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Abstract

This paper is devoted to the investigation of an unstirred chemostat system modeling the interactions of two essential nutrients (i.e., nitrogen and phosphorus), harmful algae (i.e., P. parvum and cyanobacteria), and a small-bodied zooplankton in an ecosystem. To obtain a weakly repelling property of a compact and invariant set on the boundary, we introduce an associated principal elliptic eigenvalue problem. It turns out that the model system admits a coexistence steady state and is uniformly persistent provided that the trivial steady state, two semi-trivial steady states and a global attractor on the boundary are all weak repellers.

Keywords: Chemostat, algal blooms, inhibition, global attractor, weak repellers, coexistence.
MSC(2010): 35B40, 35K57, 92D25.

1 Introduction

Harmful algal blooms (HABs) have been a serious problem in many coastal and inland waters worldwide [3, 6]. It was known that the algal species, *Prymnesium*

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parvum (golden algae), is responsible for fish-killing problem, and results in major economic damage [4]. In a reservoir, P. parvum competes for nitrogen and phosphorus with cyanobacteria, which also excrete allelopathic cyanotoxins that inhibit the growth of P. parvum. A small-bodied zooplankton population consume both types of algae for growth, but the dissolved toxins produced by P. parvum also inhibits zooplankton ingestion, growth and reproduction. In order to understand such complex interactions and reactions in an ecosystem, the authors in [5] proposed a well-mixed chemostat system to explore the dynamics of nutrients, P. parvum, toxin(s) produced by P. parvum, cyanobacteria, cyanotoxin(s) produced by cyanobacteria, and zooplankton.

A natural approach to the spatial heterogeneity is to use "unstirred" chemostat, where we will remove the assumption that interactions of nutrients and species proceeds in a well-mixed, spatially uniform habitat. The unstirred chemostat can be regarded as a spatially distributed habitat in which inflow of nutrients occur at one point and outflow at another, with diffusive transport of nutrients and organisms between these points [2, 13]. To simplify our model system, we first ignore the equations of toxins proposed in [5], and then inhibitory effects are directly determined by the densities of harmful algae. Based on the above reasons, we modify the model in [5] and incorporate the spatial variations into our system, then our governing system is the following unstirred chemostat model:

$$\begin{cases} \frac{\partial R}{\partial t} = d\frac{\partial^2 R}{\partial x^2} - q_{1r} f_1(R,S) u_1 e^{-\alpha u_2} - q_{2r} f_2(R,S) u_2, & x \in (0,1),\ t > 0, \\ \frac{\partial S}{\partial t} = d\frac{\partial^2 S}{\partial x^2} - q_{1s} f_1(R,S) u_1 e^{-\alpha u_2} - q_{2s} f_2(R,S) u_2, & x \in (0,1),\ t > 0, \\ \frac{\partial u_1}{\partial t} = d\frac{\partial^2 u_1}{\partial x^2} + f_1(R,S) u_1 e^{-\alpha u_2} - q_1 g_1(u_1) Z, & x \in (0,1),\ t > 0, \\ \frac{\partial u_2}{\partial t} = d\frac{\partial^2 u_2}{\partial x^2} + f_2(R,S) u_2 - q_2 g_2(u_2) Z, & x \in (0,1),\ t > 0, \\ \frac{\partial Z}{\partial t} = d\frac{\partial^2 Z}{\partial x^2} + G(u_1,u_2) Z, & x \in (0,1),\ t > 0, \end{cases} \tag{1.1}$$

with boundary conditions

$$\begin{cases} \frac{\partial R}{\partial x}(0,t) = -R^{(0)},\ \frac{\partial R}{\partial x}(1,t) + \gamma R(1,t) = 0,\ t > 0, \\ \frac{\partial S}{\partial x}(0,t) = -S^{(0)},\ \frac{\partial S}{\partial x}(1,t) + \gamma S(1,t) = 0,\ t > 0, \\ \frac{\partial u_i}{\partial x}(0,t) = \frac{\partial u_i}{\partial x}(1,t) + \gamma u_i(1,t) = 0,\ t > 0,\ i = 1,2, \\ \frac{\partial Z}{\partial x}(0,t) = \frac{\partial Z}{\partial x}(1,t) + \gamma Z(1,t) = 0,\ t > 0, \end{cases} \tag{1.2}$$

and initial conditions

$$\begin{cases} R(x,0) = R^0(x) \geq 0, S(x,0) = S^0(x) \geq 0, & x \in (0,1), \\ u_i(x,0) = u_i^0(x) \geq 0,\ Z(x,0) = Z^0(x) \geq 0, & x \in (0,1),\ i = 1,2, \end{cases} \tag{1.3}$$

where $R(x,t)$ and $S(x,t)$ denote the complementary nutrient (nitrogen and phosphorus) concentrations at position x and time t; $u_1(x,t)$ and $u_2(x,t)$ represent the densities of P. parvum (golden algae) and cyanobacteria, respectively; $Z(x,t)$ represents the density of small-bodied zooplankton population. $R^{(0)}$ and $S^{(0)}$ are input concentration of nutrients; q_{ir} and q_{is}, $i=1,2$, are the constant nutrient quotas; q_i, $i=1,2$, is the constant algal quota; the constant γ in (1.2) represents the washout constant. We also assume that nutrients and algal species have the same diffusion coefficient d. The term $e^{-\alpha u_2}$ describes the inhibitory effect on $u_1(x,t)$ from $u_2(x,t)$. The response function are given by $f_i(R,S)=\min\{h_{ir}(R),h_{is}(S)\}$, $i=1,2$. The nonlinear functions $h_{ir}(R)$ ($h_{is}(S)$) describe the nutrient uptake and growth rates of species i when only nutrient R (S) is limiting. We assume that the functions $h_{ir}(R)$ and $h_{is}(S)$ satisfy

$$h_{ir}(0)=0,\ h'_{ir}(R)>0\ \forall\ R>0,\ h_{ir}\in C^2, i=1,2.$$

An usual example is the Monod function

$$h_{ir}(R)=\frac{m_{\mathrm{ir}}R}{K_{ir}+R},\ h_{is}(S)=\frac{m_{\mathrm{is}}S}{K_{is}+S}.$$

Both types of algae are consumed by zooplankton, and consumption of the algae supports the growth of the zooplankton. Further, P. parvum ($u_1(x,t)$) also inhibits the growth of zooplankton. The function $g_1(u_1)$ represents the relationship between zooplankton and P. parvum, which simultaneously include positive and negative effects on the growth of the zooplankton, depending on the density of $u_1(x,t)$. Then $g_1(u_1)$ takes the following form:

$$g_1(u_1)=\frac{m_{1\mathrm{z}}u_1}{K_{1z}+u_1+\eta u_1^2}\ \text{or}\ g_1(u_1)=\frac{m_{1\mathrm{z}}u_1}{K_{1z}+u_1}e^{-\beta u_1}.$$

The cyanobacteria ($u_2(x,t)$) only inhibits the growth of P. parvum ($u_1(x,t)$), and has no negative effects on zooplankton ($Z(x,t)$). The function $g_2(u_2)$ represents the relationship between zooplankton and cyanobacteria ($u_2(x,t)$), and $g_2(u_2)$ is increasing in u_2, and hence, $g_2(u_2)$ takes the following form:

$$g_2(u_2)=\frac{m_{2\mathrm{z}}u_2}{K_{2z}+u_2}.$$

Then $G(u_1,u_2)$, the growth rate of zooplankton, takes the following types

$$G(u_1,u_2)=g_1(u_1)\cdot g_2(u_2), \tag{1.4}$$

or

$$G(u_1, u_2) = \min\{g_1(u_1), g_2(u_2)\}. \tag{1.5}$$

The organization of this paper is as follows. In Section 2, we study the well-posedness of system (1.1)-(1.3). Section 3 is devoted to the study of the global dynamics of system (3.1)-(3.3) modeling the interactions of P. parvum and cyanobacteria, that is, the subsystem of (1.1)-(1.3) where we put $Z(x,t) \equiv 0$. Basically, we show that the semiflow generated by system (3.1)-(3.3) admits a global attractor $A_0 \subset \mathrm{Int}(C([0,1], \mathbb{R}^4_+))$ when the semi-trivial steady-state solutions of (3.1)-(3.3) are both unstable, by appealing to the theory of uniform persistence and chain transitive sets. In Section 4, we investigate the coexistence of harmful algae (i.e., P. parvum and cyanobacteria) and zooplankton for system (1.1)-(1.3). The main difficulty is that the zooplankton-extinct steady-state solution of system (1.1)-(1.3) is not necessarily unique, that is, the set $A_0 \times \{0\}$ may not be a singleton. To address this general case, we first introduce a continuous function, $m(x)$, involving in A_0 (see (4.3)), and the principal eigenvalue of an eigenvalue problem associated with $m(x)$ (see (4.7)) becomes a crucial index that determines whether $M_3 := A_0 \times \{0\}$ is a uniform weak repeller in the sense of (4.8). Then we use persistence theory to establish the existence of a positive (coexistence) steady state and the uniform persistence for system (1.1)-(1.3) under the assumption that its compact invariant set $M_3 := A_0 \times \{0\}$, trivial and semitrivial steady states are all weak repellers. A brief discussion section completes the paper.

