Dynamical Modeling of Toxic and Non-toxic Phytoplankton Competition

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ABSTRACT

The study of the competitive outcome associated with two consumers of the same resource, algae, is investigated under asymmetric intraguild interactions and carrying capacities that are a function of resource (algae) availability at any time. The mathematical model is motivated by our understanding of the interactions of genus *Protoperidinium* (toxin producing) and *Heterocapsa* (non-toxic producing) phytoplankton while competing by the same resource (algae). Equilibrium stability and bifurcation analysis of a general theoretical model are carried out. Two competitive outcomes have been identified, win-win and win-lose. It is shown that the system will support coexistence (win-win) at a stable equilibrium. The win-lose situation is somewhat subtle since we have shown that initial conditions can affect the outcome.

1 Introduction

The global climate change and inceasing human exploration into the limited environment have lead to a substantial increasing of toxic phytoplankton blooms. As an unexpected result, shellfish poisoning cases have increasingly reported all around the world [1, 3]. To protect the health of human and maintain sustainable shellfish harvesters, it has become critical to monitor phytoplankton blooms and to seek an understanding of the life cycles phytoplankton blooms and related biological relationships that exist among these microorganisms. Since the discovery of this toxic trait of *Protoperidinium*, this particular phytoplankton has been of great interest to biologists, ecologists, chemists, and mathematicians. In the light of this fact, the spices of *Protoperidinium* have been studied extensively [1].

Mathematical models have been extensively used in ecology to study interacting populations. Special interesting has been focused on predator-prey. The establishment of early Lotka-Volterra model for predator-prey

interaction was one of the successful examples using dynamical models [12]. Following the Lotka-Volterra model, tremendous studies can also be found for consumer-resource interactions and parasite-host interactions.

Although these models have proved helpful in numerous studies, most relationships between species tend to contain vast complications. Trying to more articulately discuss the interactions of an ecosystem brought about the idea of a new type of model known as intraguild predation (IGP) [5]. Intraguild predation can be seen as one element of a very complex food web. A guild is defined as a collection of species that takes advantage of the same class of environmental resources in a similar way [6]. Intraguild predation models focus on competition and predator prey relations within these trophic levels. Not only do they consider two species sharing the same resource, they take into account that one of these species (IGpredator) can gain sustenance by eating the other (intermediate species or IGprey) [1, 5]. In some cases IGP occurs symmetrically, where two competing species both prey on each other as well as sharing some resources. This type of model is used frequently to determine the relationship between native and invasive species [2].

Polis et al. (1989) defined intraguild predation as predation occurring between members of the same "guild", or community of species that exploit the same resources [2, 8]. The authors classified IGP into four main types, depending on the direction of predation (symmetric or asymmetric) and age structure of the population (important or relatively unimportant). Holt and Polis (1997) analyzed several models of asymmetric IGP, where the IGprey species depends on the available resources, and the IGpredator species depends on both IGprey and resource [5].

Following the idea of intraguild interactions for predator and prey, we here study the dynamical interactions between consumers and their environmental nutrition (or resource of energy). The predator-prey and the consumer-resource process have different time scales. The Predator-prey process occurs in a fast time scale, so that the killing rate has an immediate benefit to the predators. The consumer-resource process, however, happens in a rather slow time. As a result, the consumption of the resource would benefit the whole consumer population, thus increasing its carrying capacity.

This paper is organized as follows. In Section 2, we develop a mathematical model for the case where two consumers competes the same resource. The detailed analysis to the model and relevance to the biology and ecology are carried out in Section 3. Simulation results are given in Section 4. Our concluding remarks and discussion can be found in Section 5.

2   Model Description

The mathematical model are motivated by our understanding of the interactions of genus *Protoperidinium* (toxin producing) and *Heterocapsa* (non-toxic producing) phytoplankton while competing for the same resources (algae).
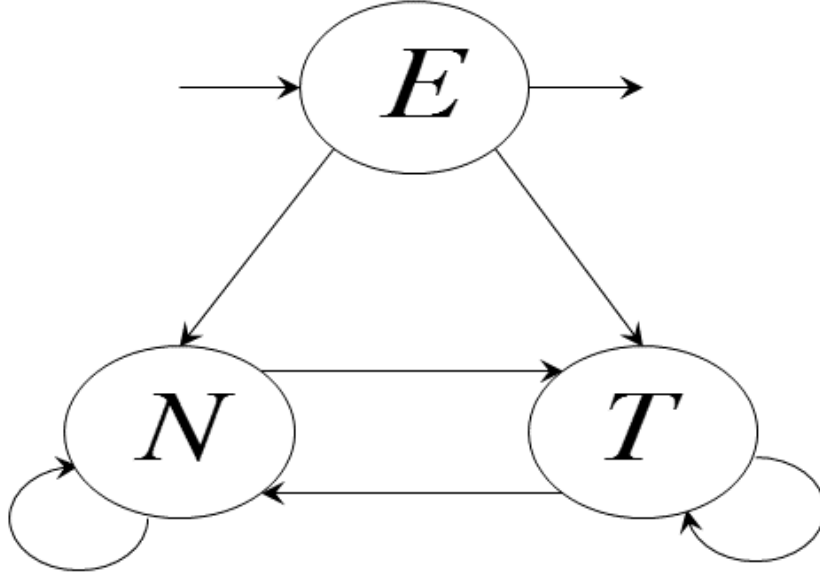
Our proposed model describes the dynamics of the populations of two intermediate consumer species, toxic phytoplankton (T) and non-toxic phytoplankton (N), as well as a shared resource (environmental nutrients (E)).

