Manuscript submitted to
AIMS' Journals
Volume **X**, Number **0X**, XX **200X**

doi:10.3934/xx.xx.xx.xx

pp. **X–XX**

COEXISTENCE SOLUTIONS OF A COMPETITION MODEL WITH TWO SPECIES IN A WATER COLUMN

Hua Nie

College of Mathematics and Information Science
Shaanxi Normal University, Xi'an, Shaanxi 710119, China.

Sze-Bi Hsu

Department of Mathematics and National Center of Theoretical Science,
National Tsing-Hua University, Hsinchu 300, Taiwan.

Jianhua Wu

College of Mathematics and Information Science
Shaanxi Normal University, Xi'an, Shaanxi 710119, China.

(Communicated by the associate editor name)

Abstract. Competition between species for resources is a fundamental ecological process, which can be modeled by the mathematical models in the chemostat culture or in the water column. The chemostat-type models for resource competition have been extensively analyzed. However, the study on the competition for resources in the water column has been relatively neglected as a result of some technical difficulties. We consider a resource competition model with two species in the water column. Firstly, the global existence and L^∞ boundedness of solutions to the model are established by inequality estimates. Secondly, the uniqueness of positive steady state solutions and some dynamical behavior of the single population model are attained by degree theory and uniform persistence theory. Finally, the structure of the coexistence solutions of the two-species system is investigated by the global bifurcation theory.

1. Introduction.

Competition between species for resources is a fundamental ecological process[7, 20]. The chemostat-type models of resource competition have been extensively analyzed (see, e.g., [10, 14, 15, 16, 22, 23, 24]). However, the study on resource competition in the water column has been relatively neglected as a result of some technical difficulties. Firstly, for the competition models in a water column, the usual reduction of the system to a competitive system of one order lower through the "conservation of nutrient" principle is lost. Thus the system with predation and competition is non-monotone, and the single population model can't be reduced to a scalar system. Hence, it is much more difficult to study the uniqueness and stability of the semitrivial nonnegative equilibria. Secondly, by virtue of the complex boundary conditions, it is hard to establish the global existence of the solutions and a priori estimates of the positive steady state solutions.

2010 *Mathematics Subject Classification.* Primary: 35K57, 35B32; Secondary: 35B50.

Key words and phrases. water column, coexistence solution, uniqueness, degree theory, global bifurcation.

The first author is supported by NSF of China(11001160, 11271236), the Program of NCET in University of MOE of China(NCET-12-0894) and the Fundamental Research Funds for the Central Universities(GK201303008, GK201302004).

Motivated by the biological significance, the study of the models in a water column began to be a problem of considerable interest recently. In [25], a mathematical model describing the vertical distribution of phytoplankton and two resources in a water column was proposed. Numerical results show a catastrophic transition between a surface maximum pattern and a subsurface maximum pattern of phytoplankton. The authors analyzed a model of competition between two phytoplankton species in a stratified water column in [26]. Multiple regions of alternative stable states are possible in parameter space by numerical simulations. In [13], the authors developed a model to explore how phytoplankton respond through growth and movement to opposing resource gradients and different mixing conditions. Numerical computation indicates that the model is able to replicate the diverse vertical distributions observed in nature and explain what underlying mechanisms drive these distributions. The mathematical analysis on competition for resources in a water column can be found in [8], which discussed the existence and uniqueness of steady-state solutions of the system with one resource and one species. Hsu and Lou[9] investigated a nonlocal reaction-diffusion-advection equation which models the growth of a single phytoplankton species in a water column where the species depends solely on light for its metabolism. The combined effect of the death rate, sinking or buoyant coefficient, water column depth, and vertical turbulent diffusion rate on the persistence of a single phytoplankton species was analyzed. Du and Mei[6] studied a general reaction-diffusion-advection equation that models the dynamics of a single phytoplankton species in a eutrophic vertical water column. The asymptotic profiles of the positive steady-state solution for small diffusion, large diffusion and deep water column are given in [6], respectively. However, the dynamical behavior of the resource competition model with two species in a water column is unclear until now.

This paper deals with a general competition model with one resource and two species in a water column

$$
\begin{aligned}
&S_t = \frac{\partial}{\partial x}\left(D_0(x)\frac{\partial S}{\partial x}\right) - \alpha_1 f_1(S)u - \alpha_2 f_2(S)v, && x\in(0,L), t>0,\\
&u_t = \frac{\partial}{\partial x}\left(D(x)\frac{\partial u}{\partial x} - \nu_1(x)u\right) + (f_1(S)-d_1)u, && x\in(0,L), t>0,\\
&v_t = \frac{\partial}{\partial x}\left(D(x)\frac{\partial v}{\partial x} - \nu_2(x)v\right) + (f_2(S)-d_2)v, && x\in(0,L), t>0
\end{aligned} \tag{1}
$$

with boundary conditions and initial conditions

$$
\begin{aligned}
&\frac{\partial S}{\partial x}(0,t)=0, \quad \frac{\partial S}{\partial x}(L,t) = \beta(S^0 - S(L,t)), && t>0,\\
&D(x)\frac{\partial u}{\partial x}(x,t) - \nu_1(x)u(x,t) = 0 \text{ at } x=0 \text{ and } L, && t>0,\\
&D(x)\frac{\partial v}{\partial x}(x,t) - \nu_2(x)v(x,t) = 0 \text{ at } x=0 \text{ and } L, && t>0,
\end{aligned} \tag{2}
$$

$$
\begin{aligned}
&S(x,0)=S_0(x)\ge 0, \quad u(x,0)=u_0(x)\ge 0, \not\equiv 0, && x\in[0,L],\\
&v(x,0)=v_0(x)\ge 0,\not\equiv 0, && x\in[0,L].
\end{aligned} \tag{3}
$$

Here $S(x,t), u(x,t), v(x,t)$ are the concentrations of the nutrient and the two species respectively. $D_0(x)$ is the vertical eddy diffusion coefficient, and $D(x)$ is the diffusion rate of species across the thermocline. $\nu_i(x)$ denotes the velocity of cells, α_i is the yield coefficient, and $d_i > 0$ is the death rate of species $i (i = 1, 2)$. L is the depth of the water column. $S^0 > 0$ is the nutrient concentration at the sediment. $\beta > 0$

is the relative transfer velocity of nutrients at the sediment interface. $f_i(S) = \frac{m_i S}{a_i + S}$ with $i = 1, 2$, which is the nutrient-limited growth rate of species i. $m_i > 0$ is the maximum growth rate, and $a_i > 0$ is the half-saturation constant. The initial concentrations of the nutrient and the two species are all assumed to be nonnegative continuous functions on the water column. The detailed biological explanation for this model can be found in [13, 25, 26].

By suitable scaling, we may take $S^0 = 1$ and $L = 1$. Then the original system (1)-(3) becomes

$$\begin{cases} S_t = (D_0(x)S_x)_x - \alpha_1 f_1(S)u - \alpha_2 f_2(S)v, & x \in (0,1), t > 0, \\ u_t = (D(x)u_x - \nu_1(x)u)_x + (f_1(S) - d_1)u, & x \in (0,1), t > 0, \\ v_t = (D(x)v_x - \nu_2(x)v)_x + (f_2(S) - d_2)v, & x \in (0,1), t > 0 \end{cases} \tag{4}$$

with boundary conditions and initial conditions

$$\begin{cases} S_x(0,t) = 0, \quad S_x(1,t) = \beta(1 - S(1,t)), & t > 0, \\ D(x)u_x(x,t) - \nu_1(x)u(x,t) = 0 \text{ at } x = 0 \text{ and } 1, & t > 0, \\ D(x)v_x(x,t) - \nu_2(x)v(x,t) = 0 \text{ at } x = 0 \text{ and } 1, & t > 0, \end{cases} \tag{5}$$

$$\begin{array}{ll} S(x,0) = S_0(x) \geq 0, \quad u(x,0) = u_0(x) \geq 0, \not\equiv 0, & x \in [0,1], \\ v(x,0) = v_0(x) \geq 0, \not\equiv 0, & x \in [0,1]. \end{array} \tag{6}$$

We concentrate on positive solutions of the following steady state system

$$\begin{cases} (D_0(x)S_x)_x - \alpha_1 f_1(S)u - \alpha_2 f_2(S)v = 0, & x \in (0,1), \\ (D(x)u_x - \nu_1(x)u)_x + (f_1(S) - d_1)u = 0, & x \in (0,1), \\ (D(x)v_x - \nu_2(x)v)_x + (f_2(S) - d_2)v = 0, & x \in (0,1), \end{cases} \tag{7}$$

with boundary conditions

$$\begin{cases} S_x(0) = 0, \quad S_x(1) = \beta(1 - S(1)), \\ D(x)u_x - \nu_1(x)u = 0 \text{ at } x = 0 \text{ and } 1, \\ D(x)v_x - \nu_2(x)v = 0 \text{ at } x = 0 \text{ and } 1. \end{cases} \tag{8}$$

Throughout this paper, we assume the diffusion rates and velocity of species satisfy the following hypotheses

(H) $\qquad D_0(x), D(x), \nu_i(x) \in C^{1+\gamma}[0,1]$ and $D_0(x), D(x) > 0$ on $[0,1]$,

where $\gamma \in (0,1), i = 1, 2$. Moreover, we can extend the response functions $f_i : [0, +\infty) \to \mathbb{R}$ to $\bar{f}_i : \mathbb{R} \to \mathbb{R}$ such that $\bar{f}_i(S) = f_i(S)$ for $S \geq 0$, $\bar{f}_i(S) < 0$ for $S < 0$, and $\bar{f}_i \in C^1(\mathbb{R})$ (see [16, 23]). We will denote $\bar{f}_i(S)$ by $f_i(S)$ for the sake of simplicity.

As mentioned before, the conservation principle is invalid, and the system with predation and competition is non-monotone. Moreover, the single population model can't be reduced to a scalar system. Hence, it is hard to study the uniqueness and stability of the semitrivial nonnegative equilibria. The organization of the paper is as follows: In Section 2, by Gronwall inequality and an indirect argument, we establish the global existence and L^∞ boundedness of solutions to the parabolic system (4)-(6). In Section 3, by the general maximum principle and a crucial spectral analysis, we show any positive solution of the single population model is nondegenerative, which produce the uniqueness of semitrivial nonnegative equilibria (see Lemma 3.3 and Theorem 3.4). Some dynamical behavior of the single population model are attained by uniform persistence theory. The structure of the coexistence solutions of the system (4)-(6) is investigated in Section 4 by bifurcation theory. The nondegeneracy of any positive solution of the single population model also plays a key role in proving the existence of the local and global bifurcation. Finally, some numerical results on the coexistence region are given, which complement the analytic results.

2. **Preliminaries.** The goal of this section is twofold. One is to provide some well-known lemmas related to our study. The other is to establish the global existence and L^∞ boundedness of solutions of the parabolic system (4)-(6).

