Single species growth consuming inorganic carbon with internal storage in a poorly mixed habitat

Sze-Bi Hsu* King-Yeung Lam † Feng-Bin Wang‡

Abstract

This paper presents a PDE system modeling the growth of a single species population consuming inorganic carbon that is stored internally in a poorly mixed habitat. Inorganic carbon takes the forms of "CO2" (dissolved CO2 and carbonic acid) and "CARB" (bicarbonate and carbonate ions), which are substitutable in their effects on algal growth. We first establish a threshold type result on the extinction/persistence of the species in terms of the sign of a principal eigenvalue associated with a nonlinear eigenvalue problem. If the habitat is the unstirred chemostat, we add biologically relevant assumptions on the uptake functions and prove the uniqueness and global attractivity of the positive steady state when the species persists.

Keywords. inorganic carbon, internal storage, extinction, persistence, global stability, a nonlinear eigenvalue problem.

AMS 2010 MSC. 35B40, 35K57, 92D25.

*Department of Mathematics, National Tsing Hua University, Hsinchu 300, Taiwan. Research supported in part by Ministry of Science and Technology, Taiwan.

†Department of Mathematics, the Ohio State University. Research partially supported by NSF grant DMS-1411476.

‡Department of Natural Science in the Center for General Education, Chang Gung University, Kwei-Shan, Taoyuan 333, Taiwan; and Community Medicine Research Center, Keelung Chang Gung Memorial Hospital, Keelung 204, Taiwan. Research supported in part by Ministry of Science and Technology, Taiwan; and National Center for Theoretical Sciences (NCTS), National Taiwan University; and Chang Gung Memorial Hospital under grants BMRPD18 and NMRPD5F0541.

1 Introduction and the model

Resource competition theory is an important topic concerning the interaction between the limiting resource(s) and the species. The most basic limiting resources for growth include nutrients (e.g., nitrogen and phosphorus), light, and inorganic carbon. Several previous works have considered the competition between the species for nutrients (e.g., nitrogen and phosphorus), or light, or both of them. However, the competition for inorganic carbon have received very little attention. The main difficulty is the biochemistry of inorganic carbon, which is much more complicated than that of nutrients and light [46]. The detailed mechanism of chemical interactions involved in the competition for inorganic carbon can be found in [37, 46]. The authors in [46] proposed a system of ODEs modeling the competition of the species for inorganic carbon that is stored internally in a well-mixed chemostat, in which dissolved CO2 and carbonic acid are regarded as one resource (denoted as "CO2"), and bicarbonate and carbonate ions are regarded as another (denoted as "CARB"). The resources "CO2" and "CARB" are substitutable in their effects on algal growth [37, 46].

To make the mathematics more tractable, we will follow the ideas used in the recent work [37] to simplify the complex processes of "CO2" and "CARB" involved, and modify the ODE system proposed in [46]. In order to model the interactions between the limiting resource(s) and the species, we need to specify the amount of resource(s) consumed in the growth of one new individual [18]. Assuming that all individuals have the same quota of resource(s) at any instant, we consider the following variable-internal-storage model in a well-mixed chemostat [18, 37, 46]:

$$\begin{cases} \frac{dR}{dt} = (R^{(0)} - R)D - f_R(R,Q)u - \omega_r R + \omega_s S, \\ \frac{dS}{dt} = (S^{(0)} - S)D - f_S(S,Q)u + \omega_r R - \omega_s S, \\ \frac{dQ}{dt} = f_R(R,Q) + f_S(S,Q) - \mu(Q)Q, \\ \frac{du}{dt} = [\mu(Q) - D]\, u, \\ R(0) \geq 0,\ S(0) \geq 0,\ Q(0) \geq Q_{\min},\ u(0) \geq 0. \end{cases} \tag{1.1}$$

Here, $R(t)$ represents the total concentration of "CO2" (i.e., dissolved CO2 and carbonic acid); $S(t)$ represents the total concentration of "CARB" (i.e., bicarbonate and carbonate ions); $u(t)$ denotes the population density of the species; $Q(t)$ stands for the cellular carbon content. The fourth equation in (1.1) describes the population density of the species, where $\mu(Q)$ is the specific growth rate of the species, and $Q_{\min}$ denotes the threshold cell quota below which no growth of the species occurs. The third equation in (1.1) describes the cellular carbon content of the species, which increases through uptake of "CO2" ($f_R(R, Q)$) and "CARB" ($f_S(S, Q)$), and decrease through consumption of cellular carbon for growth. We ignore the effect of respiration in system (1.1). The first two equations of system (1.1) describe changes in dissolved inorganic carbon in the environment. The first equation represents the changes in the concentration of dissolved "CO2" through the influx $R^{(0)}$ and efflux of water containing dissolved "CO2", through gas exchange with atmospheric CO2, and through the chemical reaction from dissolved "CO2" to "CARB" and vice versa, and through uptake of "CO2" ($f_R(R, Q)u$) by the species; the second equation describes changes in the total concentration of "CARB" through the influx $S^{(0)}$ and efflux of water containing these inorganic carbon species, through the chemical reaction from "CARB" to dissolved "CO2" and vice versa, and through uptake of "CARB" ($f_S(S, Q)u$) by the species [46]. We further assume that carbonic acid loses a proton to become bicarbonate at the rate ω_r, and the rate of the reverse reaction is denoted by ω_s [37]. All the parameters depend on the physical and chemical conditions of natural waters (e.g., temperature, pH and alkalinity) [37, 46]. The chemostat is supplied with inorganic carbon at constant concentrations ($R^{(0)}$, $S^{(0)}$) at dilution rate D. In [30, 32], the authors investigated models of two complementary/essential resources with internal storage in which growth rate for species is determined by the minimum of two Droop functions. This type of growth rate reflects that the two resources are complementary/essential, not substitutable. Two mass conservation laws can be derived for the models in [30, 32], and hence, the authors in [30, 32] can reduce their systems to monotone systems. We point out that only one mass conservation can be obtained for system (1.1), and it can not be reduced into a monotone system without imposing extra assumptions on the uptake functions. Thus, the arguments in [30, 32] can not be applied to system (1.1). We will summarize the results of system (1.1) in the Discussion section.

In [8, 9, 10, 46], the growth rate $\mu(Q)$ was taken to be

$$\mu(Q) = \mu_\infty \left(1 - \frac{Q_{\min}}{Q}\right), \ \forall\ Q \geq Q_{\min}, \tag{1.2}$$

or

$$\mu(Q) = \mu_{\max} \frac{Q - Q_{\min}}{Q_{\max} - Q_{\min}}, \ \forall\ Q_{\min} \leq Q \leq Q_{\max}, \tag{1.3}$$

where μ_∞ is the maximal growth rate at infinite quotas (i.e., as $Q \to \infty$) of the species; $\mu_{\max}$ is the maximum specific growth rate of the species; $Q_{\min}$ is its minimum cellular carbon content required for growth; $Q_{\max}$ is its maximum cellular carbon content. According to Grover [14], for $N = R,\ S$, the uptake rate $f_N(N, Q)$ takes the form:

$$f_N(N, Q) = \rho_N(Q) \frac{N}{k_N + N}. \tag{1.4}$$

The function $\rho_N(Q)$ is defined as follows:

$$\rho_N(Q) = \rho^{\text{high}}_{\max,N} - (\rho^{\text{high}}_{\max,N} - \rho^{\text{low}}_{\max,N}) \frac{Q - Q_{\min}}{Q_{\max} - Q_{\min}}, \tag{1.5}$$

or

$$\rho_N(Q) = \rho_{\max,N} \frac{Q_{\max} - Q}{Q_{\max} - Q_{\min}}, \tag{1.6}$$

where $Q_{\min} \le Q \le Q_{\max}$. The authors in [4, 5, 30] took $\rho_N(Q)$ to be a constant,

$$\rho_N(Q) = \rho_N. \tag{1.7}$$

Motivated by the above practical examples, we assume that for each $N = R,\ S$, the functions $\mu(Q)$ and $f_N(N, Q)$ satisfy the following assumptions:

(H1) $\mu(Q)$ is Lipschitz continuous for $Q \ge 0$. Moreover, $\mu'(Q) > 0$ for a.e. $Q \ge 0$, and there exists $Q_{\min} > 0$ such that $\mu(Q_{\min}) = 0$.

(H2) (i) $f_N(N, Q)$ and $\frac{\partial f_N(N,Q)}{\partial N}$ are Lipschitz continuous in $N \ge 0$ and $Q \ge 0$;

(ii) $\frac{\partial f_N(N,Q)}{\partial N} \ge 0$, $\frac{\partial f_N(N,Q)}{\partial Q} \le 0$ and $f_N(N, Q) \ge 0$ for a.e. $N \ge 0$ and $Q \ge 0$;

(iii) there exists $Q_B \in (Q_{\min}, +\infty]$ such that

$$\begin{aligned} f_N(N, Q) > 0,\ \frac{\partial f_N(N, Q)}{\partial N} > 0 \quad &\text{in } \{(N, Q) \in \mathbb{R}^2_+ : N > 0 \text{ and } Q \in [0, Q_B)\}, \\ f_N(N, Q) = 0 \quad &\text{in } \{(N, Q) \in \mathbb{R}^2_+ : N = 0 \text{ or } Q \ge Q_B\}. \end{aligned}$$

(When $Q_B = +\infty$, it is understood that $f_N(N, Q) = 0$ if and only if $N = 0$.)

One can easily use a natural way to extend the functions $\mu(Q)$ and $f_N(N, Q)$ in previous examples to be defined in $\mathbb{R}_+$ and $\mathbb{R}^2_+$, respectively, while satisfying **(H1)** and **(H2)**.

There have been several works investigating populations and dissolved nutrients that are poorly/partially mixed in spatially variable habitats [2, 3, 15, 16, 17, 20, 25, 33]. One simple, spatially distributed habitat is the unstirred chemostat [3, 25, 41], which was introduced as a poorly/partially mixed analog of the chemostat with transport of nutrients and organisms by diffusion. An advantage for the species with quota variation in spatially variable habitats is that individuals could obtain nutrients in a rich zone of a habitat and for their later use to survive when they travel to a poor zone [15, 16]. Thus, the ecological model systems with variable quotas in a spatially variable habitat are important and significant. However, such topics have received very little attention, perhaps due to the complexities and difficulties in modeling as well as mathematical analysis. In the previous works, there are three approaches of modeling to this issue. The first approach is to incorporate the physical transport equations governing spatial distributions of populations and resources into equations for population structured proposed in [6, 7]. We will give detailed descriptions about this approach in the Discussion section. The second approach is the individual-based computational model proposed in [15], where the author utilized the Lagrangian framework developed in [45] to divide the population of each species into a large number of subpopulations. Each subpopulation moves around the habitat, and its dynamics is governed by ordinary differential equations in relation to intracellular stored nutrient [10, 14], and the available nutrient satisfies a partial differential equation with a simple diffusive transport process and a consumption term. The Lagrangian/computational approach in [15, 45] can have higher accuracy for some results [16], but it requires extensive computation to achieve predictions and it cannot be analyzed mathematically. The third approach is the reaction-diffusion system [20] or the reaction-diffusion-advection system [16], which describes the dynamics of dissolved nutrient concentration, the total concentration of stored nutrient by a species at a given point, and the corresponding population density. Then the ratio of *the total concentration of stored nutrients by a species at a given point* and *the corresponding population density* can be regarded as *the average quota of individuals at a location* [16]. This approach may risk errors since population growth at each location is assumed to depend on this average quota [16]. Recently, the author in [16] compared the second approach with the third one, and he concluded that errors caused by the averaging approach were relatively modest since both approaches can have similar predictions concerning persistence/coexistence of species.

The averaging approach can be used to establish more tractable PDEs [20], and it can be regarded as an approximation of the Lagrangian/computational approach since both approaches have similar results [16]. Inspired by this fact, we intend to adopt the averaging approach in [16, 20] to incorporate spatial variations into system (1.1). For this purpose, we assume $U(t) = u(t)Q(t)$ to be the total amount of stored inorganic carbon at time t. Then (1.1) becomes

$$\begin{cases} \frac{dR}{dt} = (R^{(0)} - R)D - f_R(R, \frac{U}{u})u - \omega_r R + \omega_s S, \\ \frac{dS}{dt} = (S^{(0)} - S)D - f_S(S, \frac{U}{u})u + \omega_r R - \omega_s S, \\ \frac{dU}{dt} = f_R(R, \frac{U}{u})u + f_S(S, \frac{U}{u})u - DU, \\ \frac{du}{dt} = \left[\mu(\frac{U}{u}) - D\right] u, \\ R(0) \geq 0,\ S(0) \geq 0,\ U(0) \geq 0,\ u(0) \geq 0, \end{cases} \tag{1.8}$$

where the initial value $(u(0), U(0))$ satisfies $U(0) \geq Q_{\min} u(0)$. We propose the following "unstirred chemostat model" of system (1.1) (or (1.8)):

$$\begin{cases} R_t = dR_{xx} - f_R(R, \frac{U}{u})u - \omega_r R + \omega_s S, \quad x \in (0,1),\ t > 0, \\ S_t = dS_{xx} - f_S(S, \frac{U}{u})u + \omega_r R - \omega_s S, \quad x \in (0,1),\ t > 0, \\ U_t = dU_{xx} + f_R(R, \frac{U}{u})u + f_S(S, \frac{U}{u})u, \quad x \in (0,1),\ t > 0, \\ u_t = du_{xx} + \mu(\frac{U}{u})u, \quad x \in (0,1),\ t > 0, \\ N_x(0,t) = -N^{(0)},\ N_x(1,t) + \gamma N(1,t) = 0, \quad N = R, S,\ t > 0, \\ w_x(0,t) = 0, w_x(1,t) + \gamma w(1,t) = 0, \quad w = U, u,\ t > 0, \\ w(x,0) = w^0(x) \geq (\not\equiv) 0, \quad w = R, S, U, u,\ x \in (0,1), \end{cases} \tag{1.9}$$

where the initial value functions $u^0(x)$, and $U^0(x)$ satisfy

$$U^0(x) \geq Q_{\min} u^0(x), \text{ on } [0,1].$$

It is worth mentioning that we consider a tubular chemostat so that the spatial dimension equals one in (1.9). The constants d and γ represent the diffusion coefficient and the washout constant, respectively. Here we calculate the average quota carbon at the location x and time t as $Q(x,t) := \frac{U(x,t)}{u(x,t)}$, and apply the functions μ and f_N with the functions μ and f_N satisfying (H1) and (H2) respectively, for $N = R,\ S$.

Another natural habitat is the water column of lakes and oceans. In the poorly/partially mixed water column, the phytoplankton, which is relatively homogeneously distributed horizontally, may be moved up or down by turbulence diffusion. In addition, it also has a tendency to sink or float. Hence, our model in the water column will be a reaction-advection-diffusion system [15, 16, 24, 29, 37, 47]. The spatial coordinate $x \in [0, L]$ represents the depth of a water column, with $x = 0$ being the surface and $x = L$ the bottom. Concerning the model of phytoplankton in a water column, we shall first discuss the corresponding boundary conditions before displaying the full equation. Assuming that "CO2" (R) enters via the water-atmospheric interface ($x = 0$), whereas "CARB" (S) enters via the sedimentary interface ($x = L$), we propose the following boundary conditions for resources in the water column:

$$\begin{cases} \gamma_R R(0,t) - R_x(0,t) = \gamma_R R^{(0)}, \ R_x(L,t) = 0, \ t > 0, \\ S_x(0,t) = 0, \ S_x(L,t) + \gamma_S S(L,t) = \gamma_S S^{(0)}, \ t > 0. \end{cases} \tag{1.10}$$

Assume that $D_R(x)$ and $D_S(x)$ are the vertical turbulent diffusion coefficients of the resources R and S, respectively; γ_R represents the transfer velocity of nutrients relative to $D_R(0)$ at the surface; γ_S represents the transfer velocity of nutrients relative to $D_S(L)$ at the sediment interface [47]. The following is another type of boundary conditions for "CO2" and "CARB" used in the model of [37]:

$$\begin{cases} \gamma_R R(0,t) - R_x(0,t) = \gamma_R \hat{R}, \ R(L,t) = R^{(0)}, \ t > 0, \\ S_x(0,t) = 0, \ S(L,t) = S^{(0)}, \ t > 0, \end{cases} \tag{1.11}$$

where the positive constant $\hat{R}$ is the thermodynamic equilibrium concentration of "CO2" in water, whose biological explanations can be found in the introduction of [37]; $R^{(0)}$ and $S^{(0)}$ are the source concentration of "CO2" and "CARB" at the bottom of the water column, respectively [37]. We assume no boundary flux for the species u and the total stored resource U, that is, u and U do not leave or enter the water column at $x = 0$ and $x = L$:

$$d(x)w_x(x,t) - \nu(x)w(x,t) = 0, \ \text{for } w \in \{u, \ U\}, \ x \in \{0, \ L\}, \ \text{and } t > 0. \tag{1.12}$$

Here $d(x)$ are the vertical turbulent diffusion coefficient of u and U; $\nu(x)$ is the sinking velocity ($\nu(\cdot) > 0$) or the buoyant velocity ($\nu(\cdot) < 0$) of u and U.

We first propose general boundary conditions that can include models in the chemostat (see (1.9)) and the water column (see (1.10), (1.11), and (1.12)) as special cases. Define the following operators: for $N = R, S$,

$$\mathcal{B}_{N,x}[N] = \begin{cases} -a_{N,0}N_x(0,t) + b_{N,0}N(0,t), \ x = 0, \ t > 0, \\ a_{N,L}N_x(L,t) + b_{N,L}N(L,t), \ x = L, \ t > 0, \end{cases} \tag{1.13}$$

and for $w = U, u$,

$$\mathbb{B}^x[w] = \begin{cases} -a^0[d(0)w_x(0,t) - \nu(0)w(0,t)] + b^0 w(0,t), \ x = 0, \ t > 0, \\ a^L[d(L)w_x(L,t) - \nu(L)w(L,t)] + b^L w(L,t), \ x = L, \ t > 0, \end{cases} \tag{1.14}$$

where $a_{N,x}$, $b_{N,x}$, a^x, and b^x are non-negative, for all $N \in \{R, \ S\}$ and $x \in \{0, \ L\}$. In this paper, we shall study the general model that includes the habitats in the unstirred chemostat (see (1.9)) and in the water column (see (1.10), (1.11), and (1.12)):

$$\begin{cases} R_t = (D_R(x)R_x)_x - f_R(R, \frac{U}{u})u - \omega_r R + \omega_s S, \ x \in (0, L), \ t > 0, \\ S_t = (D_S(x)S_x)_x - f_S(S, \frac{U}{u})u + \omega_r R - \omega_s S, \ x \in (0, L), \ t > 0, \\ U_t = (d(x)U_x - \nu(x)U)_x + f_R(R, \frac{U}{u})u + f_S(S, \frac{U}{u})u - mU, \ x \in (0, L), \ t > 0, \\ u_t = (d(x)u_x - \nu(x)u)_x + \mu(\frac{U}{u})u - mu, \ x \in (0, L), \ t > 0, \\ \mathcal{B}_{N,x}[N] = c_{N,x} \geq 0, \ N = R, S, \ x = 0 \text{ or } L, \ t > 0, \\ \mathbb{B}^x[w] = 0, \ \ w = U, u, \ x = 0 \text{ or } L, \ t > 0, \\ w(x, 0) = w^0(x) \geq (\not\equiv) 0, \ w = R, S, U, u, \ x \in (0, L), \end{cases} \tag{1.15}$$

where $m \geq 0$. We will impose some assumptions on the boundary conditions in system (1.15) as follows:

(H3) $a_{N,x}, b_{N,x} \geq 0$ and $a_{N,x} + b_{N,x} > 0$ for all $(N, x) \in \{R, S\} \times \{0, L\}$; also, $b_{N,x} > 0$ for some $(N, x) \in \{R, S\} \times \{0, L\}$.

(H4) $m, a^x, b^x \geq 0$ and $a^x + b^x > 0$ for all $x \in \{0, L\}$. One of m, b^0, b^L is positive.

(H5) $D_R(x) \equiv D_S(x) \equiv D(x) \quad \forall \ x \in [0, L]$, and $a_{R,x} = a_{S,x}$, $b_{R,x} = b_{S,x}$, $\forall \ x \in \{0, L\}$.

(H6) $c_{N,x} > 0$, for some $(N, x) \in \{R, \ S\} \times \{0, \ L\}$. Moreover, if for some $(N_0, x_0) \in \{R, \ S\} \times \{0, \ L\}$ such that $c_{N_0,x_0} > 0$, then $b_{N_0,x_0} > 0$.

We point out the main distinction between this paper and the previous works in [20, 22]. The main difficulties in mathematical analysis for the system (1.15) and models in [20, 22] are caused by the singularity in the ratio U/u at the extinction steady state $(R, S, U, u) = (R^*, S^*, 0, 0)$. Thus, standard techniques such as linearization and bifurcation are not applicable. In [20], strictly positive upper/lower solutions are constructed by exploiting the underlying monotonicity of the limiting system. However, the construction requires the diffusion rate to be relatively large or small, and the question of extinction/persistence is left open for intermediate diffusion rates. The authors in [22] pushed further the results in [20] and obtained a threshold result by defining, in an abstract way, the threshold diffusion rate to be "the supremum of diffusion rates where a lower solution can be constructed". In both works [20, 22], it was essential that the limiting system is monotone, as they are based on upper/lower solution arguments. Since the general system (1.15) can not be reduced to a monotone system, the arguments developed in [20, 22] can not be applied to (1.15).

