MATHEMATICAL MODELS OF NUTRIENT RECYCLING AND TOXIN

PRODUCTION IN A GRADOSTAT

by

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To my mother Jinhong He and my father Xun Dong.

To my son Vincent Xiuqi Yang and my husband Yi Yang.

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ABSTRACT

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We discuss several gradostat models in which a microbial population excretes a biochemical that 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 lakes with fringing coves. We examine three different situations of biochemical production which is based on the algal growth rate, mortality, and nutrient concentration, respectively. Local and global stability analysis of the equilibria predicts that algal abundance and biochemical concentration can be both washed out or persistent under different environmental conditions. All theoretical results are supported by a set of numerical simulations.

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CHAPTER 1

INTRODUCTION

Harmful algae blooms can be found in inland as well as coastal waters, and have increased in both frequency and intensity [1, 2, 3]. Some of the algae release toxins that kill fish and other wildlife in the aquatic systems [4, 5], and some of the toxins even can have direct implications for human health [6, 7], such as, a toxic flagellates called *Prymnesium parvum* [8] and *cyanobacteria* producing *cylindrospermopsin* [9] and *microcystin* [10]. This paper discusses the nutrient recycling in inland aquatic ecosystems like broad rivers, lakes and riverine reservoirs [9], and focuses on the growth of a single kind of alga and its toxic production in such systems with limited nutrient supply.

The concept of chemostat occupies a central place in mathematical ecology. A chemostat is a laboratory device that can be used to model algae growth in a simple lake [11]. In order to keep the culture volume of a chemostat constant, the liquid is continuously removed from the device with new liquid added to it simultaneously [12, 13]. Basic chemostat models assume that the nutrient recycling proceeds in a well-mixed, spatially uniform habitat [4, 11], hence the mathematical approach to a chemostat is based on a system of ordinary differential equations. Setting chemostat as a starting point, this paper focuses on modeling in a gradostat, which is a combination of chemostats with the vessels connected to each other on both sides [11]. Several studies have already demonstrated the dynamics of algae growth and toxin production in a chemostat (see [14, 15, 16]). Most of the time, one is able get analytic solutions for a chemostat model, as well as a competition model in a gradostat (see

[11, 17]). However, as the complexity of an ODE model increases, for example, a gradostat model without competition, finding analytic solutions become impossible and conclusions can only be obtained using steady-states analysis.

Water flow in riverine reservoirs can wash out algae populations [9], and their toxic productions. However, fringing coves provide storage zone for both algae and their toxin that enhances algal and toxin persistence [9]. The possibility of algal persistence depends on the order of the water system. Basically, in small, low-order streams with rapid flow, no algae can be suspended in the system. However, as the order increases, the coves in broad rivers and riverine reservoirs increase the probability of the development of algal population [9]. Gradostat models are mostly used when modeling nutrient recycling and algal population growth in riverine reservoirs with fringing coves. The gradostat discussed in this paper is a two-vessel gradostat with constant volume which is used to model a main lake and its single cove. The first three models: general growth related model, limitation related model and mortality related model are derived from the gradostat model without competition [11]. Specifically, this paper discusses on two modified models derived from the general growth related model and mortality related model. Consider cyanobacteria producing cylindrospermopsin [9] and microcystin[10], which can be recycled to the system as nutrient of the cyanobacteria, hence the models are ODE systems with the toxin concentration parameters involved in the nutrient concentration equations.

The persistence of population for a species growing in an empty habitat always means the consistence of the population distribution. For example, considering the two-vessel gradostat in this study, the situation of interest is the existence of the algae population in both vessels. Namely, the algae can only be completely washed out from the ecosystem or have its population fulfill the whole ecosystem. For a gradostat model without competition, the persistence of the system always corresponds math-

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ematically to having an unstable trivial equilibrium and a globally stable positive equilibrium as a "gold standard" of persistence in a theoretical sense. In the modified models mentioned in this paper, different modes of toxin production are discussed. By examining the global behavior and the conditions for stability of both trivial and nontrivial equilibriums, one is able to conclude whether the mode of toxin production a crucial factor of the existence and stability of the algal population.

CHAPTER 2

THE GENERAL MODELS

2.1   Introduction

Mathematical modeling is used to represent the dynamic exchange of microorganisms, toxins, and nutrients in a main lake and its single cove, as shown in Fig. 2.1 [9].
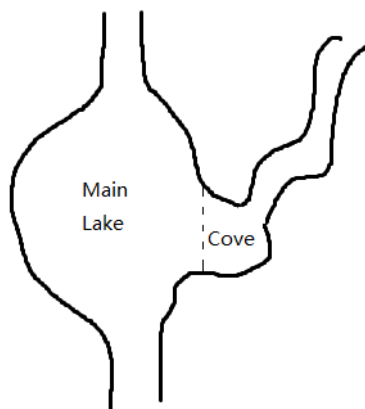
Figure 2.1. A lake and its single cove.

The models are derived from the standard model of growth without competition in a gradostat [11] by appending two equations for dynamics of the toxin produced by the algae. In addition, it is assumed that the algae produces toxin constantly, and the toxin production has no effect on growth or mortality of the algae.

2.2   The Models

In Fig. 2.2, the left vessel represents the main lake and the right vessel represents its single cove [9].

$$(1 - \phi)DR_1^{in} \qquad \phi DR_2^{in}$$

$$(1 - \psi)V \qquad \psi V$$

$$E$$

$$N_1 \qquad N_2$$
$$R_1 \qquad R_2$$
$$C_1 \qquad C_2$$

$$\phi D$$

$$D$$
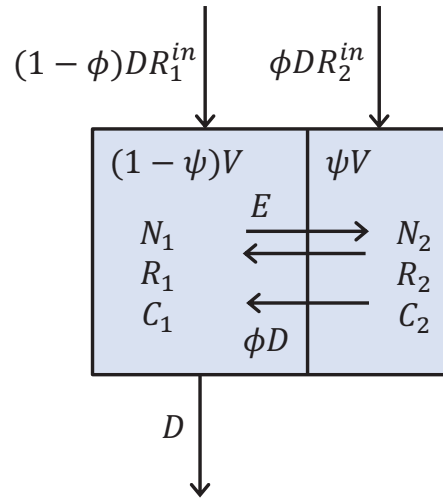
Figure 2.2. Gradostat diagram of the original system.

The parameters, units, and biological meanings are shown in Table 2.1. The limiting nutrient for the algae growth goes to the main lake and the single cove at constant concentration R_1^{in} and R_2^{in} respectively. The system dilution rate is defined as D (Day^{-1}) and the exchange rate between the the main lake and the cove is defined as E (Day^{-1}). There is also a net flow ϕD goes from the cove to the main lake to maintain constant volume. The model is constructed under the assumption that flows of algae and toxin follow those of nutrient [9].

Table 2.1. Notations.

Symbols	Meaning	Units
$N_1(t),\ N_2(t)$	Microorganism abundances	cells/mL
$C_1(t),\ C_2(t)$	Toxin concentrations	μg/L
$R_1(t),\ R_2(t)$	Nutrient concentrations	μmol/mL
D	Dilution rate	Day^{-1}
$R_1^{in},\ R_2^{in}$	Nutrient supply concentration	μmol/L
m	Mortality rate of Microorganism	Day^{-1}
E	Exchange rate	Day^{-1}
ψ	Fraction of V_2 volume in cove	None
ϕ	Fraction of inflow entering V_2	None
ϵ	Toxin production coefficient	None
q_N	Nutrient quota of algae	μmol/cell
q_C	Nutrient quota of toxin	μmol/μg

Three models are developed to represent three different ways of producing toxin, namely: growth related model, limitation related model and mortality related model [9]. The following mathematical model is a general form of the three models:

$$\frac{dN_1}{dt} = (\mu(R_1) - m)N_1 - \frac{D+E}{1-\psi}N_1 + \frac{\phi D + E}{1-\psi}N_2;$$

$$\frac{dN_2}{dt} = \frac{E}{\psi}N_1 + (\mu(R_2) - m)N_2 - \frac{\phi D + E}{\psi}N_2;$$

$$\frac{dR_1}{dt} = \frac{(1-\phi)D}{1-\psi}R_1^{in} - (\mu(R_1) - m)N_1 q_N - \frac{D+E}{1-\psi}R_1 + \frac{\phi D + E}{1-\psi}R_2;$$

$$\frac{dR_2}{dt} = \frac{\phi D}{\psi}R_2^{in} - (\mu(R_2) - m)N_2 q_N + \frac{E}{\psi}R_1 - \frac{\phi D + E}{\psi}R_2;$$

$$\frac{dC_1}{dt} = \varepsilon f_i(R_1)N_1 - \frac{D+E}{1-\psi}C_1 - kC_1 + \frac{\phi D + E}{1-\psi}C_2;$$

$$\frac{dC_2}{dt} = \varepsilon f_i(R_2)N_2 + \frac{E}{\psi}C_1 - \frac{\phi D + E}{\psi}C_2 - kC_2;$$

(2.1)

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where, $i = 1, 2, 3$. Here, N_1, N_2 represent population densities of the algae and C_1 and C_2 represent the concentration of the toxin in the two vessels, respectively. Population dynamics represent a balance between growth, removal by dilution, and mortality at per capita rates m [24]. Population growth rate depends on the nutrient concentration in the two vessels, R_1 and R_2 respectively [17]. A Michaelis-Menten formulation [25] is used for the growth-rate function, i.e., $\mu(R) = \dfrac{\mu_{max}R}{K + R}$. The function μ is monotone increasing and bounded by the maximum growth rate μ_{max}, i.e., $0 \leq \mu(R) \leq \mu_{max} < \infty$, and $d\mu/dR > 0$, where K is the half-saturation constant.

In the growth related model [18, 19], the toxin is produced proportional to the productivity of the algae, $f_1(R_j) = \mu(R_j)$. This case assumes that toxin is released to the water at a constant rate and proportional to other cellular products.[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 called *Prymnesium parvum* [20, 21, 22, 23] 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, *cyanobacteria* produces a toxin called *microcystin*, which is produced more rapidly when the mortality rate of the *cyanobacteria* is high.

2.2.1 Dimensionless Systems

To ease computation we make the following scaling changes:

$$\hat{N}_1 = N_1 q / R_1^{in}, \quad \hat{N}_2 = N_1 q / R_2^{in}, \quad \hat{R}_1 = R_1 / R_1^{in}, \quad \hat{R}_2 = R_2 / R_2^{in},$$

$$\hat{C}_1 = C_1 q / R_1^{in}, \quad \hat{C}_2 = C_2 q / R_2^{in} \quad \hat{\mu}^{max} = \mu^{max} / D,$$

$$\hat{m} = m / D, \quad \hat{t} = Dt, \quad \hat{D} = E / D, \quad \hat{R} = R_1^{in} / R_2^{in}, \quad \hat{k} = k / D.$$

Then System (2.1) becomes:

$$\frac{d\hat{N}_1}{d\hat{t}} = (\hat{\mu}(\hat{R}_1) - \hat{m})\hat{N}_1 - \frac{1 + \hat{D}}{1 - \psi}\hat{N}_1 + \frac{\phi + \hat{D}}{\hat{R}(1 - \psi)}\hat{N}_2,$$

$$\frac{d\hat{N}_2}{d\hat{t}} = \frac{\hat{D}\hat{R}}{\psi}\hat{N}_1 + (\hat{\mu}(\hat{R}_2) - \hat{m})\hat{N}_2 - \frac{\phi + \hat{D}}{\psi}\hat{N}_2,$$

$$\frac{d\hat{R}_1}{d\hat{t}} = \frac{1 - \phi}{1 - \psi} - (\hat{\mu}(\hat{R}_1) - \hat{m})\hat{N}_1 - \frac{1 + \hat{D}}{1 - \psi}\hat{R}_1 + \frac{\phi + \hat{D}}{\hat{R}(1 - \psi)}\hat{R}_2,$$

$$\frac{d\hat{R}_2}{d\hat{t}} = \frac{\phi}{\psi} - (\hat{\mu}(\hat{R}_2) - \hat{m})\hat{N}_2 + \frac{\hat{D}\hat{R}}{\psi}R_1 - \frac{\phi + \hat{D}}{\psi}\hat{R}_2,$$

$$\frac{d\hat{C}_1}{d\hat{t}} = \varepsilon\hat{f}_i(\hat{R}_1)\hat{N}_1 - \frac{1 + \hat{D}}{1 - \psi}\hat{C}_1 - \hat{k}\hat{C}_1 + \frac{\phi + \hat{D}}{\hat{R}(1 - \psi)}\hat{C}_2,$$

$$\frac{d\hat{C}_1}{d\hat{t}} = \varepsilon\hat{f}_i(\hat{R}_2)\hat{N}_1 - \frac{1 + \hat{D}}{1 - \psi}\hat{C}_1 - \hat{k}\hat{C}_1 + \frac{\phi + \hat{D}}{\hat{R}(1 - \psi)}\hat{C}_2.$$

where $\hat{\mu}(\hat{R}_i) = \dfrac{\hat{\mu}^{max}\hat{R}_i}{\hat{K} + \hat{R}_i}$; $i = 1, 2, 3$, $\hat{f}_1(\hat{R}_j) = \hat{\mu}(\hat{R}_j)$, $\hat{f}_2(\hat{R}_j) = \hat{\mu}^{max} - \hat{\mu}(\hat{R}_j)$ and $\hat{f}_3(\hat{R}_j) = \hat{m}$, $j = 1, 2$.

By dropping all the hats, the following form of a dimensionless system is obtained:

$$\frac{dN_1}{dt} = (\mu(R_1) - m)N_1 - \frac{1+D}{1-\psi}N_1 + \frac{\phi+D}{R(1-\psi)}N_2,$$

$$\frac{dN_2}{dt} = \frac{DR}{\psi}N_1 + (\mu(R_2) - m)N_2 - \frac{\phi+D}{\psi}N_2,$$

$$\frac{dR_1}{dt} = \frac{1-\phi}{1-\psi} - (\mu(R_1) - m)N_1 - \frac{1+D}{1-\psi}R_1 + \frac{\phi+D}{R(1-\psi)}R_2,$$

(2.2)

$$\frac{dR_2}{dt} = \frac{\phi}{\psi} - (\mu(R_2) - m)N_2 + \frac{DR}{\psi}R_1 - \frac{\phi+D}{\psi}R_2,$$

$$\frac{dC_1}{dt} = \varepsilon f_i(R_1)N_1 - \frac{1+D}{1-\psi}C_1 - kC_1 + \frac{\phi+D}{R(1-\psi)}C_2,$$

$$\frac{dC_2}{dt} = \varepsilon f_i(R_2)N_2 + \frac{DR}{\psi}C_1 - \frac{\phi+D}{\psi}C_2 - kC_2.$$

System (2.2) is the general form of the three models that is used in our mathematical analysis. It is trivial to show that the first quadrant is positively invariant [11] and that the system is well posed [17].

2.2.2 Dissipatedness of the Dimensionless System

Here we show that System (2.2) is dissipative [17], i.e., all the solutions lie in a bounded set [11]. All the three models have the same first four equations that are all independent of parameters C_1 and C_2.

Setting:

$$\Sigma_1 = N_1 + R_1,$$

$$\Sigma_2 = N_2 + R_2,$$

by adding the first and third equations, the second and fourth equations in System (2.2), respectively, the following ODE system is obtained:

$$\Sigma_1' = \frac{1-\phi}{1-\psi} - \frac{1+D}{1-\psi}\Sigma_1 + \frac{\phi+D}{R(1-\psi)}\Sigma_2;$$

(2.3)

$$\Sigma_2' = \frac{\phi}{\psi} + \frac{DR}{\psi}\Sigma_1 - \frac{\phi+D}{\psi}\Sigma_2.$$

As $t \to \infty$, for the equilibrium of System (2.3) we have:

$$\Sigma_1' = \Sigma_2' = 0.$$

Solving for Σ_1 and Σ_2 we obtain:

$$\Sigma_1^* = 1 + \phi - \frac{\phi}{R} = A,$$

$$\Sigma_2^* = \frac{DR - DR\phi + D\phi + \phi}{\phi + D} = B.$$

The Jacobian matrix of System (2.3) is:

$$\begin{pmatrix} -\dfrac{1+D}{1-\psi} & \dfrac{\phi+D}{R(1-\psi)} \\[2em] \dfrac{DR}{\psi} & -\dfrac{\phi+D}{\psi} \end{pmatrix}$$

and the corresponding characteristic polynomial is:

$$\lambda^2 + \left(\frac{1+D}{1-\psi} + \frac{\phi+D}{\psi}\right)\lambda + \frac{\phi+D}{\psi(1-\psi)} = 0.$$

Since

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$$\frac{1+D}{1-\psi} + \frac{\phi+D}{\psi} > 0 \quad \text{and} \quad \frac{\phi+D}{\psi(1-\psi)} > 0,$$

we have

$$Re(\lambda_1) < 0 \quad \text{and} \quad Re(\lambda_2) < 0,$$

where λ_1 and λ_2 are the eigenvalues of the matrix. Therefore, all three models represented by the dimensionless system (2.2) are dissipative and all solutions lie in the bounded set:

$$\Gamma = \{(N_1, N_2, R_1, R_2)|N_1 + R_1 \le A, N_2 + R_2 \le B\}.$$

Hence, System (2.2) can be reduced to the following form:

$$\frac{dN_1}{dt} = (\mu(A - N_1) - m)N_1 - \frac{1+D}{1-\psi}N_1 + \frac{\phi+D}{R(1-\psi)}N_2,$$

$$\frac{dN_2}{dt} = \frac{DR}{\psi}N_1 + (\mu(B - N_2) - m)N_2 - \frac{\phi+D}{\psi}N_2,$$

$$\frac{dC_1}{dt} = \varepsilon f_i(A - N_1)N_1 - \frac{1+D}{1-\psi}C_1 - kC_1 + \frac{\phi+D}{R(1-\psi)}C_2,$$

$$\frac{dC_2}{dt} = \varepsilon f_i(B - N_2)N_2 + \frac{DR}{\psi}C_1 - \frac{\phi+D}{\psi}C_2 - kC_2,$$

with $i = 1$, $f_1 = \mu(\cdot)$ in the reduced growth related model; $i = 2$, $f_2 = \mu_{max} - \mu(\cdot)$ in the reduced limitation related model; and $i = 3$, $f_3 = m$ in the reduced mortality related model. Clearly, the reduced System (2.4) has the same equilibria as the original dimensionless system (2.2) [11, 4].

