Nutrient-phytoplankton-zooplankton models with a toxin

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Abstract. Models of nutrient-plankton interaction with a toxic substance that inhibits either the growth rate of phytoplankton, zooplankton or both populations are proposed and studied. For simplicity, it is assumed that both nutrient and the toxin have the same constant input and washout rate. The effects of toxin upon the existence, magnitude, and stability of the steady states are examined. Numerical simulations demonstrate that the system can have multiple attractors when phytoplankton's nutrient uptake rate is inhibited by the toxin.

1   Introduction

Tiny plankton populates the surface waters of the oceans, rivers, and lakes. Phytoplankton is responsible for approximately 40% of the planet's total annual photosynthetic production. It has been well documented that certain chemicals interfere with phytoplankton growth. Organic (e.g. triazine herbicides, [2, 13, 14, 20]) or inorganic compounds (mainly heavy metals, [6, 13, 14, 15, 18, 19]) both may have harmful effects. For example, samples taken from the inner harbor of the Waukegan area, located in Lake County, Illinois, 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.

In addition to phytoplankton's role as a major contributor of photosynthetic production on earth, plankton populations comprise a large number

of different species and are in the bottom of the food chain. Consequently, the abundance of the populations plays a significant role in marine reserves, fishery management, etc. Due to frequent human activities over lakes, seas and oceans for the past many years, pollution has become a major problem associated with abundance of plankton and marine populations. It is the purpose of this study to investigate the effects of toxin upon the nutrient-phytoplankton-zooplankton interaction. Our models proposed here are different from those plankton systems with multiple nutrients as studied in [1, 8] and references cited therein. In those models with multiple nutrients, nutrient uptake rates of phytoplankton are functions of multiple nutrients. The models presented here consist of a single limiting nutrient, two plankton populations and an inhibitor, where the inhibitor may include agents such as pesticides and heavy metals.

In the early 1980s, Hansen and Hubbell [9] used antibiotic, nalidixic acid, to examine competition of two strains of E. coli. One strain was sensitive and the other was resistant to the inhibitor. This resistance of the population is due to a chromosomal mutation and it does not result in detoxification of the antibiotic. However, resistance by bacteria to antibiotics and heavy metals frequently comes from the acquisition of an extrachromosomal element that encodes an enzyme, which converts the inhibitor into a less toxic form. This reduces the intracellular concentration of chloramphenicol and enables the survival of bacteria that produce the enzyme. It also results in a significant reduction of the antibiotic concentration in the environment [3, 10].

This biological phenomenon motivates our models and study presented here. In one model, the zooplankton consumes 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 other model, phytoplankton is regarded as a detoxifier that uptakes the toxin while zooplankton's grazing rate is severely diminished. We acknowledge that our models are simplified real systems. However, it is a first step in understanding complex interaction between plankton populations and pollution. In doing so, we first propose a simple plankton model and summarize its dynamical consequences. We then examine the effect of toxin upon the existence, magnitude, and stability of the steady states. Criteria for coexistence of both plankton populations are also discussed. However, comparisons between more complex dynamical behavior will only be numerically simulated.

The remainder of this manuscript is organized as follows. A base nutrient-plankton model with instantaneous nutrient recycling is presented in the next

section. Section 3 studies the model when phytoplankton is inhibited by the toxin. Inhibition upon zooplankton is discussed in section 4. Numerical examples will be provided for each section to illustrate complexity of the interaction. The final section provides a brief summary and discussion.

2 The nutrient-phytoplankton-zooplankton model

In this section we shall introduce a base model which will be used to build more complicated systems involving toxic substance in later sections. For simplicity, we assume that the organisms and the nutrient are uniformly distributed over the space. It is conventional to let $N(t)$, $P(t)$, and $Z(t)$ be the nutrient concentration, the phytoplankton population, and zooplankton population at time t, respectively. For convenience, the two plankton levels are modeled 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 per capita nutrient uptake rate is denoted by f, while g is the zooplankton grazing rate. Both functions have the standard monotonic assumptions as the Michaelis-Menton kinetics, Ivelev, and Holling type III functional responses:

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

Let parameter m be the maximal nutrient uptake rate of phytoplankton and c be the maximal zooplankton ingestion rate. Parameters β and α denote the fraction 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 [7]. We assume that the input nutrient concentration is a constant and is denoted by N^0, and the rate of waters flowing in and out of the system is also a constant and denoted by D. By ignoring some biological and physical considerations, both plankton populations are also flowing out of the system with the same constant washout rate D.

It is known that phytoplankton uptakes nutrient and zooplankton preys on the phytoplankton for survival. Consequently, there are minus terms $-mf(N)P$ and $-cg(P)Z$ in the equations for $\dot{N}$ and $\dot{P}$, respectively. As there is no nutrient loss in the system, there are positive feedback terms

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$(1 - \alpha)mf(N)P$ and $(1 - \beta)cg(P)Z$ appeared in the equation for $\dot{N}$ due to instantaneous nutrient recycling. Our model with the above biological assumptions can be written as the following three dimensional ordinary differential equations.

$$\begin{aligned}
\dot{N} &= D(N^0 - N) - mf(N)P + \delta P + \epsilon Z + (1 - \beta)cg(P)Z + (1 - \alpha)mf(N)P \\
\dot{P} &= [\alpha mf(N) - \delta - D]P - cg(P)Z \qquad\qquad (2.1) \\
\dot{Z} &= [\beta cg(P) - \epsilon - D]Z \\
&\quad N(0), P(0), Z(0) \geq 0,
\end{aligned}$$

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

System (2.1) is a simple nutrient-plankton model and its asymptotic dynamics can be easily understood via standard analysis. In particular, solutions of (2.1) exist for all future time. Since $\dot{N}|_{N=0} \geq DN^0 > 0$, $\dot{P}|_{P=0} = \dot{Z}|_{Z=0} = 0$, solutions of (2.1) remain nonnegative. Let $T = N + P + Z$. Then $\dot{T} = D(N^0 - T)$ and we have $\lim_{t \to \infty} T(t) = N^0$, i.e., solutions of (2.1) are bounded. Moreover,

$$\Gamma = \{(N, P, Z) \in \mathbb{R}^3_+ : N + P + Z = N^0\}$$

is a global attractor for the system. Restricted to Γ, (2.1) has the following limiting system,

$$\begin{aligned}
\dot{P} &= [\alpha mf(N^0 - P - Z) - \delta - D]P - cg(P)Z \\
\dot{Z} &= [\beta cg(P) - \epsilon - D]Z \qquad\qquad (2.2) \\
&\quad P(0), Z(0) \geq 0, P(0) + Z(0) \leq N^0.
\end{aligned}$$

Since $N(t) + P(t) + Z(t) = N^0$ for $t \geq 0$ in Γ and solutions of (2.1) remain nonnegative, we see that $P(t) + Z(t) \leq N^0$ for $t \geq 0$, i.e., system (2.2) is well-defined.

In the remainder of this section we shall briefly discuss asymptotic dynamics of system (2.2). There exists a trivial steady state $e_0 = (0, 0)$ for all parameter values. It can be seen that boundary steady state $e_1 = (P_1^u, 0)$ exists if and only if

$$\alpha mf(N^0) > \delta + D, \qquad\qquad (2.3)$$

where P_1^u satisfies $\alpha mf(N^0 - P) = \delta + D$. For the existence of an interior steady state $e_2 = (\bar{P}^u, \bar{Z}^u)$, it is necessary that $\beta cg(P) - \epsilon - D = 0$ has a

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solution $\bar{P}^u$. It follows that $\bar{Z}^u$ must satisfy

$$[\alpha m f(N^0 - \bar{P}^u - Z) - \delta - D]\bar{P}^u = cg(\bar{P}^u)Z.$$

Consequently the above equation has a solution $\bar{Z}^u > 0$ if and only if $\alpha m f(N^0 - \bar{P}^u) > \delta + D$, in which case system (2.2) has a unique interior steady state and $\bar{P}^u + \bar{Z}^u < P_1^u$.

