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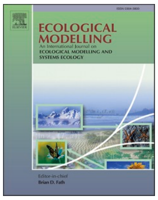

Selective grazing of zooplankton on phytoplankton defines rapid algal succession and blooms in oceans

Yanlin Zheng [a], Xiang Gong [b], Huiwang Gao [c,*]

[a] College of Mathematics and Systems Science, Shandong University of Science and Technology, Qingdao 266590, China
[b] School of Mathematics and Physics, Qingdao University of Science and Technology, Qingdao 266071, China
[c] Key Laboratory of Marine Environment and Ecology, Ocean University of China, Ministry of Education of China, Qingdao 266100, China

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ABSTRACT

In a model plankton ecosystem containing phytoplankton and zooplankton, the later usually avoids toxic phytoplankton and prefers nontoxic species by modulating its grazing rate. The toxins released by toxic phytoplankton can lead to a decreased grazing rate of zooplankton on both phytoplankton, and the presence of nontoxic phytoplankton in the system also reduces the grazing pressure of zooplankton on the toxic phytoplankton. In this study, a set of functions were given that model the selective grazing of zooplankton on various phytoplankton. Preference coefficient and avoidance coefficient were introduced in the selective grazing functions to measure the level of zooplankton preference of nontoxic phytoplankton and avoidance of toxic phytoplankton, respectively. A dynamics model was established in a nontoxic phytoplankton-toxic phytoplankton-zooplankton system based on the grazing functions of zooplankton to study the existence and stability of an interior equilibrium and Hopf-bifurcation. Our results show that zooplankton selective grazing promotes both zooplankton and toxic phytoplankton biomass, and contributes to maintain the coexistence of all species. Low grazing selectivity, i.e., low values of preference coefficient and avoidance coefficient, decreases the zooplankton population and increases the opportunity for phytoplankton blooms. A moderate level of grazing selectivity helps keep the system in balance. With high grazing selectivity on phytoplankton, toxic phytoplankton becomes the dominant species, resulting in a rapid algal succession and eventual toxic phytoplankton blooms. When the preference coefficient and avoidance coefficient in the dynamics model crossed critical values respectively, the ecosystem enters into a Hopf-bifurcation around the interior equilibrium, inducing oscillations of these populations.

1. Introduction

Selective grazing behavior has attracted the attention of ecologists for decades, and the focus varies from individual behavior to the dynamics of a predator-prey system. Many predators can distinguish different types of prey, thus avoiding the ingestion of undesirable prey, which is termed selective grazing (Mitra and Flynn, 2006; Linhart et al., 1976; Ghorai et al., 2021). In the marine plankton ecosystem, zooplankton shows a similar synergistic behavior by distinguishing between toxin-producing phytoplankton (TPP) and nontoxic phytoplankton (NTP) species (Lewis et al., 2013; Schultz and Kiørboe, 2009; Yuan et al., 2017). The cause of this phenomenon remains unknown, and the hypothesized mechanisms for selective grazing include morphology (size, shape, and colony formation), viable gut passage, and toxic chemicals produced by the prey (Porter, 1973; Frost, 1972; Zhao et al., 2018; Sterner, 1989; Liu et al., 2014). Selective grazing by copepods on toxic algae has been extensively investigated due to the potential significance of toxic algae to red tide and harmful algal bloom formations (Uye and Takamatsu, 1990; Solé et al., 2006; Agnihotri and Kaur, 2021). In selective grazing laboratory experiments of *Acartia spinicauda* (a copepod zooplankton) on *Alexandrium tamarense* (TPP) in the presence of *Platymonas subcordiformis* (NTP), the grazing rate of *A. spinicauda* on *A. tamarense* increased gradually to a maximum at a critical density of *A. tamarense*, and then decreased and continued to decline with an increasing *P. subcordiformis* density (Qi et al., 2004). These experiments suggested that *A. spinicauda* avoided the toxic *A. tamarense* and preferred the nontoxic *P. subcordiformis*.

Selective grazing not only promotes the survival of TPP populations,

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* Corresponding author.
E-mail address: hwgao@ouc.edu.cn (H. Gao).

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but it also plays an important role in their dominance over various competitors (Chakraborty et al., 2012). The population balance of zooplankton and phytoplankton is a complicated dynamic process in the marine plankton ecosystem. Nonlinear mathematical models for interacting populations have often been used to explain the dynamic behavior of the plankton system (Rosenzweig, 1971; McCann et al., 1998; Meng and Zhang 2016; Zhang et al., 2020) Chattopadhyay et al. (2004). proposed a model with three components, NTP, TPP, and zooplankton (Z), to investigate the effect of the toxin released by TPP on zooplankton grazing. They proved that all three species coexist if the grazing rate of zooplankton on TPP is bounded. They observed that when the TPP is presented the equilibrium level of NTP increases while the equilibrium level of zooplankton decreases. The result indicated that TPP plays a key role in zooplankton bloom termination. The model incorporates the Holling (1959) type II functional response to describe the grazing rate of zooplankton on TPP. Holling type II functional response is often used to explain the grazing behavior of zooplankton on phytoplankton in the predator-prey model system. It describes that the grazing rate of zooplankton tends to a maximum value as phytoplankton density increases. But Holling type II is not accurate to describe the grazing rate of zooplankton on TPP, because the grazing rate declines instead of remaining at a maximum level when TPP density is high as observed in some experiments (Qi et al., 2004).

Holling (1961) type IV incorporating prey interference with predation indicated that the per capita predation rate increased to a maximum at a critical prey density and then decreased (Sabelis, 1985; Taylor, 1984; Collings, 1997). This suggests that some phytoplankton species produce defense mechanism that reduces the grazing pressure by zooplankton (Berdalet et al., 2014) Banerjee and Venturino (2011). proposed a mathematical model for NTP-TPP-Z system by using Holling type IV to simulate this situation. Their results indicated that the avoidance behavior of zooplankton in the presence of large quantities of TPP ensured that the toxin released by TPP does not drive the zooplankton populations toward extinction. Holling type IV reflects the inhibitory effect of toxins released by TPP on zooplankton grazing, but does not take account of the ability of zooplankton to distinguish between the two species, known as grazing selectivity.

To investigate the effect of selective grazing on the survival and dominance of TPP over its nontoxic competitors, Pal et al. (2009) modified the NTP-TPP-Z model by including competition terms between TPP and NTP in grazing functions. They observed that competition was helpful for the coexistence of all three species. When the competition coefficient crosses a critical value, the ecosystem loses its stability and results in Hopf-bifurcation around the positive equilibrium depicting oscillations phenomena of the population Chaktabort et al. (2012). introduced a parameter β in the grazing functions to measure the avoidance of zooplankton for TPP in the presence of NTP. They found that high avoidance promoted the survival of the TPP population and helped to support the coexistence of all populations Fiesal et al. (2016). proposed and analyzed an ecological model that described the dynamical behavior of food web model (Nutrient-NTP-TPP-Z) with Lotka-Volterra type of functional response. These models allow for selective grazing, but ignore the fact that the large amount of toxins released by TPP would sharply reduce the grazing rate of zooplankton on TPP. some experimental results showed that zooplankton decreased the grazing rate on TPP with increasing toxins when NTP density remained unchanged (Qi et al., 2004).