2.2.3   Equilibria

To investigate the existence of equilibria for Systems (2.4), we consider the following two cases:

(a) By setting the left hand side to 0, we find from the first two equations that $N_1^0 = 0 \Leftrightarrow N_2^0 = 0$, where N_i^0, $(i = 1, 2)$ are the values of the population concentration at the equilibrium. When $N_1^0 = 0$ the first equation becomes $\dfrac{\phi + D}{R(1 - \psi)} N_2^0 = 0$, which implies $N_2^0 = 0$; similarly, when $N_2^0 = 0$ the second equation becomes $\dfrac{DR}{\psi} N_1^0 = 0$, which implies $N_1^0 = 0$.

Once we have $N_1^0 = N_2^0 = 0$, the last two equations of System (2.4) become:

$$0 = -\frac{1 + D}{1 - \psi} C_1^0 - k C_1^0 + \frac{\phi + D}{R(1 - \psi)} C_2^0,$$

$$0 = \frac{DR}{\psi} C_1^0 - \frac{\phi + D}{\psi} C_2^0 - k C_2^0,$$

where C_i^0, $(i = 1, 2)$ are the values of the toxin concentration at the equilibrium. The above system can be written in matrix form:

$$\begin{pmatrix} -\dfrac{1 + D}{1 - \psi} & \dfrac{\phi + D}{R(1 - \psi)} \\[4mm] \dfrac{DR}{\psi} & -\dfrac{\phi + D}{\psi} \end{pmatrix} \begin{pmatrix} C_1 \\[2mm] C_2 \end{pmatrix} = \begin{pmatrix} 0 \\[2mm] 0 \end{pmatrix}.$$

Since $(1 + D + k - k\psi)(\phi + D + k\psi) - D(\phi + D) \neq 0$, one can conclude that $C_1^0 = C_2^0 = 0$.

Therefore, the trivial equilibrium of System (2.2) is $E_0 = (0, 0, A, B, 0, 0)$, and the one of System (2.4) is $E_0 = (0, 0, 0, 0)$.

(b) System (2.2) could also have an interior equilibrium E^*, which lies in the interior of Ω, i.e. $N_1^* \neq 0$ and $N_2^* \neq 0$ of the equilibrium. From the first two equations of System (2.2), $N_1^* \neq 0$ and $N_2^* \neq 0$ only if R_1^* and R_2^* satisfy:

$$[(\mu(R_1) - m)(1 - \psi) - (1 + D)][(\mu(R_2) - m)\psi - (\phi + D)] = (\phi + D)D$$

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which is equivalent to

$$[(\mu(A-N_1)-m)(1-\psi)-(1+D)][(\mu(B-N_2)-m)\psi-(\phi+D)] = (\phi+D)D \quad (2.5)$$

This is the equilibrium in the interior of Γ, $E^* = (N_1^*, N_2^*, A - N_1^*, B - N_2^*, C_1^*, C_2^*)$, where $N_1^* \neq 0$ and $N_2^* \neq 0$ and $R_1^* = A - N_1^*, R_2^* = B - N_2^*$. Also, parameters C_1^* and C_2^* are both nonzero in all three models:

1. In the reduced growth related model, if we suppose that $C_1^* = 0$ and $C_2^* = 0$, then from the last two equations we have $\varepsilon\mu(A - N_1^*)N_1^* = 0$ and $\varepsilon\mu(B - N_2^*)N_2^* = 0$. This implies that $\mu(A - N_1^*) = 0$ and $\mu(B - N_2^*) = 0$, since the interior equilibria guarantees $N_1^* \neq 0$ and $N_2^* \neq 0$. Therefore, $N_1^* = A$ and $N_2 = B$, which contradicts Equation (2.5).

2. In the reduced limitation related model, if we suppose that $C_1^* = 0$ and $C_2^* = 0$, then similarly, this implies $\mu_{max} - \mu(R_1) = 0$ and $\mu_{max} - \mu(R_2) = 0$, which is impossible since $R_1^* < \infty$ and $R_2^* < \infty$ implies that the increasing function $\mu_{max} - \mu(R) > 0$. Also, if $C_1^* \neq 0$ and $C_2^* = 0$, the fifth equation of (2.4) becomes $\varepsilon(\mu^{max} - \mu(R_1^*))N_1^* + \dfrac{\phi + D}{R(1 - \psi)}C_2^* = 0$, which is impossible, since all of the parameters are positive and $\psi < 1$. Similarly, for $C_1^* = 0$ and $C_2^* \neq 0$, the sixth equation of (2.4) becomes $\varepsilon(\mu_{max} - \mu(R_2^*))N_2^* + \dfrac{DR}{\psi}C_1^* = 0$ which is also a contradiction.

3. In the reduced mortality related model, similarly to the reduced limitation related model, in the last two equations of System (2.4) the mortality rate $m > 0$, which implies that none of C_1^* and C_2^* are zero.

Therefore, all parameters of the interior equilibrium, $E^* = (N_1^*, N_2^*, A - N_1^*, B - N_2^*, C_1^*, C_2^*)$ are positive. Hence when the system achieves an interior equilibrium, it is consistent [11].

Theorem 1. *If the equilibrium E^* exists, it is unique.*

Proof. Suppose there are two equilibria (N_1^*, N_2^*) and $(\tilde{N}_1^*, \tilde{N}_2^*)$. WLOG assume $N_1^* < \tilde{N}_1^*$ [17], since μ in System (2.4) is a decreasing function of N_1 and N_2, then

$$(\mu(A - N_1^*) - m)(1 - \psi) - (1 + D) > (\mu(A - \tilde{N}_1^*) - m)(1 - \psi) - (1 + D).$$

If $\dfrac{dN_1}{dt} = 0$, then:

$$
\begin{aligned}
N_2^* \ &= \ R\frac{(\mu(A - N_1^*) - m))(1 - \psi) - (1 + D)}{-(\phi + D)}N_1^* \\
&< \ R\frac{(\mu(A - N_1^*) - m))(1 - \psi) - (1 + D)}{-(\phi + D)}\tilde{N}_1^* \\
&< \ R\frac{(\mu(A - \tilde{N}_1^*) - m))(1 - \psi) - (1 + D)}{-(\phi + D)}\tilde{N}_1^* \\
&< \ \tilde{N}_2
\end{aligned}
$$

which is impossible because they have to be equal to satisfy the condition of existence of the equilibrium [17].

Also, C_1^* and C_2^* are unique: consider the last two equations of System (2.2), the linear part of the system is nonsingular:

$$AC = b_i,$$

where

$$
A = \begin{pmatrix} -\dfrac{1 + D}{1 - \psi} - k & \dfrac{\phi + D}{R(1 - \psi)} \\[2ex] \dfrac{DR}{\psi} & -\dfrac{\phi + D}{\psi} - k \end{pmatrix}, \quad C = \begin{pmatrix} C_1^* \\[1ex] C_2^* \end{pmatrix},
$$

and

$$
b_1 = \begin{pmatrix} \varepsilon\mu(R_1^*)N_1^* \\[1ex] \varepsilon\mu(R_2^*)N_2^* \end{pmatrix}, \quad b_2 = \begin{pmatrix} \varepsilon(\mu_{max} - \mu(R_1^*))N_1^* \\[1ex] \varepsilon(\mu_{max} - \mu(R_2^*))N_2^* \end{pmatrix}, \quad b_3 = \begin{pmatrix} \varepsilon m N_1^* \\[1ex] \varepsilon m N_2^* \end{pmatrix},
$$

Since, $b_i \neq 0$ for $i = 1, 2, 3$ and

$$det[A] = \left(-\frac{1 + D}{1 - \psi} - k\right)\left(-\frac{\phi + D}{\psi} - k\right) - \left(\frac{\phi + D}{R(1 - \psi)}\right)\left(\frac{DR}{\psi}\right) > 0.$$

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Hence C_1^* and C_2^* are unique. Therefore, the interior equilibrium E^* is unique when it exists. □

The following proposition lists necessary conditions on the parameters of the three systems for the existence of the two equilibria.

Proposition 1. *For the equilibria of System (2.2), the following two cases hold:*

(a) *E_0 always exists.*

(b) *When E^* exists, it is unique, and N_1^*, N_2^* satisfy*

$$[(\mu(A - N_1^*) - m)(1 - \psi) - (1 + D)][(\mu(B - N_2^*) - m)\psi - (\phi + D)] = (\phi + D)D.$$

2.2.4 Local Stability Analysis

We now turn to the local stability analysis. The Jacobian matrix of System (2.2) has the following form:

$$J(N_1, N_2, R_1, R_2, C_1, C_2) =$$

$$\begin{pmatrix} \alpha_1 - \gamma_1 - \beta_1 - m & \gamma_3 & 0 & 0 & 0 & 0 \\ \gamma_4 & \alpha_2 - \gamma_2 - \beta_2 - m & 0 & 0 & 0 & 0 \\ -\alpha_1 - m & 0 & -\gamma_1 & \gamma_3 & 0 & 0 \\ 0 & \alpha_2 - m & \gamma_4 & -\gamma_2 & 0 & 0 \\ \varepsilon f_i(R_1) & 0 & 0 & 0 & -\gamma_1 - k & \gamma_3 \\ 0 & \varepsilon f_i(R_2) & 0 & 0 & \gamma_4 & -\gamma_2 - k \end{pmatrix},$$

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where $i = 1, 2, 3$, and

$$\alpha_1 = \mu(A - N_1), \qquad \alpha_2 = \mu(B - N_2),$$
$$\beta_1 = -N_1 \frac{d\mu}{dN_1}, \qquad \beta_2 = -N_2 \frac{d\mu}{dN_2},$$
$$\gamma_1 = \frac{1 + D}{1 - \psi}, \qquad \gamma_2 = \frac{\phi + D}{\psi},$$
$$\gamma_3 = \frac{DR}{\psi}, \qquad \gamma_4 = \frac{\phi + D}{R(1 - \psi)}.$$

Since R_i, for $i = 1, 2$ are a linear combinations of N_i, $(i = 1, 2)$, the 6×6 Jacobian matrix can be reduced to 4×4:

$$J_{NC}(N_1, N_2, C_1, C_2) =$$

$$\begin{pmatrix} \alpha_1 - \gamma_1 - \beta_1 - m & \gamma_3 & 0 & 0 \\ \gamma_4 & \alpha_2 - \gamma_2 - \beta_2 - m & 0 & 0 \\ \varepsilon f_i(A - N_1) & 0 & -\gamma_1 - k & \gamma_3 \\ 0 & \varepsilon f_i(B - N_2) & \gamma_4 & -\gamma_2 - k \end{pmatrix}$$

Since the first two equations is explicit from the last two toxin equations, steady-states analysis of (N_1, N_2) and (C_1, C_2) can be proceeded separately: The Jacobian for (N_1, N_2) is

$$J_N = \begin{pmatrix} \alpha_1 - \beta_1 - \gamma_1 - m & \gamma_3 \\ \gamma_4 & \alpha_2 - \beta_2 - \gamma_2 - m \end{pmatrix}$$

The Jacobian for (C_1, C_2) is

$$J_C = \begin{pmatrix} -\gamma_1 - k & \gamma_3 \\ \gamma_4 & -\gamma_2 - k \end{pmatrix}$$

Theorem 2. *The equilibrium E_0 is locally asymptotically stable if and only if $\alpha_1^0 + \alpha_2^0 - \gamma_1 - \gamma_2 - 2m < 0$ and $(\alpha_1^0 - \gamma_1 - m)(\alpha_2^0 - \gamma_2 - m) > \gamma_3 \gamma_4$. Where $\alpha_1^0 = \mu(A)$, $\alpha_2^0 = \mu(B)$.*

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Proof. For the equilibrium E_0, the local stability is determined by the eigenvalues of:

$$J_N(E_0) = \begin{pmatrix} \alpha_1^0 - \gamma_1 - m & \gamma_3 \\ \gamma_4 & \alpha_2^0 - \gamma_2 - m \end{pmatrix},$$

Let λ_1 and λ_2 be the eigenvalues of the matrix. For the system to be stable, we must have $Re(\lambda_1) < 0$, $Re(\lambda_2) < 0$. Apply Routh-Hurwitz Condition as follows:

$$det[J_N(E_0)] > 0$$

$$tr[J_N(E_0)] < 0,$$

which is equivalent to:

$$(\alpha_1^0 - \gamma_1 - m)(\alpha_2^0 - \gamma_2 - m) > \gamma_3\gamma_4 \tag{2.6}$$

$$\alpha_1^0 + \alpha_2^0 - \gamma_1 - \gamma_2 - 2m < 0. \tag{2.7}$$

Then we consider the Jacobian for (C_1, C_2) in this case:

$$J_C = \begin{pmatrix} -\gamma_1 - k & \gamma_3 \\ \gamma_4 & -\gamma_2 - k \end{pmatrix}$$

For the system to be stable, the following condition is satisfied:

$$-\gamma_1 - k < 0 \quad \text{and} \quad (\gamma_1 + k)(\gamma_2 + k) > \gamma_3\gamma_4$$

Since γ_i and k are positive, this condition is always true. Therefore, $E_0 = (0, 0, 0, 0)$ is always stable in this case. $\qquad\square$

Theorem 3. *The equilibrium E^* is locally asymptotically stable, whenever it exists.*

Proof. For equilibrium E^*, the local stability is determined by the eigenvalues of:

$$J_N(E^*) = \begin{pmatrix} \alpha_1^* - \beta_1^* - \gamma_1 - m & \gamma_3 \\ \gamma_4 & \alpha_2^* - \beta_2^* - \gamma_2 - m \end{pmatrix},$$

where, $\alpha_1^* = \mu(A - N_1^*)$,$\alpha_2^* = \mu(B - N_2^*)$ and $\beta_1^* = N_1^* \dfrac{d\mu}{dt}$, $\beta_2^* = N_2^* \dfrac{d\mu}{dt}$ For the system to be stable, we have the eigenvalues of the system $\lambda_1 < 0$ and $\lambda_2 < 0$, then the following conditions must be satisfied:

$$tr[J_N(E^*)] = \alpha_1^* + \alpha_2^* - \beta_1 - \beta_2 - \gamma_1 - \gamma_2 - 2m < 0,$$

$$det[J_N(E^*)] = (\alpha_1^* - \beta_1 - \gamma_1 - m)(\alpha_2^* - \beta_2 - \gamma_2 - m) - \gamma_3\gamma_4 > 0.$$

Rewrite the existence condition we have $(\alpha_1^* - \gamma_1 - m)(\alpha_2^* - \gamma_2 - m) = \gamma_3\gamma_4$, according to the first and second equations of the system respectively we have $(\alpha_1^* - \gamma_1 - m) < 0$ and $(\alpha_2^* - \gamma_2 - m) < 0$. Also, $\beta_1 > 0$ and $\beta_2 > 0$ and, then $\alpha_1^* - \beta_1 - \gamma_1 - m < \alpha_1^* - \gamma_1 - m$ and $\alpha_2^* - \beta_2 - \gamma_2 - m < \alpha_2^* - \gamma_2 - m$, which implies $(\alpha_1^* - \beta_1 - \gamma_1 - m)(\alpha_2^* - \beta_2 - \gamma_2 - m) > (\alpha_1^* - \gamma_1 - m)(\alpha_2^* - \gamma_2 - m) = \gamma_3\gamma_4$, $(\alpha_1^* - \beta_1 - \gamma_1 - m) + (\alpha_2^* - \beta_2 - \gamma_2 - m) < (\alpha_1^* - \gamma_1 - m) + (\alpha_2^* - \gamma_2 - m) < 0$. Therefore, one can conclude $tr[J_N(E^*)] < 0$ and $det[J_N(E^*)] > 0$. Now we consider the Jacobian for (C_1, C_2) in this case:

$$J_C = \begin{pmatrix} -\gamma_1 - k & \gamma_3 \\ \gamma_4 & -\gamma_2 - k \end{pmatrix}$$

Therefore, similarly (C_1^*, C_2^*) in all three cases are always stable when exist. $\qquad\square$

2.2.5 Summary

We have already proved that System (2.2) is dissipative. According to the definition in [11], the system and the reduced system (2.4) is also cooperative:

Theorem 4. *System (2.4) and System (2.2) are cooperative.*

Proof. Since

$$\frac{\partial F_1}{\partial N_2} = \frac{\phi + D}{R(1 - \psi)} > 0$$

$$\frac{\partial F_2}{\partial N_1} = \frac{DR}{\psi} > 0,$$

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where F_1 and F_2 are the first and second equation of (2.4) respectively. Hence System (2.4) and System (2.2) are cooperative. $\qquad\square$

According to Theorem 2, the stability of the trivial equilibrium E_0 implies the absence of interior equilibria. When E_0 is unstable, according to Theorems 1 and 3, there exists a unique stable interior equilibrium E^*. The results of equilibria and local stability analysis are summarized in Table 2.2, where $\Theta_1 = (\alpha_1^0 - \gamma_1 - m)$ and $\Theta_2 = (\alpha_2^0 - \gamma_2 - m)$.