Consider the linear eigenvalue problem, which is related to the study of coexistence solutions of (7)-(8),

$$\begin{array}{ll} -(D(x)\varphi_x - \nu(x)\varphi)_x + q(x)\varphi = \lambda\varphi, & 0 < x < 1 \\ D(x)\varphi_x - \nu(x)\varphi = 0 & \text{at } x = 0 \text{ and } 1, \end{array} \tag{9}$$

where $D(x)$ and $\nu(x)$ satisfy the hypothesis (H), and $q(x)$ is a continuous function in $[0, 1]$. Let $\psi = e^{-\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}\varphi(x)$. Then ψ satisfies

$$\begin{array}{l} -\left(D(x)e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}\psi_x\right)_x + q(x)e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}\psi = \lambda e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}\psi, \quad 0 < x < 1 \\ \psi_x(0) = \psi_x(1) = 0. \end{array} \tag{10}$$

Lemma 2.1. [2, 9] *All eigenvalues of (10) are real, and the smallest eigenvalue $\lambda_1(q(x), \nu(x))$ can be characterized as*

$$\lambda_1(q(x), \nu(x)) = \inf_{\psi \neq 0, \psi \in H^1(0,1)} \frac{\int_0^1 e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}(D(x)\psi_x^2 + q(x)\psi^2)\mathrm{d}x}{\int_0^1 e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}\psi^2\mathrm{d}x},$$

which corresponds to a positive eigenfunction ψ_1, and $\lambda_1(q(x), \nu(x))$ is the only eigenvalue whose corresponding eigenfunction does not change sign. Moreover,

(i) *$q_1(x) \geq q_2(x)$ implies $\lambda_1(q_1(x), \nu(x)) \geq \lambda_1(q_2(x), \nu(x))$, and the equality holds only if $q_1(x) \equiv q_2(x)$;*
(ii) *$q_n(x) \to q(x)$ in $C[0, 1]$ implies $\lambda_1(q_n(x), \nu(x)) \to \lambda_1(q(x), \nu(x))$.*

Remark 1. By Lemma 2.1, it is easy to see that if $q(x) \equiv q_0$(a constant), then $\lambda_1(q_0, \nu(x)) = q_0$ with the corresponding eigenfunction $\varphi(x) = e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}$. In particular, $\lambda_1(0, \nu(x)) = 0$.

Lemma 2.2. [21] *Let Ω is a bounded domain in $\mathbb{R}^n$ with boundary surface $\partial\Omega \in C^{2+\gamma}$, $q(x) \in C(\overline{\Omega})$ and P be a positive constant such that $P - q(x) > 0$ on $\overline{\Omega}$. Let $\sigma_1(q(x))$ be the principal eigenvalue of the eigenvalue problem*

$$\begin{array}{l} -\sum\limits_{i,j=1}^n \mathrm{D}_j(a_{ij}(x)\mathrm{D}_i\varphi) + q(x)\varphi = \sigma\varphi, \quad x \in \Omega, \\ \sum\limits_{i,j=1}^n a_{ij}(x)\mathrm{D}_i\varphi\cos(n, x_j) + b(x)\varphi = 0, \quad x \in \partial\Omega, \end{array}$$

where $a_{ij}(x), b(x) \in C(\partial\Omega)$, $b(x) \geq 0$, and n is the outward unit normal vector on $\partial\Omega$. Then the following conclusions hold

(i) *if $\sigma_1(q(x)) < 0$ then the spectral radius $r[(P - \mathrm{D}_j(a_{ij}(x)\mathrm{D}_i))^{-1}(P - q(x))] > 1$;*
(ii) *if $\sigma_1(q(x)) > 0$ then the spectral radius $r[(P - \mathrm{D}_j(a_{ij}(x)\mathrm{D}_i))^{-1}(P - q(x))] < 1$;*
(iii) *if $\sigma_1(q(x)) = 0$ then the spectral radius $r[(P - \mathrm{D}_j(a_{ij}(x)\mathrm{D}_i))^{-1}(P - q(x))] = 1$.*

Lemma 2.3. [4, 5] *Let $F : W \to W$ be a compact, continuously differentiable operator, W be a cone in the Banach space E with zero Θ. Suppose that $W - W$ is dense in E and that $\Theta \in W$ is a fixed point of F and $A_0 = F'(\Theta)$. Then the following results hold:*

(i) $\text{index}_W(F,\Theta)=1$ *if the spectral radius* $r(A_0)<1$*;*
(ii) $\text{index}_W(F,\Theta)=0$ *if* A_0 *has eigenvalue greater than 1 and* Θ *is an isolated solution of* $x=F(x)$*, that is* $h\neq A_0h$ *if* $h\in\overline{W}-\Theta$*.*

Next, we show that the parabolic system (4)-(6) has a unique solution $(S(x,t), u(x,t), v(x,t))$, which is defined for all $t>0$ and is bounded in L^∞.

Lemma 2.4. *Suppose* (H) *holds. Then for any given* $\delta_0>0$*, the initial-boundary value problem* (4)-(6) *admits a unique solution* (S,u,v) *defined for all* $x\in[0,1]$ *and* $t>0$ *provided* $d_1\geq\delta_0, d_2\geq\delta_0$*, and there exist positive constants* ρ_0,ρ_1,ρ_2 *depending only on the initial data* $S_0(x),u_0(x),v_0(x)$*, such that*

$$0<S(x,t)\leq\rho_0,\quad 0<u(x,t)\leq\rho_1,\quad 0<v(x,t)\leq\rho_2,\quad x\in[0,1],t>0.$$

Proof. The local existence and uniqueness of solutions to (4)-(6) are standard, see [19]. Next, we show the global existence and the boundedness. Let $U=ue^{-\int_0^x\frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}$ and $V=ve^{-\int_0^x\frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}$. Then (4)-(6) becomes

$$\begin{cases} S_t=(D_0(x)S_x)_x-\alpha_1f_1(S)Ue^{\int_0^x\frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}-\alpha_2f_2(S)Ve^{\int_0^x\frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi},\\ e^{\int_0^x\frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}U_t=\left(D(x)U_xe^{\int_0^x\frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}\right)_x+(f_1(S)-d_1)Ue^{\int_0^x\frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi},\\ e^{\int_0^x\frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}V_t=\left(D(x)V_xe^{\int_0^x\frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}\right)_x+(f_2(S)-d_2)Ve^{\int_0^x\frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi},\\ S_x(0,t)=0,\quad S_x(1,t)=\beta(1-S(1,t)),\quad t>0,\\ U_x(0,t)=U_x(1,t)=0,\quad V_x(0,t)=V_x(1,t)=0,\quad t>0,\\ S(x,0)=S_0(x)\geq0,\quad U(x,0)=u_0(x)e^{-\int_0^x\frac{\nu_1(\xi)}{D(\xi)}d\xi}\geq0,\not\equiv0,\\ V(x,0)=v_0(x)e^{-\int_0^x\frac{\nu_2(\xi)}{D(\xi)}d\xi}\geq0,\not\equiv0.\end{cases}\tag{11}$$

By the maximum principle of the parabolic equation, the solution $(S(x,t),U(x,t), V(x,t))$ of (11) satisfies $S(x,t)>0,U(x,t)>0,V(x,t)>0$ for all $x\in[0,1],t>0$. Moreover, it is easy to see that $\limsup_{t\to\infty}S(x,t)\leq1$, which implies for $\epsilon>0$ small there exists $T_1>0$ such that $S(x,t)\leq1+\epsilon$ for all $x\in[0,1],t\geq T_1$. Hence, there exists positive constant ρ_0 depending only on the initial data $S_0(x)$, such that $0<S(x,t)\leq\rho_0$ for all $x\in[0,1],t>0$, and we only need to show the boundedness of $U(x,t),V(x,t)$. Let $d=\min\{d_1,d_2\}$ and

$$\Phi(t)=\int_0^1(S+\alpha_1Ue^{\int_0^x\frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}+\alpha_2Ve^{\int_0^x\frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi})\mathrm{d}x.$$

By integrating each equation in (11) and summing together, we obtain

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}\Phi(t)+d\Phi(t)\quad &=D_0(1)S_x(1,t)+(d-d_1)\alpha_1\int_0^1Ue^{\int_0^x\frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}\mathrm{d}x\\ &\quad+(d-d_2)\alpha_2\int_0^1Ve^{\int_0^x\frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}\mathrm{d}x+d\int_0^1S(x,t)\mathrm{d}x\\ &\leq D_0(1)\beta+d\rho_0=\rho.\end{aligned}$$

By Gronwall inequality we get the L^1 estimates

$$\Phi(t)\leq\Phi(0)e^{-dt}+\rho\int_0^te^{-d(t-\tau)}\mathrm{d}\tau=\Phi(0)e^{-dt}+\frac{\rho}{d}(1-e^{-dt}).\tag{12}$$

Next, we show $U(x,t)$ is bounded for all $x\in[0,1]$ and $t>0$. Let $\phi(t)=\max_{x\in[0,1],\tau\in[0,t]}U(x,\tau)$. Clearly, $\phi(t)$ is nondecreasing. Suppose for contradiction that $\phi(t)\to\infty$ as $t\to\infty$. Then we can find $t_n\to\infty$ such that $\phi(t_n)=\max_{x\in[0,1]}U(x,t_n)$.

We may assume that $t_n > 1$ for all $n \geq 1$. Define $\tilde{U}_n(x,t) = \frac{U(x,t+t_n-1)}{\phi(t_n)}$. Then $\tilde{U}_n(x,t)$ satisfies

$$\begin{aligned}
&(e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}\tilde{U}_n)_t = (D(x)e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}(\tilde{U}_n)_x)_x \\
&\qquad\qquad +(f_1(S(x,t+t_n-1)) - d_1)e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}\tilde{U}_n, \quad x \in (0,1), t > 0, \\
&(\tilde{U}_n)_x(0,t) = (\tilde{U}_n)_x(1,t) = 0, \quad t > 0, \\
&0 \leq \tilde{U}_n(x,0) \leq 1.
\end{aligned}$$

Noting that $|f_1(S(x,t+t_n-1)) - d_1| \leq |f_1(\rho_0) - d_1| := \Lambda_0$, the comparison principle for parabolic system leads to $0 \leq \tilde{U}_n(x,t) \leq e^{\Lambda_0 t}$ for $x \in [0,1]$ and $t \geq 0$. Hence by the application of standard parabolic regularity, we can conclude that $\{\tilde{U}_n\}$ is bounded in $C^{1+\gamma,\gamma}([0,1] \times [\frac{1}{2},2])$ for any $\gamma \in (0,1)$. Hence, by passing to a subsequence if necessary we get $\tilde{U}_n(x,t) \to \tilde{U}$ in $C^{1,0}([0,1] \times [\frac{1}{2},2])$. Since $|f_1(S(x,t+t_n-1))-d_1| \leq \Lambda_0$, we may assume that $f_1(S(x,t+t_n-1))-d_1 \to g(x,t)$ weakly in $L^2([0,1] \times [\frac{1}{2},2])$ by passing to a further subsequence if necessary. Moreover, $|g(x,t)| \leq \Lambda_0$, and $\tilde{U}$ is a weak solution to

$$\begin{aligned}
&(e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}\tilde{U})_t = (D(x)e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}\tilde{U}_x)_x + g(x,t)e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}\tilde{U}, \quad x \in (0,1), t \in [\tfrac{1}{2},2], \\
&\tilde{U}_x(0,t) = \tilde{U}_x(1,t) = 0, \quad t \in [\tfrac{1}{2},2], \\
&0 \leq \tilde{U}(x,t) \leq e^{\Lambda_0 t}, \quad x \in [0,1], t \in [\tfrac{1}{2},2].
\end{aligned}$$

It follows from $\max\limits_{x\in[0,1]} \tilde{U}_n(x,1) = 1$ that $\max\limits_{x\in[0,1]} \tilde{U}(x,1) = 1$, which implies $\tilde{U} \not\equiv 0$. By the strong maximum principle, we deduce that $\tilde{U}(x,1) \geq \delta_1 > 0$ in [0,1]. Hence, $\tilde{U}_n(x,1) \geq \frac{\delta_1}{2}$ for all large n and $x \in [0,1]$, which leads to

$$U(x,t_n) = \tilde{U}_n(x,1)\phi(t_n) \geq \frac{\delta_1}{2}\phi(t_n) \text{ for all large } n \text{ and } x \in [0,1].$$

It follows that

$$\Phi(t_n) > \int_0^1 \alpha_1 U(x,t_n)e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}\mathrm{d}x \geq \alpha_1 \int_0^1 \frac{\delta_1}{2}\phi(t_n)e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}\mathrm{d}x \to \infty$$

as $n \to \infty$, a contradiction to (12). That is, $U(x,t)$ is bounded for all $x \in [0,1]$ and $t > 0$. In view of $U(x,t) > 0$ for all $x \in [0,1]$ and $t > 0$, we obtain that there exists $\rho_1 > 0$ such that $0 < u(x,t) \leq \rho_1$ for all $x \in [0,1]$ and $t > 0$. Repeating the same arguments as before, we assert that there exists $\rho_2 > 0$ such that $0 < v(x,t) \leq \rho_2$ for all $x \in [0,1]$ and $t > 0$. □

In order to figure out the non-trivial nonnegative solutions of (7)-(8), we derive some estimates for the nonnegative solutions of (7)-(8).