The model equations are given by:

$$E' = \lambda - \mu E - \beta_1 NE - \beta_2 TE, \tag{1}$$

$$N' = \gamma_N N(1 - \frac{N}{k_N E}) - \alpha_1 NT, \tag{2}$$

$$T' = \gamma_T T(1 - \frac{T}{k_T E}) - \alpha_2 NT. \tag{3}$$

The consumers densities are N and T and E, are the biomass of the resources. The parameter λ represents the renew rate of the resources; μ, the natural death rate; and $\beta_i, (i = 1, 2)$ the per-capita consumption rate. We use parameter α_i to express the competition rates(the rate attacking each other, irrelevant to the resource). The parameters γ_T and γ_N represents the intrinsic growth rate . Finally and most importantly, since

consumer-resource reaction undergoes in a slow time scale and considering an assumption motivated by Leslie's 1948 work [11], we propose that consumption of resources will contribute to change in the carrying capacity of consumers. Therefore, carrying capacity, $k_i E(i = T, N)$, of consumers is the proportional consumption rate. We sumarize our state variables and model parameters in Table 1.

Table 1: Parameters and descriptions.

Parameters	Description
λ	renew rate of resources
μ	natural death rate
β_1	per-capita consumption rate of N
β_2	per-capita consumption rate of T
α_1	competition rate of T on N
α_2	competition rate of N on T
γ_N	intrinsic growth rate of N
γ_T	intrinsic growth rate of T
$k_N E$	carrying capacity of N which is proportional to consumption rate of N
$k_T E$	carrying capacity of T which is proportional to consumption rate of T

Before we analyze the model, we first study a feasible biological region for the model, as can be seen in the following theorem.

Theorem 1. *Domain*

$$\Omega = \left\{ (E, N, T) | 0 \le E \le \frac{\lambda}{\mu}, 0 \le N \le k_N \frac{\lambda}{\mu}, 0 \le T \le k_T \frac{\lambda}{\mu} \right\}$$

is positively invariant for model (1-3).

Proof. From equation (1), we get

$$E' \le \lambda - \mu E.$$

Rearranging and multiplying by the integral factor gives

$$E' e^{t\mu} + \mu e^{t\mu} E \le \lambda e^{t\mu},$$

Now, integral from 0 to t gives

$$\int_0^t (Ee^{t\mu})'dt \leq \int_0^t \lambda e^{t\mu}dt.$$

which is equivalent to

$$Ee^{t\mu} - E_0 \leq \frac{\lambda}{\mu}(e^{t\mu} - 1)$$

$$Ee^{t\mu} \leq (E_0 - \frac{\lambda}{\mu}) + \frac{\lambda}{\mu}e^{t\mu}.$$

That is,

$$E(t) \leq \frac{\lambda}{\mu} + (E_0 - \frac{\lambda}{\mu})e^{-t\mu},$$

because $E_0 \leq \frac{\lambda}{\mu}$, $E \leq \frac{\lambda}{\mu}$ holds for all $t > 0$.

Next, from equation (2), we get

$$N' \leq \gamma_N N(1 - \frac{N}{k_N E}) \leq \gamma_N N(1 - \frac{N}{k_N E_\infty}), \quad \text{where } E_\infty = \frac{\lambda}{\mu}.$$

It follows from the comparison principle that $N \leq k_N E_\infty$ for all $t > 0$.

A similar argument leads to $T \leq k_T E_\infty$ for all $t > 0$. □

Theorem 2. *Resource is always persistent.*

Proof. let $\widetilde{N} = k_N \frac{\lambda}{\mu}, \widetilde{T} = k_T \frac{\lambda}{\mu}$. according to (1), we can get

$$E' \geq \lambda - \mu E - \beta_1 E\widetilde{N} - \beta_2 E\widetilde{T},$$

Rearranging and multiplying by the integral factor gives

$$E'e^{(\lambda+\beta_1\widetilde{N}+\beta_2\widetilde{T})t} + E(\lambda + \beta_1\widetilde{N} + \beta_2\widetilde{T})e^{(\lambda+\beta_1\widetilde{N}+\beta_2\widetilde{T})t} \geq \lambda e^{(\lambda+\beta_1\widetilde{N}+\beta_2\widetilde{T})t},$$

which is equivalent to

$$\int_0^t E'e^{(\lambda+\beta_1\widetilde{N}+\beta_2\widetilde{T})t}dt \geq \int_0^t \lambda e^{(\lambda+\beta_1\widetilde{N}+\beta_2\widetilde{T})t}dt,$$

now, integral from 0 to t gives

$$Ee^{(\lambda+\beta_1\widetilde{N}+\beta_2\widetilde{T})t} - E_0 \geq \frac{\lambda e^{(\lambda+\beta_1\widetilde{N}+\beta_2\widetilde{T})t} - \lambda}{\lambda + \beta_1\widetilde{N} + \beta_2\widetilde{T}},$$

we obtain that

$$E \geq (E_0 - \frac{\lambda}{\lambda + \beta_1\widetilde{N} + \beta_2\widetilde{T}})e^{-(\lambda+\beta_1\widetilde{N}+\beta_2\widetilde{T})t} + \frac{\lambda}{\lambda + \beta_1\widetilde{N} + \beta_2\widetilde{T}}.$$

when $t \gg T$, we obtain

$$E(t) \geq \frac{\lambda}{\lambda + \beta_1 \widetilde{N} + \beta_2 \widetilde{T}} - \varepsilon = \frac{\lambda}{2(\lambda + \beta_1 \widetilde{N} + \beta_2 \widetilde{T})}.$$

when $0 < t < T$, the right of the inequality is a increasing function, so $E \geq E_0$.