2 Well-posedness

We first study the well-posedness of the initial-boundary-value problem (1.1)-(1.3). Let $\mathbb{X} = C([0,1], \mathbb{R}^5_+)$ be the positive cone in the Banach space $C([0,1], \mathbb{R}^5)$ with the usual supremum norm. In order to simplify notations, we set $v_1 = R$, $v_2 = S$, $v_3 = u_1$, $v_4 = u_2$, $v_5 = Z$ and $\mathbf{v} = (v_1, v_2, v_3, v_4, v_5)$. We assume that the initial data in (1.3) satisfying $\mathbf{v}^0 = (v_1^0, v_2^0, v_3^0, v_4^0, v_5^0) := (R^0, S^0, u_1^0, u_2^0, Z^0) \in \mathbb{X}$. For the local existence and positivity of solutions in the space $\mathbb{X}$, we appeal to the theory developed in [7] where existence and uniqueness and positivity are treated simultaneously (taking delay as zero). The idea is to view the system (1.1)-(1.3) as the abstract ordinary differential equation in $\mathbb{X}$ and the so-called mild solutions can be obtained for any given initial data. More precisely,

$$\begin{cases} v_1(t) = V_R(t,0)v_1^0 + \int_0^t T(t-s)B_1(\mathbf{v}(s))ds, \\ v_2(t) = V_S(t,0)v_2^0 + \int_0^t T(t-s)B_2(\mathbf{v}(s))ds, \\ v_i(t) = T(t)v_i^0 + \int_0^t T(t-s)B_i(\mathbf{v}(s))ds, \ i = 3,4,5, \end{cases}$$

where $T(t)$ is the positive, non-expansive, analytic semigroup on $C([0,1],\mathbb{R})$ (see, e.g., [12, Chapter 7]) such that $v = T(t)v^0$ satisfies the linear initial value problem

$$\begin{cases} \frac{\partial v}{\partial t} = d\frac{\partial^2 v}{\partial x^2}, \ t > 0, 0 < x < 1, \\ -\frac{\partial v}{\partial x}(0,t) = 0, \ \frac{\partial v}{\partial x}(1,t) + \gamma v(1,t) = 0, \ t > 0, \\ v(x,0) = v^0(x). \end{cases}$$

For $N = R,\ S$, we assume that $V_N(t,s)$, $t > s$, is the family of affine operators on $C([0,1],\mathbb{R})$ (see, e.g., [10, Chapter 5]) such that $v = V_N(t,s)v^0$ satisfies the linear system with nonhomogeneous boundary conditions, with start time s, given by

$$\begin{cases} \frac{\partial v}{\partial t} = d\frac{\partial^2 v}{\partial x^2}, \ t > 0, 0 < x < 1, \\ -\frac{\partial v}{\partial x}(0,t) = N^{(0)}, \ \frac{\partial v}{\partial x}(1,t) + \gamma v(1,t) = 0, \ t > s, \\ v(x,s) = v^0(x). \end{cases}$$

The nonlinear operators $B_1, B_2, B_i : C([0,1],\mathbb{R}_+) \to C([0,1],\mathbb{R})$, $i = 3,4,5$, are defined by

$$\begin{cases} B_1(\mathbf{v}) = -q_{1r}f_1(v_1,v_2)v_3e^{-\alpha v_4} - q_{2r}f_2(v_1,v_2)v_4, \\ B_2(\mathbf{v}) = -q_{1s}f_1(v_1,v_2)v_3e^{-\alpha v_4} - q_{2s}f_2(v_1,v_2)v_4, \\ B_3(\mathbf{v}) = f_1(v_1,v_2)v_3e^{-\alpha v_4} - q_1g_1(v_3)v_5, \\ B_4(\mathbf{v}) = f_2(v_1,v_2)v_4 - q_2g_2(v_4)v_5, \\ B_5(\mathbf{v}) = G(v_3,v_4)v_5, \end{cases}$$

By standard maximum principle arguments (see, e.g., [12, Chapter 7]), it follows that $V_N(t,s)C([0,1],\mathbb{R}_+) \subset C([0,1],\mathbb{R}_+)$, $\forall\, t > s$, $N = R, S$ and $T(t)C([0,1],\mathbb{R}_+) \subset C([0,1],\mathbb{R}_+)$, $\forall\ t > 0$. Since $g_1(0) = 0$ and $g_2(0) = 0$, it follows that $B_i(\mathbf{v}) \geq 0$ whenever $v_i \equiv 0$, $i = 1,2,3,4,5$. Hence, $\mathbf{B} := (B_1,B_2,B_3,B_4,B_5)$ is quasipositive (see, e.g., [7, Remark 1.1]). By [7, Theorem 1 and Remark 1.1], it follows that the system (1.1)-(1.3) has a unique noncontinuable solution and the solutions to (1.1)-(1.3) remain non-negative on their interval of existence if they are non-negative initially. More precisely, we have the following results:

Lemma 2.1. *For every initial value function* $\mathbf{v}^0 \in \mathbb{X} = C([0,1], \mathbb{R}^5_+)$*, system* (1.1)-(1.3) *has a unique mild solution* $\mathbf{v}(x,t,\mathbf{v}^0)$ *on* $(0, \tau_{\mathbf{v}^0})$ *with* $\mathbf{v}(\cdot, 0, \mathbf{v}^0) = \mathbf{v}^0$*, where* $\tau_{\mathbf{v}^0} \le \infty$*. Furthermore,* $\mathbf{v}(\cdot, t, \mathbf{v}^0) \in \mathbb{X}$*,* $\forall\ t \in (0, \tau_{\mathbf{v}^0})$ *and* $\mathbf{v}(x,t,\mathbf{v}^0)$ *is a classical solution of* (1.1)-(1.3)*,* $\forall\ t > 0$.

For $N = R,\ S$, we consider

$$\begin{cases} \frac{\partial W_N}{\partial t} = d\frac{\partial^2 W_N}{\partial x^2},\ x \in (0,1),\ t > 0, \\ \frac{\partial W_N}{\partial x}(0,t) = -N^{(0)},\ \frac{\partial W_N}{\partial x}(1,t) + \gamma W_N(1,t) = 0,\ t > 0, \\ W_N(x,0) = W_N^0(x),\ x \in (0,1). \end{cases} \tag{2.1}$$

Then $W_N(x,t)$ satisfies (see, e. g., [2])

$$\lim_{t\to\infty} W_N(x,t) = w_N(x),\ \text{uniformly in } x \in [0,1], \tag{2.2}$$

where $w_N(x) = N^{(0)}(\frac{1+\gamma}{\gamma} - x)$.

Next, we show that solutions of (1.1)-(1.3) are ultimately bounded.

Lemma 2.2. *Any solution with initial value function in* $\mathbb{X}$ *of the system* (1.1)-(1.3) *exists globally on* $[0, \infty)$*. Moreover, solutions are ultimately bounded.*

Proof. We first consider the case where $G(u_1, u_2)$ takes the form (1.5). Let

$$Y_R(x,t) = R(x,t) + q_{1r}u_1(x,t) + q_{2r}u_2(x,t) + \min\{q_1q_{1r}, q_2q_{2r}\}Z,$$

and

$$Y_S(x,t) = S(x,t) + q_{1s}u_1(x,t) + q_{2s}u_2(x,t) + \min\{q_1q_{1s}, q_2q_{2s}\}Z.$$

Then $Y_R(x,t)$ satisfies

$$\begin{aligned} \frac{\partial Y_R}{\partial t} &= d\frac{\partial^2 Y_R}{\partial x^2} + \{\min\{q_1q_{1r}, q_2q_{2r}\}\min\{g_1(u_1), g_2(u_2)\} - q_1q_{1r}g_1(u_1) - q_2q_{2r}g_2(u_2)\}Z \\ &\le d\frac{\partial^2 Y_R}{\partial x^2},\ x \in (0,1),\ t > 0. \end{aligned}$$

That is, $Y_R(x,t)$ satisfies

$$\begin{cases} \frac{\partial Y_R}{\partial t} \le d\frac{\partial^2 Y_R}{\partial x^2},\ x \in (0,1),\ t > 0, \\ \frac{\partial Y_R}{\partial x}(0,t) = -R^{(0)},\ \frac{\partial Y_R}{\partial x}(1,t) + \gamma Y_R(1,t) = 0,\ t > 0, \\ Y_R(x,0) = Y_R^0(x),\ x \in (0,1). \end{cases} \tag{2.3}$$

Comparing system (2.3) with (2.1), it follows that $Y_R(x,t) \leq W_R(x,t),\ x \in [0,1],\ t > 0$, where we have put $N = R$ and $Y_R^0(\cdot) \equiv W_R^0(\cdot)$ in (2.1). Thus,

$$\limsup_{t\to\infty} Y_R(x,t) \leq w_R(x) := R^{(0)}(\frac{1+\gamma}{\gamma} - x),\ x \in [0,1]. \tag{2.4}$$

Similarly, we can show that

$$\limsup_{t\to\infty} Y_S(x,t) \leq w_S(x) := S^{(0)}(\frac{1+\gamma}{\gamma} - x),\ x \in [0,1]. \tag{2.5}$$

From Lemma 2.1, (2.4), and (2.5), it follows that R, S, u_1, u_2, and Z are ultimately bounded.

For the case where $G(u_1, u_2)$ takes the form (1.4), it follows that

$$G(u_1, u_2) = g_1(u_1) \cdot g_2(u_2) \leq m_{1\text{z}} g_2(u_2).$$

Setting

$$Y_R(x,t) = R(x,t) + q_{1r}u_1(x,t) + q_{2r}u_2(x,t) + \frac{q_2 q_{2r}}{m_{1\text{z}}} Z,$$

and

$$Y_S(x,t) = S(x,t) + q_{1s}u_1(x,t) + q_{2s}u_2(x,t) + \frac{q_2 q_{2s}}{m_{1\text{z}}} Z.$$

By the same arguments as before, we are able to show that $Y_R(x,t)$ and $Y_S(x,t)$ are ultimately bounded. So are R, S, u_1, u_2, and Z. $\square$

By the strong maximum principle and the Hopf boundary lemma (see [11]), we have the following result.

