Global Dynamics of Zooplankton and Harmful Algae in Flowing Habitats

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Abstract

This paper is devoted to the study of two advection-dispersion-reaction models arising from the dynamics of harmful algae and zooplankton in flowing-water habitats where a main channel is coupled to a hydraulic storage zone, representing an ensemble of fringing coves on the shoreline. For the system modeling the dynamics of algae and their toxin that contains little limiting nutrient, we establish a threshold type result on the global attractivity in terms of the basic reproduction ratio for algae. For the model with zooplankton that eat the algae and are inhibited by the toxin produced by algae, we show that there exists a coexistence steady state and the zooplankton is uniformly persistent provided that two basic reproduction ratios for algae and zooplankton are greater than unity.

Keywords: Harmful algae, zooplankton, hydraulic storage zone, steady states, global attractivity, and uniform persistence.

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1 Introduction

Prymnesium parvum (a haptophyte alga), also called "golden algae", occurs worldwide and is capable of forming large fish-killing blooms in coastal and inland water

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environments. The first recorded P. parvum bloom occurred in 1985 in a semiarid region of the country in a stretch of the Pecos River in Texas [12]. Since this event, blooms of P. parvum have increased in the inland waters of Texas and other parts of USA ([25, 28]). A viable phytoplankton community usually emerges during the occurrence of harmful algal blooms in riverine ecosystems. It is important to understand the persistence of algae in the presence of flow and the spatial variation of algal abundance and toxicity during bloom and flow events. Recently, it has been suggested that management of flow is a possible strategy to control harmful algal blooms and mitigate their effects in some river systems ([17, 18, 29]). Another fact is that coves along the shoreline of riverine reservoirs might represent habitats where dynamics of harmful algae differ from the main reservoir. Motivated by those observations, a theoretical exploration of harmful algal dynamics in flowing conditions was proposed in [8].

In flowing-water habitats, the flow enters at one boundary supplying nutrient resource(s), and exits at another, removing nutrients and organisms, while both advection and diffusion transport organisms and nutrient across the habitat domain [1, 2, 16, 30]. A basic question on persistence remains to be answered. Rapid advective flow in such habitats can prevent persistence even for one species and realistic parameters. The presence of hydraulic storage zones in flowing-water habitats is a possible resolution of the persistence paradox [27]. Although nutrient concentration and population densities vary with location in both the flowing channel and the storage zone, advective and diffusive transport occur only in the flowing zone, not the storage zone. The flow reactor and its modifications are especially important because they provide a simple model for riverine reservoirs and fluvial lakes formed in drowned river valleys, which have strong advective flows [8]. In order to study the longitudinal distribution of algal abundance and toxicity under various flows, the authors of [8] conceived of an idealized riverine reservoir where a main channel with advective transport and dispersion is coupled to a hydraulic storage zone, representing an ensemble of fringing coves on the shoreline.

In this paper, a one-dimensional model with simple habitat geometry and transport processes [8] will be investigated to study spatial variations of harmful algae and its toxin production and decay, in riverine reservoirs. Here, we further adopt a continuum approach using an advection-dispersion-reaction system to resolve transport and biochemical reaction kinetics along the main channel of a riverine reservoir. We neglect several potential complications including vertical stratification, light limitation, and higher trophic levels. Those simplifications in this model permit us to concentrate on the study of population dynamics and toxin production and decay. The model structures are simplified but they support elaboration with details necessary for modeling specific flowing water systems in Texas, where harmful blooms have occurred. Hence, the model could be modified to represent conditions found in other riverine systems worldwide [8].

The organization of the paper is as follows. Some physical setting are introduced in next section. In section 3, we study the model describing the dynamics of algae and their toxin that contains little limiting nutrient. By appealing to the theory of monotone dynamical systems and chain transitive sets, we are able to prove that the washout steady state is globally stable if the basic reproduction ratio for algae is less than unity, and there exists a globally stable coexistence steady state if this ratio is greater than unity. In section 4, we consider the model with zooplankton that eat the algae and are inhibited by its toxin. The main result for this model shows that there exists a coexistence steady state and the zooplankton is uniformly persistent provided that two basic reproduction ratios for algae and zooplankton are greater than unity. A brief discussion is presented in section 5. The proofs involving chain transitive sets and persistence theory are deferred to the Appendix.

2 Basic settings

We shall study spatially explicit models that describe the dynamic interactions of a main lake and its coves via an advection-dispersion-reaction system. This continuum approach has one spatial dimension, the longitudinal axis (x) of a riverine reservoir from the headwaters ($x = 0$) to the dam ($x = L$) (see, e.g., [8, Fig. 1]). The main channel is connected to an ensemble of fringing coves treated as a hydraulic storage zone [3]. We assume that advective and diffusive transport occur only in the main flowing zone, not the storage zone. The cross-section of the channel is partitioned into a flowing zone of area A, and a static storage zone of area A_S (assumed to be constants here). Exchange of nutrient and populations between the flowing and storage zones occurs by Fickian diffusion with rate α (time^{-1}). A flow of water enters at the upstream end ($x = 0$), with discharge F (dimensions length^3 / time). An equal flow exits at the downstream end ($x = L$), which is assumed to be a dam. Based on this flow, a dilution rate D (dimensions time^{-1}) is defined as F/V. The advective flow within the channel is set to maintain water balance, by transporting water with a net velocity $\nu = DL$. Flow enters the headwaters at a rate F (dimensions length^3 / time), carrying the limiting nutrient for algal growth at a concentration $R^{(0)}$ (μmol / liter), and a balancing flow exits at the dam, removing algae, nutrients, and algal toxin.

In the following, the assumptions for algal population growth, and toxin production and decay will be imposed. Algal growth is a Monod function of the limiting nutrient concentration (R) at a given location:

$$f(R) = \frac{\mu_{\max} R}{K + R}. \tag{2.1}$$

Here, $\mu_{\max}$ (time^{-1}) represents the maximal growth rate and K (μmol / liter) represents the half saturation constant.

There are two types of production for dissolved toxins. The first assumes that the rate of toxin production p (μg toxin liter^{-1} time^{-1}) is proportional to the degree of algal nutrient limitation and to algal abundance N (cells/liter):

$$\epsilon p(R, N) = \epsilon[\mu_{\max} - f(R)]N = \epsilon \frac{\mu_{\max} K}{K + R} N, \tag{2.2}$$

where ϵ (μg toxin/cell) is a constant coefficient. We refer to this as the flagellate case since some toxic flagellates (e.g. Prymnesium parvum) have been observed to produce toxins more rapidly when stressed by nutrient limitation ([4, 7, 13, 15]).

The second type of toxin production assumes that the rate of production is proportional to algal productivity, i.e. to the product of growth rate and abundance:

$$\epsilon p(R, N) = \epsilon f(R) N = \epsilon \frac{\mu_{\max} R}{K + R} N. \tag{2.3}$$

This case assumes that toxin is produced in proportion to other cellular products, and is then released to the water at a constant rate. We refer to this as the cylindrospermopsin case [6, 10].

3 The model for harmful algae

Suppose $R(x,t)$, $N(x,t)$ and $C(x,t)$ denote dissolved nutrient concentration, algal abundance and dissolved toxin concentration at location x and time t in the flowing channel, respectively; Suppose $R_S(x,t)$, $N_S(x,t)$ and $C_S(x,t)$ denote dissolved nutrient concentration, algal abundance and dissolved toxin concentration at location x and time t in the storage zone, respectively. For simplicity, we suppose that the nutrient content of algae that die is instantaneously and locally recycled. Further, toxin degradation is assumed to follow first order kinetics with a decay coefficient k (time^{-1}). For many flagellate toxins, the toxin contains little or none of the limiting nutrient [21] and the governing equations take the following form [8]:

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

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

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

and initial conditions

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

in $x \in (0,L)$. Here the mortality of algae is assumed to be a constant rate m (time^{-1}); q_N(μmol/cell) represents the constant quota of algae.

3.1 The well-posedness

We first study the well-posedness of the initial-boundary-value problem (3.1)-(3.3). Let $X^+ = C([0,L], \mathbb{R}_+^6)$ be the positive cone of the Banach space $X = C([0,L], \mathbb{R}^6)$ 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 (3.3) 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 [20] where existence and uniqueness and positivity are treated simultaneously (taking delay as zero). The idea is to view the system (3.1)-(3.3) as the abstract ordinary differential equation in X^+ and the so-called mild solutions can be obtained for any given initial data. More precisely,

$$\begin{cases} u_0(t) = V(t)u_0^0 + \int_0^t T_0(t-s)B_0(\mathbf{u}(s))ds, \\ u_i(t) = T_i(t)u_i^0 + \int_0^t T_i(t-s)B_i(\mathbf{u}(s))ds, \ i = 1,2, \\ u_i(t) = u_i^0 + \int_0^t B_i(\mathbf{u}(s))ds, \ i = 3,4,5, \end{cases} \tag{3.4}$$

where $T_i(t)$ is the positive, non-expansive, analytic semigroup on $C([0,L], \mathbb{R})$ (see, e.g., [30, Chapter 7]) such that $u = T_i(t)u_i^0$, $i = 0,1,2$, satisfies the linear initial value problem

$$\begin{cases} \frac{\partial u}{\partial t} = \delta \frac{\partial^2 u}{\partial x^2} - \nu \frac{\partial u}{\partial x}, \ t > 0, 0 < x < L, \\ \nu u(0,t) - \delta \frac{\partial u}{\partial x}(0,t) = \frac{\partial u}{\partial x}(L,t) = 0, \ t > 0, \\ u(x,0) = u_i^0(x), \ i = 0,1,2. \end{cases} \tag{3.5}$$

$V(t)$, $t > 0$, is the family of affine operators on $C([0, L], \mathbb{R})$ (see, e.g., [24, Chapter 5]) such that $u = V(t)u_0^0$ satisfies the linear system with nonhomogeneous, boundary condition given by

$$\begin{cases} \frac{\partial u}{\partial t} = \delta \frac{\partial^2 u}{\partial x^2} - \nu \frac{\partial u}{\partial x}, \ t > 0, \ 0 < x < L, \\ \nu u(0,t) - \delta \frac{\partial u}{\partial x}(0,t) = \nu R^{(0)}, \ \frac{\partial u}{\partial x}(L,t) = 0, \ t > 0, \\ u(x,0) = u_0^0(x). \end{cases} \tag{3.6}$$

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

$$\begin{cases} B_0(\mathbf{u}) = -q_N[f(u_0) - m]u_1 + \alpha(u_3 - u_0), \\ B_1(\mathbf{u}) = \alpha(u_4 - u_1) + [f(u_0) - m]u_1, \\ B_2(\mathbf{u}) = \alpha(u_5 - u_2) + \epsilon p(u_0, u_1) - k u_2, \\ B_3(\mathbf{u}) = -\alpha \frac{A}{A_S}(u_3 - u_0) - q_N[f(u_3) - m]u_4, \\ B_4(\mathbf{u}) = -\alpha \frac{A}{A_S}(u_4 - u_1) + [f(u_3) - m]u_4, \\ B_5(\mathbf{u}) = -\alpha \frac{A}{A_S}(u_5 - u_2) + \epsilon p(u_3, u_4) - k u_5. \end{cases} \tag{3.7}$$

By standard maximum principle arguments (see, e.g., [30, Chapter 7]), it follows that $V(t)C([0, L], \mathbb{R}_+) \subset C([0, L], \mathbb{R}_+)$ and $T_i(t)C([0, L], \mathbb{R}_+) \subset C([0, L], \mathbb{R}_+)$, $\forall\, t > 0$. The operator V and semi-group T_0 are related to [20, 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., [20, Remark 1.1]). By [20, Theorem 1 and Remark 1.1], we have the following result.

Lemma 3.1. *The system* (3.1)-(3.3) *has a unique noncontinuable solution and the solutions to* (3.1)-(3.3) *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 (3.1)-(3.3). Let

$$W(x,t) = R(x,t) + q_N N(x,t) \text{ and } W_S(x,t) = R_S(x,t) + q_N N_S(x,t). \tag{3.8}$$

Then $W(x, t)$ and $W_S(x, t)$ satisfy the following coupled differential equations

$$\begin{cases} \frac{\partial W}{\partial t} = \delta \frac{\partial^2 W}{\partial x^2} - \nu \frac{\partial W}{\partial x} + \alpha W_S - \alpha W, \ 0 < x < L, \ t > 0, \\ \frac{\partial W_S}{\partial t} = -\alpha \frac{A}{A_S} W_S + \alpha \frac{A}{A_S} W, \ 0 < x < L, \ t > 0, \\ \nu W(0,t) - \delta \frac{\partial W}{\partial x}(0,t) = \nu R^{(0)}, \ \frac{\partial W}{\partial x}(L,t) = 0, \ t > 0, \\ W(x,0) = W^0(x) \geq 0, \ W_S(x,0) = W_S^0(x) \geq 0. \end{cases} \tag{3.9}$$

By similar arguments to those in [9] and [11, Lemma 2.3], we have the following results on the global dynamics of system (3.9).

Lemma 3.2. *The system* (3.9) *admit a positive steady-state solution* $(R^{(0)}, R^{(0)})$ *such that any mild solution* $(W(x,t), W_S(x,t))$ *of* (3.9) *with* $(W(\cdot,0), W_S(\cdot,0)) \in C([0,L],\mathbb{R}^2)$ *satisfies* $\lim_{t\to\infty}(W(x,t), W_S(x,t)) = (R^{(0)}, R^{(0)})$ *uniformly for* $x \in [0,L]$.

3.2 The basic reproduction ratio for algae

In order to find a trivial steady-state solution of (3.1)-(3.3), we let the densities of the algae compartments (N and N_S) be zero. Since (R, R_S) satisfies (3.9), it follows from Lemma 3.2 that

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

Further, (C, C_S) satisfies

$$\begin{cases} \frac{\partial C}{\partial t} = \delta \frac{\partial^2 C}{\partial x^2} - \nu \frac{\partial C}{\partial x} - (\alpha + k)C + \alpha C_S, \ 0 < x < L, \ t > 0, \\ \frac{\partial C_S}{\partial t} = -(\alpha \frac{A}{A_S} + k)C_S + \alpha \frac{A}{A_S} C, \ 0 < x < L, \ t > 0, \\ \nu C(0,t) - \delta \frac{\partial C}{\partial x}(0,t) = \frac{\partial C}{\partial x}(L,t) = 0, \ t > 0, \\ C(x,0) = C^0(x) \geq 0, \ C_S(x,0) = C_S^0(x) \geq 0, \ 0 < x < L. \end{cases} \tag{3.10}$$

Let $\mathcal{T}(t)$ be the solution semigroup generated by (3.10) on $C([0,L],\mathbb{R}^2)$. It is easy to see that $\mathcal{T}(t)$ is a positive C_0-semigroup on $C([0,L],\mathbb{R}^2)$, and its generator $\mathcal{B}$ can be written as

$$\mathcal{B} = \begin{pmatrix} \delta \frac{\partial^2}{\partial x^2} - \nu \frac{\partial}{\partial x} - (\alpha + k) & \alpha \\ \alpha \frac{A}{A_S} & -(\alpha \frac{A}{A_S} + k) \end{pmatrix}.$$

Further, $\mathcal{B}$ is a closed and resolvent positive operator (see, e.g., [33, Theorem 3.12]).