Table 2.2. Summary of the three cases

Equilibrium	Conditions for existence	Conditions for Local stability
E_0	Always exists	$\Theta_1 + \Theta_2 < 0$ $\Theta_1\Theta_2 > \gamma_3\gamma_4$
E^*	$\Theta_1 + \Theta_2 \geq 0$ or $\Theta_1\Theta_2 < \gamma_3\gamma_4$	E^* exists

Table 2.2 implies that E^* exists and E_0 unstable when one of the growth-loss balance is positive, i.e., one of the following inequalities must be true:

$$\mu(A) > \frac{1+D}{1-\psi} + m, \tag{2.8}$$

$$\mu(B) > \frac{\phi+D}{\psi} + m. \tag{2.9}$$

Since A represents the maximal nutrient concentration in the first vessel, then the term $\mu(A)$ is larger than the maximal growth rate of the microorganism in the first vessel. The term $\dfrac{1+D}{1-\psi} + m$ represents the sum of mortality rate, washout rate, and exchange rate. Hence, Inequality (2.8) is satisfied when the maximal growth rate of the microorganism is less than the sum of mortality rate and the washout rate and exchange rate minus a positive term. Inequality (2.9) can be similarly analyzed,

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holding true when the maximal growth rate of the microorganism is less than the sum of mortality rate, washout rate, and exchange rate minus a positive term in the second vessel [17].

However, the system can also be persistent when both growth-loss balances in both vessels are negative, that is when the first part of Theorem 2 is true but the second part of it is violated, i.e., $(\mu(A) - \frac{1+D}{1-\psi} - m)(\mu(B) - \frac{\phi+D}{\psi} - m) < \frac{D(\phi+D)}{\psi(1-\psi)}$, with both $\mu(A) - \frac{1+D}{1-\psi} - m < 0$ and $\mu(B) - \frac{\phi+D}{\psi} - m < 0$. Hence, just negative growth-loss balance is not enough for the local stability of the trivial equilibrium E_0 – it requires that the growth rate μ at the trivial equilibrium be sufficiently small. As a matter of fact, the local stability of the trivial equilibrium E_0 requires both the following conditions to be satisfied:

$$\mu(A) < \frac{1+D}{1-\psi} + m - \frac{D(\phi+D)}{(\phi+D+\psi m)(1-\psi)}, \tag{2.10}$$

$$\mu(B) < \frac{\phi+D}{\psi} + m - \frac{D(\phi+D)}{(1+D+m-\psi m)\psi}. \tag{2.11}$$

Therefore, a negative growth-loss balance could lead to persistence, which shows that the presence of a cove in a lake system would enhance algal and toxin persistence.

2.2.6 Global Stability Analysis

After obtaining the conditions for locally stability of the two equilibria, we continuing analysis on the globally behavior. Since the system is dissipative and cooperative [11], the there's no limit cycles and the population does not turns out to be infinity [11]. Therefore, we have the following conclusions:

Theorem 5. *The equilibrium E_0 is globally stable when (2.6) and (2.7) are both established.*

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Proof. Since the system is dissipative and the first quadrant is positively invariant, we know that all trajectories end up in Γ_0. Also, the systems are cooperative, hence there is no possibility of limit cycles[11]. The Poincare-Bendixson theorem [11] guarantees that every trajectory must go to E_0, which implies E_0 is a global attractor. $\square$

Similarly, we also have the following:

Theorem 6. *The equilibrium E^* is globally stable when it exists.*

Proof. Theorem 6 tells that when either of (2.6) and (2.7) is not true, E_0 is a repeller or saddle point in the interior of Γ [11]. Also, there's no limit cycles in a cooperative system [11], and the interior equilibrium is unique. Thus all the trajectories must approach E^*, i.e. E^* is a global attractor whenever it exist. $\square$

2.3   Numerical Simulations

Numerical simulations are performed to support the conclusions that have been made in mathematical analysis in the previous sections, for the models having the form System (2.1). Numerical verification of the local results of E_0 and E^* applied to ordinary differential equation System (2.2) are obtained by using the adaptive **MatLab** solvers `ode45` and `ode23`. The following data are used in each simulation: For E_0 we set: $m = 16, D = 30, \psi = 0.01, \phi = 0.001, R = 0.1, \varepsilon = 0.5, k = 1$, and $\mu_{max} = 12$ for growth and mortality related cases, $\mu_{max} = 6$ for limitation related case, the half-saturation constant $K = 0.01$; for E^* we set $m = 2, D = 6$, other things equal. The initial condition for each case is $(N_1, N_2, R_1, R_2, C_1, C_2)(0) = (0.7, 0.1, 0.01, 0.09, 0.3, 0.06)$, and the simulations are shown in Fig. 2.3, Fig. 2.4, and Fig. 2.5. (The data are determined based on [9].)

A visualization of the N_1 and N_2 components of several simulations each with different initial values of N_1 and N_2, is displayed in Fig. 2.6.

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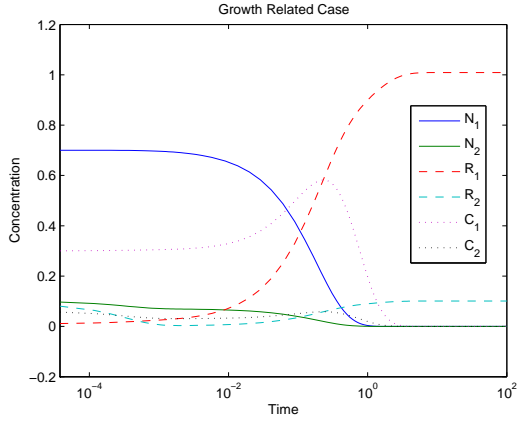
(a) Solution trajectories approaching E_0
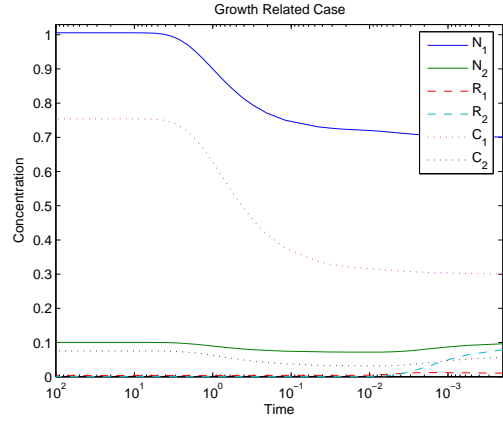
(b) Solution trajectories approaching E^*

Figure 2.3. Local stability of both equilibria of the growth related case.

(a) Solution trajectories approaching E_0
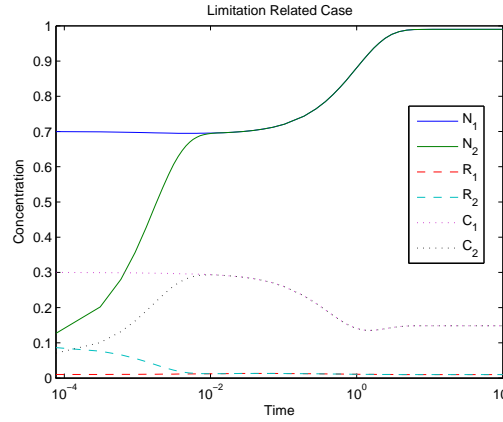
(b) Solution trajectories approaching E^*

Figure 2.4. Local stability of both equilibria of limitation related case.

The simulations are obtained by using **Mathematica** `NDSolve` applied to models having the form (2.2) using the following parameters: $\varepsilon = 0.5, \gamma_1 = 4, \gamma_2 = 3.2, \gamma_3 = 4, \gamma_4 = 1.6, A = 0.7, B = 1.25, k = 0.7, K = 0.6$ and $\mu_{max} = 1$ for Fig. 2.6 (a); and $\mu_{max} = 10$ for Fig 2.6 (b).
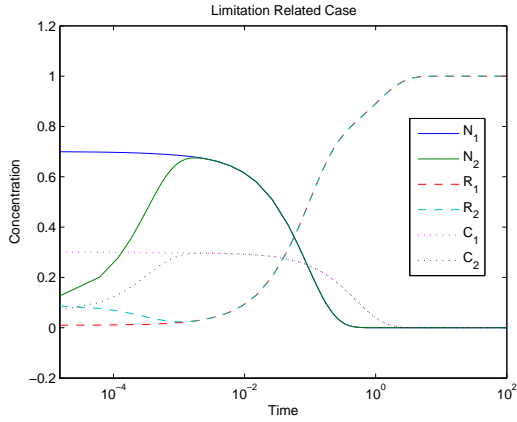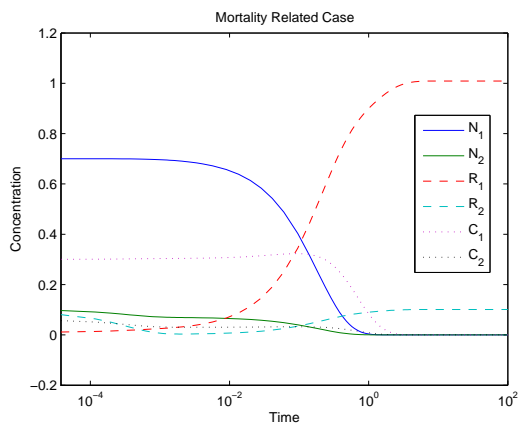
(a) Solution trajectories approaching E_0
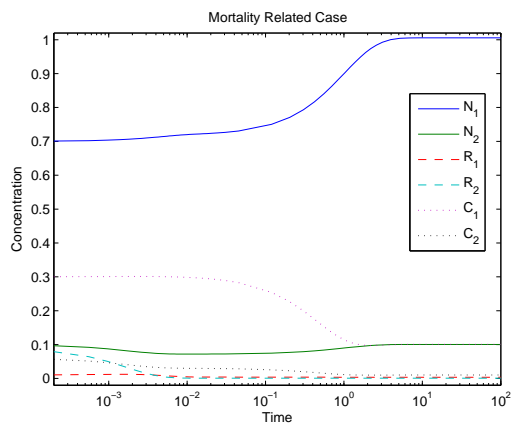
(b) Solution trajectories approaching E^*

Figure 2.5. Local stability of both equilibria of mortality related case.
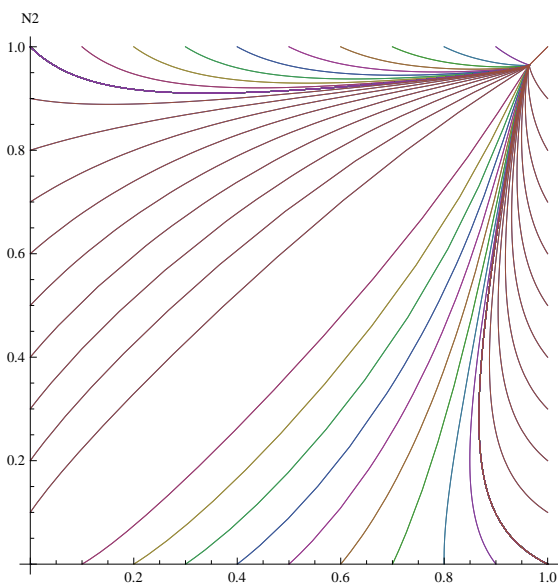
(a) E^* attracts all solutions
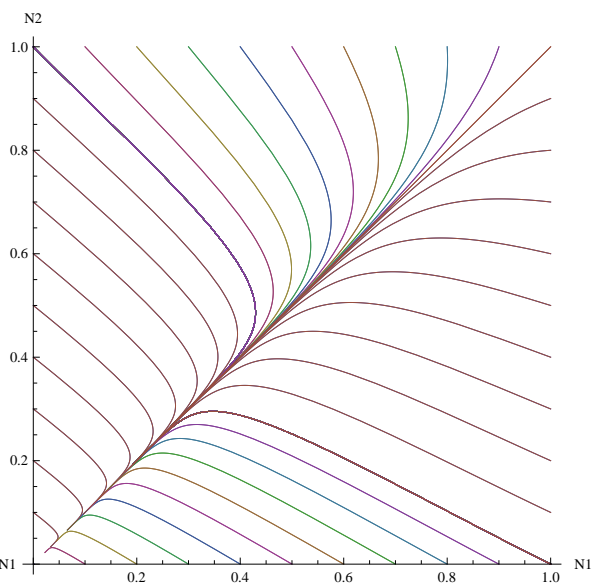
(b) E_0 attracts all solutions

Figure 2.6. Global stability of both equilibria of the three cases.

CHAPTER 3

THE MODIFIED GROWTH RELATED MODEL

3.1   Introduction

This model is derived from the previous case of growth related model. Some toxin produced by *cyanobacteria* contain potential limiting nutrient, hence the bacteria excretes a biochemical that can get recycled back into the system as a nutrient source [9]. Nutrient is partitioned between cell production and toxin production, where ε is a dimensionless coefficient specify the allocation to toxin production [9]. Similarly, the mathematical model consists of six ordinary differential equations and it represents the dynamics of algal that produces toxin in proportion to the growth rate and lives in lakes with its single coves [9].

3.2   The Model

Dynamic mass balance for the nutrient then leads to the following model:

$$\frac{dN_1}{dt} = [(1-\varepsilon)\mu(R_1) - m]N_1 - \frac{D+E}{1-\psi}N_1 + \frac{\phi D + E}{1-\psi}N_2,$$

$$\frac{dN_2}{dt} = \frac{E}{\psi}N_1 + [(1-\varepsilon)\mu(R_2) - m]N_2 - \frac{\phi D + E}{\psi}N_2,$$

$$\frac{dR_1}{dt} = \frac{(1-\phi)D}{1-\psi}R_1^{in} - (\mu(R_1) - m)N_1 q_N - \frac{D+E}{1-\psi}R_1 + \frac{\phi D + E}{1-\psi}R_2 + kC_2 q_C,$$

$$\frac{dR_2}{dt} = \frac{\phi D}{\psi}R_2^{in} - (\mu(R_2) - m)N_2 q_N + \frac{E}{\psi}R_1 - \frac{\phi D + E}{\psi}N_2 + kC_2 q_C,$$

$$\frac{dC_1}{dt} = \varepsilon\mu(R_1)N_1\frac{q_N}{q_C} - \frac{D+E}{1-\psi}C_1 - kC_1 + \frac{\phi D + E}{1-\psi}C_2,$$

$$\frac{dC_2}{dt} = \varepsilon\mu(R_2)N_2\frac{q_N}{q_C} + \frac{E}{\psi}C_1 - \frac{\phi D + E}{\psi}C_2 - kC_2.$$

$$(3.1)$$

All the parameters have the same biological meanings and units of the previous case (see notation Table 2.1), and the nutrient content of the toxin is q_C (mol/g) [9]. The terms $[(1-\varepsilon)\mu(R_i) - m]N_i$, $i = 1, 2$, specify that only a part, $1 - \varepsilon$, of the nutrient is used for population growth of the microorganism, and the rest of it is used for toxin production (see terms $\varepsilon\mu(R_i)N_i$, $i = 1, 2$ in the last two equations). The two terms $kC_i q_C$, $i = 1, 2$ adding to the two equations for nutrient concentration specify that the toxin is transferred to nutrient with quota q_C.

3.2.1 Dimensionless System

Ease calculation complexity to obtain an overall clarity by rescaling the variables in System (3.1) to dimensionless:

$$\hat{N}_1 = N_1 q_N / R_1^{in}, \quad \hat{N}_2 = N_1 q_N / R_2^{in}, \quad \hat{R}_1 = R_1 / R_1^{in}, \quad \hat{R}_2 = R_2 / R_2^{in},$$

$$\hat{C}_1 = C_1 q_C / R_1^{in}, \quad \hat{C}_2 = C_2 q_C / R_2^{in} \quad \hat{\mu}^{max} = \mu^{max} / D,$$

$$\hat{m} = m/D, \quad \hat{t} = Dt, \quad \hat{D} = E/D, \quad \hat{R} = R_1^{in} / R_2^{in}, \quad \hat{k} = k/D.$$

System (3.1) becomes:

$$\frac{d\hat{N}_1}{d\hat{t}} = [(1 - \varepsilon)\hat{\mu}(\hat{R}_1) - \hat{m}]\hat{N}_1 - \frac{1 + \hat{D}}{1 - \psi}\hat{N}_1 + \frac{\phi + \hat{D}}{\hat{R}(1 - \psi)}\hat{N}_2,$$

$$\frac{d\hat{N}_2}{d\hat{t}} = \frac{\hat{D}\hat{R}}{\psi}\hat{N}_1 + [(1 - \varepsilon)\hat{\mu}(\hat{R}_2) - \hat{m}]\hat{N}_2 - \frac{\phi + \hat{D}}{\psi}\hat{N}_2,$$

$$\frac{d\hat{R}_1}{d\hat{t}} = \frac{1 - \phi}{1 - \psi} - (\hat{\mu}(\hat{R}_1) - \hat{m})\hat{N}_1 - \frac{1 + \hat{D}}{1 - \psi}\hat{R}_1 + \frac{\phi + \hat{D}}{\hat{R}(1 - \psi)}\hat{R}_2 + k\hat{C}_1,$$

$$\frac{d\hat{R}_2}{d\hat{t}} = \frac{\phi}{\psi} - (\hat{\mu}(\hat{R}_2) - \hat{m})\hat{N}_2 + \frac{\hat{D}\hat{R}}{\psi}R_1 - \frac{\phi + \hat{D}}{\psi}\hat{N}_2 + k\hat{C}_2,$$

$$\frac{d\hat{C}_1}{d\hat{t}} = \varepsilon\hat{\mu}(\hat{R}_1)\hat{N}_1 - \frac{1 + \hat{D}}{1 - \psi}\hat{C}_1 - \hat{k}\hat{C}_1 + \frac{\phi + \hat{D}}{\hat{R}(1 - \psi)}\hat{C}_2,$$

$$\frac{d\hat{C}_1}{d\hat{t}} = \varepsilon\hat{\mu}(\hat{R}_1)\hat{N}_1 - \frac{1 + \hat{D}}{1 - \psi}\hat{C}_1 - \hat{k}\hat{C}_1 + \frac{\phi + \hat{D}}{\hat{R}(1 - \psi)}\hat{C}_2.$$

where $\hat{\mu}(\hat{R}_i) = \dfrac{\hat{\mu}^{max}\hat{R}_i}{\hat{K} + \hat{R}_i}$.