If $\alpha m f(N^0) < \delta + D$, then by the above existence conditions for the boundary state states, we see that e_0 is the only steady state for system (2.2). Moreover,

$$\dot{P} \le [\alpha m f(N^0) - \delta - D]P$$

implies $\lim_{t \to \infty} P(t) = 0$ and thus $\lim_{t \to \infty} Z(t) = 0$, i.e, e_0 is globally asymptotically stable for (2.2) if $\alpha m f(N^0) < \delta + D$.

Suppose on the other hand, $\alpha m f(N^0) > \delta + D$, so that $P_1^u > 0$ exists. If in addition $\beta c g(P_1^u) < \epsilon + D$, we claim that there is no interior equilibrium for (2.2). This is trivial if $\beta c g(P) < \epsilon + D$ for $P \ge 0$. Suppose $g(P) = \dfrac{\epsilon + D}{\beta c}$ has a solution $\bar{P}^u > 0$. Then $P_1^u < \bar{P}^u$ and thus $f(N^0 - \bar{P}^u) < f(N^0 - P_1^u) = \dfrac{\delta + D}{\alpha m}$ and therefore there is no positive steady state. It is then easy to prove that solutions of (2.2) with $P(0) > 0$ converge to e_1. Indeed, since $\dot{P} \le [\alpha m f(N^0 - P) - \delta - D]P$ and $\alpha m f(N^0) > \delta + D$, steady state 0 for the scalar equation $\dot{x} = [\alpha m f(N^0 - x) - \delta - D]x$ is unstable and solutions with $x(0) > 0$ all converge to the steady state P_1^u. Thus we see that $\limsup_{t \to \infty} P(t) \le P_1^u$ for any solution of (2.2). Hence for any $\eta > 0$ there exist $t_1 > 0$ such that $P(t) \le P_1^u + \eta$ for $t \ge t_1$. Since we assume $g(P_1^u) < \dfrac{\epsilon + D}{\beta c}$, we can choose $\eta > 0$ such that $g(P_1^u + \eta) < \dfrac{\epsilon + D}{\beta c}$. It then follows from the second equation of (2.2) that $\lim_{t \to \infty} Z(t) = 0$. As a result, we can prove $\liminf_{t \to \infty} P(t) \ge P_1^u$ if $P(0) > 0$. Therefore solutions of (2.2) with $P(0) > 0$ converge to the steady state e_1 if $\alpha m f(N^0) > \delta + D$ and $\beta c g(P_1^u) < \epsilon + D$.

Suppose now $\alpha m f(N^0) > \delta + D$ and $\beta c g(P_1^u) > \epsilon + D$. Then E_0 and E_1 are saddle points. Apply a similar argument as above, it can be shown that steady state $e_2 = (\bar{P}^u, \bar{Z}^u)$ exists. Also from the Jacobian matrix of (2.2) evaluated at e_2 that e_2 is locally asymptotically stable if $\alpha m f(x) - \delta - D - \alpha m f'(x)\bar{P}^u - cg'(\bar{P}^u)\bar{Z}^u < 0$ where $x = N^0 - \bar{P}^u - \bar{Z}^u$. Moreover, solutions of (2.2) satisfy $P(t) + Z(t) \le P_1^u$ for all t large. Since the stable manifold of e_0

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and e_1 lies on the Z and P-axis, respectively, there is no cyclic trajectories on the boundary. It follows that system (2.2) is uniformly persistent by Thieme [21], i.e., coexistence of both populations results. In the following we shall use LaSalle's invariance principle to prove global asymptotic stability of e_2 in the interior of $\mathbb{R}^2_+$.

Consider a Liapunov function defined on $\mathbb{R}^2_+$ by

$$V(P, Z) = \int_{\bar{P}^u}^{P} \frac{\beta c g(x) - \epsilon - D}{c g(x)} dx + \int_{\bar{Z}^u}^{Z} \frac{x - \bar{Z}^u}{x} dx.$$

Notice that $V \geq 0$ and $V(P, Z) = 0$ if and only if $P = \bar{P}^u$ and $Z = \bar{Z}^u$. The time derivative of V along trajectories of (2.2) after some simplifications becomes

$$\dot{V}(P, Z) = \beta c [g(P) - g(\bar{P}^u)][\frac{\alpha m f(N^0 - P - Z)P - (\delta + D)P}{c g(P)} - \bar{Z}^u].$$

Since $g'(P) > 0$ for $P \geq 0$, we impose condition

$$\beta c (P - \bar{P}^u)[\frac{\alpha m f(N^0 - P - Z)P - (\delta + D)P}{c g(P)} - \bar{Z}^u] \ < \ 0 \qquad (2.4)$$

for $P > 0$, $Z > 0$ and $P + Z \leq P_1^u$. As a result, $\dot{V} \leq 0$ and $\dot{V} = 0$ if and only if $P = \bar{P}^u$. Since the only invariant subset of $\{(P, Z) \in \mathbb{R}^2_+ : \dot{V} = 0\}$ is e_2, it follows that e_2 is globally asymptotically stable in the interior of $\mathbb{R}^2_+$ [5]. The asymptotic dynamics of (2.1) can be summarized below.

Theorem 2.1 *Dynamics of system (2.1) are described below.*

(a) *If $\alpha m f(N^0) < \delta + D$, then $E_0^u = (N^0, 0, 0)$ is the only steady state for (2.1) and solutions of (2.1) all converge to E_0.*

(b) *If $\alpha m f(N^0) > \delta + D$, then (2.1) has two steady states E_0^u and $E_1^u = (N^0 - P_1^u, P_1^u, 0)$. In addition if $\beta c g(P_1^u) < \epsilon + D$, then solutions of (2.1) with $P(0) > 0$ converge to E_1^u.*

(c) *If $\alpha m f(N^0) > \delta + D$ and $\beta c g(P_1^u) > \epsilon + D$, then (2.1) has three steady states E_0^u, E_1^u, and the interior steady state $E_2^u = (N^0 - \bar{P}^u - \bar{Z}^u, \bar{P}^u, \bar{Z}^u)$, and system (2.1) is uniformly persistent. Moreover, solutions of (2.1) with positive initial conditions converge to E_2^u if in addition (2.4) holds.*

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3 A nutrient-plankton-toxin model with inhibition on the phytoplankton

Motivated by the discussion in Section 1, we will consider the situation when toxic substance has a negative effect 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. Our goal is to study toxic effect on the natural nutrient-plankton system by investigating simple solutions and asymptotic dynamics analytically whenever it is possible.

Let $S(t)$ denote the toxic concentration at time t. In addition to the nutrient concentration, it is assumed that the toxin is continuously pouring into the system with the constant input concentration S^0 and the same constant input rate D as the nutrient. It is assumed that zooplankton can uptake the substance without any effect while phytoplankton's uptake rate is decreased by a function $h(S)$ depending on the toxin level S. The toxin uptake rate of zooplankton is denoted by u. Functions h and u are assumed to satisfy the following assumptions.

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

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

The choices of h such as $\lim_{x\to\infty} h(x) = 0$ or $\lim_{x\to\infty} h(x) > 0$ depend on the types of toxin and how harmful it is to the phytoplankton. If $h(\infty) = 0$, then the phytoplankton population growth rate will be severely inhibited when the toxin concentration is abundant. If $h(\infty) > 0$, then the population growth rate is inhibited but is not completely diminished even when there is a large amount of toxin in the system. Let $b > 0$ denote the maximum zooplankton toxin uptake rate.

