A Phytoplankton Bloom Model with Seasonal Nutrient Input

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Abstract: - A model for nutrient-phytoplankton dynamics is constructed and analyzed. A theoretical analysis shows that changes in the nutrient input can significantly change the qualitative behavior of the phytoplankton dynamics. In particular, the behavior can change from asymptotically stable to periodic. Numerical solutions of the model are carried out for seasonal nutrient inputs of a range of different frequencies and amplitudes. The numerical solutions confirm the non-oscillatory and oscillatory behaviors predicted from the theoretical analysis. The numerical simulations show that a periodic nutrient input can cause phytoplankton blooms and that changes in the frequency of the input can produce blooms with a wide range of different dynamical behaviors. In addition, it is shown that in some regions of parameter space, the oscillatory behavior recurs annually and agrees with observational data.

Key-Words: - Bloom dynamics, Frequencies, Nutrient-phytoplankton interaction, Oscillatory behavior, Periodically forced damped system, Seasonal nutrient input.

1 Introduction

Marine ecosystems contain many different organisms, e.g., plankton, fish, shellfish, corals, plants etc. Among them, phytoplankton plays an important role as a fundamental food source at the bottom of the marine food chain or food web. Phytoplankton behaves like a plant, i.e., it absorbs carbon dioxide and produces oxygen during photosynthesis and reverses the process during respiration. Excessive phytoplankton populations, however, can severely damage marine life. Some examples of these damaging effects are depletion of oxygen in the sea-water, reduction of water quality, and creation of dead zones. These environmental phenomena are known as red tide, algal bloom, or eutrophication. The first two terms are used when excess plankton population growth is the main concern while the last term is used when excessive concentrations of nutrient are primarily considered. Although growth of the phytoplankton population depends on many factors, the availability of nutrient, especially nitrate and phosphate, is often a key factor [1]. Excessive concentrations of nutrients can be a major cause of algal bloom. This excess can be due to human activities, e.g., uncontrolled
run-off of nutrient-rich water from agricultural fields or disposal of untreated sewage into rivers, lakes and coastal seas [2].

In addition to the effects mentioned above, blooms of some algae are directly toxic to marine organisms. These blooms are called harmful algal blooms (HABs) and can be caused by toxic plankton species such as *chrysochromulina* spp [3]. These blooms can kill a wide range of wild organisms as well as farmed fish [4]. In 2005, Sarkar et al. [1] constructed a model for these HABs consisting of two harmful phytoplankton and zooplankton species and studied its qualitative behavior.

A variety of different mathematical models of phytoplankton dynamics have been proposed in the literature. Several models have been based on classical predator-prey models [1, 5, 6] or chemostat models [3]. Nutrient-phytoplankton-zooplankton (NPZ) models have recently become popular models for studying marine ecosystems, (see, e.g. [5, 6, 7]). Usually, the functional forms used in each model are varied depending on the author’s assumptions. For example, the rate of nutrient uptake may be described as a saturating function of nutrient [2, 3]. Edwards and his colleagues [5, 6] have developed a model using Michaelis-Menten kinetics to describe the nutrient uptake by phytoplankton. Franks [7] has studied the behavior of NPZ models for a variety of choices of functional forms.

Huppert, Blasius, and Stone [8] proposed that eutrophication can often be understood using a model that includes only nutrient and phytoplankton in 2002. Support for the idea that “bloom is strongly controlled by nutrient rather than by higher tropic levels” comes from the phytoplankton *Peridinium*. This is a phytoplankton that is rarely grazed by zooplankton. Huppert et al used a “bottom-up” approach model to study the behavior of the phytoplankton dynamics for a constant nutrient input. 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 [3] 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.

In this paper, we consider a model for seasonal algal blooms in which the seasonal effects are due to periodic changes in the nutrient input. The structure of this paper is as follows. In section 2, we summarize field information on the recurrence of algal blooms and the seasonal pattern of coastal nutrient concentration caused, for example, by freshwater runoff. In section 3, models of nutrient-phytoplankton interaction are proposed and their properties are analyzed theoretically. Two different types of nutrient input are considered, namely, constant nutrient input and periodic nutrient input. Section 4 shows results of numerical simulations revealing the wide variety of different types of asymptotic behavior of algal blooms that can occur as the frequency of the nutrient input is changed. The final section is discussion and conclusions.

