A Reaction-Diffusion-Advection Model of Harmful Algae Growth with Toxin Degradation

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Abstract

This paper is devoted to the study of a reaction-diffusion-advection system modeling the dynamics of a single nutrient, harmful algae and algal toxin in a flowing water habitat with a hydraulic storage zone. We introduce the basic reproduction ratio $\mathcal{R}_0$ for algae and show that $\mathcal{R}_0$ serves as a threshold value for persistence and extinction of the algae. More precisely, we prove that the washout steady state is globally attractive if $\mathcal{R}_0 < 1$, while there exists a positive steady state and the algae is uniformly persistent if $\mathcal{R}_0 > 1$. With an additional assumption, we obtain the uniqueness and global attractivity of the positive steady state in the case where $\mathcal{R}_0 > 1$.

Keywords: Spatial model of harmful algae, steady states, basic reproduction ratio, threshold dynamics, global attractor.

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1 Introduction

Blooms of the harmful algae have increased the intensity worldwide in coastal as well as inland waters. The blooms have direct impacts for human health, and food webs in aquatic ecosystems [3]. For example, *Prymnesium parvum* (golden algae) is responsible for such harmful algal blooms worldwide that have caused large fish

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kills and millions of dollars in economic losses. There is a paradox in the persistence of harmful algae [15]. Intuitively, strong flow washes out suspended algae, and continual strong flow can overcome the reproductive capacity of planktonic algae. On the other hand, the characteristics of the shorelines and the bed of the channel can reduce the speed of flow, producing slow-flowing regions constituting a hydraulic storage zone that affects the persistence of harmful algae and their toxins [3, 4]. Thus, we may expect that the reproductive capacity of algae may suffice to permit population growth, even to bloom proportions. This prediction was confirmed by Grover et al. [4, Section 3.3]. Recently, a potential technique was suggested to manage and mitigate harmful algal blooms through flow manipulations in some riverine systems [8, 9, 17]. This possibility motivates the theoretical modeling of harmful algal dynamics in flowing habitats [3]. In order to investigate the differences between a fringing cove and a main lake arising in a single cove, Grover et al. [3] proposed two-compartment models in which one compartment is a small cove connected to a larger lake. Hsu et al. [5] further analyzed such a two-compartment model with seasonal temperature variations.

To understand longitudinal patterns arising along the axis of flow, the authors in [3] proposed two reaction-diffusion-advection systems modeling the dynamics of one nutrient, one single population of algae, and algal toxin with spatial variations in an idealized riverine reservoir where a main channel was coupled to a hydraulic storage zone. Next, we shall adopt notations and physical settings used in [3] to describe the model systems. Suppose that L represents the length of the channel; A and A_S represent cross-section area of a flowing zone, and a static storage zone, respectively. We assume that advective and diffusive transport occur only in the main flowing zone, not the storage zone; α (time^{-1}) represents the exchange rate of nutrient, algae, and toxin between the flowing and storage zones. Flow enters at the upstream end of the channel ($x = 0$), and an equal flow exits at the downstream end ($x = L$). Flow is parameterized as a constant dilution rate D (time^{-1}), and assuming constant water volume in the channel implies that advection occurs at a speed ν ($\nu = DL$). The flow of water in the channel in the direction of increasing x brings fresh nutrient for algal growth at a concentration $R^{(0)}$ into the reactor at $x = 0$, and a balancing flow exits at the dam ($x = L$), removing algae, nutrients, and algal toxin. Nutrient, algae, and algal toxin are assumed to diffuse throughout the main channel with the same diffusivity δ. Both advective and diffusive transport occur at the upstream boundary ($x = 0$). The downstream boundary is assumed to be a dam, over which there is advective flow but through which no diffusion can take place.

The nonlinear function $f(R)$ describes the nutrient uptake and algal growth at the limiting nutrient concentration (R). We assume that $f(R)$ satisfies

$$f(0) = 0,\ \ f'(R) > 0,\ \ f \in C^2.$$

A typical example is the Monod function

$$f(R) = \frac{\mu_{\max} R}{K + R},$$

where $\mu_{\max}$ (day^{-1}) represents the maximal growth rate and K (μM) represents the half saturation constant. Let $R(x,t)$, $N(x,t)$ and $C(x,t)$ ($R_S(x,t)$, $N_S(x,t)$ and $C_S(x,t)$) be the dissolved nutrient concentration, algal abundance and dissolved toxin concentration at location x and time t in the flowing channel (the storage zone), respectively. Assume that m (day^{-1}) and k (day^{-1}) represent the mortality of algae and toxin degradation, respectively. It was known that many cyanotoxins produced by cyanobacteria that contain nitrogen, a potential limiting nutrient for algae [1]. Because of this fact, these toxins can get recycled back into the system as a nutrient resource after they decompose. We assume ϵ is a dimensionless coefficient that specifies the allocation of the limiting nutrient to toxin production [1]. For such case, the authors in [3] proposed the following reaction-diffusion-advection system modeling the dynamics of limiting nutrient, harmful algae and their toxins:

$$\begin{cases} \frac{\partial R}{\partial t} = \delta \frac{\partial^2 R}{\partial x^2} - \nu \frac{\partial R}{\partial x} - q_N[f(R) - m]N + \alpha(R_S - R) + kq_C C, \\ \frac{\partial N}{\partial t} = \delta \frac{\partial^2 N}{\partial x^2} - \nu \frac{\partial N}{\partial x} + \alpha(N_S - N) + [(1-\epsilon)f(R) - m]N, \\ \frac{\partial C}{\partial t} = \delta \frac{\partial^2 C}{\partial x^2} - \nu \frac{\partial C}{\partial x} + \alpha(C_S - C) + \epsilon f(R)\frac{q_N}{q_C}N - kC, \\ \frac{\partial R_S}{\partial t} = -\alpha \frac{A}{A_S}(R_S - R) - q_N[f(R_S) - m]N_S + kq_C C_S, \\ \frac{\partial N_S}{\partial t} = -\alpha \frac{A}{A_S}(N_S - N) + [(1-\epsilon)f(R_S) - m]N_S, \\ \frac{\partial C_S}{\partial t} = -\alpha \frac{A}{A_S}(C_S - C) + \epsilon f(R_S)\frac{q_N}{q_C}N_S - kC_S, \end{cases} \tag{1.1}$$

for $(x,t) \in (0,L) \times (0,\infty)$ with boundary conditions

$$\begin{cases} \nu R(0,t) - \delta \frac{\partial R}{\partial x}(0,t) = \nu R^{(0)}, \\ \nu N(0,t) - \delta \frac{\partial N}{\partial x}(0,t) = \nu C(0,t) - \delta \frac{\partial C}{\partial x}(0,t) = 0, \\ \frac{\partial R}{\partial x}(L,t) = \frac{\partial N}{\partial x}(L,t) = \frac{\partial C}{\partial x}(L,t) = 0, \end{cases} \tag{1.2}$$

and initial conditions

$$\begin{cases} R(x,0) = R^0(x) \geq 0, \ N(x,0) = N^0(x) \geq 0, \ C(x,0) = C^0(x) \geq 0, \\ R_S(x,0) = R_S^0(x) \geq 0, \ N_S(x,0) = N_S^0(x) \geq 0, \ C_S(x,0) = C_S^0(x) \geq 0, \end{cases} \tag{1.3}$$

for $x \in (0,L)$, where q_N (q_C) represents the nutrient quota of algae (toxin).

We should point out that another reaction-diffusion-advection model in [3] (see system (4) therein) was mathematically analyzed in [7]. For many flagellate toxins, the toxin contains little of the limiting nutrient [11]. In such a case, the model (4) in [3] is more appropriate. As a continuation of the work in [7], our current paper is devoted to the study of the global dynamics of model (1.1). Next, we compare the main differences of mathematical approach between system (1.1)-(1.3) in the current paper and system (3.1)-(3.3) in [7] (i.e., system (4) in [3]). Since the equations C and C_S of system (3.1)-(3.3) in [7] are decoupled from the equations R, R_S, N, and N_S, it suffices to study the subsystem (3.25)-(3.27) in [7], which can be further reduced into a cooperative and subhomogeneous system (see system (3.21)-(3.23) in [7]). One can use the theory of monotone semiflows to establish the uniqueness and global stability of positive steady state for system (3.21)-(3.23) in [7]. Then the theory of chain transitive sets can be applied to prove the uniqueness and global stability of positive steady state for system (3.1)-(3.3) in [7]. However, we may not drop the C and C_S equations from system (1.1)-(1.3) in the current paper due to the recycling terms $kq_C C$ and $kq_C C_S$ appearing in the first and fourth equations of system (1.1), respectively. With the help of a conservation (see Lemma 2.2), system (1.1)-(1.3) can be reduced into a subsystem (see (3.1)-(3.3)). Notice that, without any additional assumptions, system (3.1)-(3.3) is neither a cooperative system nor a subhomogeneous system, and hence, the mathematical arguments used in [7, Section 3] no longer work for our case. Thus, the uniqueness and global attractivity of the positive steady state becomes a challenging problem. Our strategy here is to obtain a threshold result on the global extinction and persistence of the algae for system (1.1)-(1.3) by appealing to the theory of uniform persistence and chain transitive sets (see Theorem 3.3). Under an additional assumption $m = k$, we find that system (3.1)-(3.3) can be reduced into a cooperative and subhomogeneous system (see (4.4)-(4.6)), and hence, the uniqueness and global stability of positive steady state of system (1.1)-(1.3) can be obtained by using the similar arguments in [7, Section 3] (see Theorem 4.1).

The organization of this paper is as follows. In section 2, we study the well-posedness and introduce the basic reproduction ratio $\mathcal{R}_0$ for system (1.1)-(1.3), which can determine the local stability of the trivial steady state. In section 3, we prove that the solution semiflow associated with system (1.1)-(1.3) is asymptotically compact and admits a global attractor under appropriate conditions. Then we establish a threshold result on the global extinction and persistence in terms of $\mathcal{R}_0$ by appealing to the theory of uniformly persistence and chain transitive sets. In section 4, under the assumption that the mortality of algae coincides with toxin degradation ($m = k$), we find another conservation law (4.2) and then reduce (1.1)-(1.3) to a limiting system which generates a monotone semiflow. We further prove the global attractivity of the positive steady state in the case where $\mathcal{R}_0 > 1$. A brief discussion section completes the paper.

2 The basic reproduction ratio

In this section, we first study the well-posedness of the initial-boundary-value problem (1.1)-(1.3), and then introduce the basic reproduction ratio for algae growth.