With these biological assumptions, our model is given below.

$$
\begin{aligned}
\dot{N} &= D(N^0 - N) - mf(N)h(S)P + \delta P + \epsilon Z + (1-\beta)cg(P)Z \\
&\quad + (1-\alpha)mf(N)h(S)P \\
\dot{P} &= [\alpha mf(N)h(S) - \delta - D]P - cg(P)Z \\
\dot{Z} &= [\beta cg(P) - \epsilon - D]Z \\
\dot{S} &= D(S^0 - S) - bu(S)Z \\
&\quad N(0), P(0), Z(0), S(0) \geq 0,
\end{aligned}
\tag{3.1}
$$

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

Clearly solutions of (3.1) exist and remain nonnegative for $t \geq 0$. Similar to the discussion for system (2.1), if we let $T = N + P + Z$, then $\dot{T} = D(N^0 - T)$ and thus $\lim_{t \to \infty} T(t) = N^0$. On the other hand, $\dot{S} \leq D(S^0 - S)$ implies $\limsup_{t \to \infty} S(t) \leq S^0$ for any solution of (3.1). Therefore, solutions of (3.1) are bounded and we have the following lemma.

Lemma 3.1 *Solutions of (3.1) remain nonnegative and are bounded for $t \geq 0$.*

Since ω-limit sets of solutions of (3.1) lie in

$$\Omega = \{(N, P, Z, S) \in \mathbb{R}_+^4 : N + P + Z = N^0\}, \tag{3.2}$$

system (3.1) has the following limiting system

$$\begin{aligned}
\dot{P} &= [\alpha m f(N^0 - P - Z)h(S) - \delta - D]P - cg(P)Z \\
\dot{Z} &= [\beta cg(P) - \epsilon - D]Z \\
\dot{S} &= D(S^0 - S) - bu(S)Z \\
&\quad P(0), Z(0), S(0) \geq 0, P(0) + Z(0) \leq N^0.
\end{aligned} \tag{3.3}$$

Notice that system (3.3) is well defined as $P(t) + Z(t) \leq N^0$ for $t \geq 0$ for all solutions of (3.1) with $N(0) + P(0) + Z(0) = N^0$. As before, we first examine steady state solutions of (3.3). Clearly steady state $\hat{e}_0 = (0, 0, S^0)$ always exists for (3.2). Steady state $\hat{e}_1 = (\hat{P}_1, 0, S^0)$ exists if and only if

$$\alpha m f(N^0)h(S^0) > \delta + D, \tag{3.4}$$

where $\hat{P}_1$ satisfies $\alpha m f(N^0 - P)h(S^0) = \delta + D$. Comparing inequalities (3.4) and (2.3), we see that (2.3) is more likely to occur. Therefore in order for the phytoplankton to survive when there is an external toxin inhibiting the growth rate of phytoplankton, it is necessary to have a higher input nutrient concentration N^0. In particular, the higher the toxin input S^0 to the system, the higher the nutrient concentration N^0. Moreover, since $S^0 > 0$, $0 < h(S^0) < 1$, we see that

$$\hat{P}_1 < P_1^u,$$

where P_1^u is the P-component of the steady state e_1 for system (2.2), i.e., toxic substance inhibiting the growth rate of phytoplankton can reduce the phytoplankton population size of the equilibrium with the absence of zooplankton.

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Since there is no steady state of the form $(0, Z, S)$ with $Z, S > 0$, we turn to investigate the effect of toxin upon the existence and magnitude of an interior steady state $(\bar{P}, \bar{Z}, \bar{S})$. We see from the equilibrium equations that $\bar{P}$ must solve

$$\beta c g(P) = \epsilon + D.$$

Since Z can be written in terms of S as

$$Z = \frac{D(S^0 - S)}{bu(S)} = \hat{g}(S),$$

the S component of an interior steady state, $\bar{S}$, must satisfy

$$[\alpha m f(N^0 - \bar{P} - \hat{g}(S))h(S) - \delta - D]\bar{P} \;=\; cg(\bar{P})\hat{g}(S). \qquad (3.5)$$

Clearly $\hat{g}'(S) < 0$ for $0 < S \leq S^0$, and (3.5) has no positive solution if $\alpha m f(N^0 - \bar{P} - \hat{g}(S))h(S) < \delta + D$ for all $S, 0 < S \leq S^0$. However, if the above inequality is reversed for some $S, 0 < S \leq S^0$, then it is inconclusive as to whether (3.5) has no positive solutions, a unique positive solution, or multiple positive solutions. Consequently, the number of interior steady states of (3.3) can not be determined. We will use numerical examples to demonstrate our finding.

On the other hand, suppose an interior steady state $\hat{e}_2 = (\bar{P}, \bar{Z}, \bar{S})$ does exist for (3.3). Then

$$\bar{P} = \bar{P}^u,$$

and from the P equation we can conclude that

$$\bar{Z} < \bar{Z}^u.$$

Therefore toxic effect on the growth rate of phytoplankton can lower the zooplankton population size at the coexisting equilibrium, but not on the phytoplankton population. This is different from our earlier conclusion for the steady state of the form $(P, 0, S)$. It seems counterintuitive. However, since zooplankton uptakes toxin and the toxin has a negative effect on the phytoplankton if there is no zooplankton population to detoxify the environment, we see that $P_1 < P_1^u$ in the steady state of the form $(P, 0, S)$ when there is no zooplankton present. On the other hand due to the presence of zooplankton to consume toxin, we have $\bar{P} = \bar{P}^u$ for the interior steady states. But then zooplankton has a lower population size at least in the interior steady state as the population uses part of its energy to detoxify the toxin.

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We now turn to discuss asymptotic dynamics of system (3.3). It is clear that $\lim_{t \to \infty} P(t) = 0$ if $\alpha m f(N^0) < \delta + D$. Furthermore, as

$$\dot{P} \leq [\alpha m f(N^0 - P) - \delta - D]P,$$

we see that solutions $(P(t), Z(t), S(t))$ of (3.2) satisfy $\limsup_{t \to \infty} P(t) \leq P_1^u$ if $\alpha m f(N^0) > \delta + D$. The Jacobian matrix of (3.3) at the trivial steady state $\hat{e}_0 = (0, 0, S^0)$ has a lower triangular form and $\hat{e}_0$ is asymptotically stable if

$$\alpha m f(N^0) h(S^0) \quad < \quad \delta + D. \tag{3.6}$$

Since $h(S^0) < 1$, we immediately conclude that it is more likely for both populations to become extinct than that of the uninhibited model (2.2) as the above inequality is more likely to occur than $\alpha m f(N^0) < \delta + D$. Moreover, there exists no steady state of the form $\hat{e}_1 = (P_1, 0, S^0)$ and there are also no interior equilibria when (3.6) holds.

Similar to model (2.2), it can be easily shown that if inequality (2.3) holds, i.e., if $\alpha m f(N^0) < \delta + D$, then steady state $\hat{e}_0 = (0, 0, S^0)$ is globally asymptotically stable. However, it is in general not true that $\hat{e}_0$ is globally asymptotically stable when (3.6) is satisfied. Our numerical example given below demonstrates that there is an interior steady state which is moreover locally asymptotically stable when (3.6) holds. Therefore dynamics of system (3.3) are much more complicated than system (2.1). There are multiple attractors even when the trivial steady state is locally asymptotically stable. On the other hand, it can be easily proven that $\hat{e}_0$ is globally asymptotically stable on the nonnegative PS-coordinate plane if (3.6) holds. Furthermore, in addition to (3.6), if
$$\beta c g(P_1^u) \leq \epsilon + D$$
is satisfied, then it is straightforward to show that $\lim_{t \to \infty} Z(t) = 0$, $\lim_{t \to \infty} S(t) = S^0$, and solutions of (3.3) converge to $\hat{e}_0$. The nutrient-plankton interactions are much more complicated than the uninhibited model (2.1). In particular, coexistence of both populations is possible and it depends on initial conditions even when (3.6) holds.

