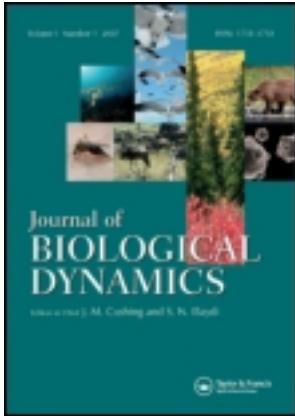


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Plankton-toxin interaction with a variable input nutrient

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A simple model of phytoplankton–zooplankton interaction with a periodic input nutrient is presented. The model is then used to study a nutrient–plankton interaction with a toxic substance that inhibits the growth rate of plankton populations. The effects of the toxin upon the existence, magnitude, and stability of the periodic solutions are discussed. Numerical simulations are also provided to illustrate analytical results and to compare more complicated dynamical behaviour.

Keywords: phytoplankton; zooplankton; toxin; Poincaré map; uniform persistence

1. Introduction

Surface water bodies in the ocean, lakes, and rivers are inhabited by microscopically small autotrophic organisms, the phytoplankton. Through the activity of the photosystem II, phytoplankton organisms are responsible for much of the oxygen present in the Earth's atmosphere. They convert inorganic materials into new organic compounds by the process of photosynthesis [22]. Hence, these tiny planktonic algae play a significant role in global primary productivity and thus are important within the biogeochemical cycling of carbon to support fish stocks. In terms of numbers, the most important groups of phytoplankton are the diatoms, cyanobacteria, and dinoflagellates, although many other groups of algae are sometimes abundant.

Pollution of freshwater and marine systems by anthropogenic sources has become a concern over the last several decades. Organic (*e.g.* triazine herbicides) [3,28–30,39,4] and inorganic compounds (*e.g.* heavy metals) [9,2,29–31,36,37] both may have harmful effects to the organisms. For example, samples taken from the inner harbour of the Waukegan area, located in Lake County, IL, USA, on the west shore of Lake Michigan, have shown that photosynthesis of the green algae *Selenastrum capricornutum* is inhibited due to pollutants originating from industrial and recreational sources (<http://www.epa.gov/glnpo/aoc/waukegan.html>).

This study investigates the possible effects of toxic substances upon nutrient–phytoplankton–zooplankton interaction in a seasonal environment. The model consists of a single limiting nutrient,

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two plankton populations, and an inhibitor, where the inhibitor may include agents such as pesticides or heavy metals. The phytoplankton takes up the nutrients and zooplankton grazes on phytoplankton. In the first model, the zooplankton absorbs the inhibitor without effect, while phytoplankton's uptake rate and consequently its growth rate are inhibited due to the presence of an external inhibitor. In the second model, phytoplankton can uptake toxin without any effect but zooplankton's grazing rate is diminished due to the external toxin. Although our models are simplified systems, it is the first step in understanding complex interaction between the first two trophic levels and pollution. The effects of multiple nutrients on planktonic systems are described *e.g.* [3]. To the best of our knowledge, this research along with a study in [19] are the first investigations of using mathematical models to explore toxic effects upon plankton interaction.

We first propose a simple plankton model with a periodic input of nutrients and summarize its dynamical consequences (Section 2). In the following two sections, we examine the effect of a toxin upon the existence, magnitude, and stability of the periodic solutions by comparing the resulting models with the base model without the toxin. Section 3 studies the model when phytoplankton is inhibited by the toxin and Section 4 presents a model that is identical to the one presented in Section 3, but the toxin has a negative effect on the zooplankton only. Criteria for the coexistence of both plankton populations are also discussed. However, comparisons between more complex dynamical behaviour will only be numerically simulated. The final section provides a brief summary and discussion.

2. The nutrient–phytoplankton–zooplankton model

In this section, we introduce the basic model that will be used in subsequent sections to study the effects of toxin upon the plankton interactions. For simplicity, it is assumed that the organisms and the nutrient are uniformly distributed over the space. Let $N(t)$, $P(t)$, and $Z(t)$ denote the nutrient concentration, the phytoplankton population, and zooplankton population at time t , respectively. For convenience, the two plankton levels are modelled in terms of nutrient content and therefore their units are nitrogen or nitrate per unit volume. We let δ and ϵ denote the per capita natural death rate of phytoplankton and zooplankton, respectively. The phytoplankton's nutrient uptake rate is denoted by f , while g is the zooplankton's grazing rate. Since plankton populations are measured in terms of nutrient concentration, f and g are functions of nutrient concentration. Both functions have the standard monotonic assumptions as the classical Ivlev and Holling types II and III functional responses given below:

$$(H1) \quad f, g \in C^1(0, \infty), \quad f(0) = g(0) = 0, \quad f'(x), g'(x) > 0 \quad \text{for } x \geq 0 \quad \text{and} \quad \lim_{x \rightarrow \infty} f(x) = \lim_{x \rightarrow \infty} g(x) = 1.$$

Parameter m is the maximal nutrient uptake rate of phytoplankton and c denotes the maximal zooplankton ingestion rate, while β and α are the fractions of zooplankton grazing conversion and phytoplankton nutrient conversion, respectively. In natural nutrient–plankton systems, waters flowing into the system bring input of fluxes of nutrients and outflows also carry out nutrients [4,10,32,33]. The rate of waters flowing in and out of the system is a constant and denoted by D . However, unlike the study in [19], we assume that the input nutrient concentration $N^0(t)$ is varied periodically around N^0 with $N^0(t) = N^0 + ar(t)$, where $N^0 > 0$, $0 < a < N^0$, and $r(t)$ is τ -periodic with mean value zero and $|r(t)| \leq 1$ for $t \geq 0$. The consideration of periodic input of nutrients is motivated by the tidal, day/night, or seasonal cycles occurring in nature. Periodical influxes of nutrients are common features in freshwater and marine ecosystem. The periodicity may occur on a daily (*e.g.* triggered by the release of vertical migrating planktonic organisms), tidal or on seasonal basis (*e.g.* by seasonal upwelling, or enhanced input by rivers in late winter/early

spring to temperate shelf seas). Both plankton populations are also assumed to be flowing out of the system with the same constant washout rate D .

Nutrients are consumed by the phytoplankton, which in turn is grazed upon by the herbivorous zooplankton. Consequently, there are minus terms $-mf(N)P$ and $-cg(P)Z$ in the equations for \dot{N} and \dot{P} , respectively. For simplicity, we assume that the system under study is closed and hence there are positive feedback terms δP , ϵZ , $(1 - \alpha)mf(N)P$, and $(1 - \beta)cg(P)Z$ appeared in the equation for \dot{N} . The model with the above biological assumptions can be written as the following three dimensional nonautonomous ordinary differential equations:

$$\begin{aligned}\dot{N} &= D(N^0(t) - N) - mf(N)P + \delta P + \epsilon Z + (1 - \beta)cg(P)Z + (1 - \alpha)mf(N)P, \\ \dot{P} &= [\alpha mf(N) - \delta - D]P - cg(P)Z, \\ \dot{Z} &= [\beta cg(P) - \epsilon - D]Z, \quad N(0), \quad P(0), \quad Z(0) \geq 0,\end{aligned}\tag{1}$$

where $0 < \alpha, \beta \leq 1$ and $D, N^0, m, c, \epsilon, \delta > 0$.