Based on this observation, in this study, we extended the model proposed by Chaktabort et al. (2012) by introducing the term dP_2^2 (P_2 is the densities of TPP while d is the avoidance coefficient) in the denominator of the grazing function to measure the avoidance of zooplankton for TPP due to its toxins. We also investigate its effect on the dynamics of the system. We focus on the explanation of selective grazing modulations on rapid algal succession and blooms in a marine environment. To meet these goals, we first establish the selective grazing functions in NTP-TPP-Z system, and then present an ecosystem dynamics model to analyze and simulate the nonlinear behaviors of the system Fig. 5.

2. Methods

2.1. . Selective grazing functions

In the NTP-TPP-Z system, let P_1, P_2 be the densities of NTP and TPP, respectively. Let I_2 be the grazing function of zooplankton on TPP. I_2 is defined by the following equation:

$$I_2 = \sigma(\omega - \delta I_2)P_2 \tag{1}$$

where, σ is the searching effectiveness which refers to the percentage of prey found by a predator in unit time, ω is the total time available for predation, and δ is the handling time for attack and ingestion (Holling, 1961). Obviously, a lower searching effectiveness and longer handling time equate to a lower grazing rate of zooplankton on TPP. Considering that the existence of NTP reduces searching effectiveness σ and that the toxins released by TPP prolong the handling time δ, we modified the equations given by Collings (1997) and define

$$\sigma = \sigma_0(1 + c_1P_1)^{-1} \tag{2}$$

$$\delta = \delta_0(1 + dP_2) \tag{3}$$

so that σ decreases and δ increases as P_1 and P_2 increase. Here, σ_0 is maximum searching effectiveness and δ_0 is the minimum handling time. The parameter $c_1 \geq 0$ measures the level of NTP interference with zooplankton searching for TPP. $d \geq 0$ indicates that the toxins released by TPP prolongs the handling time. Substitute (2) and (3) into (1) and solve for I_2 to get

$$I_2 = \frac{\sigma_0\omega P_2}{1 + c_1P_1 + \sigma_0\delta_0(1 + dP_2)P_2} \tag{4}$$

Let $a = \frac{\omega}{\delta_0}$, $b = \frac{1}{\sigma_0\delta_0}$, $c = \frac{c_1}{\sigma_0\delta_0}$, we get the grazing function

$$I_2 = \frac{aP_2}{b + cP_1 + dP_2^2 + P_2} \tag{5}$$

The parameter $c \geq 0$, termed the "preference coefficient", measures the preference of zooplankton for NTP. $c = 0$ produces a system where zooplankton does not discriminate between NTP and TPP, whereas high $c$results in a decrease in TPP uptake by zooplankton in the presence of NTP. The parameter $d \geq 0$, termed the "avoidance coefficient", measures the avoidance of TPP by zooplankton. $d = 0$ represents that TPP does not release toxins and the grazing rate I_2 increases with TPP density to near the maximum a. Parameter a is the maximal zooplankton per capita grazing rate and b is the density of TPP necessary to achieve one-half that rate when $c = 0$ and $d = 0$. When $c > 0$ and $d > 0$, a provides an upper boundary for the per capita grazing rate since I_2 attains a maximum of $\frac{a}{2\sqrt{d(b+cP_1)}+1}$ at $P_2 = \sqrt{\frac{b+cP_1}{d}}$. We reduced (5) to the following function to indicate the grazing rate:

$$I_2 = \frac{aP_2}{b + cP_1 + dP_2^2} \tag{6}$$

Obviously, (6) has the same mathematical property as (5): Firstly, the grazing function I_2 in (5) and (6) have the same maximum point $P_2 = \sqrt{\frac{b+cP_1}{d}}$ when P_1 remains constant; Secondly, I_2 in both (5) and (6) decrease with the increase of P_1 when P_2 remains constant. Formulas (5) and (6) reflect the experimental results of Qi et al. (2004) where the avoidance of TPP and preference for NTP reduces the grazing rate of zooplankton on TPP ($c > 0, d > 0$). Formulas (5) and (6) are called selective grazing functions.

To facilitate the functional property analysis, we modified (5) and (6) as follows:

$$I_2 = \frac{P_2}{b' + c'P_1 + d'P_2^2 + e'P_2} \tag{7}$$

$$I_2 = \frac{P_2}{b' + c'P_1 + d'P_2^2} \tag{8}$$

Here,

$$b' = \frac{b}{a}, c' = \frac{c}{a}, d' = \frac{d}{a}, e' = \frac{1}{a}$$

To investigate how the grazing of zooplankton on TPP changes with NTP and TPP densities, we perform a multiple nonlinear regression analysis of models (7) and (8) using experimental data from Qi et al. (2004).

From Table 1, we find that the grazing rate of zooplankton on P_2 increased to a maximum at $P_2 = 2000$ and then decreased with the density of P_2 when $P_1 =$ 600, 1200, and 2300. It means that zooplankton reduced grazing P_2 to avoid the toxin. The grazing rate decreased with the density of P_2 when $P_1 = 4600$ and had a small fluctuation in the decline when $P_1 = 9000$. When $P_2 = 2000$, the grazing rate decreased obviously with the increase of P_1, which means that the zooplankton preferred P_1 to P_2 when P_1 is abundant. The grazing rate of zooplankton on P_2 was low when the density of P_2 was in very low and high levels, so the decline trends of P_2 were not obvious when $P_2 = 400$ and 4000.

For simplicity we let

$$x = P_1 \times 10^{-3}, \quad y = P_2 \times 10^{-3}, \quad f_i = I_2 \times 10^{-3} \ (i = 1, 2)$$

in (7) and (8). We got the regression coefficients of the model (7) and (8) by using a nonlinear regression analysis with the data in Table 1. The R^2 and P value in Table 2 indicate that (7) and (8) are reasonable to describe the grazing rate of zooplankton on TPP. The results show that f_1 and f_2 fit the data well Table 2) Fig. 1. provides the fitting surface of data in Table 1 Figs. 2 and 3. provide the fitting surfaces of selective grazing models f_1,f_2, respectively. When NTP density was low, the grazing rate of zooplankton on TPP increased to a maximum and then decreased with increasing density of TPP Fig. 4. provides the section lines of the fitting surface of f_2 on a series of planes parallel to the coordinate planes. It shows two different trends of the grazing rate I_2 caused by the increasing densities of NTP and TPP. We conclude that the selective grazing functions ((5) and (6) have similar functional properties, and they describe the characteristics of selective grazing behavior of zooplankton on phytoplankton in the NTP-TPP-Z system. Considering that the form of function (5) is too complex to be analyzed for nonlinear dynamics although it fits the data better than function (6), we select (6) as a function of zooplankton grazing on TPP for its relatively simple form to build the NTP-TPP-Z system models.