Let $X = C([0, L], \mathbb{R}^6)$ and $X^+ = C([0, L], \mathbb{R}^6_+)$. Then (X, X^+) is an ordered Banach space equipped with the usual supremum norm. In order to simplify notations, we set $u_0 = R$, $u_1 = N$, $u_2 = C$, $u_3 = R_S$, $u_4 = N_S$, $u_5 = C_S$ and $\mathbf{u} = (u_0, u_1, u_2, u_3, u_4, u_5)$. We assume that the initial data in (1.3) satisfying

$$(u_0^0, u_1^0, u_2^0, u_3^0, u_4^0, u_5^0) := (R^0, N^0, C^0, R_S^0, N_S^0, C_S^0) \in X^+.$$

For the local existence and positivity of solutions, we appeal to the theory developed in [10] where the 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 X^+ and the so-called mild solutions can be obtained for any given initial data. More precisely, we consider the following integral form:

$$\begin{cases} u_0(t) = V(t)u_0^0 + \int_0^t T_0(t-s)B_0(\mathbf{u}(s))ds, \\ u_i(t) = T_i(t)u_i^0 + \int_0^t T_i(t-s)B_i(\mathbf{u}(s))ds, \ i = 1, 2, \\ u_i(t) = u_i^0 + \int_0^t B_i(\mathbf{u}(s))ds, \ i = 3, 4, 5, \end{cases}$$

where $T_i(t)$ is the positive, non-expansive, analytic semigroup on $C([0, L], \mathbb{R})$ (see, e.g., [18, Chapter 7]) such that $u = T_i(t)u_i^0$, $i = 0, 1, 2$, satisfies the linear initial value problem

$$\begin{cases} \frac{\partial u}{\partial t} = \delta \frac{\partial^2 u}{\partial x^2} - \nu \frac{\partial u}{\partial x}, \ t > 0, \ 0 < x < L, \\ \nu u(0, t) - \delta \frac{\partial u}{\partial x}(0, t) = \frac{\partial u}{\partial x}(L, t) = 0, \ t > 0, \\ u(x, 0) = u_i^0(x), \ i = 0, 1, 2, \end{cases}$$

$\{V(t)\}_{t \geq 0}$ is the family of affine operators on $C([0, L], \mathbb{R})$ (see, e.g., [13, Chapter 5]) such that $u = V(t)u_0^0$ satisfies the linear system with nonhomogeneous boundary condition given by

$$\begin{cases} \frac{\partial u}{\partial t} = \delta \frac{\partial^2 u}{\partial x^2} - \nu \frac{\partial u}{\partial x}, \ t > 0, \ 0 < x < L, \\ \nu u(0, t) - \delta \frac{\partial u}{\partial x}(0, t) = \nu R^{(0)}, \ \frac{\partial u}{\partial x}(L, t) = 0, \ t > 0, \\ u(x, 0) = u_0^0(x), \end{cases}$$

and the nonlinear operator $B_i : C([0,L],\mathbb{R}_+^6) \to C([0,L],\mathbb{R})$ is defined by

$$\begin{cases} B_0(\mathbf{u}) = -q_N[f(u_0) - m]u_1 + \alpha(u_3 - u_0) + kq_C u_2, \\ B_1(\mathbf{u}) = \alpha(u_4 - u_1) + [(1-\epsilon)f(u_0) - m]u_1, \\ B_2(\mathbf{u}) = \alpha(u_5 - u_2) + \epsilon f(u_0)\frac{q_N}{q_C}u_1 - ku_2, \\ B_3(\mathbf{u}) = -\alpha\frac{A}{A_S}(u_3 - u_0) - q_N[f(u_3) - m]u_4 + kq_C u_5, \\ B_4(\mathbf{u}) = -\alpha\frac{A}{A_S}(u_4 - u_1) + [(1-\epsilon)f(u_3) - m]u_4, \\ B_5(\mathbf{u}) = -\alpha\frac{A}{A_S}(u_5 - u_2) + \epsilon f(u_3)\frac{q_N}{q_C}u_4 - ku_5. \end{cases}$$

By the standard maximum principle arguments (see, e.g., [18, Chapter 7]), it follows that $V(t)C([0,L],\mathbb{R}_+) \subset C([0,L],\mathbb{R}_+)$ and $T_i(t)C([0,L],\mathbb{R}_+) \subset C([0,L],\mathbb{R}_+)$ for all $t \geq 0$. The operator V and semi-group T_0 are related to [10, Eq.(1.9)] by setting $\beta(x,t) \equiv \nu R^{(0)}$. Since $f(0) = 0$, it follows that $B_i(\mathbf{u}) \geq 0$ whenever $u_i \equiv 0$, $\forall\, 0 \leq i \leq 5$, and hence, $\tilde{\mathbf{B}} := (B_0, B_1, B_2, B_3, B_4, B_5)$ is quasipositive (see, e.g., [10, Remark 1.1]). By [10, Theorem 1 and Remark 1.1], we have the following result.

Lemma 2.1. *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.*

In the following, we will demonstrate that mass conservation is satisfied in the flow and storage zones for the equations given by (1.1)-(1.3). Let

$$\begin{cases} V(x,t) = R(x,t) + q_N N(x,t) + q_C C(x,t), \\ V_S(x,t) = R_S(x,t) + q_N N_S(x,t) + q_C C_S(x,t). \end{cases} \tag{2.1}$$

Then $V(x,t)$ and $V_S(x,t)$ satisfy the following coupled differential equations

$$\begin{cases} \frac{\partial V}{\partial t} = \delta\frac{\partial^2 V}{\partial x^2} - \nu\frac{\partial V}{\partial x} + \alpha V_S - \alpha V, \ 0 < x < L, \ t > 0, \\ \frac{\partial V_S}{\partial t} = -\alpha\frac{A}{A_S}V_S + \alpha\frac{A}{A_S}V, \ 0 < x < L, \ t > 0, \\ \nu V(0,t) - \delta\frac{\partial V}{\partial x}(0,t) = \nu R^{(0)}, \ \frac{\partial V}{\partial x}(L,t) = 0, \ t > 0, \\ V(x,0) = V^0(x) \geq 0, \ V_S(x,0) = V_S^0(x) \geq 0. \end{cases} \tag{2.2}$$

By similar arguments to those in [4] and [6, Lemma 2.3], we have the following results on the global dynamics of system (2.2).

Lemma 2.2. *System* (2.2) *admit a unique positive steady-state solution* $(R^{(0)}, R^{(0)})$ *and for any* $(V^0(x), V_S^0(x)) \in C([0,L],\mathbb{R}^2)$*, the unique mild solution* $(V(x,t), V_S(x,t))$ *of* (2.2) *with* $(V(x,0), V_S(x,0)) = (V^0(x), V_S^0(x))$ *satisfies*

$$\lim_{t\to\infty}(V(x,t), V_S(x,t)) = (R^{(0)}, R^{(0)}) \text{ uniformly for } x \in [0,L].$$

It is easy to see that $(R^{(0)}, 0, 0, R^{(0)}, 0, 0)$ is a steady state solution of system (1.1)-(1.3). Linearizing system (1.1)-(1.3) at $(R^{(0)}, 0, 0, R^{(0)}, 0, 0)$, we get the following cooperative system for (N, N_S) compartments:

$$\begin{cases} \frac{\partial N}{\partial t} = \delta \frac{\partial^2 N}{\partial x^2} - \nu \frac{\partial N}{\partial x} + \alpha(N_S - N) + [(1-\epsilon)f(R^{(0)}) - m]N, \\ \frac{\partial N_S}{\partial t} = -\alpha \frac{A}{A_S}(N_S - N) + [(1-\epsilon)f(R^{(0)}) - m]N_S, \end{cases} \tag{2.3}$$

in $(x, t) \in (0, L) \times (0, \infty)$ with boundary conditions

$$\nu N(0, t) - \delta \frac{\partial N}{\partial x}(0, t) = \frac{\partial N}{\partial x}(L, t) = 0, \tag{2.4}$$

and initial conditions

$$N(x, 0) = N^0(x) \geq 0, N_S(x, 0) = N_S^0(x) \geq 0. \tag{2.5}$$

Substituting $N(x, t) = e^{\lambda t} w(x)$ and $N_S(x, t) = e^{\lambda t} w_S(x)$ into (2.3), we obtain the associated eigenvalue problem

$$\begin{cases} \lambda w = \delta w'' - \nu w' + \alpha(w_S - w) + [(1-\epsilon)f(R^{(0)}) - m]w, \\ \lambda w_S = -\alpha \frac{A}{A_S}(w_S - w) + [(1-\epsilon)f(R^{(0)}) - m]w_S, \\ \nu w(0) - \delta w'(0) = w'(L) = 0. \end{cases} \tag{2.6}$$

We impose the following condition

$$\alpha \frac{A}{A_S} > (1-\epsilon)f(R^{(0)}) - m. \tag{2.7}$$

By similar arguments to those in [7, Lemma 3.3], we have the following result.

Lemma 2.3. *Assume that condition* (2.7) *holds. Then the eigenvalue problem* (2.6) *has a principal eigenvalue, denoted by* λ^*, *with an associated eigenvector* $(w^*(\cdot), w_S^*(\cdot)) \gg 0$.

In the following, we shall adopt the ideas in [21, 22] to define the basic reproduction ratio for algae. Let $S(t) : C([0, L], \mathbb{R}^2) \to C([0, L], \mathbb{R}^2)$ be the C_0-semigroup generated by the following system

$$\begin{cases} \frac{\partial N}{\partial t} = \delta \frac{\partial^2 N}{\partial x^2} - \nu \frac{\partial N}{\partial x} + \alpha(N_S - N) - mN, \ 0 < x < L, \ t > 0, \\ \frac{\partial N_S}{\partial t} = -\alpha \frac{A}{A_S}(N_S - N) - mN_S, \ 0 < x < L, \ t > 0, \\ \nu N(0, t) - \delta \frac{\partial N}{\partial x}(0, t) = \frac{\partial N}{\partial x}(L, t) = 0, \ t > 0. \end{cases}$$

It is easy to see that $S(t)$ is a positive C_0-semigroup on $C([0, L], \mathbb{R}^2)$.

In order to define the basic reproduction ratio for algae, we assume that both algae individuals in the flow and storage zones are near the state $(0,0)$, and introduce fertile individuals at time $t=0$, where the distribution of initial algae individuals in the flow and storage zones is described by $\varphi := (\varphi_2, \varphi_5) \in C(\bar{\Omega}, \mathbb{R}^2)$. Thus, it is easy to see that $S(t)\varphi$ represents the distribution of fertile algae individuals at time $t \geq 0$.

Let $\mathbf{L} : C([0,L], \mathbb{R}^2) \to C([0,L], \mathbb{R}^2)$ be defined by

$$\mathbf{L}(\varphi)(\cdot) = \int_0^\infty \begin{pmatrix} (1-\epsilon)f(R^{(0)}) & 0 \\ 0 & (1-\epsilon)f(R^{(0)}) \end{pmatrix} (S(t)\varphi)(\cdot)dt.$$

It then follows that $\mathbf{L}(\varphi)(\cdot)$ represents the distribution of the total new population generated by initial fertile algae individuals $\varphi := (\varphi_2, \varphi_5)$, and hence, $\mathbf{L}$ is the next generation operator. We define the spectral radius of $\mathbf{L}$ as the basic reproduction ratio for algae, that is,

$$\mathcal{R}_0 := r(\mathbf{L}).$$

By [22, Theorem 3.1 (i) and Remark 3.1], we have the following observation.

Lemma 2.4. $\mathcal{R}_0 - 1$ *and* λ^* *have the same sign.*

3 Threshold dynamics

In this section, we establish a threshold type result on the persistence and extinction of algae population in terms of $\mathcal{R}_0$.