By contrast, we pursue a more fundamental approach here by studying the nonlinear eigenvalue problem in the special positive cones of functions motivated by the ratio dependence. The principal eigenvalue, given by a recent Krein-Rutman type theorem involving two separate cones $C \subset D$ due to [35], is shown to characterize the threshold for persistence/extinction of the general system (1.15). We also note that the previous constructions of upper/lower solution in [20, 22] are based on some scalar eigenvalue problems, which are defined technically. Actually, one can construct another upper/lower solution for the limiting system in [20, 22] using a nonlinear eigenvalue problem similar to (2.8) in this paper, and one can easily obtains the threshold dynamics of the model in [20], and same conclusions in [22]. Although homogeneous eigenvalue problems have been used before to find threshold parameters for the dynamics of PDE models [27, 28], this is the first application of the Krein-Rutman Theorem involving two cones to study population dynamics. Furthermore, unlike previous works in phytoplankton models the mass conservation is not assumed for the general system (1.15), and as a result the boundedness of solution is proved in this paper separately. This paper is one of the the first attempts in characterizing the threshold dynamics in ratio-dependent PDE systems and we expect the methods in this paper to be applied to other PDE models with ratio-dependence.

2 Main results of system (1.15)

In this section, we state the main theorems of this paper, the proofs of which will be given in the subsequent sections. Consider first the following linear cooperative system modeling the available resources in a phytoplankton-free environment:

$$\begin{cases} R_t = (D_R(x)R_x)_x - \omega_r R + \omega_s S, & x \in (0, L),\ t > 0, \\ S_t = (D_S(x)S_x)_x + \omega_r R - \omega_s S, & x \in (0, L),\ t > 0, \\ \mathcal{B}_{N,x}[N] = c_{N,x} \geq 0,\ N = R, S, & x = 0 \text{ or } L,\ t > 0, \\ w(x, 0) = w^0(x),\ w = R, S, & x \in (0, L). \end{cases} \tag{2.1}$$

The following result concerning the dynamics of the phytoplankton-free system (2.1) is proved in section 3.

Proposition 2.1. *Suppose (H3), and one of (H5)-(H6) hold. Then system* (2.1) *admits a unique positive steady-state solution* $(R^*(x), S^*(x))$ *which is globally asymptotically stable among solutions with initial data in* $C([0, L]; \mathbb{R}^2_+)$*. Furthermore, there exists* $C \geq 1$ *independent of initial conditions* $(R^0(x), S^0(x))$ *such that*

$$\|(R(\cdot, t), S(\cdot, t))\| \leq C(1 + \|R^0(\cdot), S^0(\cdot)\|) \quad \textit{for all } t \geq 0.$$

Let $\mathbf{X} = C([0, L]; \mathbb{R}^4_+)$, $D = C^0([0, L], \mathbb{R}^2_+)$, and $\leq_D$ be the partial order in $C^0([0, L]; \mathbb{R}^2)$ generated by the cone D (see, e.g., [40, Section 1.1]), i.e.

$$(R_1(\cdot), S_1(\cdot)) \leq_D (R_2(\cdot), S_2(\cdot)) \quad \text{if} \quad R_1(x) \leq R_2(x) \text{ and } S_1(x) \leq S_2(x)\, \forall x \in [0, L]. \tag{2.2}$$

From now on, $(R^*(x), S^*(x))$ stands for the unique positive steady-state solution of system (2.1). We define next Q^* to be the unique positive number so that

$$Q^* = \inf\{Q > 0 : f_R(R^*(x), Q) + f_S(S^*(x), Q) - \mu(Q)Q \leq 0 \ \text{ in } [0, L]\}. \tag{2.3}$$

Remark 2.1.
(i) $Q_{\min} < Q^* < Q_B$, *where* $Q_{\min}$ *and* Q_B *are given by (H1) and (H2) respectively.*

(ii) *By (H2), for any* $0 < \epsilon_0 < Q_B/Q^* - 1$*, and for* $N = R, S$*,*

$$f_N(N, Q) > 0 \quad \textit{for all } N > 0 \textit{ and } 0 \leq Q \leq (1 + \epsilon_0)Q^*.$$

(iii) *The definition of* Q^* *in* (2.3) *is motivated by the ODE system* (1.1)*. For system* (1.1)*, its phytoplankton-free equilibrium is* $(R, S, Q, u) = (R^*, S^*, Q^*, 0)$*, where*

$$(R^*, S^*) := \left(\frac{DR^{(0)} + \omega_s R^{(0)} + \omega_s S^{(0)}}{D + \omega_r + \omega_s}, \frac{DS^{(0)} + \omega_r S^{(0)} + \omega_r R^{(0)}}{D + \omega_r + \omega_s}\right), \tag{2.4}$$

and Q^* *is uniquely determined by*

$$f_R(R^*, Q^*) + f_S(S^*, Q^*) - \mu(Q^*)Q^* = 0. \tag{2.5}$$

Biologically, Q^* *represents the quota that a species can obtain when the resources concentration is at its long-term upper bound* (R^*, S^*)*.*

Theorem 2.1. *Assume* (H1), (H2), (H3), (H4) *and one of* (H5), (H6) *hold. Then*

(i) *System* (1.15) *generates a semiflow in*

$$\mathbf{Y} = \{(R^0, S^0, U^0, u^0) \in \mathbf{X} : \exists \tilde{Q} > 0 \ s.t.\ U^0(x) \le \tilde{Q}u^0(x)\ \forall x \in [0, L]\}, \tag{2.6}$$

in the sense that for each initial condition in $\mathbf{Y}$*, system* (1.15) *has a unique classical solution* (R, S, U, u) *that exists for all* $t > 0$*. Moreover, the solution satisfies* $(R(\cdot,t), S(\cdot,t), U(\cdot,t), u(\cdot,t)) \in \mathbf{Y}$ *for all* $t > 0$*.*

(ii) *For each* $\bar{Q} > 0$*, the solution depends continuously on initial data in*

$$\mathbf{Y}_{\bar{Q}} := \{(R^0, S^0, U^0, u^0) \in \mathbf{Y} : U^0(x) \le \bar{Q}u^0(x) \text{ for all } x \in [0, L]\}.$$

(iii) *Let* $Q^* \in (Q_{\min}, Q_B)$ *be given by* (2.3)*. Then the subset*

$$\begin{aligned} \mathbf{Y}_1 = \{(R^0, S^0, U^0, u^0) \in \mathbf{X} : Q_{\min}u^0(\cdot) \le U^0(\cdot) \le Q^*u^0(\cdot), \\ \text{and } (R^0(\cdot), S^0(\cdot)) \le_D (R^*(\cdot), S^*(\cdot)) \text{ in } [0, L]\}. \end{aligned} \tag{2.7}$$

attracts all trajectories in $\mathbf{Y}$*.*

(iv) *The steady state* $(R^*(x), S^*(x), 0, 0) \in \mathbf{X}$ *attracts all trajectories in*

$$\partial\mathbf{Y}_0 = \{(R^0, S^0, U^0, u^0) \in \mathbf{Y} : u^0 \equiv 0\}.$$

Here $(R^*(x), S^*(x))$ *is given in Proposition 2.1.*

We further show the eventual boundedness of trajectories, which is essential for the application of persistence theory.

Proposition 2.2. *Suppose (H1)-(H4), and one of (H5)-(H6) hold. There exists a constant* $C > 0$ *independent of initial conditions in* $\mathbf{Y}$ *such that for any solution* (R, S, U, u) *of system* (1.15)*, we have*

$$\limsup_{t\to\infty} \|(R(\cdot,t), S(\cdot,t), U(\cdot,t), u(\cdot,t))\| \le C.$$

The boundedness of trajectories enables the use of persistence theory. It turns out that the persistence/extinction of the phytoplankton species is characterized by the principal eigenvalue $\Lambda^0 \in \mathbb{R}$ of the following nonlinear eigenvalue problem:

$$\begin{cases} (d(x)\varphi'(x) - \nu(x)\varphi(x))' + f_R\left(R^*(x), \frac{\varphi(x)}{\phi(x)}\right)\phi(x) \\ \qquad +f_S\left(S^*(x), \frac{\varphi(x)}{\phi(x)}\right)\phi(x) + \Lambda\varphi(x) = 0, \quad x \in (0, L), \\ (d(x)\phi'(x) - \nu(x)\phi(x))' + \mu\left(\frac{\varphi(x)}{\phi(x)}\right)\phi(x) + \Lambda\phi(x) = 0, \quad x \in (0, L), \\ \mathbb{B}^x[w] = 0, \quad \text{for } w = \varphi, \phi, \quad \text{and } x = 0, L. \end{cases} \tag{2.8}$$

The existence of the principal eigenvalue Λ^0 of the nonlinear eigenvalue problem (2.8) will be proved in section 5.

Theorem 2.2. *Under the hypothesis of Theorem 2.1,* (2.8) *has a principal eigenvalue Λ^0, characterized as the unique eigenvalue of* (2.8) *with a strictly positive eigenfunction. Furthermore, $-\Lambda^0$ is the critical death rate in the sense that*

(i) If $m \geq -\Lambda^0$, then $(R^*(\cdot), S^*(\cdot), 0, 0)$ attracts all trajectories in $\mathbf{Y}$.

(ii) If $m < -\Lambda^0$, then there exists $\sigma > 0$ independent of initial conditions in $\mathbf{Y}$ so that whenever $u^0 \not\equiv 0$,

$$\liminf_{t\to\infty}\left[\inf_{0\leq x\leq L} U(x,t)\right] \geq \sigma, \quad \text{and} \quad \liminf_{t\to\infty}\left[\inf_{0\leq x\leq L} u(x,t)\right] \geq \sigma, \tag{2.9}$$

and (1.15) *has at least one positive steady state.*

Finally, we have the following result if we specialize to system (1.9), i.e. the model of an unstirred chemostat.

Theorem 2.3. *Assume (H1) and (H2). System* (1.9) *generates a semiflow in $\mathbf{Y}$ with a critical diffusion rate $d_0 > 0$ such that*

(i) If $d \in [d_0, +\infty)$ then the steady state $(R^*(\cdot), S^*(\cdot), 0, 0)$ attracts all trajectories in $\mathbf{Y}$.

(ii) If $d \in (0, d_0)$, then there exists $\sigma > 0$ independent of initial conditions in $\mathbf{Y}$ so that any solution of (1.9) *with $u^0 \not\equiv 0$ satisfies*

$$\liminf_{t\to\infty}\left[\inf_{0\leq x\leq L} U(x,t)\right] \geq \sigma, \quad \text{and} \quad \liminf_{t\to\infty}\left[\inf_{0\leq x\leq L} u(x,t)\right] \geq \sigma.$$

If we assume in addition that

(H7) $\omega_s + \frac{\partial f_R}{\partial Q}(R, Q) \geq 0$, *and* $\omega_r + \frac{\partial f_S}{\partial Q}(S, Q) \geq 0$, *for a.e.* $R \geq 0$, $S \geq 0$, $Q \geq 0$.

Then (ii) can be strengthened to

(ii') If $d \in (0, d_0)$, *then* (1.9) *has a unique positive steady state* $(\hat{R}, \hat{S}, \hat{U}, \hat{u})$ *that attracts all trajectories in* $\mathbf{Y}$ *such that* $u^0 \not\equiv 0$.

Remark 2.2. (i) *Using* $m = 0$ *here and Theorem 2.2, we comment that in Theorem 2.3 (i),* $\Lambda^0 \geq 0$, *and in Theorem 2.3 (ii),* $\Lambda^0 < 0$. *In fact,* $\Lambda^0 := \Lambda^0(d)$ *depends on the diffusion coefficient* d. *We will show that* $\Lambda^0 > 0$ *for* $d \in (d_0, +\infty)$, *and* $\Lambda^0 < 0$ *for* $d \in (0, d_0)$ *(see Lemma 7.1).*

(ii) *In the Discussion section, we will give practical examples of* $f_R(R, Q)$ *and* $f_S(S, Q)$ *such that the inequalities in* (H7) *hold, where the parameters are in a realistic parameter range.*

We outline the rest of the paper as follows: In Section 3, we discuss the chemical dynamics of the phytoplankton-free system and prove Proposition 2.1. In Section 4, we prove the well-posedness results of Theorem 2.1. In Section 5, we adapt a non-linear version of Krein-Rutman Theorem, due to Mallet-Paret and Nussbaum [35], to study the local stability of phytoplankton-free steady state $(R^*(\cdot), S^*(\cdot), 0, 0)$. In Section 6, we prove the eventual boundedness of trajectories (Subsection 6.1) and apply persistence theory to prove the threshold dynamics contained in Theorem 2.2. In Section 7, we specialize to the unstirred chemostat system (1.9) and prove Theorem 2.3. We close with some discussion in Section 8.

3 Dynamics of the phytoplankton-free system (2.1)

Recall that $D = C^0([0, L], \mathbb{R}^2_+)$ and $\leq_D$ is the partial order in $C^0([0, L]; \mathbb{R}^2)$ defined in (2.2). We first consider a slightly more general version of the phytoplankton-free system (2.1):

$$\begin{cases} R_t = (D_R(x)R_x)_x - F_R(x, R) - \omega_r R + \omega_s S, \;\; x \in (0, L), \; t > 0, \\ S_t = (D_S(x)S_x)_x - F_S(x, S) + \omega_r R - \omega_s S, \;\; x \in (0, L), \; t > 0, \\ \mathcal{B}_{N,x}[N] = c_{N,x} \geq 0, \;\; N = R, S, \;\; x = 0 \text{ or } L, \;\; t > 0, \\ N(x, 0) = N^0(x), \;\; N = R, S, \;\; x \in (0, L). \end{cases} \tag{3.1}$$

Lemma 3.1. *Suppose (H3), and one of (H5)-(H6) hold. For $N = R, S$, assume that*

$$F_N(\cdot, 0) = 0 \quad \text{and} \quad \frac{\partial}{\partial N} F_N(\cdot, N) \geq 0 \ \ \forall N \geq 0. \tag{3.2}$$

Then the following statements are valid.

(i) *System* (3.1) *admits a unique positive steady-state solution* $(R_F^{**}(x), S_F^{**}(x))$, *which is globally asymptotically stable among all non-negative solutions. Furthermore, there exists a number $C \geq 1$ independent of initial data $(R^0, S^0) \in C([0, L]; \mathbb{R}_+^2)$ such that*

$$\|(R(\cdot, t), S(\cdot, t))\| \leq C(1 + \|(R^0(\cdot), S^0(\cdot))\|) \quad \text{for } t \geq 0.$$

(ii) *If $G_N(\cdot, N)$ satisfies a similar condition as* (3.2) *for $N = R, S$, and*

$$(G_R(x, R), G_S(x, S)) \geq_D (F_R(x, R), F_S(x, S)), \ \text{for all } x \in [0, L], \ \ R, S \geq 0,$$

then

$$(R_G^{**}(x), S_G^{**}(x)) \leq_D (R_F^{**}(x), S_F^{**}(x)), \quad \text{for every } x \in [0, L], \tag{3.3}$$

where $(R_G^{**}(x), S_G^{**}(x))$ is the unique steady-state solution of system (3.1) *with the the replacement of F by G. Additionally, if we further assume that $(G_R(\cdot, R), G_S(\cdot, S)) \geq_D, \not\equiv (F_R(\cdot, R), F_S(\cdot, S))$, then $(R_G^{**}(\cdot), S_G^{**}(\cdot)) \ll_D (R_F^{**}(\cdot), S_F^{**}(\cdot))$.*

Proof. From the assumptions in (3.2), it is easy to see that system (3.1) is a cooperative system. Let $(\underline{R}, \underline{S}) = (0, 0)$, and

$$(\overline{R}, \overline{S}) = \begin{cases} C\Phi^0(x)\,(\omega_s, \omega_r) & \text{if (H3) and (H5) hold,} \\ C \max_{(N,x)\in\Gamma}\{\frac{c_{N,x}}{b_{N,x}}\}\,(\omega_s, \omega_r) & \text{if (H3) and (H6) hold,} \end{cases} \tag{3.4}$$

where $C \geq \frac{1}{\omega_s} + \frac{1}{\omega_r}$, and $\Gamma = \{(N, x) \in \{R,\ S\} \times \{0,\ L\} |\ b_{N,x} > 0\}$ is nonempty, due to assumption (H3); $\Phi^0(x)$ being the unique positive solution to

$$\begin{cases} (D_R(x)\Phi_x^0)_x = 0, \ x \in (0, L), \\ -a_{R,0}\Phi_x^0(0) + b_{R,0}\Phi^0(0) = \max\{c_{R,0}, c_{S,0}\}, \\ a_{R,L}\Phi_x^0(L) + b_{R,L}\Phi^0(L) = \max\{c_{R,L}, c_{S,L}\}. \end{cases} \tag{3.5}$$

To show the existence of $\Phi^0(x)$, we apply Fredholm's alternative. It remains to show that $\Phi^0(x)$ is uniquely determined by system (3.5) under the assumptions (H3) and (H5). To this end, we assume that $\Phi_1^0(x)$ and $\Phi_2^0(x)$ solve system (3.5). Let $\bar{\Phi}^0(x) := \Phi_1^0(x) - \Phi_2^0(x)$. Then $\bar{\Phi}^0(x)$ satisfies

$$\begin{cases} \left(D_R(x)\bar{\Phi}_x^0\right)_x = 0, \quad x \in (0, L), \\ -a_{R,0}\bar{\Phi}_x^0(0) + b_{R,0}\bar{\Phi}^0(0) = 0, \quad a_{R,L}\bar{\Phi}_x^0(L) + b_{R,L}\bar{\Phi}^0(L) = 0. \end{cases} \tag{3.6}$$

Multiply (3.6) by $\bar{\Phi}^0$ and integrate by parts, we have

$$\int_0^L D_R(x)(\bar{\Phi}_x^0)^2 = [D_R(x)\bar{\Phi}_x^0(x)\bar{\Phi}^0(x)]\,|_0^L \leq 0.$$

This implies that $\bar{\Phi}_x^0 \equiv$ constant. By the assumption (H3), (H5) and the boundary condition of $\bar{\Phi}^0$ in (3.5), we conclude that either $\bar{\Phi}^0(0) = 0$ or $\bar{\Phi}^0(L) = 0$, which ensures that $\bar{\Phi}^0 \equiv 0$. Thus, $\Phi^0(x)$ is uniquely determined by system (3.5). It is not hard to see that for all $C \geq \frac{1}{\omega_s} + \frac{1}{\omega_r}$, $(\underline{R}, \underline{S})$ and $(\overline{R}, \overline{S})$ forms a pair of strict sub- and supersolutions of (3.1). We can then conclude that the minimal and maximal steady states of system (3.1) (with respect to $\leq_D$) exist, which we denote by $(R_F^{\min}(x), S_F^{\min}(x))$ and $(R_F^{\max}(x), S_F^{\max}(x))$ respectively. It remains to prove that

$$(R_F^{\min}(x), S_F^{\min}(x)) \equiv (R_F^{\max}(x), S_F^{\max}(x)). \tag{3.7}$$

To this end, we let $R_F(x) = R_F^{\max}(x) - R_F^{\min}(x)$, $S_F(x) = S_F^{\max}(x) - S_F^{\min}(x)$. Then $(R_F(x), S_F(x)) \geq_D (0, 0)$, and $(R_F(x), S_F(x))$ satisfies

$$\begin{cases} (D_R(x)(R_F)_x)_x - h_R(x)R_F(x) - \omega_r R_F(x) + \omega_s S_F(x) = 0, \ x \in (0, L), \\ (D_S(x)(S_F)_x)_x - h_S(x)S_F(x) + \omega_r R_F(x) - \omega_s S_F(x) = 0, \ x \in (0, L), \\ \mathcal{B}_{N,x}[N_F] = 0, \ N = R, \ S, \ x = 0 \text{ or } L, \end{cases} \tag{3.8}$$

where

$$h_R(x) = \int_0^1 \frac{\partial F_R}{\partial R}\left(x, \tau R_F^{\max}(x) + (1-\tau)R_F^{\min}(x)\right) d\tau \geq 0,$$

$$h_S(x) = \int_0^1 \frac{\partial F_S}{\partial S}\left(x, \tau S_F^{\max}(x) + (1-\tau)S_F^{\min}(x)\right) d\tau \geq 0,$$

and

$$\mathcal{B}_{N,x}[N_F] = \begin{cases} -a_{N,0}(N_F)_x(0,t) + b_{N,0}N_F(0,t), \ x = 0, \ t > 0, \\ a_{N,L}(N_F)_x(L,t) + b_{N,L}N_F(L,t), \ x = L, \ t > 0. \end{cases}$$

Claim 3.1. *The following results are valid:*

(i) If $\max_{\tilde{x}=0,L}\{b_{R,\tilde{x}}\} > 0$*, then either* $R_F \equiv 0$ *or* $\max_{\tilde{x}=0,L}(-1)^{\tilde{x}/L}R_F'(\tilde{x}) > 0$.

(ii) If $\max_{\tilde{x}=0,L}\{b_{S,\tilde{x}}\} > 0$*, then either* $S_F \equiv 0$ *or* $\max_{\tilde{x}=0,L}(-1)^{\tilde{x}/L}S_F'(\tilde{x}) > 0$.

(iii) $(-1)^{\tilde{x}/L}N_F'(\tilde{x}) = 0$ *for all* $(N, \tilde{x}) \in \{R, S\} \times \{0, L\}$.