In the same way, let I_1 be the grazing rate of zooplankton on NTP. We defined the toxins released by TPP interfered with the searching effectiveness of zooplankton for NTP. I_1 is defined by the equations

$$I_1 = \sigma(\omega - \delta I_1)P_1 \tag{9}$$

$$\sigma = \sigma_0(1 + c_2P_2)^{-1}, \ \delta = \delta_0 \tag{10}$$

Table 1

Grazing rate (cells /(per capita·d)) of Acartia spinicauda on Alexandrium tamarense with various densities of A. tamarense and Platymonas subcordiformis.

Densities of Alexandrium tamarenseP_2(cells /ml)	Densities of *Platymonas subcordiformis*P_1(cells /ml)				
	600	1200	2300	9000	4600
400	2270	2530	1830	4120	2440
2000	11040	9340	7220	3040	1190
4000	3630	2210	2250	2560	2020

Table 2

Nonlinear regression analysis for zooplankton grazing on TPP.

Model	P	R^2
$f_1 = \frac{y}{0.21 + 0.07x + 0.16y^2 - 0.36y}$	$P = 0.0001$	$R^2 = 0.84$
$f_2 = \frac{y}{0.04 + 0.066x + 0.044y^2}$	$P = 0.01$	$R^2 = 0.6$

Table 3

Parameters used for a numerical analysis of NTP-TPP-Z system.

Parameter name	Definition	Value/ Unit	Reference*
r_1	growth rate of NTP	4.5/d	(1)
r_2	growth rate of TPP	1.5/d	(2)
α	maximal grazing rate of Zooplankton on NTP	10/d	(2)
a	maximal grazing rate of Zooplankton on TPP	1/d	(2)
K	carrying capacity of algae	10/ml	(1)
μ	mortality rate of Zooplankton	0.1/d	(1)
θ	conversion efficiency of NTP to Zooplankton	1/d	-
θ_1	toxin liberation rate	0.1/d	-
b	constant	0.04	(3)
β	constant	1	-

* Parameter values for the numerical analysis in Table 3 are taken from (1) Chattopadhyay et al. (2004), (2) Qi et al. (2004), and (3) Table 2. TPP, toxin-producing phytoplankton; NTP, nontoxic phytoplankton.

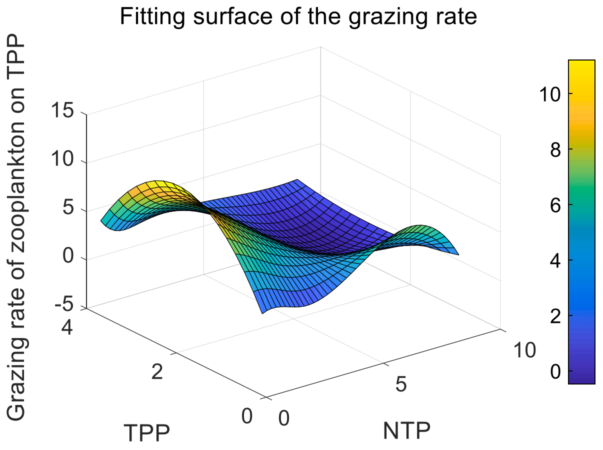

Fig. 1. Fitting surface of data in Table 1. TPP, toxin-producing phytoplankton; NTP, nontoxic phytoplankton.

where, ω, σ_0 and δ_0 in each of the expressions are defined as provided in (1)–(3). We get the grazing function

$$I_1 = \frac{\sigma_0 \omega P_1}{1 + c_2P_2 + \sigma_0\delta_0P_1} \tag{11}$$

For mathematical simplicity we let $c_2 = \sigma_0\delta_0$ in (10) and get the reduced form of I_1 as follows

$$I_1 = \frac{\alpha P_1}{\beta + P_1 + P_2} \tag{12}$$

where, $\alpha = \frac{\omega}{\delta_0}$, $\beta = \frac{1}{\sigma_0\delta_0}$. α is the upper boundary for the grazing rate of zooplankton on NTP when $P_1 \rightarrow \infty$. This function is similar to the one in a deterministic model given by Pal et al. (2009) used to describe the grazing rate of zooplankton on NTP when TPP exists.

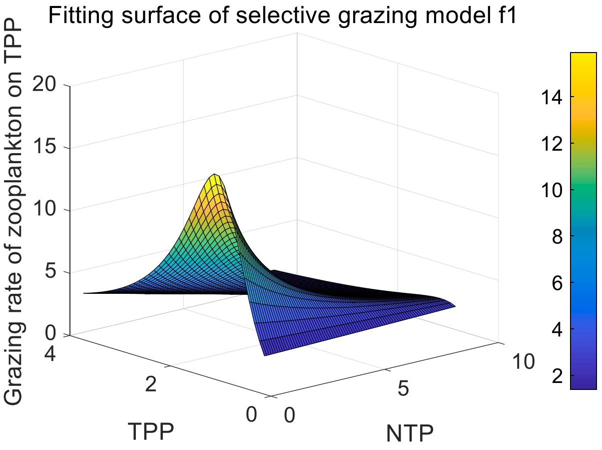

Fig. 2. Fitting surface of selective grazing rate estimated by model f_1. TPP, toxin-producing phytoplankton; NTP, nontoxic phytoplankton.

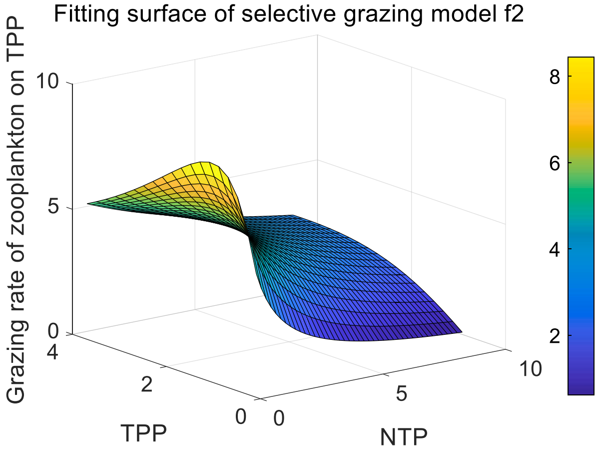

Fig. 3. Fitting surface of selective grazing model f_2. TPP, toxin-producing phytoplankton; NTP, nontoxic phytoplankton.

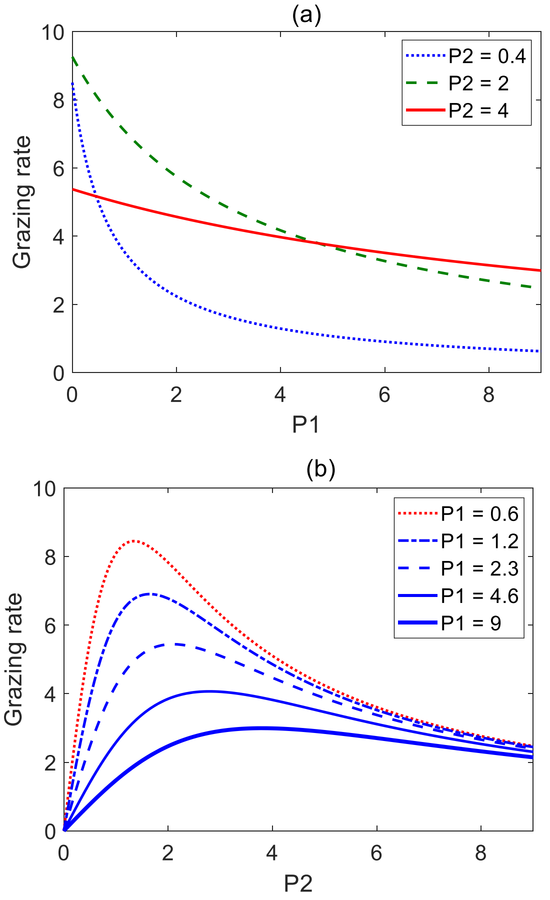

Fig. 4. Predicted value of the grazing rate of zooplankton on P_2 (*Alexandrium tamarense*) at different densities of P_1(*Platymonas subcordiformis*) (a) and P_2 (*Alexandrium tamarense*) (b) by the selective grazing function f_2.