For all t, $E \geq \min\left\{\frac{\lambda}{2(\lambda + \beta_1 \widetilde{N} + \beta_2 \widetilde{T})}, E_0\right\}$, so, E have lower bound.

$\square$

3 Model Analysis

3.1 Rescale

Letting $E = \frac{\lambda}{\mu}x, N = \frac{\mu}{\beta_1}y, T = \frac{\mu}{\beta_2}z$, and $t = \frac{\tau}{\mu}$ in system (1-3), we obtain the resulting dimensionless system,

$$\frac{dx}{d\tau} = 1 - x - xy - xz,$$

$$\frac{dy}{d\tau} = \frac{\gamma_N}{\mu}y\left(1 - \frac{\mu^2}{k_N\beta_1\lambda}\frac{y}{x}\right) - \frac{\alpha_1}{\beta_2}yz$$

$$\frac{dz}{d\tau} = \frac{\gamma_T}{\mu}z\left(1 - \frac{\mu^2}{k_T\beta_2\lambda}\frac{z}{x}\right) - \frac{\alpha_2}{\beta_1}yz.$$

Using the following the shorthand notation,
$A_1 = \frac{\gamma_N}{\mu}$, $A_2 = \frac{\mu^2}{k_N\beta_1\lambda}$, $A_3 = \frac{\alpha_1}{\beta_2}$, $A_4 = \frac{\gamma_T}{\mu}$, $A_5 = \frac{\mu^2}{k_T\beta_2\lambda}$ and $A_6 = \frac{\alpha_2}{\beta_1}$,
leads to further simplification of our oringinal model into:

$$\frac{dx}{d\tau} = 1 - x - xy - xz, \tag{4}$$

$$\frac{dy}{d\tau} = A_1 y\left(1 - A_2\frac{y}{x}\right) - A_3 yz, \tag{5}$$

$$\frac{dz}{d\tau} = A_4 z\left(1 - A_5\frac{z}{x}\right) - A_6 yz. \tag{6}$$

We will carry our analysis on model (4-6).

3.2 Boundary Equilibria

The system (4-6) has three boundary equilibria, denoted by E_i for $i = 0, 1, 2$:

1. Phytoplankton Free Equilibrium: $E_0 = (1, 0, 0)$,

2. Toxic Phytoplankton Free Equilibrium: $E_1 = \left(\frac{2A_2}{A_2 + \sqrt{A_2^2 + 4A_2}}, \frac{-A_2 + \sqrt{A_2^2 + 4A_2}}{2A_2}, 0\right)$,

3. Non-Toxic Phytoplankton Free Equilibrium: $E_2 = \left(\frac{2A_5}{A_5 + \sqrt{A_5^2 + 4A_5}}, 0, \frac{-A_5 + \sqrt{A_5^2 + 4A_5}}{2A_5} \right)$,

In order to analyze the local stability of the equilibria, we compute the Jacobian of the system (4-6), which is

$$
J(x,y,z) = \begin{pmatrix} -1 - y - z & -x & -x \\ A_1 A_2 \frac{y^2}{x^2} & A_1 - \frac{2A_1 A_2 y}{x} - A_3 z & -A_3 y \\ A_4 A_5 \frac{z^2}{x^2} & -A_6 z & A_4 - \frac{2A_4 A_5 z}{x} - A_6 y \end{pmatrix}.
$$

3.3 Phytoplankton Free Equilibrium

The Jacobian of system (4-6) about E_0 is

$$
J(E_0) = \begin{pmatrix} -1 & -1 & -1 \\ 0 & A_1 & 0 \\ 0 & 0 & A_4 \end{pmatrix}.
$$

Since this matrix has positive eigenvalues A_1 and A_4, equilibrium $E_0 = (1, 0, 0)$ is always unstable.

This just means that if resource is available, it is impossible for both consumers go to extinction.