Lemma 2.5. *Suppose* (H) *holds, and* (S,u,v) *is a nonnegative solution of* $(7)-(8)$ *with* $u \not\equiv 0$ *and* $v \not\equiv 0$. *Then*

(i) $0 < S < 1$ *in* $[0,1]$, $u > 0$ *and* $v > 0$ *in* $[0,1]$, *and* $S(x)$ *is strictly increasing on* $[0,1]$;

(ii) $0 < d_1 < f_1(1)$ *and* $0 < d_2 < f_2(1)$;

(iii) $D(x)u_x - \nu_1(x)u > 0$ *and* $D(x)v_x - \nu_2(x)v > 0$ *in* $(0,1)$, *and for any given* $\delta_0 > 0$, *there exists a positive constant* $C(\delta_0)$ *such that* $\|u\|_\infty + \|v\|_\infty \leq C$ *if* $d_1 \in [\delta_0, f_1(1))$ *and* $d_2 \in [\delta_0, f_2(1))$.

Proof. (i)At first, for any nonnegative solution (S,u,v) of (7)-(8), we have $S(0) > 0$. Indeed, if $S(0) = 0$, then it follows from the existence and uniqueness of the solution to the ordinary differential equation that $S \equiv 0$, which is a contradiction to the boundary condition $S_x(1) = \beta(1 - S(1))$. Note that

$$\begin{aligned}
&-(D_0(x)S_x)_x + \left(\alpha_1 u \int_0^1 f_1'(\tau S)\mathrm{d}\tau + \alpha_2 v \int_0^1 f_2'(\tau S)\mathrm{d}\tau\right) S = 0,\\
&S_x(0) = 0, \quad S_x(1) + \beta S(1) = \beta > 0.
\end{aligned}$$

It follows from the maximum principle that $S > 0$ on $[0, 1]$. Let $U = ue^{-\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}$. Similarly, for any nonnegative solution (S, u, v) of (7)-(8) with $u \not\equiv 0, v \not\equiv 0$, we have $U(0) > 0$, $U(1) > 0$, and

$$\begin{aligned}
&-\left(D(x)U_x e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}\right)_x + d_1 e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi} U = f_1(S)Ue^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi} \geq 0, \not\equiv 0,\\
&U_x(0) = 0, \quad U_x(1) = 0.
\end{aligned}$$

It follows from the strong maximum principle that $U > 0$ on $[0, 1]$, and hence $u > 0$ on $[0, 1]$. Similar arguments imply $v > 0$ on $[0, 1]$. From the equation for S, we get $(D_0(x)S_x)_x = \alpha_1 f_1(S)u + \alpha_2 f_2(S)v > 0$ and $S_x(0) = 0$. Hence, $D_0(x)S_x > 0$ in $(0, 1]$. By hypothesis (H), $S_x > 0$ in $(0, 1]$. Namely, S is strictly increasing on $[0, 1]$. Meanwhile, noting that $S_x(1) = \beta(1 - S(1)) > 0$, we have $S(1) < 1$, and for any $x \in [0, 1]$, $S(x) < S(1) < 1$.

(ii) From the equation for u and the positivity of u, we obtain $-d_1 = \lambda_1(-f_1(S))$. It follows from (i) that $-f_1(1) = \lambda_1(-f_1(1)) < \lambda_1(-f_1(S)) < \lambda_1(0) = 0$. Hence, we have $0 < d_1 < f_1(1)$. Similarly, we have $0 < d_2 < f_2(1)$.

(iii) Integrating the equation for u, we get $\int_0^1 (f_1(S) - d_1)u\mathrm{d}x = 0$. Noting that $S(x)$ is strictly monotone increasing in $(0, 1)$, one can assert that $f_1(S(x)) - d_1$ is strictly monotone increasing with respect to x in $(0, 1)$. Hence, there exists some $x_0 \in (0, 1)$ such that $f_1(S(x)) - d_1 < 0$ for $x \in (0, x_0)$; and $f_1(S(x)) - d_1 > 0$ for $x \in (x_0, 1)$. It follows from the equation of u that $(D(x)u_x - \nu_1(x)u)_x > 0$ in $(0, x_0)$, and $(D(x)u_x - \nu_1(x)u)_x < 0$ in $(x_0, 1)$. Noting that $D(x)u_x - \nu_1(x)u = 0$ at $x = 0$ and 1, we have $D(x)u_x - \nu_1(x)u > 0$ in $(0, 1)$. In particular, $u_x > 0$ in $(0, 1)$ if $\nu_1(x) > 0$ in $(0, 1)$. Repeating the similar arguments as above, we obtain $D(x)v_x - \nu_2(x)v > 0$ in $(0, 1)$.

Next, we establish a priori estimates for u and v by an indirect argument. To this end, for any $\delta_0 > 0$, suppose there exists a sequence $(d_1^{(i)}, d_2^{(i)}) \in [\delta_0, f_1(1) - \delta_0] \times [\delta_0, f_2(1) - \delta_0]$ and positive solution (S_i, u_i, v_i) to (7)-(8) with $d_1 = d_1^{(i)}, d_2 = d_2^{(i)}$ such that $\|u_i\|_\infty + \|v_i\|_\infty \to \infty$ as $i \to \infty$. Without loss of generality, we assume $\|u_i\|_\infty \to \infty$ as $i \to \infty$. Let $U_i = e^{-\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi} u_i$. Then $\|U_i\|_\infty \to \infty$ and U_i satisfies

$$\begin{aligned}
&\left(D(x)(U_i)_x e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}\right)_x + (f_1(S_i) - d_1^{(i)})U_i e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi} = 0,\\
&(U_i)_x(0) = (U_i)_x(1) = 0.
\end{aligned}$$

Set $\tilde{U}_i = \frac{U_i}{\|U_i\|_\infty}$. Then

$$\begin{aligned}
&\left(D(x)(\tilde{U}_i)_x e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}\right)_x + (f_1(S_i) - d_1^{(i)})\tilde{U}_i e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi} = 0,\\
&(\tilde{U}_i)_x(0) = (\tilde{U}_i)_x(1) = 0.
\end{aligned}$$

Since $0 \leq f_1(S_i) \leq f_1(1)$, we can assume $f_1(S_i) \to h_1(x)$ weakly in $L^2(0, 1)$, and $0 \leq h_1(x) \leq f_1(1)$. Note that $D(x) \in C^{1+\gamma}[0, 1]$ and $D(x) > 0$ on $[0, 1]$. Passing to a sequence if necessary, we may assume by passing to a subsequence $d_1^{(i)} \to d_1 \in$

$[\delta_0, f_1(1)-\delta_0]$, $\tilde{U}_i \to \tilde{U}$ in $C^1[0,1]$, and $\tilde{U}$ is a weak solution to

$$\begin{aligned}&\left(D(x)\tilde{U}_x e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}\right)_x + (h_1(x)-d_1)\tilde{U}e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi} = 0,\\ &\tilde{U}_x(0) = \tilde{U}_x(1) = 0.\end{aligned} \tag{13}$$

It follows from the strong maximum principle that $\tilde{U} > 0$ on $[0, 1]$. From the equation for S_i, we obtain

$$\begin{aligned}&(D_0(x)(S_i)_x)_x = \alpha_1 f_1(S_i)e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}\|U_i\|_\infty \tilde{U}_i + \alpha_2 f_2(S_i)v_i,\\ &(S_i)_x(0) = 0,\ (S_i)_x(1) = \beta(1-S_i(1)).\end{aligned}$$

Multiplying this equation by a smooth function $\varphi \in \{\varphi \in C^\infty[0,1] : \varphi_x(0) = \varphi_x(1) = 0\}$ and $\varphi > 0$ on $[0, 1]$, and integrating by parts, we obtain

$$\begin{aligned}&D_0(1)\beta(1-S_i(1)) + \textstyle\int_0^1 (D_0(x))_x\varphi_x S_i \mathrm{d}x + \int_0^1 D_0(x)\varphi_{xx}S_i\mathrm{d}x\\ &> \alpha_1\|U_i\|_\infty \textstyle\int_0^1 f_1(S_i)e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}\tilde{U}_i\varphi\mathrm{d}x > 0.\end{aligned}$$

Dividing this inequality by $\|U_i\|_\infty$, and letting $i \to \infty$, we get

$$\int_0^1 h_1(x)e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}\tilde{U}\varphi\mathrm{d}x = 0,$$

which yields $h_1(x) \equiv 0$ a.e. in $(0, 1)$. It follows from (13) that $d_1 = 0$, a contradiction. □

3. **Dynamical behavior of single population model.**

In order to investigate positive solutions of the two-species system (4)-(6), we first study the following single population model

$$\begin{cases} S_t = (D_0(x)S_x)_x - \alpha f(S)u, & x \in (0,1), t > 0,\\ u_t = (D(x)u_x - \nu(x)u)_x + (f(S)-d)u, & x \in (0,1), t > 0,\\ S_x(0,t) = 0, \quad S_x(1,t) = \beta(1-S(1,t)), & t > 0,\\ D(x)u_x(x,t) - \nu(x)u(x,t) = 0 & \text{at } x = 0, 1, t > 0,\\ S(x,0) = S_0(x) \ge 0, \quad u(x,0) = u_0(x) \ge 0, \not\equiv 0, & x \in [0,1],\end{cases} \tag{14}$$

where $f(S), \alpha, \nu$ and d are exactly the simplification of the associated parameters or variables with subscript $i = 1$ or 2. Moreover, the vertical diffusion rates $D_0(x), D(x)$ and the velocity of species $\nu(x)$ still satisfy the hypothesis (H). The first step is to work out the properties of solutions to the steady state system

$$\begin{aligned}&(D_0(x)S_x)_x - \alpha f(S)u = 0, && x \in (0,1),\\ &(D(x)u_x - \nu(x)u)_x + (f(S)-d)u = 0, && x \in (0,1),\\ &S_x(0) = 0, \quad S_x(1) = \beta(1-S(1)),\\ &D(x)u_x(x) - \nu(x)u(x) = 0 \text{ at } x = 0, 1.\end{aligned} \tag{15}$$

It follows from Lemma 2.5 that the following lemma holds, which establishes a priori estimates for nonnegative solutions of (15).