2.2. NTP-TPP-Z model and nonlinear analysis

We assumed that $P_1(t), P_2(t), Z(t)$ are the densities of NTP, TPP, and Z, at time t, respectively. We also assumed that NTP and TPP grow in a logistic function and that the growth of zooplankton depends on the predation of NTP only. We assumed that NTP and TPP share the same environmental carrying capacity and resources for growth. Finally, we assumed that the predation on TPP reduces the zooplankton population. We selected (6) and (12) as the grazing functions of zooplankton on TPP and NTP, respectively. With these assumptions, we proposed the following model to describe the variations of relationships among them:

$$\begin{aligned}
\frac{dP_1}{dt} &= r_1P_1\left(1-\frac{P_1}{K}\right)-\frac{\alpha P_1Z}{\beta+P_1+P_2}\\
\frac{dP_2}{dt} &= r_2P_2\left(1-\frac{P_2}{K}\right)-\frac{aP_2Z}{b+dP_2^2+cP_1}\\
\frac{dZ}{dt} &= \frac{\theta\alpha P_1Z}{\beta+P_1+P_2}-\frac{\theta_1aP_2Z}{b+dP_2^2+cP_1}-\mu Z
\end{aligned} \tag{13}$$

Here, let r_1, r_2 be the growth rates of NTP and TPP, respectively, and K be the environmental carrying capacity for phytoplankton. α and a are the maximal grazing rates of zooplankton on NTP and TPP, respectively. θ is the conversion efficiency of TPP into zooplankton biomass, θ_1 denotes the rate of toxin liberation by TPP, and μ is the death rate of zooplankton. The parameters d and c represent an avoidance coefficient and preference coefficient, respectively, while β, b are constants. The analysis was simplified by introducing dimensionless variables and parameters

$$x=\frac{P_1}{K},\ y=\frac{P_2}{K}, z=\frac{Z}{K} \tag{14}$$

and then using $\tau = r_1t$ as dimensionless time. For convenience in the following, time τ is replaced by t as the dimensionless time. We got the following dimensionless equations

$$\begin{aligned}
\frac{dx}{dt} &= x(1-x)-\frac{\alpha' xz}{\gamma+x+y}\\
\frac{dy}{dt} &= r'y(1-y)-\frac{\theta' yz}{1+b_2y^2+b_1x}\\
\frac{dz}{dt} &= \frac{\beta' xz}{\gamma+x+y}-\frac{\theta_1yz}{1+b_2y^2+b_1x}-\mu' z
\end{aligned} \tag{15}$$

where

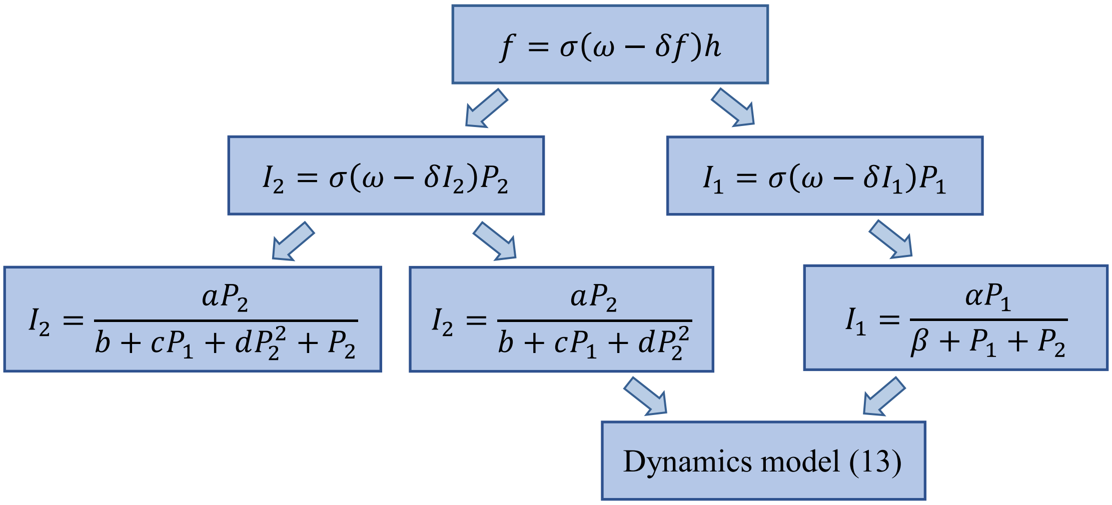

Fig. 5. Flow chart of modeling method.

$$\alpha'=\frac{\alpha}{r_1},\gamma=\frac{\beta}{K},r'=\frac{r_2}{r_1},\theta'=\frac{aK}{r_1b},b_1=\frac{cK}{b},b_2=\frac{dK^2}{b},$$
$$\beta'=\frac{\theta\alpha}{r_1},\theta_1^{'}=\frac{\theta_1aK^2}{b},\mu'=\frac{\mu}{r_1}. \tag{16}$$

System (15) was analyzed with the following initial conditions

$$x(0)\geq 0,\ y(0)\geq 0,\ z(0)\geq 0 \tag{17}$$

Holling (1961) proposed the equation

$$f=\sigma(\omega-\delta f)h \tag{18}$$

to define the functional response $f(h)$ in a predator–prey interaction model. Here, h is the density of prey, and f is the grazing rate of predator. Based on this equation, the grazing rates of zooplankton on TPP and NTP were defined in Eqs. (1) and (9) in the NTP-TPP-Z system. Considering the different characteristics of zooplankton grazing on TPP and NTP, the selective grazing functions (5) and (12) were deduced respectively from these equations. We reduced (5) to function (6) for its relatively simple form. Then the dynamics model of the NTP-TPP-Z system was established and simulated to discuss the influence of zooplankton selective grazing on the system. Let P_1,P_2 be the densities of NTP and TPP, and I_1, I_2 be the grazing rates of zooplankton on NTP and TPP, the flow chart was given as follow in Figure 5:

3. Results and discussion

3.1. . Boundedness of the system

All of the solutions of (15), which initiate in $R_+^3=\{(x,y,z)|x\geq 0,y\geq 0,z\geq 0\}$, were ultimately bounded. The proof is obvious.