System (1) is very similar to a model studied by Ruan [33] where it was assumed that zooplankton also uptakes nutrients. In this study, the zooplankton population only grazes upon phytoplankton for survival, *i.e.*, zooplankton is obligate, and our analysis is based on the methods used in the study of periodic chemostat systems [35, Chapter 7]. Notice the scalar periodic equation

$$\dot{N} = D(N^0(t) - N), \quad N(0) \geq 0,\tag{2}$$

has a unique positive τ -periodic solution

$$N^*(t) = \frac{De^{-Dt}}{e^{D\tau} - 1} \int_t^{t+\tau} e^{Ds} [N^0 + ar(s)] ds$$

and solutions of Equation (2) are asymptotic to the periodic solution $N^*(t)$ as $t \rightarrow \infty$. Since $\dot{N}|_{N=0} \geq DN^0(t) \geq 0$, $\dot{P}|_{P=0} = \dot{Z}|_{Z=0} = 0$, solutions of Equation (1) remain nonnegative.

Let $U = N^*(t) - N - P - Z$. Then $\dot{U} = -DU$ and thus solutions of Equation (1) are bounded. Moreover, system (1) can be rewritten as

$$\begin{aligned}\dot{U} &= -DU, \\ \dot{P} &= [\alpha mf(N^*(t) - U - P - Z) - \delta - D]P - cg(P)Z, \\ \dot{Z} &= [\beta cg(P) - \epsilon - D]Z.\end{aligned}\tag{3}$$

Since the ω -limit set of Equation (3) lies on the set $U = 0$, Equation (1) has the following limiting system:

$$\begin{aligned}\dot{P} &= [\alpha mf(N^*(t) - P - Z) - \delta - D]P - cg(P)Z, \\ \dot{Z} &= [\beta cg(P) - \epsilon - D]Z, \quad P(0), \quad Z(0) \geq 0, \quad P(0) + Z(0) \leq N^*(0).\end{aligned}\tag{4}$$

As $N(t) + P(t) + Z(t) = N^*(t)$ for $t \geq 0$ on the ω -limit set and solutions of Equation (1) remain nonnegative, we see that $P(t) + Z(t) \leq N^*(t)$ for $t \geq 0$, *i.e.*, system (4) is well-defined.

Let

$$\Gamma = \{(P, Z) \in R_+^2 : P + Z \leq N^*(0)\}.$$

The Poincaré maps can be exploited to study periodic system (4). We refer the reader to Chapter 7 of Smith and Waltman [35] for more in-depth information on periodic chemostat systems. Clearly, system (4) always has a steady state solution $(0, 0)$ in which both plankton populations are extinct.

The Jacobian derivative of the Poincaré map induced by system (4) evaluated at $(0, 0)$ is given by $\Phi_0(t)$, where $\Phi_0(t)$ is the fundamental matrix solution of $\dot{X} = J_0X$ with

$$J_0 = \begin{pmatrix} \alpha mf(N^*(t)) - \delta - D & 0 \\ 0 & -\epsilon - D \end{pmatrix}. \tag{5}$$

Let

$$\sigma_0 = \frac{1}{\tau} \int_0^\tau [\alpha mf(N^*(t)) - \delta - D] dt. \tag{6}$$

Since $N^*(t)$ is the maximal nutrient concentration available at any time t when both plankton populations are not present, σ_0 is the average maximal growth rate of the phytoplankton $1/\tau \int_0^\tau \alpha mf(N^*(t)) dt$ minus the total removal rate $\delta + D$ due to death and washout. Hence σ_0 can be viewed as the average net growth rate of the phytoplankton.

PROPOSITION 2.1 *If $\sigma_0 < 0$, then solutions of Equation (4) satisfy $\lim_{t \rightarrow \infty} P(t) = \lim_{t \rightarrow \infty} Z(t) = 0$.*

Proof We may assume $P(0) > 0$. Since $\dot{P} \leq [\alpha mf(N^*(t)) - \delta - D]P$ for $t \geq 0$, consider the following equation

$$\dot{x} = [\alpha mf(N^*(t)) - \delta - D]x$$

with $x(0) = P(0)$. The solution can be written explicitly as

$$\begin{aligned} x(t) &= x(0)e^{\int_0^t [\alpha mf(N^*(r)) - \delta - D] dr} \\ &= x(0)e^{\int_0^{t_0} [\alpha mf(N^*(r)) - \delta - D] dr} e^{\int_{t_0}^{n\tau+t_0} [\alpha mf(N^*(r)) - \delta - D] dr} \\ &= x(0)e^{\int_0^{t_0} [\alpha mf(N^*(r)) - \delta - D] dr} e^{\int_0^{n\tau} [\alpha mf(N^*(r)) - \delta - D] dr} \end{aligned}$$

for some $0 \leq t_0 < \tau$ and $n > 0$, where t_0 and n depend on t . Notice $t \rightarrow \infty$ if and only if $n \rightarrow \infty$. Hence $\lim_{t \rightarrow \infty} x(t) = 0$ as $\sigma_0 < 0$. As a result, $\lim_{t \rightarrow \infty} P(t) = 0$, and thus $\lim_{t \rightarrow \infty} Z(t) = 0$. ■

Suppose now $\sigma_0 > 0$. Consider the linear periodic system

$$\dot{X} = J_0X \tag{7}$$

where J_0 is given in Equation (5). Let $\Phi(t)$ be the fundamental matrix solution of the linear system (7) with $\Phi(0) = I$, the identity matrix. Then the Floquet multipliers of $(0, 0)$ are the eigenvalues of $\Phi(\tau)$ [8]. Since

$$\Phi(\tau) = \begin{pmatrix} e^{\int_0^\tau [\alpha mf(N^*(t)) - \delta - D] dt} & 0 \\ 0 & e^{-(\epsilon + D)\tau} \end{pmatrix} \tag{8}$$

and $\sigma_0 > 0$, we see that $(0, 0)$ is unstable.

PROPOSITION 2.2 *Suppose $\sigma_0 > 0$. Then Equation (4) has a unique τ -periodic solution of the form $(\bar{P}(t), 0)$ where $\bar{P}(t) > 0$. Moreover, solutions of Equation (4) with $P(0) > 0$ and $Z(0) = 0$ converge to $(\bar{P}(t), 0)$ as $t \rightarrow \infty$.*

Proof Since $Z(t) = 0$ for $t \geq 0$, we consider the following equation

$$\dot{P} = [\alpha mf(N^*(t) - P) - \delta - D]P, \quad 0 \leq P(0) \leq N^*(0). \tag{9}$$

Let $T_0 : [0, N^*(0)] \rightarrow [0, N^*(0)]$ denote the Poincaré map induced by Equation (9), i.e., $T_0(P_0) = P(\tau, P_0)$, where $P(t, P_0)$ is the solution of Equation (9) with $P(0) = P_0$.

Notice $T_0(0) = 0$, $T_0(N^*(0)) < N^*(0)$, and $\dot{T}_0 = \partial P(\tau, P_0)/\partial P_0 = v(\tau)$, where $v(t)$ satisfies

$$\begin{aligned} \dot{v} &= [\alpha m f(N^*(t) - P) - \delta - D - \alpha m f'(N^*(t) - P)P]v \\ v(0) &= 1. \end{aligned}$$

Therefore, $\dot{T}_0 > 0$, and in particular when $P_0 = 0$, we have

$$v(\tau) = e^{\int_0^\tau [\alpha m f(N^*(t)) - \delta - D] dt} > 1.$$

Thus, $\dot{T}_0(0) > 1$, and the map T_0 has a unique positive fixed point \bar{p} , $\bar{p} < N^*(0)$, which corresponds to a unique positive τ -periodic solution $\bar{P}(t)$ for Equation (9). Since the map T_0 is monotone increasing, it can be easily shown that $\lim_{n \rightarrow \infty} T_0^n(p) = \bar{p}$ for $0 < p \leq N^*(0)$. Consequently, solutions of (9) with $P(0) > 0$ satisfy $\lim_{t \rightarrow \infty} (P(t) - \bar{P}(t)) = 0$. ■

Assume $\sigma_0 > 0$ and let

$$\sigma_1 = \frac{1}{\tau} \int_0^\tau [\beta c g(\bar{P}(t)) - \epsilon - D] dt. \quad (10)$$

Similar to σ_0 , σ_1 can be viewed as the average maximal growth rate of zooplankton when phytoplankton population is stabilized at $\bar{P}(t)$ minus the total zooplankton removal rate $\epsilon + D$.