By dropping all the hats, the following form of dimensionless system is obtained:

$$\frac{dN_1}{dt} = [(1 - \varepsilon)\mu(R_1) - m]N_1 - \frac{1 + D}{1 - \psi}N_1 + \frac{\phi + D}{R(1 - \psi)}N_2,$$

$$\frac{dN_2}{dt} = \frac{DR}{\psi}N_1 + [(1 - \varepsilon)\mu(R_2) - m]N_2 - \frac{\phi + D}{\psi}N_2,$$

$$\frac{dR_1}{dt} = \frac{1 - \phi}{1 - \psi} - (\mu(R_1) - m)N_1 - \frac{1 + D}{1 - \psi}R_1 + \frac{\phi + D}{R(1 - \psi)}R_2 + kC_1,$$

(3.2)

$$\frac{dR_2}{dt} = \frac{\phi}{\psi} - (\mu(R_2) - m)N_2 + \frac{DR}{\psi}R_1 - \frac{\phi + D}{\psi}N_2 + kC_2,$$

$$\frac{dC_1}{dt} = \varepsilon\mu(R_1)N_1 - \frac{1 + D}{1 - \psi}C_1 - kC_1 + \frac{\phi + D}{R(1 - \psi)}C_2,$$

$$\frac{dC_2}{dt} = \varepsilon\mu(R_2)N_2 + \frac{DR}{\psi}C_1 - \frac{\phi + D}{\psi}C_2 - kC_2.$$

System (3.2) is the form that is used in our mathematical analysis. It is trivial to show that the first quadrant is positively invariant [11] and that the system is well posed [17].

3.2.2 Dissipatedness of the Dimensionless System

Here we show that System (3.2) is dissipative [17], i.e., all the solutions lie in a bounded set [11]. Unlike the previous case, C_1 and C_2 are involved in in calculation. Setting:

$$\Sigma_1 = N_1 + R_1 + C_1,$$

(3.3)

$$\Sigma_2 = N_2 + R_2 + C_2$$

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by adding the first and third equations, the second and fourth equations in System (3.2), respectively, the following ODE system is obtained:

$$\Sigma_1' = \frac{1-\phi}{1-\psi} - \frac{1+D}{1-\psi}\Sigma_1 + \frac{\phi+D}{R(1-\psi)}\Sigma_2.$$

$$\Sigma_2' = \frac{\phi}{\psi} + \frac{DR}{\psi}\Sigma_1 - \frac{\phi+D}{\psi}\Sigma_2.$$

The equilibrium of System (3.3) is

$$\Sigma_1^* = 1 + \phi - \frac{\phi}{R} = A,$$

$$\Sigma_2^* = \frac{DR - DR\phi + D\phi + \phi}{\phi + D} = B.$$

(3.4)

The Jacobian matrix of System (3.3) is:

$$J = \begin{pmatrix} -\dfrac{1+D}{1-\psi} & \dfrac{\phi+D}{R(1-\psi)} \\[4mm] \dfrac{DR}{\psi} & -\dfrac{\phi+D}{\psi} \end{pmatrix}.$$

(3.5)

Since all the parameters are positive, the following condition is satisfied:

$$det[J] = -\frac{\phi+D}{\psi(1-\psi)} > 0$$

$$tr[J] = -\frac{1+D}{1-\psi} - \frac{\phi+D}{\psi} < 0,$$

we have

$$Re(\lambda_1) < 0 \quad \text{and} \quad Re(\lambda_2) < 0.$$

here λ_1 and λ_2 are the eigenvalues of the matrix. Therefore, the model represented by the dimensionless system (3.2) are dissipative and all solutions lie in the bounded set:

$$\Gamma_1 = \{(N_1, N_2, R_1, R_2, C_1, C_2) | N_1 + R_1 + C_1 \le A, N_2 + R_2 + C_2 \le B\}.$$

Hence System (3.2) can be reduced to the system as following form:

$$\frac{dN_1}{dt} = ((1 - \varepsilon)\mu(A - N_1 - C_1) - m)N_1 - \frac{1 + D}{1 - \psi}N_1 + \frac{\phi + D}{R(1 - \psi)}N_2,$$

$$\frac{dN_2}{dt} = \frac{DR}{\psi}N_1 + ((1 - \varepsilon)\mu(B - N_2 - C_2) - m)N_2 - \frac{\phi + D}{\psi}N_2,$$

$$(3.6)$$

$$\frac{dC_1}{dt} = \varepsilon(\mu(A - N_1 - C_1) - m)N_1 - \frac{1 + D}{1 - \psi}C_1 - kC_1 + \frac{\phi + D}{R(1 - \psi)}C_2,$$

$$\frac{dC_2}{dt} = \varepsilon(\mu(B - N_2 - C_2) - m)N_2 + \frac{DR}{\psi}C_1 - \frac{\phi + D}{\psi}C_2 - kC_2.$$

Clearly, the reduced System (3.6) has the same equilibria as the original dimensionless system (3.2) [11, 4].

3.2.3 Equilibria

To investigate the existence of equilibria for System (3.6) we consider the following two cases:

(a) Similarly, the first two equations imply that $N_1^{(0)} = 0 \Leftrightarrow N_2^{(0)} = 0$. Hence the trivial equilibrium is

$$E_0 = (0, 0, A - C_1^{(0)}, B - C_2^{(0)}, C_1^{(0)}, C_2^{(0)});$$

Also, $N_1^{(0)} = N_2^{(0)} = 0$, implies $C_1^{(0)} = C_2^{(0)} = 0$ from the last two equations. Therefore, the trivial equilibrium $E_0 = (0, 0, A, B, 0, 0)$ is the only equilibrium on the boundary.

(b) There also possibility of the existence of interior equilibria s.t $N_1^* \neq 0$ and $N_2^* \neq 0$, if $N_1^* \neq 0$ and $N_2^* \neq 0$ only if R_1^* and R_2^* satisfy:

$$[((1-\varepsilon)\mu(R_1)-m)(1-\psi)-(1+D)][((1-\varepsilon)\mu(R_2)-m)\psi-(\phi+D)] = (\phi+D)D$$

which is equivalent to

$$\begin{aligned}
&[((1-\varepsilon)\mu(A-N_1-C_1)-m)(1-\psi)-(1+D)] \\
&\cdot[((1-\varepsilon)\mu(B-N_2-C_2)-m)\psi-(\phi+D)] = (\phi+D)D
\end{aligned} \tag{3.7}$$

The following theorem illustrates the uniqueness of the interior equilibrium.

Theorem 7. *If an interior equilibrium exists, it is the only interior equilibrium in the System (3.6).*

Proof. Suppose there are two equilibria lie in the interior of Γ_1, say E^* and $\tilde{E}^*$ and $E^* \neq \tilde{E}^*$. Studying the relations of the first two parameters of these two equilibria, there are seven possibilities as following:

(i) $N_1^* = \tilde{N}_1^*$ and $N_2^* = \tilde{N}_2^*$;

(ii) $N_1^* = \tilde{N}_1^*$ and $N_2^* \neq \tilde{N}_2^*$;

(iii) $N_1^* \neq \tilde{N}_1^*$ or $N_2^* = \tilde{N}_2^*$;

(iv) $N_1^* > \tilde{N}_1^*$ and $N_2^* > \tilde{N}_2^*$;

(v) $N_1^* < \tilde{N}_1^*$ and $N_2^* < \tilde{N}_2^*$;

(vi) $N_1^* > \tilde{N}_1^*$ and $N_2^* < \tilde{N}_2^*$;

(vii) $N_1^* < \tilde{N}_1^*$ and $N_2^* > \tilde{N}_2^*$;

Disprove all assumptions above to obtain the uniqueness:

Let $\gamma_1 = \dfrac{1+D}{1-\psi}, \gamma_2 = \dfrac{\phi+D}{\psi}, \gamma_3 = \dfrac{DR}{\psi}$ and $\gamma_4 = \dfrac{\phi+D}{R(1-\psi)}$. Setting the left hand side of the last two equations of (3.6) to zero, we get $C_1^* = a_1 N_1^* + b_1 N_2^*$ and $C_2^* = a_2 N_1^* + b_2 N_2^*$, where $a_1 = \dfrac{\varepsilon\mu_1(\gamma_2+k)}{(\gamma_1+k)(\gamma_2+k)-\gamma_3\gamma_4} > 0$, $b_1 = \dfrac{\varepsilon\mu_2\gamma_4}{(\gamma_1+k)(\gamma_2+k)-\gamma_3\gamma_4} > 0$, $a_2 = \dfrac{\varepsilon\mu_1\gamma_3}{(\gamma_1+k)(\gamma_2+k)-\gamma_3\gamma_4} > 0$ and $b_2 = \dfrac{\varepsilon\mu_2(\gamma_2+k)}{(\gamma_1+k)(\gamma_2+k)-\gamma_3\gamma_4} > 0$.

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(i) According the the results of C_1^* and C_2^* from above, $N_1^* = \tilde{N}_1^*$ and $N_2^* = \tilde{N}_2^*$ implies $C_1^* = \tilde{N}_1^*$ and $C_2^* = \tilde{N}_2^*$, hence contradicts the hypothesis $E^* \neq \tilde{E}^*$.

(ii) $N_1^* = \tilde{N}_1^*$ and without loss of generality, assume that $N_2^* > \tilde{N}_2^*$, from the second equation of (3.6), $[N_2^*((1-\varepsilon)\mu(B - N_2^* - C_2^*) - m - \gamma_2)]/\gamma_3 = [\tilde{N}_2^*((1-\varepsilon)\mu(B - \tilde{N}_2^* - \tilde{C}_2^*) - m - \gamma_2)]/\gamma_3$, implies $\mu(B - N_2^* - C_2^*) > \mu(B - \tilde{N}_2^* - \tilde{C}_2^*)$, which implies $N_2^* + C_2^* < \tilde{N}_2^* + \tilde{C}_2^*$, hence $C_2^* < \tilde{C}_2^*$; from the first equation of (3.6), we have the following relation: $N_2^* = [N_1^*((1-\varepsilon)\mu(A - N_1^* - C_1^*) - m - \gamma_1)]/\gamma_4 > \tilde{N}_1^*((1-\varepsilon)\mu(A - \tilde{N}_1^* - \tilde{C}_1^*) - m - \gamma_1)]/\gamma_4 = \tilde{N}_2^*$, since $N_1^* = \tilde{N}_1^*$, $\mu(A - N_1^* - C_1^*) > \mu(A - \tilde{N}_1^* - \tilde{C}_1^*)$. Therefore $C_2^* = a_2 N_1^* + b_2 N_2^*$, $\tilde{C}_2^* = \tilde{a}_2 \tilde{N}_1^* + \tilde{b}_2 \tilde{N}_2$, and $b_2 N_2^* = \tilde{b}_2 \tilde{N}_2$, $N_1^* = \tilde{N}_1^*$, $a_2 > \tilde{a}_2$ together imply $C_2^* > \tilde{C}_2^*$ which contradicts the previous conclusion $C_2^* < \tilde{C}_2^*$.

(iii) Similar to (ii), we get contradiction from this possibility.

(iv) $N_1^* > \tilde{N}_1^*$ and $N_2^* > \tilde{N}_2^*$ implies $C_1^* > \tilde{C}_1^*$ and $C_2^* > \tilde{C}_2^*$, hence $\mu(A - N_1^* - C_1^*) < \mu(A - \tilde{N}_1^* - \tilde{C}_1^*)$ and $\mu(A - N_2^* - C_2^*) < \mu(A - \tilde{N}_2^* - \tilde{C}_2^*)$, then $[(1-\varepsilon)\mu(A - N_1^* - C_1^*) - m - \gamma_1][(1-\varepsilon)\mu(A - N_2^* - C_2^*) - m - \gamma_2] > [(1-\varepsilon)\mu(A - \tilde{N}_1^* - \tilde{C}_1^*) - m - \gamma_1][(1-\varepsilon)\mu(A - \tilde{N}_2^* - \tilde{C}_2^*) - m - \gamma_2] = \gamma_3\gamma_4$, contradicts the existence condition (3.7).

(v) Similar to (iv), we get contradiction from this possibility.

(vi) $N_1^* > \tilde{N}_1^*$ and $N_2^* < \tilde{N}_2^*$, from the first equation of (3.6), $|(1-\varepsilon)\mu(A - N_1^* - C_1^*) - m - \gamma_1| = \frac{\gamma_4 N_2^*}{N_1^*} < \frac{\gamma_4 \tilde{N}_2^*}{\tilde{N}_1^*} = |(1-\varepsilon)\mu(A - \tilde{N}_1^* - \tilde{C}_1^*) - m - \gamma_1|$, hence $\mu(A - N_1^* - C_1^*) > \mu(A - \tilde{N}_1^* - \tilde{C}_1^*)$, which implies $N_1^* + C_1^* < \tilde{N}_1^* + \tilde{C}_1^*$, and $C_1^* < \tilde{C}_1^*$, from the third equation of (3.6), $C_2^* = [(\gamma_1 + k)C_1^* - \varepsilon\mu_1 N_1^*]/\gamma_4 < [(\gamma_1 + k)\tilde{C}_1^* - \varepsilon\mu_1 N_1^*]/\gamma_4 < [(\gamma_1 + k)\tilde{C}_1^* - \varepsilon\tilde{\mu}_1 \tilde{N}_1^*]/\gamma_4 = \tilde{C}_2^*$, since $N_2^* < \tilde{N}_2^*$, we have $N_2^* + C_2^* < \tilde{N}_2^* + \tilde{C}_2^*$. Applying the same procedure in (iv), this contradicts the existence condition (3.7).

(vii) Similar to (vi), we get contradiction from this possibility.

Since the seven possibilities are disproved, one can make a conclusion that there can be at most one interior equilibrium in the system. $\square$

The uniqueness of the interior equilibrium is obtained, hence the modified growth related system (3.2) has the same equilibria as the growth related case of System (2.2). It is now necessary to compare the population concentration components and the toxin concentration components of the two equilibria respectively, in order to study if the toxin that is retrieved back to the system as nutrient affects the final equilibrium.

Theorem 8. *Let us introduce the notations* $(\widetilde{N_1^*}, \widetilde{N_1^*})$ *and* $(\widehat{N_1^*}, \widehat{N_2^*})$ *for the population concentration components of the interior equilibria of Systems (2.2) and (3.2), respectfully, then* $\widehat{N_1^*} < \widetilde{N_1^*}$, *and* $\widehat{N_2^*} < \widetilde{N_2^*}$.

Proof. Assume that the interior equilibria exist for both Systems (2.2) and (3.2). Combining (2.6) and (3.7) we get:

$$
[((1-\varepsilon)\mu(A - \widehat{N_1^*} - C_1^*) - m) - \frac{1+D}{1-\psi}][((1-\varepsilon)\mu(B - \widehat{N_2^*} - C_2^*) - m) - \frac{\phi+D}{\psi}]
$$
$$
= [(\mu(A - \widetilde{N_1^*}) - m) - \frac{1+D}{1-\psi}][(\mu(B - \widetilde{N_2^*}) - m) - \frac{\phi+D}{\psi}]
$$

We consider the following two cases:

(i) If $((1-\varepsilon)\mu(A - \widehat{N_1^*} - C_1^*) - m)(1-\psi) - (1+D) = (\mu(A - \widetilde{N_1^*}) - m)(1-\psi) - (1+D)$ and $((1-\varepsilon)\mu(B - \widehat{N_2^*} - C_2^*) - m)\psi - (\phi+D) = (\mu(B - \widetilde{N_2^*}) - m)\psi - (\phi+D)$, $\mu(A - \widetilde{N_1^*}) = (1-\varepsilon)\mu(A - \widehat{N_1^*} - C_1^*)$. Since $0 < 1-\varepsilon < 1$, we have $\mu(A - \widetilde{N_1^*}) < \mu(A - \widehat{N_1^*} - C_1^*)$, which implies $A - \widetilde{N_1^*} < A - \widehat{N_1^*} - C_1^*$, hence $\widetilde{N_1^*} > \widehat{N_1^*} + C_1^*$ and therefore, $\widetilde{N_1^*} > \widehat{N_1^*}$.

