# Stochastic modeling of phytoplankton allelopathy

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ABSTRACT

The study of dynamic interactions between two competing phytoplankton species in the presence of toxic substances is an active field of research due to the global increase of harmful phytoplankton blooms. Ordinary differential equation models for two competing phytoplankton species, when one or both the species liberate toxic substances, are unable to capture the oscillatory and highly variable growth of phytoplankton populations. The deterministic formulation never predicts the sudden localized extinction of certain species. These obstacles of mathematical modeling can be overcome if we include stochastic variability in our modeling approach. In this investigation, we construct stochastic models of allelopathic interactions between two competing phytoplankton species as a continuous time Markov chain model as well as an Itô stochastic differential equation model. Approximate extinction probabilities for both species are obtained analytically for the continuous time Markov chain model. Analytical estimates are validated with the help of numerical simulations.

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## 1. Introduction

Almost all aquatic life is based upon plankton – the freely floating and weakly swimming organisms near the surface of most aquatic environments, namely, lakes, rivers, estuaries and oceans [1]. The plant form of a plankton community is known as phytoplankton, capable of photosynthesis in the presence of sunlight; algae are the most common form of phytoplankton. Phytoplankton occupy the first trophic level for many aquatic food chains and therefore, serve as a basic food resource. They release oxygen during photosynthesis and absorb carbon dioxide from the surrounding environment [2]. The most common features of phytoplankton populations are rapid increase of biomass due to rapid cell proliferation and after a given period of time, almost equally rapid decrease of biomass, referred to as a "bloom". In the last two decades, there has been a global increase in harmful algal blooms (HAB) of both toxic as well as non-toxic algal species [3–6]. Considerable attention has been directed toward HAB because of their negative impact on the ecology and the environment. Investigations have been undertaken to understand the exact bio-physical reason behind harmful toxic blooms but well accepted reasons behind this phenomenon are unknown [3,5–13].

The fluctuation of phytoplankton densities within a marine environment is affected by several important external factors including variation of essential nutrients and environmental forcing arising from seasonal changes (for other factors see [14]). Another important factor affecting phytoplankton growth is known as allelopathy, studied in this investigation. The term "allelopathy" was first introduced by Molisch in 1937 [15] and applied extensively to phytoplankton communities by Rice [15]. Allelopathy is the effect of one plant species on the growth of another through the release of chemical compounds into the surrounding environment [15,16]. The chemical compounds are known as "allelochemicals".

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Allelochemicals often have an inhibitory effect on some species (HAB) but are not always harmful to some phytoplankton; sometimes they act as stimulator to growth. For example, *Enteromorpha linza* produces allelochemicals which are auto-stimulatory and also stimulatory to the growth of *Enteromorpha* species [10]. *Chlorella vulgaris*, a unicellular green alga, produces an autotoxin which regulates its own growth and also inhibits the growth of *Asterionella formosa* and *Nitzschia frustulum* [8,11].

Competition for resources among plankton communities may alter the allelopathic effects of bloom-forming algae [17]. *Karenia brevis*, a red tide dinoflagellate, known to be allelopathic to the diatom *Skeletonema costatum*, was shown to have highly variable allelophathic effects that depended on growth conditions [17]. When cultured *S. costatum* was grown with field samples of *K. brevis* bloom extract that did not contain *S. costatum*, a significant reduction in growth was observed, whereas only marginally significant reduction in growth was observed when the bloom extract already contained *S. costatum* [17]. In this latter case, competition between the two algae species was hypothesized as a possible factor in the reduction of the allelopathic potency [17]. According to Smayda [7], flagellates generally have lower nutrient uptake affinity than diatoms and allelochemicals may help offset this disadvantage. Although the experimental results in [17] showed statistical significance, they were also highly variable. In this investigation, we focus on the qualitative effects of allelopathy on two competing phytoplankton species.

