma = 0.1$, Nutrient factor = 0.2, odd interval = 10, even interval = 50, $\omega_1 = 0$, $\omega_2 = 0$.

Fig. 10 shows the behavior when the total time interval *T* is 60 days, which is less than the natural 90 day period. It can be seen that the behavior is periodic with the same period as the uptake function.

Fig. 11 shows the time series solution for the case where the total time interval *T* is 800 days or 1 year, which is much greater than the natural period of 90 days. In this case, the nutrient concentration and the phytoplankton density appear to converge to the nontrivial equilibrium states corresponding to the upper and the lower amplitudes (compare Fig. 7).

D. Periodic Step Function Nutrient Input with Sinusoidal Amplitude Variation

We use the time varying input shown as case 2 in section IIID, i.e.,

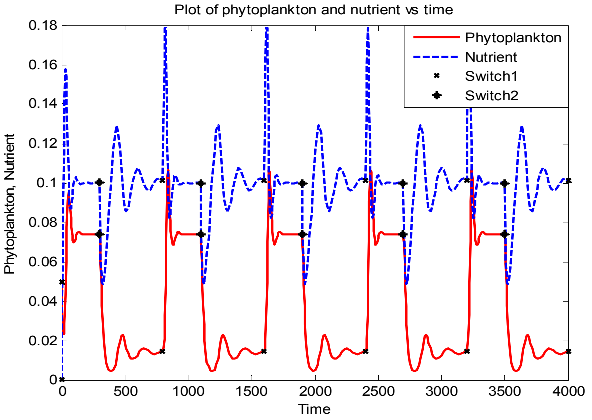

Fig. 11 The time series of the solution to the system for Lotka-Volterra uptake function and step function with $Q = 0.0075$, $\gamma = \beta = 1$, $\phi = 0.001$, $\sigma = 0.1$, Nutrient factor = 0.2, odd interval = 300, even interval l= 500, $\omega_1 = 0$, $\omega_2 = 0$.

$$\lambda(t_m) = \begin{cases} \alpha_1(1+\cos(\omega_1 t_m))/2, & t_m \in [mT, mT+\tau) \\ \alpha_2(1+\cos(\omega_2 t_m))/2, & t_m \in [mT+\tau, (m+1)T) \end{cases}$$

As in section *C,* in figure captions, the value of α_1 is "*Q*", the value of α_2 is "Nutrient factor times *Q*", the value of τ is "odd interval" and the value of $T-\tau$ is "even interval".

Fig. 12 shows the behavior when the total time *T* is 360 days. The nutrient input is high for 60 days each year and low for 300 days. It can be seen that the phytoplankton density shows peaks corresponding to algal blooms each year, but that the amplitude of the bloom varies each year depending on the actual level of nutrient input during the high input period. This response is similar to the observed data in Fig. 1.

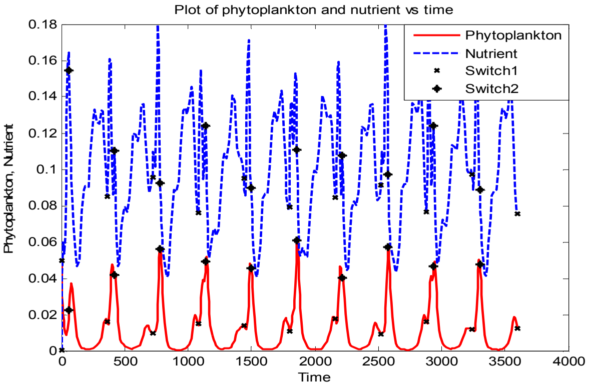

Fig. 12 The time series of the solution to the system for Lotka-Volterra uptake function and step function with $Q = 0.0075$, $\gamma = \beta = 1$, $\phi = 0.001$, $\sigma = 0.1$, Nutrient factor = 0.2, odd interval = 60, even interval = 300, $\omega_1 = 0.15$, $\omega_2 = 0.08$.

Fig. 13 shows the response when the period of the nutrient input function is short compared with the natural period and Fig. 14 shows the response when the period of the nutrient input function is long compared with the natural period.