(ii) If $((1-\varepsilon)\mu(A - \widehat{N_1^*} - C_1^*) - m)(1-\psi) - (1+D) < (\mu(A - \widetilde{N_1^*}) - m)(1-\psi) - (1+D)$ and $((1-\varepsilon)\mu(B - \widehat{N_2^*} - C_2^*) - m)\psi - (\phi+D) > (\mu(B - \widetilde{N_2^*}) - m)\psi - (\phi+D)$ (If

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it is the other way, the proof is similar), from the same procedure in i we get $\widetilde{N_1^*} > N_1^*$. According to the second equation in both System (2.2) and System (3.2), to achieve an equilibrium, one must have $(1 - \varepsilon)\mu(A - \widehat{N_1^*} - C_1^*) - m)(1 - \psi) - (1 + D) < 0$ and $(\mu(A - \widetilde{N_1^*}) - m)(1 - \psi) - (1 + D) < 0$. Therefore, $0 < m + \frac{1+D}{1-\psi} - \mu(A - \widetilde{N_1^*} < m + \frac{1+D}{1-\psi} - (1 - \varepsilon)\mu(A - \widehat{N_1^*} - C_1^*)$. Hence from the second equation in both System (2.2) and System (3.2), $m + \frac{\phi+D}{R\psi} - \mu(B - \widetilde{N_2^*})\widetilde{N_2^*} = \frac{DR}{\psi}\widetilde{N_1^*} > \frac{DR}{\psi}N_1^* = (m + \frac{1+D}{1-\psi} - (1 - \varepsilon)\mu(A - \widehat{N_1^*} - C_1^*))N_2^* > 0$, then we have $\widetilde{N_2^*} > N_2^*$

$\square$

Theorem 8 shows the relationship of the two population concentrations at equilibrium (N_1^*, N_2^*) between the original growth-related model (System (2.2)), and the modified growth-related model (System (3.2))in which the toxin contains the limiting nutrient. Other things being equal, equilibrium populations are larger in the original model. This result follows from the partitioning of nutrient between dissolved nutrient, populations, and toxin, combined with the conservation of nutrient mass. At equilibrium, total nutrient mass in each compartment of the gradostat is constrained by the asymptotic conservation principle. The populations in either model have the same loss rates, and so their break even concentrations are the same. Therefore, the nutrient that partitions into the toxin can only be taken from the portion that partitions into populations, and so population concentrations at equilibrium are lower in modified model.

3.2.4   Local Stability Analysis

We now turn to the local stability analysis. The Jacobian of System (3.2) is

$$J(N_1, N_2, R_1, R_2, C_1, C_2) =$$

$$
\begin{pmatrix}
J_{11} & \gamma_3 & 0 & 0 & (1-\varepsilon)\beta_3 & 0 \\
\gamma_4 & J_{22} & 0 & 0 & 0 & (1-\varepsilon)\beta_4 \\
-\alpha_1 - m & 0 & -\gamma_1 & \gamma_3 & k & 0 \\
0 & \alpha_2 - m & \gamma_4 & -\gamma_2 & 0 & k \\
\varepsilon(\alpha_1 + \beta_1) & 0 & 0 & 0 & -\varepsilon\beta_1 - \gamma_1 - k & \gamma_3 \\
0 & \varepsilon(\alpha_2 + \beta_2) & 0 & 0 & \gamma_4 & -\varepsilon\beta_2 - \gamma_2 - k
\end{pmatrix},
\tag{3.8}
$$

where

$$\alpha_1 = \mu(A - N_1 - C_1), \qquad \alpha_2 = \mu(B - N_2 - C_2),$$
$$\beta_1 = -N_1 \frac{d\mu}{dN_1}, \qquad \beta_2 = -N_2 \frac{d\mu}{dN_2},$$
$$\beta_3 = -N_1 \frac{d\mu}{dC_1}, \qquad \beta_4 = -N_2 \frac{d\mu}{dC_2},$$
$$\gamma_1 = \frac{1 + D}{1 - \psi}, \qquad \gamma_2 = \frac{\phi + D}{\psi},$$
$$\gamma_3 = \frac{DR}{\psi}, \qquad \gamma_4 = \frac{\phi + D}{R(1 - \psi)},$$

and $J_{11} = (1-\varepsilon)\alpha_1 - \gamma_1 - \beta_1 - m$, $J_{22} = (1-\varepsilon)\alpha_2 - \gamma_2 - \beta_2 - m$. Since R_i^* can be written as a linear combination of N_i^* and C_i^*, where$(i = 1, 2)$, the 6×6 Jacobian can be reduced to 4×4:

$$
\begin{pmatrix}
J_{11} & \gamma_3 & (1-\varepsilon)\beta_3 & 0 \\
\gamma_4 & J_{22} & 0 & (1-\varepsilon)\beta_4 \\
\varepsilon(\alpha_1 + \beta_1) & 0 & -\varepsilon\beta_1 - \gamma_1 - k & \gamma_3 \\
0 & \varepsilon(\alpha_2 + \beta_2) & \gamma_4 & -\varepsilon\beta_2 - \gamma_2 - k
\end{pmatrix}
$$

Theorem 9. *The equilibrium E_0 is locally asymptotically stable if and only if $\alpha_1 + \alpha_2 - \gamma_1 - \gamma_2 - 2m < 0$ and $((1-\varepsilon)\alpha_1 - \gamma_1 - m)((1-\varepsilon)\alpha_2 - \gamma_2 - m) - \gamma_3\gamma_4 > 0$. Where $\alpha_1^0 = \mu(A)$, and $\alpha_2^0 = \mu(B)$.*

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Proof. For the equilibrium E_0, the local stability is determined by the eigenvalues of:

$$J_{NC}(E_0) = \begin{pmatrix} (1-\varepsilon)\alpha_1^0 - \gamma_1 - m & \gamma_3 & 0 & 0 \\ \gamma_4 & (1-\varepsilon)\alpha_2^0 - \gamma_2 - m & 0 & 0 \\ \varepsilon\alpha_1^0 & 0 & -\gamma_1 - k & \gamma_3 \\ 0 & \varepsilon\alpha_2^0 & \gamma_4 & -\gamma_2 - k \end{pmatrix}$$

where $\alpha_1^0 = \mu(A)$ and $\alpha_2^0 = \mu(B)$, both of them are constant. The 4×4 matrix has the same eigenvalues of the following two 2×2 matrix (see Appendix A):

$$J_N(E_0) = \begin{pmatrix} (1-\varepsilon)\alpha_1^0 - \gamma_2 - m & \gamma_3 \\ \gamma_4 & (1-\varepsilon)\alpha_2^0 - \gamma_2 - m \end{pmatrix}, \tag{3.9}$$

and those of:

$$J_C(E_0) = \begin{pmatrix} -\gamma_1 - k & \gamma_3 \\ \gamma_4 & -\gamma_2 - k \end{pmatrix}. \tag{3.10}$$

Both (3.1) and (3.3) must negative real parts for eigenvalues to achieve the asymptotical stability of E_0. Apply Routh-Hurwitz Condition as follows:

$$det[J_N(E_0)] = ((1-\varepsilon)\alpha_1^0 - \gamma_2 - m)((1-\varepsilon)\alpha_2^0 - \gamma_2 - m) - \gamma_3\gamma_4 > 0, \tag{3.11}$$

$$tr[J_N(E_0)] = (1-\varepsilon)\alpha_1^0 - \gamma_2 - m + ((1-\varepsilon)\alpha_2^0 - \gamma_2 - m) < 0, \tag{3.12}$$

$$det[J_C(E_0)] = (\gamma_1 - k)(\gamma_2 - k) - \gamma_3\gamma_4 > 0, \tag{3.13}$$

$$tr[J_C(E_0)] = -\gamma_1 - k - \gamma_2 - k. \tag{3.14}$$

Inequalities (3.13) and (3.14) are always true, since all the parameters are positive, Inequalities (3.11) and (3.12) imply that (3.9) and (3.10) both have only negative real parts for eigenvalues, hence the asymptotical stability of E_0. □

Theorem 10. *The interior equilibrium E^* is locally asymptotically stable whenever it exists.*

Proof. The Jacobian matrix for E^*:

$$J_N(E^*) = \begin{pmatrix} J_{11} & \gamma_3 & (1-\varepsilon)\beta_3 & 0 \\ \gamma_4 & J_{22} & 0 & (1-\varepsilon)\beta_4 \\ \varepsilon(\alpha_1 + \beta_1) & 0 & -\varepsilon\beta_1 - \gamma_1 - k & \gamma_3 \\ 0 & \varepsilon(\alpha_2 + \beta_2) & \gamma_4 & -\varepsilon\beta_2 - \gamma_2 - k \end{pmatrix} \quad (3.15)$$

Consider the principle minors of Matrix (3.15) [17, 4]:

$$d_1 = (1-\varepsilon)\alpha_1 - \gamma_1 - \beta_1 - m < 0,$$

$$d_2 = ((1-\varepsilon)\alpha_1 - \beta_1 - \gamma_1 - m)((1-\varepsilon)\alpha_2 - \beta_2 - \gamma_2 - m) - \gamma_3\gamma_4 > 0,$$

$$d_3 = d_2(-\varepsilon\beta_1 - \gamma_1 - k) + (1-\varepsilon)\varepsilon\beta_3(\alpha_1 + \beta_1)[(1-\varepsilon)\alpha_2 - \beta_2 - \gamma_2 - m] < 0$$

Since $d_2 > 0, (-\varepsilon\beta_1 - \gamma_1 - k) < 0$, also $(\alpha_1 + \beta_1) > 0$ and $(1-\varepsilon)\alpha_2 - \beta_2 - \gamma_2 - m < 0$.

$$\begin{aligned} d_4 = {} & ((1-\varepsilon)\alpha_1 - \beta_1)[((1-\varepsilon)\alpha_2 - \beta_2 - \gamma_2)(-\varepsilon\beta_1 - \gamma_1 - k)(-\varepsilon\beta_2 - \gamma_2 - k)] \\ & -\gamma_3[\gamma_4(-\varepsilon\beta_1 - \gamma_1 - k)(-\varepsilon\beta_2 - \gamma_2 - k) - (1-\varepsilon)\varepsilon^2\beta_4(\alpha_1 + \beta_1)(\alpha_2 + \beta_2)] \\ & -(1-\varepsilon)\beta_3[-(1-\varepsilon)\varepsilon\gamma_3\gamma_4(\alpha_2 + \beta_2) \\ & -(\alpha_2 - \beta_2 - \gamma_2 - m)\varepsilon(\alpha_2 + \beta_2)(-\varepsilon\beta_2 - \gamma_2 - k)] > 0 \end{aligned}$$

According to the theorem in Appendix, all the eigenvalues of Matrix (3.15) have negative real parts, hence the interior equilibrium is asymptotically stable as long as it exists. $\qquad\square$

3.2.5   Summary

According to Theorem 9, the stability of the trivial equilibrium E_0 implies the absence of interior equilibria. When E_0 is unstable, according to Theorems 7 and

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10, there exists a unique stable interior equilibrium E^*. The results of equilibria and local stability analysis are summarized in Table 3.1, where $\Theta_1 = (\alpha_1^0 - \gamma_1 - m)$ and $\Theta_2 = (\alpha_2^0 - \gamma_2 - m)$.

Table 3.1. Summary of the modified growth related cases

Equilibrium	Conditions for existence	Conditions for Local stability
E_0	Always exists	$\Theta_1 + \Theta_2 < 0$ $\Theta_1 \Theta_2 > \gamma_3 \gamma_4$
E^*	$\Theta_1 + \Theta_2 \geq 0$ or $\Theta_1 \Theta_2 < \gamma_3 \gamma_4$	E^* exists

Table 3.1 implies that E^* exists and E_0 unstable when one of the growth-loss balance is positive, i.e., at least one of the following inequalities must be true:

$$\mu(A) < \frac{1}{1-\varepsilon}\left(\frac{1+D}{1-\psi} + m\right), \tag{3.16}$$

$$\mu(B) < \frac{1}{1-\varepsilon}\left(\frac{\phi+D}{\psi} + m\right). \tag{3.17}$$

Since A represents the maximal nutrient concentration in the first vessel, then the term $(1-\varepsilon)\mu(A)$ is larger than the maximal growth rate of the microorganism in the first vessel. The term $\frac{1+D}{1-\psi} + m$ represents the sum of mortality rate, washout rate, and exchange rate. Hence, Inequality (3.16) is satisfied when the maximal growth rate of the microorganism is less than the sum of mortality rate and the washout rate and exchange rate minus a positive term. Inequality (3.17) can be similarly analyzed, holding true when the maximal growth rate of the microorganism is less than the sum of mortality rate, washout rate, and exchange rate minus a positive term in the second vessel [17].

However, the system can also be persistent when both growth-loss balances in both vessels are negative, that is when the first part of Theorem 9 is true but the second part of it is violated, i.e., $((1-\varepsilon)\mu(A) - \frac{1+D}{1-\psi} - m)((1-\varepsilon)\mu(B) - \frac{\phi+D}{\psi} - m) < \frac{D(\phi+D)}{\psi(1-\psi)}$, with both $(1-\varepsilon)\mu(A) - \frac{1+D}{1-\psi} - m < 0$ and $(1-\varepsilon)\mu(B) - \frac{\phi+D}{\psi} - m < 0$. Hence, just negative growth-loss balance is not enough for the local stability of the trivial equilibrium E_0 – it requires that the growth rate μ at the trivial equilibrium be sufficiently small. As a matter of fact, the local stability of the trivial equilibrium E_0 requires both the following conditions to be satisfied:

$$\mu(A) < \frac{1}{1-\varepsilon}\left(\frac{1+D}{1-\psi} + m - \frac{D(\phi+D)}{(\phi+D+\psi m)(1-\psi)}\right), \qquad (3.18)$$

$$\mu(B) < \frac{1}{1-\varepsilon}\left(\frac{\phi+D}{\psi} + m - \frac{D(\phi+D)}{(1+D+m-\psi m)\psi}\right). \qquad (3.19)$$

Therefore, a negative growth-loss balance could lead to persistence, which shows that the presence of a cove in a lake system would enhance algal and toxin persistence.

3.2.6 Global Stability Analysis

Theorem 11. *If trivial equilibrium E_0 is locally asymptotically stable, it is globally stable.*

Proof. When E_0 is asymptotically stable, it is the only equilibrium in the reduced system. Hence it is a global attractor.

Since the reduced system has the same equilibrium as of the original dimensionless model, it is a global attractor of the original dimensionless system. $\square$

Theorem 12. *If the interior equilibrium E^* is locally asymptotically stable, it is globally stable.*

Proof. E^* is asymptotically stable, and it is the only interior equilibrium of the reduced System (3.6). Hence we only need to prove the stable manifold of E_0, M_0^+ lies exterior to Γ_1, then E^* is a global attractor attracts all the trajectories with initial conditions in the interior of Γ_1. The Jacobian matrix at E_0 takes the form:

$$J_N(E_0) = \begin{pmatrix} (1-\varepsilon)\alpha_1^0 - \gamma_1 - m & \gamma_3 & 0 & 0 \\ \gamma_4 & (1-\varepsilon)\alpha_2^0 - \gamma_2 - m & 0 & 0 \\ \varepsilon\alpha_1^0 & 0 & -\gamma_1 - k & \gamma_3 \\ 0 & \varepsilon\alpha_2^0 & \gamma_4 & -\gamma_2 - k \end{pmatrix}$$

The zero block in the upper right corner eases the computation of eigenvalues:

$$[\lambda^2 - ((1-\varepsilon)(\alpha_1^0 + \alpha_2^0) - \gamma_1 - \gamma_2 - 2m)\lambda$$
$$+((1-\varepsilon)\alpha_1^0 - \gamma_1 - m)((1-\varepsilon)\alpha_2^0 - \gamma_2 - m) - \gamma_3\gamma_4] \tag{3.20}$$
$$\cdot[\lambda^2 + (\gamma_1 + \gamma_2 + 2k)\lambda + (\gamma_1 + k)(\gamma_2 + k) - \gamma_3\gamma_4] = 0$$

The eigenvalues corresponding to the first square bracket in Equation (3.20) satisfy

$$\lambda = \frac{((1-\varepsilon)\alpha_1^0 - \gamma_1 + (1-\varepsilon)\alpha_2^0 - \gamma_2 - 2m)}{2}$$

$$\pm \frac{\sqrt{((1-\varepsilon)\alpha_1^0 - \gamma_1 - (1-\varepsilon)\alpha_2^0 + \gamma_2)^2 + 4\gamma_3\gamma_4}}{2}.$$

The eigenvalues are real, E_0 is unstable, and $((1-\varepsilon)\alpha_1^0 - \gamma_1 - m)((1-\varepsilon)\alpha_2^0 + \gamma_2 - m) \neq \gamma_3\gamma_4$, one can conclude that $((1-\varepsilon)\alpha_1^0 - \gamma_1 - m)((1-\varepsilon)\alpha_2^0 + \gamma_2 - m) < \gamma_3\gamma_4$, there is one negative and one positive eigenvalue. Since the negative eigenvalue λ^- satisfies:

$$\lambda^- + ((1-\varepsilon)\alpha_1^0 - \gamma_1 - m)$$
$$= \frac{((1-\varepsilon)(\alpha_1^0 + \alpha_2^0) - \gamma_1 - \gamma_2 - 2m) - \sqrt{((1-\varepsilon)(\alpha_1^0 - \alpha_2^0) - \gamma_1 + \gamma_2)^2 + 4\gamma_3\gamma_4}}{2} < 0.$$

Let $z = (z_1, z_2, z_3, z_4)$ be the corresponding eigenvector, $\lambda^- + (\alpha_1^0 - \gamma_1 - m)z_3 = z_4$. In particular, the stable manifold of E_0 does not intersect the interior of the positive cone, hence E^* is globally stable [11]. □

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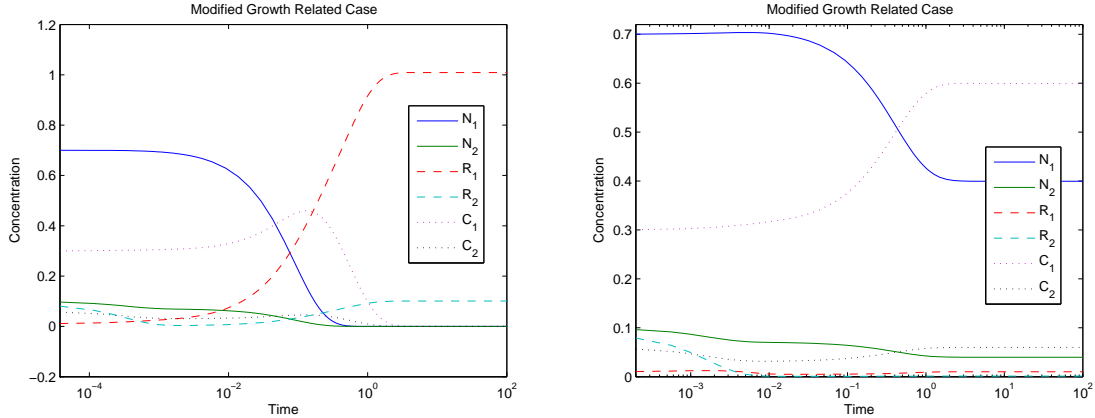
(a) Solution trajectories approaching E_0 (b) Solution trajectories approaching E^*

Figure 3.1. Local stability of both equilibria of the modified growth related case.