Lemma 2.3. *Let*

$$(v_1(x,t), v_2(x,t), v_3(x,t), v_4(x,t), v_5(x,t)) := (R(x,t), S(x,t), u_1(x,t), u_2(x,t), Z(x,t))$$

be the solution of system (1.1)-(1.3) *with initial data* $\mathbf{v}^0 \in \mathbb{X}$. *If there is a* $t_0 \geq 0$ *such that* $v_i(\cdot, t_0) \not\equiv 0$, *for some* $i \in \{1,2,3,4,5\}$, *then* $v_i(x,t) > 0$, *for all* $x \in [0,1]$ *and* $t > t_0$.

3 Dynamics of harmful algae

In this section, we put $Z = 0$ in (1.1)-(1.3) and consider the following system:

$$\begin{cases} \frac{\partial R}{\partial t} = d\frac{\partial^2 R}{\partial x^2} - q_{1r} f_1(R,S) u_1 e^{-\alpha u_2} - q_{2r} f_2(R,S) u_2, & x \in (0,1),\ t > 0, \\ \frac{\partial S}{\partial t} = d\frac{\partial^2 S}{\partial x^2} - q_{1s} f_1(R,S) u_1 e^{-\alpha u_2} - q_{2s} f_2(R,S) u_2, & x \in (0,1),\ t > 0, \\ \frac{\partial u_1}{\partial t} = d\frac{\partial^2 u_1}{\partial x^2} + f_1(R,S) u_1 e^{-\alpha u_2}, & x \in (0,1),\ t > 0, \\ \frac{\partial u_2}{\partial t} = d\frac{\partial^2 u_2}{\partial x^2} + f_2(R,S) u_2, & x \in (0,1),\ t > 0, \end{cases} \tag{3.1}$$

with boundary conditions

$$\begin{cases} \frac{\partial R}{\partial x}(0,t) = -R^{(0)},\ \frac{\partial R}{\partial x}(1,t) + \gamma R(1,t) = 0,\ t > 0, \\ \frac{\partial S}{\partial x}(0,t) = -S^{(0)},\ \frac{\partial S}{\partial x}(1,t) + \gamma S(1,t) = 0,\ t > 0, \\ \frac{\partial u_i}{\partial x}(0,t) = \frac{\partial u_i}{\partial x}(1,t) + \gamma u_i(1,t) = 0,\ t > 0,\ i = 1,2, \end{cases} \tag{3.2}$$

and initial conditions

$$\begin{cases} R(x,0) = R^0(x) \geq 0, S(x,0) = S^0(x) \geq 0, & x \in (0,1), \\ u_i(x,0) = u_i^0(x) \geq 0, & x \in (0,1),\ i = 1,2. \end{cases} \tag{3.3}$$

3.1 A single population model

For $i = 1,2$, we first consider the following system related to the single population model of (3.1)-(3.3):

$$\begin{cases} \frac{\partial R}{\partial t} = d\frac{\partial^2 R}{\partial x^2} - q_{ir} f_i(R,S) u_i, & x \in (0,1),\ t > 0, \\ \frac{\partial S}{\partial t} = d\frac{\partial^2 S}{\partial x^2} - q_{is} f_i(R,S) u_i, & x \in (0,1),\ t > 0, \\ \frac{\partial u_i}{\partial t} = d\frac{\partial^2 u_i}{\partial x^2} + f_i(R,S) u_i, & x \in (0,1),\ t > 0, \end{cases} \tag{3.4}$$

with boundary conditions

$$\begin{cases} \frac{\partial R}{\partial x}(0,t) = -R^{(0)},\ \frac{\partial R}{\partial x}(1,t) + \gamma R(1,t) = 0,\ t > 0, \\ \frac{\partial S}{\partial x}(0,t) = -S^{(0)},\ \frac{\partial S}{\partial x}(1,t) + \gamma S(1,t) = 0,\ t > 0, \\ \frac{\partial u_i}{\partial x}(0,t) = \frac{\partial u_i}{\partial x}(1,t) + \gamma u_i(1,t) = 0,\ t > 0, \end{cases} \tag{3.5}$$

and initial conditions

$$\begin{cases} R(x,0) = R^0(x) \geq 0, S(x,0) = S^0(x) \geq 0, & x \in (0,1), \\ u_i(x,0) = u_i^0(x) \geq 0, & x \in (0,1). \end{cases} \tag{3.6}$$

Note that if we put $u_2 = 0$ ($u_1 = 0$) in (3.1)-(3.3), then we obtain the system (3.4)-(3.6) with $i = 1$ ($i = 2$).

For $i = 1, 2$, introducing the new variable $W_{iR}(x,t) = R(x,t) + q_{ir}u_i(x,t)$ into (3.4)-(3.6), then $W_{iR}(x,t)$ satisfies (2.1) with $N = R$. Hence,

$$\lim_{t\to\infty} W_{iR}(x,t) = w_R(x) := R^{(0)}(\frac{1+\gamma}{\gamma} - x), \text{ uniformly in } x \in [0,1],$$

Similarly, introducing the new variable $W_{iS}(x,t) = S(x,t) + q_{is}u_i(x,t)$ into (3.4)-(3.6), it follows that

$$\lim_{t\to\infty} W_{iS}(x,t) = w_S(x) := S^{(0)}(\frac{1+\gamma}{\gamma} - x), \text{ uniformly in } x \in [0,1].$$

Then we conclude the limiting system of (3.4)-(3.6) takes the form, $i = 1, 2$,

$$\begin{cases} \frac{\partial u_i}{\partial t} = d\frac{\partial^2 u_i}{\partial x^2} + f_i(w_R(x) - q_{ir}u_i, w_S(x) - q_{is}u_i)u_i, & x \in (0,1),\ t > 0, \\ \frac{\partial u_i}{\partial x}(0,t) = \frac{\partial u_i}{\partial x}(1,t) + \gamma u_i(1,t) = 0, & t > 0, \\ u_i(x,0) = u_i^0(x) \geq 0, & x \in (0,1). \end{cases} \tag{3.7}$$

We denote λ_i^0 to be the principal eigenvalue of the eigenvalue problem

$$\begin{cases} d\varphi''(x) + f_i(w_R(x), w_S(x))\varphi(x) = \lambda_i\varphi(x), \ x \in (0,1), \\ \varphi'(0) = \varphi'(1) + \gamma\varphi(1) = 0. \end{cases} \tag{3.8}$$

with the corresponding positive eigenfunctions uniquely determined by the normalization.

By the similar arguments to those in [9, 15, 17], we have the following results concerned with the global stability of system (3.7).

Lemma 3.1. *For any nonnegative initial function $u_i^0(x)$, $i = 1, 2$, with $q_{ir}u_i^0(x) \leq w_R(x)$ and $q_{is}u_i^0(x) \leq w_S(x)$, there exists a unique nonnegative solution $u_i(x,t)$ of (3.7) defined for $t > 0$. Furthermore,*

(i) *If $\lambda_i^0 \leq 0$, then $\lim_{t\to\infty} u_i(x,t) = 0$, uniformly for $x \in [0,1]$.*

(ii) *If $\lambda_i^0 > 0$, then there exists a unique positive solution $u_i^*(x)$ with $q_{ir}u_i^*(x) < w_R(x)$ and $q_{is}u_i^*(x) < w_S(x)$ on $[0,1]$ such that*

$$\lim_{t\to\infty} u_i(x,t) = u_i^*(x),$$

uniformly for $x \in [0,1]$ provided that $u_i^0(\cdot) \not\equiv 0$.

With Lemma 3.1, we can adopt the similar arguments to those in [16, Theorem 2.2] to lift the dynamics of the limiting system (3.7) to the system (3.4)-(3.6) by using the theory of chain transitive sets [14, 18].

Lemma 3.2. *For any nonnegative initial function* $(R^0(x), S^0(x), u_i^0(x))$ *with* $u_i^0(x) \geq 0$*, there exists a unique nonnegative solution* $(R(x,t), S(x,t), u_i(x,t))$ *of* (3.4)-(3.6) *defined for* $t > 0$*. Furthermore,*

(i) *If* $\lambda_i^0 \leq 0$*, then* $\lim_{t\to\infty}(R(x,t), S(x,t), u_i(x,t)) = (w_R(x), w_S(x), 0)$*, uniformly for* $x \in [0,1]$.

(ii) *If* $\lambda_i^0 > 0$*, then there exists a unique positive solution* $(R_i^*(x), S_i^*(x), u_i^*(x))$ *on* $[0,1]$ *such that*

$$\lim_{t\to\infty}(R(x,t), S(x,t), u_i(x,t)) = (R_i^*(x), S_i^*(x), u_i^*(x)),$$

uniformly for $x \in [0,1]$ *provided that* $u_i^0(\cdot) \not\equiv 0$*. Here,* $u_i^*(x)$ *is defined in Lemma 3.1, and*

$$R_i^*(x) = w_R(x) - q_{ir}u_i^*(x), \;\; S_i^*(x) = w_S(x) - q_{is}u_i^*(x), \;\; i = 1, 2. \tag{3.9}$$

3.2 Coexistence of harmful algae

This section is devoted to the study of the global dynamics of system (3.1)-(3.3). From Lemma 3.2, it is easy to see that system (3.1)-(3.3) has the following possible steady-state solutions:

(i) Trivial steady-state solution $E_0 = (R, S, u_1, u_2) = (w_R(x), w_S(x), 0, 0)$ always exists;

(ii) Semi-trivial steady-state solution $E_1 = (R, S, u_1, u_2) = (R_1^*(x), S_1^*(x), u_1^*(x), 0)$ exists provided that $\lambda_1^0 > 0$, where $(R_1^*(x), S_1^*(x), u_1^*(x))$ is the unique steady-state solution of system (3.4)-(3.6) with $i = 1$ (see Lemma 3.2 (ii));

(iii) Semi-trivial steady-state solution $E_2 = (R, S, u_1, u_2) = (R_2^*(x), S_2^*(x), 0, u_2^*(x))$ exists provided that $\lambda_2^0 > 0$, where $(R_2^*(x), S_2^*(x), u_2^*(x))$ is the unique steady-state solution of system (3.4)-(3.6) with $i = 2$ (see Lemma 3.2 (ii));

Of course, there may be additional steady-state solutions as well and these must be positive. The two algae can coexist if a positive steady-state solution exists.