First we show Claim 3.1(i). Suppose $b_{R,\tilde{x}} > 0$ for some $\tilde{x} \in \{0, L\}$, and $R_F \not\equiv 0$. Let $\min_{x\in[0,L]} R_F(x) = R_F(x_0)$. If $x_0 \in (0, L)$, then we may apply the strong maximum principle to the equation

$$\begin{cases} (D_R(x)(R_F)_x)_x + [-h_R(x) - \omega_r]R_F(x) = -\omega_s S_F(x) \leq 0, & x \in (0, L), \\ \mathcal{B}_{R,x}[R_F] = 0, & x = 0 \text{ or } L, \end{cases}$$

to conclude that $R_F(\cdot)$ is constant on $[0, L]$. Since $b_{R,\tilde{x}} > 0$ for some $\tilde{x} \in \{0, L\}$, we deduce from the boundary conditions that in fact $R_F(\cdot) \equiv 0$, contradiction. Hence if $R_F(\cdot) \not\equiv 0$, then we must have $x_0 \in \{0, L\}$. But then by Hopf's Lemma [13, Sect. 2.5, Theorem 14], we have $(-1)^{\tilde{x}/L}R_F'(x_0) > 0$ for some $x_0 \in \{0, L\}$. This proves Claim 3.1(i). The proof of Claim 3.1(ii) is analogous and is skipped.

Before proving (iii), we first show that

$$(-1)^{\tilde{x}/L}N_F'(\tilde{x}) \geq 0 \text{ for all } (N, \tilde{x}) \in \{R, S\} \times \{0, L\}. \tag{3.9}$$

If $a_{N,\tilde{x}} > 0$, for some $(N, \tilde{x}) \in \{R, S\}\times\{0, L\}$, then $(-1)^{\tilde{x}/L}N_F'(\tilde{x}) = \frac{b_{N,\tilde{x}}}{a_{N,\tilde{x}}}N_F(\tilde{x}) \geq 0$. Alternatively, if $a_{N,\tilde{x}} = 0$, then $N_F(\tilde{x}) = 0$ is a boundary minimum so that again $(-1)^{\tilde{x}/L}N_F'(\tilde{x}) \geq 0$. Thus, (3.9) holds. For Claim 3.1(iii), we add the first two equations in (3.8) and integrate over $x \in [0, L]$ to obtain

$$0 \leq \int_0^L [h_R(x)R_F(x) + h_S(x)S_F(x)]dx = \sum_{N=R,S}\sum_{\tilde{x}=0,L} -D_N(\tilde{x})(-1)^{\tilde{x}/L}N_F'(\tilde{x}).$$

By (3.9), each term on the right is non-positive and thus identically zero. This yields (iii) and finishes the proof of Claim 3.1.

Now, by assumption (H3), either $\max_{\tilde{x}=0,L}\{b_{R,\tilde{x}}\} > 0$ or $\max_{\tilde{x}=0,L}\{b_{S,\tilde{x}}\} > 0$. By Claim 3.1, either $R_F(\cdot) \equiv 0$ or $S_F(\cdot) \equiv 0$. Plugging into (3.8) we must have $R_F(\cdot) \equiv S_F(\cdot) \equiv 0$. This proves (3.7). By the compactness of forward trajectories, we see that the unique steady state $(R_F^{**}(\cdot), S_F^{**}(\cdot))$ of system (3.1) is globally asymptotically stable among all non-negative solutions [26, Theorem D]. This proves Part (i).

For Part (ii), let (R_G^{**}, S_G^{**}) be the unique steady state of (3.1) with F_R, F_S being replaced with G_R, G_S. Then (R_G^{**}, S_G^{**}) is a strict subsolution of (3.1). Since the latter has a unique, globally asymptotically stable steady state (R_F^{**}, S_F^{**}), it follows by comparison that (3.3) holds. □

Proof of Proposition 2.1. This is a special case of Lemma 3.1(i), when $F_R \equiv F_S \equiv 0$. □

4 Well-posedness Results

In this section, we shall provide the proof of Theorem 2.1.

4.1 Estimates

Recall that $\mathbf{X} = C^0([0, L]; \mathbb{R}_+^4)$, $\mathbf{Y}$ and $\mathbf{Y}_1$ are defined in (2.6) and (2.7). Also Q^* is given in (2.3) and $(R^*(\cdot), S^*(\cdot))$ is the unique steady state of (2.1) (see Proposition 2.1). Note that $\mathbf{Y}_1 \subseteq \mathbf{Y} \subseteq \mathbf{X}$.

Lemma 4.1. *Suppose (H3), and one of (H5)-(H6) hold. Let*

$$(R(x,t), S(x,t), U(x,t), u(x,t))$$

be a solution of (1.15) *for* $t \in [0, \tau)$. *Then*

(i) If $(R^0(\cdot), S^0(\cdot)) \le_D (R^*(\cdot), S^*(\cdot))$, *then* $(R(\cdot,t), S(\cdot,t)) \le_D (R^*(\cdot), S^*(\cdot))$ *for all* $t \in [0, \tau)$.

(ii) There exists a constant $C \ge 1$ *independent of* τ *and initial conditions*

$$(R^0(\cdot), S^0(\cdot), U^0(\cdot), u^0(\cdot)) \in \mathbf{Y}$$

such that

$$\sup_{t\in[0,\tau)} \|(R(\cdot,t), S(\cdot,t))\| \le C(1 + \|(R^0(\cdot), S^0(\cdot))\|).$$

Moreover, if $\tau = +\infty$, *then*

$$\limsup_{t\to\infty} (R(x,t), S(x,t)) \le_D (R^*(x), S^*(x))$$

uniformly for $x \in [0, L]$. i.e. for each $\epsilon > 0$ there exists $t_0 > 0$ such that

$$R(x,t) \le R^*(x) + \epsilon \quad \text{and} \quad S(x,t) \le S^*(x) + \epsilon$$

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

Proof. Let (R, S, U, u) be a solution of (1.15) for $t \in [0, \tau)$ with initial data $(R^0, S^0, U^0, u^0) \in \mathbf{Y}$. By comparison principle, we have

$$(R(x,t), S(x,t)) \le_D (\hat{R}(x,t), \hat{S}(x,t)),$$

where $(\hat{R}(x,t), \hat{S}(x,t))$ is the unique solution to (2.1) with initial conditions $(R^0(x), S^0(x))$. The rest follows from Proposition 2.1. □

Lemma 4.2. *Suppose the hypotheses of Theorem 2.1 hold. Let*

$$(R(x,t), S(x,t), U(x,t), u(x,t))$$

be a solution of (1.15) for $t \in [0, \tau)$, with initial data $(R^0, S^0, U^0, u^0) \in \mathbf{Y}$. Then

(i) It holds that

$$\inf_{x\in[0,L]} \frac{U(x,t)}{u(x,t)} \ge \min\left\{ Q_{\min}\,,\ \inf_{[0,L]} \frac{U^0(x)}{u^0(x)} \right\} \quad \text{for all } t \in [0,\tau). \tag{4.1}$$

(ii) There exists $\overline{Q} \in [Q^*, +\infty)$ depending on $\|(R^0, S^0)\|$ and $\|U^0/u^0\|$ such that

$$\sup_{x\in[0,L]} \frac{U(x,t)}{u(x,t)} \le \overline{Q} \quad \text{for all } t \in [0,\tau). \tag{4.2}$$

Moreover, if $\tau = +\infty$, then

$$\liminf_{t\to\infty} \left[\inf_{x\in[0,L]} (U(x,t) - Q_{\min} u(x,t)) \right] \ge 0 \tag{4.3}$$

and for each $Q > Q^*$,

$$\limsup_{t\to\infty} \left[\sup_{x\in[0,L]} (U(x,t) - Q u(x,t)) \right] \le 0. \tag{4.4}$$

Furthermore, if $\|u(\cdot,t)\|$ is bounded uniformly in $t > 0$, then (4.4) holds for $Q = Q^*$.

Proof of Lemma 4.2. The following arguments are motivated by [16] and [33]. Let $\underline{Q}$ be a number in $[0, Q_{\min}]$ to be specified later. Then one can write

$$\mu\left(\frac{U(x,t)}{u(x,t)}\right) = \mu(\underline{Q}) + \xi(x,t;\underline{Q})\left(\frac{U(x,t)}{u(x,t)} - \underline{Q}\right)$$

where for each $Q \geq 0$,

$$\xi(x,t;Q) = \int_0^1 \mu'\left(s\frac{U(x,t)}{u(x,t)} + (1-s)Q\right) ds > 0. \tag{4.5}$$

Let $H(x,t) = U(x,t) - \underline{Q}u(x,t)$. Then $\mu\left(\frac{U}{u}\right) = \mu(\underline{Q}) + \xi(x,t;\underline{Q})\frac{H}{u}$, and

$$\begin{cases} H_t - (d(x)H_x - \nu(x)H)_x + \xi(x,t;\underline{Q})\underline{Q}H + mH \\ = -\mu(\underline{Q})\underline{Q}\,u + f_R\left(R, \frac{U}{u}\right)u + f_S\left(S, \frac{U}{u}\right)u \geq 0, \quad \text{for } x \in [0,L], t \in [0,\tau), \\ \mathbb{B}^x[H] = 0, \;\; x = 0 \text{ or } L, \quad \text{for } t \in [0,\tau), \end{cases}$$

where we used the fact that $f_N \geq 0$ for $N = R, S$ and $\mu(\underline{Q}) \leq 0$ since $\underline{Q} \in [0, Q_{\min}]$. Taking

$$\underline{Q} := \min\left\{Q_{\min}\,,\; \inf_{[0,L]} \frac{U^0(x)}{u^0(x)}\right\}.$$

Then $H(x,0) = U^0(x) - \underline{Q}u^0(x) \geq 0$ and we have, by maximum principle for linear parabolic equations, $H(\cdot,t) \geq 0$ in $[0,L]$ for all $t \in [0,\tau)$. This proves (4.1).

Consider the case where $\tau = \infty$. We are going to show (4.3). For this purpose, we take $\underline{Q} = Q_{\min}$. Let

$$\rho_0(x,t) = \exp\left(-(m+\sigma_0)t + \int_0^x \frac{\nu(y)}{d(y)}dy\right), \tag{4.6}$$

where σ_0 satisfies

$$0 < \sigma_0 < \xi(x,t;Q_{\min})Q_{\min}, \;\; \forall\; x \in [0,L], \;\; t \in [0,\infty). \tag{4.7}$$

Define $\underline{H}(x,t) = -B\rho_0(x,t)$, where $B > 0$ is chosen such that $\underline{H}(x,0) = -B\rho_0(x,0) \leq H(x,0)$, for $x \in [0,L]$. Then $\underline{H}(x,t)$ satisfies

$$\begin{cases} \underline{H}_t - (d(x)\underline{H}_x - \nu(x)\underline{H})_x + \xi(x,t;Q_{\min})Q_{\min}\underline{H} + m\underline{H} \\ = [\xi(x,t;Q_{\min})Q_{\min} - \sigma_0]\underline{H}(x,t) \leq 0, \quad \text{for } x \in [0,L], \;\; t > 0, \\ \mathbb{B}^x[\underline{H}] = b^x\underline{H}(x,t) \leq 0, \;\; x = 0 \text{ or } L, \quad \text{for } t > 0, \\ \underline{H}(x,0) \leq H(x,0) = U^0(x) - Q_{\min}u^0(x), \quad \text{for } x \in [0,L]. \end{cases}$$

By comparison principle, $H(x,t) \geq \underline{H}(x,t)$. Using the fact that $\underline{H}(\cdot,t) \to 0$ uniformly in x as $t \to \infty$, we obtain (4.3). It remains to show (4.2) and (4.4).

Next, we show (4.2). Fix a solution (R,S,U,u) of (1.15) that exists up to time $\tau \in (0,\infty]$. By Lemma 4.1, there exists a number $\overline{Q} \geq \sup_{[0,L]} \frac{U^0(x)}{u^0(x)}$ depending possibly on initial data (R^0, S^0), such that

$$f_R(R(x,t),\overline{Q}) + f_S(S(x,t),\overline{Q}) - \mu(\overline{Q})\overline{Q} \leq 0 \quad \text{for } x \in [0,L],\ t \in [0,\tau). \tag{4.8}$$

Then one can write

$$f_N\left(N(x,t), \frac{U(x,t)}{u(x,t)}\right) = f_N(N(x,t),\overline{Q}) + \vartheta_N(x,t;\overline{Q})\left(\frac{U(x,t)}{u(x,t)} - \overline{Q}\right)$$

for $N = R, S$, where

$$\vartheta_N(x,t;\overline{Q}) = \int_0^1 \frac{\partial f_N}{\partial Q}\left(N(x,t), s\frac{U(x,t)}{u(x,t)} + (1-s)\overline{Q}\right) ds \leq 0;$$

and also

$$\mu\left(\frac{U(x,t)}{u(x,t)}\right) = \mu(\overline{Q}) + \xi(x,t;\overline{Q})\left(\frac{U(x,t)}{u(x,t)} - \overline{Q}\right),$$

where $\xi(x,t;Q)$ is given in (4.5). Then $\tilde{H} := U - \overline{Q}u$ satisfies the differential inequality

$$\begin{aligned}
&\tilde{H}_t - \left(d(x)\tilde{H}_x - \nu(x)\tilde{H}\right)_x + m\tilde{H} \\
&= f_R\left(R, \frac{U}{u}\right)u + f_S\left(S, \frac{U}{u}\right)u - \mu\left(\frac{U}{u}\right)\overline{Q}\ u \\
&= [\vartheta_R(x,t;\overline{Q}) + \vartheta_S(x,t;\overline{Q}) - \xi(x,t;\overline{Q})\overline{Q}]\left(\frac{U(x,t)}{u(x,t)} - \overline{Q}\right)u \\
&\qquad + [f_R(R,\overline{Q}) + f_S(S,\overline{Q}) - \mu(\overline{Q})\overline{Q}]u \\
&\leq \tilde{E}(x,t)\tilde{H},
\end{aligned}$$

where we used (4.8), and

$$\tilde{E}(x,t) = \vartheta_R(x,t;\overline{Q}) + \vartheta_S(x,t;\overline{Q}) - \xi(x,t;\overline{Q})\overline{Q} < 0,$$

due to (H1) and (H2). Since $\tilde{H}$ also satisfies the homogeneous boundary condition

$$\mathbb{B}^x[\tilde{H}] = 0, \quad \text{for } x = 0 \text{ or } L,\ t \in [0,\tau),$$

and, by our choice of $\overline{Q}$, $\tilde{H}(x,0) \le 0$, we deduce by comparison that $U(x,t) - \overline{Q}u(x,t) = \tilde{H}(x,t) \le 0$ for all $x \in [0,L]$ and $t \in [0,\tau)$. This proves (4.2).

Finally, we prove (4.4). From (2.3), it follows that for each $\eta > 0$, there exists an $\epsilon > 0$ such that

$$f_R(R^*(x)+\epsilon, Q^*+\eta)+f_S(S^*(x)+\epsilon, Q^*+\eta)-\mu(Q^*+\eta)(Q^*+\eta) \le 0 \quad \text{for } x \in [0,L]. \tag{4.9}$$

By Lemma 4.1, we may assume without loss (by translation in t) that

$$R(x,t) \le R^*(x)+\epsilon \quad \text{and} \quad S(x,t) \le S^*(x)+\epsilon \quad \text{for all } x \in [0,L], t \ge 0. \tag{4.10}$$

Given a solution (R,S,U,u), define by Mean Value Theorem the functions

$$\vartheta_N(x,t;Q^*+\eta) = \int_0^1 \frac{\partial f_N}{\partial Q}\left(N(x,t), s\frac{U(x,t)}{u(x,t)} + (1-s)(Q^*+\eta)\right) ds \le 0,$$

and

$$\xi(x,t;Q^*+\eta) = \int_0^1 \mu'\left(s\frac{U(x,t)}{u(x,t)} + (1-s)(Q^*+\eta)\right) ds > 0,$$

so that

$$f_N\left(N, \frac{U}{u}\right) = f_N(N, Q^*+\eta) + \vartheta_N(x,t;Q^*+\eta)\left(\frac{U}{u} - Q^* - \eta\right)$$

for $N = R, S$, and

$$\mu\left(\frac{U}{u}\right) = \mu(Q^*+\eta) + \xi(x,t;Q^*+\eta)\left(\frac{U}{u} - Q^* - \eta\right).$$

Then $H_\eta := U - (Q^*+\eta)u$ satisfies

$$\begin{aligned}
&(H_\eta)_t - (d(x)(H_\eta)_x - \nu(x)H_\eta)_x + mH_\eta \\
&= f_R\left(R, \frac{U}{u}\right)u + f_S\left(S, \frac{U}{u}\right)u - \mu\left(\frac{U}{u}\right)(Q^*+\eta)u \\
&= [\vartheta_R(x,t;Q^*+\eta) + \vartheta_S(x,t;Q^*+\eta) - \xi(x,t;Q^*+\eta)(Q^*+\eta)]\left(\frac{U}{u} - Q^* - \eta\right)u \\
&\qquad + [f_R(R,Q^*+\eta) + f_S(S,Q^*+\eta) - \mu(Q^*+\eta)(Q^*+\eta)]u \\
&\le E(x,t)H_\eta,
\end{aligned}$$

where

$$E(x,t) = \vartheta_R(x,t;Q^*+\eta) + \vartheta_S(x,t;Q^*+\eta) - \xi(x,t;Q^*+\eta)(Q^*+\eta) < 0$$

by (4.9) and (4.10). Hence we may once again conclude by comparison with $\overline{H}(x,t) = B\rho_0(x,t)$ that

$$\limsup_{t\to\infty}\left\{\sup_{x\in[0,L]}[U(x,t)-(Q^*+\eta)u(x,t)]\right\} \leq 0, \text{ for all } \eta > 0.$$

This proves that (4.4) hols for all $Q > Q^*$. The last claim follows by letting $\eta \searrow 0$, which is possible if $\|u(\cdot,t)\|$ is bounded uniformly in t. □

Corollary 4.1. *Suppose the hypothesis of Theorem 2.1 hold. Let*

$$(R(x,t), S(x,t), U(x,t), u(x,t))$$

be a solution of (1.15) *for* $t \in [0,\tau)$. *If the initial data satisfies* $(R^0, S^0, U^0, u^0) \in \mathbf{Y}$ *(resp.* $\mathbf{Y}_1$*), then* $(R(\cdot,t), S(\cdot,t), U(\cdot,t), u(\cdot,t)) \in \mathbf{Y}$ *(resp.* $\mathbf{Y}_1$*) for all* $t \in [0,\tau)$.

Proof. It suffices to show that if $(R_0, S_0, U_0, u_))\in \mathbf{Y}_1$, then $(R,S,U,u) \in \mathbf{Y}_1$ for all $t > 0$, for the rest of the corollary follows immediately from Lemma 4.2. Note that $(R_0, S_0) \leq_D (R^*, S^*)$ and $U_0 - Q^* u_0 \leq 0$, and Lemma 4.1 says that $(R(\cdot,t), S(\cdot,t) \leq_D (R^*, S^*)$ for all $t > 0$. Hence one may actually take $\eta = 0$ in the proof of (4.4) to show that $H_0 := U - Q^* u \leq 0$ for all x and t. □

4.2 Proof of Theorem 2.1

Proof of Theorem 2.1. We rewrite μ, f_N $(N = R, S)$ as follows:

$$\tilde{\mu}(U,u) = \begin{cases} 0 & \text{when } u = 0, \\ \mu(U/u)u & \text{when } u > 0, \end{cases} \tag{4.11}$$

and

$$\tilde{f}_N(N,U,u) = \begin{cases} 0 & \text{when } u = 0, \\ f_N(N,U/u)u & \text{when } u > 0, \end{cases} \tag{4.12}$$

Then (1.15) can be written as

$$\begin{cases} R_t = (D_R(x)R_x)_x - \tilde{f}_R(R,U,u) - \omega_r R + \omega_s S, \ x \in (0,L), \ t>0, \\ S_t = (D_S(x)S_x)_x - \tilde{f}_S(S,U,u) + \omega_r R - \omega_s S, \ x \in (0,L), \ t>0, \\ U_t = (d(x)U_x - \nu(x)U)_x + \tilde{f}_R(R,U,u) + \tilde{f}_S(S,U,u) - mU, \ x \in (0,L), \ t>0, \\ u_t = (d(x)u_x - \nu(x)u)_x + \tilde{\mu}(U,u)u - mu, \ x \in (0,L), \ t>0, \\ \mathcal{B}_{N,x}[N] = c_{N,x} \geq 0, \ N = R,S, \ x = 0 \text{ or } L, \ t>0, \\ \mathbb{B}^x[w] = 0, \ \ w = U,u, \ x = 0 \text{ or } L, \ t>0, \\ w(x,0) = w^0(x) \geq (\not\equiv) 0, \ w = R,S,U,u, \ x \in (0,L). \end{cases} \tag{4.13}$$

Observe that $\tilde{\mu}$ and $\tilde{f}_N$ $(N = R,S)$, when regarded as mappings in $\mathbf{Y}$, are Lipschitz continuous. It follows from Lemma 4.2 and [19, Thm 3.3.3] that for each initial condition $(R^0,S^0,U^0,u^0) \in \mathbf{Y}$, there exists $\tau > 0$ and a unique solution (R,S,U,u) of (4.13) in $[0,\tau)$ satisfying $(R(\cdot,t),S(\cdot,t),U(\cdot,t),u(\cdot,t)) \in \mathbf{Y}$. Next we claim that every solution of (1.15) with initial condition in $\mathbf{Y}$ exists for all time, i.e. $\tau = +\infty$. Observe that by Lemmas 4.1 and 4.2, $\|(R,S)\|$ and the ratio $\|U/u\|$ remains bounded uniformly in $t \in [0,\tau)$. Therefore if $\tau < +\infty$, then we must have $\lim_{t \nearrow \tau} \|(U(\cdot,t),u(\cdot,t))\| = +\infty$. However, by regarding the equations for (U,u) in (1.15) as a linear equation with bounded coefficients, we deduce that

$$\sup_{[0,\tau)} \|(U(\cdot,t),u(\cdot,t))\| < +\infty \text{ if } \ \tau < +\infty.$$

This contradiction proves that $\tau = +\infty$, i.e., solutions to system (1.15) exists for all time. This proves (i).