Suppose now $\alpha m f(N^0) h(S^0) > \delta + D$ so that $\hat{e}_1$ exists. From the Jacobian matrix of (3.3) at $\hat{e}_1 = (\hat{P}_1, 0, S^0)$, we see that $\hat{e}_1$ is asymptotically stable if

$$\beta c g(\hat{P}_1) < \epsilon + D.$$

Similar to the discussion for the existence of interior steady states, we are unable to reach the conclusion as whether or not the system has an interior steady state when the above inequality is true. However, when the above inequality and (3.6) are reversed, system (3.3) is uniformly persistent. By using the theory of asymptotic autonomous systems we see that the same is true for the original 4-D system.

Theorem 3.2 *Dynamics of system (3.1) can be summarized below.*

(a) *If $\alpha m f(N^0)h(S^0) < \delta + D$ and $\beta c \leq \epsilon + D$, then $\hat{E}_0 = (N^0, 0, 0, S^0)$ is globally asymptotically stable for system (3.1).*

(b) *If $\alpha m f(N^0)h(S^0) > \delta + D$ and $\beta c g(\hat{P}_1) > \epsilon + D$, then system (3.1) is uniformly persistent.*

Since $\hat{P}_1$ increases with increasing nutrient input N^0, we see from Theorem 3.2(b) that in order for both populations to coexist with each other it is necessary to have a larger nutrient input when there is a toxin concentration inhibiting phytoplankton growth rate.

We now use a numerical example to illustrate complexity of the model. Let $f(x) = \dfrac{x}{2+x}$, $g(x) = \dfrac{x}{1+x}$, $u(S) = \dfrac{S}{6+S}$ and $h(S) = e^{-2S}$. Then system (3.2) becomes

$$
\begin{aligned}
\dot{P} &= [\frac{\alpha m(N^0 - P - Z)}{2 + N^0 - P - Z}h(S) - \delta - D]P - \frac{cP}{1+P}Z \\
\dot{Z} &= [\frac{\beta cP}{1+P} - \epsilon - D]Z \\
\dot{S} &= D(S^0 - S) - \frac{bS}{6+S}Z \\
&\quad P(0), Z(0), S(0) \geq 0, P(0) + Z(0) \leq N^0.
\end{aligned}
\tag{3.7}
$$

Choosing $N^0 = 4.85$, $D = 0.05$, $\delta = 0.4$, $\epsilon = 10^{-5}$, $c = 0.1$, $m = 5$, $\alpha = 0.9$, $\beta = 0.99$, $b = 2$ and $S^0 = 4$, then it is easy to verify that $\alpha m f(N^0)h(S^0) < \delta + D$ and $\alpha m f(N^0) > \delta + D$. Therefore the trivial steady state $E_0 = (0,0,4)$ is locally asymptotically stable. However, numerical simulations showing the existence of an interior steady state and it is also locally asymptotically stable. Consequently, asymptotic behavior of solutions of system (3.7) depend on initial conditions even when (3.6) holds. These plots are given as Figures 1 and 2.

If we use $h(S) = e^{-0.8S}$, $D = 0.07$, $\delta = 0.04$, $c = 0.3$, $\beta = 0.4$, $b = 2$ and the rest of the parameter values are the same as given above, then inequality (3.6) is reversed so that system (3.7) has a steady state $(\hat{P}, 0, S^0) = (1.8540, 0, 4)$. In this case, numerical simulations yield an interior steady state $(2.000, 2.6131, 0.3118)$ and solution with initial condition $(2.5, 2, 3)$ converges to the interior steady state and solution with initial condition $(0.1, 0.2, 7)$ goes to the steady state on the PS-coordinate plane as shown by figure 3. However, we are unable to find multiple interior steady states using these functional forms with various parameter values.

4 The nutrient-plankton-toxin model with inhibition on the zooplankton

In this section we assume that phytoplankton can uptake the toxin without any effect while zooplankton's grazing rate is inhibited by the presence of the toxin. We use the same notation h to represent reduction factor of zooplankton grazing rate. The toxin uptake rate of phytoplankton is denoted by v, where h and v depend on the toxin level S and have the same mathematical assumptions as h and u in the previous section. Moreover, parameter d is the maximal phytoplankton toxin uptake rate. Building upon the base model given in section 2, our model with this biological consideration can be described by the following system of ordinary differential equations.

$$
\begin{aligned}
\dot{N} &= D(N^0 - N) - mf(N)P + \delta P + \epsilon Z + (1 - \beta)cg(P)h(S)Z \\
&\quad + (1 - \alpha)mf(N)P \\
\dot{P} &= [\alpha mf(N) - \delta - D]P - cg(P)h(S)Z \\
\dot{Z} &= [\beta cg(P)h(S) - \epsilon - D]Z \\
\dot{S} &= D(S^0 - S) - dv(S)P \\
&\quad N(0), P(0), Z(0), S(0) \geq 0,
\end{aligned}
\tag{4.1}
$$

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

It can be easily shown that solutions of (4.1) exist, remain nonnegative and are bounded for all $t \geq 0$. The set Ω as defined in (3.2) is also a global

attractor for (4.1), and (4.1) restricted to Ω has the following limiting system

$$
\begin{aligned}
\dot{P} &= [\alpha m f(N^0 - P - Z) - \delta - D]P - cg(P)h(S)Z \\
\dot{Z} &= [\beta cg(P)h(S) - \epsilon - D]Z \\
\dot{S} &= D(S^0 - S) - dv(S)P
\end{aligned} \tag{4.2}
$$
$$
P(0), Z(0), S(0) \geq 0, P(0) + Z(0) \leq N^0.
$$

Similar to system (3.3), (4.2) always has a trivial steady state $e_0^* = (0, 0, S^0)$ and steady state $e_1^* = (P_1^*, 0, S_1^*)$ exists if and only if

$$
\alpha m f(N^0) > \delta + D,
$$

where $P_1^* = P_1^u$ and S_1^* solves

$$
D(S^0 - S) = dv(S)P_1^*.
$$

Moreover

$$
S_1^* < S^0 \text{ and } \hat{P}_1 < P_1^* = P_1^u,
$$

where $\hat{P}_1$ and S^0 are the P, S-components of the steady state $\hat{e}_1 = (\hat{P}_1, 0, S^0)$ for system (3.3). Therefore toxic concentration in the steady state with the absence of zooplankton is smaller in model (4.2) than in system (3.3). This is owing to the fact that phytoplankton can detoxify the environment so that the toxic concentration is lower than the model presented in the previous section, where zooplankton population can uptake the toxin.