By Lemma 2.2, it follows that the limiting system of (1.1)-(1.3) takes the form

$$\begin{aligned}
\frac{\partial N}{\partial t} &= \delta \frac{\partial^2 N}{\partial x^2} - \nu \frac{\partial N}{\partial x} + \alpha(N_S - N) + [(1-\epsilon)f(R^{(0)} - q_N N - q_C C) - m]N, \\
\frac{\partial C}{\partial t} &= \delta \frac{\partial^2 C}{\partial x^2} - \nu \frac{\partial C}{\partial x} + \alpha(C_S - C) + \epsilon \frac{q_N}{q_C} f(R^{(0)} - q_N N - q_C C)N - kC, \\
\frac{\partial N_S}{\partial t} &= -\alpha \frac{A}{A_S}(N_S - N) + [(1-\epsilon)f(R^{(0)} - q_N N_S - q_C C_S) - m]N_S, \\
\frac{\partial C_S}{\partial t} &= -\alpha \frac{A}{A_S}(C_S - C) + \epsilon \frac{q_N}{q_C} f(R^{(0)} - q_N N_S - q_C C_S)N_S - kC_S,
\end{aligned} \tag{3.1}$$

for $(x,t) \in (0,L) \times (0,\infty)$ with boundary conditions

$$\begin{cases} \nu N(0,t) - \delta \frac{\partial N}{\partial x}(0,t) = \nu C(0,t) - \delta \frac{\partial C}{\partial x}(0,t) = 0, \\ \frac{\partial N}{\partial x}(L,t) = \frac{\partial C}{\partial x}(L,t) = 0, \end{cases} \tag{3.2}$$

and initial conditions

$$\begin{cases} N(x,0) = N^0(x) \geq 0, N_S(x,0) = N_S^0(x) \geq 0, \\ C(x,0) = C^0(x) \geq 0,\ C_S(x,0) = C_S^0(x) \geq 0,\ 0 < x < L. \end{cases} \tag{3.3}$$

We first study the dynamics of system (3.1)-(3.3). The biologically relevant domain for system (3.1)-(3.3) is given by

$$\Sigma = \{(N^0, C^0, N_S^0, C_S^0) \in C([0,L], \mathbb{R}_+^4) : \, q_N N^0(x) + q_C C^0(x) \leq R^{(0)}, \\ q_N N_S^0(x) + q_C C_S^0(x) \leq R^{(0)} \text{ on } [0,L]\}. \quad (3.4)$$

The following result shows that the set Σ is positively invariant for the solution semiflow associated with (3.1)-(3.3) .

Lemma 3.1. *For any $\phi := (\phi_1, \phi_2, \phi_3, \phi_4) \in \Sigma$, system* (3.1)-(3.3) *has a unique mild solution $(N(x,t), C(x,t), N_S(x,t), C_S(x,t))$ on $[0, \infty)$ with initial data ϕ, and $(N(x,t), C(x,t), N_S(x,t), C_S(x,t)) \in \Sigma$ for all $t \geq 0$.*

Proof. Let $\mathbf{T}_1(t)$ and $\mathbf{T}_2(t)$ be the semigroups generated by

$$\begin{cases} \frac{\partial u}{\partial t} = \delta \frac{\partial^2 u}{\partial x^2} - \nu \frac{\partial u}{\partial x} - (\alpha + m)u, \; 0 < x < L, \; t > 0, \\ \nu u(0,t) - \delta \frac{\partial u}{\partial x}(0,t) = 0, \; \frac{\partial u}{\partial x}(L,t) = 0, \end{cases}$$

and

$$\begin{cases} \frac{\partial u}{\partial t} = \delta \frac{\partial^2 u}{\partial x^2} - \nu \frac{\partial u}{\partial x} - (\alpha + k)u, \; 0 < x < L, \; t > 0, \\ \nu u(0,t) - \delta \frac{\partial u}{\partial x}(0,t) = 0, \; \frac{\partial u}{\partial x}(L,t) = 0, \end{cases}$$

respectively, $\mathbf{T}_3(t)\phi_3 = e^{-(\frac{\alpha A}{A_S} + m)t}\phi_3$ and $\mathbf{T}_4(t)\phi_4 = e^{-(\frac{\alpha A}{A_S} + k)t}\phi_4$. Set

$$\mathbf{u}(t) = \begin{pmatrix} N(t) \\ C(t) \\ N_S(t) \\ C_S(t) \end{pmatrix}, \qquad \mathbf{T}(t) = \begin{pmatrix} \mathbf{T}_1(t) & 0 & 0 & 0 \\ 0 & \mathbf{T}_2(t) & 0 & 0 \\ 0 & 0 & \mathbf{T}_3(t) & 0 \\ 0 & 0 & 0 & \mathbf{T}_4(t) \end{pmatrix}.$$

Then (3.1)-(3.3) can be written as the following integral equation

$$\mathbf{u}(t) = \mathbf{T}(t)\phi + \int_0^t \mathbf{T}(t-s)F(\mathbf{u}(s))ds,$$

where $F = (F_1, F_2, F_3, F_4) : \Sigma \to C([0,L], \mathbb{R}^4)$ by

$$\begin{aligned} F_1(\phi) &= \alpha\phi_3 + (1-\epsilon)f(R^{(0)} - q_N\phi_1 - q_C\phi_2)\phi_1, \\ F_2(\phi) &= \alpha\phi_4 + \epsilon\frac{q_N}{q_C}f(R^{(0)} - q_N\phi_1 - q_C\phi_2)\phi_1, \\ F_3(\phi) &= \alpha\frac{A}{A_S}\phi_1 + (1-\epsilon)f(R^{(0)} - q_N\phi_3 - q_C\phi_4)\phi_3, \\ F_4(\phi) &= \alpha\frac{A}{A_S}\phi_2 + \epsilon\frac{q_N}{q_C}f(R^{(0)} - q_N\phi_3 - q_C\phi_4)\phi_3. \end{aligned}$$

By [10, Corollary 4] or [18, Theorem 7.3.1], it suffices to show that

$$\lim_{h\to 0^+} dist(\phi + hF(\phi), \Sigma) = 0, \ \forall \ \phi \in \Sigma. \tag{3.5}$$

For any $\phi \in \Sigma$ and $h \geqslant 0$, we have

$$\phi + hF(\phi) = \begin{pmatrix} \phi_1 + hF_1(\phi) \\ \phi_2 + hF_2(\phi) \\ \phi_3 + hF_3(\phi) \\ \phi_4 + hF_4(\phi) \end{pmatrix} \geqslant \begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}. \tag{3.6}$$

By our assumption on f, it is easy to see that

$$f(R) = H(R)R, \quad \text{where } H(R) = \int_0^1 f'(\tau R)d\tau, \ \forall \ R \geq 0.$$

Then we have

$$\begin{aligned} &R^{(0)} - [q_N(\phi_1 + hF_1(\phi)) + q_C(\phi_2 + hF_2(\phi))] \\ &= (R^{(0)} - q_N\phi_1 - q_C\phi_2)[1 - hq_N\phi_1 H(R^{(0)} - q_N\phi_1 - q_C\phi_2)] - h\alpha(q_N\phi_3 + q_C\phi_4) \\ &\geq (R^{(0)} - q_N\phi_1 - q_C\phi_2)[1 - hq_N\phi_1 H(R^{(0)} - q_N\phi_1 - q_C\phi_2)] - h\alpha R^{(0)}, \end{aligned} \tag{3.7}$$

and

$$\begin{aligned} &R^{(0)} - [q_N(\phi_3 + hF_3(\phi)) + q_C(\phi_4 + hF_4(\phi))] \\ &= (R^{(0)} - q_N\phi_3 - q_C\phi_4)[1 - hq_N\phi_3 H(R^{(0)} - q_N\phi_3 - q_C\phi_4)] - h\alpha\frac{A}{A_S}(q_N\phi_1 + q_C\phi_2) \\ &\geq (R^{(0)} - q_N\phi_3 - q_C\phi_4)[1 - hq_N\phi_3 H(R^{(0)} - q_N\phi_3 - q_C\phi_4)] - h\alpha\frac{A}{A_S}R^{(0)}. \end{aligned} \tag{3.8}$$

By (3.6), (3.7) and (3.8), it follows that (3.5) is true. □

In view of Lemma 3.1, we can define the solution semiflow $\Pi_t : \Sigma \to \Sigma$ associated with (3.1)-(3.3) by

$$\Pi_t(P) = (N(\cdot, t, P), C(\cdot, t, P), N_S(\cdot, t, P), C_S(\cdot, t, P)), \ \forall \ t \geq 0, \tag{3.9}$$

where $P := (N^0(\cdot), C^0(\cdot), \ N_S^0(\cdot), \ C_S^0(\cdot)) \in \Sigma$.

Since two equations in (3.1) have no diffusion terms, its solution semiflow Π_t is not compact. To obtain the existence of the global attractor of Π_t, we further assume that there is a constant $r > 0$ such that for any $(N, C, N_S, C_S) \in \Sigma$, we have

$$\mathbf{x}^T \mathcal{M}(N, C, N_S, C_S)\mathbf{x} \leq -r\mathbf{x}^T\mathbf{x}, \quad \forall \ \mathbf{x} \in \mathbb{R}^2, \tag{3.10}$$

where

$$\mathcal{M}(N, C, N_S, C_S) = \begin{pmatrix} m_{11} & m_{12} \\ m_{21} & m_{22} \end{pmatrix},$$

and

$$\begin{aligned} m_{11} &= -\alpha\frac{A}{A_S} + [(1-\epsilon)f(R^{(0)} - q_N N_S - q_C C_S) - m], \\ &\quad -q_N(1-\epsilon)f'(R^{(0)} - q_N N_S - q_C C_S)N_S, \\ m_{21} &= \epsilon\frac{q_N}{q_C}f(R^{(0)} - q_N N_S - q_C C_S) - \epsilon\frac{q_N^2}{q_C}f'(R^{(0)} - q_N N_S - q_C C_S)N_S, \\ m_{12} &= -q_C(1-\epsilon)f'(R^{(0)} - q_N N_S - q_C C_S)N_S, \\ m_{22} &= -\alpha\frac{A}{A_S} - k - \epsilon q_N f'(R^{(0)} - q_N N_S - q_C C_S)N_S. \end{aligned}$$

Remark 3.1. *Assume that* $f(R) = \frac{\mu_{max}R}{K_\mu + R}$ *and*

$$\alpha\frac{A}{A_S} > (1-\epsilon)f(R^{(0)}) - \min\{m, k\} + \frac{1}{2}\frac{\mu_{\max}R^{(0)}}{K_\mu}\left[2\epsilon\frac{q_N}{q_C} + (1-\epsilon)\frac{q_C}{q_N}\right]. \quad (3.11)$$

Then (3.11) *implies* (2.7) *and* (3.10)*. Biologically, the condition* (3.11) *means that the cross section of the main channel is large compared to that of the storage zone, or the exchange rate is sufficiently large.*

Next, we introduce the Kuratowski measure of noncompactness (see, e.g., [2])

$$\kappa(B) := \inf\{r : B \text{ has a finite cover of diameter} < r\}$$

for any bounded set B. We set $\kappa(B) = \infty$ whenever B is unbounded. It is easy to see that B is precompact(i.e., $\bar{B}$ is compact) if and only if $\kappa(B) = 0$. By similar arguments to those in [6, Lemma 4.1], we have the following result.