One of the first mathematical models for the allelopathic interaction between two competing species was studied by Maynard-Smith [19]. This model was based on two-species Lotka–Volterra type competition with an additional term representing the effect of toxic substances released by one species that negatively impact the second species. Several mathematical models have been analyzed, based on the model proposed by Maynard-Smith, with the hypothetical functional form for the allelopathic interaction term [13,20–22]. A recent experimental study on the two phytoplankton species, *C. polylepis* and *H. triquetra*, applied a more realistic allelopathic interaction rate between two phytoplankton species $N_i, i = 1, 2$. This allelopathic interaction rate has the form: $(N_1N_2)^2$ [13,16]. The experiment was based on batch cultures but interspecific competition terms were neglected due to the fact that the growth curve of the toxic alga was similar for mono-cultures and for all mixed cultures of various initial concentrations of the two species. The model proposed by Solé et al. [16] was extended by Bandyopadhyay [13] to incorporate inter-specific competition terms into the growth equations of both the toxic phytoplankton and the non-toxic phytoplankton populations. Conditions were derived for local and global stability of a coexisting equilibrium. Recently, Bandyopadhyay et al. [12] considered a delay differential equation model for toxic and non-toxic phytoplankton interaction within a fluctuating environment by introducing multiplicative white noise terms into the growth rates of two phytoplankton species. The population fluctuation intensity around the equilibrium point was obtained through Fourier transform methods [12].

We review the basic mathematical models developed for allelopathy in the presence of two phytoplankton species. We extend the deterministic model of Bandyopadhyay [13] for two competing species with one species allelopathic to the other, to two new stochastic models based on continuous time Markov chain (CTMC) models and on stochastic differential equations (SDEs). These new theoretical models account for the inherent variability in proliferation, competition and inhibition induced by allelochemicals at a small spatial scale that may be observed in controlled experimental settings [17,18]. Some new theoretical results concerning the moments of the population distributions are derived for the stochastic models. Numerical simulations are used to compare the dynamics of the stochastic models to the deterministic models in two cases. For the model of Bandyopadhyay [13], the first case represents persistence of both competitors, whereas the second case represents the bistable case, where the outcome depends on the initial density. The SDE models illustrate the high variability in plankton densities that depend on the spatial scale and on the assumptions regarding the birth and death rates. The CTMC models illustrate the importance of the initial density of plankton cells to population establishment.

## 2. Deterministic mathematical models

The model for two competing phytoplankton species with allelopathic interaction introduced by Maynard-Smith [19] was studied extensively by Chattopadhyay [23]. This mathematical model is a system of ordinary differential equations (ODEs):

$$\frac{dN_1(t)}{dt} = N_1(t)[\alpha_1 - \beta_1 N_1(t) - v_1 N_2(t) - \gamma_1 N_1(t)N_2(t)], \tag{1}$$

$$\frac{dN_2(t)}{dt} = N_2(t)[\alpha_2 - \beta_2 N_2(t) - v_2 N_1(t) - \gamma_2 N_1(t)N_2(t)], \tag{2}$$

with non-negative initial conditions $N_1(0) = N_{10} \geqslant 0$ and $N_2(0) = N_{20} \geqslant 0$. In model (1) and (2), $N_1(t)$ and $N_2(t)$ are the densities of two competing phytoplankton species at time $t$ (number of cells per fixed volume). The parameters $\alpha_1$ and $\alpha_2$ are the cell proliferation rate per day; parameters $\beta_1$ and $\beta_2$ are intra-specific competition coefficients for species 1 and 2, respectively; parameters $v_1$ and $v_2$ are the inter-specific competition coefficients. Parameters $\gamma_1$ and $\gamma_2$ are the toxic inhibition coefficients for the first species by the second and vice versa. The ratios $\alpha_1/\beta_1$ and $\alpha_2/\beta_2$ are the environmental carrying capacities of the two phytoplankton species, in the absence of competition and inhibition. The allelopathic interaction between two competing species is proportional to the product of the square of the concentration of the toxin-inhibiting species with the concentration of the toxin-producing species.

That is, the allelopathic interaction terms take the form $\gamma_i N_i^2 N_j$ with the allelopathic parameter equal to $\gamma_i$. This nonlinear functional form for the allelopathic interaction was proposed by Smith [19]. In this model, both species act as