Examining the existence of an interior steady state, we see from the third equilibrium equation that P-component of the steady state must satisfy

$$
P = \frac{D(S^0 - S)}{dv(S)} = g^*(S),
$$

where $\lim_{S \to 0^+} g^*(S) = \infty$ and $\dfrac{dg^*(S)}{dS} < 0$ for $0 < S \leq S^0$. Substituting $g^*(S)$ for P in the second equilibrium equation, we have

$$
\beta cg(g^*(S))h(S) = \epsilon + D.
$$

Since $g' > 0$, $h' < 0$, and $\dfrac{dg^*(S)}{dS} < 0$ for $0 < S \leq S^0$, the above equation has a solution $\bar{S}^* < S^0$ if and only if

$$
\beta c > \epsilon + D. \tag{4.3}
$$

Consequently from the first equilibrium equation we see that $\bar{Z}^* > 0$ exists if and only if

$$\alpha m f(N^0 - \bar{P}^*) > \delta + D. \tag{4.4}$$

Therefore steady state $(\bar{P}^*, \bar{Z}^*, \bar{S}^*)$ exists if and only if (4.3) and (4.4) hold; and the interior equilibrium is unique if it exists. Moreover, it is clear that $\bar{P}^* < \bar{P}^u$ and thus $\alpha m f(N^0 - \bar{P}^*) > \delta + D$ is more likely to occur than $\alpha m f(N^0 - \bar{P}^u) > \delta + D$. Consequently, toxic substance inhibits the grazing rate of zooplankton can promote coexistence of both populations in the interior steady state. However, it can lower phytoplankton population level at least in the interior steady state.

We next turn to discuss asymptotic dynamics of system (4.2). Analysis of model (4.2) is parallel to that of system (2.2). In particular, if $\alpha m f(N^0) < \delta + D$, then $e_0^* = (0, 0, S^0)$ is the only steady state and it is globally asymptotically stable. If the inequality is reversed, then steady state $e_1^* = (P_1^*, 0, S_1^*)$ exists. In addition if $\beta c g(P_1^*) h(S_1^*) < \epsilon + D$, then the interior steady state does not exist and it can be easily shown that solutions of (4.2) with $P(0) > 0$ all converge to e_1^*. If $\alpha m f(N^0) > \delta + D$ and $\beta c g(P_1^*) h(S_1^*) > \epsilon + D$, then it is standard to prove uniform persistence of the system. The discussion of model (4.1) is summarized below.

Theorem 4.1 *Dynamics of system (4.1) are described below.*

(a) *If $\alpha m f(N^0) < \delta + D$, then $E_0^* = (N^0, 0, 0, S^0)$ is the only steady state for (4.1) and solutions of (4.1) all converge to E_0^*.*

(b) *If $\alpha m f(N^0) > \delta + D$, then (4.1) has two steady states E_0^* and $E_1^* = (N^0 - P_1^*, P_1^*, 0, S^*)$. In addition if $\beta c g(P_1^*) < \epsilon + D$, then solutions of (4.1) with $P(0) > 0$ converge to E_1^*.*

(c) *If $\alpha m f(N^0) > \delta + D$ and $\beta c g(P_1^*) > \epsilon + D$, then (4.1) has three steady states E_0^*, E_1^*, and the interior steady state $E_2^* = (N^0 - \bar{P}^* - \bar{Z}^*, \bar{P}^*, \bar{Z}^*, \bar{S}^*)$, and system (4.1) is uniformly persistent.*

Let $f(x) = \dfrac{x}{2+x}$, $g(x) = \dfrac{x}{1+x}$, $v(S) = \dfrac{S}{3+S}$ and $h(S) = e^{-2S}$. Then

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system (4.2) becomes

$$\begin{aligned}
\dot{P} &= [\frac{\alpha m(N^0 - P - Z)}{2 + N^0 - P - Z} - \delta - D]P - \frac{cPe^{-2S}}{1+P}Z \\
\dot{Z} &= [\frac{\beta cPe^{-2S}}{1+P} - \epsilon - D]Z \qquad\qquad (4.5) \\
\dot{S} &= D(S^0 - S) - \frac{bS}{3+S}P \\
&\quad P(0), Z(0), S(0) \geq 0, P(0) + Z(0) \leq N^0.
\end{aligned}$$

Choosing $N^0 = 4.85$, $D = 0.05$, $\delta = 0.4$, $\epsilon = 10^{-5}$, $c = 0.1$, $m = 5$, $\alpha = 0.9$, $\beta = 0.99$, $b = 2$ and $S^0 = 4$, we have $\alpha m f(N^0) > \delta + D$ so that steady state $(P_1^*, 0, S_1^*)$ exists. In this case $\beta cf(P_1^*)h(S_1^*) > \epsilon + D$. Numerical simulations showing the existence of an interior steady state and it is locally asymptotically stable. Therefore, the system with an inhibitor that inhibits the grazing rate of zooplankton is more stable. It has a very similar dynamic behavior as the uninhibited system (2.1). Numerical simulations of this system is given in Figure 4.

5   Discussion

Nutrient-phytoplankton-zooplankton models are proposed to study the effects of pollutants upon the nutrient-plankton interaction. Our models consist of a single limiting nutrient, two plankton populations, and a toxin, where the toxin may be harmful to either phytoplankton or zooplankton. The toxin can be regarded as either an organic or inorganic substance. The inclusion of this toxic inhibitor is motivated by the study in [3, 9, 10], and the problems of declining marine populations, and heavy pollution in our marine and aquatic systems. Although more complicated models can be built to incorporate multiple nutrients and/or with spatial dimensions, we focused on simple models to study the biological problem.

We contrasted the proposed models with each other and with a base nutrient-plankton system. It is found that it is necessary to have a higher nutrient input N^0 when there is a toxin inhibits either phytoplankton's growth rate or zooplankton's grazing rate. The model exhibits complicated behavior with multiple attractors when phytoplankton's growth rate is inhibited. In the following we present two simulations where growth rates of both plankton populations are diminished. In one model phytoplankton can uptake toxin

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and in the other model zooplankton can uptake toxin. The systems exhibit multiple positive periodic solutions. However, we are unable to find more complicated dynamical behavior.

A simple model with both populations inhibited by the toxin and only phytoplankton can consume the toxin is given below.

$$
\begin{aligned}
\dot{P} &= [\frac{\alpha m(N^0 - P - Z)e^{-2S}}{2 + N^0 - P - Z} - \delta - D]P - \frac{cP}{(1+P)(1+S)}Z \\
\dot{Z} &= [\frac{\beta cP}{(1+P)(1+S)} - \epsilon - D]Z \\
\dot{S} &= D(S^0 - S) - \frac{qS}{5 + 5S}P \\
& \quad P(0), Z(0), S(0) \geq 0, P(0) + Z(0) \leq N^0,
\end{aligned}
\tag{5.1}
$$

Using $N^0 = 4.85$, $D = 0.05$, $\delta = 0.1$, $\epsilon = 10^{-5}$, $c = 0.5$, $m = 5$, $\alpha = 0.9$, $\beta = 0.99$, $q = 2$ and $S^0 = 1$, we have $\alpha m f(N^0) > \delta + D$. Numerical simulations yield multiple periodic solutions as given in Figure 5.

The following model captures the phenomenon when zooplankton can uptake toxin while both plankton populations are inhibited by the toxin.

$$
\begin{aligned}
\dot{P} &= [\frac{\alpha m(N^0 - P - Z)e^{-2S}}{2 + N^0 - P - Z} - \delta - D]P - \frac{cP}{(1+P)(1+S)}Z \\
\dot{Z} &= [\frac{\beta cP}{(1+P)(1+S)} - \epsilon - D]Z \\
\dot{S} &= D(S^0 - S) - \frac{qS}{5 + 5S}Z \\
& \quad P(0), Z(0), S(0) \geq 0, P(0) + Z(0) \leq N^0.
\end{aligned}
\tag{5.2}
$$

The parameter values for system (5.2) are $N^0 = 4.85$, $D = 0.05$, $\delta = 0.05$, $\epsilon = 10^{-5}$, $c = 0.5$, $m = 1$, $\alpha = 0.7$, $\beta = 0.99$, $q = 3$ and $S^0 = 2.1$. Numerical simulations also yield multiple periodic solutions as given in Figure 6.

Although our models are simplified real systems, one can conclude from this study that nutrient-plankton interactions have multiple attractors when there is a toxin inhibiting either the growth rate of phytoplankton or both plankton populations. Survival of both species may depend on initial population sizes. However, a larger input nutrient concentration will in general promote the coexistence of both populations.