Lemma 3.2. *Assume that* (3.10) *holds. Then the solution semiflow* $\Pi(t)$ *is* κ*-contracting in the sense that* $\lim_{t\to\infty}\kappa(\Pi(t)(B)) = 0$ *for any bounded set* $B \subset \Sigma$*.*

The following result shows that solutions of system (3.1)-(3.3) converge to a compact attractor in Σ.

Theorem 3.1. *Assume that* (3.10) *holds. Then* $\Pi(t)$ *admits a global attractor on* Σ*.*

Proof. By Lemma 3.2, it follows that $\Pi(t)$ is κ-contracting on Σ. By Lemma 3.1, it follows that $\Pi(t)$ is point dissipative on Σ, and forward orbits of bounded subsets of Σ for $\Pi(t)$ are bounded. By the continuous-time version of [12, Theorem 2.6], $\Pi(t)$ has a compact global attractor that attracts every point in Σ. □

By the strong maximum principle and the Hopf boundary lemma (see [14]), we have the following result.

Lemma 3.3. *Let*

$$(u_1(x,t,\phi), u_2(x,t,\phi), u_3(x,t,\phi), u_4(x,t,\phi)) := (N(x,t), C(x,t), N_S(x,t), C_S(x,t))$$

be the solution of system (3.1)-(3.3) *with initial data* $\phi \in \Sigma$. *If there is a* $t_0 \geq 0$ *such that* $u_i(\cdot, t_0, \phi) \not\equiv 0$, *for some* $i \in \{1,2,3,4\}$, *then* $u_i(x,t,\phi) > 0$ *for all* $x \in [0,L]$ *and* $t > t_0$.

The following result indicates that $\mathcal{R}_0$ is a threshold index for global extinction and persistence of the algae.

Theorem 3.2. *Assume that conditions* (2.7) *and* (3.10) *hold. Let*

$$\mathbb{W}_0 = \{\phi = (\phi_1, \phi_2, \phi_3, \phi_4) \in \Sigma : \phi_1(\cdot) \not\equiv 0 \text{ and } \phi_3(\cdot) \not\equiv 0\},$$

and

$$\partial\mathbb{W}_0 = \Sigma \backslash \mathbb{W}_0 = \{\phi \in \Sigma : \phi_1(\cdot) \equiv 0 \text{ or } \phi_3(\cdot) \equiv 0\}.$$

Let $(N(x,t,\phi), C(x,t,\phi), N_S(x,t,\phi), C_S(x,t,\phi))$ *be the solution of system* (3.1)-(3.3) *with initial data* $\phi \in \Sigma$. *Then the following statements hold true:*

- (i) *If* $\mathcal{R}_0 < 1$, *then the trivial solution* $\hat{0} := (0,0,0,0)$ *is globally attractive in* Σ.
- (ii) *If* $\mathcal{R}_0 > 1$, *then system* (3.1)-(3.3) *admits at least one positive steady state* $(\hat{N}(x), \hat{N}_S(x), \hat{C}(x), \hat{C}_S(x))$, *and there exists an* $\eta > 0$ *such that for any* $\phi \in \mathbb{W}_0$, *we have*

$$\liminf_{t\to\infty} N(x,t,\phi) > \eta \text{ and } \liminf_{t\to\infty} N_S(x,t,\phi) > \eta,$$

uniformly for all $x \in [0,L]$. *Furthermore, any compact internal chain transitive set* $\mathcal{I}$ *of* $\Pi(t)$ *with* $\mathcal{I} \neq \{\hat{0}\}$ *satisfies* $\min_{\phi\in\mathcal{I}} p(\phi) > \eta$, *where* $p(\phi) := \min\{\min_{x\in[0,L]} \phi_1(x), \min_{x\in[0,L]} \phi_3(x)\}$.

Proof. We first assume that $\mathcal{R}_0 < 1$. By Lemma 2.4, it follows that $\lambda^* < 0$. From the first and third equations of (3.1), it follows that

$$\begin{cases} \frac{\partial N}{\partial t} \leq \delta \frac{\partial^2 N}{\partial x^2} - \nu \frac{\partial N}{\partial x} + \alpha(N_S - N) + [(1-\epsilon) f(R^{(0)}) - m]N, \ t > 0, \\ \frac{\partial N_S}{\partial t} \leq -\alpha \frac{A}{A_S}(N_S - N) + [(1-\epsilon) f(R^{(0)}) - m]N_S, \ t > 0, \\ \nu N(0,t) - \delta \frac{\partial N}{\partial x}(0,t) = \frac{\partial N}{\partial x}(L,t) = 0, \ t > 0. \end{cases} \tag{3.12}$$

By Lemma 2.3, there is a strongly positive eigenfunction $\hat{w} := (w_1, w_{1S})$ corresponding to λ^*. Since for any given $\phi \in \Sigma$, there exists some $a > 0$ such that

$(N(x,0,\phi), N_S(x,0,\phi)) \le a\hat{w}(x),\ \forall\ x \in [0,L]$. Note that $ae^{\lambda^* t}\hat{w}(x)$ is a solution to (2.3)-(2.5) on $[0,\infty)$ with initial data $a\hat{w}(x)$. Then the comparison principle implies that

$$(N(x,t,\phi), N_S(x,t,\phi)) \le ae^{\lambda^* t}\hat{w}(x),\ \forall\ t \ge 0,$$

and hence, $\lim_{t\to\infty}(N(x,t,\phi), N_S(x,t,\phi)) = 0$ uniformly for $x \in [0,L]$. Thus, the equations for (C, C_S) in (3.1) are asymptotic to the following linear system

$$\begin{cases} \frac{\partial C}{\partial t} = \delta\frac{\partial^2 C}{\partial x^2} - \nu\frac{\partial C}{\partial x} - (\alpha+k)C + \alpha C_S,\ 0<x<L,\ t>0, \\ \frac{\partial C_S}{\partial t} = -(\alpha\frac{A}{A_S} + k)C_S + \alpha\frac{A}{A_S}C,\ 0<x<L,\ t>0, \\ \nu C(0,t) - \delta\frac{\partial C}{\partial x}(0,t) = \frac{\partial C}{\partial x}(L,t) = 0,\ t>0, \\ C(x,0) = C^0(x) \ge 0,\ C_S(x,0) = C_S^0(x) \ge 0,\ 0<x<L. \end{cases} \tag{3.13}$$

By [7, Lemma 3.3] and the theory of asymptotically autonomous semiflows (see, e.g., [20, Corollary 4.3]), it follows that $\lim_{t\to\infty}(C(x,t,\phi), C_S(x,t,\phi)) = (0,0)$ uniformly for $x \in [0,L]$. This proves statement (i).

Next we assume that $\mathcal{R}_0 > 1$. Then Lemma 2.4 implies that $\lambda^* > 0$. By (2.7) and similar arguments to those in [7, Lemma 3.3] (see also Lemma 2.3), it follows that there exists a sufficiently small positive number ξ_0 such that

$$\alpha\frac{A}{A_S} > (1-\epsilon)f(R^{(0)}) - \xi_0 - m,$$

and $\lambda^*_{\xi_0} > 0$ is the principal eigenvalue of the eigenvalue problem

$$\begin{cases} \lambda w = \delta w'' - \nu w' + \alpha(w_S - w) + [(1-\epsilon)f(R^{(0)}) - \xi_0 - m]w, \\ \lambda w_S = -\alpha\frac{A}{A_S}(w_S - w) + [(1-\epsilon)f(R^{(0)}) - \xi_0 - m]w_S, \\ \nu w(0) - \delta w'(0) = w'(L) = 0. \end{cases} \tag{3.14}$$

Furthermore, $\tilde{w} := (w_2, w_{2S})$ is the strongly positive eigenfunction corresponding to $\lambda^*_{\xi_0}$.

By Lemma 3.3, it follows that for any $\phi \in \mathbb{W}_0$, we have

$$N(x,t,\phi) > 0,\ N_S(x,t,\phi) > 0,\ \forall\ x \in [0,L],\ t > 0.$$

This implies that $\Pi(t)\mathbb{W}_0 \subseteq \mathbb{W}_0$ for all $t \ge 0$. Let

$$M_\partial := \{\phi \in \partial\mathbb{W}_0 : \Pi(t)\phi \in \partial\mathbb{W}_0, \forall\ t \ge 0\},$$

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

Claim 1. $\omega(\psi) = \{\hat{0}\},\ \forall\ \psi \in M_\partial$.

For any given $\psi \in M_\partial$, we have $\Pi(t)\psi \in M_\partial,\ \forall\ t \geq 0$. Thus, for any given $t \geq 0$, we have $N(\cdot,t,\psi) \equiv 0$ or $N_S(\cdot,t,\psi) \equiv 0$. In the case where $N(\cdot,t,\psi) \equiv 0$ for all $t \geq 0$, substituting $N(\cdot,t,\psi) \equiv 0$ into the first equation of (3.1), we obtain $N_S(\cdot,t,\psi) \equiv 0,\ \forall\ t \geq 0$. Then the equations for (C, C_S) satisfies the system (3.13), and hence

$$\lim_{t\to\infty}(C(x,t,\psi), C_S(x,t,\psi)) = (0,0),$$

uniformly for $x \in [0, L]$. In the case where $N(\cdot,\tilde{t}_0,\psi) \not\equiv 0$ for some $\tilde{t}_0 \geq 0$, Lemma 3.3 implies that $N(x,t,\psi) > 0,\ \forall\ x \in \bar{\Omega}, \forall\ t > \tilde{t}_0$. Thus, $N_S(\cdot,t,\psi) \equiv 0,\ \forall\, t > \tilde{t}_0$. From the third equation of (3.1), it follows that $N(\cdot,t,\psi) \equiv 0,\ \forall\ t > \tilde{t}_0$, which is impossible. This shows that $\omega(\psi) = \{\hat{0}\}$.

Note that

$$\lim_{(N,C)\to(0,0)} f(R^{(0)}-q_N N-q_C C) = f(R^{(0)}),\ \lim_{(N_S,C_S)\to(0,0)} f(R^{(0)}-q_N N_S-q_C C_S) = f(R^{(0)}).$$

It then follows that there is a $\sigma_0 >$ such tat

$$f(R^{(0)} - q_N N - q_C C) > f(R^{(0)}) - \frac{\xi_0}{1-\epsilon},\ \forall\ \|(N, C)\| < \sigma_0.$$

and

$$f(R^{(0)} - q_N N_S - q_C C_S) > f(R^{(0)}) - \frac{\xi_0}{1-\epsilon},\ \forall\ \|(N_S, C_S)\| < \sigma_0.$$

Claim 2. $\hat{0}$ is a uniform weak repeller for $\mathbb{W}_0$ in the sense that $\limsup_{t\to\infty} \|\Pi(t)\phi\| \geq \sigma_0,\ \forall\ \phi \in \mathbb{W}_0$.