3.2. . Equilibriums and their existence condition

The system (15) possesses the following equilibrium points:

(1) $E_0=(0,0,0),\ E_1=(1,0,0),\ E_2=(0,1,0),\ E_3=(1,1,0)$.

(2) $E_4=(x^*,0,z^*)$, where $x^*=\frac{\gamma\mu'}{\beta'-\mu'},z^*=\frac{\gamma}{\alpha'}\left(1-\frac{\gamma\mu'}{\beta'-\mu'}\right)\left(1+\frac{\mu'}{\beta'-\mu'}\right)$.

The existence criterion of E_4 is $\beta'>(\gamma+1)\mu'$.

(3) If avoidance of TPP and preference to NTP by zooplankton remain at a higher level, there may be a possibility of coexistence of all three species, named $E_5=(x^*,y^*,z^*)$, $0<x^*,y^*,z^*<1$.

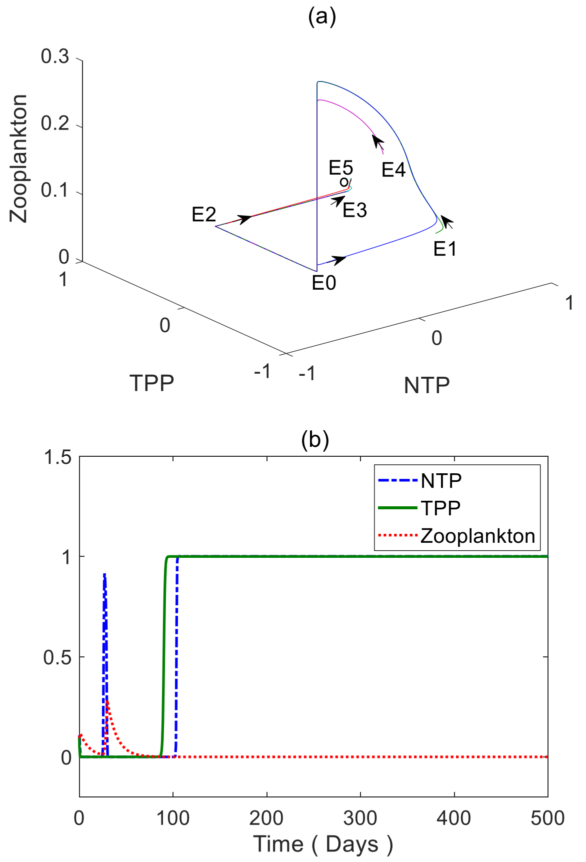

Fig. 6. c = 0.066, d = 0.02. (a) E_0,E_1,E_2,E_3,E_4 are saddle points while the interior equilibrium E_5 is a stable focus; (b) Zooplankton tends to become extinct in the system with an initial density (0.1, 0.1, 0.1).

3.3. . Eigenvalue analysis to establish local asymptotic stability

By computing the Jacobian matrix for the equilibriums of system (15), we found that E_0,E_1,E_2 are unstable, and a feasible NTP and TPP steady state E_3 as well as a feasible NTP and zooplankton steady state E_4 exist. If $\frac{\beta'}{2+\gamma}-\frac{\theta_1^{'}}{1+b_2+b_1}-\mu'>0$ then E_3 is unstable. If $r'-\frac{\theta' z^*}{1+b_1x^*}>0$ then

E_4 is unstable. Due to the complexity, an analytical study of the stability properties of E_5 is difficult; hence, we next performed a numerical investigation to identify the existence of an interior equilibrium point E_5 in the next work.

3.4. . Numerical analysis

We performed a numerical analysis of the system (13) to study the effect of the preference coefficient c and avoidance coefficient d on the dynamical behavior of the system with different parameter setup scenarios (Table 3). We then observed the role of selective grazing for maintaining system stability and the occurrence of a plankton bloom by illustrating the existence of the interior equilibriums.

From Fig. 6, we found that the zooplankton population is extremely low when the values of the preference coefficient $c = 0.066$ and avoidance coefficient $d = 0.02$. E_0, E_1, E_2, E_3, E_4 are saddle points while the interior equilibrium E_5 is locally asymptotically stable. Zooplankton tends to become extinct in the system, resulting in algal blooms. When the value of d increased from 0.02 to 0.044, retaining other parameter values the same as in Fig. 6, we observed that all populations coexist through oscillation, depicting regular recurrent phytoplankton blooms (Fig. 7). From Fig. 8, we observed that the interior E_5 is a stable limit cycle when the value of c increases to 17, which indicates that the high preference for NTP develops in zooplankton populations and induces a rapid phytoplankton succession. E_5 changes to a stable focus when the value of c increases from 17 to 40 (Fig. 9). It shows that the preference coefficient has a critical value $c^*(17 < c^* < 40)$ while the avoidance coefficient is low ($d = 0.044$). The stable coexistence equilibrium changes to a limit cycle when the preference coefficient c crosses that critical value $c^*(17 < c^* < 40)$, resulting in a Hopf-bifurcation around the positive equilibrium depicting oscillation phenomena of all populations and increasing the opportunity of TPP blooms.

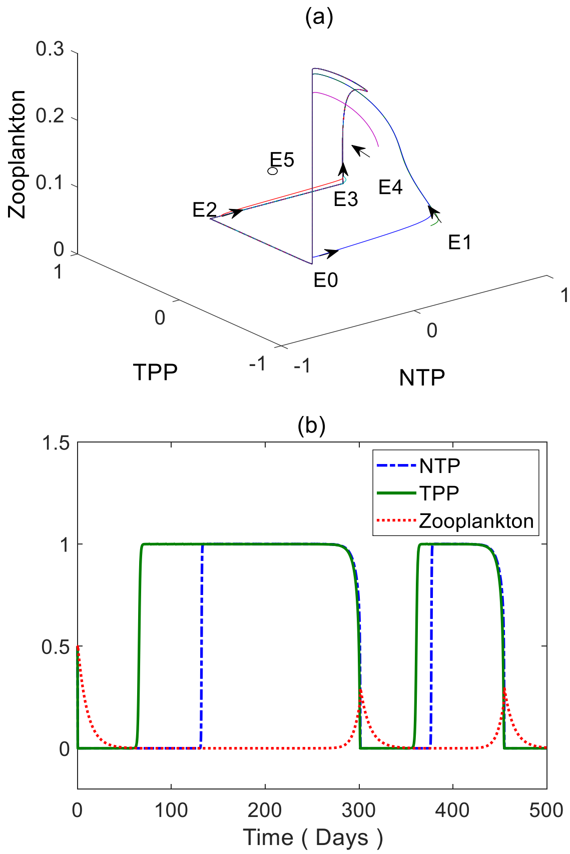

Fig. 7. $c = 0.066, d = 0.044$. (a) E_0, E_1, E_2, E_3, E_4 are saddle points while the interior equilibrium E_5 is a limit cycle; (b) All populations coexist through periodic oscillation giving rise to bi-species blooms with an initial density $(0.1, 0.1, 0.1)$.We used a different time scale to show the clear dynamics of all populations over time.