3.4 Toxic Phytoplankton Free Equilibrium

Theorem 3. *If* $\beta_1 < \frac{k_N \lambda \alpha_2^2 - \mu \alpha_2 \gamma_T}{\gamma_T^2}$ *and* $\gamma_T < \frac{\lambda}{\mu} k_N \alpha_2$, *then* E_1 *is locally asymptotically stable.*

Proof. The Jacobian of system (4-6) about E_1 is

$$
J(E_1) = \begin{pmatrix} -1 - y_1^* & -x_1^* & -x_1^* \\ A_1 A_2 \frac{y_1^{*2}}{x_1^{*2}} & -A_1 & -A_3 y_1^* \\ 0 & 0 & A_4 - A_6 y_1^* \end{pmatrix}.
$$

Obviously, $J(E_1)$ has an eigenvalue $A_4 - A_6 y_1^*$. Local stability of this equilibrium depends on the eigenvalue $A_4 - A_6 y_1^*$ and eigenvalues of matrix B_1, where,

$$
B_1 = \begin{pmatrix} -1 - y_1^* & -x_1^* \\ A_1 A_2 \frac{y_1^{*2}}{x_1^{*2}} & -A_1 \end{pmatrix}.
$$

So, this equilibrium is locally stable if and only if $A_4 - A_6 y_1^* < 0$, $|B_1| > 0$ and $tr(B_1) < 0$, where

$$
|B_1| = (-1 - y_1^*)(-A_1) + A_1 A_2 \frac{y_1^{*2}}{x_1^*} > 0, \text{ and}
$$

$$
tr(B_1) = (-1 - y_1^*) + (-A_1) < 0.
$$

$A_4 - A_6 y_1^* < 0$ implies $\frac{2A_2 A_4}{A_6} + A_2 < \sqrt{A_2^2 + 4A_2}$. To understand the biological meaning, we rewrite the inequality in terms of the original parameters, to get $\beta_1 < \frac{k_N \lambda \alpha_2^2 - \mu \alpha_2 \gamma_T}{\gamma_T^2}$ and $\gamma_T < \frac{\lambda}{\mu} k_N \alpha_2$. $\qquad\square$

Biologically, since the intrinsic growth rate of consumer T is less than the attacking rate by its competitor, population T eventually dies out.

3.5   Non-Toxic Phytoplankton Free Equilibrium

Analogously to the interpretation in Section 3.3. Biologically, since the intrinsic growth rate of consumer N is less than the attacking rate by its competitor, population N eventually dies out.

Theorem 4. *If* $\beta_2 < \frac{k_T \lambda \alpha_1^2 - \mu \alpha_1 \gamma_N}{\gamma_N^2}$ *and* $\gamma_N < \frac{\lambda}{\mu} k_T \alpha_1$, *then* E_2 *is locally asymptotically stable.*

Proof. The Jacobian at E_2 is given by

$$J(E_2) = \begin{pmatrix} -1 - z_1^* & -x_1^* & -x_1^* \\ 0 & A_1 - A_3 z_1^* & 0 \\ A_4 A_5 \frac{z_1^{*2}}{x_1^{*2}} & -A_6 z_1^* & -A_4 \end{pmatrix}.$$

Obviously, $J(E_2)$ has an eigenvalue $A_1 - A_3 z_1^*$. Stability of this equilibrium depends on the eigenvalue $A_1 - A_3 z_1^*$ and eigenvalues of matrix B_2, where

$$B_2 = \begin{pmatrix} -1 - z_1^* & -x_1^* \\ A_4 A_5 \frac{z_1^{*2}}{x_1^{*2}} & -A_4 \end{pmatrix},$$

So, this equilibrium is locally asymptotically stable if and only if $A_1 - A_3 z_1^* < 0$, $|B_2| > 0$ and $tr(B_2) < 0$, where

$$|B_2| = (-1 - z_1^*)(-A_4) + A_4 A_5 \frac{z_1^{*2}}{x_1^*} > 0, \text{ and}$$

$$tr(B_2) = (-1 - z_1^*) + (-A_4) < 0.$$

It is not hard to deserve that $A_1 - A_3 z_1^* < 0$ implies $\frac{2A_1 A_5}{A_3} + A_5 < \sqrt{A_5^2 + 4A_5}$. In order to understand the biological meaning, we rewrite the above inequality in terms of the original parameters, to get
$\beta_2 < \frac{k_T \lambda \alpha_1^2 - \mu \alpha_1 \gamma_N}{\gamma_N^2}$ and $\gamma_N < \frac{\lambda}{\mu} k_T \alpha_1$. $\qquad\square$

3.6 A Special Case: $\alpha_1 = \alpha_2 = 0$.

If we ignore attacking between N and T, when $\alpha_1 = \alpha_2 = 0$, the system (1-3) becomes

$$E' = \lambda - \mu E - \beta_1 N E - \beta_2 T E, \tag{7}$$

$$N' = \gamma_N N \left(1 - \frac{N}{k_N E}\right), \tag{8}$$

$$T' = \gamma_T T \left(1 - \frac{T}{k_T E}\right). \tag{9}$$

Rewriting the system in dimensionless form, give

$$\frac{dx}{d\tau} = 1 - x - xy - xz, \tag{10}$$

$$\frac{dy}{d\tau} = A_1 y \left(1 - A_2 \frac{y}{x}\right), \tag{11}$$

$$\frac{dz}{d\tau} = A_4 z \left(1 - A_5 \frac{z}{x}\right). \tag{12}$$

The system has four equilibria, which are given by
$E_0^* = (1, 0, 0)$,
$E_1^* = \left(\frac{2A_2}{A_2 + \sqrt{A_2^2 + 4A_2}}, \frac{-A_2 + \sqrt{A_2^2 + 4A_2}}{2A_2}, 0\right)$,
$E_2^* = \left(\frac{2A_5}{A_5 + \sqrt{A_5^2 + 4A_5}}, 0, \frac{-A_5 + \sqrt{A_5^2 + 4A_5}}{2A_5}\right)$,
$E_3^* = (x^*, y^*, z^*)$, with $x^* = \frac{-A_2 A_5 + \sqrt{A_2^2 A_5^2 + 4A_2 A_5(A_2 + A_5)}}{2(A_2 + A_5)}, y^* = \frac{-A_2 A_5 + \sqrt{A_2^2 A_5^2 + 4A_2 A_5(A_2 + A_5)}}{2A_2(A_2 + A_5)}$
and $z^* = \frac{-A_2 A_5 + \sqrt{A_2^2 A_5^2 + 4A_2 A_5(A_2 + A_5)}}{2A_5(A_2 + A_5)}$.