Lemma 3.1. *Suppose (H) holds, and let (S, u) be a nonnegative solution of (15) with $u \not\equiv 0$. Then*

(i) *$0 < S < 1$ in $[0, 1]$, $u > 0$ in $[0, 1]$, and S is strictly increasing on $[0, 1]$;*
(ii) *$0 < d < f(1)$;*
(iii) *$D(x)u_x - \nu(x)u > 0$ in $(0, 1)$, and for any given $\delta_0 > 0$, there exists a positive constant $C_1(\delta_0)$ such that $\|u\|_\infty \le C_1$ provided that $d \in [\delta_0, f(1))$.*

Next, we show the uniqueness of positive equilibrium of (15) by degree theory. To this end, let $\chi = 1 - S, U = e^{-\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi} u(x)$. Then (15) is equivalent to

$$\begin{cases} (D_0(x)\chi_x)_x + \alpha f(1-\chi)e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi} U = 0, & x \in (0,1), \\ (D(x)e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi} U_x)_x + (f(1-\chi) - d)e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi} U = 0, & x \in (0,1), \\ \chi_x(0) = 0, \quad \chi_x(1) + \beta\chi(1) = 0, \qquad U_x(0) = U_x(1) = 0. \end{cases} \tag{16}$$

It follows from Lemma 3.1 that any nonnegative solution of (16) with $U \not\equiv 0$ satisfies

$$0 < \chi < 1, \quad 0 < U \le C_1 \max_{[0,1]} e^{-\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi} \text{ on } [0,1].$$

We introduce the spaces:

$$\begin{aligned} &X = C[0,1] \times C[0,1], \\ &W = \{(u,v) \in X | u \ge 0, v \ge 0 \ \text{ for } \ x \in [0,1]\}, \\ &\Omega = \{(u,v) \in W | u < 2, v < C_1 \max_{[0,1]} e^{-\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi} + 1\}, \end{aligned}$$

Then W is a cone of X and Ω is a bounded open set in W. Since $f(1-\chi) \ge f(1) - B_1\chi$ for some positive constant $B_1 > 0$, we can define $A_\tau : [0,1] \times X \to X$ by

$$A_\tau(\chi, U) := \begin{pmatrix} K_0(\alpha f(1-\chi)e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi} U + M\chi) \\ K((\tau f(1-\chi) - d)e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi} U + MU) \end{pmatrix},$$

where K_0, K are the solution operators $\phi = K_0(h_1(x))$ and $\psi = K(h_2(x))$ for the problems respectively

$$-(D_0(x)\phi_x)_x + M\phi = h_1(x),\ x \in (0,1), \quad \phi_x(0) = 0,\ \phi_x(1) + \beta\phi(1) = 0,$$

$$-(D(x)e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}\psi_x)_x + M\psi = h_2(x),\ x \in (0,1), \quad \psi_x(0) = 0,\ \psi_x(1) = 0.$$

M is large enough such that $M - \alpha B_1 \chi e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi} U > 0$ and $M + (\tau f(1-\chi) - d)e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi} > 0$ for all $(\chi, U) \in \Omega$, $\tau \in [0,1]$ and $x \in [0,1]$. Hence, for any $\tau \in [0,1]$, we have $A_\tau : \Omega \to W$. It follows from standard elliptic regularity theory that A_τ is compact and continuously differentiable. Let $A = A_1$. By Lemma 3.1, (16) (or (15) equivalently) has nonnegative solutions if and only if the operator A has a fixed point in Ω. Moreover, similar arguments as in Lemma 3.1 indicate that A_τ has no fixed point on $\partial\Omega$.

Lemma 3.2. (i) $\mathrm{index}(A, \Omega, W) = 1$; (ii) $\mathrm{index}(A, (0,0), W) = 0$ *provided that* $\delta \le d < f(1)$.

Proof. (i) It follows from similar arguments as in Lemma 3.1 that A_τ has no fixed point on $\partial\Omega$. By the homotopic invariance of the degree, we obtain

$$\mathrm{index}(A, \Omega, W) = \mathrm{index}(A_\tau, \Omega, W) = \mathrm{index}(A_0, \Omega, W).$$

Clearly, $(0,0)$ is the unique fixed point of A_0 in Ω. Hence,

$$\mathrm{index}(A, \Omega, W) = \mathrm{index}(A_0, \Omega, W) = \mathrm{index}(A_0, (0,0), W).$$

By some standard calculations, we have $\mathrm{index}(A_0, (0,0), W) = 1$. Hence,

$$\mathrm{index}(A, \Omega, W) = 1.$$

(ii) Let $A'(0,0)$ be the Fréchet derivative of A at $(0,0)$ with respect to (χ, U). Suppose $A'(0,0)(\phi,\psi)^\top = (\phi,\psi)^\top$ with $(\phi,\psi) \in \overline{W} - (0,0)$. Then

$$\begin{array}{ll} -\left(D_0(x)\phi_x\right)_x - \alpha f(1) e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}\psi = 0, & x \in (0,1), \\ -\left(D(x) e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}\psi_x\right)_x - (f(1)-d) e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}\psi = 0, & x \in (0,1), \\ \phi_x(0) = 0, \quad \phi_x(1) + \beta\phi(1) = 0, \quad \psi_x(0) = \psi_x(1) = 0. & \end{array}$$

Since $f(1) - d > 0$ and $\psi \geq 0$, it is easy to see that $\psi \equiv 0$, which implies $\phi \equiv 0$, a contradiction to $(\phi,\psi) \in \overline{W} - (0,0)$. Hence, $(0,0)$ is an isolated fixed point of A in W.

Let $A'(0,0)(\phi,\psi)^\top = \lambda(\phi,\psi)^\top$. Then

$$\begin{array}{l} -\lambda\left(D_0(x)\phi_x\right)_x + (\lambda-1)M\phi = \alpha f(1) e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}\psi, \ x \in (0,1), \\ -\left(D(x) e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}\psi_x\right)_x + M\psi = \frac{1}{\lambda}\left(M - (d - f(1)) e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}\psi\right), \ x \in (0,1), \\ \phi_x(0) = 0, \quad \phi_x(1) + \beta\phi(1) = 0, \quad \psi_x(0) = \psi_x(1) = 0. \end{array} \tag{17}$$

Consider the eigenvalue problem

$$-\left(D(x) e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}\psi_x\right)_x + (d - f(1)) e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}\psi = \sigma\psi, \ \psi_x(0) = \psi_x(1) = 0. \tag{18}$$

In view of $d < f(1)$, we can find that the least eigenvalue $\sigma_1 < 0$ of (18). It follows from Lemma 2.2 that the spectral radius

$$\lambda_0 := r\left(M - \frac{\partial}{\partial x}\left(D(x) e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}\frac{\partial}{\partial x}\right)^{-1}\left(M - (d - f(1)) e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}\right)\right) > 1$$

Note that $-\lambda\frac{\partial}{\partial x}\left(D_0(x)\frac{\partial}{\partial x}\right) + (\lambda-1)M$ is invertible subject to the boundary conditions $\phi_x(0) = 0$, $\phi_x(1) + \beta\phi(1) = 0$ when $\lambda > 1$. We can conclude that the spectral radius λ_0 is an eigenvalue of $A'(0,0)$. Hence, $A'(0,0)$ has an eigenvalue greater than 1. It follows from Lemma 2.3 that $\operatorname{index}(A,(0,0),W) = 0$ provided that $\delta \leq d < f(1)$. ☐

Lemma 3.3. *Suppose (S_0,u_0) is a positive solution of (15). Then (S_0,u_0) is nondegenerative, and* $\operatorname{index}(A,(\chi_0,U_0),W) = 1$, *where* $(\chi_0,U_0) = (1-S_0, e^{-\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}u_0)$.

Proof. In order to show the nondegeneracy of (S_0,u_0), we only need to show the linearization of (15) at (S_0,u_0) with respect to (S,u)

$$\begin{array}{ll} \left(D_0(x)\phi_x\right)_x - \alpha f'(S_0)u_0\phi - \alpha f(S_0)\psi = 0, & x \in (0,1), \\ \left(D(x)\psi_x - \nu(x)\psi\right)_x + (f(S_0)-d)\psi + f'(S_0)u_0\phi = 0, & x \in (0,1), \\ \phi_x(0) = 0, \quad \phi_x(1) + \beta\phi(1) = 0, & \\ D(x)\psi_x(x) - \nu(x)\psi(x) = 0 \text{ at } x = 0,1 & \end{array} \tag{19}$$

only has trivial solution. The idea is motivated by [11]. Suppose $(\phi,\psi) \not\equiv (0,0)$. Let $\Psi = e^{-\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}\psi(x)$. Then (19) is equivalent to

$$\begin{array}{ll} L_1\phi = \alpha f(S_0)\Psi e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}, & x \in (0,1), \\ L_2\Psi = -f'(S_0)u_0\phi, & x \in (0,1), \\ \phi_x(0) = 0, \quad \phi_x(1) + \beta\phi(1) = 0, \quad \Psi_x(0) = \Psi_x(1) = 0 & \end{array} \tag{20}$$

where $L_1\phi = \left(D_0(x)\phi_x\right)_x - \alpha f'(S_0)u_0\phi$, $L_2\Psi = \left(D(x) e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}\Psi_x\right)_x + (f(S_0) - d) e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}\Psi$. It follows from $\alpha f'(S_0)u_0 > 0$ that the operator L_1 is invertible subject to the boundary conditions $\phi_x(0) = 0,\ \phi_x(1) + \beta\phi(1) = 0$, and the principal eigenvalue of L_1 satisfies $\lambda_1(L_1) < 0$. Noting that

$$\begin{cases} (D(x)e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}(U_0)_x)_x + (f(S_0) - d)e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}U_0 = 0,\ x \in (0,1), \\ (U_0)_x(0) = (U_0)_x(1) = 0, \end{cases} \tag{21}$$

we have $\lambda_1(L_2) = 0$.

We first claim that both ϕ, Ψ must change sign in (0, 1). Suppose $\Psi > 0$ in (0, 1) without loss of generality. Then it follows from the first equation of (20) that $L_1\phi > 0$ in (0, 1). By the strong maximum principle, we have $\phi < 0$ on [0, 1]. Multiplying the second equation of (20) by U_0 and (21) by Ψ, integrating over (0, 1), and applying Green's formula, we have

$$-\int_0^1 f'(S_0)u_0\phi U_0 \mathrm{d}x = 0,$$

a contradiction to $-\int_0^1 f'(S_0)u_0\phi U_0\mathrm{d}x > 0$. Assume $\phi > 0$ in (0, 1). Similar arguments as above lead to $-\int_0^1 f'(S_0)u_0\phi U_0\mathrm{d}x = 0$, a contradiction. Hence, both ϕ, Ψ must change sign in (0, 1).

Second, we claim that ϕ, Ψ have at most finitely many zeros in (0,1). Suppose $\phi(x_n) = 0$ for an infinite sequence of distinct points $\{x_n\} \subset [0, 1]$. By compactness, we may assume there is a $x_\infty \in [0, 1]$ such that $x_n \to x_\infty (n \to \infty)$ by passing to a subsequence if necessary. By the mean value theorem, we conclude that $\phi(x_\infty) = 0, \phi_x(x_\infty) = 0, \phi_{xx}(x_\infty) = 0$. It follows from the first equation of (20) that $\Psi(x_\infty) = 0$. The maximum principle applied to the first equation of (20) shows that Ψ must change sign in any neighborhood of x_∞. Thus $\Psi_x(x_\infty) = 0$. It follows from the uniqueness of the Cauchy problem associated with (20) that $(\phi, \Psi) = (0, 0)$, which is a contradiction to $(\phi, \Psi) \neq (0, 0)$. The same assertion holds for the zeros where Ψ changes sign.