### 2 Field Observations

![Fig. 1: Phytoplankton blooms from 1970-1999](image)

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.

![Fig. 2: Sampled nutrient data from 1990-2002](image)

Fig. 2 shows time series of monthly average concentrations of nutrients measured off southern Norway from 1990 to 2002 [4]. The time series data was obtained by sampling nutrient levels every
second to third week at depths between 0-30 m. Obviously, the pattern of nutrient concentrations behaves like a periodic function. This data gives good guidance for developing a bottom-up model of seasonal nutrient control of algal blooms. We will assume that the seasonal nutrient input can be approximated as a sinusoidal function.

3 Theoretical Results

A general forced model of nutrient-phytoplankton interaction can be written as follows

\[
\frac{dN}{dt} = \lambda(t)Q - f(N, P) - \phi N
\]

\[
\frac{dP}{dt} = g(N, P) - \sigma P,
\]

where the following assumptions are made. The system is composed of homogenous compartments of nutrient and phytoplankton. Units are calculated in terms of concentration and biomass density, respectively. Equation (1) describes the changing rate of nutrient concentration \(N\). The term \(\lambda(t)Q\) shows an increasing rate of \(N\) due to an external nutrient input, the term \(f(N, P)\) explains a decreasing rate of \(N\) due to phytoplankton uptake, and the term \(\phi N\) expresses a loss rate of nutrient due to sinking to depths below the phytoplankton. Equation (2) shows 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 \(\sigma P\) expresses the decreasing rate of phytoplankton due to death.

There are a variety of assumptions that have been made in the literature for the functional forms for nutrient input, phytoplankton growth functions, and phytoplankton uptake [7]. Commonly used growth functions are Malthus exponential growth, logistic growth, and Gompertz growth. These growth functions do not explicitly include the effect of nutrient on population. Alternative growth functions which explicitly include the effect of nutrient are the Lotka-Volterra interaction, the Monod type, and the Holling type III. In plankton dynamics models, it is usually assumed that the plankton growth depends directly on the amount of nutrient consumed, and therefore the functional forms of growth rate and uptake rate are usually assumed to be identical. In a chemostat environment, the nutrient input can be easily controlled to be a constant. However, in the real world, the nutrient input should be considered as a function of time. According to section 2, a good choice for seasonal nutrient input is a periodic function.

3.1 Constant Nutrient Input

Without loss of generality, we assume \(\lambda(t) = 1\). We also assume that the functional forms of the growth rate and uptake functions are identical in separable and linear forms in \(P\). That is, \(f(N, P) = \gamma h(N)P\) 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,

\[
\frac{dN}{dt} = Q - \gamma h(N)P - \phi N
\]

\[
\frac{dP}{dt} = (\beta h(N) - \sigma)P.
\]

An equilibrium solution \((N^*, P^*)\) must satisfy \(dN/dt = 0\) and \(dP/dt = 0\). Obviously, \((Q/\phi, 0)\) always exists. This equilibrium solution is locally asymptotically stable if \(\beta h(N^*) - \sigma < 0\) and unstable if \(\beta h(N^*) - \sigma > 0\).

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

\[
h(N^*) = \frac{\sigma}{\beta} \quad \text{and} \quad P^* = \frac{Q - \phi N^*}{\gamma h(N^*)}.
\]

Positive solutions for (5) exist iff \(\max \beta h(N) \geq \sigma\) and \(Q > \phi N^*\). If this second equilibrium point exists, it is always asymptotically stable. We now consider two special cases.

Case 1 Lotka-Volterra type interactions [9]

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

This system contains two nonnegative equilibrium points, an unstable point \((N_1^*, P_1^*) = (Q/\phi, 0)\) and a stable point \((N_2^*, P_2^*) = (\sigma/\beta, (\beta Q/\sigma - \phi)/\gamma)\), where \(\beta Q > \phi \sigma\). In this case, \((N_2^*, P_2^*)\) is not only asymptotically stable but is also globally stable because we can construct a Liapunov function

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

Case 2 \(f(N, P) = g(N, P)\), \(\sigma = \phi\).