The Jacobian of system (10-12) is given by

$$J^*(x, y, z) = \begin{pmatrix} -1 - y - z & -x & -x \\ A_1 A_2 \frac{y^2}{x^2} & A_1 - \frac{2A_1 A_2 y}{x} - A_3 z & 0 \\ A_4 A_5 \frac{z^2}{x^2} & 0 & A_4 - \frac{2A_4 A_5 z}{x} - A_6 y \end{pmatrix},$$

and specifically

$$J^*(E_0^*) = \begin{pmatrix} -1 & -1 & -1 \\ 0 & A_1 & 0 \\ 0 & 0 & A_4 \end{pmatrix},$$

$$J^*(E_1^*) = \begin{pmatrix} -1 - y^* & -x^* & -x^* \\ A_1 A_2 \frac{y^{*2}}{x^{*2}} & -A_1 & 0 \\ 0 & 0 & A_4 \end{pmatrix},$$

$$J^*(E_2^*) = \begin{pmatrix} -1 - z^* & -x^* & -x^* \\ 0 & A_1 & 0 \\ A_4 A_5 \frac{z^{*2}}{x^{*2}} & 0 & -A_4 \end{pmatrix},$$

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and

$$J^*(E_3^*) = \begin{pmatrix} -1 - y^* - z^* & -x^* & -x^* \\ A_1 A_2 \frac{y^2}{x^2} & -A_1 & 0 \\ A_4 A_5 \frac{z^{*2}}{x^{*2}} & 0 & -A_4 \end{pmatrix},$$

where $x^* = A_2 y^*, x^* = A_5 z^*$.

Obviously, E_0, E_1 and E_2 are unstable.

Biologically, neither consumers can go to extinction. The next theorem describe the long term behavior of the system.

Theorem 5. E_3^* *is always locally asymptotically stable.*

Proof. The stability of E_3^* can be determined by using the Routh-Hurwitz criterion, this requires $\omega_1, \omega_2, \omega_3, \omega_2 \omega_3 - \omega_1 > 0$, where the quantities are defined as

$$
\begin{aligned}
\omega_1 &= -det(J^*(E_3^*)) \\
&= -[(-1 - y^* - z^*)(-A_1)(-A_4) + x^*(-A_1)\frac{A_4}{A_5} + x^*\frac{A_1}{A_2}(-A_4)] \\
&= (1 + y^* + z^*)A_1 A_4 + A_1 A_4 z^* + A_1 A_4 y^* > 0, \\
\omega_2 &= -[(-1 - y^* - z^*) + (-A_1) + (-A_4)] \\
&= 1 + y^* + z^* + A_1 + A_4 > 0, \\
\omega_3 &= M_{11} + M_{22} + M_{33} \\
&= A_1(1 + y^* + z^*) + A_1 y^* + A_4(1 + y^* + z^*) + A_4 z^* + A_1 A_4 > 0 \\
\omega_2 \omega_3 &= (1 + y^* + z^* + A_1 + A_4)[A_1(1 + y^* + z^*) + A_1 y^* + A_4(1 + y^* + z^*) + A_4 z^* + A_1 A_4] \\
&= (A_1 + A_4)(1 + y^* + z^*)^2 + (A_1 y^* + A_4 z^*)(1 + y^* + z^*) + A_1 A_4(1 + y^* + z^*) \\
&\quad + (A_1 + A_4)^2(1 + y^* + z^*) + (A_1 + A_4)(A_1 y^* + A_4 z^*) + A_1 A_4(A_1 + A_4) \\
&> (1 + y^* + z^*)A_1 A_4 + A_1 A_4 z^* + A_1 A_4 y^* = \omega_1,
\end{aligned}
$$

where M_{ii} is the (i, i) minor of matrix $J^*(E_3^*)$.

So, E_3^* is locally asymptotically stable. □

Biologically, N and T consume the same resource, but do not attack each other. So, co-existence is the only option.