The following result is concerned with the global dynamics of system (3.10).

Lemma 3.3. *Let* $\sigma(\mathcal{B})$ *be the spectral set and* $s(\mathcal{B}) = \sup\{Re\lambda : \lambda \in \sigma(\mathcal{B})\}$ *be the spectral bound of* $\mathcal{B}$*. Then the following statements are valid:*

(i) $s(\mathcal{B})$ *is a geometrically simple eigenvalue of* $\mathcal{B}$ *with a positive eigenvector.*

(ii) *The steady-state solution* $(0,0)$ *is globally asymptotically stable on* $C([0,L],\mathbb{R}^2)$ *for* (3.10)*, and hence,* $(0,0)$ *is the unique steady-state solution for* (3.10)*. More precisely,* $\lim_{t\to\infty}(C(x,t), C_S(x,t)) = (0,0)$ *uniformly for* $x \in [0,L]$.

Proof. We first consider part (i). In order to make use of [35, Theorem 2.3], we define an one-parameter family of linear operators on $C([0,L],\mathbb{R})$:

$$\mathcal{L}_\Lambda = \delta \frac{\partial^2}{\partial x^2} - \nu \frac{\partial}{\partial x} - (\alpha + k) + \frac{\frac{\alpha^2 A}{A_S}}{\Lambda + (\alpha A/A_S) + k}, \ \forall \ \Lambda > -\frac{\alpha A}{A_S} - k.$$

According to [30, pp.147-148], the eigenvalue problem

$$\begin{cases} \Lambda\phi(x) = \delta\phi''(x) - \nu\phi'(x), \ 0 < x < L, \\ \nu\phi(0) - \delta\phi'(0) = \phi'(L) = 0, \end{cases} \tag{3.11}$$

has a principal eigenvalue, denoted by Λ^0, with an associated eigenvector $\phi^0 \gg 0$, and $\Lambda^0 < 0$. Let

$$Q(\Lambda) = \Lambda^2 + [\frac{\alpha A}{A_S} + \alpha + 2k - \Lambda^0]\Lambda + (\alpha + k - \Lambda^0)(\frac{\alpha A}{A_S} + k) - \frac{\alpha^2 A}{A_S}.$$

Then $Q(-\frac{\alpha A}{A_S} - k) = -\frac{\alpha^2 A}{A_S} < 0$. This implies that there are two distinct real roots of the algebraic equation $Q(\Lambda) = 0$, and we denote the largest root by Λ^*. Thus, $\Lambda^* > -\frac{\alpha A}{A_S} - k$. Since $\delta\frac{\partial^2\phi^0(x)}{\partial x^2} - \nu\frac{\partial\phi^0(x)}{\partial x} = \Lambda^0\phi^0(x)$, it follows that

$$\mathcal{L}_{\Lambda^*}\phi^0(x) = \frac{\Lambda^*(\Lambda^0 - \alpha - k) - [(\alpha + k - \Lambda^0)(\frac{\alpha A}{A_S} + k) - \frac{\alpha^2 A}{A_S}]}{\Lambda^* + (\alpha A/A_S) + k}\phi^0(x) = \Lambda^*\phi^0(x). \tag{3.12}$$

By [35, Theorem 2.3 (i)], it follows that $s(\mathcal{B})$ is a geometrically simple eigenvalue of $\mathcal{B}$ with a positive eigenvector $(\phi^*(\cdot), \phi_S^*(\cdot))$.

We are in a position to prove part (ii). Substituting $C(x,t) = e^{\Lambda t}\phi(x)$ and $C_S(x,t) = e^{\Lambda t}\phi_S(x)$ into (3.10), we obtain the associated eigenvalue problem

$$\begin{cases} \Lambda\phi(x) = \delta\phi''(x) - \nu\phi'(x) - (\alpha + k)\phi(x) + \alpha\phi_S(x), \ 0 < x < L, \\ \Lambda\phi_S(x) = -(\alpha\frac{A}{A_S} + k)\phi_S(x) + \alpha\frac{A}{A_S}\phi(x), \ 0 < x < L, \\ \nu\phi(0) - \delta\phi'(0) = \phi'(L) = 0. \end{cases} \tag{3.13}$$

Then $s(\mathcal{B})$ and $(\phi^*(\cdot), \phi_S^*(\cdot))$ are eigenvalue and eigenvector of (3.13). From (3.12), it is easy to see that $s(\mathcal{L}_{\Lambda^*}) = \Lambda^*$. It then follows from [35, Theorem 2.3 (ii)] that $s(\mathcal{B}) = \Lambda^*$. Since $Q(0) = (\alpha + k - \Lambda^0)(\frac{\alpha A}{A_S} + k) - \frac{\alpha^2 A}{A_S} > 0$, it follows that $\Lambda^* < 0$. Further, for each $t > 0$, the spectrum radius of $\mathcal{T}(t)$, $r(\mathcal{T}(t))$, is the principal eigenvalue of $\mathcal{T}(t)$, and hence,

$$r(\mathcal{T}(t)) = e^{\Lambda^* t}, \ \forall\, t > 0. \tag{3.14}$$

In view of (3.14) and the fact that $\Lambda^* < 0$, we see that $r(\mathcal{T}(t)) < 1$ for each $t > 0$. This implies that $(0,0)$ is globally asymptotically stable on $C([0,L], \mathbb{R}^2)$ for (3.10), and hence, $(0,0)$ is the unique steady-state solution for (3.10). $\square$

Linearizing system (3.1)-(3.3) at the steady-state solution $(R^{(0)}, 0, 0, R^{(0)}, 0, 0)$, we get the following cooperative system for the algae population:

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

Substituting $N(x,t) = e^{\lambda t}\phi(x)$ and $N_S(x,t) = e^{\lambda t}\phi_S(x)$ into (3.15), we obtain the associated eigenvalue problem

$$\begin{cases} \lambda\phi(x) = \delta\phi''(x) - \nu\phi'(x) + \alpha(\phi_S(x) - \phi(x)) + [f(R^{(0)}) - m]\phi(x), \ 0 < x < L, \\ \lambda\phi_S(x) = -\alpha\frac{A}{A_S}(\phi_S(x) - \phi(x)) + [f(R^{(0)}) - m]\phi_S(x), \ 0 < x < L, \\ \nu\phi(0) - \delta\phi'(0) = \phi'(L) = 0. \end{cases} \tag{3.16}$$

By similar arguments to those in Lemma 3.3 (i), we can show that the eigenvalue problem (3.16) has a principal eigenvalue, denoted by λ^0, with a positive eigenvector $(\phi(\cdot), \phi_S(\cdot)) \gg 0$ provided that

$$\alpha\frac{A}{A_S} + m > f(R^{(0)}). \tag{3.17}$$

In the following, we shall adopt the ideas in [34, 35] 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

$$\begin{cases} \frac{\partial N}{\partial t} = \delta \frac{\partial^2 N}{\partial x^2} - \nu \frac{\partial N}{\partial x} + \alpha(N_S - N) - mN, \ 0 < x < L, \ t > 0, \\ \frac{\partial N_S}{\partial t} = -\alpha\frac{A}{A_S}(N_S - N) - mN_S, \ 0 < x < L, \ t > 0, \\ \nu N(0,t) - \delta\frac{\partial N}{\partial x}(0,t) = \frac{\partial N}{\partial x}(L,t) = 0, \ t > 0. \end{cases} \tag{3.18}$$

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 trivial steady-state solution $(0,0)$ for (3.15), 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

$$\mathbf{L}(\varphi)(\cdot) = \int_0^\infty \begin{pmatrix} f(R^{(0)}) & 0 \\ 0 & f(R^{(0)}) \end{pmatrix} (S(t)\varphi)(\cdot)dt. \tag{3.19}$$

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,

$$\mathcal{R}_0 := r(\mathbf{L}). \tag{3.20}$$

By [35, Theorem 3.1 (i) and Remark 3.1], we have the following observation.

Lemma 3.4. $\mathcal{R}_0 - 1$ *and* λ^0 *have the same sign.*

3.3 The global stability

We first consider the following auxiliary system which will be used in our subsequent discussions:

$$\begin{cases} \frac{\partial N}{\partial t} = \delta \frac{\partial^2 N}{\partial x^2} - \nu \frac{\partial N}{\partial x} + \alpha(N_S - N) + [f(R^{(0)} - q_N N) - m]N, \\ \frac{\partial N_S}{\partial t} = -\alpha \frac{A}{A_S}(N_S - N) + [f(R^{(0)} - q_N N_S) - m]N_S, \end{cases} \tag{3.21}$$

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

$$\nu N(0,t) - \delta \frac{\partial N}{\partial x}(0,t) = \frac{\partial N}{\partial x}(L,t) = 0,\ t > 0, \tag{3.22}$$

and initial conditions

$$N(x, 0) = N^0(x) \geq 0,\ N_S(x, 0) = N_S^0(x) \geq 0,\ 0 < x < L. \tag{3.23}$$

The biologically relevant domain for the system (3.21)-(3.23) is given by

$$Y^+ = \left\{ (N^0, N_S^0) \in C([0, L], \mathbb{R}_+^2) :\ 0 \leq N^0(\cdot) \leq \frac{R^{(0)}}{q_N},\ 0 \leq N_S^0(\cdot) \leq \frac{R^{(0)}}{q_N} \right\}.$$

For convenience, we let $Y_0 = Y^+ \backslash \{(0,0)\}$, $\partial Y_0 := Y^+ \backslash Y_0 = \{(0,0)\}$. By similar arguments to those in [11, Lemma 3.1], we have the following result.

Lemma 3.5. *For any* $(N^0, N_S^0) \in Y^+$*, system* (3.21)-(3.23) *has a unique mild solution* $(N(\cdot,t), N_S(\cdot,t))$ *with* $(N(\cdot,0), N_S(\cdot,0)) = (N^0, N_S^0)$ *and* $(N(\cdot,t), N_S(\cdot,t)) \in Y^+$ *for all* $t \geq 0$.

By Lemma 3.5, we can define the solution semiflow $\Phi_1(t) : Y^+ \to Y^+$ of (3.21)-(3.23) by

$$\Phi_1(t)(P) = (N(\cdot, t, P), N_S(\cdot, t, P)),\ \forall P := (N^0(\cdot),\ N_S^0(\cdot)) \in Y^+,\ t \geq 0. \tag{3.24}$$

By similar arguments to those in [11, Lemma 3.2, Theorem 3.1 and Theorem 3.2], we have the following result.

Lemma 3.6. *Assume that* (3.17) *holds and* λ^0 *is principal eigenvalue of* (3.16). *For any* $(N^0(\cdot),\ N_S^0(\cdot)) \in Y^+$, *let* $(N(\cdot,t), N_S(\cdot,t))$ *be the solution of* (3.21)-(3.23). *Then the following statements are valid:*

(i) *If* $\lambda^0 \le 0$, *then* $\lim_{t\to\infty}(N(x,t), N_S(x,t)) = (0,0)$ *uniformly for* $x \in [0,L]$;

(ii) *If* $\lambda^0 > 0$, *then* (3.21)-(3.23) *admit a unique positive steady-state solution* $(N^*(x), N_S^*(x))$ *and for any* $(N^0(\cdot),\ N_S^0(\cdot)) \in Y_0$, *we have*

$$\lim_{t\to\infty}(N(x,t), N_S(x,t)) = (N^*(x), N_S^*(x)),\ \ \textit{uniformly for } x \in [0,L].$$

Since the equations of R, N, R_S and N_S in (3.1) are independent of the equations of C and C_S, we first study the following subsystem:

$$\begin{cases} \frac{\partial R}{\partial t} = \delta\frac{\partial^2 R}{\partial x^2} - \nu\frac{\partial R}{\partial x} - q_N[f(R)-m]N + \alpha(R_S - R), \\ \frac{\partial N}{\partial t} = \delta\frac{\partial^2 N}{\partial x^2} - \nu\frac{\partial N}{\partial x} + \alpha(N_S - N) + [f(R)-m]N, \\ \frac{\partial R_S}{\partial t} = -\alpha\frac{A}{A_S}(R_S - R) - q_N[f(R_S)-m]N_S, \\ \frac{\partial N_S}{\partial t} = -\alpha\frac{A}{A_S}(N_S - N) + [f(R_S)-m]N_S, \end{cases} \tag{3.25}$$

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

$$\begin{cases} \nu R(0,t) - \delta\frac{\partial R}{\partial x}(0,t) = \nu R^{(0)}, \\ \nu N(0,t) - \delta\frac{\partial N}{\partial x}(0,t) = 0, \\ \frac{\partial R}{\partial x}(L,t) = \frac{\partial N}{\partial x}(L,t) = 0, \end{cases} \tag{3.26}$$

and initial conditions

$$\begin{cases} R(x,0) = R^0(x) \ge 0,\ \ N(x,0) = N^0(x) \ge 0, \\ R_S(x,0) = R_S^0(x) \ge 0,\ \ N_S(x,0) = N_S^0(x) \ge 0,\ \ 0 < x < L. \end{cases} \tag{3.27}$$

By similar arguments to those in Lemma 3.1, we have the following result.