In this case a simple solution for \(N(t) + P(t)\) can be found from (3) and (4) even when the nutrient input is time-dependent. 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

\[(N + P)(t) = e^{-\sigma t} \left[\int_0^t \lambda(\tau)Qe^{\sigma \tau} d\tau + C\right].\]
where $C$ is an arbitrary constant.

### 3.2 Periodic Nutrient Input

We assume that $\lambda(t) = (1 + \cos \omega t)/2$. 

#### Case 3

After substituting $s = N + P$, we obtain the first order linear equation which can be solved by the integrating-factor method

$$s(t) = e^{at}[\Phi(t) + C]$$

where $C = s(0)$ and $\Phi(t) = \int_0^t e^{a(t-\tau)}(\lambda(t)Qd\tau$.

Using Euler’s formula $z = re^{i\theta} = r(\cos \theta + i\sin \theta)$, multiplying the numerator and denominator by $\sigma - i\omega$, rearranging, and substituting, we obtain

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

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. Therefore, nutrient and phytoplankton have 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. [11]. We then 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.

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

(6)

It can be shown to have a trivial $\omega$-periodic solution $(\vec{N}(t), 0)$ where $\vec{N}(t)$ is a unique $\omega$-period solution of the form

$$\vec{N}(t) = \frac{\phi e^{\omega t}}{e^{\phi t} - 1} \int_0^{\omega} e^{\omega s} \lambda(s)Qd\sigma$$

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

$$N(t) = \vec{N}(t) + (N(0) - \vec{N}(0))e^{\omega t}.$$  

So $N(t) \to \vec{N}(t)$ as $t \to \infty$.

#### Lemma

Solutions of (6) are nonnegative and the system is dissipative.

**Proof.** Let $s = N + P$ and suppose $L = \min\{\sigma, \phi\}$. $\lambda(t)$ is a sinusoidal function so $|\lambda(t)| < M$. Since $N|_{s_0=0} = \lambda(t)Q > 0$ and $P|_{s_0=0} = 0$, the solution of the system remains nonnegative for $t \geq 0$. Then, $\dot{s} \leq \lambda(t)Q - \phi N - \sigma P \leq MQ - Ls$.

It follows that $\limsup_{t \to \infty} (N(t) + P(t)) \leq MQ / L$.

Finally, we have $N(t) + P(t) \leq \frac{MQ}{L}$ for all $t$ large. Therefore the system is dissipative.

#### Theorem

If $\mu_0 = \int_0^\omega (\beta \vec{N}(t) - \sigma)dt < 0$, the solution $(N(t), P(t))$ of (6) satisfies $\lim_{t \to \infty} (N(t) - \vec{N}(t)) = \lim_{t \to \infty} P(t) = 0$.

**Proof.** From $\vec{N} \leq \lambda(t)Q - \phi N$, for $t \geq 0$,

$$N(t) \leq \vec{N}(t) + (N(0) - \vec{N}(0))e^{\omega t}.$$  

For any $\epsilon > 0$, there exists $t_0 \geq 0$ such that for $t \geq t_0$ $N(t) \leq \vec{N}(t) + \epsilon$. After choosing $\epsilon > 0$, we obtain

$$\int_0^\omega (\beta(\vec{N}(t) + \epsilon) - \sigma)dt < 0$$

From $\dot{P} \leq P(\beta - \sigma)$, for some $n = n(t) > 0$,

$$P(t) \leq P(0)e^{\int_0^t[\beta(\vec{N}(\tau) + \epsilon) - \sigma]d\tau}.$$  

Thus $\lim_{t \to \infty} P(t) = 0$. Next consider $\lim_{t \to \infty} N(t) - \vec{N}(t)$.