4   Schematic Interpretation in Parameter Space

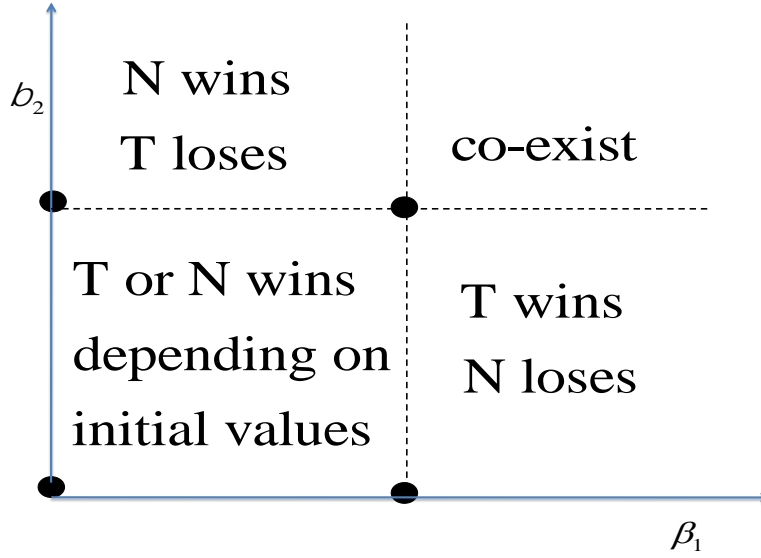Theorem 3 and Theorem 4 can be schematically presented in Figure 1:

Figure 1:

(1) When $0 < \beta_1 < \frac{k_N \lambda \alpha_2^2 - \mu \alpha_2 \gamma_T}{\gamma_T^2}, \beta_2 > \frac{k_T \lambda \alpha_1^2 - \mu \alpha_1 \gamma_N}{\gamma_N^2}$, N Wins, T Loses.

(2) When $\beta_1 > \frac{k_N \lambda \alpha_2^2 - \mu \alpha_2 \gamma_T}{\gamma_T^2}, 0 < \beta_2 < \frac{k_T \lambda \alpha_1^2 - \mu \alpha_1 \gamma_N}{\gamma_N^2}$, T Wins, N Loses.

(3) When $0 < \beta_1 < \frac{k_N \lambda \alpha_2^2 - \mu \alpha_2 \gamma_T}{\gamma_T^2}, 0 < \beta_2 < \frac{k_T \lambda \alpha_1^2 - \mu \alpha_1 \gamma_N}{\gamma_N^2}$, N or T can win, depending on initial conditions (see Figure 2).

(4) When $\beta_1 > \frac{k_N \lambda \alpha_2^2 - \mu \alpha_2 \gamma_T}{\gamma_T^2}, \beta_2 > \frac{k_T \lambda \alpha_1^2 - \mu \alpha_1 \gamma_N}{\gamma_N^2}$, N and T can Co-exist.

From Figure 1, when $0 < \beta_1 < \frac{k_N \lambda \alpha_2^2 - \mu \alpha_2 \gamma_T}{\gamma_T^2}, 0 < \beta_2 < \frac{k_T \lambda \alpha_1^2 - \mu \alpha_1 \gamma_N}{\gamma_N^2}$, N or T can win, depending on initial conditions. This is verified in Figure 2.
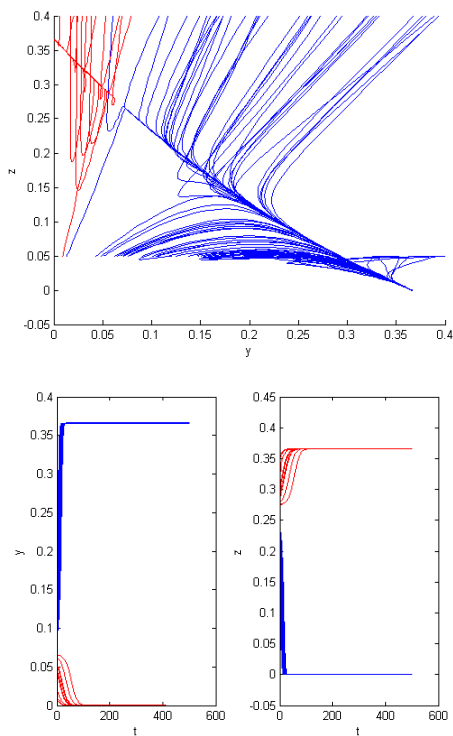
Figure 2: For the same parameter values $A_1 = 1.0, A_2 = 2.0, A_3 = 3.0, A_4 = 1.0, A_5 = 2.0, A_6 = 4.0$. The red lines approach to a stable point, and the blue lines approach to another stable point.

5 The Ratio of the Non-toxic Phytoplankton to the Total Phytoplankton

In the special case, The ratio of the non-toxic phytoplankton to the total phytoplankton is given by

$$\frac{k_N \beta_1}{k_N \beta_1 + k_T \beta_2}.$$

Next, we study the ratio of the non-toxic phytoplankton to the total phytoplankton in the general model.

12
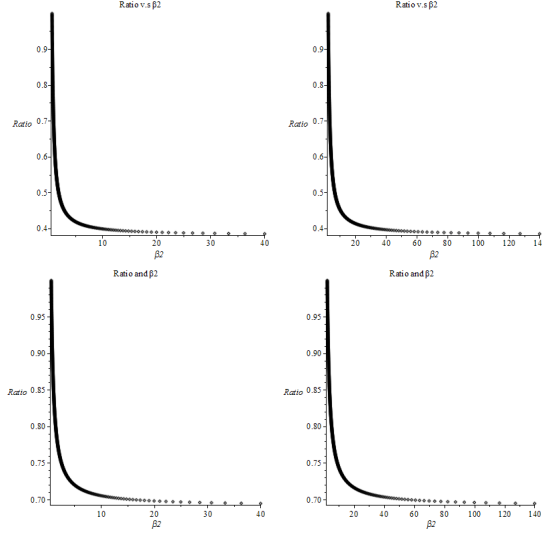
From every piture, we can see the ratio have related to β_2. The same lines, we change the α_1, but the ratio don't change, it proved that the impact of α_1 to the ratio is ignorable. In the same ranks, we change the β_1, we can clearly see the ratio's change, so, the consumption rates have a significant impact on the ratio of the non-toxic phytoplankton to the total phytoplankton.