For (ii), fix $\bar{Q} > Q^*$ and $C_0 > 0$, then there is $\hat{Q} \gg 1$ such that any initial condition in $\{(R,S,U,u) \in \mathbf{Y}_{\bar{Q}} : \|(R,S)\| \leq C_0\}$ determines uniquely a trajectory $(R(\cdot,t),S(\cdot,t),U(\cdot,t),u(\cdot,t))$ in $\mathbf{Y}_{\hat{Q}}$, where $\mathbf{Y}_{\bar{Q}}$ is defined in Theorem 2.1 (ii). So that we may use the Lipschitz dependence of $\tilde{\mu}$, $\tilde{f}_N$ defined at the beginning of the proof to show that solutions depends continuously in their initial conditions in $\{(R,S,U,u) \in \mathbf{Y}_{\bar{Q}} : \|(R,S)\| \leq C_0\}$. Since $C_0 > 0$ is arbitrary, we have proved (ii).

Finally, (iii) and (iv) follow from (4.3) and Proposition 2.1 respectively. □

5 A nonlinear eigenvalue problem

We will use a recent generalization of Krein-Rutman Theorem involving two different cones due to Mallet-Paret and Nussbaum [35]. We start by giving some notations.

Let $(\tilde{\mathbf{X}}, \|\cdot\|)$ be a *normed linear space* (or NLS) over $\mathbb{R}$. We call a subset $C \subset \tilde{\mathbf{X}}$ a *cone* if (i) C is convex, (ii) $tC \subset C$ for all $t \geq 0$, and (iii) $C \cap (-C) = \{0\}$. A cone C is said to be *solid* if it has non-empty interior. It is *normal* if there exists $M > 0$ such that $\|x\| \leq M\|y\|$ whenever $x \leq_C y$.

If C is a cone and also a complete metric space in the metric induced by the norm on $\tilde{\mathbf{X}}$, we call C a complete cone. A cone C in an NLS $(\tilde{\mathbf{X}}, \|\cdot\|)$ induces a partial ordering $\leq_C$ on $\tilde{\mathbf{X}}$ by $x \leq_C y$ if and only if $y - x \in C$. If C is a solid cone, we say that $x \ll_C y$ if and only if $y - x \in \operatorname{Int} C$. Observe that if C is a solid cone, $0 \ll_C x$ and $0 \ll_C y$, then $tx \ll_C y$ for some $t > 0$.

A mapping $\mathbf{T} : C \to C$ is *homogeneous of degree one* if, for each $t \geq 0$ and each $x \in C$,

$$\mathbf{T}(tx) = t\mathbf{T}(x).$$

Let $D \subset \tilde{\mathbf{X}}$ be another cone such that $C \subset D$. A mapping $\mathbf{T} : C \to C$ is *D-order-preserving* if $\mathbf{T}(x) \leq_D \mathbf{T}(y)$ whenever $x, y \in C$ satisfy $x \leq_D y$. Here $\leq_D$ is the partial order generated by the cone D. If D is a solid cone, we say that $\mathbf{T}$ is *D-strongly-order-preserving* if $\mathbf{T}(x) \ll_D \mathbf{T}(y)$ whenever $x, y \in C$ satisfy $x \leq_D y$ and $x \neq y$. Recall also the *Bonsall cone spectral radius* (see [34, 35, 44])

$$\tilde{r}_C(\mathbf{T}) := \lim_{m\to\infty} \|\mathbf{T}^m\|_C^{1/m} = \inf_{m\geq 1} \|\mathbf{T}^m\|_C^{1/m},$$

where $\|\mathbf{T}^m\|_C := \sup\{\|\mathbf{T}^m(x)\| : x \in C \text{ and } \|x\| \leq 1\}$. We impose the following:

(C) Let $C \subset D$ be complete cones in an NLS $(\tilde{\mathbf{X}}, \|\cdot\|)$, D be normal, and $\mathbf{T} : C \to C$ be (i) continuous, (ii) compact, (iii) homogeneous of degree one, and (iv) D-order-preserving.

Theorem 5.1 ([35, Theorem 4.9])**.** *Assume* **(C)** *holds. If the Bonsall cone spectral radius satisfies $\tilde{r}_C(\mathbf{T}) > 0$, then there is $v \in C \setminus \{0\}$ such that $\mathbf{T}v = \tilde{r}_C v$.*

Proof. This is a special case of [35, Theorem 4.9], by setting the operator g in the statement of the theorem to be zero. □

Corollary 5.2. *Assume* **(C)** *holds. If, in addition, D is a solid cone and $\mathbf{T}$ is D-strongly-order-preserving, then*

(a) $\tilde{r} = \tilde{r}_C(\mathbf{T}) > 0$ and there is a non-zero eigenvector $\tilde{x} \in C \cap \operatorname{int} D$ such that

$$\mathbf{T}\tilde{x} = \tilde{r}\tilde{x}.$$

(b) If $x' \in C$ is an eigenvector of $\mathbf{T}$, then $x' \in span\{\tilde{x}\}$ and $\mathbf{T}x' = \tilde{r}x'$.

Proof. Take any $y_0 \in C \setminus \{0\}$, then $\mathbf{T}y_0 \gg_D 0$ and hence $\mathbf{T}y_0 \geq_D r_0 y_0$ for some $r_0 > 0$ and hence $\tilde{r} = \tilde{r}_C(\mathbf{T}) \geq r_0 > 0$. It then follows from Theorem 5.1 that $T\tilde{x} = \tilde{r}\tilde{x}$ for some non-zero eigenvector $\tilde{x} \in C \setminus \{0\}$. Moreover, $\tilde{x} \in C \cap \operatorname{Int} D$ since $\mathbf{T}$ is D-strongly-order-preserving. This proves (a).

Next, we show (b). First, let $x' \in C \setminus \{0\}$ be an eigenvector of $\tilde{r}$, i.e. $\mathbf{T}x' = \tilde{r}x'$. We have $c_1 := \inf\{c > 0 : x' \leq_D c\tilde{x}\}$ is positive. By monotonicity of $\mathbf{T}$,

$$x' = \frac{1}{\tilde{r}}\mathbf{T}x' \leq_D \frac{1}{\tilde{r}}\mathbf{T}(c_1\tilde{x}) = c_1\tilde{x} \tag{5.1}$$

By definition of c_1, we see that $\mathbf{T}x' \ll_D \mathbf{T}(c_1\tilde{x})$ is impossible. Hence, by D-strongly-order-preserving property of $\mathbf{T}$, equality holds in (5.1). In particular, $x' = c_1\tilde{x}$. This proves that $\tilde{r}$ is simple.

It remains to show that $\tilde{r}$ is the unique eigenvalue of $\mathbf{T}$ corresponding to an eigenvector in $C \setminus \{0\}$. Suppose $\mathbf{T}x' = r'x'$, for some $r' \in \mathbb{C}$ and $x' \in C \setminus \{0\}$. By definition of $\mathbf{T}$ and the cone C, it must be the case that $r' \in \mathbb{R}$. As $\mathbf{T}x', x' \in C \setminus \{0\}$ and $C \cap (-C) = \{0\}$, we must have $r' \geq 0$. Also, $\mathbf{T}$ is D-strongly-order-preserving, so that $r' > 0$ and $x' \in C \cap \operatorname{Int} D$. In particular $\tilde{x}, x' \in C \cap \operatorname{Int} D$ and there are positive constants c_2, c_3 such that $c_2\tilde{x} \ll_D x' \ll_D c_3\tilde{x}$. Applying $\mathbf{T}^n$, we have

$$c_2\tilde{r}^n\tilde{x} \leq_D (r')^n x' \leq_D c_3\tilde{r}^n\tilde{x} \qquad \text{for all } n \geq 1.$$

This proves that $r' = \tilde{r}$ and completes the proof of assertion (b). □

The following result is concerned with the existence of the principal eigenvalue of the nonlinear eigenvalue problem (2.8). From this point onwards, let $D = C^0([0,L], \mathbb{R}^2_+)$ and

$$C = \{(U,u) \in D : Q_{\min}u(x) \leq U(x) \leq Q^* u(x) \text{ for } x \in [0,L]\},$$

where Q^* is given in (2.3). It is clear that both are complete cones and that D is both normal and solid.

Lemma 5.1. *Suppose the hypotheses of Theorem 2.1 hold. For each $d(x) > 0$ and $\nu(x) \geq 0$, the eigenvalue problem* (2.8) *admits a principal eigenvalue Λ^0 corresponding to which there is a strongly positive eigenfunction $(\varphi^0(x), \phi^0(x)) \gg_D 0$.*

Proof of Lemma 5.1. We first consider the following system

$$\begin{cases} U_t = (d(x)U_x - \nu(x)U)_x + f_R(R^*(x), \frac{U}{u})u + f_S(S^*(x), \frac{U}{u})u, \ \ x \in (0, L), \ t > 0, \\ u_t = (d(x)u_x - \nu(x)u)_x + \mu(\frac{U}{u})u, \ \ x \in (0, L), \ t > 0, \\ \mathbb{B}^x[w] = 0, \ \ w = U, u, \ x = 0 \text{ or } L, \ t > 0, \\ w(x, 0) = w^0(x) \geq (\not\equiv) 0, \ \ w = U, u, \ x \in (0, L), \end{cases} \tag{5.2}$$

where $(R^*(x), S^*(x))$ is given by Proposition 2.1. Substituting $U(x,t) = e^{-\Lambda t}\varphi(x)$, and $u(x,t) = e^{-\Lambda t}\phi(x)$ into (5.2), we obtain the associated nonlinear eigenvalue problem (2.8).

By an argument analogous to Theorem 2.1, one may deduce that (5.2) generates a semiflow Φ_t on C. It is easy to see that for all $t > 0$, Φ_t is continuous, compact and homogeneous of degree one. To apply Corollary 5.2, we need to show that for each $t > 0$, $\Phi_t : C \to C$ is D-strongly-order-preserving. For this purposes, suppose $(U_1, u_1) <_D (U_2, u_2)$ (i.e. $(U_1, u_1) \leq_D (U_2, u_2)$ but $(U_1, u_1) \neq (U_2, u_2)$). Then by rewriting f_R, f_S, μ as in (4.11) and (4.12), one can deduce that $(U_2 - U_1, u_2 - u_1)$ satisfies a linear cooperative system, whose coefficients are L^∞ bounded by the fact that $(U_i, u_i) \in C$ for $i = 1, 2$. By the (strong) maximum principle for linear cooperative system [38], the semiflow is D-strongly-order-preserving. Hence for each $t > 0$, we may apply Corollary 5.2 to the operator $\Phi_t : C \to C$ to obtain $\tilde{r}(t)$ and $(\varphi(t), \phi(t)) \in C \cap \operatorname{Int} D$ with $\|(\varphi(t), \phi(t))\| = 1$ such that

$$\Phi_t(\varphi(t), \phi(t)) = \tilde{r}(t)(\varphi(t), \phi(t)). \tag{5.3}$$

Claim 5.1. *$t^{-1} \log \tilde{r}(t)$ and $(\varphi(t), \phi(t))$ are independent of $t > 0$.*

To this end, we take $t_n = 2^{-n}$. Now, for any $0 \leq n \leq m$, observe that

$$\Phi_{t_n}(\varphi(t_m), \phi(t_m)) = (\tilde{r}(t_m))^{t_n/t_m}(\varphi(t_m), \phi(t_m))$$

so that $(\varphi(t_m), \phi(t_m))$ is an eigenfunction of Φ_{t_n} in C as well. As Corollary 5.2 asserts that there is only one possible normalized eigenfunction in C, we must then have $(\varphi(t_m), \phi(t_m)) = (\varphi(t_n), \phi(t_n))$ and $\tilde{r}(2^{-n}) = [\tilde{r}(2^{-m})]^{2^{m-n}}$. Thus Claim 5.1

holds for all dyadic numbers $t = k2^{-n}$ for $k, n \in \mathbb{N}$. Finally, Claim 5.1 follows by continuity.

Finally, we define

$$\Lambda^0 := -t^{-1} \log \tilde{r}(t) \equiv -\log \tilde{r}(1), \tag{5.4}$$

where $\tilde{r}(1)$ is the Bonsall cone spectral radius of $\Phi_1 : C \to C$, so that $\Lambda^0 \in \mathbb{R}$ is the principal eigenvalue of (2.8). $\square$

6 Threshold Dynamics of System (1.15)

In Subsection 6.1, we prove the eventual boundedness of trajectories for system (1.15). In Subsection 6.2, we apply the results of Section 5 and persistence theory to prove Theorem 2.2.

6.1 Eventual Boundedness of Solutions

In this subsection we give a proof of Proposition 2.2.

Proof of Proposition 2.2. For each $(\Theta_R(x),\ \Theta_S(x)) \in C([0, L]; \mathbb{R}_+^2)$, consider the following eigenvalue problem

$$\begin{cases} (d(x)\varphi'(x) - \nu(x)\varphi(x))' + f_R\left(\Theta_R(x), \frac{\varphi(x)}{\phi(x)}\right)\phi(x) \\ \qquad +f_S\left(\Theta_S(x), \frac{\varphi(x)}{\phi(x)}\right)\phi(x) - m\varphi(x) + \Lambda\varphi(x) = 0, \ \ x \in (0, L), \\ (d(x)\phi'(x) - \nu(x)\phi(x))' + \mu\left(\frac{\varphi(x)}{\phi(x)}\right)\phi(x) - m\phi(x) + \Lambda\phi(x) = 0, \ \ x \in (0, L), \\ \mathbb{B}^x[w] = 0, \ \ w = \varphi,\ \phi,\ x = 0 \text{ or } L. \end{cases} \tag{6.1}$$

Let $(R^*(x), S^*(x))$ be given by Proposition 2.1. We recall the definition of Q^* from (2.3).

Claim 6.1. *Let condition (H4) hold, and σ_1 be the principal eigenvalue of the eigenvalue problem*

$$\begin{cases} (d(x)\phi'(x) - \nu(x)\phi(x))' - m\phi(x) + \sigma\phi(x) = 0, \ \ x \in (0, L), \\ \mathbb{B}^x[\phi] = 0, \ x = 0 \ \textit{or} \ L. \end{cases} \tag{6.2}$$

Then $\sigma_1 > 0$.

It is easy to see that $\phi_0(x) = \exp\left(\int_0^x \frac{\nu(y)}{d(y)}\right) dy > 0$ satisfies

$$\begin{cases}(d(x)\phi_0'(x) - \nu(x)\phi_0(x))' - m\phi_0(x) = -m\phi_0(x) \leq 0, \;\; x \in (0, L), \\ \mathbb{B}^x[\phi_0] = b^x\phi_0(x) \geq 0, \;\; x = 0 \text{ or } L,\end{cases}$$

such that one of the inequalities is strict (due to (H4)), i.e. ϕ_0 is a strict supersolution. Then Claim 6.1 follows from [1, Theorem 2.4].

Claim 6.2. *There exists* $(\Theta_R(x), \Theta_S(x)) \in C([0, L]; \mathbb{R}^2_+)$ *satisfying*

$$\begin{cases} (0, 0) \ll_D (\Theta_R(x), \Theta_S(x)) \ll_D (R^*(x), S^*(x)), \;\; \forall\, x \in [0, L], \\ \mathcal{B}_{N,x}[\Theta_N(x)] = c_{N,x}, \;\; N = R, S, \;\; x = 0 \text{ or } L.\end{cases}$$

such that if we denote the corresponding principal eigenvalue and eigenfunction of (6.1) *by* $\bar{\Lambda}_0^{\Theta}$ *and* $(\bar{\varphi}_0^{\Theta}, \bar{\phi}_0^{\Theta})$ *respectively, then* $\bar{\Lambda}_0^{\Theta} > 0$.

For $(\Theta_R(\cdot), \Theta_S(\cdot)) \leq_D (R^*(\cdot), S^*(\cdot)),\ \forall\, x \in [0, L]$, we can use the same arguments in Lemma 5.1 to show that the eigenvalue problem (6.1) admits a principal eigenvalue $\bar{\Lambda}_0^{\Theta} := \bar{\Lambda}_0(\Theta_R(x), \Theta_S(x))$ corresponding to which there is a strongly positive eigenfunction $(\bar{\varphi}_0^{\Theta}(x), \bar{\phi}_0^{\Theta}(x))$ satisfying $Q_{\min}\bar{\phi}_0^{\Theta}(x) \leq \bar{\varphi}_0^{\Theta}(x) \leq Q^*\bar{\phi}_0^{\Theta}(x)$ for $x \in [0, L]$. Further, we can use compactness arguments to show that

$$\bar{\Lambda}_0(\Theta_R(x), \Theta_S(x)) \to \sigma_1 > 0 \text{ as } (\Theta_R(x), \Theta_S(x)) \to (0, 0) \text{ in } C([0, L]; \mathbb{R}^2_+),$$

where σ_1 is the principal eigenvalue of (6.2). This proves Claim 6.2.

By Theorem 2.1(iii), $\mathbf{Y}_1$ is globally attracting, so given a solution (R, S, U, u) of (1.15), we may assume without loss (by replacing t with $t + C$) that

$$(R(x, t), S(x, t)) \leq_D 2(R^*(x), S^*(x)), \;\; \forall\, x \in [0, L], \;\; t \geq 0, \tag{6.3}$$

and that

$$Q_{\min}u(x, t) - 1 \leq U(x, t) \leq 2Q^*u(x, t) + Q^*, \;\; \forall\, x \in [0, L], \;\; t \geq 0, \tag{6.4}$$

where Q^* is given in (2.3). Let

$$M(t) = \max\{\|U(\cdot, t)\|, \; \|u(\cdot, t)\|\}.$$

Claim 6.3. *There exists* $M_1 > 1$ *such that if* $M(t_1) = M_1$, *then*

$$(R(x, t), S(x, t)) \leq_D (\Theta_R(x), \Theta_S(x)), \;\; \forall\, x \in [0, L], \;\; t \in [t_1 + 2, t_1 + 3].$$

We will specify M_1 later. To prove Claim 6.3, we first note that if $M(t_1) = M_1$, then

$$\text{either } \|U(\cdot, t_1)\| = M_1 \text{ or } \|u(\cdot, t_1)\| = M_1.$$

Regarding $f_N(N, \frac{U}{u})$ and $\mu(\frac{U}{u})$ as the given functions, and using the boundedness of $\frac{U}{u}$, R, and S, we may apply the parabolic Harnack inequality [31, Theorem 7.36] to deduce that

$$\inf_{0<x<L,\ t_1+1<t<t_1+3} U(x,t) \geq C_1 M_1 \quad \text{or} \quad \inf_{0<x<L,\ t_1+1<t<t_1+3} u(x,t) \geq C_1 M_1, \tag{6.5}$$

for some $C_1 > 0$ independent of M_1. By (6.4) and (6.5), it follows that

$$\inf_{[0,L]\times[t_1+1,t_1+3]} U(x,t) \geq C_2 M_1 - 1 \quad \text{and} \quad \inf_{[0,L]\times[t_1+1,t_1+3]} u(x,t) \geq C_2 M_1 - 1, \tag{6.6}$$

where $C_2 = C_1 \min\{Q_{\min}, 1/(2Q^*)\}$ is again independent of M_1.