Lemma 3.7. *The system* (3.25)-(3.27) *has a unique noncontinuable solution and the solutions to* (3.25)-(3.27) *remain non-negative on their interval of existence if they are non-negative initially.*

We rewrite the system (3.25)-(3.27) as follows:

$$\begin{cases} \frac{\partial W}{\partial t} = \delta\frac{\partial^2 W}{\partial x^2} - \nu\frac{\partial W}{\partial x} + \alpha W_S - \alpha W, \\ \frac{\partial W_S}{\partial t} = -\alpha\frac{A}{A_S}W_S + \alpha\frac{A}{A_S}W, \\ \frac{\partial N}{\partial t} = \delta\frac{\partial^2 N}{\partial x^2} - \nu\frac{\partial N}{\partial x} + \alpha(N_S - N) + [f(W - q_N N)-m]N, \\ \frac{\partial N_S}{\partial t} = -\alpha\frac{A}{A_S}(N_S - N) + [f(W_S - q_N N_S)-m]N_S, \end{cases} \tag{3.28}$$

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

$$\begin{cases} \nu W(0,t) - \delta \frac{\partial W}{\partial x}(0,t) = \nu R^{(0)}, \\ \nu N(0,t) - \delta \frac{\partial N}{\partial x}(0,t) = \frac{\partial W}{\partial x}(L,t) = \frac{\partial N}{\partial x}(L,t) = 0, \ t > 0, \end{cases} \tag{3.29}$$

and initial conditions

$$\begin{cases} W(x,0) = W^0(x) \geq 0, \ N(x,0) = N^0(x) \geq 0, \\ W_S(x,0) = W_S^0(x) \geq 0, \ N_S(x,0) = N_S^0(x) \geq 0, \ x \in (0,L), \end{cases} \tag{3.30}$$

where W and W_S are defined in (3.8).

Let

$$\Sigma = \{(W^0, W_S^0, N^0, N_S^0) \in C([0,L], \mathbb{R}_+^4) : q_N N^0(\cdot) \leq W^0(\cdot) \text{ and } q_N N_S^0(\cdot) \leq W_S^0(\cdot)\},$$

and

$$\Sigma_0 = \{(W^0, W_S^0, N^0, N_S^0) \in \Sigma : (N^0, N_S^0) \neq (0,0)\}.$$

Lemma 3.8. *If $P \in \Sigma$, then the solution of* (3.28)-(3.29) *through P satisfies*

$$(W(\cdot,t,P), W_S(\cdot,t,P), N(\cdot,t,P), N_S(\cdot,t,P)) \in \Sigma, \ \forall \ t \geq 0.$$

Proof. Let $R(x,t) = W(x,t) - q_N N(x,t)$ and $R_S(x,t) = W_S(x,t) - q_N N_S(x,t)$. Then $(R(x,t), N(x,t), R_S(x,t), N_S(x,t))$ satisfies (3.25)-(3.27). By Lemma 3.7, it follows that

$$(R(\cdot,t,P), N(\cdot,t,P), R_S(\cdot,t,P), N_S(\cdot,t,P)) \geq 0, \ \forall \ t \geq 0.$$

This completes our proof. $\square$

Let $\mathcal{X}^+ = C([0,L], \mathbb{R}_+^4)$, $\mathcal{X}_0 = \mathcal{X}^+ \backslash \{(R^{(0)}, 0, R^{(0)}, 0)\}$, $\partial \mathcal{X}_0 := \mathcal{X}^+ \backslash \mathcal{X}_0 = \{(R^{(0)}, 0, R^{(0)}, 0)\}$. Then we have the following threshold type result, whose proof is given in the Appendix.

Theorem 3.1. *Assume that* (3.17) *holds. Let*

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

be the solution of (3.25)-(3.27) *with initial data in $\mathcal{X}^+$. Then the following statements are valid:*

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

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

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

(ii) *If* $\mathcal{R}_0 > 1$*, then* (3.25)-(3.27) *admit a unique positive steady-state solution* $(R^*(x), N^*(x), R_S^*(x), N_S^*(x))$*, and for any*

$$(R^0(\cdot), N^0(\cdot), R_S^0(\cdot), N_S^0(\cdot)) \in \mathcal{X}_0,$$

we have

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

In order to discuss the global dynamics of the full system of (3.1)-(3.3), we first consider the following system:

$$\begin{cases} \frac{\partial C}{\partial t} = \delta\frac{\partial^2 C}{\partial x^2} - \nu\frac{\partial C}{\partial x} + \epsilon p(R^*(x), N^*(x)) - (\alpha + k)C + \alpha C_S, \ 0 < x < L, \ t > 0, \\ \frac{\partial C_S}{\partial t} = \epsilon p(R_S^*(x), N_S^*(x)) - (\alpha\frac{A}{A_S} + k)C_S + \alpha\frac{A}{A_S}C, \ 0 < x < L, \ t > 0, \\ \nu C(0,t) - \delta\frac{\partial C}{\partial x}(0,t) = \frac{\partial C}{\partial x}(L,t) = 0, \ t > 0, \\ C(x,0) = C^0(x) \geq 0, \ C_S(x,0) = C_S^0(x) \geq 0, \ 0 < x < L, \end{cases} \tag{3.31}$$

where $(R^*(x), N^*(x), R_S^*(x), N_S^*(x))$ is the unique positive steady-state solution of (3.25)-(3.27). It is easy to see that system (3.10) is the homogenous linear system of (3.31), and $(0,0)$ is linearly stable for system (3.10) by Lemma 3.3. By the arguments similar to those in [11, Lemma 2.3], we have the following result on the global dynamics of system (3.31).

Lemma 3.9. *The system* (3.31) *admit a positive steady-state solution* $(C^*(x), C_S^*(x))$ *such that any solution* $(C(x,t), C_S(x,t))$ *of system* (3.31) *with* $(C(\cdot,0), C_S(\cdot,0)) \in C([0,L],\mathbb{R}^2)$ *satisfies* $\lim_{t\to\infty}(C(x,t), C_S(x,t)) = (C^*(x), C_S^*(x))$ *uniformly for* $x \in [0, L]$.

Recall that $X^+ = C([0,L], \mathbb{R}_+^6)$ is the biologically relevant domain for the system (3.1)-(3.3). For convenience, we set $X_0 := X^+\backslash\{(R^{(0)}, 0, 0, R^{(0)}, 0, 0)\}$, $\partial X_0 := X^+\backslash X_0 = \{(R^{(0)}, 0, 0, R^{(0)}, 0, 0)\}$.

Theorem 3.2. *Assume that* (3.17) *holds. Let* $(R^*(x), N^*(x), R_S^*(x), N_S^*(x))$ *and* $(C^*(x), C_S^*(x))$ *be the positive steady-state solutions of* (3.25)-(3.27) *and* (3.31)*, respectively, and 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* (3.1)-(3.3) *with initial data in* X^+*. Then the following statements are valid:*

(i) *If* $\mathcal{R}_0 \leq 1$*, 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* (3.1)-(3.3) *admit a unique positive steady-state solution* $(R^*(x), N^*(x), C^*(x), R_S^*(x), N_S^*(x), C_S^*(x))$, *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

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

Proof. Suppose that $\mathcal{R}_0 \le 1$. Then Theorem 3.1 (i) implies that the equation for C and C_S in (3.1)-(3.3) is asymptotic to the system (3.10). Thus, Lemma 3.3 and the theory for asymptotically autonomous semiflows (see, e.g., [32, Corollary 4.3]) imply that

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

uniformly for $x \in [0, L]$. This proves statement (i).

Suppose that $\mathcal{R}_0 > 1$. Then Theorem 3.1 (ii) implies that the equation for C and C_S in (3.1)-(3.3) is asymptotic to the system (3.31). Thus, Lemma 3.9 and the theory for asymptotically autonomous semiflows (see, e.g., [32, Corollary 4.3]) implies that $\lim_{t\to\infty}(C(x,t), C_S(x,t)) = (C^*(x), C_S^*(x))$ uniformly for $x \in [0, L]$. This proves statement (ii). □

4 The model for harmful algae and zooplankton

In this section, we introduce the zooplankton into the model (3.1)-(3.3). Suppose Z and Z_S represent the densities of zooplankton in the flow and storage zones; q_Z is the constant nutrient quota for zooplankton; m_Z is the mortality of zooplankton. Then the governing equations take the following form:

$$\begin{cases}\frac{\partial R}{\partial t} = \delta\frac{\partial^2 R}{\partial x^2} - \nu\frac{\partial R}{\partial x} - q_N[f(R) - m]N + \alpha(R_S - R),\\ \frac{\partial N}{\partial t} = \delta\frac{\partial^2 N}{\partial x^2} - \nu\frac{\partial N}{\partial x} + \alpha(N_S - N) + [f(R) - m]N - q_Z g(N)e^{-\eta C}Z,\\ \frac{\partial C}{\partial t} = \delta\frac{\partial^2 C}{\partial x^2} - \nu\frac{\partial C}{\partial x} + \alpha(C_S - C) + \epsilon p(R, N) - kC,\\ \frac{\partial Z}{\partial t} = \delta\frac{\partial^2 Z}{\partial x^2} - \nu\frac{\partial Z}{\partial x} + \alpha(Z_S - Z) + [g(N)e^{-\eta C} - m_Z]Z,\\ \frac{\partial R_S}{\partial t} = -\alpha\frac{A}{A_S}(R_S - R) - q_N[f(R_S) - m]N_S,\\ \frac{\partial N_S}{\partial t} = -\alpha\frac{A}{A_S}(N_S - N) + [f(R_S) - m]N_S - q_Z g(N_S)e^{-\eta C_S}Z_S,\\ \frac{\partial C_S}{\partial t} = -\alpha\frac{A}{A_S}(C_S - C) + \epsilon p(R_S, N_S) - kC_S,\\ \frac{\partial Z_S}{\partial t} = -\alpha\frac{A}{A_S}(Z_S - Z) + [g(N_S)e^{-\eta C_S} - m_Z]Z_S,\end{cases} \tag{4.1}$$

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

$$\begin{cases} \nu R(0,t) - \delta \frac{\partial R}{\partial x}(0,t) = \nu R^{(0)}, \\ \nu N(0,t) - \delta \frac{\partial N}{\partial x}(0,t) = \nu C(0,t) - \delta \frac{\partial C}{\partial x}(0,t) = \nu Z(0,t) - \delta \frac{\partial Z}{\partial x}(0,t) = 0, \\ \frac{\partial R}{\partial x}(L,t) = \frac{\partial N}{\partial x}(L,t) = \frac{\partial C}{\partial x}(L,t) = \frac{\partial Z}{\partial x}(L,t) = 0, \end{cases} \tag{4.2}$$

and initial conditions

$$\begin{cases} R(x,0) = R^0(x) \geq 0, \ N(x,0) = N^0(x) \geq 0, \\ C(x,0) = C^0(x) \geq 0, \ Z(x,0) = Z^0(x) \geq 0, \\ R_S(x,0) = R_S^0(x) \geq 0, \ N_S(x,0) = N_S^0(x) \geq 0, \\ C_S(x,0) = C_S^0(x) \geq 0, \ Z_S(x,0) = Z_S^0(x) \geq 0, \end{cases} \tag{4.3}$$

in $x \in (0,L)$. Here $\eta > 0$ is a constant and represents the effect of the inhibitor on zooplankton, the term $e^{-\eta C}$ represents the degree of inhibition of C on the growth rate of zooplankton, and the function $g(N)$ has the following form:

$$g(N) = \frac{\hat{\mu}_{\max} N}{\hat{K} + N}. \tag{4.4}$$

4.1 The well-posedness

Let $\mathbb{X} := C([0,L], \mathbb{R}^8)$ be the Banach space with the supremum norm $\|\cdot\|_{\mathbb{X}}$. Define $\mathbb{X}^+ := C([0,L], \mathbb{R}_+^8)$. Then $(\mathbb{X}, \mathbb{X}^+)$ is a strongly ordered space. By the arguments similar to those in Lemma 3.1, we obtain the following basic properties of the set $\mathbb{X}^+$.

Lemma 4.1. *For every initial value functions $\phi \in \mathbb{X}^+$, system* (4.1)-(4.3) *has a unique mild solution $u(x,t,\phi)$ on $(0,\tau_\phi)$ with $u(\cdot,0,\phi) = \phi$, where $\tau_\phi \leq \infty$. Furthermore, $u(\cdot,t,\phi) \in \mathbb{X}^+$, $\forall\ t \in (0,\tau_\phi)$, and $u(x,t,\phi)$ is a classical solution of* (4.1)-(4.3) *for $t > 0$.*

We first show that solutions of system (4.1)-(4.3) exist globally on $[0,\infty)$, and ultimately bounded and uniformly bounded in $\mathbb{X}^+$.

Lemma 4.2. *For every initial value functions $\phi \in \mathbb{X}^+$, system* (4.1)-(4.3) *has a unique solution $u(x,t,\phi)$ on $[0,\infty)$ with $u(\cdot,0,\phi) = \phi$, and solutions of* (4.1)-(4.3) *are ultimately bounded and uniformly bounded in $\mathbb{X}^+$.*

Proof. Let

$$U(x,t) = R(x,t) + q_N N(x,t) \text{ and } U_S(x,t) = R_S(x,t) + q_N N_S(x,t). \tag{4.5}$$

Then $U(x,t)$ and $U_S(x,t)$ satisfy the following coupled differential equations

$$\begin{cases} \frac{\partial U}{\partial t} = \delta\frac{\partial^2 U}{\partial x^2} - \nu\frac{\partial U}{\partial x} + \alpha U_S - \alpha U - q_N q_Z g(N)e^{-\eta C}Z,\ 0 < x < L,\ t > 0, \\ \frac{\partial U_S}{\partial t} = -\alpha\frac{A}{A_S}U_S + \alpha\frac{A}{A_S}U - q_N q_Z g(N_S)e^{-\eta C_S}Z_S,\ 0 < x < L,\ t > 0, \\ \nu U(0,t) - \delta\frac{\partial U}{\partial x}(0,t) = \nu R^{(0)},\ \frac{\partial U}{\partial x}(L,t) = 0,\ t > 0, \\ U(x,0) = U^0(x) \geq 0,\ U_S(x,0) = U_S^0(x) \geq 0. \end{cases} \tag{4.6}$$

In view of Lemma 4.1 and (4.6), it follows that

$$\begin{cases} \frac{\partial U}{\partial t} \leq \delta\frac{\partial^2 U}{\partial x^2} - \nu\frac{\partial U}{\partial x} + \alpha U_S - \alpha U,\ 0 < x < L,\ t > 0, \\ \frac{\partial U_S}{\partial t} \leq -\alpha\frac{A}{A_S}U_S + \alpha\frac{A}{A_S}U,\ 0 < x < L,\ t > 0, \\ \nu U(0,t) - \delta\frac{\partial U}{\partial x}(0,t) = \nu R^{(0)},\ \frac{\partial U}{\partial x}(L,t) = 0,\ t > 0, \\ U(x,0) = U^0(x) \geq 0,\ U_S(x,0) = U_S^0(x) \geq 0. \end{cases} \tag{4.7}$$

The comparison principle implies that $U(x,t)$ and $U_S(x,t)$ are uniformly bounded, and hence, so are $R(x,t)$, $R_S(x,t)$, $N(x,t)$ and $N_S(x,t)$. This, together with the comparison arguments, implies that $C(x,t)$, $C_S(x,t)$, $Z(x,t)$ and $Z_S(x,t)$ are also uniformly bounded.