3.3 Numerical Simulations

Numerical simulations are performed to support the conclusions that have been made in mathematical analysis in the previous sections, for the modified growth related model. Numerical verification of the local results of E_0 and E^* applied to ordinary differential equation System (3.2) are obtained by using the adaptive **MatLab** solvers `ode45` and `ode23`. The following data are used in each simulation:

For E_0 we set: $m = 16, D = 30, \psi = 0.01, \phi = 0.001, R = 0.1, \varepsilon = 0.5, k = 1$, and $\mu_{max} = 12$, the half-saturation constant $K = 0.01$; for E^* we set $m = 2, D = 6$, other things equal. The initial condition is $(N_1, N_2, R_1, R_2, C_1, C_2)(0) = (0.7, 0.1, 0.01, 0.09, 0.3, 0.06)$, and the simulations are shown in Fig. 3.1. (The data are determined based on [9].)

A visualization of the N_1 and N_2 components of several simulations each with different initial values of N_1 and N_2, is displayed in Fig. 3.3.

The simulations are obtained by using **Mathematica** `NDSolve` applied to the modified growth related model (3.2). using the following parameters: $\varepsilon = 0.5, \gamma_1 =$

$4, \gamma_2 = 3.2, \gamma_3 = 4, \gamma_4 = 1.6, A = 0.7, B = 1.25, k = 0.7, K = 0.6$ and $\mu_{max} = 1$ for

Fig. 3.3 (a); and $\mu_{max} = 10$ for Fig 3.3 (b).

(a) E_0 attracts all solutions
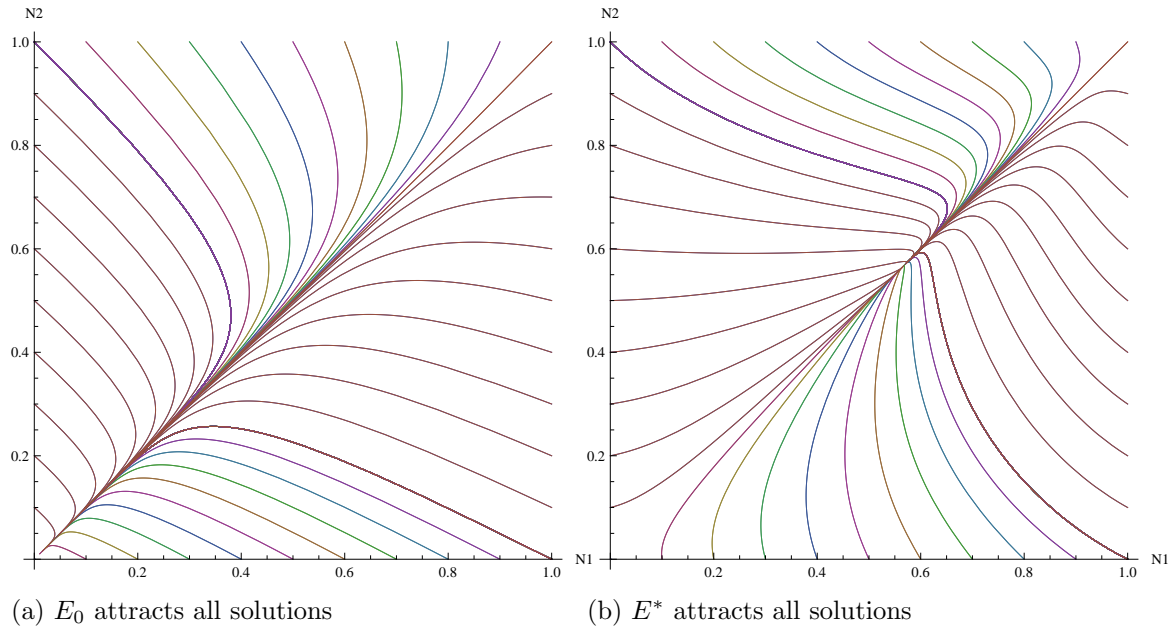
(b) E^* attracts all solutions

Figure 3.2. Global stability of both equilibria of the modified growth related case.

CHAPTER 4

THE MODIFIED MORTALITY RELATED MODEL

4.1   Introduction

This model is derived from the previous case of mortality related model. Similarly, the mathematical model consists of six ordinary differential equations and represents the dynamics of microorganism in a lake with its single coves [9], and the algal produces toxin in proportion to its mortality rate.

4.2   The Model

The original model has the following form:

$$\frac{dN_1}{dt} = [\mu(R_1) - m]N_1 - \frac{D + E}{1 - \psi}N_1 + \frac{\phi D + E}{1 - \psi}N_2;$$

$$\frac{dN_2}{dt} = \frac{E}{\psi}N_1 + [\mu(R_2) - m]N_2 - \frac{\phi D + E}{\psi}N_2;$$

$$\frac{dR_1}{dt} = \frac{(1 - \phi)D}{1 - \psi}R_1^{in} - (\mu(R_1) - (1 - \varepsilon)m)N_1 q_N$$
$$- \frac{D + E}{1 - \psi}R_1 + \frac{\phi D + E}{1 - \psi}R_2 + kC_2 q_C;$$

$$\frac{dR_2}{dt} = \frac{\phi D}{\psi}R_2^{in} - (\mu(R_2) - (1 - \varepsilon)m)N_2 q_N + \frac{E}{\psi}R_1 - \frac{\phi D + E}{\psi}N_2 + kC_2 q_C;$$

$$\frac{dC_1}{dt} = \varepsilon m N_1 \frac{q_N}{q_C} - \frac{D + E}{1 - \psi}C_1 - kC_1 + \frac{\phi D + E}{1 - \psi}C_2;$$

$$\frac{dC_2}{dt} = \varepsilon m N_2 \frac{q_N}{q_C} + \frac{E}{\psi}C_1 - \frac{\phi D + E}{\psi}C_2 - kC_2.$$

All the parameters have the same biological meanings and units in Table 2.1, and the nutrient content of the toxin is q_C (mol/g) [9] and ε is a dimensionless coefficient. The terms $(\mu(R_i) - (1-\varepsilon)m)N_i q_N$, $i = 1, 2$, specify that a fraction, ε, of the mortality generates toxin. When the algal die, they become part of the toxin (see terms εN_i, $i = 1, 2$ in the last two equations). The two terms $kC_i q_C$, $i = 1, 2$ adding to the two equations for nutrient concentration specify that the toxin was transferred to nutrient with quota q_C

4.2.1 Dimensionless system

Apply the same strategy in previous cases to obtain the dimensionless system as follows:

$$\frac{dN_1}{dt} = [\mu(R_1) - m]N_1 - \frac{1+D}{1-\psi}N_1 + \frac{\phi+D}{R(1-\psi)}N_2,$$

$$\frac{dN_2}{dt} = \frac{DR}{\psi}N_1 + [\mu(R_2) - m]N_2 - \frac{\phi+D}{\psi}N_2,$$

$$\frac{dR_1}{dt} = \frac{1-\phi}{1-\psi} - (\mu(R_1) - (1-\varepsilon)m)N_1 - \frac{1+D}{1-\psi}R_1 + \frac{\phi+D}{R(1-\psi)}R_2 + kC_1,$$

$$(4.1)$$

$$\frac{dR_2}{dt} = \frac{\phi}{\psi} - (\mu(R_2) - (1-\varepsilon)m)N_2 + \frac{DR}{\psi}R_1 - \frac{\phi+D}{\psi}N_2 + kC_2,$$

$$\frac{dC_1}{dt} = \varepsilon m N_1 - \frac{1+D}{1-\psi}C_1 - kC_1 + \frac{\phi+D}{R(1-\psi)}C_2,$$

$$\frac{dC_2}{dt} = \varepsilon m N_2 + \frac{DR}{\psi}C_1 - \frac{\phi+D}{\psi}C_2 - kC_2.$$

System (4.1) is the form that is used in our mathematical analysis. It is trivial to show that the first quadrant is positively invariant [11] and that the system is well posed [17].

4.2.2 Dissipatedness of The Dimensionless system

Similar as in the modified growth related case, by setting

$$\Sigma_1 = N_1 + R_1 + C_1,$$

$$\Sigma_2 = N_2 + R_2 + C_2$$

(4.2)

we obtain the same dissipative system:

$$\Sigma_1' = \frac{1-\phi}{1-\psi} - \frac{1+D}{1-\psi}\Sigma_1 + \frac{\phi+D}{R(1-\psi)}\Sigma_2,$$

$$\Sigma_2' = \frac{\phi}{\psi} + \frac{DR}{\psi}\Sigma_1 - \frac{\phi+D}{\psi}\Sigma_2,$$

and the same equilibrium:

$$\Sigma_1^* = 1 + \phi - \frac{\phi}{R} = A,$$

$$\Sigma_2^* = \frac{DR - DR\phi + D\phi + \phi}{\phi + D} = B.$$

Hence System (4.1) can be reduced to the following form:

$$\frac{dN_1}{dt} = (\mu(A - N_1 - C_1) - m)N_1 - \frac{1+D}{1-\psi}N_1 + \frac{\phi+D}{R(1-\psi)}N_2,$$

$$\frac{dN_2}{dt} = \frac{DR}{\psi}N_1 + (\mu(B - N_2 - C_2) - m)N_2 - \frac{\phi+D}{\psi}N_2,$$

$$\frac{dC_1}{dt} = \varepsilon m N_1 - \frac{1+D}{1-\psi}C_1 - kC_1 + \frac{\phi+D}{R(1-\psi)}C_2,$$

$$\frac{dC_2}{dt} = \varepsilon m N_2 + \frac{DR}{\psi}C_1 - \frac{\phi+D}{\psi}C_2 - kC_2.$$

(4.3)

System (4.3) has the same equilibrium as System (4.1) and the model represented by

the dimensionless system (4.1) are dissipative and all solutions lie in the bounded set:

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$\Gamma_2 = \{(N_1, N_2, C_1, C_2)|N_1 + R_1 + C_1 \le A, N_2 + R_2 + C_2 \le B\}$. To investigate the existence of equilibrium for System (4.3) we consider the following two cases:

(a) Similarly, the first two equations can easily conclude that $N_1^{(0)} = 0 \Leftrightarrow N_2^{(0)} = 0$. Hence the trivial equilibrium is

$$E_0 = (0, 0, A - C_1^{(0)}, B - C_2^{(0)}, C_1^{(0)}, C_2^{(0)});$$

Also, $N_1^{(0)} = N_2^{(0)} = 0$, implies $C_1^{(0)} = C_2^{(0)} = 0$ from the last two equations. Therefore, we have our trivial equilibrium is $E_0 = (0, 0, 0, 0)$, which is the only equilibrium on the boundary.

(b) There also a possibility of the existence of interior equilibriums $E^* = (N_1^*, N_2^*, C_1^*, C_2^*)$ where $N_1^* \ne 0$, $N_2^* \ne 0$, $C_1^* \ne 0$ and $C_2^* \ne 0$. From the first two equations of each system, $N_1^* \ne 0$ and $N_2^* \ne 0$ only if R_1^* and R_2^* satisfy:

$$[(\mu(R_1^*) - m)(1 - \psi) - (1 + D)][(\mu(R_2^*) - m)\psi - (\phi + D)] = (\phi + D)D$$

which is equivalent to

$$[(\mu(A - N_1^* - C_1^*) - m)(1 - \psi) - (1 + D)][(\mu(B - N_2^* - C_2^*) - m)\psi - (\phi + D)] = (\phi + D)D$$

$$(4.4)$$

From the last two equations in System (4.3), $N_1^* \ne 0$ and $N_2^* \ne 0$ implies $C_1^* \ne 0$ and $C_2^* \ne 0$, hence this equilibrium E^* lies in the interior of Ω.

Theorem 13. *If the interior equilibrium exists, it is the only nontrivial equilibrium in the System (4.3).*

Proof. Suppose there are two equilibriums lies in the interior of Γ_2, say E^* and $\tilde{E}^*$ and $E^* \ne \tilde{E}^*$. Studying the relations of the first two parameters of these two equilibriums, there are seven possibilities as following:

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(i) $N_1^* = \tilde{N}_1^*$ and $N_2^* = \tilde{N}_2^*$;

(ii) $N_1^* = \tilde{N}_1^*$ and $N_2^* \neq \tilde{N}_2^*$;

(iii) $N_1^* \neq \tilde{N}_1^*$ or $N_2^* = \tilde{N}_2^*$;

(iv) $N_1^* > \tilde{N}_1^*$ and $N_2^* > \tilde{N}_2^*$;

(v) $N_1^* < \tilde{N}_1^*$ and $N_2^* < \tilde{N}_2^*$;

(vi) $N_1^* > \tilde{N}_1^*$ and $N_2^* < \tilde{N}_2^*$;

(vii) $N_1^* < \tilde{N}_1^*$ and $N_2^* > \tilde{N}_2^*$;

Disprove all of the above assumptions to obtain the uniqueness: Let $\gamma_1 = \dfrac{1+D}{1-\psi}, \gamma_2 = \dfrac{\phi+D}{\psi}, \gamma_3 = \dfrac{DR}{\psi}$ and $\gamma_4 = \dfrac{\phi+D}{R(1-\psi)}$. Setting the left hand side of the last two equations of (4.3) to zero, we get $C_1^* = a_1 N_1^* + b_1 N_2^*$ and $C_2^* = a_2 N_1^* + b_2 N_2^*$, where $a_1 = \dfrac{\varepsilon m(\gamma_2 + k)}{(\gamma_1 + k)(\gamma_2 + k) - \gamma_3\gamma_4} > 0, \ b_1 = \dfrac{\varepsilon m\gamma_4}{(\gamma_1 + k)(\gamma_2 + k) - \gamma_3\gamma_4} > 0, \ a_2 = \dfrac{\varepsilon m\gamma_3}{(\gamma_1 + k)(\gamma_2 + k) - \gamma_3\gamma_4} > 0$ and $b_2 = \dfrac{\varepsilon m(\gamma_2 + k)}{(\gamma_1 + k)(\gamma_2 + k) - \gamma_3\gamma_4} > 0$.

(i) According the the results of C_1^* and C_2^* from above, $N_1^* = \tilde{N}_1^*$ and $N_2^* = \tilde{N}_2^*$ implies $C_1^* = \tilde{N}_1^*$ and $C_2^* = \tilde{N}_2^*$, hence contradicts the hypothesis $E^* \neq \tilde{E}^*$.

(ii) $N_1^* = \tilde{N}_1^*$ and without loss of generality, assume that $N_2^* > \tilde{N}_2^*$, from the second equation of (4.3), $[N_2^*(\mu(A - N_2^* - C_2^*) - m - \gamma_2)]/\gamma_3 = [\tilde{N}_2^*(\mu(A - \tilde{N}_2^* - \tilde{C}_2^*) - m - \gamma_2)]/\gamma_3$, implies $\mu(A - N_2^* - C_2^*) > \mu(A - \tilde{N}_2^* - \tilde{C}_2^*)$, which implies $N_2^* + C_2^* < \tilde{N}_2^* + \tilde{C}_2^*$ hence $C_2^* < \tilde{C}_2^*$, but $C_2^* = a_2 N_1^* + b_2 N_2^* > a_2 N_1^* + b_2 \tilde{N}_2^* = \tilde{C}_2^*$, contradiction.

(iii) Similar to (ii), we get contradiction from this possibility.

(iv) $N_1^* > \tilde{N}_1^*$ and $N_2^* > \tilde{N}_2^*$ implies $C_1^* > \tilde{C}_1^*$ and $C_2^* > \tilde{C}_2^*$, hence $\mu(A - N_1^* - C_1^*) < \mu(A - \tilde{N}_1^* - \tilde{C}_1^*)$ and $\mu(A - N_2^* - C_2^*) < \mu(A - \tilde{N}_2^* - \tilde{C}_2^*)$, then $[\mu(A - N_1^* - C_1^*) - m - \gamma_1][\mu(A - N_2^* - C_2^*) - m - \gamma_2] > [\mu(A - \tilde{N}_1^* - \tilde{C}_1^*) - m - \gamma_1][\mu(A - \tilde{N}_2^* - \tilde{C}_2^*) - m - \gamma_2] = \gamma_3\gamma_4$, contradicts the existence condition (4.4).

(v) Similar to (iv), we get contradiction from this possibility.