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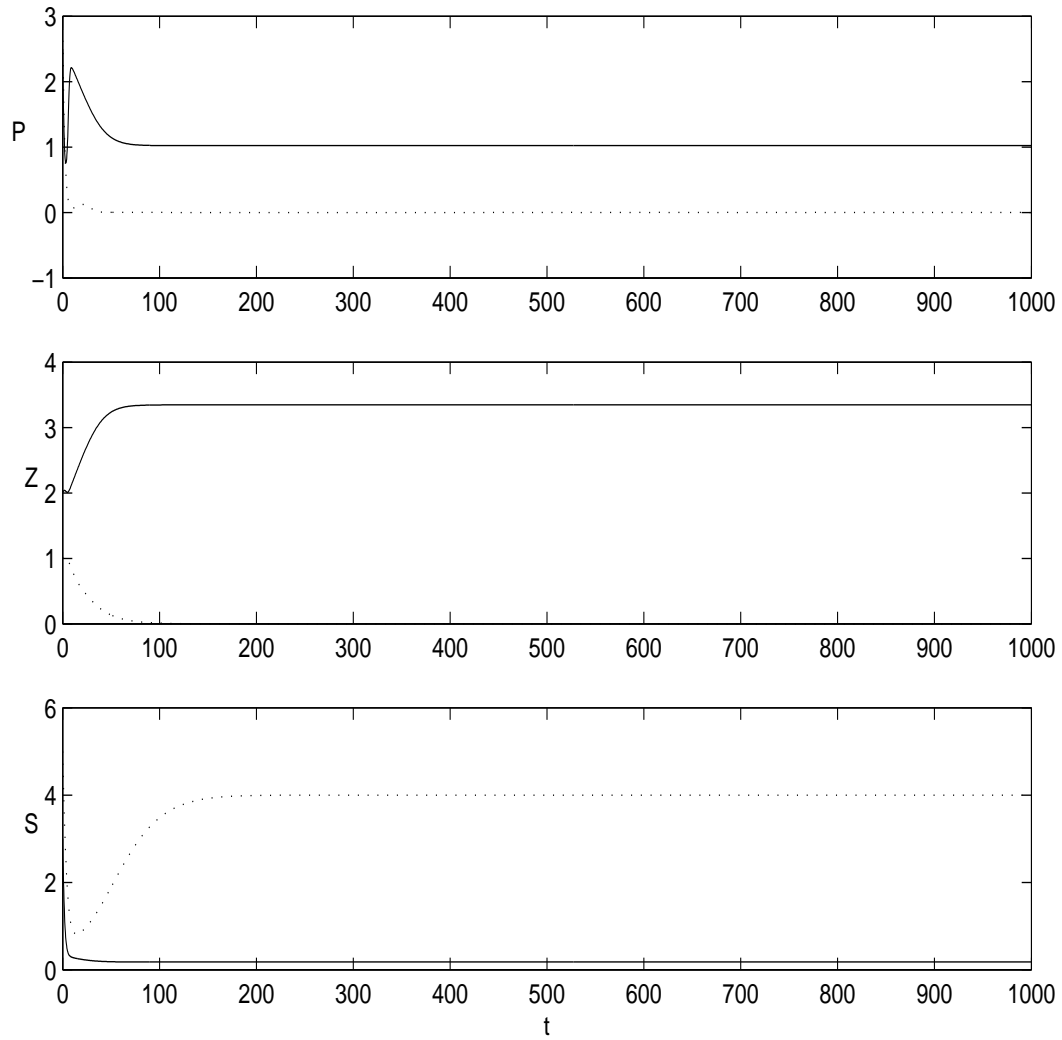
Figure 1: System (3.7) has an interior steady state. Solution with initial condition (2.5, 2, 3) converges to the interior steady state (1.0208, 3.3457, 0.1765) while solution with initial condition (3, 1, 5) goes to the trivial steady state (0, 0, 4).
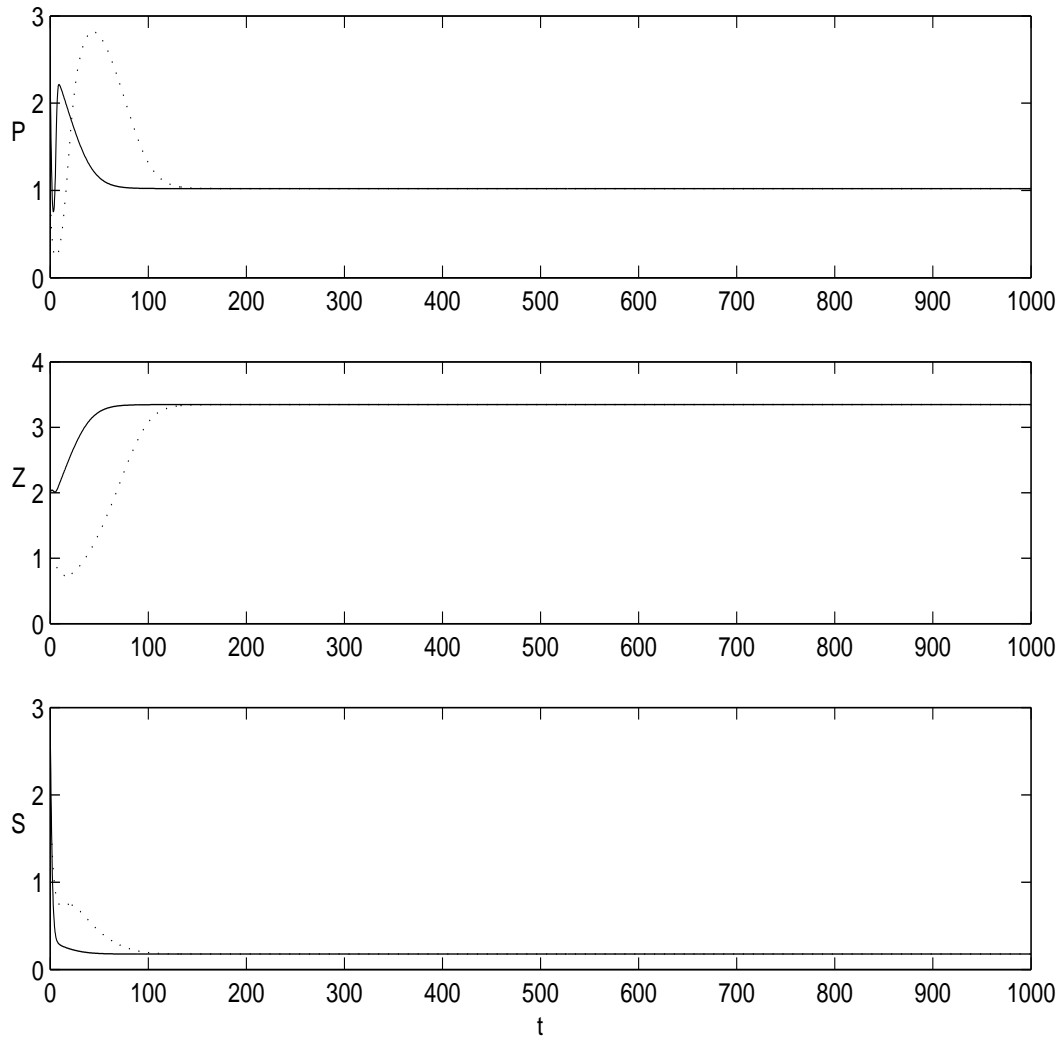
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Figure 2: With the same parameter values as in Figure 1, System (3.7) has an interior steady state $(1.0208, 3.3457, 0.1765)$ which is locally asymptotically stable even when condition (3.6) is satisfied. Initial conditions are $(2.5, 2, 3)$ and $(1, 1, 2)$ for the solid and dashed lines, respectively.