Comparing (4.7) with (3.9), we see from Lemma 3.2 and the comparison principle that

$$\lim_{t\to\infty} U(x,t) \leq R^{(0)} \text{ and } \lim_{t\to\infty} U_S(x,t) \leq R^{(0)} \text{ uniformly for } x \in [0,L]. \tag{4.8}$$

More precisely, there is a $t_1 > 0$ such that

$$U(\cdot,t),\ U_S(\cdot,t) \leq 2R^{(0)},\ \forall\ t \geq t_1.$$

This implies that $R(x,t)$, $R_S(x,t)$, $N(x,t)$ and $N_S(x,t)$ are ultimately bounded and

$$R(\cdot,t),\ R_S(\cdot,t) \leq 2R^{(0)};\ N(\cdot,t),\ N_S(\cdot,t) \leq \frac{2R^{(0)}}{q_N},\ \forall\ t \geq t_1.$$

It then follows from (2.2) and (2.3) that

$$\epsilon p(R(\cdot,t),N(\cdot,t)) \leq \frac{2\epsilon\mu_{\max}R^{(0)}}{q_N},\ \forall\ t \geq t_1. \tag{4.9}$$

In view of (4.1) and (4.9), it follows that

$$\begin{cases} \frac{\partial C}{\partial t} \leq \delta\frac{\partial^2 C}{\partial x^2} - \nu\frac{\partial C}{\partial x} + \alpha(C_S - C) + \tilde{Q} - kC,\ t > t_1,\ 0 < x < L, \\ \frac{\partial C_S}{\partial t} \leq -\alpha\frac{A}{A_S}(C_S - C) + \tilde{Q} - kC_S,\ t > t_1,\ 0 < x < L, \\ \nu C(0,t) - \delta\frac{\partial Z}{\partial x}(0,t) = \frac{\partial C}{\partial x}(L,t) = 0,\ t > t_1, \end{cases} \tag{4.10}$$

where $\tilde{Q} = \frac{2\epsilon\mu_{\max}R^{(0)}}{q_N}$. We consider the following system:

$$\begin{cases} \frac{\partial\tilde{C}}{\partial t} = \delta\frac{\partial^2\tilde{C}}{\partial x^2} - \nu\frac{\partial\tilde{C}}{\partial x} + \alpha(\tilde{C}_S - \tilde{C}) + \tilde{Q} - k\tilde{C},\ t > t_1,\ 0 < x < L, \\ \frac{\partial\tilde{C}_S}{\partial t} = -\alpha\frac{A}{A_S}(\tilde{C}_S - \tilde{C}) + \tilde{Q} - k\tilde{C}_S,\ t > t_1,\ 0 < x < L, \\ \nu\tilde{C}(0,t) - \delta\frac{\partial\tilde{C}}{\partial x}(0,t) = \frac{\partial\tilde{C}}{\partial x}(L,t) = 0,\ t > t_1. \end{cases} \tag{4.11}$$

By the same arguments as in Lemma 3.9, we can show that system (4.11) admit a positive steady state $(\tilde{C}^*(x), \tilde{C}_S^*(x))$ such that any solution $(\tilde{C}(x,t), \tilde{C}_S(x,t))$ of (4.11) with $(\tilde{C}(\cdot,0), \tilde{C}_S(\cdot,0)) \in C([0,L],\mathbb{R}^2)$ satisfies

$$\lim_{t\to\infty}(\tilde{C}(x,t), \tilde{C}_S(x,t)) = (\tilde{C}^*(x), \tilde{C}_S^*(x)),\ \text{uniformly for } x \in [0,L].$$

It then follows that

$$\lim_{t\to\infty} C(x,t) \le \tilde{C}^*(x) \text{ and } \lim_{t\to\infty} C_S(x,t) \le \tilde{C}_S^*(x),\ \text{uniformly for } x \in [0,L]. \tag{4.12}$$

Let

$$V(x,t) = N(x,t) + q_Z Z(x,t) \text{ and } V_S(x,t) = N_S(x,t) + q_Z Z_S(x,t). \tag{4.13}$$

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

$$\begin{cases} \frac{\partial V}{\partial t} = \delta\frac{\partial^2 V}{\partial x^2} - \nu\frac{\partial V}{\partial x} + \alpha(V_S - V) - m_Z V + [f(R) - m + m_Z]N,\ 0 < x < L,\ t > 0, \\ \frac{\partial V_S}{\partial t} = -\alpha\frac{A}{A_S}(V_S - V) - m_Z V_S + [f(R_S) - m + m_Z]N_S,\ 0 < x < L,\ t > 0, \\ \nu V(0,t) - \delta\frac{\partial V}{\partial x}(0,t) = 0,\ \frac{\partial V}{\partial x}(L,t) = 0,\ t > 0. \end{cases} \tag{4.14}$$

Thus, we have

$$\begin{cases} \frac{\partial V}{\partial t} \le \delta\frac{\partial^2 V}{\partial x^2} - \nu\frac{\partial V}{\partial x} + \alpha(V_S - V) + \hat{Q} - m_Z V,\ 0 < x < L,\ t > t_1, \\ \frac{\partial V_S}{\partial t} \le -\alpha\frac{A}{A_S}(V_S - V) + \hat{Q} - m_Z V_S,\ 0 < x < L,\ t > t_1, \\ \nu V(0,t) - \delta\frac{\partial V}{\partial x}(0,t) = 0,\ \frac{\partial V}{\partial x}(L,t) = 0,\ t > t_1, \end{cases} \tag{4.15}$$

where $\hat{Q} = \frac{2R^{(0)}(\mu_{\max} + m_Z)}{q_N}$. Similarly, we can show that

$$\lim_{t\to\infty} V(x,t) \le \hat{V}^*(x) \text{ and } \lim_{t\to\infty} V_S(x,t) \le \hat{V}_S^*(x) \text{ uniformly for } x \in [0,L], \tag{4.16}$$

where $(\hat{V}^*(x), \hat{V}_S^*(x))$ is the unique positive steady-state solution of

$$\begin{cases} \frac{\partial\hat{V}}{\partial t} = \delta\frac{\partial^2\hat{V}}{\partial x^2} - \nu\frac{\partial\hat{V}}{\partial x} + \alpha(\hat{V}_S - \hat{V}) + \hat{Q} - m_Z\hat{V},\ 0 < x < L,\ t > 0, \\ \frac{\partial\hat{V}_S}{\partial t} = -\alpha\frac{A}{A_S}(\hat{V}_S - \hat{V}) + \hat{Q} - m_Z\hat{V}_S,\ 0 < x < L,\ t > 0, \\ \nu\hat{V}(0,t) - \delta\frac{\partial\hat{V}}{\partial x}(0,t) = 0,\ \frac{\partial\hat{V}}{\partial x}(L,t) = 0,\ t > 0. \end{cases} \tag{4.17}$$

By the above discussions, it follows that $C(x,t)$, $C_S(x,t)$, $Z(x,t)$ and $Z_S(x,t)$ are also ultimately bounded. $\square$

From the proof of Lemma 4.2, we see that there exist $t_2 \geq t_1$ such that

$$R(\cdot,t),\ R_S(\cdot,t) \leq 2R^{(0)};\ N(\cdot,t),\ N_S(\cdot,t) \leq \frac{2R^{(0)}}{q_N},\ \forall\, t \geq t_2$$

and

$$C(\cdot,t) \leq 2\tilde{C}^*(\cdot),\ C_S(\cdot,t) \leq 2\tilde{C}_S^*(\cdot); Z(\cdot,t) \leq \frac{2\hat{V}^*(\cdot)}{q_Z},\ Z_S(\cdot,t) \leq \frac{2\hat{V}_S^*(\cdot)}{q_Z},\ \forall\, t \geq t_2,$$

where $(\tilde{C}^*(x), \tilde{C}_S^*(x))$ and $(\hat{V}^*(x), \hat{V}_S^*(x))$ are the positive steady-state solution of the system (4.11) and (4.17), respectively.

Let

$$\mathcal{D} = \Bigg\{(R,N,C,Z,R_S,N_S,C_S,Z_S) \in \mathbb{X}^+ : R(\cdot),\ R_S(\cdot) \leq 2R^{(0)}; N(\cdot),\ N_S(\cdot) \leq \frac{2R^{(0)}}{q_N};$$
$$C(\cdot) \leq 2\tilde{C}^*(\cdot);\ C_S(\cdot) \leq 2\tilde{C}_S^*(\cdot);\ Z(\cdot) \leq \frac{2\hat{V}^*(\cdot)}{q_Z};\ Z_S(\cdot) \leq \frac{2\hat{V}_S^*(\cdot)}{q_Z}\Bigg\}.$$

Define the solution semiflow $\Psi(t) : \mathbb{X}^+ \to \mathbb{X}^+$ of (4.1)-(4.3) by

$$\Psi(t)\phi = u(\cdot,t,\phi), \quad \forall t \geq 0,\ \phi \in \mathbb{X}^+,$$

where $u(x,t,\phi)$ is the solution of (4.1)-(4.3) with $u(\cdot,0,\phi) = \phi \in \mathbb{X}^+$. Then

$$\Psi(t)(\phi) \in \mathcal{D},\ \forall\, t \geq t_2,\ \phi \in \mathbb{X}^+.$$

Moreover, it is easy to see that $(2R^{(0)}, 2R^{(0)})$, $(2\tilde{C}^*(x), 2\tilde{C}_S^*(x))$ and $(2\hat{V}^*(x), 2\hat{V}_S^*(x))$ are upper solutions of systems (3.9), (4.11) and (4.17), respectively. Those facts, together with the comparison arguments, imply that $\mathcal{D}$ is positively invariant for $\Psi(t)$ in the sense that

$$\Psi(t)(\phi) \in \mathcal{D},\ \forall\, t \geq 0,\ \phi \in \mathcal{D}.$$

With the assumption (3.17), it is easy to see that whenever $\alpha\frac{A}{A_S}$ is sufficiently large, there exists a constant $r > 0$ such that

$$\mathbf{v}^T\mathcal{M}(\phi(x))\mathbf{v} \leq -r\mathbf{v}^T\mathbf{v}, \quad \forall\phi \in \mathcal{D},\, x \in [0,L],\, \mathbf{v} \in \mathbb{R}^4, \tag{4.18}$$

where $\mathcal{M}(R,N,C,Z,R_S,N_S,C_S,Z_S) =$

$$\begin{pmatrix} m_{11} & m_{12} & 0 & 0 \\ f'(R_S)N_S & m_{22} & m_{23} & m_{24} \\ \epsilon\frac{\partial p(R_S,N_S)}{\partial R_S} & \epsilon\frac{\partial p(R_S,N_S)}{\partial N_S} & -\alpha\frac{A}{A_S} - k & 0 \\ 0 & m_{42} & m_{43} & m_{44} \end{pmatrix},$$

and

$$
\begin{aligned}
m_{11} &= -\alpha \frac{A}{A_S} - q_N f'(R_S) N_S,\ m_{12} = -q_N [f(R_S) - m], \\
m_{22} &= -\alpha \frac{A}{A_S} + [f(R_S) - m] - q_Z g'(N_S) e^{-\eta C_S} Z_S, \\
m_{23} &= \eta q_Z g(N_S) e^{-\eta C_S} Z_S,\ m_{42} = g'(N_S) e^{-\eta C_S} Z_S, \\
m_{43} &= -\eta g(N_S) e^{-\eta C_S} Z_S,\ m_{24} = -q_Z g(N_S) e^{-\eta C_S}, \\
m_{44} &= -\alpha \frac{A}{A_S} + g(N_S) e^{-\eta C_S} - m_Z.
\end{aligned}
$$

Since the last four equations in system (4.1)-(4.3) have no diffusion terms, its solution map $\Psi(t)$ is not compact. In order to overcome this problem, we use the Kuratowski measure of noncompactness (see [5]), κ, which is defined by

$$
\kappa(B) := \inf\{r : B \text{ has a finite cover of diameter} < r\}, \tag{4.19}
$$

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 [11, Lemma 4.1], we have the following result.

Lemma 4.3. *Let* (3.17) *and* (4.18) *hold. Then the solution semiflow* $\Psi(t)$ *is* κ-*contracting in the sense that* $\lim_{t\to\infty} \kappa(\Psi(t)(B)) = 0$ *for any bounded set* $B \subset \mathbb{X}^+$.

Theorem 4.1. *Let* (3.17) *and* (4.18) *hold. Then* $\Psi(t)$ *admits a global attractor on* $\mathbb{X}^+$.

Proof. By Lemma 4.3, it follows that $\Psi(t)$ is κ-contracting on $\mathbb{X}^+$. By Lemma 4.2, it follows that $\Psi(t)$ is point dissipative on $\mathbb{X}^+$, and forward orbits of bounded subsets of $\mathbb{X}^+$ for $\Psi(t)$ are bounded. By [22, Theorem 2.6], $\Psi(t)$ has a global attractor that attracts each bounded set in $\mathbb{X}^+$. $\square$

4.2 The basic reproduction ratio for zooplankton

It is easy to see that the system (4.1)-(4.3) has the following possible equilibrium points: $E_0 := (R^{(0)}, 0, 0, 0, R^{(0)}, 0, 0, 0)$ and

$$
E_1 := (R^*(x), N^*(x), C^*(x), 0, R_S^*(x), N_S^*(x), C_S^*(x), 0) \text{ provided that } \lambda^0 > 0,
$$

where λ^0 is the principal eigenvalue of the eigenvalue problem (3.16) and

$$
(R^*(x), N^*(x), C^*(x), R_S^*(x), N_S^*(x), C_S^*(x))
$$

is the unique positive steady-state solution of (3.1)-(3.3).