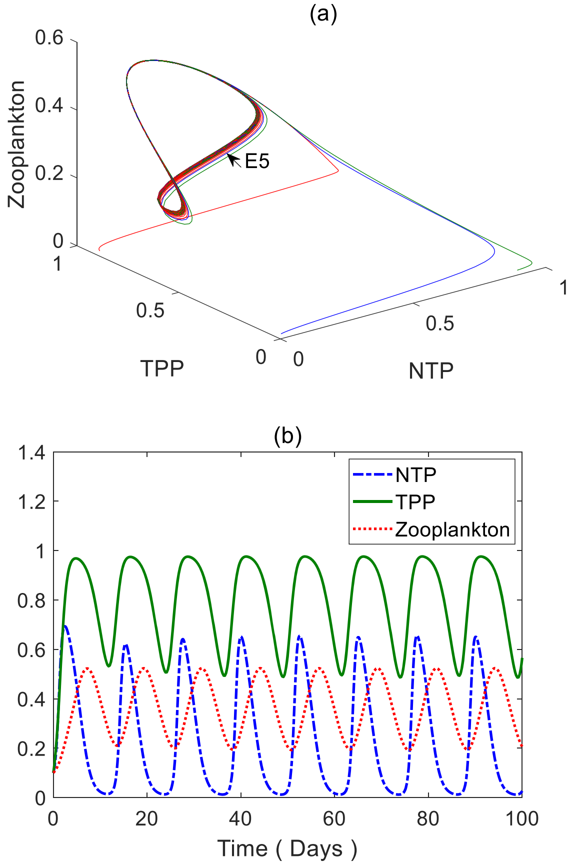

Fig. 8. $c = 17, d = 0.044$. (a) E_5 is a limit cycle; (b) All populations coexist through oscillation with an initial density $(0.1, 0.1, 0.1)$. We used a different time scale to show the clear dynamics of all populations over time.

From Figs. 10 and 11 we find that the stable focus E_5 changes to a limit cycle when the avoidance coefficient d crosses a critical value d^* $(0.15 < d^* < 0.25)$ at $c = 6.6$, resulting in a Hopf-bifurcation around the stable equilibrium. This suggests that the high avoidance of TPP by zooplankton develops both TPP and zooplankton populations in the system Fig. 12. indicates that three species achieve the internal stable equilibrium point after a long period of oscillation when the selective grazing level of zooplankton is low ($c = 0.8, d = 0.25$). When the selective grazing level is high ($c = 10, d = 2.5$), TPP dominates in the system and tends to the environmental carrying capacity, implying the development of TPP blooms.

Three scenarios were studied in numerical simulations: when the zooplankton grazing selectivity level was low, i.e. the ability of zooplankton to distinguish TPP from NTP was low($c = 0.066, d = 0.02$), zooplankton populations tended to become extinct in the system, resulting in algal blooms. When zooplankton grazing selectivity

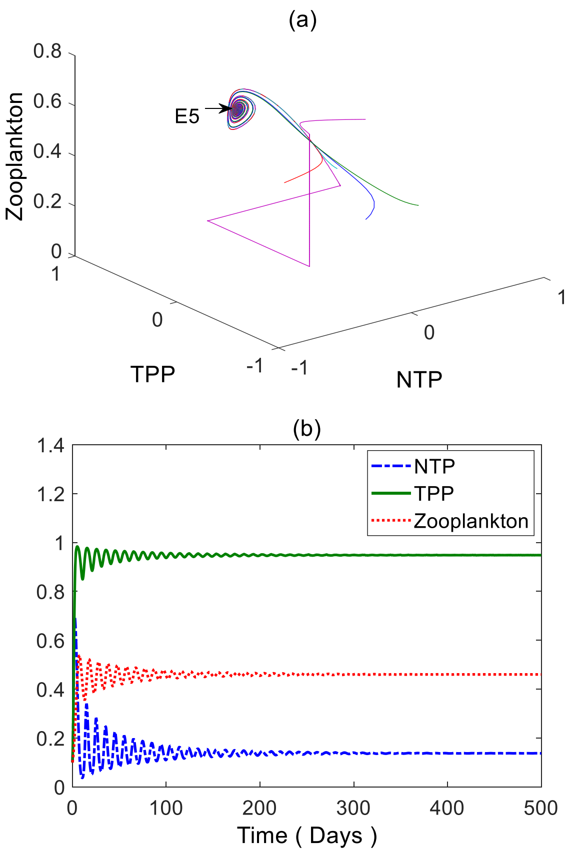

Fig. 9. $c = 40, d = 0.044$. (a) E_5 is a stable focus; (b) All populations coexist at E_5 after a long period of oscillation with an initial density $(0.1, 0.1, 0.1)$.

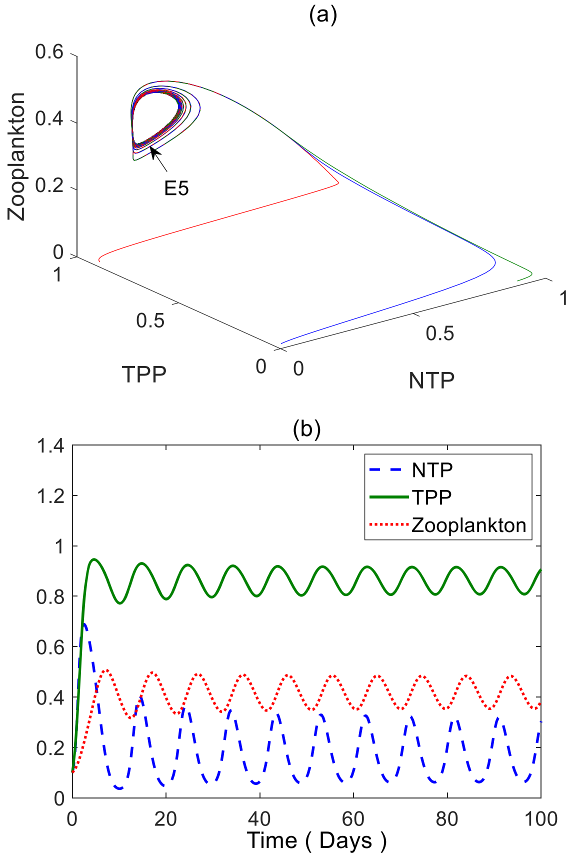

Fig. 10. $c = 6.6, d = 0.15$. (a) E_5 is a limit cycle; (b) All populations coexist through oscillation with an initial density $(0.1,\ 0.\ 1,\ 0.1)$.

increases($c = 6.6$, $d = 0.25$), the system enters a stable equilibrium point. As selectivity levels continued to rise($c = 10$, $d = 2.5$), TPP blooms outbreak. The simulation results show that when the zooplankton selectivity level remains at a high level, there are critical values of preference coefficient$c^*$$(17 < c^* < 40)$ and avoidance coefficientd^* $(0.15 < d^* < 0.25)$ in the system, and Hopf bifurcation occurs when the two selective coefficients pass through their respective critical values.