PROPOSITION 2.3 *Let $\sigma_0 > 0$ and $\sigma_1 < 0$. Then solutions of Equation (4) with $P(0) > 0$ satisfy $\lim_{t \rightarrow \infty} (P(t) - \bar{P}(t)) = \lim_{t \rightarrow \infty} Z(t) = 0$.*

Proof We claim that $\lim_{t \rightarrow \infty} Z(t) = 0$. Since $\dot{P} \leq [\alpha m f(N^*(t) - P) - \delta - D]P$ for all $t \geq 0$, consider the following equation:

$$\dot{x} = [\alpha m f(N^*(t) - x) - \delta - D]x, \quad x(0) = P(0). \quad (11)$$

Observe that $P(t) \leq x(t)$ for $t \geq 0$. Since $x(t) \rightarrow \bar{P}(t)$ as $t \rightarrow \infty$ by Proposition 2.2, $\liminf_{t \rightarrow \infty} (x(t) - \bar{P}(t)) = 0$. Hence for any $\eta > 0$ given, there exists $t_0 > 0$ such that $x(t) \leq \bar{P}(t) + \eta$ for $t \geq t_0$. As a result, $P(t) \leq \bar{P}(t) + \eta$ for $t \geq t_0$. By our assumption $\sigma_1 < 0$, we can choose $\eta > 0$ such that

$$\int_0^\tau [\beta c g(\bar{P}(t) + \eta) - \epsilon - D] dt < 0.$$

Consequently, $\dot{Z} \leq [\beta c g(\bar{P}(t) + \eta) - \epsilon - D]Z$ for $t \geq t_0$ implies $\lim_{t \rightarrow \infty} Z(t) = 0$.

It remains to show that $\lim_{t \rightarrow \infty} (\bar{P}(t) - P(t)) = 0$. Consider the Poincaré map T induced by system (4), $T(P_0, Z_0) = (P(\tau), Z(\tau))$, where $(P(t), Z(t))$ is the solution of Equation (4) with initial condition (P_0, Z_0) . Since $\lim_{t \rightarrow \infty} Z(t) = 0$, $\lim_{n \rightarrow \infty} T^n(P_0, Z_0)$ lies on the P -axis. Moreover, $T^n(P_0, 0) = (T_0^n P_0, 0)$, where T_0 is the Poincaré map associated with Equation (9). Since T_0 has a unique positive fixed point \bar{p} which is moreover globally asymptotically stable for T_0 in $(0, N^*(0)]$, it follows that $T^n(P_0, 0)$ converges to the fixed point $(\bar{p}, 0)$. Therefore the periodic solution $(\bar{P}(t), 0)$ is globally asymptotically stable. ■

Suppose now $\sigma_0 > 0$ and $\sigma_1 > 0$. Then the floquet multipliers of the periodic solution $(\bar{P}(t), 0)$ are the eigenvalues of $\Phi_1(\tau)$, where $\Phi_1(t)$ is the fundamental matrix solution of $\dot{X} = J_1 X$ with

$$J_1 = \begin{pmatrix} J_{11} & -\alpha m f'(N^*(t) - \bar{P}(t))\bar{P}(t) - c g(\bar{P}(t)) \\ 0 & \beta c g(\bar{P}(t)) - \epsilon - D \end{pmatrix}, \tag{12}$$

where

$$J_{11} = \alpha m f(N^*(t) - \bar{P}(t)) - \delta - D - \alpha m f'(N^*(t) - \bar{P}(t))\bar{P}(t).$$

It follows that the periodic solution $(\bar{P}(t), 0)$ is unstable as $\sigma_1 > 0$. Similar to the arguments used in [18,42], we can prove that both populations can coexist by using the concepts of uniform persistence.

THEOREM 2.4 *The asymptotic dynamics of system (1) are summarized below.*

- (a) *If $\sigma_0 < 0$, then solutions of Equation (1) are asymptotic to $(N^*(t), 0, 0)$.*
- (b) *If $\sigma_0 > 0$ and $\sigma_1 < 0$, then solutions $(N(t), P(t), Z(t))$ of Equation (1) with $P(0) > 0$ are asymptotic to $(N^*(t) - \bar{P}(t), \bar{P}(t), 0)$ as $t \rightarrow \infty$*
- (c) *If $\sigma_0, \sigma_1 > 0$, then system (1) is uniformly persistent and has a positive τ -periodic solution.*

Proof We rewrite system (4) as $\dot{Y} = F(Y, t)$ and system (3) as $\dot{X} = F(X, t) + R(X, t)$. Notice there exists $C = D \max_{0 \leq t \leq \tau} N^*(t)$ such that $|R(X, t)| \leq C e^{-Dt}$ for $t \geq 0$ for all solution $X(t)$ of system (3). As a result, Lemma A.4 of Hale and Somolinos [14] implies that the asymptotic behaviour of Equations (3) and (4) are the same. Since systems (1) and (3) are equivalent, we can conclude that systems (1) and (4) have the same asymptotic dynamics. Therefore, the proof of (a) and (b) follows from Propositions 2.1 and 2.3, respectively.

To prove (c), we first apply Theorem 3.1 of Butler and Waltman [5] to show uniform persistence of the limiting system (4). Let \mathcal{F} be the flow generated by system (4) and $\partial\mathcal{F}$ be \mathcal{F} restricted to the boundary of Γ . We need to verify that $\partial\mathcal{F}$ is isolated and acyclic. Let $M_0 = \{(0, 0)\}$ and $M_1 = \{(\bar{P}(t), 0) : 0 \leq t \leq \tau\}$. Then the invariant set of $\partial\mathcal{F}$ is $\{M_0, M_1\}$. It is clear that $\partial\mathcal{F}$ is acyclic as M_0 and M_1 are globally attracting on the positive Z -axis and P -axis, respectively, and thus no subset of $\{M_0, M_1\}$ can form a cycle.

It remains to prove that each M_i is isolated for $\partial\mathcal{F}$ and for \mathcal{F} , respectively, for $i = 0, 1$. We only verify that M_0 is isolated for \mathcal{F} as the remaining assertion can be argued similarly. Let $c_0 = \max_{0 \leq P \leq N^*(0)} g'(P)$. By our assumption, we can choose $\rho > 0$ such that

$$\frac{1}{\tau} \int_0^\tau [\alpha m f(N^*(t) - \rho) - \delta - D - c c_0 \rho] dt > 0. \tag{13}$$

Let $\mathcal{N} = \{(P, Z) \in \Gamma : d((P, Z), M_0) < \rho\}$, where d is the Euclidean metric on \mathbb{R}^2 . We show that \mathcal{N} is an isolated neighbourhood of M_0 in Γ .