Clearly, $\phi(0) \neq 0$ or $\Psi(0) \neq 0$. Otherwise, $\phi(0) = 0, \Psi(0) = 0$. By the uniqueness of the Cauchy problem associated with (20), we have $(\phi, \Psi) \equiv (0, 0)$, a contradiction. Hence, we may assume $\phi(0) > 0$ and $0 < x_1 < x_2 < \cdots < x_p < 1$ are the finite sequence of zeros of ϕ in (0,1) where it changes sign. Then $\phi > 0$ on $(0, x_1)$. We claim that

$$(-1)^j\Psi(x_j) > 0, \quad j \in \{1, 2, \cdots, p\}.$$

We first claim that $\Psi(x_1) < 0$ by an indirect argument. Suppose $\Psi(x_1) \geq 0$. Note that

$$L_2\Psi = -af'(S_0)u_0\phi < 0 \text{ in } (0, x_1), \quad \Psi_x(0) = 0,\ \Psi(x_1) \geq 0,$$

and $L_2U_0 = 0$ in $(0, x_1)$. The general maximum principle implies Ψ/U_0 cannot reach its non-positive minimum in $(0, x_1)$. If $\min\limits_{x\in[0,1]} \Psi/U_0 = \Psi(0)/U_0(0) \leq 0$, then $\left(\frac{\Psi}{U_0}\right)_x|_{x=0} > 0$ by the general maximum principle, which is a contradiction to $\left(\frac{\Psi}{U_0}\right)_x|_{x=0} = 0$. Suppose $\min\limits_{x\in[0,1]} \Psi/U_0 = \Psi(x_1)/U_0(x_1) \leq 0$. In view of $\Psi(x_1) \geq 0$, we have $\Psi(x_1) = 0$ and $\Psi > 0$ in $(0, x_1)$. Hence,

$$L_1\phi = \alpha f(S_0)\Psi e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi} > 0 \text{ in } (0, 1), \quad \phi_x(0) = 0,\ \phi(x_1) = 0.$$

By the strong maximum principle, we obtain $\phi < 0$ in $(0, x_1)$, a contradiction to $\phi > 0$ in $(0, x_1)$. Thus $\Psi(x_1) < 0$.

It remain to prove that $\Psi(x_i)\cdot\Psi(x_{i+1})<0$ for $i\in\{1,2,\cdots,p-1\}$. Suppose $\Psi(x_i)<0$ and $\phi<0$ in (x_i,x_{i+1}). We prove $\Psi(x_{i+1})>0$ by an indirect argument. Suppose $\Psi(x_{i+1})\le 0$. Note that

$$L_2\Psi=-af'(S_0)u_0\phi>0 \text{ in } (x_i,x_{i+1}), \quad \text{and } L_2U_0=0 \text{ in } (x_i,x_{i+1}).$$

The general maximum principle implies Ψ/U_0 cannot reach its nonnegative maximum in (x_i,x_{i+1}). By virtue of $\Psi(x_i)<0$, one can conclude that Ψ/U_0 cannot reach its nonnegative maximum at $x=x_i$. Assume $\max\limits_{x\in[x_i,x_{i+1}]}\Psi/U_0=\Psi(x_{i+1})/U_0(x_{i+1})\ge 0$. By the hypothesis $\Psi(x_{i+1})\le 0$, we get $\Psi(x_{i+1})=0$ and $\Psi(x)/U_0(x)<0$ in (x_i,x_{i+1}). Hence,

$$L_1\phi=\alpha f(S_0)\Psi e^{\int_0^x\frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}<0 \text{ in } (x_i,x_{i+1}), \quad \phi(x_i)=0,\, \phi(x_{i+1})=0.$$

By the strong maximum principle, we obtain $\phi>0$ in (x_i,x_{i+1}), a contradiction to $\phi<0$ in (x_i,x_{i+1}). Thus $\Psi(x_{i+1})>0$. Similar arguments show that if $\Psi(x_i)>0$ and $\phi>0$ in (x_i,x_{i+1}), then $\Psi(x_{i+1})<0$. These implies $(-1)^j\Psi(x_j)>0,\quad j\in\{1,2,\cdots,p\}$.

At last, we focus on the last interval to establish a contradiction. We have two possibility to consider: (i) $\phi>0$ in $(x_p,1)$; (ii) $\phi<0$ in $(x_p,1)$.

(i) The case of $\phi>0$ in $(x_p,1)$. By the above arguments, we have $\Psi(x_p)>0$. Note that

$$L_2\Psi=-af'(S_0)u_0\phi<0 \text{ in } (x_p,1), \quad \text{and } L_2U_0=0 \text{ in } (x_p,1).$$

The general maximum principle implies Ψ/U_0 cannot reach its non-positive minimum in $(x_p,1)$. By virtue of $\Psi(x_p)>0$, one can conclude that Ψ/U_0 cannot reach its non-positive minimum at $x=x_p$. Then $\min\limits_{x\in[x_p,1]}\Psi/U_0=\Psi(1)/U_0(1)\le 0$. By the general maximum principle again, we have $\left(\frac{\Psi}{U_0}\right)_x|_{x=1}<0$. On the other hand, it is easy to see that $\left(\frac{\Psi}{U_0}\right)_x|_{x=1}=\frac{\Psi_x(1)U_0(1)-\Psi(1)(U_0)_x(1)}{U_0^2(1)}=0$, a contradiction.

(ii) The case of $\phi<0$ in $(x_p,1)$. By the above arguments, we have $\Psi(x_p)<0$. Note that

$$L_2\Psi=-af'(S_0)u_0\phi>0 \text{ in } (x_p,1), \quad \text{and } L_2U_0=0 \text{ in } (x_p,1).$$

The general maximum principle implies Ψ/U_0 cannot reach its nonnegative maximum in $(x_p,1)$. Noting that $\Psi(x_p)<0$, one can conclude that Ψ/U_0 cannot reach its nonnegative maximum at $x=x_p$. Then $\max\limits_{x\in[x_p,1]}\Psi/U_0=\Psi(1)/U_0(1)\ge 0$. By the general maximum principle again, we have $\left(\frac{\Psi}{U_0}\right)_x|_{x=1}>0$, a contradiction to $\left(\frac{\Psi}{U_0}\right)_x|_{x=1}=\frac{\Psi_x(1)U_0(1)-\Psi(1)(U_0)_x(1)}{U_0^2(1)}=0$. Therefore, we have $(\phi,\Psi)\equiv(0,0)$, that is, $(\phi,\psi)\equiv(0,0)$, which implies any positive solution of (15) is non-degenerative.

The remain task is to show $\mathrm{index}(A,(\chi_0,U_0),W)=1$, where $(\chi_0,U_0)=(1-S_0,e^{-\int_0^x\frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}u_0)$. To this end, let $A'(\chi_0,U_0)$ be the Fréchet derivative operator of A at (χ_0,U_0) with respect to (χ,U). It follows from the arguments above that 1 is not an eigenvalue of $A'(\chi_0,U_0)$, and (χ_0,U_0) is a nondegenerate fixed-point of A in W. Hence,

$$\mathrm{index}(A,(\chi_0,U_0),W)=\mathrm{index}(A,(\chi_0,U_0),X)=\mathrm{index}(A'(\chi_0,U_0),(0,0),X)=(-1)^\sigma$$

by the Leray-Schauder formula, where σ is the sum of the multiplicities of all eigenvalues of $A'(\chi_0,U_0)$ which are greater than one. Suppose $\lambda>1$ is an eigenvalue of $A'(\chi_0, U_0)$ with the corresponding eigenfunction (ϕ, ψ). Then

$$\begin{aligned}
&A'(\chi_0, U_0)(\phi, \psi)^\top \\
&= \begin{pmatrix} K_0(-\alpha f'(1-\chi_0)e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}U_0\phi + M\phi + \alpha f(1-\chi_0)e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}\psi) \\ K((f(1-\chi_0)-d)e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}\psi + M\psi - f'(1-\chi_0)e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}U_0\phi) \end{pmatrix} \\
&= \lambda(\phi, \psi)^\top,
\end{aligned}$$

which is equivalent to

$$\begin{aligned}
&\mathfrak{L}_1(\lambda)\phi = \alpha f(1-\chi_0)e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}\psi, \qquad x \in (0,1), \\
&\mathfrak{L}_2(\lambda)\psi = -f'(1-\chi_0)e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}U_0\phi, \qquad x \in (0,1), \\
&\phi_x(0) = 0, \quad \phi_x(1) + \beta\phi(1) = 0, \qquad \psi_x(0) = \psi_x(1) = 0
\end{aligned}$$

where

$$\mathfrak{L}_1(\lambda)\phi = -\lambda\left(D_0(x)\phi_x\right)_x + (\lambda-1)M\phi + \alpha f'(1-\chi_0)e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}U_0\phi,$$

$$\mathfrak{L}_2(\lambda)\psi = -\lambda(D(x)e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}\psi_x)_x + (\lambda-1)M\psi - (f(1-\chi_0)-d)e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}\psi.$$

It follows from $\lambda > 1$ and $\alpha f'(1-\chi_0)e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}U_0 > 0$ that the operator $\mathfrak{L}_1(\lambda)$ is invertible subject to the boundary conditions $\phi_x(0) = 0$, $\phi_x(1) + \beta\phi(1) = 0$, and the principal eigenvalue of $\mathfrak{L}_1(\lambda)$ satisfies $\lambda_1(\mathfrak{L}_1(\lambda)) > 0$. Noting that the equation (21) and $\lambda > 1$, we have $\lambda_1(\mathfrak{L}_2(\lambda)) > 0$ by Lemma 2.1. By similar arguments as we dealt with (20), we can show $(\phi, \psi) = (0, 0)$. Hence, $A'(\chi_0, U_0)$ has no eigenvalue greater than 1. Thus $\mathrm{index}(A, (\chi_0, U_0), W) = (-1)^0 = 1$. □

Theorem 3.4. *Suppose (H) holds. Then*

(i) *the trivial solution (1, 0) of (15) is the unique nonnegative solution if $d \geq f(1)$;*
(ii) *for any $\delta > 0$, there exists a unique positive solution of (15) if $\delta \leq d < f(1)$, denoted by $(S_d(x), u_d(x))$.*

Proof. (i) is a direct result of Lemma 3.1(ii).

(ii) It follows from Lemma 3.1 that the fixed points of A in Ω are two types, which are the trivial fixed point $(0, 0)$ and the positive fixed points (χ, U). It follows from Lemma 3.3 that any positive fixed points (χ_0, U_0) of A is non-degenerative and $\mathrm{index}(A, (\chi_0, U_0), W) = 1$. Meanwhile, by the compactness argument on the operator A and the non-degeneracy of its fixed points (including $(0, 0)$ and positive fixed points), one knows that there are at most finitely many positive fixed points in Ω. Let them be $(\chi_i, U_i)(i = 1, 2, \cdots, l)$. Then $\mathrm{index}(A, (\chi_i, U_i), W) = 1$ for $i = 1, 2, \cdots, l$. By the additivity property of the fixed point index and Lemma 3.2, we have

$$1 = \mathrm{index}(A, \Omega, W) = \mathrm{index}(A, (0, 0), W) + \sum_{i=1}^{l} \mathrm{index}(A, (\chi_i, U_i), W) = l.$$

That is, for any $\delta > 0$, there exists a unique positive solution of (15) if $\delta \leq d < f(1)$. □

Lemma 3.5. *Suppose (H) holds and $f(1) > d$. Let $(S_d(x), u_d(x))$ be the unique positive solution of (15) when $d \in [\delta_0, f(1) - \delta_0]$, where δ_0 is given in Lemma 3.1. Then $(S_d(x), u_d(x))$ is continuous with respect to d from $[\delta_0, f(1) - \delta_0]$ to $C^2[0, 1] \times C^2[0, 1]$.*

Proof. The continuity of the map $d \to (S_d(x), u_d(x))$ from $[\delta_0, f(1)-\delta_0]$ to $C^1[0,1]\times C^1[0,1]$ follows from a standard compactness and uniqueness consideration. Indeed, if $d_n \to d_0 \in [\delta_0, f(1)-\delta_0]$, then there exists a sequence of $(S_{d_n}(x), u_{d_n}(x))$ converges in $C^1[0,1]\times C^1[0,1]$ to a positive solution of (15) with $d = d_0$. By the uniqueness, this positive solution must be $(S_{d_0}(x), u_{d_0}(x))$. Therefore the entire sequence converges to $(S_{d_0}(x), u_{d_0}(x))$. Moreover, from the equations of $S_{d_n}(x)$ and $u_{d_n}(x)$, we easily see that $(S_{d_n}(x), u_{d_n}(x)) \to (S_{d_0}(x), u_{d_0}(x))$ in $C^1[0,1]\times C^1[0,1]$ implies $(S_{d_n}(x), u_{d_n}(x)) \to (S_{d_0}(x), u_{d_0}(x))$ in $C^2[0,1]\times C^2[0,1]$. □

Remark 2. By application of a standard bifurcation arguments, $(f(1);1,0)$ is a simple bifurcation point, and (15) has an unbounded connected branch of positive solutions bifurcating from $(f(1);1,0)$. Moreover, we can show that the branch of positive solutions can only become unbounded through $(d;S_d,u_d)$ belongs to the branch and satisfies $d\to 0$, and $\|u_d\|_\infty \to \infty$, which leads to $f(S_d)\to 0$ in $(0,1)$.