(vi) $N_1^* > \tilde{N}_1^*$ and $N_2^* < \tilde{N}_2^*$, from the first equation of (4.3), $|\mu(A - N_1^* - C_1^*) - m - \gamma_1| = \frac{\gamma_4 N_2^*}{N_1^*} < \frac{\gamma_4 \tilde{N}_2^*}{\tilde{N}_1^*} = |\mu(A - \tilde{N}_1^* - \tilde{C}_1^*) - m - \gamma_1|$, hence $\mu(A - N_1^* - C_1^*) > \mu(A - \tilde{N}_1^* - \tilde{C}_1^*) - m - \gamma_1$, which implies $N_1^* + C_1^* < \tilde{N}_1^* + \tilde{C}_1^*$, and $C_1^* < \tilde{C}_1^*$, from the third equation of (4.3), $C_2^* = [(\gamma_1 + k)C_1^* - \varepsilon m N_1^*]/\gamma_4 < [(\gamma_1 + k)\tilde{C}_1^* - \varepsilon m N_1^*]/\gamma_4 < [(\gamma_1 + k)\tilde{C}_1^* - \varepsilon m \tilde{N}_1^*]/\gamma_4 = \tilde{C}_2^*$, since $N_2^* < \tilde{N}_2^*$, we have $N_2^* + C_2^* < \tilde{N}_2^* + \tilde{C}_2^*$. Applying the same procedure in (iv), this contradicts the existence condition (4.4).

(vii) Similar to (vi), we get contradiction from this possibility.

Since the seven possibilities are disproved, there can be at most one interior equilibrium of the system. $\qquad\square$

4.2.3 Local Stability Analysis

We now turn to the local stability analysis. The Jacobian matrix of System (4.3) is:

$$J(N_1, N_2, R_1, R_2, C_1, C_2) =$$

$$
\begin{pmatrix}
\alpha_1 - \gamma_1 - \beta_1 - m & \gamma_3 & 0 & 0 & \beta_3 & 0 \\
\gamma_4 & \alpha_2 - \gamma_2 - \beta_2 - m & 0 & 0 & 0 & \beta_4 \\
-\alpha_1 - (1 - \varepsilon)m & 0 & -\gamma_1 & \gamma_3 & k & 0 \\
0 & -\alpha_2 - (1 - \varepsilon)m & \gamma_4 & -\gamma_2 & 0 & k \\
\varepsilon m & 0 & 0 & 0 & -\gamma_1 - k & \gamma_3 \\
0 & \varepsilon m & 0 & 0 & \gamma_4 & -\gamma_2 - k
\end{pmatrix},
$$

where

$$\alpha_1 = \mu(A - N_1 - C_1), \qquad \alpha_2 = \mu(B - N_2 - C_2),$$

$$\beta_1 = -N_1 \frac{d\mu}{dN_1}, \qquad \beta_2 = -N_2 \frac{d\mu}{dN_2},$$

$$\beta_3 = -N_1 \frac{d\mu}{dC_1} \qquad \beta_4 = -N_2 \frac{d\mu}{dC_2},$$

$$\gamma_1 = \frac{1 + D}{1 - \psi}, \qquad \gamma_2 = \frac{\phi + D}{\psi},$$

$$\gamma_3 = \frac{DR}{\psi}, \qquad \gamma_4 = \frac{\phi + D}{R(1 - \psi)}.$$

Since R_i can be written as a linear combination of N_i and $C_i (i = 1, 2)$, the 6×6 Jacobian can be reduced to 4×4:

$$\begin{pmatrix} \alpha_1 - \gamma_1 - \beta_1 - m & \gamma_3 & \beta_3 & 0 \\ \gamma_4 & \alpha_2 - \gamma_2 - \beta_2 - m & 0 & \beta_4 \\ \varepsilon m & 0 & -\gamma_1 - k & \gamma_3 \\ 0 & \varepsilon m & -\gamma_4 & -\gamma_2 - k \end{pmatrix}$$

Theorem 14. *The equilibrium E_0 is locally asymptotically stable if and only if $(\alpha_1 - \gamma_1 - m) + (\alpha_2 - \gamma_2 - m) < 0$ and $(\alpha_1 - \gamma_1 - m)(\alpha_2 - \gamma_2 - m) > \gamma_3 \gamma_4$. Where $\alpha_1^0 = \mu(A)$, and $\alpha_2^0 = \mu(B)$.*

Proof. For the equilibrium E_0, the local stability is determined by the eigenvalues of:

$$J_{NC}(E_0) = \begin{pmatrix} \alpha_1^0 - \gamma_1 - m & \gamma_3 & 0 & 0 \\ \gamma_4 & \alpha_2^0 - \gamma_2 - m & 0 & 0 \\ \varepsilon m & 0 & -\gamma_1 - k & \gamma_3 \\ 0 & \varepsilon m & \gamma_4 & -\gamma_2 - k \end{pmatrix}$$

We can reduce the 4×4 matrix to two 2×2 matrix: For the equilibrium E_0, the local stability is determined by the eigenvalues of:

$$J_N(E_0) = \begin{pmatrix} \alpha_1 - \gamma_2 - m & \gamma_3 \\ \gamma_4 & \alpha_2 - \gamma_2 - m \end{pmatrix}, \tag{4.5}$$

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and those of:

$$J_C(E_0) = \begin{pmatrix} -\gamma_1 - k & \gamma_3 \\ \gamma_4 & -\gamma_2 - k \end{pmatrix}, \tag{4.6}$$

For achieving the asymptotical stability of E_0, both (4.5) and (4.6) must real negative eigenvalues. Apply Routh-Hurwitz Condition as follows:

$$det[J_N(E_0)] = (\alpha_1^0 - \gamma_2 - m)(\alpha_2^0 - \gamma_2 - m) - \gamma_3\gamma_4 > 0 \tag{4.7}$$

$$tr[J_N(E_0)] = \alpha_1^0 - \gamma_2 - m + (\alpha_2^0 - \gamma_2 - m) < 0 \tag{4.8}$$

$$det[J_C(E_0)] = (\gamma_1 - k)(\gamma_2 - k) - \gamma_3\gamma_4 > 0 \tag{4.9}$$

$$tr[J_C(E_0)] = -\gamma_1 - k - \gamma_2 - k. \tag{4.10}$$

(4.9) and (4.10) are always true, since all the parameters are positive, then the truth of (4.7) and (4.8) imply that (4.5) and (4.6) both have only negative real eigenvalues, hence the asymptotical stability of E_0. ☐

Theorem 15. *The equilibrium E^* is stable, whenever it exists.*

Proof. The local stability of the equilibrium E^* is determined by the eigenvalues of matrix:

$$J_N(E_3) = \begin{pmatrix} \alpha_1 - \beta_1 - \gamma_1 - m & \gamma_3 & \beta_3 & 0 \\ \gamma_4 & \alpha_2 - \beta_2 - \gamma_2 - m & 0 & \beta_4 \\ \varepsilon m & 0 & -\gamma_1 - k & \gamma_3 \\ 0 & \varepsilon m & \gamma_4 & -\gamma_2 - k \end{pmatrix} \tag{4.11}$$

Considering the principle minors of the matrix(4.11) [17, 4]:

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$$
\begin{aligned}
d_1 &= \alpha_1 - \gamma_1 - \beta_1 - m < 0, \\
d_2 &= (\alpha_1 - \beta_1 - \gamma_1 - m)(\alpha_2 - \beta_2 - \gamma_2 - m) - \gamma_3\gamma_4 > 0, \\
d_3 &= d_2(-\gamma_1 - k) + \varepsilon\beta_3 m(\alpha_2 - \beta_2 - \gamma_2 - m) < 0
\end{aligned}
$$

Since $d_2 > 0, (-\varepsilon\beta_1 - \gamma_1 - k) < 0$, also $(\alpha_1 - \beta_1) > 0$
and $(1 - \varepsilon)\alpha_2 - \beta_2 - \gamma_2 - m < 0$.

$$
\begin{aligned}
d_4 &= (\alpha_1 - \beta_1)[(\alpha_2 - \beta_2 - \gamma_2)(-\gamma_1 - k)(-\gamma_2 - k)] \\
&\quad - \gamma_3[\gamma_4(-\gamma_1 - k)(-\gamma_2 - k) - \varepsilon^2\beta_4(\alpha_1 + \beta_1)(\alpha_2 + \beta_2)] \\
&\quad - \beta_3[-\varepsilon\gamma_3\gamma_4(\alpha_2 + \beta_2) - (\alpha_2 - \beta_2 - \gamma_2 - m)\varepsilon(\alpha_2 + \beta_2)(-\gamma_2 - k)] > 0
\end{aligned}
$$

Therefore, the eigenvalues of Matrix (4.11) all have negative real parts, E^* is stable when it exists. $\qquad\square$

4.2.4 Summary

According to Theorem 14, the stability of the trivial equilibrium E_0 implies the absence of interior equilibria. When E_0 is unstable, according to Theorems 13 and 15, there exists a unique stable interior equilibrium E^*. The results of equilibria and local stability analysis are summarized in Table 4.1, where $\Theta_1 = (\alpha_1^0 - \gamma_1 - m)$ and $\Theta_2 = (\alpha_2^0 - \gamma_2 - m)$.

Table 4.1 shows that for the equilibrium E^* to exist at least one of the growth-loss balances must be positive, i.e., at least one of the following inequalities must be true:

$$
\mu(A) > \frac{1 + D}{1 - \psi} + m, \tag{4.12}
$$

Table 4.1. Summary of the modified mortality cases

Equilibrium	Conditions for existence	Conditions for Local stability
E_0	Always exists	$\Theta_1 + \Theta_2 < 0$
		$\Theta_1 \Theta_2 > \gamma_3 \gamma_4$
E^*	$\Theta_1 + \Theta_2 \geq 0$ or	E^* exists
	$\Theta_1 \Theta_2 < \gamma_3 \gamma_4$	

$$\mu(B) > \frac{\phi + D}{\psi} + m. \tag{4.13}$$

Since A represents the maximal nutrient concentration in the first vessel, then the term $\mu(A)$ is larger than the maximal growth rate of the microorganism in the first vessel. The term $\frac{1 + D}{1 - \psi} + m$ represents the sum of mortality rate, washout rate, and exchange rate. Hence, Inequality (4.12) is satisfied when the maximal growth rate of the microorganism is less than the sum of mortality rate and the washout rate and exchange rate minus a positive term. Inequality (4.13) can be similarly analyzed, holding true when the maximal growth rate of the microorganism is less than the sum of mortality rate, washout rate, and exchange rate minus a positive term in the second vessel [17].

However, the system can also be persistent when both growth-loss balances in both vessels are negative, that is when the first part of Theorem 14 is true but the second part of it is violated, i.e., $(\mu(A) - \frac{1 + D}{1 - \psi} - m)(\mu(B) - \frac{\phi + D}{\psi} - m) < \frac{D(\phi + D)}{\psi(1 - \psi)}$, with both $\mu(A) - \frac{1 + D}{1 - \psi} - m < 0$ and $\mu(B) - \frac{\phi + D}{\psi} - m < 0$. Hence, just negative growth-loss balance is not enough for the local stability of the trivial equilibrium E_0 – it requires that the growth rate μ at the trivial equilibrium be sufficiently small.

As a matter of fact, the local stability of the trivial equilibrium E_0 requires both the following conditions to be satisfied:

$$\mu(A) < \frac{1+D}{1-\psi} + m - \frac{D(\phi+D)}{(\phi+D+\psi m)(1-\psi)}, \tag{4.14}$$

$$\mu(B) < \frac{\phi+D}{\psi} + m - \frac{D(\phi+D)}{(1+D+m-\psi m)\psi}. \tag{4.15}$$

Therefore, a negative growth-loss balance could lead to persistence, which shows that the presence of a cove in a lake system would enhance algal and toxin persistence.

4.2.5 Global Stability Analysis

Theorem 16. *If trivial equilibrium E_0 is locally asymptotic stable, it's globally stable.*

Proof. When E_0 is asymptotically stable, it's the only equilibrium in the reduced system. Hence it's a global attractor.

Since the reduced system has the same equilibrium as of the original dimensionless model, it's a global attractor of the original dimensionless system. □

Theorem 17. *If the interior equilibrium E^* is locally asymptotically stable, it is globally stable.*

Proof. When E^* is locally asymptotically stable, it's the only interior equilibrium of the reduced system, if the stable manifold of E_0, M_0^+ lies exterior to Γ_2, therefore, E^* is a global attractor attracts all the trajectories with initial conditions in the interior of Γ_2. The Jacobian matrix at E_0 takes the form:

$$J_N(E_0) = \begin{pmatrix} \alpha_1^0 - \gamma_1 - m & \gamma_3 & 0 & 0 \\ \gamma_4 & \alpha_2^0 - \gamma_2 - m & 0 & 0 \\ \varepsilon m & 0 & -\gamma_1 - k & \gamma_3 \\ 0 & \varepsilon m & \gamma_4 & -\gamma_2 - k \end{pmatrix}.$$

The zero block in the upper right corner eases the computation of eigenvalues:

$$[\lambda^2 - (\alpha_1^0 - \gamma_1 - m + \alpha_2^0 - \gamma_2 - m)\lambda + (\alpha_1^0 - \gamma_1 - m)(\alpha_2^0 - \gamma_2 - m) - \gamma_3\gamma_4]$$

$$\times [\lambda^2 + (\gamma_1 + \gamma_2 + 2k)\lambda + (\gamma_1 + k)(\gamma_2 + k) - \gamma_3\gamma_4] = 0 \tag{4.16}$$

The eigenvalues corresponding to the first square bracket in (4.16) satisfy

$$\lambda = \frac{(\alpha_1^0 - \gamma_1 + \alpha_2^0 - \gamma_2 - 2m) \pm \sqrt{(\alpha_1^0 - \gamma_1 - \alpha_2^0 + \gamma_2)^2 + 4\gamma_3\gamma_4}}{2}.$$

The eigenvalues are real,and since E_0 is unstable, $(\alpha_1^0 - \gamma_1 - m)(\alpha_2^0 + \gamma_2 - m) \neq \gamma_3\gamma_4$, one can conclude that $(\alpha_1^0 - \gamma_1 - m)(\alpha_2^0 + \gamma_2 - m) < \gamma_3\gamma_4$, there is on negative and one positive eigenvalue. Since the negative eigenvalue λ^- satisfies:

$$\lambda^- + (\alpha_1^0 - \gamma_1 - m) = \frac{(\alpha_1^0 - \gamma_1 + \alpha_2^0 - \gamma_2 - 2m) - \sqrt{(\alpha_1^0 - \gamma_1 - \alpha_2^0 + \gamma_2)^2 + 4\gamma_3\gamma_4}}{2} < 0$$

Let $z = (z_1, z_2, z_3, z_4)$ be the corresponding eigenvector, $\lambda^- + (\alpha_1^0 - \gamma_1 - m)z_3 = z_4$. In particular, the stable manifold of E_0 does not intersect the interior of the positive cone, hence E^* is globally stable [11]. □

4.3 Numerical Simulations

Numerical simulations are performed to support the conclusions that have been made in mathematical analysis in the previous sections, for the modified mortality related model. Numerical verification of the local results of E_0 and E^* applied to ordinary differential equation System (4.1) are obtained by using the adaptive **MatLab** solvers `ode45` and `ode23`. The following data are used in each simulation:

For E_0 we set: $m = 16, D = 30, \psi = 0.01, \phi = 0.001, R = 0.1, \varepsilon = 0.5, k = 1$, and $\mu_{max} = 12$, the half-saturation constant $K = 0.01$; for E^* we set $m = 2, D = 6$, other things equal. The initial condition is $(N_1, N_2, R_1, R_2, C_1, C_2)(0) = (0.7, 0.1, 0.01, 0.09, 0.3, 0.06)$, and the simulations are shown in Fig. 4.1. (The data are determined based on [9].)
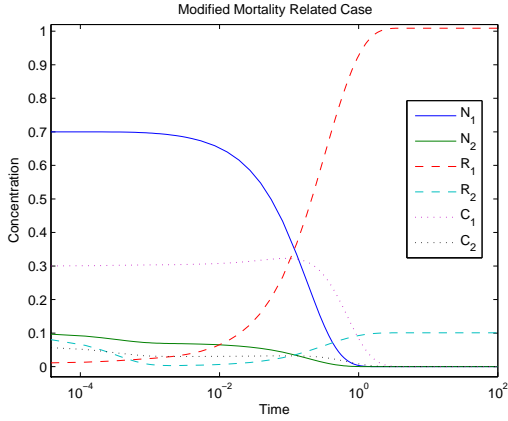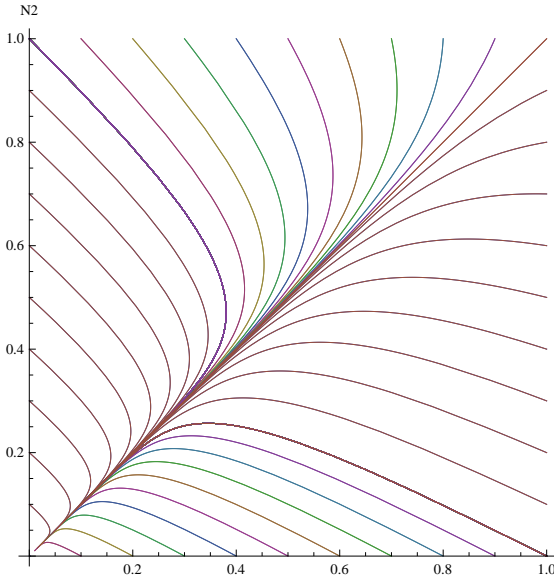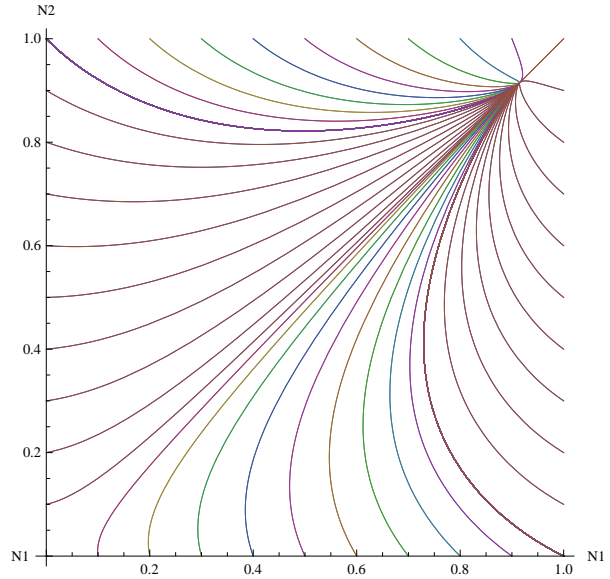
(a) Solution trajectories approaching E_0
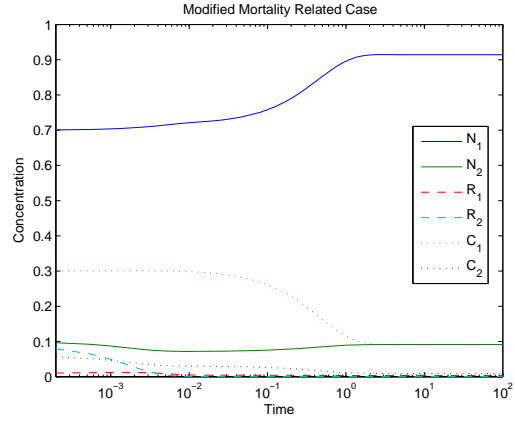
(b) Solution trajectories approaching E^*

Figure 4.1. Local stability of both equilibria of the modified mortality related case.