In order to investigate the local stability of E_1 for system (3.1)-(3.3), we consider the following linear system:

$$\begin{cases} \frac{\partial u_2}{\partial t} = d\frac{\partial^2 u_2}{\partial x^2} + f_2(R_1^*(x), S_1^*(x))u_2, & x \in (0,1),\ t > 0, \\ \frac{\partial u_2}{\partial x}(0,t) = \frac{\partial u_2}{\partial x}(1,t) + \gamma u_2(1,t) = 0, & t > 0, \\ u_2(x,0) = u_2^0(x) \geq 0, & x \in (0,1). \end{cases} \tag{3.10}$$

Then we denote Λ_1^0 to be the principal eigenvalue of the eigenvalue problem

$$\begin{cases} d\varphi''(x) + f_2(R_1^*(x), S_1^*(x))\varphi(x) = \Lambda_1\varphi(x),\ x \in (0,1), \\ \varphi'(0) = \varphi'(1) + \gamma\varphi(1) = 0. \end{cases} \tag{3.11}$$

with the corresponding positive eigenfunctions uniquely determined by the normalization. In order to investigate the local stability of E_2 for system (3.1)-(3.3), we consider the following linear system:

$$\begin{cases} \frac{\partial u_1}{\partial t} = d\frac{\partial^2 u_1}{\partial x^2} + f_1(R_2^*(x), S_2^*(x))e^{-\alpha u_2^*(x)}u_1, & x \in (0,1),\ t > 0, \\ \frac{\partial u_1}{\partial x}(0,t) = \frac{\partial u_1}{\partial x}(1,t) + \gamma u_1(1,t) = 0, & t > 0, \\ u_1(x,0) = u_1^0(x) \geq 0, & x \in (0,1). \end{cases} \tag{3.12}$$

Then we denote Λ_2^0 to be the principal eigenvalue of the eigenvalue problem

$$\begin{cases} d\varphi''(x) + f_1(R_2^*(x), S_2^*(x))e^{-\alpha u_2^*(x)}\varphi(x) = \Lambda_2\varphi(x),\ x \in (0,1), \\ \varphi'(0) = \varphi'(1) + \gamma\varphi(1) = 0. \end{cases} \tag{3.13}$$

with the corresponding positive eigenfunctions uniquely determined by the normalization.

Introducing the new variable $W_R(x,t) = R(x,t) + q_{1r}u_1(x,t) + q_{2r}u_2(x,t)$, and $W_S(x,t) = S(x,t) + q_{1s}u_1(x,t) + q_{2s}u_2(x,t)$ into (3.1)-(3.3), respectively. Then $W_N(x,t)$ satisfies (2.1) with $N = R,\ S$, and hence,

$$\lim_{t\to\infty} W_N(x,t) = w_N(x) := N^{(0)}(\frac{1+\gamma}{\gamma} - x),\ \text{uniformly in } x \in [0,1]. \tag{3.14}$$

Let $\Omega = C([0,1], \mathbb{R}_+^4)$ be the positive cone of the Banach space $C([0,1], \mathbb{R}^4)$ with the usual supremum norm. By (3.14) and the similar arguments in Lemma 2.2, we can show that any solution with initial value function in Ω of the system (3.1)-(3.3) exists globally on $[0,\infty)$, and solutions are ultimately bounded. Let $\Pi(t):\Omega\to\Omega$ be the semiflow generated by system (3.1)-(3.3). Then $\Pi(t):\Omega\to\Omega$ is compact, point dissipative, $\forall\ t>0$. By [1, Theorem 3.4.8], it follows that $\Pi(t)$ admits a global compact attractor in Ω. Setting

$$\Omega_0=\{(R^0(\cdot),S^0(\cdot),u_1^0(\cdot),u_2^0(\cdot))\in\Omega:u_1^0(\cdot)\not\equiv 0,\ u_2^0(\cdot)\not\equiv 0\},\quad \partial\Omega_0=\Omega\backslash\Omega_0,$$

Theorem 3.1. *Assume that*

$$\lambda_i^0>0 \text{ and } \Lambda_i^0>0,\ i=1,2. \tag{3.15}$$

Then $\Pi(t):\Omega\to\Omega$ is uniformly persistent with respect to $(\Omega_0,\partial\Omega_0)$ in the sense that there exists $\tilde\eta>0$ such that

$$\liminf_{t\to\infty}u_i(\cdot,t,Q^0)\geq\tilde\eta,\ i=1,2,\ \forall\ Q^0\in\Omega_0.$$

Further, system (3.1)-(3.3) admits at least one positive steady-state solutions

$$(\tilde R(x),\tilde S(x),\tilde u_1(x),\tilde u_2(x)).$$

Proof. By the same arguments in Lemma 2.3, it follows that for any $Q^0\in\Omega_0$, we have

$$u_1(x,t,Q^0)>0,\ u_2(x,t,Q^0)>0,\ \forall\ x\in[0,1],\ t>0.$$

This implies that $\Pi(t)\Omega_0\subseteq\Omega_0$ for all $t\geq 0$. Let

$$\tilde M_\partial:=\{Q^0\in\partial\Omega_0:\Pi(t)Q^0\in\partial\Omega_0,\forall\ t\geq 0\},$$

and $\tilde\omega(Q^0)$ be the omega limit set of the orbit $O^+(Q^0):=\{\Pi(t)Q^0:t\geq 0\}$. We further prove the following claims.

Claim 1. $\tilde\omega(\varphi)\subset\tilde M_0\cup\tilde M_1\cup\tilde M_2,\ \forall\ \varphi\in\tilde M_\partial$, where $\tilde M_i=\{E_i\}$, $i=0,1,2$.

Since $\varphi\in\tilde M_\partial$, we have $\Pi(t)\varphi\in\tilde M_\partial,\ \forall\, t\geqslant 0$. Thus $u_1(\cdot,t,\varphi)\equiv 0$ or $u_2(\cdot,t,\varphi)\equiv 0,\ \forall\, t\geqslant 0$. In case where $u_1(\cdot,t,\varphi)\equiv 0,\ \forall\, t\geqslant 0$. Then (R,S,u_2) satisfies (3.4)-(3.6) with $i=2$. By Lemma 3.2, it follows that either

$$\lim_{t\to\infty}(R(x,t,\varphi),S(x,t,\varphi),u_2(x,t,\varphi))=(w_R(x),w_S(x),0),\ \text{ uniformly for } x\in[0,1],$$

or

$$\lim_{t\to\infty}(R(x,t,\varphi),S(x,t,\varphi),u_2(x,t,\varphi))=(R_2^*(x),S_2^*(x),u_2^*(x)),\ \text{uniformly for } x\in[0,1].$$

In case where $u_1(\cdot, t_0, \varphi) \not\equiv 0$, for some $t_0 \geqslant 0$. Then the strong maximum principle and the Hopf boundary lemma (see [11]) implies that $u_1(\cdot, t, \varphi) > 0$, for all $t > t_0$. Thus, $u_2(\cdot, t, \varphi) \equiv 0$, $\forall\ t > t_0$, and hence, the (R, S, u_1) equation in (3.1)-(3.3) satisfies (3.4)-(3.6) with $i = 1$, for all $t > t_0$. Again, from Lemma 3.2, it follows that either

$$\lim_{t\to\infty} (R(x,t,\varphi), S(x,t,\varphi), u_1(x,t,\varphi)) = (w_R(x), w_S(x), 0),\ \text{uniformly for } x \in [0,1],$$

or

$$\lim_{t\to\infty} (R(x,t,\varphi), S(x,t,\varphi), u_1(x,t,\varphi)) = (R_1^*(x), S_1^*(x), u_1^*(x)),\ \text{uniformly for } x \in [0,1].$$

This ends the proof of Claim 1.

Claim 2. For $i = 0, 1, 2$, $\tilde{M}_i$ is a uniform weak repeller for Ω_0 in the sense that there exists $\tilde{\delta}_i > 0$ such that $\limsup_{t\to\infty} \|\Pi(t)Q - \tilde{M}_i\| \geq \tilde{\delta}_i$, $\forall\ Q \in \Omega_0$.