Linearizing system (4.1)-(4.3) at the equilibrium E_1, we get the following system for the zooplankton compartments (Z, Z_S):

$$\begin{cases} \frac{\partial Z}{\partial t} = \delta \frac{\partial^2 Z}{\partial x^2} - \nu \frac{\partial Z}{\partial x} + \alpha(Z_S - Z) \\ \qquad\qquad\qquad\qquad +[g(N^*)e^{-\eta C^*} - m_Z]Z, \ 0 < x < L, \ t > 0, \\ \frac{\partial Z_S}{\partial t} = -\alpha \frac{A}{A_S}(Z_S - Z) + [g(N_S^*)e^{-\eta C_S^*} - m_Z]Z_S, \ 0 < x < L, \ t > 0, \\ \nu Z(0,t) - \delta \frac{\partial Z}{\partial x}(0,t) = 0, \ \frac{\partial Z}{\partial x}(L,t) = 0, \ t > 0, \\ Z(x,0) = Z^0(x) \geq 0, \ Z_S(x,0) = Z_S^0(x) \geq 0, \ 0 < x < L. \end{cases} \tag{4.20}$$

Let $\mathbf{T}(t)$ be the solution semigroup generated by (4.20) on $C([0,L], \mathbb{R}^2)$. It is easy to see that $\mathbf{T}(t)$ is a positive C_0-semigroup on $C([0,L], \mathbb{R}^2)$, and its generator $\mathbf{B}$ can be written as

$$\mathbf{B} = \begin{pmatrix} \delta \frac{\partial^2}{\partial x^2} - \nu \frac{\partial}{\partial x} - \alpha + \beta_1(x) & \alpha \\ \alpha \frac{A}{A_S} & -\alpha \frac{A}{A_S} + \beta_2(x) \end{pmatrix}$$

with $\beta_1(x) := g(N^*(x))e^{-\eta C^*(x)} - m_Z$ and $\beta_2(x) := g(N_S^*(x))e^{-\eta C_S^*(x)} - m_Z$. Further, $\mathbf{B}$ is a closed and resolvent positive operator (see, e.g., [33, Theorem 3.12]). The following eigenvalue problem is associated with (4.20):

$$\begin{cases} \mu\psi(x) = \delta\psi'' - \nu\psi' + \alpha(\psi_S - \psi) \\ \qquad\qquad\qquad\qquad +[g(N^*)e^{-\eta C^*} - m_Z]\psi(x), \ 0 < x < L, \\ \mu\psi_S(x) = -\alpha \frac{A}{A_S}(\psi_S - \psi) + [g(N_S^*)e^{-\eta C_S^*} - m_Z]\psi_S, \ 0 < x < L, \\ \nu\psi(0) - \delta\psi'(0) = 0, \ \psi'(L) = 0. \end{cases} \tag{4.21}$$

Let

$$\alpha \frac{A}{A_S} + m_Z > g(N_S^*(x))e^{-\eta C_S^*(x)}, \ \forall \, x \in [0, L]. \tag{4.22}$$

By a generalized Krein-Rutman Theorem (see, e.g., [23]), we have the following result.

Lemma 4.4. *Let $\mu^* := s(\mathbf{B})$ be the spectral bound of $\mathbf{B}$ and the condition (4.22) be true. If $\mu^* \geq 0$, then μ^* is the principal eigenvalue of the eigenvalue problem (4.21) with a strongly positive eigenfunction.*

Proof. By (4.22), it follows that

$$\alpha \frac{A}{A_S} + m_Z - g(N_S^*(x))e^{-\eta C_S^*(x)} \geq a, \ \forall \, x \in [0, L], \text{ and } a \text{ is a positive number.}$$

By similar arguments to those in [11, Lemma 3.3], we can show that $\mathbf{T}(t)$ is an κ-contraction on $C([0,L], \mathbb{R}^2)$ with a contracting function e^{-at} in the following sense:

$$\kappa(\mathbf{T}(t)\mathcal{C}) \leq e^{-at}\kappa(\mathcal{C}), \text{ for any bounded set } \mathcal{C} \text{ in } C([0,L], \mathbb{R}^2) \text{ with } \kappa(\mathcal{C}) > 0, \ \forall \, t > 0.$$

This implies that the essential spectral radius $r_e(\mathbf{T}(t))$ of $\mathbf{T}(t)$ satisfies

$$r_e(\mathbf{T}(t)) \leq e^{-at} < 1, \ \forall \ t > 0.$$

On the other hand, the spectral radius $r(\mathbf{T}(t))$ of $\mathbf{T}(t)$ satisfies

$$r(\mathbf{T}(t)) = e^{s(\mathbf{B})t} \geq 1, \ \forall \ t > 0.$$

This implies that $r_e(\mathbf{T}(t)) < r(\mathbf{T}(t))$, $\forall \ t > 0$. Since $\mathbf{T}(t)$ is a strongly positive and bounded operator on $C([0, L], \mathbb{R}^2)$, our conclusion follows from a generalized Krein-Rutman Theorem (see, e.g., [23]). □

We also consider the following perturbed system of (4.20):

$$\begin{cases} \frac{\partial Z}{\partial t} = \delta \frac{\partial^2 Z}{\partial x^2} - \nu \frac{\partial Z}{\partial x} + \alpha(Z_S - Z) \\ \qquad\qquad\qquad\qquad +[g(N^*)e^{-\eta C^*} - m_Z - \varrho]Z, \ 0 < x < L, \ t > 0, \\ \frac{\partial Z_S}{\partial t} = -\alpha \frac{A}{A_S}(Z_S - Z) + [g(N_S^*)e^{-\eta C_S^*} - m_Z - \varrho]Z_S, \ 0 < x < L, \ t > 0, \\ \nu Z(0, t) - \delta \frac{\partial Z}{\partial x}(0, t) = 0, \ \frac{\partial Z}{\partial x}(L, t) = 0, \ t > 0, \\ Z(x, 0) = Z^0(x) \geq 0, \ Z_S(x, 0) = Z_S^0(x) \geq 0, \ 0 < x < L, \end{cases} \tag{4.23}$$

and its associated eigenvalue problem:

$$\begin{cases} \mu\psi(x) = \delta\psi'' - \nu\psi' + \alpha(\psi_S - \psi) \\ \qquad\qquad\qquad\qquad +[g(N^*)e^{-\eta C^*} - m_Z - \varrho]\psi(x), \ 0 < x < L, \\ \mu\psi_S(x) = -\alpha \frac{A}{A_S}(\psi_S - \psi) + [g(N_S^*)e^{-\eta C_S^*} - m_Z - \varrho]\psi_S, \ 0 < x < L, \\ \nu\psi(0) - \delta\psi'(0) = 0, \ \psi'(L) = 0. \end{cases} \tag{4.24}$$

Lemma 4.5. *Let $\mu^* := s(\mathbf{B})$ be the spectral bound of $\mathbf{B}$ and the condition* (4.22) *be true. If $\mu^* > 0$, then there is a small $\tilde{\varrho} > 0$ such that the eigenvalue problem* (4.24) *has the principal eigenvalue $\mu_\varrho^* > 0$ with a strongly positive eigenfunction for all $0 < \varrho < \tilde{\varrho}$.*

Proof. Let $\mathbf{T}_\varrho(t)$ be the strongly positive C_0-semigroup generated by (4.23) on $C([0, L], \mathbb{R}^2)$. Fix $t_0 > 0$ and then it is easy to see that there is a $\tilde{\varrho}_1 > 0$ such that $\mathbf{T}_\varrho(t_0)$ is an κ-contraction on $C([0, L], \mathbb{R}^2)$, $\forall \ 0 < \varrho < \tilde{\varrho}_1$. This implies that the essential spectral radius $r_e(\mathbf{T}_\varrho(t_0))$ of $\mathbf{T}_\varrho(t_0)$ satisfies

$$r_e(\mathbf{T}_\varrho(t_0)) < 1, \ \forall \ 0 < \varrho < \tilde{\varrho}_1.$$

On the other hand, it follows from the assumption $\mu^* > 0$ and the proof in Lemma 4.4 that the spectral radius $r(\mathbf{T}(t_0))$ of $\mathbf{T}(t_0)$ satisfies

$$r(\mathbf{T}(t_0)) > 1.$$

Thus, there is a $\tilde{\varrho}_2 > 0$ such that $r(\mathbf{T}_\varrho(t_0)) > 1\ \forall\ 0 < \varrho < \tilde{\varrho}_2$, that is, the spectral radius of $\mathbf{T}_\varrho(t_0)$ is still greater than one under small perturbations (see, e.g., [14]). Let $\tilde{\varrho} := \min\{\tilde{\varrho}_1, \tilde{\varrho}_2\}$. Then

$$r_e(\mathbf{T}_\varrho(t_0)) < 1 < r(\mathbf{T}_\varrho(t_0)),\ \forall\ 0 < \varrho < \tilde{\varrho}.$$

It then follows from a generalized Krein-Rutman Theorem (see, e.g., [23]) that the perturbed eigenvalue problem (4.24) has a positive principal eigenvalue with positive eigenfunction. □

In the following, we shall adopt the ideas in [34, 35] to define the basic reproduction ratio for zooplankton. Let $\mathbb{S}(t) : C([0, L], \mathbb{R}^2) \to C([0, L], \mathbb{R}^2)$ be the C_0-semigroup generated by the following system

$$\begin{cases} \frac{\partial Z}{\partial t} = \delta \frac{\partial^2 Z}{\partial x^2} - \nu \frac{\partial Z}{\partial x} + \alpha(Z_S - Z) - m_Z Z,\ 0 < x < L,\ t > 0, \\ \frac{\partial Z_S}{\partial t} = -\alpha \frac{A}{A_S}(Z_S - Z) - m_Z Z_S,\ 0 < x < L,\ t > 0, \\ \nu Z(0, t) - \delta \frac{\partial Z}{\partial x}(0, t) = 0,\ \frac{\partial Z}{\partial x}(L, t) = 0,\ t > 0. \end{cases} \tag{4.25}$$

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

In order to define the basic reproduction ratio for zooplankton, we assume that both zooplankton individuals in the flow and storage zones are near the trivial steady-state solution $(0, 0)$ for (4.20), and introduce fertile individuals at time $t = 0$, where the distribution of initial zooplankton individuals in the flow and storage zones is described by $\varphi := (\varphi_4, \varphi_8) \in C([0, L], \mathbb{R}^2)$. Thus, it is easy to see that $\mathbb{S}(t)\varphi$ represents the distribution of fertile zooplankton individuals at time $t \geq 0$.

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

$$\mathbb{L}(\varphi)(\cdot) = \int_0^\infty \begin{pmatrix} g(N_S^*(\cdot))e^{-\eta C_S^*(\cdot)} & 0 \\ 0 & g(N_S^*(\cdot))e^{-\eta C_S^*(\cdot)} \end{pmatrix} (\mathbb{S}(t)\varphi)(\cdot)dt. \tag{4.26}$$

It then follows that $\mathbb{L}(\varphi)(\cdot)$ represents the distribution of the total new population generated by initial fertile zooplankton individuals $\varphi := (\varphi_4, \varphi_8)$, and hence, $\mathbb{L}$ is the next generation operator. We define the spectral radius of $\mathbb{L}$ the basic reproduction ratio of zooplankton compartments for system (4.1)-(4.3), that is,

$$\mathcal{R}_0^z := r(\mathbb{L}). \tag{4.27}$$

By [35, Theorem 3.1 (i) and Remark 3.1], we have the following observation.

Lemma 4.6. $\mathcal{R}_0^z - 1$ *and* μ^* *have the same sign.*

4.3 The global dynamics

The following result will play an important role in establishing the uniform persistence of solutions of (4.1)-(4.3).

Lemma 4.7. *Suppose $u(x,t,\phi)$ is the solution of system (4.1)-(4.3) with $u(\cdot,0,\phi) = \phi \in \mathbb{X}^+$.*

(i) *If there exists some $t_0 \geq 0$ such that $N(x,t_0,\phi) \not\equiv 0$ and $N_S(x,t_0,\phi) \geq 0$, then $N(x,t,\phi) > 0,\ N_S(x,t,\phi) > 0,\ \forall\ x \in [0,L],\ t > t_0$;*

(ii) *If there exists some $t_0 \geq 0$ such that $C(x,t_0,\phi) \not\equiv 0$ and $C_S(x,t_0,\phi) \geq 0$, then $C(x,t,\phi) > 0,\ C_S(x,t,\phi) > 0,\ \forall\ x \in [0,L],\ t > t_0$;*

(iii) *If there exists some $t_0 \geq 0$ such that $Z(x,t_0,\phi) \not\equiv 0$ and $Z_S(x,t_0,\phi) \geq 0$, then $Z(x,t,\phi) > 0,\ Z_S(x,t,\phi) > 0,\ \forall\ x \in [0,L],\ t > t_0$;*

(iv) *For any $\phi \in \mathbb{X}^+$, we have $R(x,t,\phi) > 0,\ R_S(x,t,\phi) > 0,\ \forall\ x \in [0,L],\ t > 0$.*

Proof. It is easy to see that N satisfies the following inequalities:

$$\begin{cases} \frac{\partial N}{\partial t} \geq \delta \frac{\partial^2 N}{\partial x^2} - \nu \frac{\partial N}{\partial x} \\ \qquad\qquad -[\alpha + m + q_Z e^{-\eta C} Z \int_0^1 g'(\theta N) d\theta] N,\ 0 < x < L,\ t > 0, \\ \nu N(0,t) - \delta \frac{\partial N}{\partial x}(0,t) = 0,\ \frac{\partial N}{\partial x}(L,t) = 0,\ t > 0. \end{cases} \tag{4.28}$$

By the standard comparison arguments, it follows that $N(\cdot,t,\phi) > 0,\ \forall\ t > t_0$.

From the N_S equation of (4.1), we see that

$$\frac{\partial N_S}{\partial t} = -a(\cdot,t) N_S + b(\cdot,t),$$

where $a(\cdot,t) := \alpha \frac{A}{A_S} + m + q_Z e^{-\eta C_S} Z_S \int_0^1 g'(\theta N_S) d\theta$; $b(\cdot,t) := \alpha \frac{A}{A_S} N(\cdot,t) + f(R_S) N_S(\cdot,t)$. This implies that

$$N_S(\cdot,t) = e^{-\int_{t_0}^t a(\cdot,s_1) ds_1} \left[\int_{t_0}^t e^{\int_{t_0}^{s_2} a(\cdot,s_1) ds_1} b(\cdot,s_2) ds_2 + N_S(\cdot,t_0) \right],\ \forall\ t \geq t_0.$$

Since $N(\cdot,t,\phi) > 0,\ N_S(\cdot,t,\phi) \geq 0,\ \forall\ t > t_0$, it follows that $b(\cdot,t) > 0,\ \forall\ t > t_0$, and hence, $N_S(\cdot,t) > 0,\ \forall\ t > t_0$. This proves Part(i). Similarly, Part (ii)-(iii) can be proved.