Suppose, by contradiction, there exists $\phi_0 \in \mathbb{W}_0$ such that $\limsup_{t\to\infty} \|\Pi(t)\phi_0 - \hat{0}\| < \sigma_0$. Then there exists $t_1 > 0$ such that

$$\|(N(x,t,\phi_0, C(x,t,\phi_0)\| < \sigma_0 \text{ and } \|(N_S(x,t,\phi_0, C_S(x,t,\phi_0)\| < \sigma_0, \forall\, t \geq t_1,\ x \in [0, L].$$

It follows that the equation for N and N_S in (3.1) satisfy

$$\begin{cases} \frac{\partial N}{\partial t} \geq \delta\frac{\partial^2 N}{\partial x^2} - \nu\frac{\partial N}{\partial x} + \alpha(N_S - N) + [(1-\epsilon)f(R^{(0)}) - \xi_0 - m]N,\ t \geq t_1 \\ \frac{\partial N_S}{\partial t} \geq -\alpha\frac{A}{A_S}(N_S - N) + [(1-\epsilon)f(R^{(0)}) - \xi_0 - m]N_S,\ t \geq t_1 \\ \nu N(0,t) - \delta\frac{\partial N}{\partial x}(0,t) = \frac{\partial N}{\partial x}(L,t) = 0,\ t \geq t_1. \end{cases} \tag{3.15}$$

Recall that $\tilde{w} := (w_2, w_{2S})$ is the strongly positive eigenfunction corresponding to $\lambda^*_{\xi_0}$. Since $N(x,t,\phi_0) > 0, N_S(x,t,\phi_0) > 0,\ \forall\ x \in [0, L],\ t > 0$, there exists a sufficiently small number $\rho_0 > 0$ such that $(N(x,t_1,\phi_0) > 0, N_S(x,t_1,\phi_0)) \geq \rho_0\tilde{w}$. Note that $\rho_0 e^{\lambda^*_{\xi_0}(t-t_1)}\tilde{w},\ t \geq t_1$, is a solution of the following linear system:

$$\begin{cases} \frac{\partial N}{\partial t} = \delta\frac{\partial^2 N}{\partial x^2} - \nu\frac{\partial N}{\partial x} + \alpha(N_S - N) + [(1-\epsilon)f(R^{(0)}) - \xi_0 - m]N,\ t \geq t_1 \\ \frac{\partial N_S}{\partial t} = -\alpha\frac{A}{A_S}(N_S - N) + [(1-\epsilon)f(R^{(0)}) - \xi_0 - m]N_S,\ t \geq t_1 \\ \nu N(0,t) - \delta\frac{\partial N}{\partial x}(0,t) = \frac{\partial N}{\partial x}(L,t) = 0,\ t \geq t_1, \end{cases} \tag{3.16}$$

with initial data $\rho_0\tilde{w}$. Then the comparison principle implies that

$$(N(x,t,\phi_0), N_S(x,t,\phi_0)) \geq \rho_0 e^{\lambda^*_{\xi_0}(t-t_1)}\tilde{w},\ \forall\ t \geq t_1,\ x \in [0,L].$$

Since $\lambda^*_{\xi_0} > 0$, we see that $(N(x,t,\phi_0), N_S(x,t,\phi_0))$ is unbounded. This contradiction proves the claim.

Define a continuous function $p : \Sigma \to [0,\infty)$ by

$$p(\phi) := \min\left\{\min_{x\in[0,L]} \phi_1(x), \min_{x\in[0,L]} \phi_3(x)\right\},\ \forall\ \phi \in \Sigma. \tag{3.17}$$

By Lemma 3.3, it follows that $p^{-1}(0,\infty) \subseteq \mathbb{W}_0$ and p has the property that if $p(\phi) > 0$ or $\phi \in \mathbb{W}_0$ with $p(\phi) = 0$, then $p(\Pi(t)\phi) > 0,\ \forall\ t > 0$. Thus, p is a generalized distance function for the semiflow $\Pi(t) : \Sigma \to \Sigma$ (see, e.g., [19]). By Claims 1 and 2 above, it follows that any forward orbit of $\Pi(t)$ in M_∂ converges to $\hat{0}$, $\hat{0}$ is isolated invariant set in Σ, and $W^s(\hat{0}) \cap \mathbb{W}_0 = \emptyset$, where $W^s(\hat{0})$ is the stable set of $\hat{0}$. It is obvious that there is no cycle from $\hat{0}$ to $\hat{0}$ in M_∂. By [19, Theorem 3], there exists an $\eta > 0$ such that any compact internal chain transitive set $\mathcal{I}$ of $\Pi(t)$ with $\mathcal{I} \neq \{\hat{0}\}$ satisfies $\min_{\phi\in\mathcal{I}} p(\phi) > \eta$. For any $\phi \in \mathbb{W}_0$, we see from Claim 2 that $\omega(\phi) \neq \{\hat{0}\}$. Letting $\mathcal{I} = \omega(\phi)$, we then obtain $\min_{\psi\in\omega(\phi)} p(\psi) > \eta$ for all $\phi \in \mathbb{W}_0$. This implies the uniform persistence stated in statement (ii). By [12, Theorem 3.7 and Remark 3.10], it follows that $\Pi(t) : \Sigma \to \Sigma$ has a global attractor A_0. It then follows from [12, Theorem 4.7] that $\Pi(t)$ has an equilibrium $(\hat{N}, \hat{C}, \hat{N}_S, \hat{C}_S) \in \mathbb{W}_0$, which satisfies $\hat{N}(x) > 0$, $\hat{C}(x) \geq 0$, $\hat{N}_S(x) > 0$, $\hat{C}_S(x) \geq 0$, $\forall\ x \in [0,L]$.

From the second equation of (3.1), it is easy to see that $\hat{C}(x)$ satisfies

$$\begin{cases} \delta\hat{C}''(x) - \nu\hat{C}'(x) - (\alpha+k)\hat{C}(x) \\ = -\alpha\hat{C}_S(x) - \epsilon\frac{q_N}{q_C} f(R^{(0)} - q_N\hat{N} - q_C\hat{C}(x))\hat{N} \leq 0,\ x \in (0,L), \\ \nu\hat{C}(0) - \delta\hat{C}'(0) = \hat{C}'(L) = 0. \end{cases}$$

By the strong maximum principle and the Hopf boundary lemma (see [14]), we obtain $\hat{C}(x) > 0,\ \forall\ x \in [0,L]$. From the fourth equation of (3.1), it is easy to see that $\hat{C}_S(x)$ satisfies

$$(\alpha\frac{A}{A_S} + k)\hat{C}_S(x) = \alpha\frac{A}{A_S}\hat{C}(x) + \epsilon\frac{q_N}{q_C} f(R^{(0)} - q_N\hat{N}_S - q_C\hat{C}_S)\hat{N}_S(x) \geq \alpha\frac{A}{A_S}\hat{C}(x),$$

which implies that $\hat{C}_S(x) > 0,\ \forall\ 0 \leq x \leq L$. Therefore, $(\hat{N}(x), \hat{C}(x), \hat{N}_S(x), \hat{C}_S(x))$ is a positive steady state solution of (3.1)-(3.3). □

Recall that $X^+ = C([0,L], \mathbb{R}^6_+)$ is the biologically relevant domain for system (1.1)-(1.3). For convenience, we set

$$X_0 := \{(R^0(\cdot), N^0(\cdot), C^0(\cdot), R^0_S(\cdot), N^0_S(\cdot), C^0_S(\cdot)) \in X^+ : N^0(\cdot) \not\equiv 0 \text{ and } N^0_S(\cdot) \not\equiv 0\},$$

and $\partial X_0 := X^+ \backslash X_0$.

By appealing to the theory of chain transitive sets, we are able to lift the dynamics of (3.1)-(3.3) to the full system (1.1)-(1.3).

Theorem 3.3. *Assume that conditions* (2.7) *and* (3.10) *hold. Let*

$$(R(x,t), N(x,t), C(x,t), R_S(x,t), N_S(x,t), C_S(x,t))$$

be the solution of (1.1)-(1.3) *with initial data in* X^+*. Then the following statements are valid:*

(i) *If* $\mathcal{R}_0 < 1$*, then*

$$\lim_{t\to\infty}(R(x,t), N(x,t), C(x,t), R_S(x,t), N_S(x,t), C_S(x,t)) = (R^{(0)}, 0, 0, R^{(0)}, 0, 0),$$

uniformly for $x \in [0, L]$.

(ii) *If* $\mathcal{R}_0 > 1$*, then* (1.1)-(1.3) *admits at least one positive steady-state solution* $(\hat{R}(x), \hat{N}(x), \hat{C}(x), \hat{R}_S(x), \hat{N}_S(x), \hat{C}_S(x))$*, and there exists an* $\eta > 0$ *such that for any*

$$(R^0(\cdot), N^0(\cdot), C^0(\cdot), R^0_S(\cdot), N^0_S(\cdot), C^0_S(\cdot)) \in X_0,$$

we have

$$\liminf_{t\to\infty} N(x,t,\phi) > \eta \text{ and } \liminf_{t\to\infty} N_S(x,t,\phi) > \eta,$$

uniformly for all $x \in [0, L]$.

Proof. Note that system (1.1)-(1.3) is equivalent to the following one:

$$\begin{cases} \frac{\partial N}{\partial t} = \delta\frac{\partial^2 N}{\partial x^2} - \nu\frac{\partial N}{\partial x} + \alpha(N_S - N) + [(1-\epsilon)f(V - q_N N - q_C C) - m]N, \\ \frac{\partial C}{\partial t} = \delta\frac{\partial^2 C}{\partial x^2} - \nu\frac{\partial C}{\partial x} + \alpha(C_S - C) + \epsilon\frac{q_N}{q_C}f(V - q_N N - q_C C)N - kC, \\ \frac{\partial N_S}{\partial t} = -\alpha\frac{A}{A_S}(N_S - N) + [(1-\epsilon)f(V_S - q_N N_S - q_C C_S) - m]N_S, \\ \frac{\partial C_S}{\partial t} = -\alpha\frac{A}{A_S}(C_S - C) + \epsilon\frac{q_N}{q_C}f(V_S - q_N N_S - q_C C_S)N_S - kC_S, \\ \frac{\partial V}{\partial t} = \delta\frac{\partial^2 V}{\partial x^2} - \nu\frac{\partial V}{\partial x} + \alpha(V_S - V), \\ \frac{\partial V_S}{\partial t} = -\alpha\frac{A}{A_S}(V_S - V), \end{cases} \tag{3.18}$$

for $(x,t) \in (0,L) \times (0,\infty)$ with boundary conditions

$$\begin{cases} \nu N(0,t) - \delta\frac{\partial N}{\partial x}(0,t) = \nu C(0,t) - \delta\frac{\partial C}{\partial x}(0,t) = 0, \\ \nu V(0,t) - \delta\frac{\partial V}{\partial x}(0,t) = \nu R^{(0)}, \\ \frac{\partial N}{\partial x}(L,t) = \frac{\partial C}{\partial x}(L,t) = \frac{\partial V}{\partial x}(L,t) = 0, \end{cases} \tag{3.19}$$

and initial conditions

$$\begin{cases} N(x,0) = N^0(x) \geq 0,\ C(x,0) = C^0(x) \geq 0,\ N_S(x,0) = N_S^0(x) \geq 0, \\ C_S(x,0) = C_S^0(x) \geq 0,\ V(x,0) = V^0(x) \geq 0,\ V_S(x,0) = V_S^0(x) \geq 0, \end{cases} \tag{3.20}$$

for $x \in (0, L)$, where V and V_S are defined in (2.1).