Since $\frac{d}{dt}Ne^{\omega t} = e^{\omega t}(\lambda(t)Q - \gamma PN)$, we obtain

$$N(t) = N(0)e^{\omega t} + \phi e^{\omega t} \int_0^t e^{\omega s} \lambda(s)Qd\sigma - re^{\omega t} \int_0^\omega N(r)P(r)e^{\omega dr}.$$  

Because $\lim_{t \to \infty} P(t) = 0$ and $N(t)$ is bounded, we get

$$\lim_{t \to \infty} \gamma e^{\omega t} \int_0^\omega N(r)P(r)e^{\omega dr} = 0.$$  

So $N(0)e^{\omega t} + \phi e^{\omega t} \int_0^t e^{\omega s} \lambda(s)Qd\sigma$ is a solution of (6) with initial condition $N(0)$. Thus, $N(t) \to \vec{N}(t)$ as $t \to \infty$.

As a conclusion, $\mu_0 < 0$ implies that nutrient input is insufficient to support the phytoplankton population. Consequently, it becomes extinct. The stability of the $\omega$-periodic solution $(\vec{N}(t), 0)$ can be considered via Floquet multipliers which are all eigenvalues of the fundamental matrix solution $\Phi(t)$ of the following linear system

$$\dot{Z} = \left[\begin{array}{cc} -\phi & -\gamma \vec{N} \\ 0 & \beta \vec{N} - \sigma \end{array}\right] Z$$

where $\Phi(0) = I$. In Case 4, all eigenvalues of $\Phi(t)$ are $e^{\int_0^t[\beta N(t) - \sigma]dt}$ and $e^{\omega t}$. Thus $(\vec{N}(t), 0)$ is unstable if $\mu_0 > 0$. In order to show that (6) has a nontrivial $\omega$-periodic solution $(\vec{N}(t), \vec{P}(t))$, similarly to Jang et al. [11], more lemmas and theorem are required.
4 Numerical Results

In this section we mainly investigate the system behavior starting from the damped system in Case 1 to the forced system in Case 4 with the same values of parameters given in Huppert et al. [8], i.e., \( Q = 0.000375, \gamma = \beta = 1, \phi = 0.001, \sigma = 0.1 \), and with the initial condition \((N, P) = (0.0005, 0.05)\). The ODE solver \textit{ode45} in Matlab has been used.

Fig. 3 shows the solution to the system in Case 1. The phytoplankton density and nutrient concentration initially oscillate but eventually tend to the stable equilibrium solutions of the second type with nonzero \((N^*_2, P^*_2) = \left(\frac{\sigma}{\gamma}(\beta Q/\sigma - \phi)/\gamma\right)\). It can be seen that the minima of the nutrient concentration approximately correspond to the maxima of the phytoplankton density. For the parameter values used, the analytic solution gives \((N^*_2, P^*_2) = (0.1, 0.00275)\). The behavior looks like a damped oscillation with a period of approximately 250 days and a decay time of approximately 1100 days.

Fig. 4 displays the oscillatory behavior that occurs for Case 4 when the forcing frequency of the nutrient input is \( \omega = 0.02 \). This forcing frequency corresponds to a period that is approximately 320 days, which is slightly greater than the period of approximately 250 days shown in Fig. 3 for constant 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, minima in nutrient concentration correspond approximately to maxima in phytoplankton density.

Fig. 5 shows the oscillatory behavior that occurs for Case 4 when the input frequency is \( \omega = 0.001 \). This frequency corresponds to a period much greater than the period of approximately 250 days in Fig. 3. The observed behavior in Fig. 5 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. 5 would be expected to occur. As before, minima in nutrient concentration respond to maxima in phytoplankton density.
the solution looks like a constant input solution, but with small superimposed rapid fluctuations. As usual, minima in nutrient concentration correspond approximately to maxima in phytoplankton density.

Fig. 6: The time series of the solution to the system in Case 4 with $Q = 0.000375$, $\gamma = \beta = 1$, $\phi = 0.001$, $\sigma = 0.1$, $\omega = 0.1$.

5 Conclusion
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. Three distinct types of behavior have been observed depending 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 input of similar period to the natural phytoplankton period, the blooms show initial fluctuations which are eventually replaced by blooms that closely follow the nutrient input. 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. In all cases, minima in nutrient concentrations correspond approximately to maxima in phytoplankton density [3]. Although there are differences in detail, the solution shown in Fig. 4 is in broad qualitative agreement with the observed field data shown in Fig. 1 and 2.

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