If this is not true, then there exists an invariant set V in Γ such that $M_0 \subset V \subset \mathcal{N}$ and $V \setminus M_0 \neq \emptyset$. Notice, we can find $P(0), Z(0) > 0$ such that $(P(0), Z(0)) \in V \setminus M_0$. On the other hand, $V \subset \mathcal{N}$ implies

$$\begin{aligned} \frac{\dot{P}}{P} &= \alpha m f(N^*(t) - P - Z) - \delta - D - \frac{c g(P)}{P} Z \\ &\geq \alpha m f(N^*(t) - \rho) - \delta - D - c c_0 \rho. \end{aligned}$$

Hence,

$$P(t) \geq P(0) e^{\int_0^t [\alpha m f(N^*(s) - \rho) - \delta - D - c c_0 \rho] ds}$$

and we have $\lim_{t \rightarrow \infty} P(t) = \infty$ by inequality (13). This is impossible as solutions of Equation(4) are bounded. Therefore, M_0 must be isolated in $\partial\mathcal{F}$. Furthermore, let $\overset{\circ}{\Gamma}$ denote the interior of

Γ and $W^+(M_i)$ be the stable manifold of M_i , $i = 0, 1$. It follows from the Floquet multipliers of M_i that $W^+(M_i)$ is disjoint from $\overset{\circ}{\Gamma}$ for $i = 0, 1$. Hence, Equation (4) is uniformly persistent by Butler and Waltman [5]. The existence of a τ -periodic solution in the interior of Γ follows from a result of Yang and Freedman [42] as the system is dissipative and uniformly persistent. ■

Simulations reveal that the positive periodic solution in Theorem 2.4 (c) is unique and locally stable when $\sigma_1 > 0$ is small and it becomes unstable as we increase σ_1 . Indeed, we let $N^0(t) = 10 + 5 \sin(\pi t/10)$, $f(x) = x/2 + x'$, and $g(x) = x/1 + x$. Notice Michaelis-Menton functions f and g have been frequently used in the literature to model plankton uptake rates. We first choose the following parameter values: $D = 0.2$, $\delta = 9$, $\epsilon = 0.01$, $c = 2$, $m = 13$, $\alpha = 0.9$, $\beta = 0.2$, $d = 2$, and $b = 10$. Then $\sigma_0 = 0.4993$ and $\sigma_1 = 0.0475$. Figure 1(a) plots two solutions with initial conditions $(P(0), Z(0)) = (3, 1)$ for the solid line, and with $(P(0), Z(0)) = (3.1, 2.9)$ for the dashed line. Both solutions converge to the positive periodic solution. When we change c to 8, $\sigma_1 = 0.8200$ becomes larger. Figure 1(b) demonstrates that the positive periodic solution becomes unstable. In this simulation, we use the same initial conditions as for Figure 1(a).

We can summarize our results of Theorem 2.4 in biological terms as follows. If the average maximal growth rate $1/\tau \int_0^\tau \alpha m f(N^*(t)) dt$ of phytoplankton is less than the total removal rate $\delta + D$, i.e., $\sigma_0 < 0$, then phytoplankton population goes extinct and so does the zooplankton. If the average maximal growth rate of phytoplankton exceeds its total removal rate, i.e., $\sigma_0 > 0$, then the phytoplankton population can stabilize in a positive periodic solution fashion in the absence of zooplankton, namely $\bar{P}(t)$. Consequently, zooplankton population becomes extinct if its average maximal growth rate $1/\tau \int_0^\tau \beta c g(\bar{P}(t)) dt$ when phytoplankton is stabilized is less than its total removal rate $\epsilon + D$, and both populations can coexist if these average maximal growth rates are greater than the total removal rates.

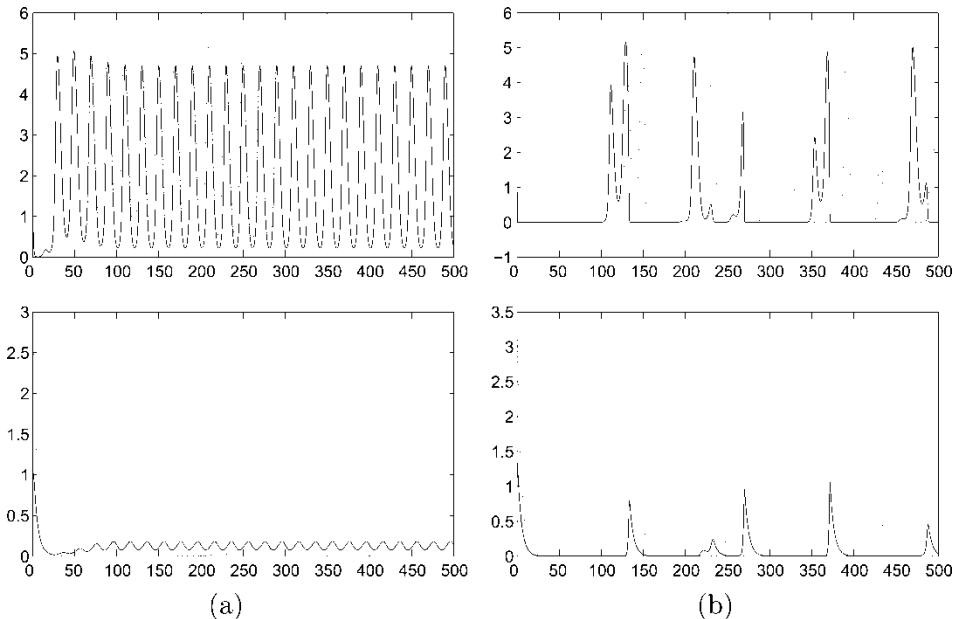


Figure 1. This figure plots solutions of system (1). Two solutions are given in (a) when $\sigma_0 = 0.4993$ and $\sigma_1 = 0.0475$. Two solutions are provided in (b) when $\sigma_0 = 0.4993$ and $\sigma_1 = 0.8200$.

3. A nutrient–plankton–toxin model with inhibition of the phytoplankton

Motivated by the discussion of Section 1, in this section we will consider the situation when a toxic substance has negative effects on the phytoplankton. Specifically, the uptake rate and consequently the growth rate of phytoplankton is inhibited by the presence of the toxin, but zooplankton can consume the substance without any effect. For example, in a marine planktonic community comprising mainly diatoms and herbivorous copepods in a low silicate, elevated copper environment [34], copper will harm only diatoms and not crustaceans. At low concentrations, the herbicide triazine also affects primary producers directly by inhibiting photosynthesis, while effects on subsequent trophic levels only would be indirect [34]. Our goal is to study toxic effects on the nutrient–plankton system by investigating simple solutions and asymptotic dynamics analytically whenever it is possible.

It is assumed that the toxin is continuously pouring into the system with constant input concentration S^0 at the same constant rate D as the nutrient. As a first guess one would expect nutrient and contaminant input to be regularly coupled (*e.g.* both compounds being equally diluted by periodical rainfall, or as river water laden with both compounds discharging into a lake or an coastal area [34]). This is the case for pulsed river diversions in Louisiana [36]. But, there are also several scenarios where nutrient input is uncoupled from the influx or the concentration of contaminants. These are the scenarios we are referring to in this paper. Some examples are related to the fact that in aquatic as well as terrestrial environments consumers often regulate the input and cycling of nutrients [37].

Diel vertical migration of the zooplankton is a well-known predator avoidance mechanism taking place in lakes as well as in coastal or open oceans systems [39,41]. Zooplankton is known to be able to release relevant amounts of nutrients, both nitrogen and phosphorus, to the surrounding water [2,12,23]. With the zooplankton largely higher abundant in the euphotic layer at night this will imply a night-time nutrient pulse available for the phytoplankton that is uncoupled from a potential contaminant background. Beside these active migrations of zooplankton triggering the pulsed nutrient input passive accumulation of zooplankton by periodically tidal currents are known [20,43] generating identical effects of pulsed nutrient enrichments.

Some diatoms or cyanobacteria are able to actively regulate their buoyancy and hence can vertically migrate [11,15,25]. In contrast to the zooplankton these organisms perform diel vertical migrations to gather nutrients in the deeper water at night-time [1,38,40]. At daytime they float up into the euphotic layer where they use the nutrients collected during night to perform photosynthesis in the less nutrient rich upper layer. Since every plankton cell is leaky to a certain extent, and substances can be additionally released by sloppy grazing, some of the nutrients gathered in the deep are released to the water in the upper layer. This again represents a periodical input of nutrients to a system while potential toxin levels remain unchanged.