Next, we study the dynamical behavior of the solution $(S(x,t), u(x,t))$ of (14). It follows from Lemma 2.4 that for every initial value function $(S^0, u^0)\in W$, the system (14) has a unique solution $(S(x,t), u(x,t))$ on $[0,\infty)$ with $(S(x,0), u(x,0)) = (S_0, u_0)$, and the solutions of (14) are ultimately bounded and uniformly bounded in W. Here $W = \{(S,u)\in X : S\ge 0, u\ge 0 \text{ on } [0,1]\}$, and $X = C[0,1]\times C[0,1]$. More precisely, we have the following result.

Lemma 3.6. *Suppose* (H) *holds. Then for any given* $\delta_0>0$*, the initial-boundary value problem* (14) *admits a unique solution* (S,u) *defined for all* $x\in[0,1]$ *and* $t>0$ *provided* $d\ge\delta_0$*, and there exist positive constants* ρ_0,ρ_1 *depending only on the initial data* $S_0(x), u_0(x)$*, such that* $0<S(x,t)\le\rho_0,\quad 0<u(x,t)\le\rho_1,\quad x\in[0,1], t>0$.

Theorem 3.7. *Suppose* (H) *holds and* $d>f(1)$*. Then the solution* (S,u) *of* (14) *converges to* $(1,0)$ *uniformly on* $[0,1]$.

Proof. By the maximum principle of the parabolic equation, it is easy to see that the solution $(S(x,t), u(x,t))$ of (14) satisfies $S(x,t)>0, u(x,t)>0$. Moreover, it is easy to see that $\limsup\limits_{t\to\infty} S(x,t)\le 1$, which implies for $\epsilon>0$ small there exists $T_1>0$ such that $S(x,t)\le 1+\epsilon$ for all $x\in[0,1], t\ge T_1$. Let $U = e^{-\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}u$. Then for $t\ge T_1$,

$$\begin{aligned} e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}U_t &= \left(D(x)e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}U_x\right)_x + (f(S)-d)Ue^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi} \\ &\le \left(D(x)e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}U_x\right)_x + (f(1+\epsilon)-d)Ue^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}. \end{aligned}$$

Noting that $d>f(1)$, there is ϵ small enough such that $d>f(1+\epsilon)$. Hence the comparison principle leads to $U(x,t)\to 0$ as $t\to\infty$ uniformly on $[0,1]$. Thus $\lim\limits_{t\to\infty} u(x,t) = 0$ uniformly on $[0,1]$ provided $d>f(1)$, which leads to there exists $T_2\ge T_1$ so that $0<u(x,t)\le\epsilon$ for $t\ge T_2$. Therefore for $t\ge T_2$,

$$S_t \ge (D_0(x)S_x)_x - \alpha f(S)\epsilon \ge (D_0(x)S_x)_x - \alpha f(1+\epsilon)\epsilon.$$

The comparison principle implies $S(x,t)\ge S_\epsilon(x,t)$ for $t\ge T_2$, where $S_\epsilon(x,t)$ is the solution of

$$\begin{aligned} &(S_\epsilon)_t = (D_0(x)(S_\epsilon)_x)_x - \alpha\epsilon f(1+\epsilon), && x\in[0,1], t>T_2, \\ &(S_\epsilon)_x(0,t) = 0,\quad (S_\epsilon)_x(1,t) = \beta(1-S_\epsilon(1,t)), && t>T_2 \\ &S_\epsilon(x,T_2) = S(x,T_2), && x\in[0,1]. \end{aligned}$$

Obviously, $S_\epsilon(x,t) \to 1$ as $t \to \infty$ and $\epsilon \to 0$. Hence, we have $(S(x,t), u(x,t)) \to (1,0)$ as $t \to \infty$. □

Theorem 3.8. *Suppose (H) holds. Then for any given $\delta_0 > 0$, the system (14) is uniformly persistent (i.e. there exists $\epsilon_0 > 0$ such that the solution $(S(x,t), u(x,t))$ of (14) satisfies $\liminf_{t\to\infty} u(\cdot,t) \geq \epsilon_0$) provided $\delta_0 < d < f(1)$.*

Proof. We prove it by making use of the abstract persistence theory, see [18]. Let $\Psi(t)$ be the solution semiflow generated by the system (14) on the state space W. Set $X_0 := \{(S,u) \in W : u(x) \not\equiv 0\}$ and $\partial X_0 := W \backslash X_0$. Let $M_\partial := \{(S_0,u_0) \in \partial X_0 : \Psi(t)(S_0,u_0) \in \partial X_0, \forall t \geq 0\}$ and $\omega((S_0,u_0))$ be the omega limit set of the forward orbit $\gamma^+((S_0,u_0)) := \{\Psi(t)(S_0,u_0) : t \geq 0\}$. Then X_0 is open in W and forward invariant under the dynamics generated by (14) and ∂X_0 contains the washout equilibrium $(1,0)$.

We first claim that $\cup_{\Phi\in M_\partial}\omega(\Phi) \subset \{(1,0)\}$. For any given $(S_0,u_0) \in M_\partial$, we have $\Psi(t)(S_0,u_0) \in M_\partial, \forall t \geq 0$, which implies for each $t \geq 0$, we have $u(\cdot,t,(S_0,u_0)) \equiv 0$. Thus $S(\cdot,t,(S_0,u_0))$ satisfies

$$\begin{array}{ll} S_t = (D_0(x)S_x)_x, & x \in (0,1), t > 0, \\ S_x(0,t) = 0, \quad S_x(1,t) = \beta(1 - S(1,t)), & t > 0, \\ S(x,0) = S_0(x) \geq 0, & x \in [0,1], \end{array}$$

which implies $\lim_{t\to\infty} S = 1$ uniformly for $x \in [0,1]$. Hence, the claim is proved.

Next, we claim that $(1,0)$ is uniform weak repeller in the sense that

$$\limsup_{t\to\infty} \|\Psi(t)(S_0,u_0) - (1,0)\| \geq \delta$$

for all $(S_0,u_0) \in X_0$. Assume to the contrary that $(1,0)$ is not a weak repeller. Then for any $\delta > 0$, there exists $(S_0,u_0) \in X_0$ such that $\limsup_{t\to\infty} \|\Psi(t)(S_0,u_0) - (1,0)\| < \delta$. Therefore, there exists $t_0 > 0$ such that for $t \geq t_0$, we have

$$\|S(\cdot,t,(S_0,u_0)) - 1\| < \delta, \quad \|u(\cdot,t,(S_0,u_0))\| < \delta,$$

which implies $S(x,t,(S_0,u_0)) > 1 - \delta$ for $x \in [0,1]$ and $t \geq t_0$. Consequently, $f(S(x,t,(S_0,u_0))) > f(1-\delta)$ for $x \in [0,1]$ and $t \geq t_0$. This implies that

$$\begin{array}{l} u_t \geq (D(x)u_x - \nu(x)u)_x + (f(1-\delta) - d)u, \quad x \in (0,1),\, t \geq t_0, \\ D(x)u_x - \nu(x)u = 0 \quad \text{at } x = 0,1,\, t \geq t_0. \end{array}$$

In view of $(S_0,u_0) \in X_0$, it is not hard to conclude that $u(\cdot,t,(S_0,u_0)) > 0$ for $x \in [0,1]$ and $t > 0$. Since $-f(1-\delta) + d$ is a constant, it follows from Remark 1 that $\lambda_1(-f(1-\delta) + d, \nu(x)) = -f(1-\delta) + d$ with the associated eigenfunction $\varphi_\delta = e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}$. Choosing $u(\cdot,t_0,(S_0,u_0)) \geq \delta_1 e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}$, by comparison principle, $u(\cdot,t,(S_0,u_0)) \geq \delta_1 e^{-\lambda_\delta(t-t_0)} \cdot e^{\int_0^x \frac{\nu(\xi)}{D(\xi)}\mathrm{d}\xi}$ for $t > t_0$, where $\lambda_\delta = d - f(1-\delta)$. Since $d < f(1)$, by the continuity of f, we can choose $\delta > 0$ small enough such that $d < f(1-\delta)$, which implies $\lambda_\delta < 0$ and $\lim_{t\to\infty} u(\cdot,t,(S_0,u_0)) = \infty$. This is a contradiction to $\|u(\cdot,t,(S_0,u_0))\| < \delta$ for $t > t_0$. Hence, we conclude that $(1,0)$ is a uniform weak repeller and $\{(1,0)\}$ is an isolated invariant set in W.

Define a continuous function $\mathbf{p} : W \to [0,\infty)$ by $\mathbf{p}((S,u)) := \min_{x\in[0,1]} u(x)$ for any $(S,u) \in W$. It follows from the standard comparison principle that $\mathbf{p}^{-1}(0,\infty) \subseteq X_0$ and $\mathbf{p}$ satisfies that if $\mathbf{p}((S,u)) > 0$ or $(S,u) \in X_0$ with $\mathbf{p}((S,u)) = 0$, then $\mathbf{p}(\Psi(t)(S,u)) > 0$ for all $t > 0$. That is, $\mathbf{p}$ is a generalized distance function for the semiflow $\Psi(t): W \to W$(see [18]). It follows from $\cup_{\Phi \in M_\partial}\omega(\Phi) \subset \{(1,0)\}$ that any forward orbit of $\Psi(t)$ in M_∂ converges to $(1,0)$. Note that $\{(1,0)\}$ is an isolated invariant set in W, and the stable set $W^s(\{(1,0)\}) \cap X_0 = \emptyset$. Hence, there is no subsets of $\{(1,0)\}$ forms a cycle in M_∂. Meanwhile, it follows from Lemma 3.6 that $\Psi(t)$ is point dissipative on W, and forward orbits of bounded subsets of W for $\Psi(t)$ are bounded. By Theorem 2.6 in [12], $\Psi(t)$ has a global attractor that attracts each bounded set in W. It follows from Theorem 3 in [18] that there exists a ϵ_0 such that for any $\Phi \in X_0$, $\min_{(S_0,u_0)\in\omega((S,u))} \mathbf{p}((S_0,u_0)) > \epsilon_0$, which implies that for any $(S,u) \in X_0$, $\liminf_{t\to\infty} u(\cdot,t) \geq \epsilon_0$. □

4. **Coexistence of the two-species model.** The aim of this section is devoted to study the structure of the nonnegative solutions of the steady state system (7)-(8). Clearly, there are three types of nonnegative solutions of (7)-(8):

(i) The unique trivial solution $(S,u,v) = (1,0,0)$, which exists for all $d_1, d_2 > 0$.

(ii) It follows from Theorem 3.4 that (7)-(8) has exactly two semi-trivial solutions $(S,u,v) = (S_{d_1}(x), u_{d_1}(x), 0)$ provided that $d_1 \in (0, f_1(1))$ and $(S,u,v) = (S_{d_2}(x), 0, v_{d_2}(x))$ provided that $d_2 \in (0, f_2(1))$.