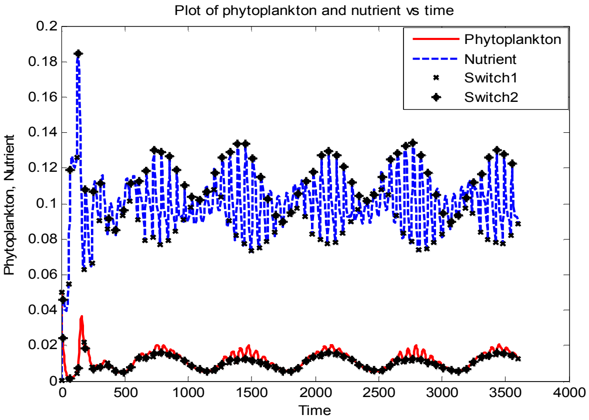

Fig. 13 The time series of the solution to the system for Lotka-Volterra uptake function and step function with $Q = 0.0075$, $\gamma = \beta = 1$, $\phi = 0.001$, $\sigma = 0.1$, Nutrient factor = 0.2, odd interval = 10, even interval = 50, $\omega_1 = 0.1$, $\omega_2 = 0.2$.

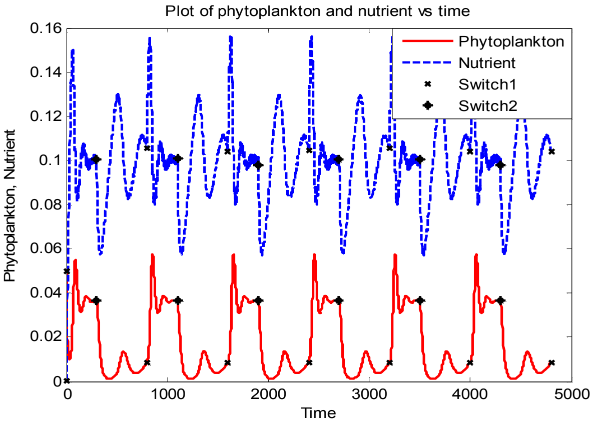

Fig. 14 The time series of the solution to the system for Lotka-Volterra uptake function and step function with $Q = 0.0075$, $\gamma = \beta = 1$, $\phi = 0.001$, $\sigma = 0.1$, Nutrient factor = 0.2, odd interval = 300, even interval = 500, $\omega_1 = 2$, $\omega_2 = 1$.

V. DISCUSSION AND CONCLUSIONS

We have studied a nutrient-phytoplankton model both analytically and numerically. For constant nutrient input of sufficiently large amplitude, phytoplankton blooms can occur that initially fluctuate but then tend to a locally and globally stable equilibrium solution with nonzero nutrient concentration and phytoplankton density. The model shows that large nutrient increases are generally followed by bloom events. The effect of seasonal periodic nutrient has been studied numerically for three different types of input for a range of values for the periods of the inputs. The three different types of periodic input are 1) sinusoidal, 2) step function with constant upper and lower amplitudes, 3) step function with time dependent upper and lower amplitudes. We have shown that the qualitative behavior depends on the ratio of the nutrient period to the natural damped oscillating period of the phytoplankton. For long-period nutrient input, the phytoplankton solutions show a series of blooms each similar to a constant-input bloom. For short-period input, the phytoplankton bloom is similar to the bloom produced by a constant input equal to the time-average of the periodic input. For inputs of type 1) and 2) and of similar period to the natural phytoplankton period, the blooms show initial fluctuations which are eventually replaced by blooms that closely follow the periodic behavior of the nutrient input. In particular, the amplitudes of the bloom is the same in each period. For inputs of type 3) of similar period to the natural period, the blooms again show initial fluctuations which are eventually replaced by blooms of similar period to the nutrient period, but the bloom amplitudes show random fluctuations with different amplitudes at each period. In all cases, maxima and minima in phytoplankton densities follow after maxima and minima for nutrient concentrations. The closest agreement between the observed blooms in Fig. 1 and the model behavior occurs for inputs of type 3) with nutrient input periods comparable with the natural transient decay period of the phytoplankton.

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