We only show the case where $i = 2$ since the other cases can be proved in the similar way. From the fact that $\Lambda_2^0 > 0$, we may assume that there exists an $\epsilon_0 > 0$ such that $\Lambda_2^{\epsilon_0} > 0$, where $\Lambda_2^{\epsilon_0}$ is the principal eigenvalue of the eigenvalue problem

$$\begin{cases} d\varphi''(x) + [f_1(R_2^*(x), S_2^*(x))e^{-\alpha u_2^*(x)} - \epsilon_0]\varphi(x) = \Lambda_2 \varphi(x),\ x \in (0,1), \\ \varphi'(0) = \varphi'(1) + \gamma\varphi(1) = 0. \end{cases}$$

The positive eigenfunction corresponding to $\Lambda_2^{\epsilon_0}$ can be uniquely determined by the normalization, and we denote it by $\varphi_{\epsilon_0}(x)$. By continuity of f_1, we can choose $\tilde{\delta}_2 > 0$ such that if $\|(R_2, S_2, u_2) - (R_2^*(\cdot), S_2^*(\cdot), u_2^*(\cdot))\| < \tilde{\delta}_2$, then

$$f_1(R_2, S_2)e^{-\alpha u_2} > f_1(R_2^*(\cdot), S_2^*(\cdot))e^{-\alpha u_2^*(\cdot)} - \epsilon_0. \tag{3.16}$$

Then we show that

$$\limsup_{t\to\infty} \|\Pi(t)Q - \tilde{M}_2\| \geq \tilde{\delta}_2,\ \forall\ Q \in \Omega_0. \tag{3.17}$$

Suppose, by contradiction, there exists $Q^0 \in \Omega_0$ such that $\limsup_{t\to\infty} \|\Pi(t)Q^0 - \tilde{M}_2\| < \tilde{\delta}_2$. Then there exists $t_0 > 0$ such that for $t \geq t_0$ and $x \in [0,1]$, we have

$$\|(R(x,t,Q^0), S(x,t,Q^0), u_2(x,t,Q^0)) - (R_2^*(x), S_2^*(x), u_2^*(x))\| < \tilde{\delta}_2.$$

It then follows from (3.16) that

$$f_1(R(\cdot,t,Q^0),S(\cdot,t,Q^0))e^{-\alpha u_2(\cdot,t,Q^0)} > f_1(R_2^*(\cdot),S_2^*(\cdot))e^{-\alpha u_2^*(\cdot)} - \epsilon_2,\ t \geq t_0. \quad (3.18)$$

With (3.18), it follows from the third equation of (1.1) that

$$\begin{cases} \frac{\partial u_1}{\partial t} \geq d\frac{\partial^2 u_1}{\partial x^2} + [f_1(R_2^*(\cdot),S_2^*(\cdot))e^{-\alpha u_2^*(\cdot)} - \epsilon_0]u_1, & x \in (0,1),\ t \geq t_0, \\ \frac{\partial u_1}{\partial x}(0,t) = \frac{\partial u_1}{\partial x}(1,t) + \gamma u_1(1,t) = 0,\ t \geq t_0. \end{cases} \quad (3.19)$$

Since $Q^0 \in \Omega_0$, we can further show that $u_1(x,t,Q^0) > 0,\ \forall\ x \in [0,1],\ t > 0$. Thus, there exists a sufficiently small number $a > 0$ such that $u_1(x,t_0,Q^0) \geq a\varphi_{\epsilon_0}(x),\ \forall\ x \in [0,1]$. Note that $\hat{u}_1(x,t) := ae^{\Lambda_2^{\epsilon_0}(t-t_0)}\varphi_{\epsilon_0}(x),\ t \geq t_0$, is a solution of the following linear system:

$$\begin{cases} \frac{\partial u_1}{\partial t} = d\frac{\partial^2 u_1}{\partial x^2} + [f_1(R_2^*(\cdot),S_2^*(\cdot))e^{-\alpha u_2^*(\cdot)} - \epsilon_0]u_1, & x \in (0,1),\ t \geq t_0, \\ \frac{\partial u_1}{\partial x}(0,t) = \frac{\partial u_1}{\partial x}(1,t) + \gamma u_1(1,t) = 0,\ t \geq t_0, \end{cases} \quad (3.20)$$

with initial data $\hat{u}_1(x,t_0) := a\varphi_{\epsilon_0}(x)$. Then the comparison principle implies that

$$u_1(x,t,Q^0) \geq \hat{u}_1(x,t) := ae^{\Lambda_2^{\epsilon_0}(t-t_0)}\varphi_{\epsilon_0}(x),\ \forall\ x \in [0,1],\ t \geq t_0.$$

Since $\Lambda_2^{\epsilon_0} > 0$, it follows that $u_1(x,t,Q^0)$ is unbounded. This contradiction proves the result in (3.17). Thus, Claim 2 holds.

Define a continuous function $\rho : \Omega \to [0,\infty)$ by

$$\rho(Q) := \min_{3\leq i\leq 4}\{\min_{x\in[0,1]} Q_i(x)\},\ \forall\ Q := (Q_1,Q_2,Q_3,Q_4) \in \Omega.$$

By the strong maximum principle and the Hopf boundary lemma (see [11]), we can prove that that $\rho^{-1}(0,\infty) \subseteq \Omega_0$ and ρ has the property that if $\rho(Q) > 0$ or $Q \in \Omega_0$ with $\rho(Q) = 0$, then $\rho(\Pi(t)Q) > 0,\ \forall\ t > 0$. That is, ρ is a generalized distance function for the semiflow $\Pi(t) : \Omega \to \Omega$ (see, e.g., [14]). By the above claims, it follows that any forward orbit of $\Pi(t)$ in $\tilde{M}_\partial$ converges to either $\tilde{M}_0$ or $\tilde{M}_1$ or $\tilde{M}_2$. Further, $\tilde{M}_0$, $\tilde{M}_1$, and $\tilde{M}_2$ are isolated in Ω and $W^s(\tilde{M}_i) \cap \Omega_0 = \emptyset,\ \forall\ i = 0,1,2$, where $W^s(\tilde{M}_i)$ is the stable set of $\tilde{M}_i,\ i = 0,1,2$ (see [14]). It is easy that no subsets of $\tilde{M}_0, \tilde{M}_1, \tilde{M}_2$ forms a cycle in $\tilde{M}_\partial$.

Since $\Pi(t) : \Omega \to \Omega$ admits a global compact attractor in Ω, it follows from [14, Theorem 3] that there exists an $\tilde{\eta} > 0$ such that

$$\min_{\varphi\in\omega(Q)} \rho(\varphi) > \tilde{\eta},\ \forall\ Q \in \Omega_0.$$

This implies that the uniform persistence stated in our theorem is valid. By [8, Theorem 3.7 and Remark 3.10], it then follows that $\Pi(t) : \Omega_0 \to \Omega_0$ has a global attractor. It then follows from [8, Theorem 4.7] that $\Pi(t)$ has an steady-state solution $(\hat{R}(\cdot), \hat{S}(\cdot), \hat{u}_1(\cdot), \hat{u}_2(\cdot), \hat{Z}(\cdot)) \in \Omega_0$. $\square$

Remark 3.1. *From Theorem 3.1, we have that* $\Pi(t) : \Omega \to \Omega$ *is uniformly persistent with respect to* $(\Omega_0, \partial\Omega_0)$ *provided that* (3.15) *is met. It follows from [8, Theorem 3.8] that* $\Pi(t) : \Omega_0 \to \Omega_0$ *admits a global attractor* A_0*. Since* $A_0 \subset \Omega_0$ *and* $A_0 = \Pi(t)(A_0)$*, we further have* $A_0 \subset \mathrm{Int}(C([0,1], \mathbb{R}^4_+))$.

4 Coexistence of harmful algae and zooplankton

In this section, we explore the possibility of coexistence of harmful algae and zooplankton. That is, we are going to establish the existence of positive (coexistence) steady-state solutions of system (1.1)-(1.3). Since zooplankton population growth rate $G(u_1, u_2)$ takes the form (1.4) or (1.5), it follows that $G(0, u_2) = G(u_1, 0) = 0$. This implies that the following types of steady-state solutions of (1.1)-(1.3) cannot occur:

$$(R, S, u_1, u_2, Z) = (\check{R}_1(x), \check{S}_1(x), \check{u}_1(x)(x), 0, \check{Z}_1(x)) \text{ with } \check{u}_1(\cdot), \check{Z}_1(\cdot) \gg 0, \quad (4.1)$$

and

$$(R, S, u_1, u_2, Z) = (\check{R}_2(x), \check{S}_2(x), 0, \check{u}_2(x)(x), \check{Z}_2(x)) \text{ with } \check{u}_2(\cdot), \check{Z}_2(\cdot) \gg 0. \quad (4.2)$$

Thus, system (1.1)-(1.3) has the following possible steady-state solutions:

(i) Trivial steady-state solution $\mathcal{E}_0 = (R, S, u_1, u_2, Z) = (w_R(x), w_S(x), 0, 0, 0)$ always exists (see Lemma 3.2 (i));

(ii) Semi-trivial steady-state solution $\mathcal{E}_1 = (R, S, u_1, u_2, Z) = (R_1^*(x), S_1^*(x), u_1^*(x), 0, 0)$ exists provided that $\lambda_1^0 > 0$, where $(R_1^*(x), S_1^*(x), u_1^*(x))$ is the unique steady-state solution of system (3.4)-(3.6) with $i = 1$ (see Lemma 3.2 (ii));

(iii) Semi-trivial steady-state solution $\mathcal{E}_2 = (R, S, u_1, u_2, Z) = (R_2^*(x), S_2^*(x), 0, u_2^*(x), 0)$ exists provided that $\lambda_2^0 > 0$, where $(R_2^*(x), S_2^*(x), u_2^*(x))$ is the unique steady-state solution of system (3.4)-(3.6) with $i = 2$ (see Lemma 3.2 (ii));

(iv) Zooplankton-extinct steady-state solution

$$\mathcal{E}_3 = (R, S, u_1, u_2, Z) = (\tilde{R}(x), \tilde{S}(x), \tilde{u}_1(x), \tilde{u}_2(x), 0)$$

exists provided that (3.15) holds. Here $(\tilde{R}(x), \tilde{S}(x), \tilde{u}_1(x), \tilde{u}_2(x))$ is a positive steady-state solution of (3.1)-(3.3), which is is not necessarily unique (see Theorem 3.1 and Remark 3.1).

Biologically, the most interesting question is whether both harmful algae and zooplankton can coexist in the unstirred chemostat. Mathematically, we want to show the existence of positive (coexistence) steady-state solutions of system (1.1)-(1.3) under suitable conditions.