The biologically relevant domain for system (3.18)-(3.20) is given by

$$\begin{aligned} \widetilde{\Sigma} = \{(N^0, C^0, N_S^0, C_S^0, V^0, V_S^0) \in C([0,L], \mathbb{R}_+^6) :\ & q_N N^0(x) + q_C C^0(x) \leq V^0(x), \\ & q_N N_S^0(x) + q_C C_S^0(x) \leq V_S^0(x) \text{ on } [0,L]\}. \end{aligned} \tag{3.21}$$

For convenience, we define

$$\widetilde{\Sigma}_0 := \{(N^0, C^0, N_S^0, C_S^0, V^0, V_S^0) \in \widetilde{\Sigma} : N^0(\cdot) \not\equiv 0 \text{ and } N_S^0(\cdot) \not\equiv 0\},$$

and $\partial\widetilde{\Sigma}_0 := \widetilde{\Sigma} \backslash \widetilde{\Sigma}_0$. We first show that $\widetilde{\Sigma}$ is positively invariant for system (3.18)-(3.20). Indeed, let $Q := (N^0(\cdot), C^0(\cdot), N_S^0(\cdot), C_S^0(\cdot), V^0(\cdot), V_S^0(\cdot)) \in \widetilde{\Sigma}$ and let

$$(N(\cdot,t,Q), C(\cdot,t,Q), N_S(\cdot,t,Q), C_S(\cdot,t,Q), V(\cdot,t,Q), V_S(\cdot,t,Q))$$

be the solution of system (3.18)-(3.20) with initial data Q. Recall that

$$\begin{cases} R(x,t) = V(x,t) - q_N N(x,t) - q_C C(x,t), \\ R_S(x,t) = V_S(x,t) - q_N N_S(x,t) - q_C C_S(x,t). \end{cases} \tag{3.22}$$

Then $(R(\cdot,t,Q), N(\cdot,t,Q), C(\cdot,t,Q), R_S(\cdot,t,Q), N_S(\cdot,t,Q), C_S(\cdot,t,Q))$ satisfies (1.1)-(1.3) and $R(\cdot,0,Q) \geq 0,\ N(\cdot,0,Q) \geq 0,\ C(\cdot,0,Q) \geq 0,\ R_S(\cdot,0,Q) \geq 0,\ N_S(\cdot,0,Q) \geq 0,\ C_S(\cdot,0,Q) \geq 0$. By Lemma 2.1, it follows that

$$(R(\cdot,t,Q), N(\cdot,t,Q), C(\cdot,t,Q), R_S(\cdot,t,Q), N_S(\cdot,t,Q), C_S(\cdot,t,Q)) \geq 0,\ \forall\, t \geq 0.$$

This implies that

$$(N(\cdot,t,Q), C(\cdot,t,Q), N_S(\cdot,t,Q), C_S(\cdot,t,Q), V(\cdot,t,Q), V_S(\cdot,t,Q)) \in \widetilde{\Sigma},\ \forall\, t \geq 0.$$

Thus, we can define the solution semiflow $\widetilde{\Pi}_t : \widetilde{\Sigma} \to \widetilde{\Sigma}$ of (3.18)-(3.20) by

$$\widetilde{\Pi}_t(Q) = (N(\cdot,t,Q), C(\cdot,t,Q), N_S(\cdot,t,Q), C_S(\cdot,t,Q), V(\cdot,t,Q), V_S(\cdot,t,Q)),\ \forall\, t \geq 0,$$

where $Q := (N^0(\cdot), C^0(\cdot), N_S^0(\cdot), C_S^0(\cdot), V^0(\cdot), V_S^0(\cdot)) \in \widetilde{\Sigma}$. For any $Q \in \widetilde{\Sigma}$, let $\widetilde{\omega} := \widetilde{\omega}(Q)$ be the omega limit set of Q for $\widetilde{\Pi}_t$. It is easy to see that

$$(R^0(\cdot), N^0(\cdot), C^0(\cdot), R_S^0(\cdot), N_S^0(\cdot), C_S^0(\cdot)) \in X_0$$

if and only if $(N^0, C^0, N_S^0, C_S^0, V^0, V_S^0) \in \widetilde{\Sigma}_0$.

By Lemma 2.2, we have

$$\lim_{t\to\infty}(V(x,t), V_S(x,t)) = (R^{(0)}, R^{(0)}) \text{ uniformly for } x \in [0, L].$$

It then follows that for any $(N(\cdot), C(\cdot), N_S(\cdot), C_S(\cdot)) \in C([0, L], \mathbb{R}_+^4)$ with

$$((N(\cdot), C(\cdot), N_S(\cdot), C_S(\cdot)), V(\cdot), V_S(\cdot)) \in \widetilde{\omega},$$

there holds $(V(\cdot), V_S(\cdot)) = (R^{(0)}, R^{(0)})$. Thus, there exists a set $\mathcal{I} \subset C([0, L], \mathbb{R}_+^4)$ such that $\widetilde{\omega} = \mathcal{I} \times \{(R^{(0)}, R^{(0)})\}$. Since $\widetilde{\Sigma}$ is closed, it follows that $\widetilde{\omega} \subset \widetilde{\Sigma}$. For any given $(N(\cdot), C(\cdot), N_S(\cdot), C_S(\cdot)) \in \mathcal{I}$, we have

$$(N(\cdot), C(\cdot), N_S(\cdot), C_S(\cdot), R^{(0)}, R^{(0)}) \in \widetilde{\omega} \subset \widetilde{\Sigma}.$$

By the definition of $\widetilde{\Sigma}$, we obtain $(N(\cdot), C(\cdot), N_S(\cdot), C_S(\cdot)) \in \Sigma$. This shows that $\mathcal{I} \subset \Sigma$.

In view of [23, Lemma 1.2.1′], we see that $\widetilde{\omega}$ is a compact, invariant and internal chain transitive set for $\widetilde{\Pi}_t$. Moreover, for any $(N(\cdot), C(\cdot), N_S(\cdot), C_S(\cdot)) \in C([0, L], \mathbb{R}_+^4)$ with $(N(\cdot), C(\cdot), N_S(\cdot), C_S(\cdot)), V(\cdot), V_S(\cdot)) \in \widetilde{\omega}$, there holds

$$\widetilde{\Pi}_t \mid_{\widetilde{\omega}} (N(\cdot), C(\cdot), N_S(\cdot), C_S(\cdot), V(\cdot), V_S(\cdot)) = (\Pi_t(N(\cdot), C(\cdot), N_S(\cdot), C_S(\cdot)), R^{(0)}, R^{(0)}),$$

where Π_t is the semiflows associated with (3.1)-(3.3) on Σ. It then easily follows that $\mathcal{I}$ is a compact, invariant and internal chain transitive set for $\Pi_t : \Sigma \to \Sigma$.

In the case where $\mathcal{R}_0 < 1$, it follows from Theorem 3.2 (i) that $\hat{0}$ is a global attractor for $\Pi_t : \Sigma \to \Sigma$. By the continuous-time version of [23, Theorem 1.2.1], we obtain $\mathcal{I} = \{\hat{0}\}$, and hence, $\widetilde{\omega} = \mathcal{I} \times \{(R^{(0)}, R^{(0)})\} = \{(0, 0, 0, 0, R^{(0)}, R^{(0)})\}$. This implies that $(0, 0, 0, 0, R^{(0)}, R^{(0)})$ is globally attractive for $\widetilde{\Pi}_t$ in $\widetilde{\Sigma}$, that is, system (3.18)-(3.20) has a globally attractive steady state $(0, 0, 0, 0, R^{(0)}, R^{(0)})$ in $\widetilde{\Sigma}$. In view of (2.1), we see that statement (i) holds true.

In the case where $\mathcal{R}_0 > 1$, it follows from Lemma 2.4 that $\lambda^* > 0$. Thus, there exists a $\rho > 0$ such that

$$\alpha\frac{A}{A_S} > (1 - \epsilon)f(R^{(0)}) - m - \rho,$$

and the eigenvalue problem

$$\begin{cases} \lambda w = \delta w'' - \nu w' + \alpha(w_S - w) + [(1 - \epsilon)f(R^{(0)}) - m - \rho]w, \\ \lambda w_S = -\alpha\frac{A}{A_S}(w_S - w) + [(1 - \epsilon)f(R^{(0)}) - m - \rho]w_S, \\ \nu w(0) - \delta w'(0) = w'(L) = 0, \end{cases} \tag{3.23}$$

has a principal eigenvalue, denoted by $\lambda_\rho^* > 0$, with an associated eigenvector $(w_\rho^*(\cdot), w_{S\rho}^*(\cdot) \gg 0$. We further show that $\mathcal{I} \neq \{\hat{0}\}$. Otherwise, we have $\widetilde{\omega} = \mathcal{I} \times \{(R^{(0)}, R^{(0)})\} = \{(0,0,0,0,R^{(0)},R^{(0)})\}$. This implies that

$$\lim_{t\to\infty} ||(N(\cdot,t), C(\cdot,t), N_S(\cdot,t), C_S(\cdot,t), V(\cdot,t), V_S(\cdot,t)) - (0,0,0,0,R^{(0)},R^{(0)})|| = 0.$$

It follows that

$$\lim_{t\to\infty} ||(V(\cdot,t) - q_N N(\cdot,t) - q_C C(\cdot,t)) - R^{(0)}|| = 0,$$

and

$$\lim_{t\to\infty} ||(V_S(\cdot,t) - q_N N_S(\cdot,t) - q_C C_S(\cdot,t)) - R^{(0)}|| = 0.$$

Consequently, there exists a $t_1 > 0$ such that

$$f(V(\cdot,t) - q_N N(\cdot,t) - q_C C(\cdot,t)) > f(R^{(0)}) - \frac{\rho}{1-\epsilon},\ \forall\ t \geq t_1,$$

and

$$f(V_S(\cdot,t) - q_N N_S(\cdot,t) - q_C C_S(\cdot,t)) > f(R^{(0)}) - \frac{\rho}{1-\epsilon},\ \forall\ t \geq t_1.$$

From the first and third equations in (3.18), we have

$$\begin{cases} \frac{\partial N}{\partial t} \geq \delta \frac{\partial^2 N}{\partial x^2} - \nu \frac{\partial N}{\partial x} + \alpha(N_S - N) + [(1-\epsilon) f(R^{(0)}) - m - \rho]N,\ 0 < x < L,\ t \geq t_1, \\ \frac{\partial N_S}{\partial t} \geq -\alpha \frac{A}{A_S}(N_S - N) + [(1-\epsilon) f(R^{(0)}) - m - \rho]N_S,\ 0 < x < L,\ t \geq t_1, \\ \nu N(0,t) - \delta \frac{\partial N}{\partial x}(0,t) = \frac{\partial N}{\partial x}(L,t) = 0,\ t \geq 0. \end{cases}$$

Since $N^0(\cdot) \not\equiv 0$ and $N_S^0(\cdot) \not\equiv 0$, it follows from the strong maximum principle (see, e. g., [14, p. 172, Theorem 4]) and the Hopf boundary lemma (see, e.g., [14, p. 170, Theorem 3]) that $N(\cdot,t) > 0,\ N_S(\cdot,t) > 0,\ \forall\ t > 0$. Hence, there exists a sufficiently small number $a > 0$ such that $(N(\cdot,t_1),\ N_S(\cdot,t_1)) \geq a(w_\rho^*(\cdot), w_{S\rho}^*(\cdot))$. By the comparison theorem, it follows that

$$(N(\cdot,t),\ N_S(\cdot,t)) \geq a e^{\lambda_\rho^*(t-t_1)}(w_\rho^*(\cdot), w_{S\rho}^*(\cdot))\ ,\forall\ t \geq t_1,\ x \in [0,L].$$

Since $\lambda_\rho^* > 0$, $(N(x,t),\ N_S(x,t))$ is unbounded, which is a contradiction. In view of $\mathcal{I} \neq \{\hat{0}\}$, we see from Theorem 3.2 (ii) that $\min_{\phi\in\mathcal{I}} p(\phi) > \eta$. Since $\widetilde{\omega} = \mathcal{I} \times \{(R^{(0)}, R^{(0)})\}$, it then follows that statement (ii) is valid. □

4 Global attractivity

In this section, we established the uniqueness and global stability of the positive steady state for system (1.1)-(1.3) under the condition that $m = k$.