It is easy to see that R satisfies the following inequalities:

$$\begin{cases} \frac{\partial R}{\partial t} \geq \delta \frac{\partial^2 R}{\partial x^2} - \nu \frac{\partial R}{\partial x} - [\alpha + q_N N \int_0^1 f'(\theta R) d\theta] R,\ 0 < x < L,\ t > 0, \\ \nu R(0,t) - \delta \frac{\partial R}{\partial x}(0,t) = \nu R^{(0)},\ \frac{\partial R}{\partial x}(L,t) = 0,\ t > 0. \end{cases} \tag{4.29}$$

The standard comparison arguments implies that $R(x,t) > 0,\ \forall\, 0 \le x \le L,\ t > 0$.

Suppose that $R_S(\tilde{x}, \tilde{t}) = 0$, for some $(\tilde{x}, \tilde{t}) \in [0, L] \times (0, \infty)$, that is, $R_S(\tilde{x}, t)$ attains its minimum at a point $t = \tilde{t} \in (0, \infty)$. This implies that

$$0 = \frac{\partial R_S}{\partial t}(\tilde{x}, \tilde{t}) = -\alpha \frac{A}{A_S}(R_S(\tilde{x}, \tilde{t}) - R(\tilde{x}, \tilde{t})) - q_N[f(R_S(\tilde{x}, \tilde{t})) - m]N_S(\tilde{x}, \tilde{t}),$$

and hence,

$$0 = \frac{\partial R_S}{\partial t}(\tilde{x}, \tilde{t}) = \alpha \frac{A}{A_S} R(\tilde{x}, \tilde{t}) + q_N m N_S(\tilde{x}, \tilde{t}) > 0,$$

which is a contradiction. Thus, $R_S(x,t) > 0$ for all $0 \le x \le L$ and $t > 0$. $\square$

Now we are in a position to state the main result of this section, whose proof is given in the Appendix.

Theorem 4.2. *Assume* (3.17), (4.18) *and* (4.22) *are true. Let*

$$\mathbb{X}_0 := \{(R, N, C, Z, R_S, N_S, C_S, Z_S) \in \mathbb{X}^+ : Z(\cdot) \not\equiv 0 \text{ and } Z_S(\cdot) \not\equiv 0\}$$

and

$$\partial\mathbb{X}_0 := \mathbb{X}^+ \backslash \mathbb{X}_0.$$

Then the following statements hold:

(i) *If* $\mathcal{R}_0 < 1$, *then the trivial solution* E_0 *is globally attractive in* $\mathbb{X}^+$ *for* (4.1)-(4.3).

(ii) *If* $\mathcal{R}_0 > 1$ *and* $\mathcal{R}_0^z > 1$, *then system* (4.1)-(4.3) *admits at least one (componentwise) positive equilibrium*

$$(\hat{R}(\cdot), \hat{N}(\cdot), \hat{C}(\cdot), \hat{Z}(\cdot), \hat{R}_S(\cdot), \hat{N}_S(\cdot), \hat{C}_S(\cdot), \hat{Z}_S(\cdot)),$$

and there is a positive constant $\zeta > 0$ *such that every solution*

$$(R(\cdot,t), N(\cdot,t), C(\cdot,t), Z(\cdot,t), R_S(\cdot,t), N_S(\cdot,t), C_S(\cdot,t), Z_S(\cdot,t))$$

of (4.1)-(4.3) *with*

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

satisfies $\liminf_{t\to\infty} Z(\cdot,t) \ge \zeta$ *and* $\liminf_{t\to\infty} Z_S(\cdot,t) \ge \zeta$.

To finish this section, we remark that it remains an open problem whether E_1 is globally attractive in $\mathbb{X}^+$ for system (4.1)-(4.3) in the case where $\mathcal{R}_0 > 1$ and $\mathcal{R}_0^z < 1$.

5 Discussion

In this paper, we first analyze a model that describes the longitudinal distribution of algal abundance and toxicity produced by algae, that contains little limiting nutrient in flowing-water habitats. In such a habitat, a main channel with advective transport and dispersion was coupled to a hydraulic storage zone, representing an ensemble of fringing coves on the shoreline. We then further examined a model with zooplankton that eat the algae and are inhibited by the toxin. Due to the lack of diffusion terms in the equations for hydraulic storage zone, the solution maps are not compact. So we need to address the existence of the principal eigenvalue for the associated eigenvalue problem and the existence of global attractors for full systems. Therefore, the results of models presented in this paper are based on the assumptions (3.17), (4.18) and (4.22). Those assumptions hold if the exchange rate between the main channel and the storage zone is large (i.e., α is large) or if the cross section of the main channel is large compared to that of the storage zone (i.e., the ratio $\frac{A}{A_S}$ is large). Such biological parameters can be found in [8].

The basic reproduction number, which is defined as the expected number of secondary infections generated by a single infected individual introduced into a completely susceptible population, is one of the important quantities in epidemiology. It can be used to predict persistence or extinction of a disease. With the next generation operator approach, Mckenzie et al. [19] introduced the net reproductive rate for an advection-diffusion-reaction model of a stream population. The net reproductive rate is defined as the number of offspring produced by a single individual over its lifetime, assuming that the individual is subject to a particular spatial configuration in the river. This spatial configuration is associated with the principal eigenfunction of a next generation operator. It can be interpreted as the spatial configuration associated with the maximum long-term intergenerational growth of the population [19].

In this work, we use the theory of R_0 developed in [35, section 3] to show that the single algae growth system (3.1)-(3.3) admits a net reproductive rate $\mathcal{R}_0$, and this $\mathcal{R}_0$ is a threshold value for the persistence and extinction of the algal population. More precisely, the algae will grow if $\mathcal{R}_0 > 1$, while the algae will become extinct if $\mathcal{R}_0 < 1$ (Theorem 3.2). We also define the net reproductive rate $\mathcal{R}_0^z$ for the zooplankton-algae food chain system (4.1)-(4.3) and prove that if $\mathcal{R}_0 < 1$, then the algae and zooplankton will become extinct (Theorem 4.2 (i)); if $\mathcal{R}_0 > 1$ and $\mathcal{R}_0^z > 1$, then the algae and zooplankton will persist (Theorem 4.2 (ii)). For the case where $\mathcal{R}_0 > 1$ and $\mathcal{R}_0^z < 1$, we conjecture that the algae will persist and zooplankton will become extinct.

In [8], the development of longitudinal patterns at steady-state generally depend on flow conditions, as summarized by the dimensionless Péclet number

$$\mathrm{Pe} = L\nu/\delta.$$

The algal populations were predicted to be extinct by higher values of Pe (i.e. rapid flow). Thus, conditions for persistence of the algal population depend on the flow characteristics (advection and diffusivity). It is worth pointing out that one can use the same arguments as in [9, Section 3] to show that the algal population will be washed out as $\nu \to \infty$, while the algal population will always persist as $\nu \to 0$ for the system (3.1)-(3.3). This is consistent with the above prediction. As mentioned in [8], the model (3.1)-(3.3) ignores vertical variations and light limitation. In reality, flow interacts with stratification to affect dynamics of algal blooms in deeper riverine systems. On the other hand, to incorporate the influence of seasonal temperature variations on non-steady dynamics, the algal maximal growth rate should be a time-periodic function (see equations (9)-(10) in [8]). We leave these interesting problems for future investigation.

Appendix

In this appendix, we provide the proofs of Theorems 3.1 and 4.2.

Proof of Theorem 3.1: Since system (3.25)-(3.27) and (3.28)-(3.30) are equivalent, it suffices to study the system (3.28)-(3.30). Let $\tilde{\Phi}_1(t) : \Sigma \to \Sigma$ be the solution semiflow associated with (3.28)-(3.30), and $\tilde{\omega}_1(W^0, W_S^0, N^0, N_S^0)$ be the omega-limit set of the orbit of $\tilde{\Phi}_1(t)$ with initial values $(W^0, W_S^0, N^0, N_S^0) \in \Sigma$. From the first two equations of (3.28), it follows that

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

Thus, there exists a set $\mathcal{I}_1 \subset C([0, L], \mathbb{R}^2_+)$ such that

$$\tilde{\omega}_1(W^0, W_S^0, N^0, N_S^0) = \{(R^{(0)}, R^{(0)})\} \times \mathcal{I}_1.$$

For any given $(N^0, N_S^0) \in \mathcal{I}_1$, we have

$$(R^{(0)}, R^{(0)}, N^0, N_S^0) \in \tilde{\omega}_1(W^0, W_S^0, N^0, N_S^0) \subset \Sigma.$$

By the definition of Σ, it follows that $(N^0, N_S^0) \in Y^+$. Thus, $\mathcal{I}_1 \subset Y^+$, where Y^+ is defined in (3.3).

By [36, Lemma 1.2.1′], it follows that $\tilde{\omega}_1(W^0, W_S^0, N^0, N_S^0)$ is a compact, invariant and internal chain transitive set for $\tilde{\Phi}_1(t)$. Moreover, if $(N^0, N_S^0) \in C([0, L], \mathbb{R}^2_+)$ with $(R^{(0)}, R^{(0)}, N^0, N_S^0) \in \tilde{\omega}_1(W^0, W_S^0, N^0, N_S^0)$, there holds

$$\tilde{\Phi}_1(t) \mid_{\tilde{\omega}_1(W^0, W_S^0, N^0, N_S^0)} (R^{(0)}, R^{(0)}, N^0, N_S^0) = (R^{(0)}, R^{(0)}, \Phi_1(t)(N^0, N_S^0)),$$

where $\Phi_1(t) : Y^+ \to Y^+$ is the solution semiflow associated with (3.21)-(3.23). It then follows that $\mathcal{I}_1$ is a compact, invariant and internal chain transitive set for $\Phi_1(t) : Y^+ \to Y^+$.

In the case where $\mathcal{R}_0 \leq 1$, we have $\lambda^0 \leq 0$ by Lemma 3.4. It then follows from Lemma 3.6 (i) that (3.21)-(3.23) has a globally attractive solution $(0, 0)$ in Y^+. This implies that the unique solution $(0, 0)$ is an isolated invariant set in Y^+ and no cycle connecting $(0, 0)$ to itself in Y^+. Since $\mathcal{I}_1$ is a compact, invariant and internal chain transitive set for $\Phi_1(t) : Y^+ \to Y^+$, it follows from a convergence theorem (see, e.g., [36, Theorem 1.2.2]) that $\mathcal{I}_1$ is a steady-state solution of $\Phi_1(t)$. That is, $\mathcal{I}_1 = \{(0, 0)\}$, and hence,

$$\tilde{\omega}_1(W^0, W_S^0, N^0, N_S^0) = \{(R^{(0)}, R^{(0)})\} \times \mathcal{I}_1 = \{(R^{(0)}, R^{(0)}, 0, 0)\}.$$

This implies that $(R^{(0)}, R^{(0)}, 0, 0)$ is globally attractive for $\tilde{\Phi}_1(t)$ in Σ. In view of (3.8), statement (i) holds true.

In the case where $\mathcal{R}_0 > 1$, we have $\lambda^0 > 0$ by Lemma 3.4. It then follows from Lemma 3.6 (ii) that (3.21)-(3.23) has a globally attractive solution $(N^*(\cdot), N_S^*(\cdot))$ in Y_0^+. Note that $(0, 0)$ is also a steady-state solution of (3.21)-(3.23). This implies that the possible fixed points $(0, 0)$ and $(N^*(\cdot), N_S^*(\cdot))$ are isolated invariant sets in Y^+ and no subset of $\{(0, 0)\} \cup \{(N^*(\cdot), N_S^*(\cdot))\}$ forms a cycle in Y^+. Since $\mathcal{I}_1$ is a compact, invariant and internal chain transitive set for $\Phi_1(t) : Y^+ \to Y^+$, it follows from a convergence theorem (see, e.g., [36, Theorem 1.2.2]) that either $\mathcal{I}_1 = \{(0, 0)\}$ or $\mathcal{I}_1 = \{(N^*(\cdot), N_S^*(\cdot))\}$.

Suppose, by contradiction, that $\mathcal{I}_1 = \{(0, 0)\}$. This implies that

$$\tilde{\omega}_1(W^0, W_S^0, N^0, N_S^0) = \{(R^{(0)}, R^{(0)}, 0, 0)\}.$$

Thus, we have

$$\lim_{t \to \infty} \tilde{\Phi}_1(t)(W^0, W_S^0, N^0, N_S^0) = (R^{(0)}, R^{(0)}, 0, 0).$$

Since $\lambda^0 > 0$ and (3.17), it follows that there is a $\sigma_0 > 0$ such that

$$\alpha \frac{A}{A_S} + m + \sigma_0 > f(R^{(0)}) \text{ and } \lambda_{\sigma_0}^0 > 0,$$

where $\lambda_{\sigma_0}^0$ is the principal eigenvalue with the eigenvector $(\phi^{\sigma_0}(\cdot), \phi_S^{\sigma_0}(\cdot)) \gg 0$ of the following eigenvalue problem

$$\begin{cases} \lambda\phi(x) = \delta\phi''(x) - \nu\phi'(x) + \alpha(\phi_S(x) - \phi(x)) + [f(R^{(0)}) - m - \sigma_0]\phi(x), \ 0 < x < L, \\ \lambda\phi_S(x) = -\alpha\frac{A}{A_S}(\phi_S(x) - \phi(x)) + [f(R^{(0)}) - m - \sigma_0]\phi_S(x), \ 0 < x < L, \\ \nu\phi(0) - \delta\phi'(0) = \phi'(L) = 0. \end{cases} \tag{5.1}$$

There also exists $t_0 = t_0(\sigma_0) > 0$ such that

$$f(W(x,t) - q_N N(x,t)) > f(R^{(0)}) - \sigma_0 \text{ and } f(W_S(x,t) - q_N N_S(x,t)) > f(R^{(0)}) - \sigma_0,$$

for all $x \in [0, L]$ and $t \geq t_0$.