Recall that $\mathbb{X} = C([0,1], \mathbb{R}^5_+)$ is the positive cone of the Banach space $C([0,1], \mathbb{R}^5)$ with the usual supremum norm. From Lemma 2.1 and Lemma 2.2, we can assume that $\Sigma(t) : \mathbb{X} \to \mathbb{X}$ is the semiflow generated by system (1.1)-(1.3). Let

$$\mathbb{X}_0 = \{(R^0(\cdot), S^0(\cdot), u_1^0(\cdot), u_2^0(\cdot), Z^0(\cdot)) \in \mathbb{X} : u_1^0(\cdot) \not\equiv 0,\ u_2^0(\cdot) \not\equiv 0,\ Z^0(\cdot) \not\equiv 0\},$$

and

$$\partial\mathbb{X}_0 = \mathbb{X} \backslash \mathbb{X}_0.$$

Assume that $M_0 = \{\mathcal{E}_0\}$, $M_1 = \{\mathcal{E}_1\}$, $M_2 = \{\mathcal{E}_2\}$, and $M_3 = A_0 \times \{0\}$, where $A_0 \subset \mathrm{Int}(C([0,1], \mathbb{R}^4_+))$ is a global attractor of the semiflows generated by system (3.1)-(3.3) (see Remark 3.1).

Define a projection $\mathcal{P}$ on $C([0,1], \mathbb{R}^4_+)$ by

$$\mathcal{P}(R, S, u_1, u_2) = (u_1, u_2),\ \forall\ (R, S, u_1, u_2) \in C([0,1], \mathbb{R}^4_+).$$

Let

$$B_0 = \mathcal{P}(A_0) \text{ and } m(x) = \inf_{\phi \in B_0} G(\phi(x)),\ \forall\ x \in [0,1]. \tag{4.3}$$

Lemma 4.1. *Let $m(x)$ be defined in* (4.3). *Then $m(x)$ is continuous on* $[0,1]$.

Proof. Let $H : [0,1] \times B_0 \to \mathbb{R}$ be defined by

$$H(x, \phi) = G(\phi(x)),\ \forall\ (x, \phi) \in [0,1] \times B_0.$$

Since H is continuous on the compact set $[0,1] \times B_0$, it follows that H is uniformly continuous on $[0,1] \times B_0$. Let $\epsilon > 0$ to be given. Then there exists $\delta = \delta(\epsilon)$ such that

$$|G(\phi(x)) - G(\phi(y))| = |H(x, \phi) - H(y, \phi)| < \frac{\epsilon}{2}, \tag{4.4}$$

whenever $(x,\phi),\ (y,\phi)\in[0,1]\times B_0$ with $|x-y|<\delta$.

Let $x,y\in[0,1]$ be given such that $|x-y|<\delta$. Since $m(y)+\frac{\epsilon}{2}$ is not a lower bound of $\{G(\phi(y)):\phi\in B_0\}$, we can find $\tilde{\phi}\in B_0$ such that $m(y)+\frac{\epsilon}{2}>G(\tilde{\phi}(y))$. Using (4.4), we further have

$$m(y)+\frac{\epsilon}{2}>G(\tilde{\phi}(y))>G(\tilde{\phi}(x))-\frac{\epsilon}{2}\geq m(x)-\frac{\epsilon}{2}. \tag{4.5}$$

Similarly, $m(x)+\frac{\epsilon}{2}$ is not a lower bound of $\{G(\phi(x)):\phi\in B_0\}$, and we can find $\hat{\phi}\in B_0$ such that $m(x)+\frac{\epsilon}{2}>G(\hat{\phi}(x))$. Using (4.4) again, we obtain

$$m(x)+\frac{\epsilon}{2}>G(\hat{\phi}(x))>G(\hat{\phi}(y))-\frac{\epsilon}{2}\geq m(y)-\frac{\epsilon}{2}. \tag{4.6}$$

By (4.5) and (4.6), it follows that for any given $\epsilon>0$, if $x,y\in[0,1]$ with $|x-y|<\delta$, then $|m(x)-m(y)|<\epsilon$. This shows that $m(\cdot)$ is uniformly continuous on $[0,1]$, and hence, $m(\cdot)$ is continuous on $[0,1]$. □

Next, we denote μ^0 to be the principal eigenvalue of the eigenvalue problem

$$\begin{cases} d\psi''(x)+m(x)\psi(x)=\mu\psi(x),\ x\in(0,1),\\ \psi'(0)=\psi'(1)+\gamma\psi(1)=0 \end{cases} \tag{4.7}$$

where $m(x)$ is defined in (4.3).

Lemma 4.2. *Let* (3.15) *hold and* $\mu^0>0$. *Then* M_3 *is a uniform weak repeller in the sense that there exists* $\delta_3>0$ *such that*

$$\limsup_{t\to\infty} dist(\Sigma(t)(Q^0,Z^0),M_3)\geq\delta_3,\ \text{for all } (Q^0,Z^0)\in\mathbb{X}_0. \tag{4.8}$$

Proof. Since $\mu^0>0$, we can choose a sufficiently small $\epsilon_0>0$ such that $\mu^0_{\epsilon_0}>0$, where $\mu^0_{\epsilon_0}$ is the principal eigenvalue of the eigenvalue problem

$$\begin{cases} d\psi''(x)+[m(x)-\epsilon_0]\psi(x)=\mu\psi(x),\ x\in(0,1),\\ \psi'(0)=\psi'(1)+\gamma\psi(1)=0. \end{cases} \tag{4.9}$$

Define $\tilde{G}:B_0\to C([0,1],\mathbb{R})$ by

$$\tilde{G}(\phi)(x)=G(\phi(x)),\ \forall\ x\in[0,1],\ \phi\in B_0.$$

Then there exists $\delta_3 > 0$ such that

$$\mathrm{dist}(\tilde{G}(\phi), \tilde{G}(B_0)) < \epsilon_0,$$

whenever $\phi \in C([0,1], \mathbb{R}^2)$ with $\mathrm{dist}(\phi, B_0) < \delta_3$. Since B_0 is compact, it follows that for any $\phi \in C([0,1], \mathbb{R}^2)$ with $\mathrm{dist}(\phi, B_0) < \delta_3$, there exists $\phi_* \in B_0$ with ϕ_* depending on ϕ such that

$$\mathrm{dist}(\tilde{G}(\phi), \tilde{G}(\phi_*)) = \mathrm{dist}(\tilde{G}(\phi), \tilde{G}(B_0)) < \epsilon_0.$$

Thus, we have

$$|G(\phi(x)) - G(\phi_*(x))| = |\tilde{G}(\phi)(x) - \tilde{G}(\phi_*)(x)| < \epsilon_0, \ \forall\ x \in [0,1], \tag{4.10}$$

whenever $\phi \in C([0,1], \mathbb{R}^2)$ with $\mathrm{dist}(\phi, B_0) < \delta_3$.

Next, we prove (4.8) by contradiction. Suppose that (4.8) is not true. Then there exists $(Q^0, Z^0) \in \mathbb{X}_0$ such that

$$\limsup_{t\to\infty} \mathrm{dist}(\Sigma(t)(Q^0, Z^0), M_3) < \delta_3,$$

and hence,

$$\limsup_{t\to\infty} \mathrm{dist}((u_1(\cdot,t), u_2(\cdot,t)), B_0) < \delta_3, \tag{4.11}$$

and

$$\limsup_{t\to\infty} \|Z(\cdot,t)\| < \delta_3. \tag{4.12}$$

From (4.11), we can choose $t_0 > 0$ such that

$$\mathrm{dist}((u_1(\cdot,t), u_2(\cdot,t)), B_0) < \delta_3, \ t \geq t_0. \tag{4.13}$$

By (4.10), it follows that there exists $\phi_*^t \in B_0$ such that

$$|G((u_1(x,t), u_2(x,t)) - G(\phi_*^t(x))| < \epsilon_0, \ \forall\ x \in [0,1], \ t \geq t_0, \tag{4.14}$$

and hence,

$$G((u_1(x,t), u_2(x,t)) > G(\phi_*^t(x)) - \epsilon_0 \geq m(x) - \epsilon_0, \ \forall\ x \in [0,1], \ t \geq t_0. \tag{4.15}$$

It follows from the fifth equation of (1.1) that

$$\begin{cases} \frac{\partial Z}{\partial t} \geq d\frac{\partial^2 Z}{\partial x^2} + [m(x) - \epsilon_0]Z, \ x \in (0,1), \ t \geq t_0, \\ \frac{\partial Z}{\partial x}(0,t) = \frac{\partial Z}{\partial x}(1,t) + \gamma Z(1,t) = 0, \ t \geq t_0. \end{cases} \tag{4.16}$$

Since $Z(\cdot,t) \not\equiv 0$, we can further show that $Z(\cdot,t_0) \gg 0$, and hence, there exists a sufficiently small number $a > 0$ such that $Z(x,t_0) \geq a\psi_{\epsilon_0}(x),\ \forall\ x \in [0,1]$, where $\psi_{\epsilon_0}(x)$ is the eigenfunction corresponding to $\mu^0_{\epsilon_0}$. Then the Comparison Principle ensures that

$$Z(x,t) \geq ae^{\mu^0_{\epsilon_0}(t-t_0)}\psi_{\epsilon_0}(x),\ \forall\ x \in [0,1],\ t \geq t_0.$$

Since $\mu^0_{\epsilon_0} > 0$, we deduce that $\lim_{t\to\infty} Z(\cdot,t) = \infty$, which contradicts (4.12). This proves (4.8). □

Now we are in a position to prove the main result of this section.