Fix a smooth function $0 \leq \zeta(t) \leq 1$ satisfying

$$\zeta(t) = \begin{cases} 1, & \text{for } t \leq t_1 + 1, \\ 0, & \text{for } t \geq t_1 + 2, \end{cases}$$

and define

$$(\bar{R}(x,t), \bar{S}(x,t)) := \zeta(t) \cdot 2(R^*(x), S^*(x)) + (1 - \zeta(t))(\Theta_R(x), \Theta_S(x)).$$

We claim that, if M_1 is sufficiently large (affecting U, u which are regarded as given functions), then $(\bar{R}, \bar{S})$ is a supersolution of

$$\begin{cases} R_t = (D_R(x)R_x)_x - f_R(R, \frac{U}{u})u - \omega_r R + \omega_s S, \ x \in (0,L), \ t_1 + 1 \leq t \leq t_1 + 3, \\ S_t = (D_S(x)S_x)_x - f_S(S, \frac{U}{u})u + \omega_r R - \omega_s S, \ x \in (0,L), \ t_1 + 1 \leq t \leq t_1 + 3, \\ \mathcal{B}_{N,x}[N] = c_{N,x}, \ N = R, S, \ x = 0 \text{ or } L, \ t > 0. \end{cases} \tag{6.7}$$

To this end, we fix by Remark 2.1(ii) a constant $\epsilon_0 > 0$ so that for $N = R, S$,

$$f_N(N, Q) > 0 \quad \text{for } 0 < N \leq 2 \sup_{x\in(0,L)} N^*(x) \text{ and } Q \in [0,\ Q^*(1+\epsilon_0)]. \tag{6.8}$$

Next, observe that for $N = R,\ S$,

$$\begin{aligned} \mathcal{B}_{N,x}[\bar{N}(x,t)] &= 2\zeta(t)\mathcal{B}_{N,x}[N^*(x)] + (1-\zeta(t))\mathcal{B}_{N,x}[\Theta_N(x)] \\ &= 2\zeta(t)c_{N,x} + (1-\zeta(t))c_{N,x} \geq c_{N,x}. \end{aligned}$$

Using (6.4),

$$\frac{U}{u} \leq Q^* \left(1 + \frac{1}{u}\right) \leq Q^*(1+\epsilon_0) \quad \text{in } (0,L)\times(t_1+1, t_1+3), \tag{6.9}$$

provided that $M_1 \geq \frac{1}{C_2}\left(\frac{1}{\epsilon_0}+1\right)$, where ϵ_0 is given in (6.8). Since $(R^*(x), S^*(x))$ satisfies (2.1), we have

$$\begin{aligned}
&\bar{R}_t - \left(D_R(x)\bar{R}_x\right)_x + f_R(\bar{R}, \frac{U}{u})u + \omega_r \bar{R} - \omega_s \bar{S} \\
&= \zeta'(t)(2R^*(x) - \Theta_R(x)) + f_R(\bar{R}, \frac{U}{u})u \\
&\quad +(1-\zeta(t))[(-D_R(x)\Theta_R'(x))' + \omega_r \Theta_R(x) - \omega_s \Theta_S(x)] \\
&\geq -C_3 + f_R(\Theta_R(x), Q^*(1+\epsilon_0))) \cdot [\inf_{[0,L]\times[t_1+1,t_1+3]} u(x,t)] \\
&\geq -C_3 + C_4 M_1 \geq 0,
\end{aligned}$$

where $C_3 > 0$ is some constant independent of M_1, and, by (6.8),

$$C_4 := C_2 \inf_{x\in(0,L)} f_R(\Theta_R(x), Q^*(1+\epsilon_0))$$

is positive and independent of $M_1 \geq \frac{1}{C_2}\left(\frac{1}{\epsilon_0}+1\right)$; and we have chosen M_1 larger so that $M_1 \geq C_3/C_4$. Similarly,

$$\begin{aligned}
&\bar{S}_t - \left(D_S(x)\bar{S}_x\right)_x + f_S(\bar{S}, \frac{U}{u})u - \omega_r \bar{R} + \omega_s \bar{S} \\
&\geq -C_5 + C_6 M_1 \geq 0,
\end{aligned}$$

for some $C_5 > 0$ and $C_6 > 0$ and by choosing $M_1 \geq C_5/C_6$. By Comparison Principle, it follows that

$$(R(x,t), S(x,t)) \leq_D (\bar{R}(x,t), \bar{S}(x,t)),\ \forall\ x \in [0,L],\ t \in [t_1+1, t_1+3].$$

In particular,

$$(R(x,t), S(x,t)) \leq_D (\Theta_R(x), \Theta_S(x)),\ \forall\ x \in [0,L],\ t \in [t_1+2, t_1+3]. \tag{6.10}$$

This proves Claim 6.3.

Claim 6.4. *Let M_1 be given by Claim 6.3.*

(i) *There exists $t'_k \to \infty$ such that $M(t'_k) < M_1$.*

(ii) *There exists $T_1 > 0$ (depending on M_1 only) such that if for some $t_1 < t_2$, $M(t_1) = M(t_2) = M_1$ and $M(t) > M_1$ for $t \in (t_1, t_2)$, then $t_2 - t_1 < T_1$.*

Let $\bar\Lambda_0^\Theta > 0$ and $(\bar\varphi_0^\Theta(x), \bar\phi_0^\Theta(x))$ be given by Claim 6.2. First we show Claim 6.4(i). Assume to the contrary that $M(t) \geq M_1$ for all $t \geq t_1$. Then by Claim 6.3, it follows that $(R(x,t), S(x,t)) \leq_D (\Theta_R(x), \Theta_S(x))$, $\forall\ x \in [0, L]$, $t \geq t_1 + 2$. By (6.3) and (6.4), we see that U, u satisfies a linear system with bounded coefficients, so that there is a constant C_7 such that $M(t_1 + 2) \leq C_7 M(t_1)$. Now, if we choose C_8 such that $(1,1) \leq_D C_8(\bar\varphi_0^\Theta, \bar\phi_0^\Theta)$, then

$$(U(\cdot, t_1+2), u(\cdot, t_1+2))) \leq_D M(t_1+2)(1,1) \leq_D C_9 M(t_1)(\bar\varphi_0^\Theta, \bar\phi_0^\Theta).$$

for some constant $C_9 = C_7 C_8$ independent of initial condition. Hence,

$$(\bar U(x,t), \bar u(x,t)) := C_9 M(t_1) e^{-\bar\Lambda_0^\Theta (t - t_1 - 2)}(\bar\varphi_0^\Theta(x), \bar\phi_0^\Theta(x))$$

satisfies the following inequalities:

$$\begin{cases} \overline{U}_t = \left(d(x)\overline{U}_x - \nu(x)\overline{U}\right)_x + f_R(\Theta_R(x), \frac{\overline{U}}{\overline{u}})\overline{u} + f_S(\Theta_S(x), \frac{\overline{U}}{\overline{u}})\overline{u} - m\overline{U} \\ \geq \left(d(x)\overline{U}_x - \nu(x)\overline{U}\right)_x + f_R(R(x,t), \frac{\overline{U}}{\overline{u}})u + f_S(S(x,t), \frac{\overline{U}}{\overline{u}})\overline{u} - m\overline{U}, \quad x \in (0, L), \\ \overline{u}_t = (d(x)\overline{u}_x - \nu(x)\overline{u})_x + \mu(\frac{\overline{U}}{\overline{u}})\overline{u} - m\overline{u}, \quad x \in (0, L), \\ \mathbb{B}^x[w] = 0, \quad w = U, u, \ x = 0 \text{ or } L, \\ (\bar U(\cdot, t_1+2), \bar u(\cdot, t_1+2)) \geq_D (U(\cdot, t_1+2), u(\cdot, t_1+2)). \end{cases} \tag{6.11}$$

for the time interval $t \geq t_1 + 2$. Therefore, by comparison, we have $(U, u) \leq_D (\overline{U}, \overline{u})$ for $t \geq t_1 + 2$, i.e.

$$M(t) \leq C_9 M(t_1) e^{-\bar\Lambda_0^\Theta (t - t_1 - 2)} \qquad \text{for } t \geq t_1 + 2.$$

This contradicts $M(t) \geq M_1$ for all $t \geq t_1$, and proves Claim 6.4(i). To prove Claim 6.4(ii), let $M(t_1) = M(t_2) = M_1$ and $M(t) > M_1$ in (t_1, t_2). If $t_2 - t_1 \leq 2$, then we are done. If $t_2 - t_1 > 2$, then from the preceding arguments we have

$$M_1 = M(t_2) \leq C_9 M_1 e^{-\bar\Lambda_0^\Theta (t_2 - t_1 - 2)},$$

i.e.

$$t_2 - t_1 \leq T_1 := 2 + \frac{\log C_9}{\bar\Lambda_0^\Theta}.$$

This proves Claim 6.4(ii).

Claim 6.5. *There exists $M_2 > 0$ such that $\limsup_{t\to\infty} M(t) \leq M_2$, regardless of initial condition.*

If $M(t) \leq M_1$ for all t, then there is nothing to prove. If $M(t_0) > M_1$ for some t_0, then by Claim 6.4, we can find a finite (maximal) interval $(t_1, t_2) \ni t_0$ such that $M(t_1) = M(t_2) = M_1$, $M(t) > M_1$ in (t_1, t_2) and $t_2 - t_1 < T_1$. Since M_1 is fixed (Claim 6.3), $T_1 > 0$ is independent of initial data (Claim 6.4(ii)). One can define a constant $M_2 = M_2(M_1, T_1)$ by $M_2 := \sup M(t)$, where the supremum is taken over $0 \leq t \leq T_1$ and initial condition satisfying

$$(0,0) \leq_D (R_0, S_0) \leq_D 2(R^*(\cdot), S^*(\cdot)), \quad \|U_0\| \leq M_1 \quad \text{and} \quad \|u_0\| \leq M_1.$$

By assumption, $M(t_1) \leq M_1$, $t_2 - t_2 \leq T_1$ and $0 \leq_D (R(\cdot, t_1), S(\cdot, t_1)) \leq_D 2(R^*(\cdot), S^*(\cdot))$. Hence we conclude, by the fact that the semiflow is autonomous, that $\sup_{(t_1,t_2)} M(t) \leq M_2$. This proves Claim 6.5. □

6.2 Proof of Theorem 2.2

Recall the definition of $\mathbf{Y}$ in (2.6), and define $\mathbf{Y}_0 := \{(R, S, U, u) \in \mathbf{Y} : u \not\equiv 0 \text{ in } [0, L]\}$, and the complementary set

$$\begin{aligned}\partial\mathbf{Y}_0 := \mathbf{Y} - \mathbf{Y}_0 &= \{(R, S, U, u) \in \mathbf{Y} : u \equiv 0 \text{ in } [0, L]\} \\ &= \{(R, S, U, u) \in \mathbf{Y} : U \equiv u \equiv 0 \text{ in } [0, L]\},\end{aligned}$$

so that $\mathbf{Y} = \mathbf{Y}_0 \cup \partial\mathbf{Y}_0$. Next, we define the function $p : \mathbf{Y} \to [0, \infty)$ by

$$p(P^0) = p(R^0, S^0, U^0, u^0) = \min_{[0,L]} u^0(\cdot).$$

It is easy to see that p is continuous, and satisfies $p(\Psi_t(P^0)) > 0$ for $t > 0$ if either $p(P^0) > 0$, or $p(P^0) = 0$ with $P^0 \in \mathbf{Y}_0$. (Here we emphasize the distinction of $p : \mathbf{X} \to \mathbb{R}$ from the distance function of $\mathbf{X} = C([0, L]; \mathbb{R}^4_+)$.) We will prove the persistence result (Theorem 2.2(ii)) before the extinction results (Theorem 2.2(i)).

Since the proof of Theorem 2.2(ii) is quite lengthy, we provide a brief outline here. The goal here is to show that the semiflow is uniformly persistent with respect to the distance function p, i.e. $\liminf_{t\to\infty} p(\Phi_t(P^0)) \geq \tilde{\eta}$ for some $\tilde{\eta}$ independent of $P^0 \in \mathbf{Y}_0$. Step 1 (Claim 6.7(i)) is to show that $\{(R^*, S^*, 0, 0)\}$ is the global attractor on the invariant set $\partial\mathbf{Y}_0$. Step 2 (Claim 6.7(ii)) is to show acyclicity in $\partial\mathbf{Y}_0$. Step 3 (Claim 6.8) is to show that, for each $P^0 \in \mathbf{Y}_0$, the omega limit set (which is necessarily chain transitive) $\omega(P^0) \not\subset \{(R^*, S^*, 0, 0)\}$. Step 4 (Claim 6.9) is to show that $\{(R^*, S^*, 0, 0)\}$ is isolated in $\mathbf{Y} = \mathbf{Y}_0 \cup \partial\mathbf{Y}_0$. The above four steps allows us to apply [42, Theorem 3] (see also [39, 48]) to show that that for each compact chain transitive set L such that $L \not\subset \{(R^*, S^*, 0, 0)\}$ (such as $\omega(P^0)$, see Step 3), there exists $\tilde{\eta}$ such that $\min_{x\in L} p(x) \geq \tilde{\eta}$. Finally, by [36, Theorem 3.7 and Remark 3.10], there is a global attractor bounded away from $\partial\mathbf{Y}_0$, which implies the existence of a positive steady state.

Proof of Theorem 2.2(ii). By Lemma 4.2 (ii), $\sup_{(x,t)\in[0,L]\times[0,\infty)} \frac{U(x,t)}{u(x,t)} < \infty$ for any given trajectory. It follows then by eventual boundedness (Proposition 2.2) and standard parabolic estimates [31, Section VII.8] that system (1.15) generates a semiflow Ψ_t on $\mathbf{Y}$ with precompact trajectories in $\mathbf{X}$.

Claim 6.6. *(i) If $P^0 = (R^0, S^0, U^0, u^0) \in \mathbf{Y}_0$, then $U(x,t) > 0$ and $u(x,t) > 0$ for all $x \in [0, L]$ and $t > 0$. i.e. $\mathbf{Y}_0$ is positively invariant for Ψ_t.*

(ii) $\partial\mathbf{Y}_0$ is closed and positively invariant.

Claim 6.6 (i) follows from strong maximum principle for linear cooperative systems, and Claim 6.6 (ii) is obvious. Next, define

$$\mathbf{M} = \{(R^*(\cdot), S^*(\cdot), 0, 0)\}, \quad \text{and} \quad \mathbf{M}_\partial = \{P^0 \in \partial\mathbf{Y}_0 : \Psi_t(P^0) \in \partial\mathbf{Y}_0 \ \forall t \geq 0\},$$

where $(R^*(\cdot), S^*(\cdot))$ is the unique positive steady state of (2.1) (Proposition 2.1). By the above discussion, we see that

$$\mathbf{M}_\partial = \partial\mathbf{Y}_0.$$

Claim 6.7. *(i) $\cup_{P^0\in\mathbf{M}_\partial}\omega(P^0) = \mathbf{M}$.*

(ii) There is no homoclinic cycle from $\mathbf{M}$ to $\mathbf{M}$.

Claim 6.7 is a direct consequence of the fact that $(R^*(\cdot), S^*(\cdot), 0, 0)$ is globally asymptotically stable among all solutions of (1.15) in $M_\partial = \partial\mathbf{Y}_0$ (Proposition 2.1).

By assumption, the principal eigenvalue Λ^0 of (2.8) satisfies $\Lambda^0 + m < 0$. So there is $0 < \bar{\epsilon} \ll 1$ such that the principal eigenvalue $\bar{\Lambda}$ of the following problem is negative.

$$\begin{cases} (d(x)\varphi'(x)-\nu(x)\varphi(x))'+f_R\left(R^*(x)-\bar\epsilon,\frac{\varphi(x)}{\phi(x)}\right)\phi(x) \\ \qquad +f_S\left(S^*(x)-\bar\epsilon,\frac{\varphi(x)}{\phi(x)}\right)\phi(x)-m\varphi(x)+\bar\Lambda\varphi(x)=0,\ \ x\in(0,L), \\ (d(x)\phi'(x)-\nu(x)\phi(x))'+\mu\left(\frac{\varphi(x)}{\phi(x)}\right)\phi(x)-m\phi(x)+\bar\Lambda\phi(x)=0,\ \ x\in(0,L), \\ \mathbb{B}^x[w]=0,\ \ w=\varphi,\ \phi,\ x=0 \text{ or } L. \end{cases} \tag{6.12}$$

Claim 6.8. *There exists $\eta_1>0$ such that for any $P^0\in\mathbf{Y}_0$,*

$$\limsup_{t\to\infty}\operatorname{dist}(\Psi_t(P^0),\mathbf{M})\geq\eta_1$$

where $\operatorname{dist}((R^0(\cdot),S^0(\cdot),U^0(\cdot),u^0(\cdot)),\mathbf{M}):=\max\{\|R^0-R^*\|,\|S^0-S^*\|,\|U^0\|,\|u^0\|\}$ is the usual distance function in $\mathbf{Y}$. In particular, $W^s(R^*(\cdot),S^*(\cdot),0,0)\cap\mathbf{Y}_0=\emptyset$, where $W^s(R^*(\cdot),S^*(\cdot),0,0)$ is the stable set of $(R^*(\cdot),S^*(\cdot),0,0)$ (see [42]).

Suppose to the contrary that for some P^0, the corresponding solution $\Psi_t(P^0)=(R,S,U,u)$ satisfies $\lim_{t\to\infty}\operatorname{dist}(\Psi_t(P^0),\mathbf{M})=0$. In particular, there exists $\bar t>0$ such that

$$R(x,t)\geq R^*(x)-\bar\epsilon \quad\text{and}\quad S(x,t)\geq S^*(x)-\bar\epsilon$$

for all $x\in[0,L]$ and $t\geq\bar t$. By Claim 6.6, there exists $\bar\delta>0$ such that

$$\bar\delta\bar\varphi(x)\leq U(x,\bar t),\quad\text{and}\quad \bar\delta\bar\phi(x)\leq u(x,\bar t)\quad\text{for } x\in[0,L].$$

where $(\bar\varphi,\bar\phi)\in C\cap(\operatorname{int}D)$ is the principal eigenfunction of (6.12). Then

$$(\underline{U}(x,t),\underline{u}(x,t)):=\bar\delta e^{-\bar\Lambda(t-\bar t)}(\bar\varphi(x),\bar\phi(x)) \tag{6.13}$$

satisfies the following linear cooperative system

$$\begin{cases} \underline{U}_t=(d(x)\underline{U}_x-\nu(x)\underline{U})_x+f_R(R^*(x)-\bar\epsilon,\frac{\underline{U}}{\underline{u}})\underline{u} \\ \qquad\qquad +f_S(S^*(x)-\bar\epsilon,\frac{\underline{U}}{\underline{u}})\underline{u}-m\underline{U},\ x\in(0,L),\ t\geq\bar t, \\ \underline{u}_t=(d(x)\underline{u}_x-\nu(x)\underline{u})_x+\mu(\frac{\underline{U}}{\underline{u}})\underline{u}-m\underline{u},\ \ x\in(0,L),\ t\geq\bar t, \\ \mathbb{B}^x[w]=0,\ \ w=\underline{U},\underline{u},\ x=0 \text{ or } L,\ t\geq\bar t, \\ (\underline{U}(x,\bar t),\underline{u}(x,\bar t))\leq_D(U(x,\bar t),u(x,\bar t)),\ x\in(0,L), \end{cases}$$

for which $(U(x,t), u(x,t))$ is a supersolution in $[0,L] \times [\bar{t}, \infty)$. Therefore by comparison,

$$(U(\cdot,t), u(\cdot,t)) \geq_D (\underline{U}(\cdot,t), \underline{u}(\cdot,t)) \quad \text{for all } t \geq \bar{t}.$$

This is a contradiction as (U,u) needs to stay close to $(0,0)$, yet $\bar{\Lambda} < 0$ in (6.13). This proves Claim 6.8.

Claim 6.9. $\mathbf{M}$ *is isolated in* $\mathbf{Y}$*. i.e. there exists a neighborhood of* $\mathbf{M}$ *in* $\mathbf{Y}$ *in which* $\mathbf{M}$ *is the maximal invariant subset.*

To see Claim 6.9, it remains to show that $\mathbf{M}$ is maximal invariant in some neighborhood. Suppose there exists a bounded total trajectory $\mathbf{N}$ near to $\mathbf{M}$. By Claim 6.8, $\mathbf{N} \cap \mathbf{Y}_0 = \emptyset$ and hence $\mathbf{N} \subset \partial \mathbf{Y}_0$ and $\Psi_t(\mathbf{N}) = \mathbf{N}$ for all $t > 0$, but this contradicts the fact that $\operatorname{dist}(\Psi_t(\mathbf{N}), \mathbf{M}) \to 0$ as $t \to \infty$ (Proposition 2.1). This proves Claim 6.9.

Finally, by the precompactness of trajectories of the semiflow Ψ_t, together with Claims 6.6, 6.7, 6.8 and 6.9, we may apply the uniform persistence results of [42, Theorems 3 and 4] to show the existence of $\tilde{\eta} > 0$ such that

$$\min_{P' \in \omega(P^0)} p(P') \geq \tilde{\eta} \quad \text{for all } P^0 \in \mathbf{Y}_0.$$

i.e. there exists some $\tilde{\eta} > 0$ independent of initial condition $P^0 \in \mathbf{Y}_0$ such that $\liminf_{t\to\infty} u(\cdot,t) \geq \tilde{\eta}$. By Theorem 2.1(iii), every trajectory approaches $\mathbf{Y}_1$, where $\mathbf{Y}_1$ is defined in (2.7). Hence,

$$\liminf_{t\to\infty} U(x,t) \geq Q_{\min} \liminf_{t\to\infty} u(x,t) \geq Q_{\min}\tilde{\eta}, \ \forall\, x \in [0,L].$$

Therefore, (2.9) holds for $\sigma = \min\{\tilde{\eta}, Q_{\min}\tilde{\eta},\ \min_{x\in[0,L]} \check{R}(x),\ \min_{x\in[0,L]} \check{S}(x)\}$.

By [36, Theorem 3.7 and Remark 3.10], it follows that $\Psi(t) : \mathbf{Y}_0 \to \mathbf{Y}_0$ has a global attractor $A_0 \subset \mathbf{Y}_0$. It then follows from [36, Theorem 4.7] that $\Psi(t)$ has a steady-state solution

$$(R_c(\cdot), S_c(\cdot), U_c(\cdot), u_c(\cdot)) \in \mathbf{Y}_0.$$

By (2.9), it follows that $u_c(\cdot) > 0$ and $U_c(\cdot) > 0$. It follows from (4.3) that $U_c(\cdot) \leq Q^* u_c(\cdot)$. Then $F_N(\cdot, N) := f_N(N, \frac{U_c(\cdot)}{u_c(\cdot)})u_c(\cdot) > 0$. We may then apply Lemma 3.1 to deduce that $R_c(\cdot) > 0$ and $S_c(\cdot) > 0$. Theorem 2.2(ii) is proved.