Let $S(t)$ denote the toxic concentration at time t . It is assumed that zooplankton can uptake the substance without any effect while phytoplankton's nutrient uptake rate is decreased by a fraction, $h(S)$, depending only on the toxin level S . Zooplankton's toxin uptake rate is denoted by u . Functions h and u are assumed to satisfy the following assumptions.

$$(H2) \quad h \in C^1[0, \infty), \quad h(0) = 1, \quad h'(x) < 0 \quad \text{and} \quad h(x) > 0 \quad \text{for all} \quad x \geq 0.$$

$$(H3) \quad u \in C^1[0, \infty), \quad u(0) = 0, \quad u'(x) > 0 \quad \text{for} \quad x \geq 0 \quad \text{and} \quad \lim_{x \rightarrow \infty} u(x) = 1.$$

Let $b > 0$ denote the maximum zooplankton toxin uptake rate. Similar to the previous model, we assume that the ecosystem under study is closed. With the above biological assumptions, the

plankton–toxin interaction is given below.

$$\begin{aligned}\dot{N} &= D(N^0(t) - N) - mf(N)h(S)P + \delta P + \epsilon Z + (1 - \beta)cg(P)Z + (1 - \alpha)mf(N)h(S)P, \\ \dot{P} &= [\alpha mf(N)h(S) - \delta - D]P - cg(P)Z, \\ \dot{Z} &= [\beta cg(P) - \epsilon - D]Z, \\ \dot{S} &= D(S^0 - S) - bu(S)Z, \quad N(0), P(0), Z(0), S(0) \geq 0,\end{aligned}\tag{14}$$

where $0 < \alpha, \beta \leq 1$, and $D, N^0, S^0, m, b, c, \epsilon, \delta > 0$.

Notice f and g have the same assumption as in Section 2. Although the phytoplankton may uptake the toxin so that its growth rate is inhibited, however, since the toxin concentration is usually very small, we assume that the uptake function f does not depend on S explicitly. System (14) can be regarded as an approximation of a more realistic model.

Since $\dot{S}(t) \leq D(S^0 - S(t))$ for $t \geq 0$, $\limsup_{t \rightarrow \infty} S(t) \leq S^0$. Consequently, using the same argument as we did for system (1), it can be easily seen that solutions of Equation (14) remain nonnegative and are bounded. Therefore, it can be shown that solutions of Equation (14) satisfy

$$0 < \liminf_{t \rightarrow \infty} S(t) \leq \limsup_{t \rightarrow \infty} S(t) \leq S^0.\tag{15}$$

Indeed, if $\liminf_{t \rightarrow \infty} S(t) = 0$, then there exists a sequence $\{t_n\}$, $t_n \rightarrow \infty$, such that $\lim_{n \rightarrow \infty} S(t_n) = 0$. Notice $\lim_{n \rightarrow \infty} \dot{S}(t_n) = 0$ as the right hand side of Equation (14) is bounded. We thus obtain a contraction as $\lim_{n \rightarrow \infty} \dot{S}(t_n) = DS^0 > 0$. Hence, inequality (15) is shown. Furthermore, system (14) has the following limiting system:

$$\begin{aligned}\dot{P} &= [\alpha mf(N^*(t) - P - Z)h(S) - \delta - D]P - cg(P)Z, \\ \dot{Z} &= [\beta cg(P) - \epsilon - D]Z, \\ \dot{S} &= D(S^0 - S) - bu(S)Z, \quad P(0), Z(0), S(0) \geq 0, P(0) + Z(0) \leq N^*(0),\end{aligned}\tag{16}$$

where $N^*(t)$ is the unique positive τ -periodic solution of Equation (2). Notice that system (16) is well defined as $P(t) + Z(t) \leq N^*(t)$ for $t \geq 0$ for all solutions of Equation (16) with $P(0) + Z(0) \leq N^*(0)$. Clearly Equation (16) always has a steady state solution of the form $(0, 0, S^0)$, where both plankton populations are extinct. Let

$$\sigma_0 = \frac{1}{\tau} \int_0^\tau [\alpha mf(N^*(t)) - \delta - D]dt,$$

as defined in Equation (6), and

$$\rho_0 = \frac{1}{\tau} \int_0^\tau [\alpha mf(N^*(t))h(S^0) - \delta - D]dt.\tag{17}$$

Then

$$\rho_0 < \sigma_0.$$

Observe that ρ_0 is the average net growth rate of phytoplankton when toxin is present at its maximum level S^0 , while σ_0 can be viewed as the average net growth rate of phytoplankton when there is no toxin. It is straightforward to show that $(0, 0, S^0)$ is locally stable if $\rho_0 < 0$. Similar to Section 2, we can show that solutions of system (16) asymptotically approach $(0, 0, S^0)$ if $\sigma_0 < 0$, a stronger condition than $\rho_0 < 0$.

PROPOSITION 3.1 *If $\sigma_0 < 0$, then solutions of Equation (16) satisfy $\lim_{t \rightarrow \infty} P(t) = \lim_{t \rightarrow \infty} Z(t) = 0$ and $\lim_{t \rightarrow \infty} S(t) = S^0$.*

It is strongly suspected that complicated dynamical behaviour can occur for system (16) when $\sigma_0 > 0$ and $\rho_0 < 0$. We next use numerical examples to demonstrate the complexity of the model. We use the same functional forms $N^0(t)$, f and g as we did for Figure 1 and let $h(s) = e^{-bs}$ and $u(s) = s/6 + s$. Notice this particular form of h has been used in [24] to model inhibiting mechanism. Parameter values adopted are $D = 0.07$, $\delta = 0.04$, $\epsilon = 0.01$, $c = 0.3$, $m = 5$, $\alpha = 0.9$, $\beta = 0.4$, $b = 6$, and $S^0 = 4$. In this case, $\sigma_0 = 3.6369$ and $\rho_0 = -0.1007$. Therefore, according to Proposition 3.1 that the trivial solution $(0, 0, S^0)$ is locally stable but may not be globally attracting. Simulations exhibit the existence of a positive periodic solution, which is moreover locally stable. Figure 2(a) plots the positive periodic solution. We then use random number generator to simulate the solutions. We first fix initial condition with $S(0) = 1$ and let $P(0)$ and $Z(0)$ vary. Initial conditions that result in convergence to $(0, 0, S^0)$ are denoted by the symbol *, while initial conditions that converging to the positive periodic solution are denoted by dots. We then perform the same procedure for different initial conditions of $S(0)$. Figure 2(b) plots these initial conditions with $S(0) = 1$, $S(0) = 5$, and $S(0) = 10$, respectively. Since $N^*(0) = 8.9$, these