Theorem 4.1. *Let* (3.15) *hold and* $\mu^0 > 0$. *Then system* (1.1)-(1.3) *is uniformly persistent with respect to* $(\mathbb{X}_0, \partial\mathbb{X}_0)$ *in the following sense that there is a constant* $\eta > 0$ *such that every solution* $(R(\cdot,t), S(\cdot,t), u_1(\cdot,t), u_2(\cdot,t), Z(\cdot,t))$ *of* (1.1)-(1.3) *with* $(R(\cdot,0), S(\cdot,0), u_1(\cdot,0), u_2(\cdot,0), Z(\cdot,0)) \in \mathbb{X}_0$ *satisfying*

$$\liminf_{t\to\infty} u_i(\cdot,t) \geq \eta,\ \text{and}\ \liminf_{t\to\infty} Z(\cdot,t) \geq \eta,\ i = 1,2. \tag{4.17}$$

Furthermore, system (1.1)-(1.3) *admits at least one (componentwise) positive steady-state solution* $(\hat{R}(\cdot), \hat{S}(\cdot), \hat{u}_1(\cdot), \hat{u}_2(\cdot), \hat{Z}(\cdot))$.

Proof. By Lemma 2.3, it follows that for any $\mathbf{v}^0 \in \mathbb{X}_0$, we have

$$u_1(x,t,\mathbf{v}^0) > 0,\ u_2(x,t,\mathbf{v}^0) > 0,\ Z(x,t,\mathbf{v}^0) > 0,\ \forall\ x \in [0,1],\ t > 0.$$

This implies that $\Sigma(t)\mathbb{X}_0 \subseteq \mathbb{X}_0$ for all $t \geq 0$.

Let

$$M_\partial := \{\mathbf{v}^0 \in \partial\mathbb{X}_0 : \Sigma(t)\mathbf{v}^0 \in \partial\mathbb{X}_0, \forall\ t \geq 0\},$$

and $\omega(\mathbf{v}^0)$ be the omega limit set of the orbit $O^+(\mathbf{v}^0) := \{\Sigma(t)\mathbf{v}^0 : t \geq 0\}$. We further prove the following claims.

Claim 1. $\omega(\psi) \subset M_0 \cup M_1 \cup M_2 \cup M_3,\ \forall\ \psi \in M_\partial$.

For any given $\psi := (R^0, S^0, u_1^0, u_2^0, Z^0) \in M_\partial$, we have $\Sigma(t)\psi \in M_\partial,\ \forall\ t \geq 0$. Thus, for any given $t \geq 0$, we have $u_1(\cdot,t,\psi) \equiv 0$ or $u_2(\cdot,t,\psi) \equiv 0$ or $Z(\cdot,t,\psi) \equiv 0$.

In the case where $Z(\cdot,t,\psi) \equiv 0$ for all $t \geq 0$, substituting $Z(\cdot,t,\psi) \equiv 0$ into system (1.1)-(1.3). Then the equations for (R, S, u_1, u_2) satisfy system (3.1)-(3.3). We discuss the following four subcases:

(i) If $u_1^0 \equiv 0,\ u_2^0 \equiv 0$, then we have $u_1(\cdot,t,\psi) \equiv 0$ and $u_2(\cdot,t,\psi) \equiv 0$. Thus, $\lim_{t\to\infty} \Sigma(t)\psi = \mathcal{E}_0$.

(ii) If $u_1^0 \not\equiv 0$, $u_2^0 \equiv 0$, then we have $u_1(\cdot,t,\psi) > 0$ and $u_2(\cdot,t,\psi) \equiv 0$. Then the equations for (R,S,u_1) satisfy system (3.4)-(3.6) with $i=1$. Since $\lambda_1^0 > 0$, it follows from Lemma 3.2 that $\lim_{t\to\infty}(R(\cdot,t,\psi), S(\cdot,t,\psi), u_1(\cdot,t,\psi)) = (R_1^*(x), S_1^*(x), u_1^*(x))$, and hence, $\lim_{t\to\infty}\Sigma(t)\psi = \mathcal{E}_1$.

(iii) If $u_1^0 \equiv 0$, $u_2^0 \not\equiv 0$, then we can use the fact $\lambda_2^0 > 0$ and the same arguments as in (ii) to show that $\lim_{t\to\infty}\Sigma(t)\psi = \mathcal{E}_2$.

(iv) If $u_1^0 \not\equiv 0$, $u_2^0 \not\equiv 0$, then we have $u_1(\cdot,t,\psi) > 0$ and $u_2(\cdot,t,\psi) > 0$. Since (3.15) holds, it follows from Theorem 3.1 and Remark 3.1 that

$$(R(\cdot,t,\psi), S(\cdot,t,\psi), u_1(\cdot,t,\psi), u_2(\cdot,t,\psi))$$

will eventually enter the global attractor $A_0 \subset \mathrm{Int}(C([0,1],\mathbb{R}_+^4))$. Thus, $\Sigma(t)\psi$ will eventually enter the global attractor M_3.

In the case where $Z(\cdot,t_1,\psi) \not\equiv 0$, for some $t_1 \geq 0$. Then Lemma 2.3 implies that $Z(x,t,\psi) > 0$, $\forall\ x \in [0,1], \forall\ t > t_1$. It then follows that for each $t > t_1$, either $u_1(\cdot,t,\psi) \equiv 0$ or $u_2(\cdot,t,\psi) \equiv 0$. If $u_1(\cdot,t,\psi) \equiv 0$, for each $t > t_1$. Then $G(u_1(\cdot,t,\psi), u_2(\cdot,t,\psi)) = 0$, and hence, $Z(x,t,\psi)$ satisfies

$$\begin{cases} \frac{\partial Z}{\partial t} = d\frac{\partial^2 Z}{\partial x^2}, & x \in (0,1),\ t > 0, \\ \frac{\partial Z}{\partial x}(0,t) = \frac{\partial Z}{\partial x}(1,t) + \gamma Z(1,t) = 0, & t > 0, \\ Z(x,0) = Z^0(x) \geq 0, & x \in (0,1). \end{cases} \tag{4.18}$$

It is easy to see that $\lim_{t\to\infty} Z(\cdot,t,\psi) = 0$. Thus, either $\lim_{t\to\infty}\Sigma(t)\psi = \mathcal{E}_0$ or $\lim_{t\to\infty}\Sigma(t)\psi = \mathcal{E}_2$. If $u_1(\cdot,t_2,\psi) \not\equiv 0$, for some $t_2 > t_1$. Then Lemma 2.3 implies that $u_1(x,t,\psi) > 0$, $\forall\ x \in [0,1], \forall\ t > t_2$. It then follows that for each $t > t_2$, $u_2(\cdot,t,\psi) \equiv 0$. Thus, $G(u_1(\cdot,t,\psi), u_2(\cdot,t,\psi)) = 0$, and hence, $Z(x,t,\psi)$ satisfies (4.18). This implies that either $\lim_{t\to\infty}\Sigma(t)\psi = \mathcal{E}_0$ or $\lim_{t\to\infty}\Sigma(t)\psi = \mathcal{E}_1$. we have proved claim 1.

Claim 2. For $i = 0,1,2,3$, M_i is a uniform weak repeller for $\mathbb{X}_0$ in the sense that there exists $\delta_i > 0$ such that $\limsup_{t\to\infty}\|\Sigma(t)\mathbf{v}^0 - M_i\| \geq \delta_i$, $\forall\ \mathbf{v}^0 \in \mathbb{X}_0$.

By Lemma 4.2, it follows that claim 2 is true when $i=3$. Next, we only give the detailed arguments for the case $i=2$ since we can prove the cases where $i=0,1$ by using the similar arguments. From the fact that $\Lambda_2^0 > 0$, we may assume that there exists an $\epsilon_2 > 0$ such that $\Lambda^0_{2\epsilon} > 0$, where $\Lambda^0_{2\epsilon}$ is the principal eigenvalue of the eigenvalue problem

$$\begin{cases} d\varphi''(x) + [f_1(R_2^*(x), S_2^*(x))e^{-\alpha u_2^*(x)} - 2\epsilon_2]\varphi(x) = \Lambda_2\varphi(x), \ x \in (0,1), \\ \varphi'(0) = \varphi'(1) + \gamma\varphi(1) = 0, \end{cases}$$

where $R_2^*(x) := w_R(x) - q_{2r}u_2^*(x)$ and $S_2^*(x) := w_S(x) - q_{2s}u_2^*(x)$ (see (3.9)). The positive eigenfunction corresponding to $\Lambda^0_{2\epsilon}$ can be uniquely determined by the normalization, and we denote it by $\varphi^0_{2\epsilon}(x)$.