6 Co-exist and Hopf Bifurcation

Theorem 6. *Co-exist equilibrium, $E_h = (x_h, y_h, z_h)$, exists if $4B_2^3 + B_2^2 + 18B_1B_2 + 4B_1 - 27B_1^2 > 0$, where $B_1 = \frac{A_1A_6 + A_3A_4 + A_3A_6}{A_1A_2A_4A_5}$ and $B_2 = \frac{A_1A_2A_4 + A_1A_4A_5 + A_3A_6}{A_1A_2A_4A_5}$.*

Proof. According to (4-6), we can get a single equation about x_h,

$$(A_1A_6 + A_3A_4 + A_3A_6)x_h^3 - (A_1A_2A_4 + A_1A_4A_5 + A_3A_6)x_h^2 - A_1A_2A_4A_5x_h + A_1A_2A_4A_5 = 0.$$

Let us rewrite this equation as follows

$$G(x) = B_1 x_h^3 - B_2 x_h^2 - x + 1 = 0. \tag{13}$$

We look for a saddle-node bifurcation. Here,

$$G'(x) = 3B_1 x_h^2 - 2B_2 x_h - 1 = 0. \tag{14}$$

From equations (13) and (14), we can get parametric equations associated with the saddle-node bifurcation, which are given by

$$B_1 = \frac{2 - x_h}{x_h^3} \text{ and } B_2 = \frac{3 - 2x_h}{x_h^2}.$$

13

Finally, by eliminating x in (13) and (14), we get an explicit equation for the saddle-node bifurcation,

$$B_1 \left(\frac{\sqrt{1+3B_2}-1}{B_2} \right)^3 + \frac{\sqrt{1+3B_2}-1}{B_2} - 2 = 0.$$

Therefore, there exist positive solutions to $G(x) = 0$, if

$$B_1 \left(\frac{\sqrt{1+3B_2}-1}{B_2} \right)^3 + \frac{\sqrt{1+3B_2}-1}{B_2} - 2 < 0.$$

This inequality can be rearranged as

$$4B_2^3 + B_2^2 + 18B_1 B_2 + 4B_1 - 27B_1^2 > 0. \tag{15}$$

That is, if (15) holds, there exists a positive equilibrium. $\square$

Furthermore, we can show condition for the existence of a Hopf bifurcation. We first present a Lemma from our previous work in [2].

Lemma 1. *If $B > 0$ and $C = AB$, then the polynomial $\lambda^3 + A\lambda^2 + B\lambda + C = 0$ has the root $-A$ and a pair of purely imaginary roots $\pm\sqrt{B}i$.*

Theorem 7. *Assume $E_h = (x_h, y_h, z_h)$ exists. where*

$$D_1 = \frac{A_1^2 A_2^2 A_4 A_5 y_h^2 z_h + A_1^2 A_2^2 y_h^2 + A_1 A_2 A_4^2 A_5^2 y_h z_h^2 + A_4^2 A_5^2 z_h^2 + 2A_1 A_2 A_4 A_5 y_h z_h + A_4 A_5 z_h}{x_h^3}$$

$$+ \frac{A_1 A_2 y_h}{x_h^3} + \frac{A_3 A_4 A_5 y_h z_h^2}{x_h} + \frac{A_1^2 A_2^2 y_h^3 + A_4^2 A_5^2 z_h^3 + A_4 A_5 z_h^2 + A_1 A_2 y_h^2}{x_h^2}$$

$$D_2 = \frac{A_1 A_2 y_h^2 z_h + A_1 A_2 A_3 y_h^2 z_h + A_3 A_4 A_5 y_h z_h^2}{x_h}.$$

Let $\varepsilon = D_1 - D_2 A_6$ be the bifurcation parameter. Then the system undergoes a hopf bifurcation around $\varepsilon = 0$.

Proof. The Jacobian of (4-6) evaluated at the equilibrium E_3 is given by

$$J(E_3) = \begin{pmatrix} -\frac{1}{x_h} & x_h & x_h \\ \frac{A_1 A_2 y_h^2}{x_h^2} & -\frac{A_1 A_2 y_h}{x_h} & A_3 y_h \\ A_4 A_5 \frac{z_h^2}{x_h^2} & -A_6 z_h & -\frac{A_4 A_5 z_h}{x_h} \end{pmatrix}.$$

The corresponding characteristic equation is

$$\lambda^3 + B_1 \lambda^2 + B_2 \lambda + B_3 = 0,$$

where $B_1 = \frac{A_1 A_2 y_h + A_4 A_5 z_h + 1}{x_h}$,
$B_2 = \frac{A_1 A_2 A_4 A_5 y_h z_h + A_4 A_5 z_h + A_1 A_2 y_h + A_4 A_5 x_h z_h^2 + A_1 A_2 x_h y_h^2 - A_3 A_6 x_h^2 y_h z_h}{x_h^2}$,

$B_3 = \frac{A_1A_2A_4A_5y_hz_h + A_1A_2A_4A_5x_hy_hz_h^2 + A_1A_2A_4A_5x_hy_h^2z_h - A_3A_4A_5x_h^2y_hz_h^2 - A_1A_2A_6x_h^2y_h^2z_h - A_3A_6x_h^2y_hz_h}{x_h^3}$.