(iii) The positive solutions (S,u,v) with $S,u,v > 0$ on [0, 1], which is the focus to study the properties of nonnegative solutions of the steady state system (7)-(8).

It follows from Lemma 2.5 that the necessary conditions for the existence of a positive solution of (7)-(8) are $0 < d_1 < f_1(1), 0 < d_2 < f_2(1)$. From now on, we take $0 < d_1 < f_1(1)$ fixed, and d_2 as the bifurcation parameter. Then (7)-(8) has two semi-trivial solution branches by Theorem 3.4

$$\Gamma_u = \{(d_2, S_{d_1}(x), u_{d_1}(x), 0) : d_2 > 0\}$$

and

$$\Gamma_v = \{(d_2, S_{d_2}(x), 0, v_{d_2}(x)) : 0 < d_2 < f_2(1)\}.$$

Next, we construct a positive solution of (7)-(8) bifurcating from the semi-trivial solution branch Γ_u by the global bifurcation theorem.

Let $\chi = 1 - S$, $U = e^{-\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi} u$, $V = e^{-\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi} v$. Then the system (7)-(8) is equivalent to

$$\begin{aligned}
&-(D_0(x)\chi_x)_x = \alpha_1 f_1(1-\chi)e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}U + \alpha_2 f_2(1-\chi)e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}V,\\
&-\left(D(x)e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}U_x\right)_x = (f_1(1-\chi) - d_1)e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}U,\\
&-\left(D(x)e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}V_x\right)_x = (f_2(1-\chi) - d_2)e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}V,\\
&\chi_x(0) = 0, \quad \chi_x(1) + \beta\chi(1) = 0, \quad U_x(0) = U_x(1) = 0, \quad V_x(0) = V_x(1) = 0.
\end{aligned} \tag{22}$$

Moreover the change of variables maps the trivial solution $(S,u,v) = (1,0,0)$ of (7)-(8) to $(\chi,U,V) = (0,0,0)$, and maps the semi-trivial nonnegative solution branches Γ_u and Γ_v of (7)-(8) to the semi-trivial nonnegative ones

$$\begin{aligned}
\Gamma_U &= \{(d_2, 1 - S_{d_1}(x), e^{-\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}u_{d_1}(x), 0) : d_2 \in (0,+\infty)\},\\
\Gamma_V &= \{(d_2, 1 - S_{d_2}(x), 0, e^{-\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}v_{d_2}(x)) : d_2 \in (0, f_2(1))\}.
\end{aligned}$$

By Lemma 2.5, any nonnegative solution (χ,U,V) of (22) satisfies $0 \leq \chi < 1$ and U, V are bounded in $L^\infty(0,1)$. Hence, for $0 < d_1 < f_1(1), 0 < d_2 < f_2(1)$, there exists a positive constant M such that

$$(f_1(1-\chi) - d_1)e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi} + M > 0 \text{ and } (f_2(1-\chi) - d_2)e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi} + M > 0$$

on [0, 1].

Let $\mathbf{X} = W^{2,p}(0,1) \times W^{2,p}(0,1) \times W^{2,p}(0,1)$ with $p > 1$. Then $\mathbf{X} \hookrightarrow C^1[0,1] \times C^1[0,1] \times C^1[0,1]$. We define $T : (0,+\infty) \times \mathbf{X} \to \mathbf{X}$ by

$$T(d_2,\chi,U,V) = \begin{pmatrix} \mathbf{K}_0\left(\alpha_1 f_1(1-\chi)e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}U + \alpha_2 f_2(1-\chi)e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}V\right) \\ \mathbf{K}_1\left((f_1(1-\chi)-d_1)e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}U + MU\right) \\ \mathbf{K}_2\left((f_2(1-\chi)-d_2)e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}V + MV\right) \end{pmatrix},$$

where $\mathbf{K}_i (i = 0,1,2)$ are the solution operators $\phi = \mathbf{K}_0(h_0(x))$ and $\psi_i = \mathbf{K}_i(h_i(x))$ $(i = 1,2)$ for the problems respectively

$$-\left(D_0(x)\phi_x\right)_x = h_0(x),\ x \in (0,1), \quad \phi_x(0) = 0,\ \phi_x(1) + \beta\phi(1) = 0,$$

$$-(D(x)e^{\int_0^x \frac{\nu_i(\xi)}{D(\xi)}\mathrm{d}\xi}(\psi_i)_x)_x + M\psi_i = h_i(x),\ x \in (0,1), \quad (\psi_i)_x(0) = 0,\ (\psi_i)_x(1) = 0.$$

Clearly, $\mathbf{K}_i (i = 0,1,2)$ is a strongly positive compact operator. By standard elliptic regularity theory we know that $T : (0,+\infty) \times \mathbf{X} \to \mathbf{X}$ is completely continuous. Let

$$G(d_2,\chi,U,V) = (\chi,U,V)^\top - T(d_2,\chi,U,V).$$

Then $G : (0,+\infty) \times \mathbf{X} \to \mathbf{X}$ is C^1 smooth, and the zeros of $G(d_2,\chi,U,V) = 0$ with $0 \le \chi < 1, U \ge 0, V \ge 0$ correspond to the nonnegative solutions of (22).

Now, we begin to construct a positive solution branch $\tilde{\Gamma} = \{d_2,\chi,U,V\} \subset (0,+\infty) \times \mathbf{X}$ bifurcating from the semi-trivial solution branches Γ_U and Γ_V by the bifurcation theory [17]. To this end, we introduce

$$\hat{d}_1(d_2) = -\lambda_1(-f_1(S_{d_2}(x)),\nu_1), \quad \hat{d}_2(d_1) = -\lambda_1(-f_2(S_{d_1}(x)),\nu_2), \tag{23}$$

where $\lambda_1(-f_1(S_{d_2}(x)),\nu_1)$ and $\lambda_1(-f_2(S_{d_1}(x)),\nu_2)$ are the smallest eigenvalues of (10) with $q(x) = -f_1(S_{d_2}(x)), \nu(x) = \nu_1(x)$ and $q(x) = -f_2(S_{d_1}(x)), \nu(x) = \nu_2(x)$, respectively. It is easy to see that $0 < \hat{d}_1(d_2) < f_1(1)$, $0 < \hat{d}_2(d_1) < f_2(1)$ since $0 < S_{d_2}(x) < 1$ and $0 < S_{d_1}(x) < 1$. Moreover, $\hat{d}_1(d_2)$ is continuous with respect to d_2 by Lemma 3.5. It follows from Remark 2 that $\lim_{d_2 \to 0} \hat{d}_1(d_2) = 0$ and $\lim_{d_2 \to f_2(1)} \hat{d}_1(d_2) = f_1(1)$. Hence for any given $d_1 \in (0, f_1(1))$, there exists $\tilde{d}_2 \in (0, f_2(1))$ such that $\hat{d}_1(\tilde{d}_2) = d_1$.

Theorem 4.1. *Suppose (H) holds and let $\delta \le d_1 < f_1(1)$ fixed, where $\delta > 0$ is an arbitrary constant. Then there exists a continuum of positive solutions to (7)-(8), denoted by*

$$\Gamma = \{(d_2,S,u,v)\} \subset (0,+\infty) \times \mathbf{X},$$

which bifurcates from the semi-trivial solution branch $\Gamma_u = \{(d_2, S_{d_1}(x), u_{d_1}(x), 0) : d_2 > 0\}$ at $(\hat{d}_2, S_{d_1}(x), u_{d_1}(x), 0)$, and meets the other semi-trivial solution branch $\Gamma_v = \{(d_2, S_{d_2}(x), 0, v_{d_2}(x)) : 0 < d_2 < f_2(1)\}$ at $(\tilde{d}_2, S_{\tilde{d}_2}(x), 0, v_{\tilde{d}_2}(x))$. In particular, (7)-(8) has a positive solution (S,u,v) if d_2 lies between $\hat{d}_2$ and $\tilde{d}_2$. Here, $\hat{d}_1, \hat{d}_2$ are given by (23) and $\tilde{d}_2$ is determined by $\hat{d}_1(\tilde{d}_2) = d_1$.

Proof. Noting that the system (7)-(8) is equivalent to (22), we only need to show there exists a continuum of positive solutions to (22), denoted by

$$\tilde{\Gamma} = \{(d_2,\chi,U,V)\} \subset (0,+\infty) \times \mathbf{X},$$

which bifurcates from the semi-trivial solution branch

$$\Gamma_U = \{(d_2, 1 - S_{d_1}(x), e^{-\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi} u_{d_1}(x), 0) : d_2 > 0\}$$

at $(\hat{d}_2, 1 - S_{d_1}(x), e^{-\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi} u_{d_1}(x), 0)$, and meets the other semi-trivial solution branch

$$\Gamma_V = \{(d_2, 1 - S_{d_2}(x), 0, e^{-\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi} v_{d_2}(x)) : 0 < d_2 < f_2(1)\}$$

at $(\tilde{d}_2, 1 - S_{\tilde{d}_2}(x), 0, e^{-\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi} v_{\tilde{d}_2}(x))$. To this end, for any $\delta > 0$ and $d_1 \in [\delta, f_1(1))$ fixed, we construct the global bifurcation which corresponds to positive solutions by treating d_2 as a bifurcation parameter.

Let $U_{d_1} = e^{-\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi} u_{d_1}(x)$. The Fréchet derivative of $G(d_2, \chi, U, V)$ with respect to (χ, U, V) at $(1 - S_{d_1}(x), U_{d_1}, 0)$ is denoted by $G'_{(\chi,U,V)}(d_2, 1 - S_{d_1}, U_{d_1}, 0)$. Clearly, $G'_{(\chi,U,V)}(d_2, 1 - S_{d_1}, U_{d_1}, 0)$ is a Fredholm operator. In order to apply Crandall-Rabinowitz Theorem of bifurcation from simple eigenvalue, we first calculate the null space of $G'_{(\chi,U,V)}(d_2, 1 - S_{d_1}, U_{d_1}, 0)$. Let

$$G'_{(\chi,U,V)}(d_2, 1 - S_{d_1}, U_{d_1}, 0)(\zeta, \phi, \psi) = 0.$$

Then

$$\begin{aligned}
&-(D_0(x)\zeta_x)_x = -\alpha_1 f_1'(S_{d_1}) u_{d_1}(x)\zeta + \alpha_1 f_1(S_{d_1}) e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}\phi + \alpha_2 f_2(S_{d_1}) e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}\psi,\\
&-\left(D(x)e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}\phi_x\right)_x = (f_1(S_{d_1}) - d_1)e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}\phi - f_1'(S_{d_1})u_{d_1}(x)\zeta,\\
&-\left(D(x)e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}\psi_x\right)_x = (f_2(S_{d_1}) - d_2)e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}\psi,\\
&\zeta_x(0) = \zeta_x(1) + \beta\zeta(1) = 0, \quad \phi_x(0) = \phi_x(1) = 0, \quad \psi_x(0) = \psi_x(1) = 0.
\end{aligned}$$

If $\psi = 0$, then (ζ, ϕ) satisfies

$$\begin{aligned}
&\tilde{L}_1\zeta = -\alpha_1 f_1(S_{d_1}) e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}\phi,\\
&\tilde{L}_2\phi = f_1'(S_{d_1})u_{d_1}(x)\zeta,\\
&\zeta_x(0) = \zeta_x(1) + \beta\zeta(1) = 0, \quad \phi_x(0) = \phi_x(1) = 0,
\end{aligned} \tag{24}$$

where

$$\begin{aligned}
&\tilde{L}_1\zeta = (D_0(x)\zeta_x)_x - \alpha_1 f_1'(S_{d_1})u_{d_1}(x)\zeta\\
&\tilde{L}_2\phi = \left(D(x)e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}\phi_x\right)_x + (f_1(S_{d_1}) - d_1)e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}\phi.
\end{aligned}$$

It follows from $\alpha_1 f_1'(S_{d_1})u_{d_1}(x) > 0$ that the operator $\tilde{L}_1$ is invertible subject to the boundary conditions $\zeta_x(0) = 0$, $\zeta_x(1) + \beta\zeta(1) = 0$, and the principal eigenvalue of $\tilde{L}_1$ satisfies $\lambda_1(\tilde{L}_1) < 0$. Noting that $U_{d_1} = e^{-\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi} u_{d_1}(x)$ and

$$\begin{aligned}
&(D(x)e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}(U_{d_1})_x)_x + (f(S_{d_1}) - d_1)e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}U_{d_1} = 0,\ x \in (0,1),\\
&(U_{d_1})_x(0) = (U_{d_1})_x(1) = 0,
\end{aligned} \tag{25}$$

we have $\lambda_1(\tilde{L}_2) = 0$. It follows from the similar arguments dealt with (20) that $(\zeta, \phi) = (0, 0)$. That is, the operator

$$\mathfrak{B} := \begin{pmatrix} \tilde{L}_1 & \alpha_1 f_1(S_{d_1}) e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi} \\ -f_1'(S_{d_1})u_{d_1}(x) & \tilde{L}_2 \end{pmatrix}$$

is invertible. Hence $\psi \neq 0$.