It is easy to see that there exists $\delta_{21} > 0$ such that if $\|(R_2, S_2, u_2) - (R_2^*(\cdot), S_2^*(\cdot), u_2^*(\cdot))\| < \delta_{21}$, then

$$f_1(R_2, S_2)e^{-\alpha u_2} > f_1(R_2^*(\cdot), S_2^*(\cdot))e^{-\alpha u_2^*(\cdot)} - \epsilon_2. \tag{4.19}$$

Rewrite $q_1 g_1(u_1)Z = I(u_1, Z)u_1$, where $I(u_1, Z) = q_1\frac{g_1(u_1)}{u_1}Z$ and $I(0,0) = 0$. Then there exists $\delta_{22} > 0$ such that if $\|(u_1, Z) - (0,0)\| < \delta_{22}$, then

$$I(u_1, Z) < I(0,0) + \epsilon_2 = \epsilon_2. \tag{4.20}$$

Setting $\delta_2 := \min\{\delta_{21}, \delta_{22}\}$. Then we show that

$$\limsup_{t\to\infty} \|\Sigma(t)\mathbf{v}^0 - M_2\| \geq \delta_2, \ \forall \ \mathbf{v}^0 \in \mathbb{X}_0. \tag{4.21}$$

Suppose, by contradiction, there exists $\mathbf{v}^0_0 \in \mathbb{X}_0$ such that $\limsup_{t\to\infty} \|\Sigma(t)\mathbf{v}^0_0 - M_2\| < \delta_2$. Then there exists $\tilde{t} > 0$ such that for $t \geq \tilde{t}$ and $x \in [0,1]$, we have

$$\|(R(x,t,\mathbf{v}^0_0), S(x,t,\mathbf{v}^0_0), u_2(x,t,\mathbf{v}^0_0)) - (R_2^*(x), S_2^*(x), u_2^*(x))\| < \delta \leq \delta_{21},$$

and

$$\|(u_1(x,t,\mathbf{v}^0_0), Z(x,t,\mathbf{v}^0_0)) - (0,0)\| < \delta \leq \delta_{22}.$$

It follows from (4.19) and (4.20) that for $t \geq \tilde{t}$, we have

$$f_1(R(\cdot,t,\mathbf{v}^0_0), S(\cdot,t,\mathbf{v}^0_0))e^{-\alpha u_2(\cdot,t,\mathbf{v}^0_0)} > f_1(R_2^*(\cdot), S_2^*(\cdot))e^{-\alpha u_2^*(\cdot)} - \epsilon_2, \tag{4.22}$$

and

$$I(u_1(\cdot,t,\mathbf{v}^0_0), Z(\cdot,t,\mathbf{v}^0_0)) < \epsilon_2. \tag{4.23}$$

With (4.22) and (4.23), it follows from the third equation of (1.1) that

$$\begin{cases} \frac{\partial u_1}{\partial t} \geq d\frac{\partial^2 u_1}{\partial x^2} + [f_1(R_2^*(\cdot), S_2^*(\cdot))e^{-\alpha u_2^*(\cdot)} - 2\epsilon_2]u_1, \quad x \in (0,1), \ t \geq \tilde{t}, \\ \frac{\partial u_1}{\partial x}(0,t) = \frac{\partial u_1}{\partial x}(1,t) + \gamma u_1(1,t) = 0, \ t \geq \tilde{t}. \end{cases} \tag{4.24}$$

Since $\mathbf{v}_0^0 \in \mathbb{X}_0$, it follows from Lemma 2.3 that $u_1(x, t, \mathbf{v}_0^0) > 0,\ \forall\ x \in [0, 1],\ t > 0$. Thus, there exists a sufficiently small number $\rho_0 > 0$ such that $u_1(x, \tilde{t}, \mathbf{v}_0^0) \geq \rho_0 \varphi_{2\epsilon}^0(x),\ \forall\ x \in [0, 1]$. Note that $\tilde{u}_1(x, t) := \rho_0 e^{\Lambda_{2\epsilon}^0 (t-\tilde{t})} \varphi_{2\epsilon}^0(x),\ t \geq \tilde{t}$, is a solution of the following linear system:

$$\begin{cases} \frac{\partial u_1}{\partial t} = d\frac{\partial^2 u_1}{\partial x^2} + [f_1(R_2^*(\cdot), S_2^*(\cdot))e^{-\alpha u_2^*(\cdot)} - 2\epsilon_2]u_1, \quad x \in (0, 1),\ t \geq \tilde{t}, \\ \frac{\partial u_1}{\partial x}(0, t) = \frac{\partial u_1}{\partial x}(1, t) + \gamma u_1(1, t) = 0,\ t \geq \tilde{t}, \end{cases} \tag{4.25}$$

with initial data $\tilde{u}_1(x, \tilde{t}) := \rho_0 \varphi_{2\epsilon}^0(x)$. Then the comparison principle implies that

$$u_1(x, t, \mathbf{v}_0^0) \geq \tilde{u}_1(x, t) := \rho_0 e^{\Lambda_{2\epsilon}^0 (t-\tilde{t})} \varphi_{2\epsilon}^0(x),\ \forall\ x \in [0, 1],\ t \geq \tilde{t}.$$

Since $\Lambda_{2\epsilon}^0 > 0$, it follows that $u_1(x, t, \mathbf{v}_0^0)$ is unbounded. This contradiction proves the result in (4.21). Thus, claim 2 holds.

Define a continuous function $\mathbf{p} : \mathbb{X} \to [0, \infty)$ by

$$\mathbf{p}(\mathbf{v}^0) := \min_{3 \leq i \leq 5} \{ \min_{x \in [0,1]} \mathbf{v}_i^0(x) \},\ \forall\ \mathbf{v}^0 := (\mathbf{v}_1^0, \mathbf{v}_2^0, \mathbf{v}_3^0, \mathbf{v}_4^0, \mathbf{v}_5^0) \in \mathbb{X}.$$

By Lemma 2.3, it follows that $\mathbf{p}^{-1}(0, \infty) \subseteq \mathbb{X}_0$ and $\mathbf{p}$ has the property that if $\mathbf{p}(\mathbf{v}^0) > 0$ or $\mathbf{v}^0 \in \mathbb{X}_0$ with $\mathbf{p}(\mathbf{v}^0) = 0$, then $\mathbf{p}(\Sigma(t)\mathbf{v}^0) > 0,\ \forall\ t > 0$. That is, $\mathbf{p}$ is a generalized distance function for the semiflow $\Sigma(t) : \mathbb{X} \to \mathbb{X}$ (see, e.g., [14]). By the above claims, it follows that any forward orbit of $\Sigma(t)$ in M_∂ converges to either M_0 or M_1 or M_2 or M_3. Further, M_0, M_1, M_2, and M_3 are isolated in $\mathbb{X}$ and $W^s(M_i) \cap \mathbb{X}_0 = \emptyset,\ \forall\ i = 0, 1, 2, 3$, where $W^s(M_i)$ is the stable set of $M_i,\ i = 0, 1, 2, 3$ (see [14]). It is easy that no subsets of M_0, M_1, M_2, M_3 forms a cycle in M_∂.

By Lemma 2.2, it is easy to see that $\Sigma(t) : \mathbb{X} \to \mathbb{X}$ has a global compact attractor in $\mathbb{X}$, $\forall\ t \geq 0$. It follows from [14, Theorem 3] that there exists an $\eta > 0$ such that

$$\min_{\psi \in \omega(\mathbf{v}^0)} \mathbf{p}(\psi) > \eta,\ \forall\ \mathbf{v}^0 \in \mathbb{X}_0.$$

This implies that (4.17) holds. Hence, the uniform persistence stated in our theorem is valid. By [8, Theorem 3.7 and Remark 3.10], it then follows that $\Sigma(t) : \mathbb{X}_0 \to \mathbb{X}_0$ has a global attractor. It then follows from [8, Theorem 4.7] that $\Sigma(t)$ has an steady-state solution $(\hat{R}(\cdot), \hat{S}(\cdot), \hat{u}_1(\cdot), \hat{u}_2(\cdot), \hat{Z}(\cdot)) \in \mathbb{X}_0$. □

5 Discussion

In this paper, we propose and analyze an unstirred chemostat model of the dynamics of P. parvum, cyanobacteria, and a zooplankton population. In our system

(1.1)-(1.3), P. parvum competes for nutrients with cyanobacteria, which inhibits the growth of P. parvum. The zooplankton population grazes on P. parvum and cyanobacteria for growth, but P. parvum also inhibits the growth of zooplankton. This project is highly motivated by paper [5], in which the authors investigated a well-mixed chemostat system modeling the inhibitory/allelopathic effects of the algal toxins produced by P. parvum and cyanobacteria. Our system (1.1)-(1.3) further includes spatial variations, but neglects the compartments of algal toxins produced by P. parvum and cyanobacteria. The strength of inhibition/allelopathy is directly determined by the densities of P. parvum and cyanobacteria respectively, not their toxins, which reduces the numbers of the modeling equations.

In order to study the coexistence of system (1.1)-(1.3), we need first to find the following possible steady-state solutions: the trivial steady-state solution of (1.1)-(1.3), corresponds to the absence of both harmful algae and zooplankton, is unique (Lemma 3.2 (i)); two semi-trivial steady-state solutions, corresponds to the presence of one of the algae and the absence of the other algae and zooplankton, are both unique if they exist (Lemma 3.2 (ii)); zooplankton-extinct steady-state solution, corresponds to the presence of both harmful algae and the absence of zooplankton, is not necessarily unique (see Theorem 3.1 and Remark 3.1). After defining a suitable continuous function $m(x)$ (see Lemma 4.1), we are able to show that the compact attractor M_3 on the boundary $Z = 0$ is a uniform weak repeller for system (1.1)-(1.3) (see Lemma 4.2) under appropriate conditions. Then, we are able to show that system (1.1)-(1.3) is uniformly persistent, and system (1.1)-(1.3) admits at least one (componentwise) positive steady-state solution when the trivial steady-state solution, two semi-trivial steady-state solutions, and the compact set M_3 are all invasible (see Theorem 4.1).

Our work extended the well-mixed model in [5] to a partially-mixed system, but we also did two significant simplifications in modeling. For example, the growth rate of zooplankton $G(u_1, u_2)$ only takes the form (1.4) or (1.5), which eliminates the possibility of two types of steady-state solutions for system (1.1)-(1.3) (see (4.1) and (4.2)). If $G(u_1, u_2)$ takes the substitutable type, that is, $G(0, u_2)$ and $G(u_1, 0)$ can be both positive, then it is likely that another two types of steady-state solutions, (4.1) and (4.2), can happen. This will make the analysis much more complicated than those in the current paper. On the other hand, in order to reduce the numbers of model equations in our system, we have removed the compartments of algal toxins produced by both harmful algae, and the associated inhibition/allelopathy is directly affected by the densities of algae respectively. We will relax the aforementioned simplifications and investigate a more realistic and challenging case in the future.

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