From the numerical simulation results we conclude that, the preference of NTP and the avoidance of TPP develop zooplankton in NTP-TPP-Z system. This analysis well explains the experimental results of Pal et al. (2010), in which they observed that if there were sufficient resources in the system to make NTP abundant, zooplankton would be more inclined to graze NTP and develop zooplankton themselves. However, they also noted that if the resources in the system are insufficient resulting in a low density of NTP, the zooplankton will become extinct by eating large amounts of TPP. The results of the numerical simulation are also consistent with Chaktabort et al. (2012) that the high avoidance level of TPP helps support the coexistence of all species. The grazing function in their models assumed that the grazing rate of zooplankton on TPP would tend to gradually increase to the maximum with increasing TPP density when NTP density remained unchanged, that is, the amount of toxins released by TPP had no significant impact on the grazing rate of zooplankton. Therefore, when the NTP density in the system was low, zooplankton tended to become extinct in their models because zooplankton did not reduce grazing on TPP. In fact, because the toxins released by TPP reduce the grazing rates of zooplankton on both TPP and NTP (Yuan et al. 2017), the three populations will remain in a stable state or coexist through oscillation, describing rapid algal succession and blooms. This is the advantage of the models established in our study, that is, it measures the selective grazing level of zooplankton from both preference of NTP and avoidance of TPP. Therefore, the models established in this work has a better simulation of the real situation in terms of mathematical properties.

4. Conclusion

In this work, we modified the linear function of the densities of NTP and TPP proposed by Chaktabort et al. (2012) to a nonlinear one in the denominator of the grazing rate function through the regression analysis of experimental data. The results from the numerical analysis showed that the level of avoidance to TPP by zooplankton plays an important role in maintaining the stability of the system. The high avoidance of TPP by zooplankton develops both TPP and zooplankton populations in the system. As the values of avoidance coefficient increases, TPP populations dominate in the system and tend to increase the environmental

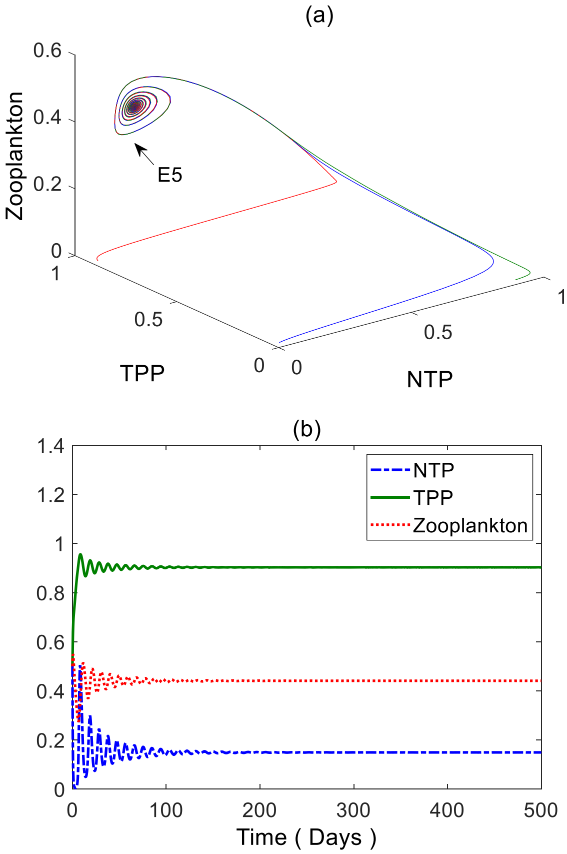

Fig. 11. $c = 6.6, d = 0.25$. (a) E_5 is a stable focus; (b) All populations coexist at E_5 after a long period of oscillation with an initial density.

carrying capacity, implying the development of TPP blooms.

In NTP-TPP-Z systems of the ocean, zooplankton prefers NTP to TPP. In this study, two key parameters, the avoidance coefficient and preference coefficient, were introduced in the selective grazing function to measure the grazing selectivity of zooplankton in NTP-TPP-Z system. The advantage of this function is that the reduction of zooplankton grazing pressure on TPP can be attributed to the presence of NTP and the inhibition of toxins released by TPP on zooplankton grazing. The results showed that selective grazing developed both zooplankton and TPP and helped to maintain the coexistence of them both. Low grazing selectivity, i.e., low values of preference coefficient and avoidance coefficient, decreased the zooplankton populations and increased the opportunity for phytoplankton blooms. High grazing selectivity increased the zooplankton and TPP populations and make TPP become the dominant species, resulting in a rapid algal succession and eventual TPP blooms.

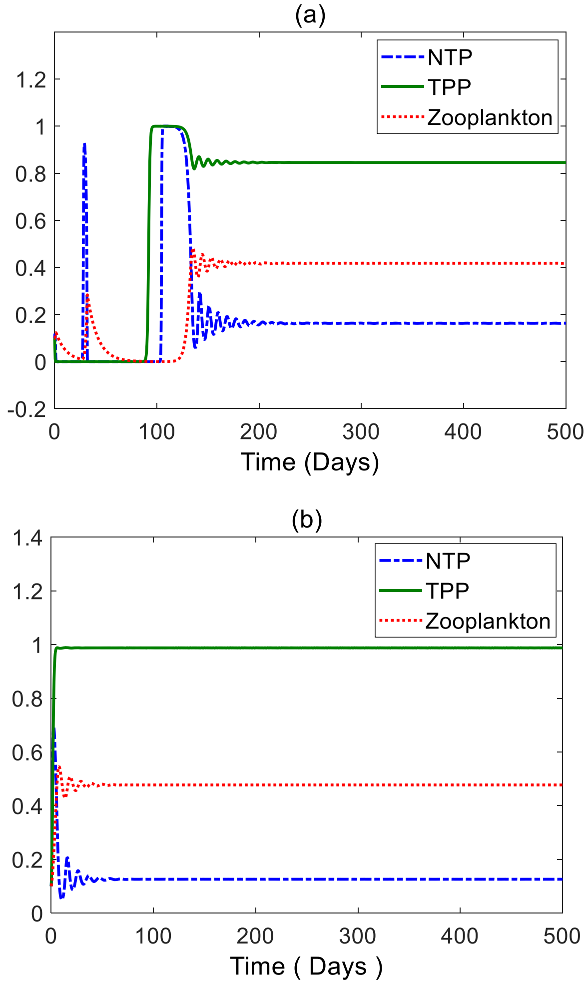

Fig. 12. The initial density is $(0.1, 0.1, 0.1)$. E_5 is a stable focus at (a) $c = 0.8, d = 0.25$and (b) $c = 10, d = 2.5$.

Evolutionary trade-off between defense against grazing and competitive ability is well known in planktonic algae, and it helps to maintain system stability Yoshida et al. (2004). grew algal populations for multiple generations in either the presence or absence of the grazing rotifer Brachionus calyciflorus and then concluded that grazed algae were better defended, yielding a rotifer growth rate 32% below that of animals fed non-grazed algae. However, they also had a diminished competitive ability, with a growth rate under nutrient-limiting conditions 28% below that of non-grazed algae. In addition, grazed algae had a smaller cell size, which influenced the system stability. For example, Zhao et al. (2018) investigated that the system went into oscillation with the increasing cell size of phytoplankton, and demonstrated that the cell size of phytoplankton increased the complexity of phytoplankton-zooplankton interaction and the possibility of phytoplankton blooms.