Let

$$\begin{cases} W(x,t) = C(x,t) - \frac{\epsilon}{1-\epsilon}\frac{q_N}{q_C}N(x,t), \\ W_S(x,t) = C_S(x,t) - \frac{\epsilon}{1-\epsilon}\frac{q_N}{q_C}N_S(x,t). \end{cases} \tag{4.1}$$

It then follows from system (3.1)-(3.3) that $W(x,t)$ and $W_S(x,t)$ satisfy

$$\begin{cases} \frac{\partial W}{\partial t} = \delta\frac{\partial^2 W}{\partial x^2} - \nu\frac{\partial W}{\partial x} - (\alpha+m)W + \alpha W_S, \ 0<x<L, \ t>0, \\ \frac{\partial W_S}{\partial t} = -(\alpha\frac{A}{A_S}+m)W_S + \alpha\frac{A}{A_S}W, \ 0<x<L, \ t>0, \\ \nu W(0,t) - \delta\frac{\partial W}{\partial x}(0,t) = \frac{\partial W}{\partial x}(L,t) = 0, \ t>0, \\ W(x,0) = W^0(x) \geq 0, \ W_S(x,0) = W_S^0(x) \geq 0, \ 0<x<L. \end{cases} \tag{4.2}$$

By [7, Lemma 3.3] with $k=m$, it follows that

$$\lim_{t\to\infty}(W(x,t), W_S(x,t)) = (0,0), \text{ uniformly for } x\in[0,L]. \tag{4.3}$$

Then system (3.1)-(3.3) can be reduced to the following one:

$$\begin{cases} \frac{\partial N}{\partial t} = \delta\frac{\partial^2 N}{\partial x^2} - \nu\frac{\partial N}{\partial x} + \alpha(N_S - N) + [(1-\epsilon)f(R^{(0)} - \frac{q_N}{1-\epsilon}N) - m]N, \\ \frac{\partial N_S}{\partial t} = -\alpha\frac{A}{A_S}(N_S - N) + [(1-\epsilon)f(R^{(0)} - \frac{q_N}{1-\epsilon}N_S) - m]N_S, \end{cases} \tag{4.4}$$

for $(x,t)\in(0,L)\times(0,\infty)$ with boundary conditions

$$\nu N(0,t) - \delta\frac{\partial N}{\partial x}(0,t) = \frac{\partial N}{\partial x}(L,t) = 0, \tag{4.5}$$

and initial conditions

$$N(x,0) = N^0(x) \geq 0, N_S(x,0) = N_S^0(x) \geq 0, \ 0<x<L. \tag{4.6}$$

The biologically relevant domain for system (4.4)-(4.6) is given by

$$\Omega = \left\{(N^0, N_S^0) \in C([0,L],\mathbb{R}_+^2) : \ \frac{q_N}{1-\epsilon}N^0(x) \leq R^{(0)}, \ \frac{q_N}{1-\epsilon}N_S^0(x) \leq R^{(0)} \text{ on } [0,L]\right\}.$$

We define the solution semiflow $\Phi_t : \Omega \to \Omega$ of (4.4)-(4.6) by

$$\Phi_t(N^0(\cdot), N_S^0(\cdot)) = (N(\cdot,t,(N^0(\cdot),N_S^0(\cdot))), N_S(\cdot,t,(N^0(\cdot),N_S^0(\cdot)))), \ \forall\, t\geq 0,$$

where $(N^0(\cdot)N_S^0(\cdot)) \in \Omega$. It is easy to see that the solution semiflow Φ_t is strongly monotone (see, e.g., [18, Chapter 7]) in the sense that

$$\Phi_t(N^0(\cdot), N_S^0(\cdot)) \gg \Phi_t(\tilde{N}^0(\cdot), \tilde{N}_S^0(\cdot)), \ \forall t>0,$$

whenever $(N^0(\cdot), N_S^0(\cdot)) > (\tilde{N}^0(\cdot), \tilde{N}_S^0(\cdot))$, and strictly subhomogeneous (see, e.g., [23, section 2.3]) in the sense that

$$\Phi_t(\theta N^0(\cdot), \theta N_S^0(\cdot)) \gg \theta\Phi_t(N^0(\cdot), N_S^0(\cdot)), \forall\, (N^0(\cdot), N_S^0(\cdot)) \gg 0, \, \theta\in(0,1).$$

For convenience, we let $\Omega_0 = \Omega\backslash\{(0,0)\}, \ \partial\Omega_0 := \Omega\backslash\Omega_0 = \{(0,0)\}$.

By similar arguments to those in [6, Lemma 3.2, Theorems 3.1 and 3.2], we have the following result.

Lemma 4.1. *Assume that* $m = k$ *and* (2.7) *holds. For any* $(N^0(\cdot),\ N_S^0(\cdot)) \in \Omega$, *let* $(N(\cdot,t), N_S(\cdot,t))$ *be the solution of* (4.4)-(4.6). *Then the following statements are valid:*

(i) *If* $\mathcal{R}_0 < 1$, *then* $\lim_{t\to\infty}(N(x,t), N_S(x,t)) = (0,0)$ *uniformly for* $x \in [0, L]$*;*

(ii) *If* $\mathcal{R}_0 > 1$, *then* (4.4)-(4.6) *admits a unique positive steady-state solution* $(\hat{N}(x), \hat{N}_S(x))$ *and for any* $(N^0(\cdot),\ N_S^0(\cdot)) \in \Omega_0$, *we have*

$$\lim_{t\to\infty}(N(x,t), N_S(x,t)) = (\hat{N}(x), \hat{N}_S(x)),\ \text{uniformly for } x \in [0, L].$$

Now we are in a position to prove the global attractivity of the positive steady state for system (1.1)-(1.3) under the additional assumption that $m = k$.

Theorem 4.1. *Assume that* $m = k$ *and* (2.7) *holds. Let*

$$(R(x,t), N(x,t), C(x,t), R_S(x,t), N_S(x,t), C_S(x,t))$$

be the solution of (1.1)-(1.3) *with initial data in* X^+. *Then the following statements are valid:*

(i) *If* $\mathcal{R}_0 < 1$, *then*

$$\lim_{t\to\infty}(R(x,t), N(x,t), C(x,t), R_S(x,t), N_S(x,t), C_S(x,t)) = (R^{(0)}, 0, 0, R^{(0)}, 0, 0),$$

uniformly for $x \in [0, L]$.

(ii) *If* $\mathcal{R}_0 > 1$, *then* (1.1)-(1.3) *admits a unique positive steady-state solution* $(\hat{R}(x), \hat{N}(x), \hat{C}(x), \hat{R}_S(x), \hat{N}_S(x), \hat{C}_S(x))$, *and for any*

$$(R^0(\cdot), N^0(\cdot), C^0(\cdot), R_S^0(\cdot), N_S^0(\cdot), C_S^0(\cdot)) \in X_0,$$

we have

$$\begin{aligned}&\lim_{t\to\infty}(R(x,t), N(x,t), C(x,t), R_S(x,t), N_S(x,t), C_S(x,t))\\ &= (\hat{R}(x), \hat{N}(x), \hat{C}(x), \hat{R}_S(x), \hat{N}_S(x), \hat{C}_S(x)),\ \text{uniformly for } x \in [0, L].\end{aligned}$$

Proof. Statement (i) follows directly from Theorem 3.3(i). In order to prove statement (ii), we rewrite the system (1.1)-(1.3) with $m = k$ as an equivalent form:

$$\begin{cases}\frac{\partial N}{\partial t} = \delta\frac{\partial^2 N}{\partial x^2} - \nu\frac{\partial N}{\partial x} + \alpha(N_S - N) + [(1-\epsilon)f(V - \frac{q_N}{1-\epsilon}N - q_C W) - m]N,\\ \frac{\partial N_S}{\partial t} = -\alpha\frac{A}{A_S}(N_S - N) + [(1-\epsilon)f(V_S - \frac{q_N}{1-\epsilon}N_S - q_C W_S) - m]N_S,\\ \frac{\partial V}{\partial t} = \delta\frac{\partial^2 V}{\partial x^2} - \nu\frac{\partial V}{\partial x} + \alpha(V_S - V),\\ \frac{\partial V_S}{\partial t} = -\alpha\frac{A}{A_S}(V_S - V),\\ \frac{\partial W}{\partial t} = \delta\frac{\partial^2 W}{\partial x^2} - \nu\frac{\partial W}{\partial x} - (\alpha + m)W + \alpha W_S,\\ \frac{\partial W_S}{\partial t} = -(\alpha\frac{A}{A_S} + m)W_S + \alpha\frac{A}{A_S}W,\end{cases} \tag{4.7}$$

for $(x,t)\in(0,L)\times(0,\infty)$ with boundary conditions

$$\begin{cases}\nu N(0,t)-\delta\frac{\partial N}{\partial x}(0,t)=0,\ \nu V(0,t)-\delta\frac{\partial V}{\partial x}(0,t)=\nu R^{(0)},\\ \nu W(0,t)-\delta\frac{\partial W}{\partial x}(0,t)=0,\\ \frac{\partial N}{\partial x}(L,t)=\frac{\partial V}{\partial x}(L,t)=\frac{\partial W}{\partial x}(L,t)=0,\end{cases}\tag{4.8}$$

and initial conditions

$$\begin{cases}N(x,0)=N^0(x)\geq 0,\ N_S(x,0)=N_S^0(x)\geq 0,\ V(x,0)=V^0(x)\geq 0,\\ V_S(x,0)=V_S^0(x)\geq 0,\ W(x,0)=W^0(x)\geq 0,\ W_S(x,0)=W_S^0(x)\geq 0,\end{cases}\tag{4.9}$$

for $x\in(0,L)$. Here (V,V_S) and (W,W_S) are defined in (2.1) and (4.1), respectively. The biologically relevant domain for system (4.7)-(4.9) is given by

$$\begin{aligned}&\widetilde{\Omega}=\{(N^0,N_S^0,V^0,V_S^0,W^0,W_S^0)\in C([0,L],\mathbb{R}_+^4)\times C([0,L],\mathbb{R}^2):\\ &\frac{q_N}{1-\epsilon}N^0(x)+q_CW^0(x)\leq V^0(x),\ \frac{q_N}{1-\epsilon}N_S^0(x)+q_CW_S^0(x)\leq V_S^0(x),\\ &W^0(x)+\frac{\epsilon}{1-\epsilon}\frac{q_N}{q_C}N^0(x)\geq 0,\ W_S^0(x)+\frac{\epsilon}{1-\epsilon}\frac{q_N}{q_C}N_S^0(x)\geq 0 \text{ on } [0,L]\}.\end{aligned}$$