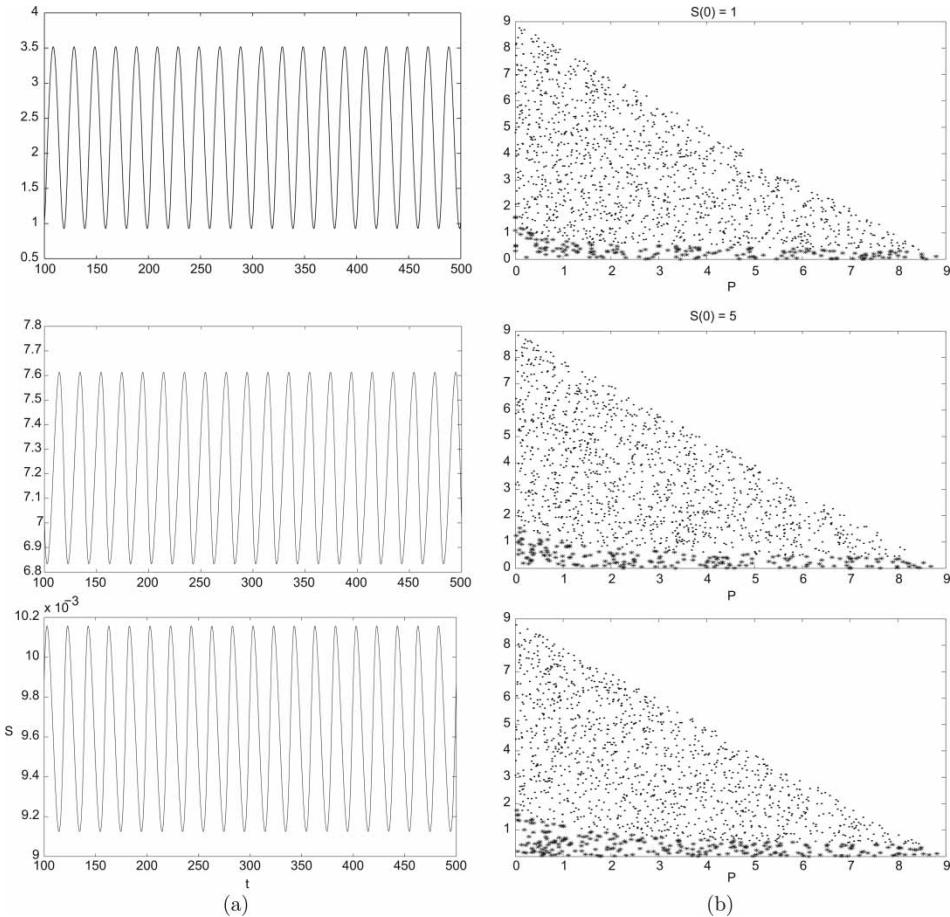


Figure 2. (a) plots the positive periodic solution for system (3.3) when $\rho_0 < 0 < \sigma_0$. (b) plots initial conditions of $P(0)$ and $Z(0)$ with $S(0) = 1$, $S(0) = 5$, and $S(0) = 10$, respectively. Initial conditions that converge to the positive periodic solution and to the steady state solution $(0, 0, S^0)$ are denoted by * and dots, respectively.

initial conditions form a triangle region: $P(0) + Z(0) \leq 8.9$. Similar plots are obtained when we increase initial values for $S(0)$. It is clear from these plots that solutions converge to $(0, 0, S^0)$ when $Z(0)$ is very small, while solutions converge to the positive periodic solution if $Z(0)$ is somewhat larger.

PROPOSITION 3.2 *If $\rho_0 > 0$, then Equation (16) has a unique τ -periodic solution of the form $(\hat{P}(t), 0, S^0)$ where $\hat{P}(t) > 0$, and solutions of Equation (16) with $P(0) > 0$ and $Z(0) = 0$ satisfy $\lim_{t \rightarrow \infty} (P(t) - \hat{P}(t)) = \lim_{t \rightarrow \infty} Z(t) = 0$ and $\lim_{t \rightarrow \infty} S(t) = S^0$.*

Proof Since $Z(t) = 0$ for $t > 0$ if $Z(0) = 0$, it is enough to consider the following system:

$$\begin{aligned}\dot{P} &= [\alpha m f(N^*(t) - P)h(S) - \delta - D]P, \\ \dot{S} &= D(S^0 - S), \quad 0 \leq P(0) \leq N^*(0), \quad S(0) \geq 0.\end{aligned}\tag{18}$$

As \dot{S} can be decoupled from P , we see that $\lim_{t \rightarrow \infty} S(t) = S^0$. Hence for any $\eta > 0$, there exists $t_0 > 0$, such that $S^0 - \eta < S(t) < S^0 + \eta$ for $t \geq t_0$. It is clear that $1/\tau \int_0^\tau [\alpha m f(N^*(t))h(S^0 - \eta) - \delta - D]dt > 0$. We choose $\eta > 0$ such that

$$\frac{1}{\tau} \int_0^\tau [\alpha m f(N^*(t))h(S^0 + \eta) - \delta - D]dt > 0.$$

Notice

$$\alpha m f(N^*(t) - P)h(S^0 + \eta) - \delta - D]P \leq \dot{P} \leq [\alpha m f(N^*(t) - P)h(S^0 - \eta) - \delta - D]P$$

for all $t \geq t_0$.

Consider the corresponding systems:

$$\dot{x} = [\alpha m f(N^*(t) - x)h(S^0 - \eta) - \delta - D]x, \quad x(0) = P(t_0) \leq N^*(0)\tag{19}$$

and

$$\dot{y} = [\alpha m f(N^*(t) - y)h(S^0 + \eta) - \delta - D]y, \quad y(0) = P(t_0) \leq N^*(0).\tag{20}$$

Let T_1 and T_2 be the Poincaré maps induced by Equations (19) and (20), respectively, *i.e.*, $T_1 : [0, N^*(0)] \rightarrow [0, N^*(0)]$ by $T_1(x_0) = x(\tau, x_0)$, where $x(t, x_0)$ is the solution of Equation (19) with initial condition x_0 , and T_2 is defined similarly. It follows that $T_i(0) = 0$, $\dot{T}_i > 0$, $T_i(N^*(0)) < N^*(0)$, and $\dot{T}_i(0) > 1$ for $i = 1, 2$ by the choice of η . Thus the map T_i has a unique positive fixed point \hat{p}_η^i , $\hat{p}_\eta^i < N^*(0)$, and solutions with positive initial conditions under forward iterations of T_i converge to \hat{p}_η^i for $i = 1, 2$. Consequently, solutions of Equations (19) and (20) converge to \hat{P}_η^i , where $\hat{P}_\eta^i(t)$ is the corresponding positive τ -periodic solution of Equations (19) and (20), respectively. On the other hand $\hat{p}_\eta^i \rightarrow \hat{p}$ as $\eta \rightarrow 0^+$ for $i = 1, 2$, where \hat{p} is the unique positive fixed point for the Poincaré map induced by the equation

$$\dot{P} = [\alpha m f(N^*(t) - P)h(S^0) - \delta - D]P, \quad 0 \leq P(0) \leq N^*(0).\tag{21}$$

Therefore, system (16) has a unique τ -periodic solution $(\hat{P}(t), 0, S^0)$. Since $y(t) \leq P(t) \leq x(t)$ for all $t \geq t_0$, we see that $\lim_{t \rightarrow \infty} (P(t) - \hat{P}(t)) = 0$ and the result follows. ■

Suppose now $\rho_0 > 0$ so that Equation (16) has the τ -periodic solution $(\hat{P}(t), 0, S^0)$. Define

$$\rho_1 = \frac{1}{\tau} \int_0^\tau [\beta c g(\hat{P}(t)) - \delta - D]dt.\tag{22}$$

Similar to σ_1 , ρ_1 is the average net growth rate of zooplankton when phytoplankton is stabilized at the level of $\hat{P}(t)$. It is clear that $(\hat{P}(t), 0, S^0)$ is locally stable if $\rho_1 < 0$. We are unable to reach the conclusion analytically as whether Equation (16) has a positive τ -periodic solution when $\rho_1 < 0$.