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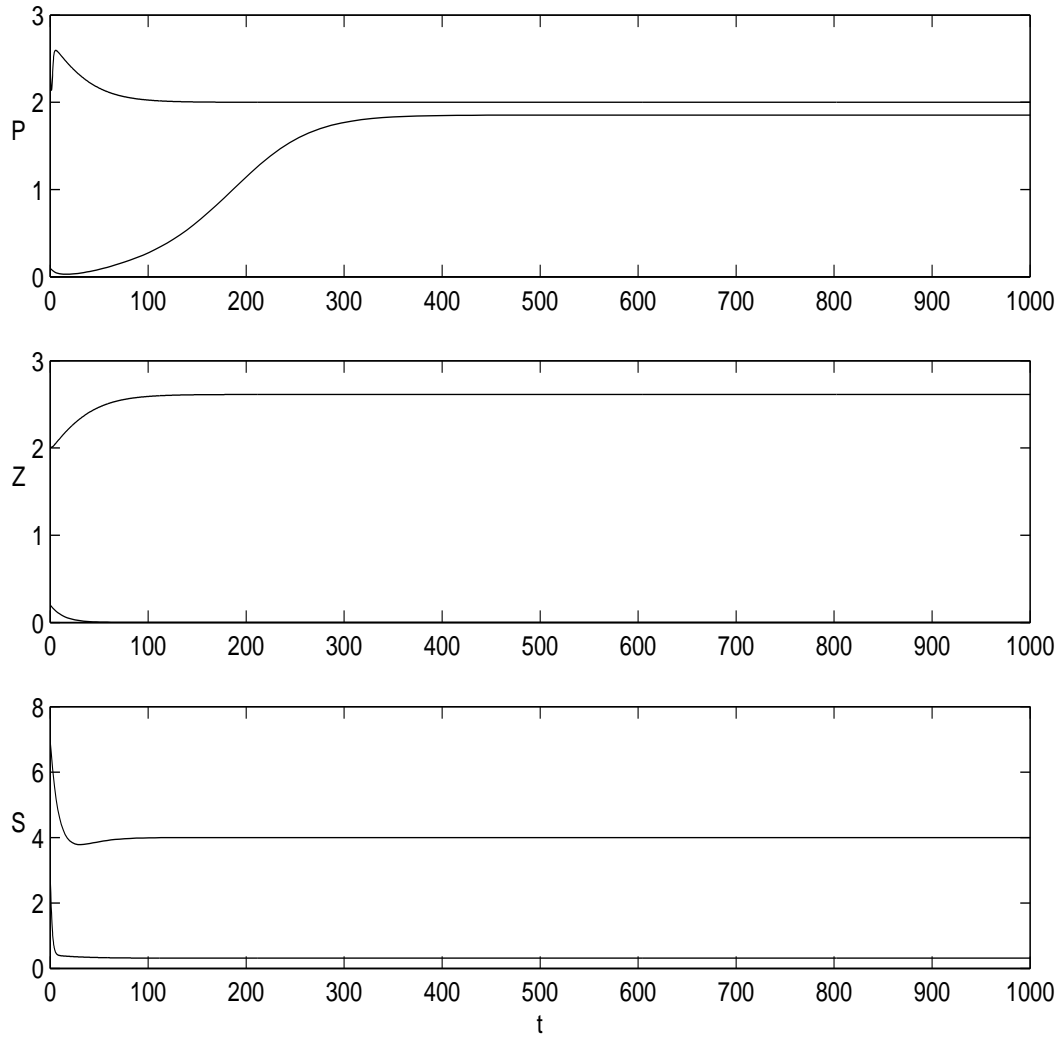
Figure 3: Solution with initial condition $(2.5, 2, 3)$ converges to the interior steady state while solution with initial condition $(0.1, 0.2, 7)$ goes to the non-trivial steady state on the PS-plane.
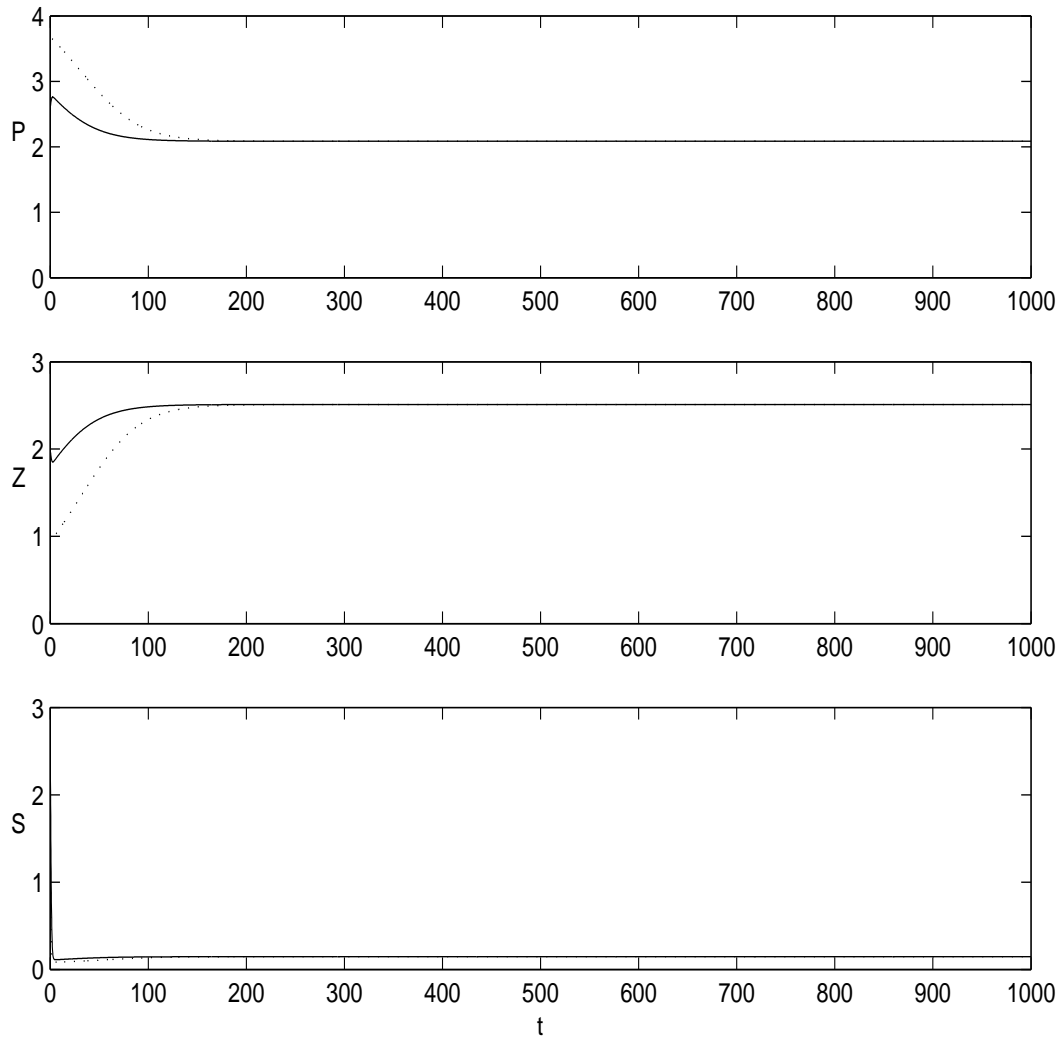
Figure 4: Solutions of system (4.5) with initial conditions $(2.5, 2, 3)$ and $(3.5, 1, 2)$ converge to the interior steady state $(2.0838, 2.5101, 