□

We supply a brief outline for the proof of Theorem 2.2(i). (Step 1) Suppose there exists $P^0 \in \mathbf{Y}_0$ such that for some $\epsilon_0 > 0$, $x_k \in [0, L]$ and $t_k \to \infty$, $\Phi_t(P^0) = (R, S, U, u)$ satisfies

$$u(x_k, t_k + 1) \geq \epsilon_0 \quad \text{for all } k. \tag{6.14}$$

(Step 2) Claim 6.10 allows one to assume without loss of generality that $(R^0, S^0) \ll_D (R^*, S^*)$. (Step 3) Define

$$c(t) := \inf\{\tau > 0 : (U(x,t), u(x,t)) \leq_D \tau(\varphi^0(x), \phi^0(x)),\ x \in [0, L]\}, \tag{6.15}$$

where $(\varphi^0(x), \phi^0(x)) \gg 0$ is the eigenfunction corresponding to Λ^0, which is the principal eigenvalue of (2.8). One can then show by comparison that $c(t)$ is strictly decreasing for all $t \geq 0$. In particular $c_0 := \lim_{t\to\infty} c(t)$ exists. By (6.14), $c_0 > 0$. (Step 4) Passing to a sequence $t_k \to \infty$, there exists an entire solution $\tilde{P}(t) = \lim_{t_k\to\infty} \Phi_{t+t_k}(P^0) \in \omega(P^0)$ such that the corresponding $c^\infty(t) \equiv c_0 > 0$. This can only happen when

$$\tilde{P}(t) = (\tilde{R}(\cdot, t), \tilde{S}(\cdot, t), c_0\varphi^0(\cdot), c_0\phi^0(\cdot)) \quad \text{for all } t \in \mathbb{R}.$$

(Step 5) Upon examining the third and fourth equation of (1.15), this implies that $m + \Lambda^0 = 0$ and

$$\tilde{P}(t) = (R^*(\cdot), S^*(\cdot), c_0\varphi^0(\cdot), c_0\phi^0(\cdot))$$

i.e. the entire solution $\tilde{P}(t)$ is actually an equilibrium. i.e. $c_0 = 0$. This is in contradiction with $c_0 > 0$ and proves the theorem.

Proof of Theorem 2.2(i). Assume that $\Lambda^0 + m \geq 0$. By Theorem 2.1(iii) and Proposition 2.2, for any $P^0 \in \mathbf{Y}$, the omega limit set $\omega(P^0) \subset \mathbf{Y}_1$, where $\mathbf{Y}_1$ is defined in (2.7). It is enough to show that for any $P^0 \in \mathbf{Y}_0$, $u(\cdot, t) \to 0$ uniformly in $[0, L]$ as $t \to \infty$.

Fix some initial data $(R^0(\cdot), S^0(\cdot), U^0(\cdot), u^0(\cdot)) \in \mathbf{Y}$. Suppose to the contrary that there exists $\epsilon_0 > 0$, a sequence $\{t_k\} \nearrow \infty$ and a sequence $\{x_k\} \to x_0 \in [0, L]$ such that (6.14) holds.

Claim 6.10. *There exists $T_0 > 0$ such that $(R(\cdot, T_0), S(\cdot, T_0)) \ll_D (R^*(\cdot), S^*(\cdot))$.*

For each positive integer k, we define

$$(R_k(x,t), S_k(x,t), U_k(x,t), u_k(x,t)) = (R(x, t_k+t), S(x, t_k+t), U(x, t_k+t), u(x, t_k+t)).$$

Then for each k, $(R_k(x,t), S_k(x,t), U_k(x,t), u_k(x,t))$ satisfies system (1.15). We are in a position to apply the L^p estimates and Embedding Theorems [31, Section VI.3 and VII.8] to the sequence $(R_k(x,t), S_k(x,t), U_k(x,t), u_k(x,t))$. By Lemma 4.2, there exists $\overline{Q} > 0$ independent of k such that

$$\sup_k \|U_k/u_k\|_{L^\infty((0,L)\times(0,\infty))} \le \overline{Q}.$$

Hence $f_R(R_k, U_k/u_k)$, $f_S(S_k, U_k/u_k)$ and $\mu(U_k/u_k)$ are uniformly bounded in $L^\infty((0,L)\times(0,\infty))$. Therefore, we may pass to a subsequence and assume

$$f_R(R_k, U_k/u_k) \rightharpoonup F_R(x,t), \quad f_S(S_k, U_k/u_k) \rightharpoonup F_S(x,t), \quad \mu(U_k/u_k) \rightharpoonup g(x,t)$$

weakly in $L^p((0,L)\times(0,T))$ for all $p > 1$ and all $T > 0$. Moreover, we may apply the parabolic L^p estimate to deduce that for each $p > 1$, and $T > 0$, we have $\| (R_k, S_k, U_k, u_k) \|_{W^{2,1,p}((0,L)\times(0,T))} \le C_2$. Then $\| (R_k, S_k, U_k, u_k) \|_{C^{1+\alpha,\frac{1+\alpha}{2}}([0,L]\times[0,T])} \le C_3$, for some $\alpha \in (0,1)$. Passing to a further "diagonal" subsequence, still denoted by (R_k, S_k, U_k, u_k), we have

$$(R_k, S_k, U_k, u_k) \to (\tilde{R}, \tilde{S}, \tilde{U}, \tilde{u}),$$

in $C_{loc}^{1+\alpha,\frac{1+\alpha}{2}}([0,L]\times[0,\infty))$ as $k \to \infty$. Moreover, $\tilde{u}$ is a solution to

$$\begin{cases} \tilde{u}_t = (d(x)\tilde{u}_x - \nu(x)\tilde{u})_x + g(x,t)\tilde{u} - m\tilde{u}, & x \in (0,L),\ t > 0, \\ \mathbb{B}^x[\tilde{u}] = 0,\ x = 0 \text{ or } L,\ t > 0, \\ \tilde{u}(x_0, 1) > 0 \quad \text{for some } x_0. \end{cases}$$

By strong maximum principle, we have $\tilde{u}(x,t) > 0$ for all $x \in [0,L]$ and $t \ge 0$. This, together with the fact that $(U_k, u_k) \to (\tilde{U}, \tilde{u})$, implies that $U_k/u_k \to \tilde{U}/\tilde{u}$ in $C_{loc}([0,L]\times[0,\infty))$. Thus, $(\tilde{R}, \tilde{S}, \tilde{U}, \tilde{u})$ satisfies the original equation (1.15) with the additional properties (by Lemma 4.1)

$$(\tilde{R}(x,t), \tilde{S}(x,t)) \le_D (R^*(x), S^*(x)) \quad \text{and} \quad \tilde{u}(x,t) > 0,$$

for all $x \in [0,L]$ and $t \ge 0$. Here $(R^*(\cdot), S^*(\cdot))$ is the unique positive solution of (2.1). Furthermore, $f_R(\tilde{R}, \frac{\tilde{U}}{\tilde{u}})\tilde{u}(x,t) > 0$ and $f_S(\tilde{S}, \frac{\tilde{U}}{\tilde{u}})\tilde{u}(x,t) > 0$ for all x and $t \ge 0$ (by (6.14)), which implies by comparison (see Lemma 3.1) that $(\tilde{R}(\cdot,t), \tilde{S}(\cdot,t)) \ll_D (R^*(\cdot), S^*(\cdot))$ for all $t > 0$. In particular

$$\lim_{k\to\infty} (R(x, t_k+1), S(x, t_k+1) = (\tilde{R}(\cdot,1), \tilde{S}(\cdot,1)) \ll_D (R^*(\cdot), S^*(\cdot))$$

from which Claim 6.10 follows.

From now on, we assume without loss that $(R^0(\cdot), S^0(\cdot)) \ll_D (R^*(\cdot), S^*(\cdot))$ (Claim 6.10) and thus $(R(\cdot,t), S(\cdot,t)) \ll_D (R^*(\cdot), S^*(\cdot))$ for all $t \geq 0$ (see proof of Lemma 4.1(i)). Next, recall the definition of $c(t)$ in (6.15). For $t \geq t_0$, it is not hard to see that

$$c(t_0)e^{-(\Lambda^0+m)(t-t_0)}(\varphi^0(x), \phi^0(x))$$

is a supersolution solution of

$$\begin{cases} U_t = (d(x)U_x - \nu(x)U)_x + f_R(R^*(x), \frac{U}{u})u + f_S(S^*(x), \frac{U}{u})u - mU, & x \in (0, L),\ t \geq t_0, \\ u_t = (d(x)u_x - \nu(x)u)_x + \mu(\frac{U}{u})u - mu, & x \in (0, L),\ t \geq t_0, \\ \mathbb{B}^x[w] = 0, \quad w = U, u,\ x = 0 \text{ or } L,\ t \geq t_0, \end{cases} \tag{6.16}$$

for $t \geq t_0$ with initial data at $t = t_0$ being given by $(U(\cdot, t_0), u(\cdot, t_0))$. For the case where $\Lambda^0 + m > 0$, we can show that $c(t) \leq e^{-(\Lambda^0+m)t}c(0)$, which implies that $c(t) \to 0$ as $t \to \infty$. Thus, $u(\cdot, t) \to 0$ as $t \to \infty$. This contradicts (6.14).

It remains to tackle the case where $\Lambda^0 + m = 0$. Given $t_1 \geq 0$, it is easy to see that $c(t_1)(\varphi^0(x), \phi^0(x))$ is an upper solution of (6.16) for $t \geq t_1$. On the other hand, using the fact that $(R^0(\cdot), S^0(\cdot)) \ll_D (R^*(\cdot), S^*(\cdot))$, we see that $(U(\cdot, t), u(\cdot, t))$ is a strict subsolution of (6.16), for $t \geq t_1$. Thus, $(U(\cdot, t), u(\cdot, t)) \ll_D c(t_1)(\varphi^0(\cdot), \phi^0(\cdot))$, for $x \in [0, L]$, $t \geq t_1$. Therefore, $c(t) < c(t_1)$, for $t > t_1$, that is, $c(t)$ is strictly decreasing in t.

Define $c_0 = \lim\limits_{t\to\infty} c(t) = \inf\limits_{t>0} c(t)$. By assumption (6.14), $c_0 > 0$.

Claim 6.11. $\lim_{t\to\infty}(U(x, t), u(x, t)) = c_0(\varphi^0(x), \phi^0(x))$, *uniformly in* $x \in [0, L]$, *where* $c_0 = \lim\limits_{t\to\infty} c(t) > 0$.

Suppose to the contrary, then there is a sequence $\{\hat{t}_k\} \nearrow \infty$ such that

$$\liminf_{k\to\infty} \sup_{x\in[0,L]} \left[c(\hat{t}_k)(\varphi^0(x), \phi^0(x)) - (U(x, \hat{t}_k), u(x, \hat{t}_k))\right] > 0. \tag{6.17}$$

Furthurmore, for each $\hat{t}_k$, we can choose by definition of $c(\hat{t}_k + 1)$ some $\hat{x}_k \in [0, L]$ such that

$$(U(\hat{x}_k, \hat{t}_k + 1), u(\hat{x}_k, \hat{t}_k + 1)) = c(\hat{t}_k + 1)(\varphi^0(\hat{x}_k), \phi^0(\hat{x}_k)), \tag{6.18}$$

and $\hat{x}_k \to \hat{x}_0$ as $k \to \infty$. For each positive integer k, we define

$$(\hat{R}_k(x, t), \hat{S}_k(x, t), \hat{U}_k(x, t), \hat{u}_k(x, t)) = (R(x, \hat{t}_k+t), S(x, \hat{t}_k+t), U(x, \hat{t}_k+t), u(x, \hat{t}_k+t)).$$

We can use the similar arguments as we did before to conclude that

$$(\hat{R}_k(x,t), \hat{S}_k(x,t), \hat{U}_k(x,t), \hat{u}_k(x,t)) \to (\hat{R}(x,t), \hat{S}(x,t), \hat{U}(x,t), \hat{u}(x,t)),$$

uniformly in $x \in [0, L]$, and locally in $t \in [0, \infty)$, as $k \to \infty$. We can further show that $(\hat{R}(x,t), \hat{S}(x,t), \hat{U}(x,t), \hat{u}(x,t))$ is a classical solution of of system (1.15) on $[0, L] \times [0, \infty)$. It follows from (6.17) and (6.18) that

$$(\hat{U}(\cdot, 0), \hat{u}(\cdot, 0)) \leq_D c_0(\varphi^0(\cdot), \phi^0(\cdot)), \quad (\hat{U}(\cdot, 0), \hat{u}(\cdot, 0)) \not\equiv c_0(\varphi^0(\cdot), \phi^0(\cdot)), \tag{6.19}$$

and

$$(\hat{U}(\hat{x}_0, 1), \hat{u}(\hat{x}_0, 1)) = c_0(\varphi^0(\hat{x}_0), \phi^0(\hat{x}_0)), \tag{6.20}$$

respectively. Note that $c_0(\varphi^0(x), \phi^0(x))$ is a supersolution of system (6.16), while $(\hat{U}(x,t), \hat{u}(x,t))$ is a subsolution of (6.16). Then the strong maximum principle contradicts (6.19) and (6.20). Thus, Claim 6.11 holds.

By Claim 6.11, it follows that the equations of R and S in (1.15) are asymptotic to the following system

$$\begin{cases} R_t = (D_R(x)R_x)_x - f_R(R, \frac{\varphi^0(x)}{\phi^0(x)})(c_0\phi^0(x)) - \omega_r R + \omega_s S, \ x \in (0, L), \ t > 0, \\ S_t = (D_S(x)S_x)_x - f_S(S, \frac{\varphi^0(x)}{\phi^0(x)})(c_0\phi^0(x)) + \omega_r R - \omega_s S, \ x \in (0, L), \ t > 0, \\ \mathcal{B}_{N,x}[N] = c_{N,x} \geq 0, \ N = R, S, \ x = 0 \text{ or } L, \ t > 0, \end{cases} \tag{6.21}$$

By the theory for asymptotically autonomous semiflows (see, e.g., [43, Corollary 4.3]) and Lemma 3.1, while making use of $F_N(x, N) = f_N(N, \frac{\varphi^0(x)}{\phi^0(x)})(c_0\phi^0(x)) > 0$, we see that $(R(\cdot, t), S(\cdot, t)) \to (R^{**}(\cdot), S^{**}(\cdot))$ such that

$$(0, 0) \ll_D (R^{**}(\cdot), S^{**}(\cdot)) \ll_D (R^*(\cdot), S^*(\cdot)).$$

Thus, we see that the equations of U and u in (1.15) are asymptotic to the following system

$$\begin{cases} U_t = (d(x)U_x - \nu(x)U)_x + f_R(R^{**}(x), \frac{U}{u})u + f_S(S^{**}(x), \frac{U}{u})u - mU, \ x \in (0, L), \ t > 0, \\ u_t = (d(x)u_x - \nu(x)u)_x + \mu(\frac{U}{u})u - mu, \ x \in (0, L), \ t > 0, \\ \mathbb{B}^x[w] = 0, \ \ w = U, u, \ x = 0 \text{ or } L, \ t > 0. \end{cases} \tag{6.22}$$

Finally, consider the following eigenvalue problem associated with (6.22):

$$\begin{cases} (d(x)\varphi'(x) - \nu(x)\varphi(x))' + f_R\left(R^{**}(x), \frac{\varphi(x)}{\phi(x)}\right)\phi(x) \\ \qquad + f_S\left(S^{**}(x), \frac{\varphi(x)}{\phi(x)}\right)\phi(x) + \Lambda\varphi(x) = 0, \quad x \in (0, L), \\ (d(x)\phi'(x) - \nu(x)\phi(x))' + \mu\left(\frac{\varphi(x)}{\phi(x)}\right)\phi(x) + \Lambda\phi(x) = 0, \quad x \in (0, L), \\ \mathbb{B}^x[w] = 0, \quad w = \varphi, \ \phi, \ x = 0 \text{ or } L. \end{cases} \tag{6.23}$$

We denote the principal eigenvalue of (6.23) by Λ^{**}. Then $\Lambda^{**} + m > \Lambda^0 + m = 0$. By the similar arguments we did for the case where $\Lambda^0 + m > 0$, it follows that $u(\cdot, t) \to 0$ as $t \to \infty$. This contradicts Claim 6.11. Thus, (6.14) is impossible. This concludes the proof of Theorem 2.2(i). □

7 The Unstirred Chemostat Model

In this section, we specialize in the chemostat model (1.9) and prove Theorem 2.3. We will first show the existence of a critical diffusion rate in Subsection 7.1. In Subsection 7.2, we show, under an additional assumption (H7), the existence of a globally attracting steady state whenever the phytoplankton species persists.

7.1 Critical Diffusion Rate

By Theorem 2.2, the persistence/extinction of the chemostat system (1.9) is determined by the associated nonlinear eigenvalue problem

$$\begin{cases} d\varphi''(x) + f_R\left(R^*(x), \frac{\varphi(x)}{\phi(x)}\right)\phi(x) + f_S\left(S^*(x), \frac{\varphi(x)}{\phi(x)}\right)\phi(x) + \Lambda\varphi(x) = 0, \quad x \in (0,1), \\ d\phi''(x) + \mu\left(\frac{\varphi(x)}{\phi(x)}\right)\phi(x) + \Lambda\phi(x) = 0, \quad x \in (0,1), \\ w_x(0) = 0, w_x(1) + \gamma w(1) = 0, \quad w = \varphi, \ \phi. \end{cases} \tag{7.1}$$

Here $(R^*(x), S^*(x))$ is the unique steady state of (2.1) (see Proposition 2.1), determined by

$$\begin{cases} dR'' - \omega_r R + \omega_s S = 0, \ x \in (0,1), \\ dS'' + \omega_r R - \omega_s S = 0, \ x \in (0,1), \\ N'(0) = -N^{(0)}, \ N'(1) + \gamma N(1) = 0, \ N = R, S. \end{cases} \tag{7.2}$$

We observe that $R^* + S^*$ satisfies a simplified equation, whence $R^*(x) + S^*(x) = (R^{(0)} + S^{(0)})\left(\frac{1+\gamma}{\gamma} - x\right)$ (see, e.g. [25]).

By Lemma 5.1, it follows that for each $d > 0$, the eigenvalue problem (7.1) admits a principal eigenvalue $\Lambda^0 := \Lambda^0(d)$ corresponding to which there is a strongly positive eigenfunction $(\varphi^0(x), \phi^0(x)) \gg_D (0, 0)$.

Lemma 7.1. *For each $d > 0$, let $\Lambda^0 := \Lambda^0(d)$ be the principal eigenvalue of the eigenvalue problem* (7.1)*. Then there is a $d_0 > 0$ such that*

$$\begin{cases} \Lambda^0(d) < 0, & \text{if } 0 < d < d_0, \\ \Lambda^0(d) = 0, & \text{if } d = d_0, \\ \Lambda^0(d) > 0, & \text{if } d > d_0. \end{cases} \tag{7.3}$$

Proof. Let $(\eta_1, w_1(x))$ be the principal eigenpair of following eigenvalue problem:

$$\begin{cases} w''(x) + \eta w(x) = 0, \ x \in (0, 1), \\ w'(0) = w'(1) + \gamma w(1) = 0. \end{cases} \tag{7.4}$$

It is standard to show that $\eta_1 > 0$, see e.g. proof of Lemma 3.1. Let

$$Q_* = \sup\{Q > 0 : f_R(R^*(x), Q) + f_S(S^*(x), Q) - \mu(Q)Q \geq 0 \ \text{ in } [0, 1].\}, \tag{7.5}$$

where $(R^*(x), S^*(x))$ is the unique positive steady-state solution of system (7.2). It is clear that $Q_{\min} < Q_*$ and

$$f_R(R^*(x), Q_*) + f_S(S^*(x), Q_*) \geq Q_*\mu(Q_*) > 0 \quad \text{for all } x \in [0, 1]. \tag{7.6}$$

Claim 7.1. *$\Lambda^0(d) < 0$ for all $d \in (0, \mu(Q_*)/\eta_1)$, where $\eta_1 > 0$ is the principal eigenvalue of* (7.4)*.*

Recall from the proof of Lemma 5.1 that $\Lambda^0 = -\log \tilde{r}(1)$, where $\tilde{r}(t)$ is the spectral radius of the semiflow map $\Phi_t : C \to C$ of

$$\begin{cases} U_t = dU_{xx} + f_R(R^*(x), \frac{U}{u})u + f_S(S^*(x), \frac{U}{u})u, \ \ x \in (0, 1), \ t > 0, \\ u_t = du_{xx} + \mu(\frac{U}{u})u, \ \ x \in (0, 1), \ t > 0, \\ w_x(0, t) = 0, w_x(1, t) + \gamma w(1, t) = 0, \ \ w = U, u, \ t > 0, \\ w(x, 0) = w^0(x) \geq (\not\equiv) 0, \ \ w = U, u, \ x \in (0, 1), \end{cases} \tag{7.7}$$

Since (7.7) is a special case of (5.2), Φ_t is also continuous, compact, and homogeneous of degree one. Define

$$\hat{U}(x) := Q_* w_1(x), \qquad \text{and} \qquad \hat{u}(x) := w_1(x).$$

It is enough to show that $(\hat{U}, \hat{u})$ is a strict lower solution of (7.7) for all sufficiently small d. Since then by strong-order-preserving property, $\Phi_t(\hat{U}, \hat{u}) \gg_D (\hat{U}, \hat{u})$. This means $\Phi_t(\hat{U}, \hat{u}) \geq_D k(\hat{U}, \hat{u})$ for some $k > 1$, whence the Bonsall cone spectral radius $\tilde{r}(t)$ must be strictly greater than 1, and by definition $\Lambda^0 = -\log \tilde{r}(1) < 0$.

Now we verify that $(\hat{U}, \hat{u})$ is a strict lower solution of (7.7) for $d \in (0, \mu(Q_*)/\eta_1)$. By computations, for $d \in (0, \mu(Q_*)/\eta_1)$, we have

$$\begin{aligned}
&d\hat{U}_{xx} + f_R(R^*(x), \frac{\hat{U}}{\hat{u}})\hat{u} + f_S(S^*(x), \frac{\hat{U}}{\hat{u}})\hat{u} \\
&= dQ_* w_1''(x) + f_R(R^*(x), Q_*)w_1(x) + f_S(S^*(x), Q_*)w_1(x) \\
&\geq dQ_* \left(-\eta_1 w_1(x)\right) + \mu(Q_*)Q_* w_1(x) = \left(\mu(Q_*) - d\eta_1\right) Q_* w_1(x) > 0,
\end{aligned}$$

(where we used (7.6)) and

$$d\hat{u}_{xx} + \mu(\frac{\hat{U}}{\hat{u}})\hat{u} = dw_1'' + \mu(Q_*)w_1 = \left(\mu(Q_*) - d\eta_1\right) w_1 > 0.$$

This proves Claim 7.1.