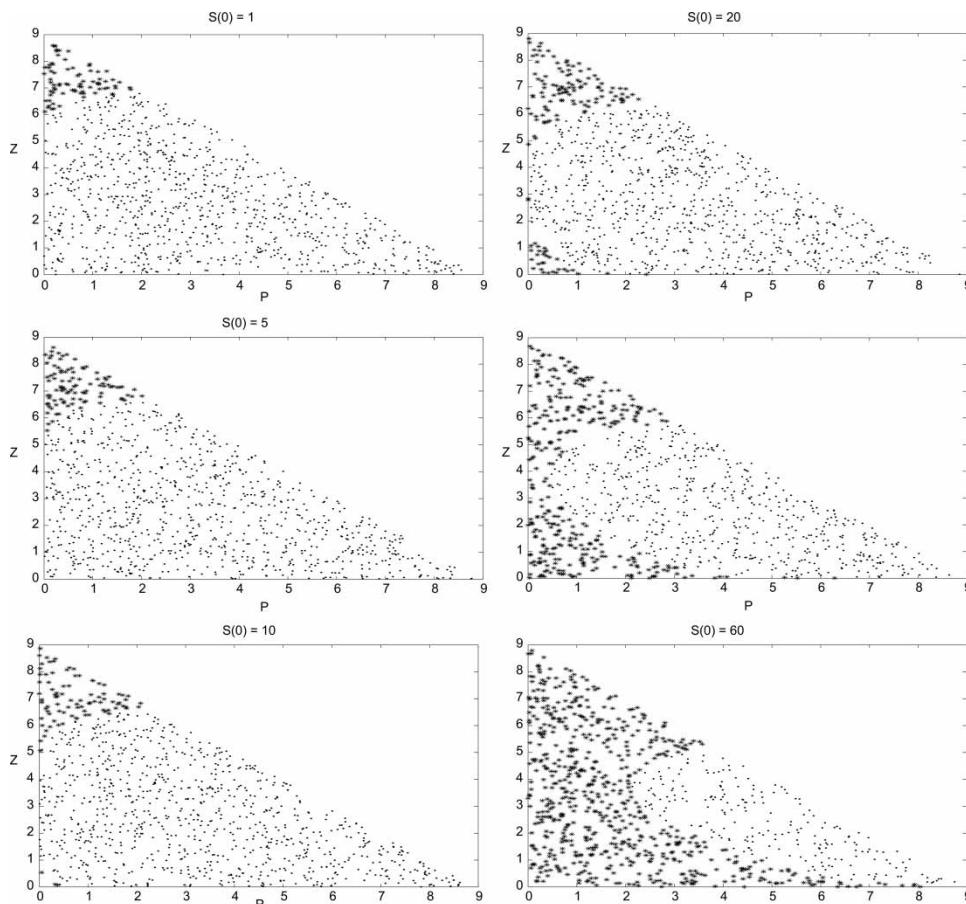


Figure 3. This figure plots initial conditions of $P(0)$ and $Z(0)$ for system (16) when $\rho_1 < 0 < \rho_0$. Initial conditions that converge to the periodic solution $(\hat{P}(t), 0, S^0)$ and to the positive periodic solution are denoted by * and dots, respectively.

We next adopt the same functionals as we did for the previous plots but with somewhat different parameter values: $\alpha = 0.15$, $\beta = 0.35$, and $S^0 = 1$. In this case, $\rho_0 = 0.5145 > 0$ and $\rho_1 = -0.0199 < 0$. The system has a periodic solution $(\hat{P}(t), 0, S^0)$, which is locally stable by the above analysis. Figure 3 plots initial conditions using random number generator for fixed $S(0)$. From Figure 3, we see that as we increase $S(0)$ the region of initial conditions of $P(0)$ and $Z(0)$ that converge to the periodic solution $(\hat{P}(t), 0, S^0)$ gets larger and thus the populations are less likely to persist.

On the other hand, if $\rho_0 > 0$ and $\rho_1 > 0$, applying a similar argument as in Theorem 2.4, one can show that system (14) is uniformly persistent. The proof of the following theorem is parallel to Theorem 2.4 and is therefore omitted.

THEOREM 3.3 *If $\rho_0 > 0$ and $\rho_1 > 0$, then system (14) is uniformly persistent.*

Similar to the interpretations of Theorem 2.4, both populations can survive if the average net growth rates of phytoplankton and zooplankton are greater than zero when phytoplankton's growth rate is inhibited due to the toxin.

4. A nutrient–plankton–toxin model with inhibition of the zooplankton

In this section, we will investigate the effects of toxin when it has a negative impact on the zooplankton's grazing rate while phytoplankton can uptake the toxin without any effect. This scenario applies to chemical defence mechanisms reported both from fresh water and marine environments as well as to the contamination of water bodies with insecticides such as carbaryl, azadirachtin, or cypermetrin. Specifically, the model takes the following form:

$$\begin{aligned}\dot{N} &= D(N^0(t) - N) - mf(N)P + \delta P + \epsilon Z + (1 - \beta)cg(P)h(S)Z + (1 - \alpha)mf(N)P, \\ \dot{P} &= [\alpha mf(N) - \delta - D]P - cg(P)h(S)Z, \\ \dot{Z} &= [\beta cg(P)h(S) - \epsilon - D]Z, \\ \dot{S} &= D(S^0 - S) - dv(S)P, \quad N(0), P(0), Z(0), S(0) \geq 0,\end{aligned}\tag{23}$$

where $0 < \alpha, \beta \leq 1$ and $D, S^0, m, d, c, \epsilon, \delta > 0$.

The functions $f, g, N^0(t)$, and h have the same assumptions as in the previous sections and v has the same hypotheses as u given in Section 3, *i.e.*, (H3). Observe that zooplankton's grazing rate does not depend on S . As in model (14) this is a first approximation to a more realistic system. Since the effects of inhibition is upon the higher trophic level, the analysis of model (23) is very similar to system (1). In particular, $S(t)$ satisfies inequality (15). All solutions of Equation (23) remain nonnegative and are bounded, and Equation (23) has the following limiting system:

$$\begin{aligned}\dot{P} &= [\alpha mf(N^*(t) - P - Z) - \delta - D]P - cg(P)h(S)Z, \\ \dot{Z} &= [\beta cg(P)h(S) - \epsilon - D]Z, \\ \dot{S} &= D(S^0 - S) - dv(S)P, \quad P(0), Z(0), S(0) \geq 0, P(0) + Z(0) \leq N^*(0),\end{aligned}\tag{24}$$

where $N^*(t)$ is the positive τ -periodic solution of Equation (2). Note Equation (24) is well-defined and has a steady state solution $(0, 0, S^0)$ for which both plankton populations are not present.

Let σ_0 be defined as in Section 2, *i.e.*,

$$\sigma_0 = 1/\tau \int_0^\tau [\alpha mf(N^*(t)) - \delta - D]dt.$$

Then $(0, 0, S^0)$ is locally stable if $\sigma_0 < 0$, and similar to Sections 2 and 3 it can be shown that all solutions of Equation (24) converge to $(0, 0, S^0)$ when $\sigma_0 < 0$.

PROPOSITION 4.1 *If $\sigma_0 < 0$, then solutions of Equation (24) satisfy $\lim_{t \rightarrow \infty} P(t) = \lim_{t \rightarrow \infty} Z(t) = 0$ and $\lim_{t \rightarrow \infty} S(t) = S^0$.*

Suppose now $\sigma_0 > 0$. Since the nonnegative PS -coordinate plane is forward invariant, we consider the following PS -subsystem:

$$\begin{aligned}\dot{P} &= [\alpha mf(N^*(t) - P) - \delta - D]P, \\ \dot{S} &= D(S^0 - S) - dv(S)P, \quad P(0), S(0) \geq 0, P(0) \leq N^*(0).\end{aligned}\tag{25}$$

As the first equation can be decoupled from the second equation and it is indeed the Equation (9), it follows that the first equation of the Equation (25) has a unique positive τ -periodic solution $\bar{P}(t)$ and solutions with $P(0) > 0$ converge to $\bar{P}(t)$. Consider the following periodic equation:

$$\dot{S} = D(S^0 - S) - dv(S)\bar{P}(t).\tag{26}$$

Let $T_2(S_0)$ denote the Poincaré map induced by the above equation, *i.e.*, $T_2(S_0) = S(\tau, S_0)$, where $S(\tau, S_0)$ is the unique solution of Equation (26) with $S(0) = S_0$. Notice $T_2(S^0) < S^0$, $T_2(0) > 0$

and $T_2'(S) > 0$ for $S \geq 0$. We conclude that T_2 has a unique positive fixed point \bar{S} , $\bar{S} < S^0$, and $\lim_{n \rightarrow \infty} T_2^n(S_0) = \bar{S}$ for all $S_0 \geq 0$. As a result, Equation (26) has a unique positive τ -periodic solution $\bar{S}(t)$, $0 < \bar{S}(t) < S^0$ for $t \geq 0$, and solutions of Equation (26) satisfy $\lim_{t \rightarrow \infty} |S(t) - \bar{S}(t)| = 0$. Moreover, it can be shown that solutions of Equation (24) with $Z(0) = 0$ are asymptotic to $(\bar{P}(t), 0, \bar{S}(t))$ as $t \rightarrow \infty$.