For convenience, we define

$$\widetilde{\Omega}_0:=\{(N^0,N_S^0,V^0,V_S^0,W^0,W_S^0)\in\widetilde{\Omega}:N^0(\cdot)\not\equiv 0 \text{ and } N_S^0(\cdot)\not\equiv 0\},$$

and $\partial\widetilde{\Omega}_0:=\widetilde{\Omega}\backslash\widetilde{\Omega}_0$. We first show that $\widetilde{\Omega}$ is positively invariant for system (4.7)-(4.9). Indeed, let $Q:=(N^0(\cdot),N_S^0(\cdot),V^0(\cdot),V_S^0(\cdot),W^0(\cdot),W_S^0(\cdot))\in\widetilde{\Omega}$ and let

$$(N(\cdot,t,Q),N_S(\cdot,t,Q),V(\cdot,t,Q),V_S(\cdot,t,Q),W(\cdot,t,Q),W_S(\cdot,t,Q))$$

be the solution of (4.7)-(4.9) with initial data Q. Recall that

$$\begin{cases}R(x,t)=V(x,t)-\frac{q_N}{1-\epsilon}N(x,t)-q_CW(x,t),\\ R_S(x,t)=V_S(x,t)-\frac{q_N}{1-\epsilon}N_S(x,t)-q_CW_S(x,t),\\ C(x,t)=W(x,t)+\frac{\epsilon}{1-\epsilon}\frac{q_N}{q_C}N(x,t),\\ C_S(x,t)=W_S(x,t)+\frac{\epsilon}{1-\epsilon}\frac{q_N}{q_C}N_S(x,t).\end{cases}\tag{4.10}$$

Then $(R(\cdot,t,Q),N(\cdot,t,Q),C(\cdot,t,Q),R_S(\cdot,t,Q),N_S(\cdot,t,Q),C_S(\cdot,t,Q))$ satisfies (1.1)-(1.3) and

$$R(\cdot,0,Q)\geq 0,\ N(\cdot,0,Q)\geq 0,\ C(\cdot,0,Q)\geq 0,$$

$$R_S(\cdot,0,Q)\geq 0,\ N_S(\cdot,0,Q)\geq 0,\ C_S(\cdot,0,Q)\geq 0.$$

By Lemma 2.1, it follows that

$$(R(\cdot,t,Q),N(\cdot,t,Q),C(\cdot,t,Q),R_S(\cdot,t,Q),N_S(\cdot,t,Q),C_S(\cdot,t,Q))\geq 0,\ \forall\ t\geq 0.$$

Thus, we can define the solution semiflows $\widetilde{\Phi}_t : \widetilde{\Omega} \to \widetilde{\Omega}$ associated with (4.7)-(4.9) by

$$\widetilde{\Phi}_t(Q) = (N(\cdot,t,Q), N_S(\cdot,t,Q), V(\cdot,t,Q), V_S(\cdot,t,Q), W(\cdot,t,Q), W_S(\cdot,t,Q)),\ \forall\, t \geq 0,$$

where $Q := (N^0(\cdot), N_S^0(\cdot), V^0(\cdot), V_S^0(\cdot), W^0(\cdot), W_S^0(\cdot)) \in \widetilde{\Omega}$. For any $Q \in \widetilde{\Omega}$, let $\widetilde{\omega}_1 := \widetilde{\omega}_1(Q)$ be the omega limit set of Q for $\widetilde{\Phi}_t$. Note that

$$(R^0(\cdot), N^0(\cdot), C^0(\cdot), R_S^0(\cdot), N_S^0(\cdot), C_S^0(\cdot)) \in X_0$$

if and only if $(N^0(\cdot), N_S^0(\cdot), V^0(\cdot), V_S^0(\cdot), W^0(\cdot), W_S^0(\cdot)) \in \widetilde{\Omega}_0$. By Lemma 2.2 and [7, Lemma 3.3], we have

$$\lim_{t\to\infty}(V(x,t), V_S(x,t)) = (R^{(0)}, R^{(0)}),\ \text{uniformly for } x \in [0,L],$$

and

$$\lim_{t\to\infty}(W(x,t), W_S(x,t)) = (0,0),\ \text{uniformly for } x \in [0,L].$$

For any $(N(\cdot), N_S(\cdot)) \in C([0,L], \mathbb{R}_+^2)$ with

$$(N(\cdot), N_S(\cdot), V(\cdot), V_S(\cdot), W(\cdot), W_S(\cdot)) \in \widetilde{\omega}_1,$$

there holds $(V(\cdot), V_S(\cdot)) = (R^{(0)}, R^{(0)})$ and $(W(\cdot), W_S(\cdot)) = (0,0)$. Thus, there exists a set $\mathcal{I}_1 \subset C([0,L], \mathbb{R}_+^2)$ such that $\widetilde{\omega}_1 = \mathcal{I}_1 \times \{(R^{(0)}, R^{(0)}, 0, 0)\}$. Since $\widetilde{\Omega}$ is closed, it follows that $\widetilde{\omega}_1 \subset \widetilde{\Omega}$. For any given $(N(\cdot), N_S(\cdot)) \in \mathcal{I}_1$, we have $(N(\cdot), N_S(\cdot), R^{(0)}, R^{(0)}, 0, 0) \in \widetilde{\omega}_1 \subset \widetilde{\Omega}$. By the definition of $\widetilde{\Omega}$, it follows that $(N(\cdot), N_S(\cdot)) \in \Omega$. This shows that $\mathcal{I}_1 \subset \Omega$.

By [23, Lemma 1.2.1′], it follows that $\widetilde{\omega}_1$ is a compact, invariant and internal chain transitive set for $\widetilde{\Phi}_t$. Moreover, for any $(N(\cdot), N_S(\cdot)) \in C([0,L], \mathbb{R}_+^2)$ with $(N(\cdot), N_S(\cdot), V(\cdot), V_S(\cdot), W(\cdot), W_S(\cdot)) \in \widetilde{\omega}_1$, there holds

$$\widetilde{\Phi}_t\,|_{\widetilde{\omega}_1}\,(N(\cdot), N_S(\cdot), V(\cdot), V_S(\cdot), W(\cdot), W_S(\cdot)) = (\Phi_t(N(\cdot), N_S(\cdot)), R^{(0)}, R^{(0)}, 0, 0),$$

where $\Phi_t(N(\cdot), N_S(\cdot))$ is the semiflows associated with (4.4)-(4.6) on Ω. It then easily follows that $\mathcal{I}_1$ is a compact, invariant and internal chain transitive set for $\Phi_t : \Omega \to \Omega$.

In the case where $\mathcal{R}_0 > 1$, it follows from Lemma 4.1 (ii) that (4.4)-(4.6) has a globally attractive steady state $(\hat{N}(\cdot), \hat{N}_S(\cdot))$ in Ω_0. Clearly, $(0,0)$ is also a steady state of system (4.4)-(4.6). Note that $(0,0)$ and $(\hat{N}(\cdot), \hat{N}_S(\cdot))$ are isolated invariant sets in Ω and no subset of $\{(0,0)\} \cup \{(\hat{N}(\cdot), \hat{N}_S(\cdot))\}$ forms a cycle in Ω. Since $\mathcal{I}_1$ is a compact, invariant and internal chain transitive set for $\Phi_t : \Omega \to \Omega$, it follows from a continuous-time version of [23, Theorem 1.2.2]) that either $\mathcal{I}_1 = \{(0,0)\}$ or $\mathcal{I}_1 = \{(\hat{N}(\cdot), \hat{N}_S(\cdot))\}$. By similar arguments to those in the proof of Theorem 3.3 (ii), we can further show that $\mathcal{I}_1 \neq \{(0,0)\}$. Thus, we have $\mathcal{I}_1 = \{(\hat{N}(\cdot), \hat{N}_S(\cdot))\}$, and hence, $\widetilde{\omega}_1 = \{(\hat{N}(\cdot), \hat{N}_S(\cdot), R^{(0)}, R^{(0)}, 0, 0)\}$. This, together with (4.10), implies that statement (ii) holds true. □

We remark that the condition $m = k$ makes sense biologically if we go one step further to set $m = k = 0$. This is a special case where algal mortality (m) and toxin decay (k) are negligible compared to flows, and hence, the loss processes are governed entirely by flow.

5 Discussion

In this paper, we analyze a reaction-diffusion-advection system modeling the longitudinal distribution of harmful algae and algal toxin that contains substantial amounts of nitrogen [1]. When the toxin contains little or none of the limiting nutrient [11], another system was proposed in [3] (see system (4) therein), that is, system (3.1)-(3.3) in [7]. Without recycling terms, the authors of [7] established a threshold type result on the global attractivity of system (3.1)-(3.3) of [7] in terms of the basic reproduction ratio for algae. For the general case of system (1.1)-(1.3) in this paper, we can only establish the global extinction and persistence of the algae (Theorems 3.2 and 3.3). Imposing an additional assumption that $m = k$, we can further obtain the global attractivity of the positive steady state of system (1.1)-(1.3) (Theorem 4.1).

It was recognized that inflows and salinity are also significant factors affecting phytoplankton community dynamics and structure. *Prymnesium parvum* (golden algae) can be tolerant of large variations in temperature and salinity, and is capable of forming large fish-killing blooms. Such kind of blooms have dramatically increased in frequency in inland waters of the United States, especially in western Texas [16]. As mentioned in [16], factors that can reduce the population of *Prymnesium parvum* might include grazing by toxin resistant zooplankton and pathogenic effects of virus. It was also known that some cyanobacteria may inhibit *Prymnesium parvum* blooms [16].

Mathematical modeling of algal dynamics is an important topic in theoretical ecology, since it can help us to understand the complex factors influencing harmful algal blooms and to gain insight that can guide mitigation and management. Based on the discussions in the last paragraph, we can extend models (1.1)-(1.3) here and (3.1)-(3.3) of [7] in several ways. For example, we may study the influence of seasonal temperature and salinity variations on the evolution dynamics. In order to understand the competition between P. parvum and cyanobacteria, the two-species model should be taken into account. As mentioned in [7, Section 4], we may also introduce the population of zooplankton into model (1.1)-(1.3) and study the resulting algae-zooplankton system. We leave these interesting problems for future investigation.

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