Claim 7.2. *$\Lambda^0(d) > 0$ for all $d \in (\mu(Q^*)/\eta_1, +\infty)$, where Q^* is given by* (2.3) *and $\eta_1 > 0$ is the principal eigenvalue of* (7.4).

Define

$$\hat{U}(x) := Q^* w_1(x), \qquad \text{and} \qquad \hat{u}(x) := w_1(x).$$

By an analogous argument as above, we can show that for $d \in (\mu(Q^*)/\eta_1, +\infty)$, $(\hat{U}, \hat{u})$ forms a strict upper solution of (7.7). This implies that $\Phi_t(\hat{U}, \hat{u}) \ll_D (\hat{U}, \hat{u})$.

We claim that this implies that the Bonsall cone spectral radius $\tilde{r}(t)$ of Φ_t is strictly less than 1 for all $t > 0$. Fix $t > 0$. By Corollary 5.2, there exists $(\varphi, \phi) \in C \setminus \{0\}$ such that $\Phi_t(\varphi, \phi) = \tilde{r}(t)(\varphi, \phi)$. Since $(\hat{U}, \hat{u}), (\varphi, \phi) \in \operatorname{int} D$, we may scale the eigenvector (φ, ϕ) so that

$$(\varphi, \phi) \leq_D (\hat{U}, \hat{u}), \qquad \text{but} \qquad k(\varphi, \phi) \not\leq_D (\hat{U}, \hat{u}) \qquad \text{for all } k > 1.$$

Then by comparison,

$$\tilde{r}(t)(\varphi, \phi) = \Phi_t(\varphi, \phi) \leq_D \Phi_t(\hat{U}, \hat{u}) \ll_D (\hat{U}, \hat{u}),$$

i.e. $\tilde{k}\tilde{r}(t)(\varphi,\phi) \leq_D (\hat{U},\hat{u})$ for some $\tilde{k} > 1$. Hence $\tilde{k}\tilde{r}(t) \leq 1$ and $\tilde{r}(t) \leq 1/\tilde{k} < 1$. i.e. $\Lambda^0 = -\log \tilde{r}(1) > 0$ for all $d \in (\mu(Q^*)/\eta_1, +\infty)$. This proves Claim 7.2.

By Claims 7.1 and 7.2, we see that there exists a $d_0 > 0$ such that $\Lambda^0(d_0) = 0$. It remains to show that

$$\begin{cases} \Lambda^0(d) < 0, & \text{for all } 0 < d < d_0, \\ \Lambda^0(d) > 0, & \text{for all } d > d_0. \end{cases} \tag{7.8}$$

Assume that $\Lambda^0(d_0) = 0$ is the principal eigenvalue of the eigenvalue problem (7.1) with $d = d_0$, that is there exists eigenfunction $(\varphi_{d_0}(x), \phi_{d_0}(x)) \in C \cap \text{int}\, D$ satisfying

$$\begin{cases} d_0\varphi''(x) + f_R\left(R^*(x), \frac{\varphi(x)}{\phi(x)}\right)\phi(x) + f_S\left(S^*(x), \frac{\varphi(x)}{\phi(x)}\right)\phi(x) = 0, \quad x \in (0,1), \\ d_0\phi''(x) + \mu\left(\frac{\varphi(x)}{\phi(x)}\right)\phi(x) = 0, \quad x \in (0,1), \\ w_x(0) = 0, w_x(1) + \gamma w(1) = 0, \quad w = \varphi,\ \phi. \end{cases} \tag{7.9}$$

Claim 7.3. *For each $d > d_0$, $\Lambda^0(d) > 0$.*

Again, it suffices to show that $(\mathbf{U}(x), \mathbf{u}(x)) := (\varphi_{d_0}(x), \phi_{d_0}(x))$ is a strict lower solution, so that $\Phi_t(\mathbf{U},\mathbf{u}) \ll_D (\mathbf{U},\mathbf{u})$ for $t > 0$. Now, we verify

$$\begin{aligned} & d\mathbf{U}_{xx} + f_R(R^*(x), \frac{\mathbf{U}}{\mathbf{u}})\mathbf{u} + f_S(S^*(x), \frac{\mathbf{U}}{\mathbf{u}})\mathbf{u} \\ &= d\varphi''_{d_0}(x) + f_R(R^*(x), \frac{\varphi_{d_0}}{\phi_{d_0}})\phi_{d_0}(x) + f_S(S^*(x), \frac{\varphi_{d_0}}{\phi_{d_0}})\phi_{d_0}(x) \\ &= \frac{d}{d_0}\left[d_0\varphi''_{d_0}(x) + \frac{d_0}{d} f_R(R^*(x), \frac{\varphi_{d_0}}{\phi_{d_0}})\phi_{d_0}(x) + \frac{d_0}{d} f_S(S^*(x), \frac{\varphi_{d_0}}{\phi_{d_0}})\phi_{d_0}(x)\right] \\ &< \frac{d}{d_0}\left[d_0\varphi''_{d_0}(x) + f_R(R^*(x), \frac{\varphi_{d_0}}{\phi_{d_0}})\phi_{d_0}(x) + f_S(S^*(x), \frac{\varphi_{d_0}}{\phi_{d_0}})\phi_{d_0}(x)\right] = 0, \end{aligned}$$

and

$$d\mathbf{u}_{xx} + \mu(\frac{\mathbf{U}}{\mathbf{u}})\mathbf{u} = d\phi''_{d_0}(x) + \mu\left(\frac{\varphi_{d_0}}{\phi_{d_0}}\right)\phi_{d_0}(x) < \frac{d}{d_0}\left[d_0\phi''_{d_0}(x) + \mu\left(\frac{\varphi_{d_0}}{\phi_{d_0}}\right)\phi_{d_0}(x)\right] = 0.$$

This proves Claim 7.3.

Claim 7.4. *For each $d < d_0$, $\Lambda^0(d) < 0$.*

Claim 7.4 follows from a similar fashion as Claim 7.3, so we skip the details. This proves Lemma 7.1. $\square$

Here we prove parts (i) and (ii) of Theorem 2.3.

Proof of Theorem 2.3 (i) and (ii). First, it follows from Theorem 2.1 that system (1.9) generates a semiflow in $\mathbf{Y}$. Let d_0 be given by Lemma 7.1. If $d \in [d_0, \infty)$, then Lemma 7.1 says that the principal eigenvalue Λ^0 of (7.1) is non-positive. Hence, Theorem 2.3(i) follows from Theorem 2.2(i). If $d \in (0, d_0)$, then Lemma 7.1 says that $\Lambda^0 < 0$. Theorem 2.3(ii) thus follows from Theorem 2.2(ii). □

7.2 Global Attractivity of system (1.9)

In this subsection, we intend to investigate the uniqueness and global stability of positive steady-state solutions of system (1.9) under the additional assumption (H7). Note that the existence of a positive steady-state solution of system (1.9) is obtained based on persistence theory in the previous section.

Let

$$\begin{cases} W_R(x,t) = R^*(x) - R(x,t), \\ W_S(x,t) = S^*(x) - S(x,t), \\ W(x,t) = W_R(x,t) + W_S(x,t) - U(x,t), \end{cases} \tag{7.10}$$

where $(R^*(x), S^*(x))$ is the unique steady state solution of (7.2). Then system (1.9) is equivalent to the following system

$$\begin{cases} (W_R)_t = d(W_R)_{xx} + f_R(R^*(x) - W_R, \frac{W_R+W_S-W}{u})u - \omega_r W_R + \omega_s W_S, \quad x \in (0,1),\ t > 0, \\ (W_S)_t = d(W_S)_{xx} + f_S(S^*(x) - W_S, \frac{W_R+W_S-W}{u})u + \omega_r W_R - \omega_s W_S, \quad x \in (0,1),\ t > 0, \\ u_t = du_{xx} + \mu(\frac{W_R+W_S-W}{u})u, \quad x \in (0,1),\ t > 0, \\ W_t = dW_{xx}, \quad x \in (0,1),\ t > 0, \\ Z_x(0,t) = 0, Z_x(1,t) + \gamma Z(1,t) = 0, \quad Z = W_R, W_S, u, W,\ t > 0, \\ Z(x,0) = Z^0(x) \geq (\not\equiv) 0, \quad Z = W_R, W_S, u, W,\ x \in (0,1). \end{cases} \tag{7.11}$$

Motivated by Theorem 2.1, the relevant domains for system (7.11) are

$$\mathbf{Y}' = \{(W_R^0(\cdot), W_S^0(\cdot), u^0(\cdot), W^0(\cdot)) \in C([0,1], \mathbb{R}_+^4) : W_R^0(x) \leq R^*(x),\ W_S^0(x) \leq S^*(x), \\ \exists \tilde{Q} > 0 \text{ such that } 0 \leq W_R^0(x) + W_S^0(x) - W^0(x) \leq u^0(x)\tilde{Q} \text{ for all } x \in [0,1]\}, \tag{7.12}$$

and

$$\mathbf{Y}'_1 = \{(W_R^0(\cdot), W_S^0(\cdot), u^0(\cdot), W^0(\cdot)) \in C([0,1], \mathbb{R}_+^4) : W_R^0(x) \leq R^*(x),\ W_S^0(x) \leq S^*(x), \\ Q_{\min} u^0(x) \leq W_R^0(x) + W_S^0(x) - W^0(x) \leq Q^* u^0(x) \text{ for all } x \in [0,1]\}, \tag{7.13}$$

where Q^* is given in (2.3).

It is easy to see that the unique steady state for the fourth equation in system (7.11) is the trivial solution. It then follows from [13, Sect. 6.5, Theorem 5] that

$$\lim_{t\to\infty} W(x,t) = 0 \text{ uniformly for } x \in [0,1].$$

Thus, the limiting system of (7.11) takes the form

$$\begin{cases} (W_R)_t = d(W_R)_{xx} + f_R(R^*(x) - W_R, \frac{W_R+W_S}{u})u - \omega_r W_R + \omega_s W_S, & x \in (0,1),\ t > 0, \\ (W_S)_t = d(W_S)_{xx} + f_S(S^*(x) - W_S, \frac{W_R+W_S}{u})u + \omega_r W_R - \omega_s W_S, & x \in (0,1),\ t > 0, \\ u_t = du_{xx} + \mu(\frac{W_R+W_S}{u})u, \quad x \in (0,1),\ t > 0, \\ Z_x(0,t) = 0, Z_x(1,t) + \gamma Z(1,t) = 0, \quad Z = W_R, W_S, u,\ t > 0, \\ Z(x,0) = Z^0(x) \geq (\not\equiv) 0, \quad Z = W_R, W_S, u,\ x \in (0,1), \end{cases} \tag{7.14}$$

where the biologically relevant domains for system (7.14) are

$$\begin{aligned} \mathbf{Y}'' = \{&(W_R^0(\cdot), W_S^0(\cdot), u^0(\cdot)) \in C([0,1], \mathbb{R}_+^3) : W_R^0(x) \leq R^*(x),\ W_S^0(x) \leq S^*(x), \\ &\exists \tilde{Q} > 0 \text{ such that } 0 \leq W_R^0(x) + W_S^0(x) \leq u^0(x)\tilde{Q} \ \text{ for all } x \in [0,1]\}, \end{aligned} \tag{7.15}$$

and

$$\begin{aligned} \mathbf{Y}_1'' = \{&(W_R^0(\cdot), W_S^0(\cdot), u^0(\cdot)) \in C([0,1], \mathbb{R}_+^3) : W_R^0(x) \leq R^*(x),\ W_S^0(x) \leq S^*(x), \\ &Q_{\min} u^0(x) \leq W_R^0(x) + W_S^0(x) \leq Q^* u^0(x) \ \text{ for all } x \in [0,1]\}, \end{aligned} \tag{7.16}$$

where Q^* is given in (2.3).

For persistence result, we set $\mathbf{Y}_0'' := \{(W_R, W_S, u) \in \mathbf{Y}'' : u \not\equiv 0 \text{ in } [0,1]\}$, and the complementary set

$$\begin{aligned} \partial \mathbf{Y}_0'' := \mathbf{Y}'' - \mathbf{Y}_0'' &= \{(W_R, W_S, u) \in \mathbf{Y}'' : u \equiv 0 \text{ in } [0,1]\} \\ &= \{(W_R, W_S, u) \in \mathbf{Y}'' : W_R = W_S = u \equiv 0 \text{ in } [0,1]\}. \end{aligned}$$

The following result is related to the global attractivity of the positive steady state of the limiting system (7.14).

Lemma 7.2. *Assume that (H1), (H2) and (H7) hold, and $\Lambda^0 := \Lambda^0(d)$ is the principal eigenvalue of (7.1). If $\Lambda^0 < 0$, then (7.14) admits a unique positive steady-state solution $(\hat{W}_R(x), \hat{W}_S(x), \hat{u}(x)) \in \mathbf{Y}''$. Moreover, any solution $(W_R(\cdot,t), W_S(\cdot,t), u(\cdot,t))$ of (7.14) with initial condition $(W_R^0, W_S^0, u^0) \in \mathbf{Y}_0''$ satisfies*

$$\lim_{t\to\infty} (W_R(x,t), W_S(x,t), u(x,t)) = (\hat{W}_R(x), \hat{W}_S(x), \hat{u}(x)), \ \text{ uniformly for } x \in [0,1].$$

Proof. By the similar arguments in Lemma 4.2 and Theorem 2.1(i), we can show that the set $\mathbf{Y}''$ is positively invariant under the semiflow Π_t generated by system (7.14). Theorem 2.2 (ii) guarantee the existence of a compact attractor $A_0'' \subset \mathrm{Int}(C([0,1],\mathbb{R}_+^3))$ for Π_t, and it suffices to show that Π_t is monotone and subhomogeneous, which imply that the attractor A_0'' is a singleton set. Fix $P^0 \in \mathbf{Y}_0''$ and let $(W_R(\cdot,t), W_S(\cdot,t), u(\cdot,t)) = \Pi_t(P^0)$, and set

$$R(x,t) = R^*(x) - W_R(x,t), \quad S(x,t) = S^*(x) - W_S(x,t),$$

and

$$U(x,t) = W_R(x,t) + W_S(x,t).$$

Then it is not hard to see that $(R(x,t), S(x,t), U(x,t), u(x,t)) \in \mathbf{Y}$ satisfies system (1.9), where $\mathbf{Y}$ is given in (2.6). By Lemma 4.2,

$$\limsup_{t\to\infty} \left[\sup_{x\in[0,L]} (U(x,t) - Q^* u(x,t)) \right] \leq 0.$$

Since $\Lambda^0 < 0$ and $u^0 \not\equiv 0$, it follows from Theorem 2.2(ii) that there exists $\eta > 0$ such that $\liminf_{t\to\infty} u(\cdot,t) \geq \eta$, so (recall that $U(x,t) = W_R(x,t) + W_S(x,t)$)

$$\limsup_{t\to\infty} \left(\frac{U(x,t)}{u(x,t)} - Q^* \right) = \limsup_{t\to\infty} \frac{U(x,t) - Q^* u(x,t)}{u(x,t)} \leq 0.$$

From the fact that $Q^* < Q_B$ (Remark 2.1), we have

$$\frac{W_R(\cdot,t) + W_S(\cdot,t)}{u(\cdot,t)} = \frac{U(\cdot,t)}{u(\cdot,t)} < Q_B, \ \forall\, t \geq t_0. \tag{7.17}$$

Note that we have also proved that Π_t is uniformly persistent with respect to $(\mathbf{Y}_0'', \partial\mathbf{Y}_0'')$ in the sense that $\liminf\limits_{t\to\infty} \mathrm{dist}(\Pi_t(P^0), \partial\mathbf{Y}_0'') \geq \eta$, $\forall\ P^0(\cdot) \in \mathbf{Y}_0''$. By (7.17), without loss of generality, we may further assume that the initial value $(W_R^0(\cdot), W_S^0(\cdot), u^0(\cdot)) \in \mathbf{Y}_0''$ and $\frac{W_R^0(\cdot)+W_S^0(\cdot)}{u^0(\cdot)} < Q_B$.

The Jacobian matrix of reaction terms in (7.14) with respect to (W_R, W_S, u) at points $(W_R, W_S, u) \in \mathbb{R}_+^3$, takes the form

$$J = \begin{pmatrix} * & a_{12} & a_{13} \\ a_{21} & * & a_{23} \\ + & + & * \end{pmatrix},$$

where

$$
\begin{aligned}
a_{21} &= \omega_r + \frac{\partial f_S}{\partial Q}(S^*(x) - W_S, \frac{W_R + W_S}{u}),\\
a_{12} &= \omega_s + \frac{\partial f_R}{\partial Q}(R^*(x) - W_R, \frac{W_R + W_S}{u}),\\
a_{13} &= f_R(R^*(x) - W_R, \frac{W_R + W_S}{u}) - \frac{W_R + W_S}{u}\frac{\partial f_R}{\partial Q}(R^*(x) - W_R, \frac{W_R + W_S}{u})\\
&\geqq f_R(R^*(x) - W_R, \frac{W_R + W_S}{u}) \geqq 0,\\
a_{23} &= f_S(S^*(x) - W_S, \frac{W_R + W_S}{u}) - \frac{W_R + W_S}{u}\frac{\partial f_S}{\partial Q}(S^*(x) - W_S, \frac{W_R + W_S}{u})\\
&\geqq f_S(S^*(x) - W_S, \frac{W_R + W_S}{u}) \geqq 0.
\end{aligned}
$$

Note that $\mu(Q)$ and $f_N(N, Q)$ are Lipschitz continuous, thus the Jacobian matrix of reaction terms, J, exists almost everywhere $(W_R, W_S, u) \in \mathbb{R}^3_+$. It follows from the assumption (H7) that $a_{21} \geq 0$ and $a_{12} \geq 0$. Thus, the Jacobian matrix J has nonnegative off-diagonal entries, and hence, the semiflow $\Pi_t : \mathbf{Y}'' \to \mathbf{Y}''$ generated by the system (7.14) is monotone [40] under the partial order $\leq_{\mathbb{D}}$ generated by the cone $\mathbb{D} := C^0([0,1], \mathbb{R}^3_+)$. Furthermore, if

$$
W_R < R^*(x),\ W_S < S^*(x) \text{ for } x \in [0,1], \text{ and } W_R + W_S < uQ_B
$$

where Q_B is given in (H2), then $a_{13} > 0$ and $a_{23} > 0$, and hence, J is irreducible [41], which implies that such a semiflow is strongly monotone in the interior of $\mathbf{Y}''$ [40]. For convenience, we denote the reaction terms of (7.14) by

$$
\begin{cases}
F_1(W_R, W_S, u) = f_R(R^*(x) - W_R, \frac{W_R+W_S}{u})u - \omega_r W_R + \omega_s W_S,\\
F_2(W_R, W_S, u) = f_S(S^*(x) - W_S, \frac{W_R+W_S}{u})u + \omega_r W_R - \omega_s W_S,\\
F_3(W_R, W_S, u) = \mu(\frac{W_R+W_S}{u})u.
\end{cases}
$$

It is easy to see that the reaction terms of (7.14) are strictly subhomogeneous in the sense that for $0 < \theta < 1$ and $(W_R, W_S, u) \in \mathbf{Y}''$, we have

$$
F_i(\theta W_R, \theta W_S, \theta u) > \theta F_i(W_R, W_S, u),\ F_3(\theta W_R, \theta W_S, \theta u) = \theta F_3(W_R, W_S, u),\ i = 1, 2.
$$

Then we can adopt the arguments in [12, Theorem 2.2] to show that for any $t > 0$, $\Pi_t : \mathbf{Y}'' \to \mathbf{Y}''$ is strictly subhomogeneous in the sense that for any $\theta \in (0,1)$,

$(W_R^0(\cdot), W_S^0(\cdot), u^0(\cdot)) \in \mathbf{Y}''$ with $u^0(\cdot) \gg 0$, we have

$$\Pi_t(\theta W_R^0(\cdot), \theta W_S^0(\cdot), \theta u^0(\cdot)) \ll_D \theta \Pi_t(W_R^0(\cdot), W_S^0(\cdot), u^0(\cdot)).$$

For $t > 0$, we have proved that Π_t is compact, point dissipative and uniformly persistent. It follows from [36, Theorem 3.8] that $\Pi_t : \mathbf{Y}_0'' \to \mathbf{Y}_0''$ admits a global attractor A_0''. Since Π_t is also strongly monotone, strictly subhomogeneous, $A_0'' \subset \mathbf{Y}_0''$ and $A_0'' = \Pi_t(A_0'')$, we further have $A_0'' \subset \text{Int}(C([0,1], \mathbb{R}_+^3))$. It then follows from [48, Theorem 2.3.2] with $K = A_0''$ that in fact $A_0'' = \{e\}$, where $e \gg_{\mathbb{D}} (0,0,0)$ is a fixed point of Π_t. This implies that e is globally attractive for Π_t in $\mathbf{Y}_0''$, and we finish the proof.

□

By appealing to Lemma 7.2 and the theory of chain transitive sets, we are able to lift the dynamics of (7.14) to the full system (1.9). That is, Theorem 2.2(ii) can be improved, and we further have the following result which contains Theorem 2.3(ii') as a special case.