Let $\varepsilon = B_1B_2 - B_3$. We can express A_6 in terms of ε,

$$A_6 = \frac{D_1 - \varepsilon}{D_2} = f(\varepsilon).$$

We choose ε as the bifurcation parameter. In the case of that $\varepsilon = 0$, from Lemma 1, the characteristic equation has one negative root $\lambda_1 = -B_1$ and a pair of purely imaginary roots $\lambda_{2,3} = \pm\sqrt{B_2}$.

If $\varepsilon \neq 0$, let the eigenvalues be denoted by $\lambda(\varepsilon) = a(\varepsilon) + b(\varepsilon)i$, with $a(0) = 0$ and $b(0) = \sqrt{B_2}$. For the appearance of a Hopf bifurcation, we need further to show that

$$\frac{da(\varepsilon)}{d\varepsilon}\Big|_{\varepsilon=0} = a'(0) \neq 0.$$

We implicitly differentiate the characteristic equation with respect to ε and
$3x_h^3\lambda^2\lambda' + 2(A_1A_2y_h + A_4A_5z_h + 1)x_h^2\lambda\lambda' + (A_1A_2A_4A_5x_hy_hz_h + A_4A_5x_hz_h + A_1A_2x_hy_h + A_4A_5x_h^2z_h^2 + A_1A_2x_h^2y_h^2)\lambda'A_3x_h^3y_hz_hf(\varepsilon)\lambda' - A_3x_h^3y_hz_hf'(\varepsilon)\lambda - (A_1A_2x_h^2y_h^2z_h + A_3x_h^2y_hz_h)f'(\varepsilon) = 0$, and evaluate it at $\varepsilon = 0, \lambda(0) = b(0)i, \lambda^2(0) = -b^2(0) = -B_2$. Since $\lambda'(0) = a'(0) + b'(0)i$, we have
$-2x_h^3b^2(0)a'(0) - 2x_h^3b^2(0)b'(0)i + 2B_1x_h^3a'(0)b(0)i - 2B_1x_h^3b(0)b'(0) - A_3x_h^3y_hz_hb(0)f'(0)i - (A_1A_2x_h^2y_h^2z_h + A_3x_h^2y_hz_h)f'(0) = 0$.

Setting the real part of the above equation to 0 and imaginary part equal to 0 yields the system

$$-2x_h^3b^2(0)a'(0) - 2B_1x_h^3b(0)b'(0) - (A_1A_2x_h^2y_h^2z_h + A_3x_h^2y_hz_h)f'(0) = 0,$$

$$-2x_h^3b^2(0)b'(0) + 2B_1x_h^3b(0)a'(0) - A_3x_h^3y_hz_hb(0)f'(0) = 0,$$

which can be written in matrix form as

$$\begin{pmatrix} -2x_h^3b^2(0) & -2B_1x_h^3b(0) \\ 2B_1x_h^3b(0) & -2x_h^3b^2(0) \end{pmatrix} \begin{pmatrix} a'(0) \\ b'(0) \end{pmatrix} = \begin{pmatrix} (A_1A - 2x_h^2y_h^2z_h + A_3x_h^2y_hz_h)f'(0) \\ A - 3x_h^3y_hz_hb(0)f'(0) \end{pmatrix}.$$

By Cramer's rule,

$$a'(0) = \frac{-2x_h^5y_hz_hb^2(0)f'(0)(A_1A_2 + A_3 - A_3B_1x_h)}{4x_h^6b^4(0) + 4B_1^2x_h^6b^2(0)}.$$

The denominator of $a'(0)$ is positive since its first term is positive and its second term is nonnegative. In order to have $a'(0) = 0$, we would need the numerator to be zero, which implies

$$-2x_h^5y_hz_hb^2(0)f'(0)(A_1A_2 + A_3 - A_3B_1x_h) = 0,$$

however,

$$-2x_h^5y_hz_hb^2(0)f'(0)(A_1A_2 + A_3 - A_3B_1x_h) > 0.$$

Since $f'(0) = -\frac{1}{D_2}$, we have $f'(0)(A_1A_2 + A_3 - A_3B_1x_h) < 0$, and the numerator of $a'(0)$ is positive. Therefore, $a'(0) \neq 0$.

$\square$

7 Conclusion

In the paper, we formulate the mathematical model of two consumers and the same resource, algae are investigated under asymmetric intraguild interactions and carrying capacities that are a function of resource (algae) availability at any time. We get the system is bounded and resource is always persistent. If the intrinsic growth rate of a consumer is less than the corresponding attacking rate of its competitor, then the consumer eventually dies out. Some competition outcomes depend on the initial conditions. If two consumers do not attack each other, then co-existence is the unique outcome. The consumption rates have a significant impact on the ratio of the non-toxic phytoplankton to the total phytoplankton. Co-existence can be in sustainable oscillation or non-oscillation.

8 Acknowledgments

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