From the last two equations of (3.28), we see that

$$\begin{cases} \frac{\partial N}{\partial t} \geq \delta \frac{\partial^2 N}{\partial x^2} - \nu \frac{\partial N}{\partial x} + \alpha(N_S - N) + [f(R^{(0)}) - m - \sigma_0]N, \ t \geq t_0 \\ \frac{\partial N_S}{\partial t} \geq -\alpha \frac{A}{A_S}(N_S - N) + [f(R^{(0)}) - m - \sigma_0]N_S, \ t \geq t_0. \end{cases}$$

Since $(W^0, W_S^0, N^0, N_S^0) \in \Sigma_0$, it follows that $(N^0, N_S^0) \neq (0, 0)$, and hence,

$$(N(\cdot, t), N_S(\cdot, t)) \gg 0, \ \forall t > 0.$$

In particular, $N(\cdot, t_0) \gg 0$ and $N_S(\cdot, t_0) \gg 0$ in Σ. Thus, there exists $\xi := \xi(\sigma_0) > 0$ such that $N(\cdot, t_0) \geq \xi \phi^{\sigma_0}(\cdot)$ and $N_{S,2}(\cdot, t_0) \geq \xi \phi_S^{\sigma_0}(\cdot)$. By the comparison theorem, it follows that

$$N(\cdot, t) \geq \xi e^{\lambda_{\sigma_0}^0 (t - t_0)} \phi^{\sigma_0}(\cdot) \text{ and } N_S(\cdot, t) \geq \xi e^{\lambda_{\sigma_0}^0 (t - t_0)} \phi_S^{\sigma_0}(\cdot), \ \forall \ t \geq t_0.$$

Since $\lambda_{\sigma_0}^0 > 0$, it follows that

$$N(\cdot, t), \ N_S(\cdot, t) \to \infty \text{ as } t \to \infty,$$

which is a contradiction. Thus, we have $\mathcal{I}_1 = \{(N^*(\cdot), N_S^*(\cdot))\}$, and hence,

$$\tilde{\omega}_1(W^0, W_S^0, N^0, N_S^0) = \{(R^{(0)}, R^{(0)})\} \times \mathcal{I}_1 = \{(R^{(0)}, R^{(0)}, N^*(\cdot), N_S^*(\cdot))\}.$$

This implies that $(R^{(0)}, R^{(0)}, N^*(\cdot), N_S^*(\cdot))$ is globally attractive for $\tilde{\Phi}_1(t)$ in Σ_0. By (3.8), letting $R^*(\cdot) = R^{(0)} - q_N N^*(\cdot)$, $R_S^*(\cdot) = R^{(0)} - q_N N_S^*(\cdot)$, we then complete the proof of statement (ii).

Proof of Theorem 4.2: Assume $\mathcal{R}_0 < 1$. It then follows from Lemma 3.4 that $\lambda^0 < 0$. Since $\lambda^0 < 0$, there exists a sufficiently small positive number ρ_0 such that $\alpha \frac{A}{A_S} + m - \rho_0 > f(R^{(0)})$ and $\lambda_{\rho_0}^0 < 0$, where $\lambda_{\rho_0}^0$ is the principal eigenvalue of the following eigenvalue problem

$$\begin{cases} \lambda_{\rho_0}^0 \hat{\phi}(x) = \delta \hat{\phi}''(x) - \nu \hat{\phi}'(x) + \alpha(\hat{\phi}_S(x) - \hat{\phi}(x)) \\ \qquad\qquad + [f(R^{(0)}) - m + \rho_0]\hat{\phi}(x), \ 0 < x < L, \\ \lambda_{\rho_0}^0 \hat{\phi}_S(x) = -\alpha \frac{A}{A_s}(\hat{\phi}_S(x) - \hat{\phi}(x)) \\ \qquad\qquad + [f(R^{(0)}) - m + \rho_0]\hat{\phi}_S(x), \ 0 < x < L, \\ \nu \hat{\phi}(0) - \delta \hat{\phi}'(0) = \hat{\phi}'(L) = 0, \end{cases} \tag{5.2}$$

with a strongly positive eigenfunction $(\hat{\phi}(\cdot), \hat{\phi}_S(\cdot))$. It is easy to see that

$$\lim_{R\to R^{(0)}} f(R) = f(R^{(0)}) \text{ and } \lim_{R_S\to R^{(0)}} f(R) = f(R^{(0)}).$$

Thus, we can choose $\tilde{\delta}_0 > 0$ such that

$$f(R) < f(R^{(0)}) + \rho_0, \ \forall\ 0 <\mid R - R^{(0)} \mid< \tilde{\delta}_0,$$

and

$$f(R_S) < f(R^{(0)}) + \rho_0, \ \forall\ 0 <\mid R_S - R^{(0)} \mid< \tilde{\delta}_0.$$

From (4.8), it follows that $\lim\limits_{t\to\infty} R(\cdot, t) \le R^{(0)}$, $\lim\limits_{t\to\infty} R_S(\cdot, t) \le R^{(0)}$, and hence there is a $\tilde{t}_0 > 0$ such that $R(\cdot, t) \le R^{(0)} + \frac{1}{2}\tilde{\delta}_0$, $R_S(\cdot, t) \le R^{(0)} + \frac{1}{2}\tilde{\delta}_0$, $\forall\ t \ge \tilde{t}_0$. Therefore,

$$f(R(\cdot, t)) \le f(R^{(0)} + \frac{1}{2}\tilde{\delta}_0) < f(R^{(0)}) + \rho_0, \text{ for any } t \ge \tilde{t}_0,$$

and

$$f(R_S(\cdot, t)) \le f(R^{(0)} + \frac{1}{2}\tilde{\delta}_0) < f(R^{(0)}) + \rho_0, \text{ for any } t \ge \tilde{t}_0.$$

By the N and N_S equations of (4.1), it follows that

$$\begin{cases} \frac{\partial N}{\partial t} \le \delta \frac{\partial^2 N}{\partial x^2} - \nu \frac{\partial N}{\partial x} + \alpha(N_S - N) + [f(R^{(0)}) + \rho_0 - m]N, \ t \ge \tilde{t}_0, \\ \frac{\partial N_S}{\partial t} \le -\alpha \frac{A}{A_S}(N_S - N) + [f(R^{(0)}) + \rho_0 - m]N_S, \ t \ge \tilde{t}_0, \\ \nu N(0, t) - \delta \frac{\partial N}{\partial x}(0, t) = 0, \ \frac{\partial N}{\partial x}(L, t) = 0. \end{cases} \tag{5.3}$$

For any given $\phi \in \mathbb{X}^+$, there exists some $a > 0$ such that

$$(N(x, \tilde{t}_0, \phi), N_S(x, \tilde{t}_0, \phi)) \le a(\hat{\phi}(x), \hat{\phi}_S(x)), \ \forall\ x \in [0, L].$$

Note that the following linear system

$$\begin{cases} \frac{\partial N}{\partial t} = \delta \frac{\partial^2 N}{\partial x^2} - \nu \frac{\partial N}{\partial x} + \alpha(N_S - N) + [f(R^{(0)}) + \rho_0 - m]N, \ t \ge \tilde{t}_0, \\ \frac{\partial N_S}{\partial t} = -\alpha \frac{A}{A_S}(N_S - N) + [f(R^{(0)}) + \rho_0 - m]N_S, \ t \ge \tilde{t}_0, \\ \nu N(0, t) - \delta \frac{\partial N}{\partial x}(0, t) = 0, \ \frac{\partial N}{\partial x}(L, t) = 0, \end{cases} \tag{5.4}$$

admits a solution $ae^{\lambda^0_{\rho_0}(t-\tilde{t}_0)}(\hat{\phi}(x), \hat{\phi}_S(x))$, $\forall\ t \ge \tilde{t}_0$. Then the comparison principle implies that

$$(N(x, t, \phi), N_S(x, t, \phi)) \le ae^{\lambda^0_{\rho_0}(t-\tilde{t}_0)}(\hat{\phi}(x), \hat{\phi}_S(x)), \ \forall\ t \ge \tilde{t}_0,$$

and hence, $\lim_{t\to\infty}(N(x, t, \phi), N_S(x, t, \phi)) = (0, 0)$, uniformly for $x \in [0, L]$. Thus, the equation for (C, C_S) is asymptotic to system (3.10). By the theory for asymptotically autonomous semiflows (see, e.g., [32, Corollary 4.3]), it follows that

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

uniformly for $x \in [0, L]$. Similarly, (Z, Z_S) is asymptotic to the following system:

$$\begin{cases} \frac{\partial Z}{\partial t} = \delta \frac{\partial^2 Z}{\partial x^2} - \nu \frac{\partial Z}{\partial x} + \alpha(Z_S - Z) - m_Z Z, \\ \frac{\partial Z_S}{\partial t} = -\alpha \frac{A}{A_S}(Z_S - Z) - m_Z Z_S, \\ \nu Z(0,t) - \delta \frac{\partial Z}{\partial x}(0,t) = 0, \ \frac{\partial Z}{\partial x}(L,t) = 0. \end{cases} \tag{5.5}$$

Therefore, we have

$$\lim_{t\to\infty}(Z(x,t), Z_S(x,t)) = (0,0)$$

uniformly for $x \in [0, L]$. This implies that the equation for (R, R_S) is asymptotic to system (3.9), and hence,

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

This proves statement (i).

Assume $\mathcal{R}_0 > 1$ and $\mathcal{R}_0^z > 1$. It then follows from Lemmas 3.4 and 4.6 that $\lambda^0 > 0$ and $\mu^* > 0$. Suppose $\Psi(t)P$ is the solution maps generated by (4.1)-(4.3) with initial value P. Set $M_\partial := \{P \in \partial\mathbb{X}_0 : \Psi(t)P \in \partial\mathbb{X}_0, \ \forall\ t \geq 0\}$ and let $\omega(P)$ be the omega limit set of the forward orbit $\gamma^+(P) := \{\Psi(t)P : t \geq 0\}$.

Claim 1. $\bigcup_{P\in M_\partial} \omega(P) \subset \{E_0\} \cup \{E_1\}$.

For any given $P \in M_\partial$, we have $\Psi(t)P \in M_\partial$, $\forall\ t \geq 0$. Then for each $t \geq 0$, we have $Z(\cdot, t, P) \equiv 0$ or $Z_S(\cdot, t, P) \equiv 0$. In the case where $Z(\cdot, t, P) \equiv 0$, $\forall\ t \geq 0$. From the fourth equation of (4.1), we see that $Z_S(\cdot, t, P) \equiv 0$, $\forall\ t \geq 0$. Thus, (R, N, C, R_S, N_S, C_S) satisfy system (3.1)-(3.3). It follows from Theorem 3.2 that either

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

or

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

In the case where $Z(\cdot, \tilde{t}_1, P) \not\equiv 0$, for some $\tilde{t}_1 \geq 0$. Then Lemma 4.7 implies that $Z(\cdot, t, P) > 0$, $\forall\ t > \tilde{t}_1$. Thus, $Z_S(\cdot, t, P) \equiv 0$, $\forall\ t > \tilde{t}_1$. It then follows from the last equation of (4.1) that $Z(\cdot, t, P) \equiv 0$, $\forall\ t \geq \tilde{t}_1$, which is a contradiction. Hence, the claim is proved.

Since $\lambda^0 > 0$ and $\mu^* > 0$, there exists a sufficiently small positive number ϱ_0 such that $\lambda^0_{\varrho_0} > 0$ and $\mu^*_{\varrho_0} > 0$, where $\lambda^0_{\varrho_0}$ is the principal eigenvalue of the following eigenvalue problem

$$\begin{cases} \lambda^0_{\varrho_0}\tilde{\phi}(x) = \delta\tilde{\phi}''(x) - \nu\tilde{\phi}'(x) + \alpha(\tilde{\phi}_S(x) - \tilde{\phi}(x)) \\ \qquad\qquad\qquad +[f(R^{(0)}) - m - \varrho_0]\tilde{\phi}(x), \ 0 < x < L, \\ \lambda^0_{\varrho_0}\tilde{\phi}_S(x) = -\alpha\frac{A}{A_s}(\tilde{\phi}_S(x) - \tilde{\phi}(x)) \\ \qquad\qquad\qquad +[f(R^{(0)}) - m - \varrho_0]\tilde{\phi}_S(x), \ 0 < x < L, \\ \nu\tilde{\phi}(0) - \delta\tilde{\phi}'(0) = \tilde{\phi}'(L) = 0, \end{cases} \tag{5.6}$$

with a strongly positive eigenfunction $(\tilde{\phi}(\cdot), \tilde{\phi}_S(\cdot))$, and $\mu^*_{\varrho_0}$ is the principal eigenvalue of the following eigenvalue problem (see Lemma 4.5):

$$\begin{cases} \mu^*_{\varrho_0}\tilde{\psi}(x) = \delta\tilde{\psi}'' - \nu\tilde{\psi}' + \alpha(\tilde{\psi}_S - \tilde{\psi}) \\ \qquad\qquad\qquad +[g(N^*)e^{-\eta C^*} - m_Z - \varrho_0]\tilde{\psi}(x), \ 0 < x < L, \\ \mu^*_{\varrho_0}\tilde{\psi}_S(x) = -\alpha\frac{A}{A_S}(\tilde{\psi}_S - \tilde{\psi}) + [g(N^*_S)e^{-\eta C^*_S} - m_Z - \varrho_0]\tilde{\psi}_S, \ 0 < x < L, \\ \nu\tilde{\psi}(0) - \delta\tilde{\psi}'(0) = 0, \ \tilde{\psi}'(L) = 0, \end{cases} \tag{5.7}$$

with a strongly positive eigenfunction $(\tilde{\psi}(\cdot), \tilde{\psi}_S(\cdot))$.

It is easy to see that

$$\lim_{R\to R^{(0)}} f(R) = f(R^{(0)}) \text{ and } \lim_{(C,Z)\to(0,0)} [e^{-\eta C}Z] = 0.$$

Thus, we can choose $\delta_1 > 0$ such that

$$f(R) > f(R^{(0)}) - \frac{\varrho_0}{2}, \text{ for any } \mid R - R^{(0)} \mid < \delta_1,$$

and

$$e^{-\eta C}Z < \frac{\varrho_0}{2q_Z}\frac{\hat{K}}{\hat{\mu}_{\max}}, \text{ for any } \|(C,Z)\| < \delta_1,$$

where $\hat{K}$ and $\hat{\mu}_{\max}$ are defined in (4.4). From (4.4), it follows that

$$g(N) = \frac{\hat{\mu}_{\max}N}{\hat{K} + N} \le \frac{\hat{\mu}_{\max}}{\hat{K}}N, \ \forall \ N \ge 0. \tag{5.8}$$

Claim 2. E_0 is a uniform weak repeller in the sense that $\limsup_{t\to\infty} \|\Psi(t)P - E_0\| \ge \delta_1$ for all $P \in \mathbb{X}_0$.