Therefore, changes in phytoplankton grazing pressure on phytoplankton lead to phytoplankton evolutionary in cell size and growth rate, which in turn affect zooplankton grazing rate. We noted that in NTP-TPP-Z system, the growth rate of phytoplankton and the toxin release rate of TPP were assumed to be constants for mathematical simplicity. In fact, when the selective grazing level was low, the growth rate of TPP decreased, and the toxin release rate increased as a defense against grazing. Then, when grazing pressure was decreased, a higher TPP growth rate was induced coupled with a lower toxin release rate. This would eventually affect the selective grazing level of zooplankton. Considering the genetic variation of phytoplankton, we should change the growth rate and toxin release rate from constants to functions of avoidance coefficient and preference coefficient in an analysis of the nonlinear behavior of the NTP-TPP-Z system in future work.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that cdocould have appeared to influence the work reported in this paper.

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Appendix

Proof of boundedness of system (15)

We defined a function

$$\omega = x + y + \frac{\alpha'}{\beta'} z$$

The time derivative of ω along the solutions of (13) is

$$\frac{d\omega}{dt} = x(1-x) + r' y(1-y) - \frac{\mu'\alpha'}{\beta'} z - \frac{\left(\theta' + \frac{\theta_1'\alpha'}{\beta'}\right) yz}{1 + b_2 y^2 + b_1 x}$$

For each $c > 0$, the following inequality holds:

$$\frac{d\omega}{dt} + c\omega \le x(1 - x + c) + r' y\left(1 - y + \frac{c}{r'}\right) + (c - \mu')\frac{\alpha'}{\beta'} z$$

Now, if we take $c < \mu'$, then we get the following inequality,

$$\frac{d\omega}{dt} + c\omega \le L$$

where, $L = \frac{1}{4}\left[(1+c)^2 + r'\left(1 + \frac{c}{r'}\right)^2\right] \Big\rangle 0$, Then we obtain

$$0 < \omega(x(t), y(t), z(t)) \le \frac{L}{c}\left(1 - e^{-ct}\right) + \omega(x(0), y(0), z(0)) e^{-ct}$$

and for $t \to \infty$, we have

$$0 < \omega < \frac{L}{c}$$

Hence, all the solutions of (15) which are initiated in $R_+^3 = \{(x, y, z) | x \ge 0, y \ge 0, z \ge 0\}$ are ultimately bounded within a region B defined by

$$B = \left\{ (x, y, z) \middle| 0 \le x(t) \le 1, 0 \le y(t) \le 1, 0 \le x(t) + y(t) + \frac{\alpha'}{\beta'} z(t) \le \frac{L}{c} \right\}$$

Stability analysis of the system (15)

The Jacobian matrix of system (15) reads

$$V = \begin{pmatrix} 1 - 2x - \alpha' A_1 & \alpha' A_2 & -\alpha' A_3 \\ \theta' A_4 & r' - 2r' y - \theta' A_5 & -\theta' A_6 \\ \beta' A_1 + \theta_1' A_4 & -\beta' A_2 - \theta_1' A_5 & \beta' A_3 - \theta_1' A_6 - \mu' \end{pmatrix}$$

where,

$$A_1 = \frac{z(\gamma + y)}{(\gamma + x + y)^2},\ A_2 = \frac{xz}{(\gamma + x + y)^2}, A_3 = \frac{x}{\gamma + x + y}$$

$$A_4 = \frac{b_1 yz}{(1 + b_2 y^2 + b_1 x)^2},\ A_5 = \frac{z(1 - b_2 y^2 + b_1 x)}{(1 + b_2 y^2 + b_1 x)^2}, A_6 = \frac{y}{1 + b_2 y^2 + b_1 x}$$

(1) $V_0 = \begin{pmatrix} 1 & 0 & 0 \\ 0 & r' & 0 \\ 0 & 0 & -\mu' \end{pmatrix}$. The eigenvalues of V_0 around the equilibrium $E_0(0, 0, 0)$ are 1, r', and $-\mu'$. Clearly this steady state is unstable.

(2) $V_1 = \begin{pmatrix} -1 & 0 & -\dfrac{\alpha^{'}}{1+\gamma} \\ 0 & r^{'} & 0 \\ 0 & 0 & \dfrac{\beta^{'}}{1+\gamma} - \mu^{'} \end{pmatrix}$. The eigenvalues of V_1 around the equilibrium $E_1(1,0,0)$ are -1, r', and $\frac{\beta'}{1+\gamma} - \mu'$. Clearly this steady state is unstable.

(3) $V_2 = \begin{pmatrix} 1 & 0 & 0 \\ 0 & -r^{'} & -\dfrac{\theta^{'}}{1+b_2} \\ 0 & 0 & -\dfrac{\theta_1^{'}}{1+b_2} - \mu^{'} \end{pmatrix}$. The eigenvalues of V_2 around the equilibrium $E_2(0,1,0)$ are 1, $-r'$, and $-\frac{\theta_1'}{1+b_2} - \mu'$. Clearly this steady state is unstable.

(4) $V_3 = \begin{pmatrix} -1 & 0 & -\dfrac{\alpha'}{2+\gamma} \\ 0 & -r' & -\dfrac{\theta'}{1+b_2+b_1} \\ 0 & 0 & \dfrac{\beta'}{2+\gamma} - \dfrac{\theta_1^{'}}{1+b_2+b_1} - \mu' \end{pmatrix}$. The eigenvalues of V_3 around the equilibrium $E_3(1,1,0)$ are -1, $-r'$, and $\frac{\beta'}{2+\gamma} - \frac{\theta_1^{'}}{1+b_2+b_1} - \mu'$.

This equilibrium is unstable when $\frac{\beta'}{2+\gamma} - \frac{\theta_1^{'}}{1+b_2+b_1} - \mu' > 0$. E_3 is stable when $\frac{\beta'}{2+\gamma} - \frac{\theta_1^{'}}{1+b_2+b_1} - \mu' < 0$.

(5) $V_4 = \begin{pmatrix} 1 - 2x^{*} - \dfrac{\alpha^{'} z^{*} \gamma}{(\gamma + x^{*})^2} & 0 & -\dfrac{\alpha^{'} x^{*}}{\gamma + x^{*}} \\ 0 & r^{'} - \dfrac{\theta^{'} z^{*}}{1 + b_1 x^{*}} & 0 \\ \dfrac{\beta^{'} z^{*} \gamma}{\gamma + x^{*}} & -\dfrac{\beta' x^{*} z^{*}}{(\gamma + x^{*})^2} - \dfrac{\theta_1^{'} z^{*}}{1 + b_1 x^{*}} & 0 \end{pmatrix}$, The eigenvalues of,$V_4$ around the equilibrium, $E_4(x^{*}, 0, z^{*})$ are,

$\lambda_1 = \lambda_2 = \lambda_3 = r' - \frac{\theta' z^{*}}{1+b_1 x^{*}}$, The equilibrium E_4 is unstable when $r' - \frac{\theta' z^{*}}{1+b_1 x^{*}} > 0$.

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