Let

$$\hat{\rho}_1 = \frac{1}{\tau} \int_0^\tau [\beta c g(\bar{P}(t)) h(\bar{S}(t)) - \epsilon - D] dt. \tag{27}$$

Parameter $\hat{\rho}_1$ is the average net growth rate of zooplankton when phytoplankton is stabilized at the level of $\bar{P}(t)$. If $\sigma_0 > 0$ and $\hat{\rho}_1 < 0$, then parallel to Proposition 2.3 we have the following result. The proof is similar to the proof of Proposition 2.3 and is omitted.

PROPOSITION 4.2 *Let $\sigma_0 > 0$ and $\hat{\rho}_1 < 0$. Then solutions $(P(t), Z(t), S(t))$ of Equation (24) with $P(0) > 0$ converge to $(\bar{P}(t), 0, \bar{S}(t))$ as $t \rightarrow \infty$.*

We next use parameter values: $D = 0.07$, $\delta = 0.04$, $\epsilon = 0.01$, $c = 0.3$, $m = 5$, $\alpha = 0.9$, $\beta = 0.1$, $d = 2$, $b = 1$, and $S^0 = 1$ for system (24). In this case, $\sigma_0 > 0$ and $\hat{\rho}_1 < 0$. Although not presented in this manuscript, simulations reveal that solutions with $P(0) > 0$ all converge to $(\bar{P}(t), 0, \bar{S}(t))$ which validates Proposition 4.2. Similar to system (1), it can be shown that system (23) is uniformly persistent if $\sigma_0 > 0$ and $\hat{\rho}_1 > 0$.

THEOREM 4.3 *The asymptotic dynamics of system (23) can be summarized below.*

- (a) *If $\sigma_0 < 0$, then solutions of Equation (23) satisfy $\lim_{t \rightarrow \infty} |N(t) - N^*(t)| = \lim_{t \rightarrow \infty} P(t) = \lim_{t \rightarrow \infty} Z(t) = 0$.*
- (b) *If $\sigma_0 > 0$ and $\hat{\rho}_1 < 0$, then solutions of Equation (23) with $P(0) > 0$ satisfy $\lim_{t \rightarrow \infty} |N(t) - (N^*(t) - \bar{P}(t))| = \lim_{t \rightarrow \infty} |P(t) - \bar{P}(t)| = \lim_{t \rightarrow \infty} |S(t) - \bar{S}(t)| = \lim_{t \rightarrow \infty} Z(t) = 0$.*
- (c) *If $\sigma_0 > 0$ and $\hat{\rho}_1 > 0$, then system (23) is uniformly persistent and has a positive τ -periodic solution.*

When we use the same parameter values as above but with $D = 0.01$ and $c = 0.5$, then $\sigma_0 = 3.6999$ and $\hat{\rho}_1 = 0.0253 > 0$. Numerical simulations demonstrate that there exists a unique positive periodic solution, which is moreover asymptotically stable.

5. Discussion

It is well documented that rivers, lakes, and oceans are polluted with either organic and/or inorganic substances. In this manuscript, we present simple mathematical models to investigate toxic effects upon the nutrient–plankton interaction. For simplicity, the proposed ecological systems are assumed to be closed. However, the input nutrient is varied periodically. Although several researchers [6,7,26,27] have studied the impact of viruses upon plankton interactions recently, to the best of our knowledge, there exist no mathematical models of plankton–toxin in the literature other than that in [14]. Moreover, Hsu and Waltman [16,17] have studied inhibition upon microorganisms with models consisting of competing populations. In this manuscript, we investigate predator–prey systems with a resource.

If nutrient concentration is input constantly instead of periodically in system (1), *i.e.*, if $N^0(t) \equiv N^0$, then σ_0 reduces to $\alpha m f(N^0) - \delta - D$, a threshold defined in [19]. The other thresholds σ_1 , ρ_0 , ρ_1 , and $\hat{\rho}_1$ are the same as those introduced in [19] when $N^0(t) \equiv N^0$. In this case, the results obtained in this study recover those results from the previous study [19]. These

thresholds can be viewed as the average net growth rates of phytoplankton and zooplankton under different circumstances when either toxin is absent, or present with effects to different trophic levels.

The dynamical consequence of the populations when zooplankton's grazing rate is inhibited is very similar to the base model (1). This is probably because the effect is upon the higher food chain level, which has less effect to the system. When toxin has a negative effect on the growth rate of phytoplankton, inequality (15) implies that toxin will always remain in the system. As a result, we cannot use σ_0 to predict the system dynamics as we do for system (1) since σ_0 is the average net growth rate of phytoplankton when toxin is absent. At the other extreme, ρ_0 is the average net growth rate of phytoplankton when the toxin is at its maximal level S^0 [inequality (15)].

The simulations in Figure 2 reveal that there exists a unique positive τ -periodic solution when $\rho_0 < 0 < \sigma_0$, and solutions with small $Z(0)$ converge to the steady state solution $(0, 0, S^0)$ where both plankton populations are extinct, while solutions with larger $Z(0)$ converge to the positive periodic solution where both plankton populations are present. This is due to the fact that zooplankton can consume the toxin with no effect. Hence, zooplankton may be regarded as a detoxifier for the environment. Both plankton populations can survive if zooplankton initially has a higher population level to uptake the toxin. If zooplankton population level is not large enough to counter-effect the negative impact of toxin upon the phytoplankton, then both populations will become extinct.

When toxin has a negative effect on the phytoplankton, then $\rho_0 > 0$ implies that the phytoplankton can survive in the absence of zooplankton (Proposition 3.2). If in addition $\rho_1 < 0$, then Figure 3 reveals that when $S(0)$ is small, solutions converge to the positive τ -periodic solution if $Z(0)$ is small. As we increase $S(0)$, we see that the region of initial conditions for which only phytoplankton population can survive includes the lower left corner of small zooplankton and phytoplankton populations, especially when $S(0)$ is larger than 20. Notice in this numerical example $S^0 = 4$. Therefore, as $S(0)$ is increased it will take longer time for $S(t)$ to get closer to S^0 especially when $Z(0)$ is small. Hence, the phytoplankton population's growth rate is severely inhibited for a considerable length of time and, as a result, the zooplankton will go extinct when its population is initially small even when phytoplankton is initially large.

The models we consider in this paper only mimic simple ecological systems. More complicated models would be necessary to describe the details of toxin and plankton interactions. Nonetheless, our results can suggest possible explanations for observed properties concerning specific plankton populations. For example, no plankton populations are present in the Derwent Estuary of Australia (<http://www.ea.gov.au/ssd/publications/ssr/129.html>) despite there being abundant nutrients in the region to support a phytoplankton population. Our results suggest that this is due to an inhibited phytoplankton growth rate and an insufficient zooplankton population to uptake the known toxic pollutants present in the system.

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