Suppose, by contradiction, there exists $P_0 \in \mathbb{X}_0$ such that

$$\limsup_{t\to\infty} \|\Psi(t)P_0 - E_0\| < \delta_1.$$

Thus, there exists $t_1 > 0$ such that

$$\mid R(\cdot,t) - R^{(0)} \mid < \delta_1 \text{ and } \mid R_S(\cdot,t) - R^{(0)} \mid < \delta_1, \ \forall \ t \ge t_1,$$

and

$$\|(C(\cdot,t),Z(\cdot,t))\| < \delta_1 \text{ and } \|(C_S(\cdot,t),Z_S(\cdot,t))\| < \delta_1,\ t \geq t_1.$$

Combining (5.8) and above relations, we obtain

$$f(R(\cdot,t)) > f(R^{(0)}) - \frac{\varrho_0}{2},\ f(R_S(\cdot,t)) > f(R^{(0)}) - \frac{\varrho_0}{2},\ \forall\, t \geq t_1,$$

and

$$g(N(\cdot,t))e^{-\eta C(\cdot,t)}Z(\cdot,t) < \frac{\varrho_0}{2q_Z}N(\cdot,t),\ g(N_S(\cdot,t))e^{-\eta C_S(\cdot,t)}Z_S(\cdot,t) < \frac{\varrho_0}{2q_Z}N_S(\cdot,t),$$

for all $t \geq t_1$. It follows from the N and N_S equations of system (4.1)-(4.3) that

$$\begin{cases} \frac{\partial N}{\partial t} \geq \delta\frac{\partial^2 N}{\partial x^2} - \nu\frac{\partial N}{\partial x} + \alpha(N_S - N) \\ \qquad\qquad\qquad +[f(R) - m - \varrho_0]N,\ 0 < x < L,\ t \geq t_1, \\ \frac{\partial N_S}{\partial t} \geq -\alpha\frac{A}{A_S}(N_S - N) + [f(R_S) - m - \varrho_0]N_S,\ 0 < x < L,\ t \geq t_1, \\ \nu N(0,t) - \delta\frac{\partial N}{\partial x}(0,t) = 0,\ \frac{\partial N}{\partial x}(L,t) = 0,\ t \geq t_1. \end{cases} \tag{5.9}$$

Recall that $(\tilde{\phi}(\cdot),\tilde{\phi}_S(\cdot))$ is the strongly positive eigenfunction corresponding to $\lambda^0_{\varrho_0}$. Since $N(\cdot,t,\phi_0) > 0,\ N_S(\cdot,t,\phi_0) > 0,\ \forall\, t > 0$, there exists $\epsilon_0 > 0$ such that $(N(\cdot,t_1,\phi_0),N_S(\cdot,t_1,\phi_0)) \geq \epsilon_0(\tilde{\phi}(\cdot),\tilde{\phi}_S(\cdot))$. Note that $\epsilon_0 e^{\lambda^0_{\varrho_0}(t-t_1)}(\tilde{\phi}(\cdot),\tilde{\phi}_S(\cdot))$ is a solution of the following linear system:

$$\begin{cases} \frac{\partial N}{\partial t} = \delta\frac{\partial^2 N}{\partial x^2} - \nu\frac{\partial N}{\partial x} + \alpha(N_S - N) \\ \qquad\qquad\qquad +[f(R) - m - \varrho_0]N,\ 0 < x < L,\ t \geq t_1, \\ \frac{\partial N_S}{\partial t} = -\alpha\frac{A}{A_S}(N_S - N) + [f(R_S) - m - \varrho_0]N_S,\ 0 < x < L,\ t \geq t_1, \\ \nu N(0,t) - \delta\frac{\partial N}{\partial x}(0,t) = 0,\ \frac{\partial N}{\partial x}(L,t) = 0,\ t \geq t_1. \end{cases} \tag{5.10}$$

Then the comparison principle implies that

$$(N(x,t,\phi_0),N_S(x,t,\phi_0)) \geq \epsilon_0 e^{\lambda^0_{\varrho_0}(t-t_1)}(\tilde{\phi}(\cdot),\tilde{\phi}_S(\cdot)),\ \forall\, t \geq t_1,\ x \in [0,L].$$

Since $\lambda^0_{\varrho_0} > 0$, it follows that $N(x,t,\phi_0)$ and $N_S(x,t,\phi_0)$ are unbounded. This contradiction proves the claim.

It is easy to see that

$$\lim_{(N,C)\to(N^*,C^*)}[g(N)e^{-\eta C}] = g(N^*)e^{-\eta C^*}$$

and

$$\lim_{(N_S,C_S)\to(N_S^*,C_S^*)}[g(N_S)e^{-\eta C_S}] = g(N_S^*)e^{-\eta C_S^*}.$$

Thus, we can choose $\delta_2 > 0$ such that

$$g(N)e^{-\eta C} > g(N^*)e^{-\eta C^*} - \varrho_0, \text{ for any } \|(N, C) - (N^*, C^*)\| < \delta_2,$$

and

$$g(N_S)e^{-\eta C_S} > g(N_S^*)e^{-\eta C_S^*} - \varrho_0, \text{ for any } \|(N_S, C_S) - (N_S^*, C_S^*)\| < \delta_2.$$

Claim 3. E_1 is a uniform weak repeller in the sense that $\limsup_{t\to\infty} \|\Psi(t)P - E_1\| \geq \delta_2$ for all $P \in \mathbb{X}_0$.

Suppose, by contradiction, there exists $\hat{P}_0 \in \mathbb{X}_0$ such that

$$\limsup_{t\to\infty} \|\Psi(t)\hat{P}_0 - E_1\| < \delta_2.$$

Thus, there exists $t_2 > 0$ such that

$$\|(N(\cdot, t), C(\cdot, t)) - (N^*(\cdot), C^*(\cdot))\| < \delta_2, \ t \geq t_2,$$

and

$$\|(N_S(\cdot, t), C_S(\cdot, t)) - (N_S^*(\cdot), C_S^*(\cdot))\| < \delta_2, \ t \geq t_2.$$

Hence,

$$g(N(\cdot, t))e^{-\eta C(\cdot,t)} > g(N^*(\cdot))e^{-\eta C^*(\cdot)} - \varrho_0, \ t \geq t_2,$$

and

$$g(N_S(\cdot, t))e^{-\eta C_S(\cdot,t)} > g(N_S^*(\cdot))e^{-\eta C_S^*(\cdot)} - \varrho_0, \ t \geq t_2.$$

It follows from the Z and Z_S equations of system (4.1)-(4.3) that

$$\begin{cases} \frac{\partial Z}{\partial t} \geq \delta\frac{\partial^2 Z}{\partial x^2} - \nu\frac{\partial Z}{\partial x} + \alpha(Z_S - Z) \\ \qquad\qquad +[g(N^*(\cdot))e^{-\eta C^*(\cdot)} - \varrho_0 - m_Z]Z, \ 0 < x < L, \ t \geq t_2, \\ \frac{\partial Z_S}{\partial t} \geq -\alpha\frac{A}{A_S}(Z_S - Z) \\ \qquad\qquad +[g(N_S^*(\cdot))e^{-\eta C_S^*(\cdot)} - \varrho_0 - m_Z]Z_S, \ 0 < x < L, \ t \geq t_2, \\ \nu Z(0, t) - \delta\frac{\partial Z}{\partial x}(0, t) = 0, \ \frac{\partial Z}{\partial x}(L, t) = 0, \ t \geq t_2. \end{cases} \tag{5.11}$$

Recall that $(\tilde{\psi}(\cdot), \tilde{\psi}_S(\cdot))$ is the strongly positive eigenfunction corresponding to $\mu^*_{\varrho_0}$. Since $Z(\cdot, t, \phi_0) > 0$, $Z_S(\cdot, t, \phi_0) > 0$, $\forall\ t > 0$, there exists $\epsilon_1 > 0$ such that $(Z(\cdot, t_2, \phi_0), Z_S(\cdot, t_2, \phi_0)) \geq \epsilon_1(\tilde{\psi}(\cdot), \tilde{\psi}_S(\cdot))$. Note that $\epsilon_1 e^{\mu^*_{\varrho_0}(t-t_2)}(\tilde{\psi}(\cdot), \tilde{\psi}_S(\cdot))$ is a solution of the following linear system:

$$\begin{cases} \frac{\partial Z}{\partial t} = \delta\frac{\partial^2 Z}{\partial x^2} - \nu\frac{\partial Z}{\partial x} + \alpha(Z_S - Z) \\ \qquad\qquad +[g(N^*(\cdot))e^{-\eta C^*(\cdot)} - \varrho_0 - m_Z]Z, \ 0 < x < L, \ t \geq t_2, \\ \frac{\partial Z_S}{\partial t} = -\alpha\frac{A}{A_S}(Z_S - Z) \\ \qquad\qquad +[g(N_S^*(\cdot))e^{-\eta C_S^*(\cdot)} - \varrho_0 - m_Z]Z_S, \ 0 < x < L, \ t \geq t_2, \\ \nu Z(0, t) - \delta\frac{\partial Z}{\partial x}(0, t) = 0, \ \frac{\partial Z}{\partial x}(L, t) = 0, \ t \geq t_2. \end{cases} \tag{5.12}$$

The comparison principle implies that

$$(Z(x,t,\phi_0), Z_S(x,t,\phi_0)) \geq \epsilon_1 e^{\mu^*_{\varrho_0}(t-t_2)}(\tilde{\psi}(\cdot), \tilde{\psi}_S(\cdot)),\ \forall\ t \geq t_2,\ x \in [0,L].$$

Since $\mu^*_{\varrho_0} > 0$, it follows that $Z(x,t,\phi_0)$ and $Z_S(x,t,\phi_0)$ are unbounded. This contradiction proves the claim.

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

$$\mathbf{p}(\phi) := \min\{\min_{x\in[0,L]} \phi_4(x),\ \min_{x\in[0,L]} \phi_8(x)\},\ \forall\ \phi \in \mathbb{X}^+.$$

By Lemma 4.7, it follows that $\mathbf{p}^{-1}(0,\infty) \subseteq \mathbb{X}_0$ and $\mathbf{p}$ has the property that if $\mathbf{p}(\phi) > 0$ or $\phi \in \mathbb{X}_0$ with $\mathbf{p}(\phi) = 0$, then $\mathbf{p}(\Psi(t)\phi) > 0,\ \forall\ t > 0$. That is, $\mathbf{p}$ is a generalized distance function for the semiflow $\Psi(t) : \mathbb{X}^+ \to \mathbb{X}^+$ (see, e.g., [31]). By the above claims, it follows that any forward orbit of $\Psi(t)$ in M_∂ converges to either $\{E_0\}$ or $\{E_1\}$. Further, $\{E_0\}$ and $\{E_1\}$ are isolated in $\mathbb{X}^+$ and $W^s(\{E_i\}) \cap \mathbb{X}_0 = \emptyset,\ \forall\ i = 0,1$, where $W^s(\{E_i\})$ is the stable set of $\{E_i\},\ i = 0,1$ (see [31]). It is easy that no subsets of $\{\{E_0\},\{E_1\}\}$ forms a cycle in M_∂. By Theorem 4.1 and [31, Theorem 3], it follows that there exists an $\zeta > 0$ such that

$$\min_{\psi\in\omega(\phi)} \mathbf{p}(\psi) > \zeta,\ \forall\ \phi \in \mathbb{X}_0.$$

This implies that

$$\liminf_{t\to\infty} Z(\cdot,t) \geq \zeta \text{ and } \liminf_{t\to\infty} Z_S(\cdot,t) \geq \zeta,\ \forall\ \phi \in \mathbb{X}_0. \tag{5.13}$$

Hence, the uniform persistence stated in statement (ii) is valid.

By Lemma 4.3 and [22, Theorem 3.7 and Remark 3.10], it follows that $\Psi(t) : \mathbb{X}_0 \to \mathbb{X}_0$ has a global attractor A_0. It then follows from [22, Theorem 4.7] that $\Psi(t)$ has an equilibrium

$$(\hat{R}(\cdot), \hat{N}(\cdot), \hat{C}(\cdot), \hat{Z}(\cdot), \hat{R}_S(\cdot), \hat{N}_S(\cdot), \hat{C}_S(\cdot), \hat{Z}_S(\cdot)) \in \mathbb{X}_0.$$

We have to prove that

$$(\hat{R}(\cdot), \hat{N}(\cdot), \hat{C}(\cdot), \hat{Z}(\cdot), \hat{R}_S(\cdot), \hat{N}_S(\cdot), \hat{C}_S(\cdot), \hat{Z}_S(\cdot))$$

is a positive steady state of (4.1)-(4.3). It is easy to see that $\hat{R}$ satisfies the following inequalities,

$$\begin{cases} \delta\hat{R}'' - \nu\hat{R}' - [\alpha + q_N \int_0^1 f'(\theta\hat{R})d\theta]\hat{R} \leq 0,\ 0 < x < L, \\ \nu\hat{R}(0) - \delta\hat{R}'(0) = \nu R^{(0)},\ \hat{R}'(L,t) = 0. \end{cases} \tag{5.14}$$

Suppose $\hat{R}$ attains a minimum $\hat{R}(\hat{x}) \leq 0$ at some point $\hat{x} \in [0,L]$. If $\hat{x} \in (0,L)$, then by the strong maximum principle (see [26, p.64,Theorem 6]), one has that

$\hat{R} \equiv \hat{R}(\hat{x})$, contradicting its boundary condition at $x = 0$. If $\hat{x} = L$, by the Hopf boundary lemma (see [26]), one has $\hat{R}'(L) < 0$, which is a contradiction. Similarly, $\hat{x} = 0$ is impossible. Thus, $\hat{R}(x) > 0, \ \forall\ 0 \leq x \leq L$. Clearly, $\hat{R}_S$ satisfies the following equalitiy,

$$\alpha \frac{A}{A_S} \hat{R}_S(x) + q_N f(\hat{R}_S(x)) \hat{N}_S(x) = \alpha \frac{A}{A_S} \hat{R}(x) + q_N m \hat{N}_S(x), \ 0 \leq x \leq L,$$

which implies that $\hat{R}_S(x) > 0, \ \forall\ 0 \leq x \leq L$. Similarly, we can prove that $\hat{N}(x) > 0, \ \hat{N}_S(x) > 0, \ \hat{C}(x) > 0, \ \hat{C}_S(x) > 0$ for all $0 \leq x \leq L$. This completes the proof.

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