

Mathematical models of nutrient recycling and toxin production in a gradostat



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ABSTRACT

We discuss several gradostat models in which a microbial population excretes a dissolved toxin, which in some cases can get recycled back into the system as a nutrient source. Each mathematical model consists of six ordinary differential equations and represents the dynamics of harmful algal blooms in a two compartment gradostat, for example representing lakes with fringing coves. We examine three different modes of toxin production, related to the algal growth rate, mortality rate, and nutrient limitation, respectively. Local and global stability analysis of the equilibria predict that algal abundance and toxin concentration can be both washed out or both persist under different environmental conditions. All theoretical results are supported by a set of numerical simulations.

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1. Introduction

Harmful algal blooms can be found in inland as well as coastal waters, and have increased in both frequency and intensity [1–3]. Some algae produce toxins that kill fish and other wildlife in the aquatic systems [4,5], and some of the toxins can even have direct implications for human health [6,7]. This paper focuses on the growth of a single kind of algae, such as the flagellate *Prymnesium parvum* [8], which produces fish-killing toxins, or species of cyanobacteria producing toxins such as cylindrospermopsin [9] or microcystin [10]. Populations of algae in inland waters, and their production of toxins, are related to nutrient supply. In some cases, the toxins contain a limiting nutrient, and chemical decomposition of the toxin results in nutrient recycling. Variations of the models analyzed here address such situations.

Water flow in reservoirs can wash out algae populations [9], and their toxins. However, fringing coves can provide a storage zone for both algae and their toxins, so that the algal and toxin persistence is enhanced. The possibility of algal persistence depends on the order of the water system [9]. Basically, in small, low-order streams with rapid flow, no algae can be suspended in the system. However, as the order increases, more coves appear in the water system, and the probability of the development of algal population increases [9]. We use a gradostat model to represent algal population growth in riverine reservoirs with fringing coves. We present three models making different assumptions about toxin production: the growth-related model, the limitation-related model, and the mortality-related model that are derived from [11,4]. We also introduce two modified models derived from the general growth-related and mortality-related models, in which chemical decomposition of the toxin results in nutrient recycling [9].

The situation of interest, considering the two-vessel gradostat in this study, is the existence of the algae population in both vessels. Namely, the algae can only either be completely washed out from the ecosystem or have its population fill the whole

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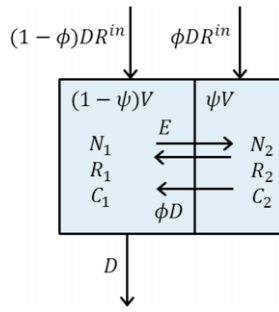


Fig. 1. Gradostat diagram of the biological system: a lake (left vessel) and its single cove (right vessel).

ecosystem. For a gradostat model without competition, the persistence of the system always corresponds mathematically to having an unstable trivial equilibrium and a globally stable positive equilibrium. By examining the global behavior and the conditions for stability of both trivial and nontrivial equilibria, we were able to conclude whether the mode of toxin production is a crucial factor of the existence and stability of the algal population.

2. The models

The mathematical models examined here are constructed from modifying single-species versions of competition models in chemostats and gradostats presented in [4,11]. In addition, it is assumed that the algae produce toxin constantly, and the toxin has no effect on mortality of the species producing the toxin, though it may have a cost of production in reduced growth. We use a two-vessel gradostat model with constant volumes (Fig. 1) to represent algal populations in a main lake with a single fringing cove. The parameters, units, and biological meanings are shown in Table 1. The limiting nutrient for algal growth enters the main lake and the single cove at a constant concentration R^{in} . The whole-system dilution rate is denoted by D and the exchange rate between the main lake and the cove is denoted by E . The model is constructed under the assumption that the flow of algae and toxin follows that of the nutrient [9].

The three different models – the growth-related model, the limitation-related model, and the mortality-related model – are developed to represent three different modes of toxin production by algae [9]. The following system of differential equations represents the general form of all three models:

$$\begin{aligned}
 \frac{dN_1}{dt} &= (\mu(R_1) - m)N_1 - \frac{D + E}{1 - \psi} N_1 + \frac{\phi D + E}{1 - \psi} N_2, \\
 \frac{dN_2}{dt} &= (\mu(R_2) - m)N_2 + \frac{E}{\psi} N_1 - \frac{\phi D + E}{\psi} N_2, \\
 \frac{dR_1}{dt} &= \frac{(1 - \phi)D}{1 - \psi} R^{in} - (\mu(R_1) - m)N_1 q_N - \frac{D + E}{1 - \psi} R_1 + \frac{\phi D + E}{1 - \psi} R_2, \\
 \frac{dR_2}{dt} &= \frac{\phi D}{\psi} R^{in} - (\mu(R_2) - m)N_2 q_N + \frac{E}{\psi} R_1 - \frac{\phi D + E}{\psi} R_2, \\
 \frac{dC_1}{dt} &= \varepsilon f_i(R_1)N_1 - \frac{D + E}{1 - \psi} C_1 + \frac{\phi D + E}{1 - \psi} C_2 - kC_1, \\
 \frac{dC_2}{dt} &= \varepsilon f_i(R_2)N_2 + \frac{E}{\psi} C_1 - \frac{\phi D + E}{\psi} C_2 - kC_2,
 \end{aligned} \tag{1}$$

where, $i = 1, 2, 3$. Here, N_1, N_2 denote the population densities of the algae and C_1 and C_2 denote the concentration of the toxin in the two vessels, respectively. Population dynamics represents a balance between growth, removal by dilution, and mortality at per capita rates m [12]. The population growth rate depends on the nutrient concentration in the two vessels, R_1 and R_2 respectively [11]. The nutrient uptake function $\mu(R_j)$, $j = 1, 2$ is assumed to be bounded and monotone increasing, i.e., $d\mu/dR_j > 0$, with $\mu(0) = 0$ and $0 \leq \mu(R_j) \leq \mu^{max} < \infty$, where μ^{max} represents the maximal growth rate. The model-specific functions, $f_i(R_j)$, $i = 1, 2, 3$, are defined as follows:

- In the growth-related model [13,14], the toxin is produced proportional to the productivity of the algae, $f_1(R_j) = \mu(R_j)$. This case assumes that toxin is produced proportional to other cellular products and released into the water at a constant rate [9].
- In the limitation-related model, the algae is assumed to produce toxin more rapidly when there is little nutrient in the system [9], $f_2(R_j) = \mu^{max} - \mu(R_j)$. For example, the flagellate *Prymnesium parvum* [15–17] produces toxin proportional to the degree of algal nutrient limitation.
- In the mortality-related model, the algae produces toxin in proportion to the mortality rate, $f_3(R_j) = m$ [9]. For example, some cyanobacteria produce a toxin called microcystin, which is contained in cells and released rapidly when the mortality rate of the cyanobacteria is high.

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