0.1455)$. Although it is not plotted, this is also true for solutions with other initial conditions.
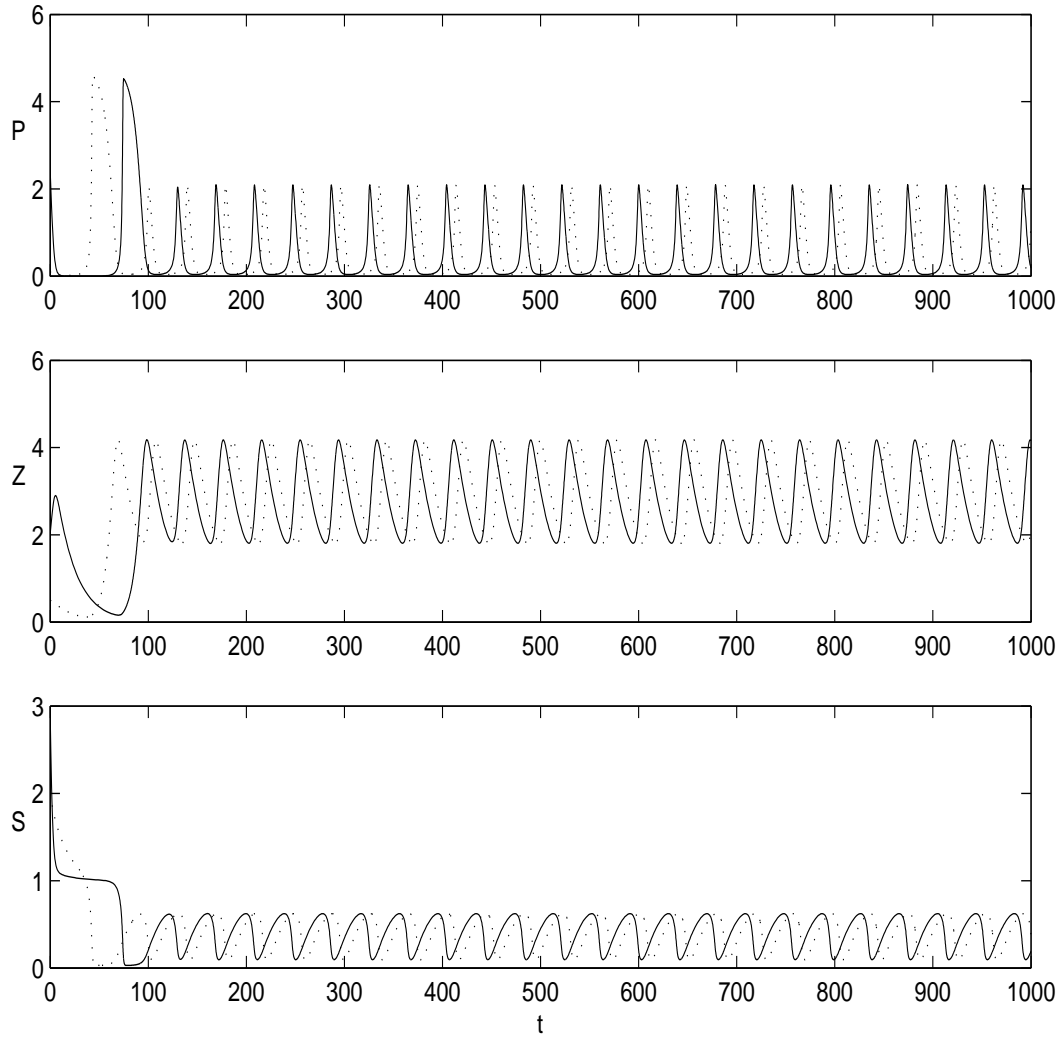
Figure 5: Solutions of system (5.1) with initial condition $(2.5, 2, 3)$ and $(0.1, 0.5, 2)$ oscillate. They generate two positive periodic solutions.
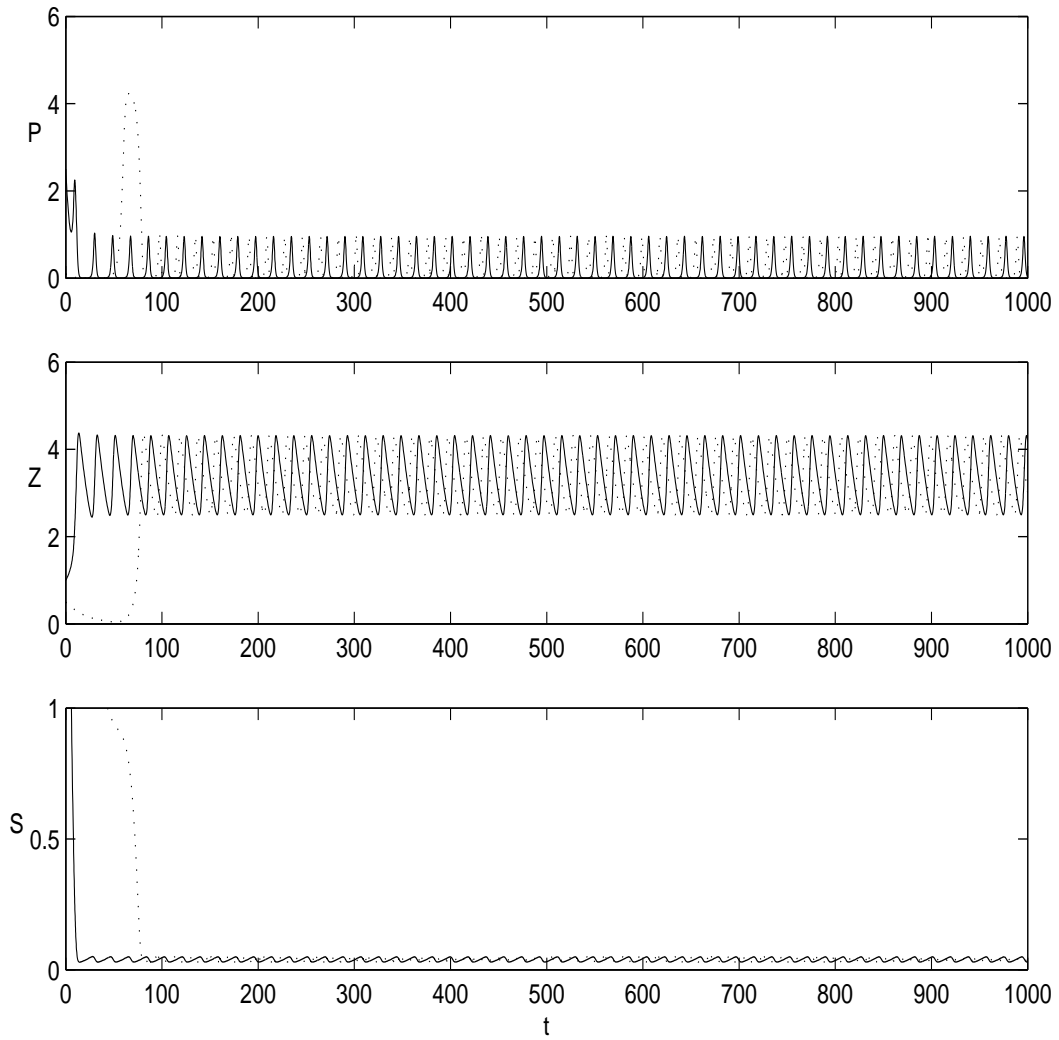
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Figure 6: Solutions of (5.2) with initial condition $(2.5, 1, 3)$ and $(0.1, 0.5, 7)$ also oscillate.