Theorem 7.1. *Assume that (H1), (H2), and (H7) hold, and* $\Lambda^0 := \Lambda^0(d)$ *is the principal eigenvalue of* (7.1). *Let* $(R(\cdot,t), S(\cdot,t), U(\cdot,t), u(\cdot,t))$ *be the solution of system* (1.9) *with initial conditon* $(R^0, S^0, U^0, u^0) \in \mathbf{Y}$.

(i) *If* $\Lambda^0 \geq 0$, *then*

$$\lim_{t\to\infty} (R(\cdot,t), S(\cdot,t), U(\cdot,t), u(\cdot,t)) = (R^*(\cdot), S^*(\cdot), 0, 0).$$

(ii) *If* $\Lambda^0 < 0$, *then system* (1.9) *admits a unique positive steady-state solution* $(\hat{R}(\cdot), \hat{S}(\cdot), \hat{U}(\cdot), \hat{u}(\cdot))$. *In addition, if the initial condition satisfies* $(R^0, S^0, U^0, u^0) \in \mathbf{Y}_0$, *then*

$$\lim_{t\to\infty} (R(x,t), S(x,t), U(x,t), u(x,t)) = (\hat{R}(x), \hat{S}(x), \hat{U}(x), \hat{u}(x)),$$

uniformly for $x \in [0,1]$, *where* $\hat{R}(\cdot) = R^*(\cdot) - \hat{W}_R(\cdot)$, $\hat{S}(\cdot) = S^*(\cdot) - \hat{W}_S(\cdot)$, $\hat{U}(\cdot) = \hat{W}_R(\cdot) + \hat{W}_S(\cdot)$, *and* $(\hat{W}_R(\cdot), \hat{W}_S(\cdot), \hat{u}(\cdot))$ *are given by Lemma 7.2.*

Proof. Part (i) was proved in Theorem 2.2(i), and we only need to prove Part (ii). Since systems (1.9) and (7.11) are equivalent, it suffices to study system (7.11) with initial data in $\mathbf{Y}'$ (see (7.12)). (Note that $(R_0, S_0, U_0, u_0) \in \mathbf{Y}$ iff $(W_R, W_S, u, W) = (R^* - R_0, S^* - S_0, u_0, W_R + W_S - U) \in \mathbf{Y}'$.)

Define $\mathbf{Y}'_0 := \{(W_R, W_S, u, W) \in \mathbf{Y}' : u \not\equiv 0\}$, and the complementary set

$$\begin{aligned}\partial \mathbf{Y}'_0 &:= \mathbf{Y}' - \mathbf{Y}'_0 = \{(W_R, W_S, u, W) \in \mathbf{Y}' : u \equiv 0 \text{ in } [0,1]\} \\ &= \{(W_R, W_S, u, W) \in \mathbf{Y}' : W_R + W_S - W \equiv u \equiv 0 \text{ in } [0,1]\}.\end{aligned}$$

We first show that $\mathbf{Y}'$ is positively invariant for system (7.11). Indeed, fix $P^0 := (W_R^0, W_S^0, u^0, W^0) \in \mathbf{Y}'$ and let $(W_R(\cdot,t), W_S(\cdot,t), u(\cdot,t), W(\cdot,t))$ be the solution of system (7.11) with initial data P^0. Motivated by (7.10), we set

$$\begin{cases} R(x,t) = R^*(x) - W_R(x,t), \\ S(x,t) = S^*(x) - W_S(x,t), \\ U(x,t) = W_R(x,t) + W_S(x,t) - W(x,t). \end{cases} \tag{7.18}$$

Then $(R(x,t), S(x,t), U(x,t), u(x,t))$ satisfies system (1.9) (by (7.12)) and $R(\cdot,0)$, $S(\cdot,0)$, $u(\cdot,0)$ are non-negative, and there exists $Q' > 0$ such that

$$U(x,0) \le Q' u(x,0) \text{ for all } x \in [0,1].$$

By Corollary 4.1, it follows that $R(\cdot,t) \ge 0$, $S(\cdot,t) \ge 0$, $u(\cdot,t) \ge 0$, and there exists $Q'' > 0$ such that

$$U(x,t) \le Q'' u(x,t) \quad \text{for all } x \in [0,1] \text{ and } t > 0.$$

This implies that

$$(W_R(\cdot,t), W_S(\cdot,t), u(\cdot,t), W(\cdot,t)) \in \mathbf{Y}' \quad \text{for all } t \ge 0.$$

Thus, we can define the solution semiflow $\widetilde{\Psi}_t : \mathbf{Y}' \to \mathbf{Y}'$ of (7.11) by

$$\widetilde{\Psi}_t(P^0) = (W_R(\cdot,t), W_S(\cdot,t), u(\cdot,t), W(\cdot,t)), \ \forall\, t \ge 0,$$

where (W_R, W_S, u, W) is the solution of (7.11) with initial data

$$P^0 = (W_R^0, W_S^0, u^0, W^0) \in \mathbf{Y}'.$$

Fix $P^0 \in \mathbf{Y}'_0$, and let $\widetilde{\omega} := \widetilde{\omega}(P^0)$ be the omega limit set of P^0 for $\widetilde{\Psi}_t$. Let

$$R^0 = R^* - W_R^0, \quad S^0 = S^* - W_S^0, \quad U^0 = W_R^0 + W_S^0 - W^0 \quad \text{for } x \in [0,L],$$

then

$$(R^0, S^0, U^0, u^0) \in \mathbf{Y}_0 \iff (W_R^0, W_S^0, u^0, W^0) \in \mathbf{Y}'_0.$$

It follows from the fourth equation in system (7.11) that $\lim_{t\to\infty} W(\cdot,t) = 0$ regardless of initial condition $P^0 \in \mathbf{Y}'$. Thus, there exists a set $\mathcal{I} \subset C([0,1], \mathbb{R}^3_+)$ such that $\widetilde{\omega} := \widetilde{\omega}(P^0) = \mathcal{I} \times \{0\}$.

Claim 7.5. $\mathcal{I} \subset \mathbf{Y}''$.

For each $(W_R^0, W_S^0, u^0) \in \mathcal{I}$, we have

$$(W_R^0, W_S^0, u^0, 0) \in \widetilde{\omega} \subset \mathbf{Y}',$$

where the last inclusion follows from Lemma 4.2. By the definition of $\mathbf{Y}'$, we deduce $(W_R^0, W_S^0, u^0) \in \mathbf{Y}''$. This proves the claim.

Claim 7.6. *$\mathcal{I}$ is compact, invariant and internal chain transitive for the semiflow $\Pi_t : \mathbf{Y}'' \to \mathbf{Y}''$.*

It is straight forward to see that $\mathcal{I} \times \{0\}$ is compact and invariant with respect to $\tilde{\Psi}_t$ iff $\mathcal{I}$ is compact and invariant with respect to Π_t. In view of Lemma 4.2, it follows that for any $(W_R(\cdot), W_S(\cdot), u(\cdot)) \in C([0,1], \mathbb{R}_+^3)$ with $(W_R(\cdot), W_S(\cdot), u(\cdot), W(\cdot)) \in \widetilde{\omega}$, there holds

$$\widetilde{\Psi}_t \mid_{\widetilde{\omega}} (W_R(\cdot), W_S(\cdot), u(\cdot), W(\cdot)) = (\Pi_t(W_R(\cdot), W_S(\cdot), u(\cdot)), 0), \tag{7.19}$$

where Π_t is the semiflows associated with (7.14) on $\mathbf{Y}''$. Given any $a,\ b \in \mathcal{I}$ and any $\epsilon, T > 0$. Since $(a, 0),\ (b, 0) \in \mathcal{I} \times \{0\} = \widetilde{\omega}$ and $\widetilde{\omega}$ is a compact, invariant and internal chain transitive set for $\widetilde{\Psi}_t$ (see, e.g., [23] or [48, Lemma 1.2.1′]), it follows from the definition (see, e.g., [23] or [48, page 8]) that there is a finite sequences $\{t_i\}_{i=1}^{n-1}$ with $t_i \geq T,\ \forall\ 1 \leq i \leq n-1$, and $\{(\chi_i, 0)\}_{i=1}^{n} \subseteq \widetilde{\omega} = \mathcal{I} \times \{0\}$ with $(\chi_1, 0) = (a, 0)$, $(\chi_n, 0) = (b, 0)$ such that

$$\text{dist}\left(\widetilde{\Psi}_{t_{i-1}}(\chi_{i-1}, 0), (\chi_i, 0)\right) < \epsilon,\ \forall\ 2 \leq i \leq n. \tag{7.20}$$

From (7.19), (7.20) as well as the above discussions, it follows that there is finite sequences $\{t_i\}_{i=1}^{n-1}$ with $t_i \geq T,\ \forall\ 1 \leq i \leq n-1$, and $\{\chi_i\}_{i=1}^{n} \subseteq \mathcal{I}$ with $\chi_1 = a$, $\chi_n = b$ such that

$$\text{dist}\left(\Pi_{t_{i-1}}(\chi_{i-1}), \chi_i\right) < \epsilon,\ \forall\ 2 \leq i \leq n.$$

This shows that $\mathcal{I}$ is a compact, invariant and internal chain transitive set for $\Pi_t : \mathbf{Y}'' \to \mathbf{Y}''$. Thus, the proof of the claim is finished.

Thus, from Lemma 7.2 and [48, Theorem 1.2.2] we can conclude that either $\mathcal{I} = \{(0,0,0)\}$ or $\mathcal{I} = \{(\hat{W}_R(\cdot), \hat{W}_S(\cdot), \hat{u}(\cdot))\}$. Since $\Lambda^0 < 0$, Theorem 2.2 (ii) says that $\liminf_{t\to\infty} u(\cdot, t) > 0$, i.e. $\mathcal{I} \neq \{(0,0,0)\}$. Therefore, we must have

$$\mathcal{I} = \{(\hat{W}_R(\cdot), \hat{W}_S(\cdot), \hat{u}(\cdot))\}.$$

This, together with (7.10), implies that Part (ii) holds. □

Proof of Theorem 2.3(ii'). First, it follows from Theorem 2.1 that system (1.9) generates a semiflow in $\mathbf{Y}$. Let d_0 be given by Lemma 7.1. If $d \in (0, d_0)$, then Lemma 7.1 says that $\Lambda^0 < 0$. Theorem 2.3(ii') follows from Theorem 7.1(ii). □

8 Discussion

In this paper, we study the growth of a single phytoplankton species consuming "CO2" (dissolved CO2 and carbonic acid) and "CARB" (bicarbonate and carbonate ions) in a poorly/partially mixed habitat (e.g., the unstirred chemostat, or the water columns of lakes and oceans), where "CO2" and "CARB" can be stored within individuals for later consumption. Our proposed system (1.9), and the general version (1.15) are motivated by the previous works [15, 16, 20, 24, 25, 29, 33, 37, 46, 47].

For the general system (1.15), we first establish the well-posedness results (Theorem 2.1 and Proposition 2.2), and investigate the extinction/persistence of the phytoplankton species (Theorem 2.2). The positive constant Q^* in (2.3) plays an important role in proof of the well-posedness results of system (1.15). From the assumptions (H1) and (H2), it is easy to see that Q^* exists. Inspired by [16, equation (5)], we will provide an explicit relation between Q^* and the parameters on the practical examples of growth rate and uptake rates. As in [16], $\mu(Q)$ takes the form in (1.2), $f_N(N, Q)$ takes the form in (1.4) together with (1.5), and we impose the following condition

$$\mu_\infty \geq \frac{\rho^{\text{low}}_{\max,R} + \rho^{\text{low}}_{\max,S}}{Q^* - Q_{\min}}. \tag{8.1}$$

Since $\mu(Q^*) = \mu_\infty \left(1 - \frac{Q_{\min}}{Q^*}\right)$, it follows that (8.1) is equivalent to

$$\rho^{\text{low}}_{\max,R} + \rho^{\text{low}}_{\max,S} - \mu(Q^*)Q^* \leq 0. \tag{8.2}$$

Note that

$$f_N(N^*(x), Q^*) = \rho_N(Q^*)\frac{N^*(x)}{k_N + N^*(x)} = \rho^{\text{low}}_{\max,N} \cdot \frac{N^*(x)}{k_N + N^*(x)} \leq \rho^{\text{low}}_{\max,N}.$$

Then (8.1) or (8.2) implies that

$$f_R(R^*(x), Q^*) + f_S(R^*(x), Q^*) - \mu(Q^*)Q^* \leq 0,$$

which coincides with the definition of Q^* in (2.3). More biological interpretations on (8.1) can be found in [16, Section 2]. In view of Theorem 2.2, we see that the extinction/persistence of the phytoplankton species is determined by the death rate m, and the principal eigenvalue Λ^0 of the nonlinear eigenvalue problem (2.8). The latter depends on $(R^*(x), S^*(x))$, the unique positive steady-state solution of system (2.1). The eigenvalue Λ^0 depends also on the conversion rate between "CO2" and "CARB" (ω_r and ω_s), the physical transport characteristics of the habitat (i.e. the diffusivity or the advection), uptake rates, and growth rate. It will be of practical interest to understand the dependence of Λ^0 on the parameters of the nonlinear eigenvalue problem (2.8). We leave this challenging problem for future investigation.

When we specialize in the chemostat model (1.9), Theorem 2.3 reveals that there is a unique critical diffusion rate d_0 such that the species will go to extinct (resp. persist) if the diffusion d is greater than or equal to d_0 (resp. d is less than d_0). If we impose the additional condition (H7), then there exists a unique positive steady state solution of system (1.9) when the species persists, and the unique positive steady state solution is globally asymptotically stable. Next, we show that several practical examples can satisfy assumption (H7):

- Assume that $f_N(N,Q) = \rho_N(Q)\frac{N}{k_N+N}$ takes the form (1.4) with (1.5) for all $N \geq 0$ and $Q_{\min} \leq Q \leq Q_{\max}$. We first extend the function $f_N(N,Q)$ in this case to be defined in $\mathbb{R}^2_+$:

$$\hat{f}_N(N,Q) = \hat{\rho}_N(Q)\frac{N}{k_N+N},$$

where

$$\hat{\rho}_N(Q) = \begin{cases} \rho(Q_{\max}) + \frac{\rho(Q_{\min})-\rho(Q_{\max})}{Q_{\min}-Q_{\max}}(Q-Q_{\max}), & \text{for } 0 \leq Q \leq Q_B, \\ 0, \quad \text{for } Q > Q_B, \end{cases}$$

and

$$Q_B = Q_{\max} + \rho(Q_{\max})\frac{\rho(Q_{\min})-\rho(Q_{\max})}{Q_{\max}-Q_{\min}} > Q_{\max}.$$

Then $\hat{f}_N(N,Q)$ satisfies (H2), and (H7) holds if

$$\begin{cases} \omega_s - \frac{\rho^{\text{high}}_{\max,R}-\rho^{\text{low}}_{\max,R}}{Q_{\max}-Q_{\min}} \geq 0, \\ \omega_r - \frac{\rho^{\text{high}}_{\max,S}-\rho^{\text{low}}_{\max,S}}{Q_{\max}-Q_{\min}} \geq 0. \end{cases}$$

- Assume that $f_N(N,Q) = \rho_N(Q)\frac{N}{k_N+N}$ takes the form (1.4) with (1.6) for all $N \geq 0$ and $Q_{\min} \leq Q \leq Q_{\max}$. For this case, $Q_{\max} = Q_B$, where Q_B is given in (H2). If

$$\begin{cases} \omega_s - \frac{\rho_{\max,R}}{Q_{\max}-Q_{\min}} \geq 0, \\ \omega_r - \frac{\rho_{\max,S}}{Q_{\max}-Q_{\min}} \geq 0, \end{cases} \tag{8.3}$$

then (H7) holds. Here, we can give some realistic parameters such that (8.3) is valid, and hence, (H7) holds. For example, ω_r ranges from 2000 d^{-1} to 4000 d^{-1}, and ω_s ranges from 15 d^{-1} to 25 d^{-1} in [37]; $Q_{\min} = 9$ μmol mm^{-3}, $Q_{\max} = 17$ μmol mm^{-3}, $\rho_{\max,R} = 8.2$ μmol mm$^{-3}d^{-1}$, and $\rho_{\max,S} = 7.3$ μmol mm$^{-3}d^{-1}$ in [46].

- If $f_N(N,Q) = \rho_N \frac{N}{k_N+N}$ takes the form (1.4) with (1.7), then (H7) automatically holds.

Understanding extinction/persistence of a single species is a first step to the study of coexistence of multiple species in competition for resources. Thus, this work paves the way for the investigation of competing system consisting of two phytoplankton species with ratio dependence. The other extensions of the model discussed in this paper is to include the factors of respiration and light availability since carbon is lost by respiration and the light reaction of photosynthesis provides the energy for carbon assimilation [46]. In the Supplementary Information of [46], the authors assumed that the respiration rate is proportional to the size of the transient carbon pool, and they further assumed that uptake rates include self-shading by the phytoplankton population, that is, an increase in population density will reduce light intensity. In order to reflect the vertical heterogeneity in the water column, light intensity usually involves nonlocal terms in depth (see e.g., [24, 29, 47]), which make mathematical analysis much more complicated. We will combine the ideas developed in this paper with those arguments in [11, 21] to study a more realistic system that phytoplankton species compete for inorganic carbon with internal storage, and light in a spatially variable habitat in which carbon is lost by respiration. We also leave this interesting project for future study.

It is worth pointing out that the main ideas used in this paper are closely related to the analysis of the ODE system (1.1) or (1.8). Recall that the phytoplankton-free equilibrium $(R,S,Q,u) = (R^*,S^*,Q^*,0)$ of (1.1) is given in (2.4) and (2.5), and it is not hard to show that its local stability is determined by the sign of $\mu(Q^*) - D$. In fact, we can further show that the population is washed out if $\mu(Q^*) - D \leq 0$, and persistence of the species occurs if $\mu(Q^*) - D > 0$. Consider the eigenvalue problem associated with the ODE system (1.1) or (1.8):

$$\begin{cases} f_R\left(R^*, \frac{\varphi}{\phi}\right)\phi + f_S\left(S^*, \frac{\varphi}{\phi}\right)\phi - D\varphi + \Lambda\varphi = 0, \\ \mu\left(\frac{\varphi}{\phi}\right)\phi - D\phi + \Lambda\phi = 0, \end{cases} \tag{8.4}$$

where φ and ϕ are both constants. Then it follows from the relations (2.4) and (2.5) that $\Lambda^0 = -(\mu(Q^*) - D)$ is the principal eigenvalue of system (8.4) corresponding to the eigenfunction $(\varphi, \phi) = (Q^*, 1) \gg (0, 0)$. Thus, the extinction/persistence of system (1.1) or (1.8) can be determined by the principal eigenvalue $\Lambda^0 = -(\mu(Q^*) - D)$, which is parallel to Theorem 2.2 for the PDE system. In order to obtain the uniqueness and global stability of the positive equilibrium of (1.1) or (1.8), we comment that a condition similar to (H7) is needed.

In closing, we describe a quota-structured system with spatial variations related to this paper. In (1.1), we have assumed that the quota per individual varies dynamically and the dynamics of quota also satisfies an ordinary differential equation. The simplest model associated with (1.1) is under the assumption that the consumption of resource and production of populations are directly proportional through a quota constant q, leading to the following system:

$$\begin{cases} \frac{dR}{dt} = (R^{(0)} - R)D - qf_R(R)u - \omega_r R + \omega_s S, \\ \frac{dS}{dt} = (S^{(0)} - S)D - qf_S(S)u + \omega_r R - \omega_s S, \\ \frac{du}{dt} = [f_R(R) + f_S(S) - D]\, u, \\ R(0) \geq 0,\ S(0) \geq 0,\ u(0) \geq 0. \end{cases} \tag{8.5}$$

The other modeling associated with system (1.1) is to assume that quotas differ among individuals at any instant, and the distribution of stored resource quota over individual cells at each location is governed by a structured population model (see, e.g., [6, 7] and section 2 of [18]). The associated system takes the forms:

$$\begin{cases} \frac{dR(t)}{dt} = (R^{(0)} - R(t))D - f_R(R)\int_{\frac{q_{min}}{2}}^{q_{max}} g(q)n(t,q)dq - \omega_r R + \omega_s S, \\ \frac{dS(t)}{dt} = (S^{(0)} - S(t))D - f_S(S)\int_{\frac{q_{min}}{2}}^{q_{max}} g(q)n(t,q)dq + \omega_r R - \omega_s S, \\ \frac{\partial n(t,q)}{\partial t} = [f_R(R) + f_S(S)]\{-\frac{\partial(g(q)n(t,q))}{\partial q} - b(q)n(t,q) + 4b(2q)n(t,2q)\} - Dn(t,q), \\ R(0) \geq 0,\ S(0) \geq 0,\ n(0,q) = n^0(q), \\ n(t, \frac{q_{min}}{2}) = 0. \end{cases} \tag{8.6}$$

Here t denotes time, q stands for the size of an individual cell. n is the population density function, that is, $\int_{q_1}^{q_2} n(t,q)dq$ represents the number of cells with size between q_1 and q_2 at time t. The functions $b(q)$ and $g(q)$ are the rates at which cells of size q divide and grow, respectively. We refer the Appendix in [6] (see also [7] and section 2 of [18]) for detailed descriptions of the following term

$$-\frac{\partial(g(q)n(t,q))}{\partial q} - b(q)n(t,q) + 4b(2q)n(t,2q),$$

which is related to the population operator proposed in [6, 7]. Encouraged by the work [18], we will also investigate a system that combines the structured population model (8.6) with the physical transport equations governing spatial distributions of populations and resources.

Acknowledgement. We are grateful to three anonymous referees for their careful reading and helpful suggestions which led to improvements of our original manuscript.

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