(a) E_0 attracts all solutions

(b) E^* attracts all solutions

Figure 4.2. Global stability of both equilibria of the mortality related case.

A visualization of the N_1 and N_2 of simulations each with different initial values of N_1 and N_2, is displayed in Fig. 4.2. The simulations are obtained by using **Mathematica** `NDSolve` applied to the modified mortality related model (4.1). Using the following parameters: $\varepsilon = 0.5, \gamma_1 = 4, \gamma_2 = 3.2, \gamma_3 = 4, \gamma_4 = 1.6, A = 0.7, B = 1.25, k = 0.7, K = 0.6$ and $\mu_{max} = 1$ for Fig. 4.2 (a); and $\mu_{max} = 10$ for Fig 4.2 (b).

CHAPTER 5

A SPECIAL CASE

5.1   Introduction

We are unable to find the analytic solutions for all the previous models due
to the complexity. This is a universal problem for all gradostat models without
competition. The special case, however, is similar to a chemostat model, the analytic
solutions of which can be easily found: consider the case that two reservoirs have
different water levels, a system which has no water exchange between each other
$(E = 0)$, but there is a net flow from the first vessel to the second vessel as seen in
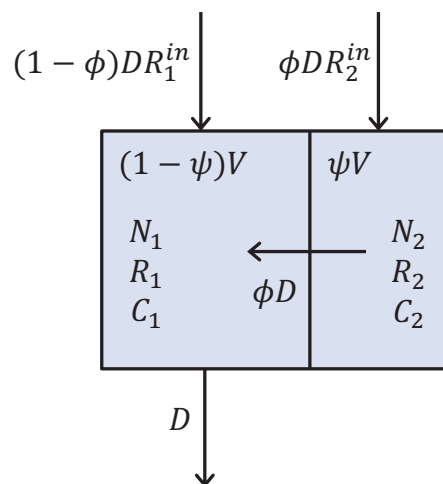Fig. 5.1.

Figure 5.1. Gradostat diagram of the special case.

5.2 The Model

There is no outflow from the first vessel to the second vessel, no exchange flow in the system, hence $E = 0$. The model is as the following form:

$$\frac{dN_1}{dt} = (\mu(R_1) - m)N_1 - \frac{D}{1-\psi}N_1 + \frac{\phi D}{1-\psi}N_2;$$

$$\frac{dN_2}{dt} = (\mu(R_2) - m)N_2 - \frac{\phi D}{\psi}N_2;$$

$$\frac{dR_1}{dt} = \frac{(1-\phi)D}{1-\psi}R_1^{in} - (\mu(R_1) - m)N_1 q_N - \frac{D}{1-\psi}R_1 + \frac{\phi D}{1-\psi}R_2;$$

$$\frac{dR_2}{dt} = \frac{\phi D}{\psi}R_2^{in} - (\mu(R_2) - N_2 q_N - \frac{\phi D}{\psi}N_2;$$

$$\frac{dC_1}{dt} = \varepsilon f_i(R_1)N_1\frac{q_N}{q_C} - \frac{D}{1-\psi}C_1 - kC_1 + \frac{\phi D}{1-\psi}C_2;$$

$$\frac{dC_2}{dt} = \varepsilon f_i(R_2)N_2\frac{q_N}{q_C} - \frac{\phi D}{\psi}C_2 - kC_2;$$

where, $i = 1, 2, 3$.

5.2.1 Dimensionless System

Apply the same strategy in the previous case to obtain the dimensionless system as following :

$$\frac{dN_1}{dt} = (\mu(R_1) - m)N_1 - \frac{1}{1 - \psi}N_1 + \frac{\phi}{R(1 - \psi)}N_2,$$

$$\frac{dN_2}{dt} = (\mu(R_2) - m)N_2 - \frac{\phi}{\psi}N_2,$$

$$\frac{dR_1}{dt} = \frac{1 - \phi}{1 - \psi} - (\mu(R_1) - N_1 - \frac{1}{1 - \psi}R_1 + \frac{\phi}{R(1 - \psi)}R_2,$$

$$\frac{dR_2}{dt} = \frac{\phi}{\psi} - (\mu(R_2) - m)N_2 - \frac{\phi}{\psi}N_2,$$

$$(5.1)$$

$$\frac{dC_1}{dt} = \varepsilon f_i(R_1)N_1 - \frac{1}{1 - \psi}C_1 - kC_1 + \frac{\phi}{R(1 - \psi)}C_2,$$

$$\frac{dC_2}{dt} = \varepsilon f_i(R_2)N_2 - \frac{\phi}{\psi}C_2 - kC_2.$$

5.2.2 Dissipatedness of the Dimensionless System

The following is a proof of dissipatedness [17], i.e. for each system all the solutions lie in a bounded set [11]. All the three systems have the same first four equations which are all independent of parameters C_1 and C_2.
Setting:

$$\Sigma_1 = N_1 + R_1,$$

$$\Sigma_2 = N_2 + R_2.$$

By simply adding the first and third equations and adding the second and fourth equations in System (5.1), the following ODE system is established:

$$\Sigma_1' = \frac{1-\phi}{1-\psi} - \frac{1}{1-\psi}\Sigma_1 + \frac{\phi}{R(1-\psi)}\Sigma_2;$$

(5.2)

$$\Sigma_2' = \frac{\phi}{\psi} - \frac{\phi}{\psi}\Sigma_2$$

as $t \to \infty$, for the equilibrium of this system:

$$\Sigma_1' = \Sigma_2' = 0.$$

Solving the ODE System (5.2) we obtain;

$$\Sigma_1^* = 1 + \phi - \frac{\phi}{R} = A \quad \text{and} \quad \Sigma_2^* = 1$$

The Jacobian matrix of (5.2) is:

$$\begin{pmatrix} -\dfrac{1}{1-\psi} & \dfrac{\phi}{R(1-\psi)} \\ 0 & -\dfrac{\phi}{\psi} \end{pmatrix}$$

λ_1 and λ_2 are the eigenvalues of the matrix, and

$$\lambda_1 = -\frac{1}{1-\psi} < 0;$$

$$\lambda_2 = -\frac{\phi}{\psi} < 0;$$

Therefore, System (5.1) is dissipative and all solutions lies in the bounded set:

$$\Omega_a = \{(N_1, N_2, R_1, R_2) | N_1 + R_1 \le A, N_2 + R_2 \le 1\}.$$

Hence System (5.1) can be reduced to the following form:

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$$\frac{dN_1}{dt} = (\mu(A - N_1) - m)N_1 - \frac{1}{1 - \psi}N_1 + \frac{\phi}{R(1 - \psi)}N_2,$$

$$\frac{dN_2}{dt} = (\mu(1 - N_2) - m)N_2 - \frac{\phi}{\psi}N_2,$$

(5.3)

$$\frac{dC_1}{dt} = \varepsilon f_i(A - N_1)N_1 - \frac{1}{1 - \psi}C_1 - kC_1 + \frac{\phi}{R(1 - \psi)}C_2,$$

$$\frac{dC_2}{dt} = \varepsilon f_i(1 - N_2)N_2 - \frac{\phi}{\psi}C_2 - kC_2.$$

5.2.3 Equilibria and Stability Analysis

The analysis of equilibria of the system is discussed here. There are three equilibria for System (5.3): $E_0 = (0, 0, 0, 0)$, and the interior equilibrium $E^* = (N_1^*, N_2^*, C_1^*, C_2^*)$, where $N_2^* = 1 - \mu^{-1}(m + \frac{\phi}{\psi}) > 0$, and $E_1 = (\tilde{N}_1^*, 0, \tilde{C}_1^*, 0)$, where $\tilde{N}_1^* = A - \mu^{-1}(m + \frac{1}{1 - \psi}) > 0$. To investigate the existence of equilibria for System (5.3), we consider the following four cases:

(a) The trivial equilibrium $E_0 = (0, 0, 0, 0)$ always exists, and the Jacobian matrix for it is

The cylindrospermopsin case:

$$J_0 = \begin{pmatrix} \mu(A) - \gamma_1 - m & 0 & 0 & 0 \\ \gamma_4 & \mu(1) - \gamma_2 - m & 0 & 0 \\ \varepsilon f_i(A) & 0 & -\gamma_1 - k & 0 \\ 0 & \varepsilon f_i(1) & \gamma_4 & -\gamma_2 - k \end{pmatrix}$$

where $i = 1, 2, 3$, and

$$\alpha_1 = \mu(A - N_1^*), \qquad \alpha_2 = \mu(1 - N_2^*),$$

$$\beta_1 = -N_1^* \frac{d\mu}{dN_1^*}, \qquad \beta_2 = -N_2^* \frac{d\mu}{dN_2^*},$$

$$\tilde{\beta}_1 = -\tilde{N}_1^* \frac{d\mu}{d\tilde{N}_1^*}, \qquad \gamma_1 = \frac{1}{1 - \psi},$$

$$\gamma_2 = \frac{\phi}{\psi}, \qquad \gamma_4 = \frac{\phi}{R(1 - \psi)}.$$

Obviously, E_0 is stable if and only if both the following are established:

$$\mu(A) < m + \frac{1}{1 - \psi} \quad \text{qnd} \quad \mu(1) < m + \frac{\phi}{\psi}.$$

Equivalently,

$$A - \mu^{-1}\left(m + \frac{1}{1 - \psi}\right) < 0,$$

(5.4)

$$1 - \mu^{-1}\left(m + \frac{\phi}{\psi}\right) < 0.$$

Therefore, no interior equilibrium and no boundary equilibrium other than E_0 exists, E_0 is the only equilibrium in the system, hence it is globally stable.

(b) If both two inequalities of (5.4) are violated, both E^* and E_1 exist. The Jacobian matrix for E^* is

$$J^* = \begin{pmatrix} \alpha_1 - \gamma_1 - \beta_1 - m & 0 & 0 & 0 \\ \gamma_4 & -\beta_2 & 0 & 0 \\ \varepsilon f_i(A - N_1^*) & 0 & -\gamma_1 - k & 0 \\ 0 & \varepsilon f_i(1 - N_2^*) & \gamma_4 & -\gamma_2 - k \end{pmatrix}.$$

According to the first equation of System (5.3), $\alpha_1 - \gamma_1 - m < 0$ (Since $N_1^* < 0$ is impossible, proof is in Appendix), then $\alpha_1 - \gamma_1 - \beta_1 - m < 0$ (β_1 and β_2 are positive), the eigenvalues of J^* are always real and negative, therefore, E^* is stable whenever it exists.

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The Jacobian matrix for E_1 is

$$
J_1 = \begin{pmatrix}
-\tilde{\beta}_1 & 0 & 0 & 0 \\
\gamma_4 & \mu(1) - \gamma_2 - m & 0 & 0 \\
\varepsilon f_i(A - \tilde{N}_1^*) & 0 & -\gamma_1 - k & 0 \\
0 & \varepsilon f_i(1) & \gamma_4 & -\gamma_2 - k
\end{pmatrix}.
$$

Since both two inequalities of (5.4) are violated, $\mu(1) > m + \dfrac{\phi}{\psi}$, J_1 has a positive eigenvalue, hence E_1 is unstable, and the one dimensional stable manifold of E_1 lies in the exterior of Ω_a, hence E^* is globally stable. There are three equilibria exist in this case, one of them is stable and globally stable.

(c) If only the first inequality of (5.4) is violated, there is no interior equilibrium but E_1 exists. Since the second inequality of (5.4) is true, $\mu(1) < m + \dfrac{\phi}{\psi}$, all the eigenvalues of J_1 are real and negative, hence E_1 is stable and he one dimensional stable manifold of E_0 lies in the exterior of Ω_a, hence E_1 is globally There are two equilibria exist in this case, one of them is stable and globally stable.

(d) If only the second inequality of (5.4) is violated, there is no boundary equilibrium other than E_0 exists. Since the first inequality of (5.4) is true, There is only one solution of N_1^* (proof in Appendix), hence the interior equilibrium is unique and all the eigenvalues of J^* are real and negative, E^* is stable and the one dimensional stable manifold of There are two equilibria exist in this case, one of them is stable and globally stable.

CHAPTER 6

DISCUSSION AND CONCLUSIONS

We have now analyzed the models of allelopathy producing toxins in an idealized gradostat environment. The existence conditions and results for steady-states of the equilibriums in each case are summarized at the end of each section, which have the implications for ecological outcomes of both extinction and persistence.

All the models, including the general cases and the modified cases, show that an unbalanced situation does not exist. Namely, the extinction or persistence in one vessel implies the same result in the other one. Biologically, this means in a flowing water system with a main lake and a single cove, the exchange flow between them is continuously and eternally carrying population from one vessel to another to keep the consistency of the system. Also, conditions for global stability and ecological persistence are found for all versions of the model. The similarity of the conditions in all cases suggests that mode of toxin production, as far as it was explored here, does not affect this property of the model (This conclusion makes rigorous the suggestions in my earlier paper that were based on numerical simulations). The models are analyzed based on the assumption that they are in an empty habitat. Hence biologically, this means that the population of the algae is not affected by their own toxic productions as far as explored here.

For local stability, Theorem 2 in the general cases and Theorem 9 for the modified cases address the trivial equilibrium with the absence of algae population in both vessels, which is stable when we have the satisfaction of both inequalities. The violation of either of the two inequalities would imply the instability of the trivial

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equilibrium, and suggests the existence of an interior equilibrium, as discussed in Theorem 3 and Theorem 10. Violation of the first inequality suggests that the trivial equilibrium is unstable with negative growth-loss balances in both vessels [4]; namely, the growth rate of the algae population is smaller than the sum of wash out rate and mortality rate in at least one vessel. In another word, if the aggregated (or average) balance of local population growth rate over local loss rates is positive there will be persistence. Violation of the second inequality suggests that only with negative growth-loss balance is not enough for the local stability of the trivial equilibrium, the growth rate needs to be sufficiently small in both vessels to have extinction of the population, as summarized in Theorem 8.

Recalling the condition for persistence in a simple chemostat [11], a negative growth-loss balance is able to generate the persistence of the system. However, this paper proves that the increase of the order of the system would enhances algal and toxin persistence [9], i.e. if the cove has lower flow (a common situation), then it has a longer residence time and acts as a storage zone which provides increases probability of population persistence. [9].

Theorem 8 shows that other things being equal, equilibrium populations are larger in the original model. This result follows from the partitioning of nutrient between dissolved nutrient, populations, and toxin, combined with the conservation of nutrient mass. At equilibrium, total nutrient mass in each compartment of the gradostat is constrained by the asymptotic conservation principle. The populations in either model have the same loss rates, and so their break even concentrations are the same. Therefore, the nutrient that partitions into the toxin can only be taken from the portion that partitions into populations, and so population concentrations at equilibrium are lower in modified model.

APPENDIX A

A BLOCK MATRIX THEOREM

In this appendix, we present a theorem about matrices with special structure in order to show that the eigenvalues of these matrices are the same as the ones of the blocks of the matrices.

Theorem 18. *Let J be a 4×4 matrix, and J has the form:*

$$J = \begin{pmatrix} A & 0 \\ C & B \end{pmatrix},$$

where

$$A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}_{2 \times 2}, B = \begin{pmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{pmatrix}_{2 \times 2}, C = \begin{pmatrix} c_{11} & c_{12} \\ c_{21} & c_{22} \end{pmatrix}_{2 \times 2},$$

then

$$det[J] = det[A]det[B]$$

Proof.

$$
\begin{aligned}
det[J] &= a_{11} \begin{vmatrix} a_{22} & 0 & 0 \\ c_{12} & b_{11} & b_{12} \\ c_{22} & b_{21} & b_{22} \end{vmatrix} - a_{12} \begin{vmatrix} a_{21} & 0 & 0 \\ c_{11} & b_{11} & b_{12} \\ c_{21} & b_{21} & b_{22} \end{vmatrix} \\
&= a_{11}a_{22}det[B] - a_{12}a_{21}det[B] = det[A]det[B]
\end{aligned}
$$

□

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BIOGRAPHICAL STATEMENT

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