Take $d_2 = \hat{d}_2,\ \psi = \hat{\psi}_1$, which is the corresponding positive eigenfunction to the eigenvalue $\lambda_1(-f_2(S_{d_1}), \nu_2)$. Then (ζ, ϕ) satisfies

$$\begin{aligned} &\mathfrak{B}(\zeta,\phi)^\top = (-\alpha_2 f_2(S_{d_1}) e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}\psi, 0)^\top, \\ &\zeta_x(0) = \zeta_x(1) + \beta\zeta(1) = 0, \quad \phi_x(0) = \phi_x(1) = 0. \end{aligned} \tag{26}$$

Noting that the operator $\mathfrak{B}$ is invertible, $(\zeta, \phi) := (\zeta_1, \phi_1)$ is uniquely determined by (26). Hence, the null space of $G'_{(\chi,U,V)}(\hat{d}_2, 1 - S_{d_1}, U_{d_1}, 0)$ is

$$\mathcal{N}(G'_{(\chi,U,V)}(\hat{d}_2, 1 - S_{d_1}, U_{d_1}, 0)) = \mathrm{span}\{(\zeta_1, \phi_1, \hat{\psi}_1)\}.$$

Suppose that $(\chi, U, V) \in \mathcal{R}(G'_{(\chi,U,V)}(\hat{d}_2, 1 - S_{d_1}, U_{d_1}, 0))$, which is the range of the operator $G'_{(\chi,U,V)}(\hat{d}_2, 1 - S_{d_1}, U_{d_1}, 0)$. Then there exists $(\zeta, \phi, \psi) \in \mathbf{X}$ such that

$$G'_{(\chi,U,V)}(\hat{d}_2, 1 - S_{d_1}, U_{d_1}, 0)(\zeta, \phi, \psi)^\top = (\chi, U, V)^\top.$$

Direct computation leads to

$$\begin{aligned} &(D_0(x)\zeta_x)_x - \alpha_1 f_1'(S_{d_1}) u_{d_1}(x)\zeta + \alpha_1 f_1(S_{d_1}) e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}\phi \\ &\qquad\qquad\qquad + \alpha_2 f_2(S_{d_1}) e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}\psi = (D_0(x)\chi_x)_x, \\ &\left(D(x) e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}\phi_x\right)_x + (f_1(S_{d_1}) - d_1) e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}\phi \\ &\qquad\qquad\qquad - f_1'(S_{d_1}) u_{d_1}(x)\zeta = \left(D(x) e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi} U_x\right)_x - MU, \\ &\left(D(x) e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}\psi_x\right)_x + (f_2(S_{d_1}) - \hat{d}_2) e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}\psi = \left(D(x) e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi} V_x\right)_x - MV, \\ &\zeta_x(0) = \zeta_x(1) + \beta\zeta(1) = 0, \quad \phi_x(0) = \phi_x(1) = 0, \quad \psi_x(0) = \psi_x(1) = 0. \end{aligned}$$

Noting that $\hat{\psi}_1$ satisfies the equation

$$\begin{aligned} &\left(D(x) e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}\hat{\psi}_{1x}\right)_x + (f_2(S_{d_1}) - \hat{d}_2) e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}\hat{\psi}_1 = 0, \quad x \in (0,1), \\ &\hat{\psi}_{1x}(0) = \hat{\psi}_{1x}(1) = 0. \end{aligned}$$

Multiplying this equation by ψ and the third equation of (4) by $\hat{\psi}_1$, and integrating over $(0, 1)$ by parts, we obtain $\int_0^1 [(f_2(S_{d_1}) - \hat{d}_2) e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi} + M]\hat{\psi}_1 V \mathrm{d}x = 0$. Namely, the range of $G'_{(\chi,U,V)}(\hat{d}_2, 1 - S_{d_1}, U_{d_1}, 0)$ is

$$\begin{aligned} &\mathcal{R}(G'_{(\chi,U,V)}(\hat{d}_2, 1 - S_{d_1}, U_{d_1}, 0)) \\ =&\{(\chi, U, V) \in \mathbf{X} : \int_0^1 [(f_2(S_{d_1}) - \hat{d}_2) e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi} + M]\hat{\psi}_1 V \mathrm{d}x = 0\}. \end{aligned}$$

At last, by virtue of $\mathbf{K}_2(e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}\hat{\psi}_1) > 0$ and $(f_2(S_{d_1}) - \hat{d}_2) e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi} + M > 0$, we have

$$\int_0^1 [(f_2(S_{d_1}) - \hat{d}_2) e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi} + M]\hat{\psi}_1 \mathbf{K}_2(e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}\hat{\psi}_1)\mathrm{d}x > 0.$$

Hence,

$$\begin{aligned} G'_{d_2(\chi,U,V)}(\hat{d}_2, 1 - S_{d_1}, U_{d_1}, 0)(\zeta_1, \phi_1, \hat{\psi}_1)^\top =&(0, 0, \mathbf{K}_2(e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}\hat{\psi}_1))^\top \\ &\notin \mathcal{R}(G'_{(\chi,U,V)}(\hat{d}_2, 1 - S_{d_1}, U_{d_1}, 0)). \end{aligned}$$

Let

$$\begin{aligned}\mathbf{Z} =&\mathcal{R}(G'_{(\chi,U,V)}(\hat{d}_2, 1-S_{d_1}, U_{d_1}, 0))\\ =&\{(\chi,U,V)\in\mathbf{X} : \int_0^1 [(f_2(S_{d_1})-\hat{d}_2)e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi} + M]\hat{\psi}_1 V \mathrm{d}x = 0\}.\end{aligned}$$

It is easy to see that $\mathbf{Z}\oplus\mathrm{span}\{(\zeta_1,\phi_1,\hat{\psi}_1)\} = \mathbf{X}$. By the application of the standard bifurcation theorem from a simple eigenvalue [3, 17], there exists a $\tau_0 > 0$ and C^1 curve $(d_2(\tau), Q(\tau), \Phi(\tau), \Psi(\tau)) : (-\tau_0, \tau_0) \mapsto (-\infty, +\infty)\times\mathbf{Z}$ such that $d_2(0) = \hat{d}_2, Q(0) = 0, \Phi(0) = 0, \Psi(0) = 0$ and

$$\begin{aligned}&(d_2, \chi(\tau), U(\tau), V(\tau))\\ =&(d_2(\tau), 1-S_{d_1} + \tau(\zeta_1 + Q(\tau)), U_{d_1} + \tau(\phi_1 + \Phi(\tau)), \tau(\hat{\psi}_1 + \Psi(\tau)))(|\tau| < \tau_0),\end{aligned}$$

which is the solution of the system (22). Let $S(\tau) = 1-\chi(\tau)$, $u(\tau) = e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}U(\tau) = u_{d_1}(x)+e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}\tau(\phi_1+\Phi(\tau))$ and $v(\tau) = e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}V(\tau) = e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}\tau(\hat{\psi}_1+\Psi(\tau))$. Then the bifurcation branch

$$\Gamma_1 = \{(d_2(\tau), S(\tau), u(\tau), v(\tau)) : \tau\in(0,\tau_0)\}$$

is exactly the positive solution of the steady state system (7)-(8).

Next, we extend the local bifurcation Γ_1 to the global one by the application of the global bifurcation results for Fredholm operators (see Theorems 4.3-4.4 in [17]). Noting that $T : (0,+\infty)\times\mathbf{X}\to\mathbf{X}$ is C^1 smooth and compact, we can conclude that the Fréchet derivative $\mathrm{D}_{(\chi,U,V)}G(d_2,\chi,U,V)$ is Fredholm with index zero for any $(d_2,\chi,U,V)\in(0,+\infty)\times\mathbf{X}$. Now we can apply Theorem 4.3 in [17] to obtain a connected component Υ of the set

$$\{(d_2,\chi,U,V)\in(0,+\infty)\times\mathbf{X} : G(d_2,\chi,U,V) = 0, (\chi,U,V)\neq(1-S_{d_1},U_{d_1},0)\}$$

emanating from Γ_U at $(\hat{d}_2, 1-S_{d_1}, U_{d_1}, 0)$. Moreover, either Υ is not compact in $(0,+\infty)\times\mathbf{X}$ or Υ contains a point $(\bar{d}_2, 1-S_{d_1}, U_{d_1}, 0)$ with $\bar{d}_2\neq\hat{d}_2$. Set

$$\Upsilon' = \{(d_2,S,u,v) : S = 1-\chi, u = e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}U, v = e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}V \text{ and } (d_2,\chi,U,V)\in\Upsilon\}.$$

Then $\Gamma_1\subset\Upsilon'$. Let $\mathbf{X}_0 = \{(S,u,v)\in C^1[0,1]\times C^1[0,1]\times C^1[0,1] : S > 0, u > 0, v > 0 \text{ on } [0,1]\}$. Then $\Upsilon'\cap(\mathbb{R}_+\times\mathbf{X}_0)\neq\emptyset$.

Let $\Gamma = \Upsilon'\cap(\mathbb{R}_+\times\mathbf{X}_0)$. Then Γ consists of the local positive solution branch Γ_1 near the bifurcation point $(\hat{d}_2, S_{d_1}(x), u_{d_1}(x), 0)$. That is, $\Gamma\subset\mathbb{R}_+\times\mathbf{X}_0$ in a small neighborhood of $(\hat{d}_2, S_{d_1}(x), u_{d_1}(x), 0)$. Let Υ^+ be the connected component of $\Upsilon'\backslash\{(d_2(\tau), S(\tau), u(\tau), v(\tau)) : \tau\in(-\tau_0, 0)\}$. Then $\Gamma\subset\Upsilon^+$. It follows from Theorem 4.4 in [17] that Υ^+ satisfies one of the following alternatives

(i) it is not compact;

(ii) it contains a point $(\bar{d}_2, S_{d_1}(x), u_{d_1}(x), 0)$ with $\bar{d}_2\neq\hat{d}_2$;

(iii) it contains a point $(d_2, S_{d_1}(x)-\chi, u_{d_1}(x)+e^{\int_0^x \frac{\nu_1(\xi)}{D(\xi)}\mathrm{d}\xi}U, e^{\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}V)$, where $(\chi,U,V)\neq 0$ and $(\chi,U,V)\in\mathbf{Z}$.

For any $(S,u,v)\in\Gamma$, we have $v > 0$ on $[0, 1]$. Noting that $V = e^{-\int_0^x \frac{\nu_2(\xi)}{D(\xi)}\mathrm{d}\xi}v > 0$ on $[0, 1]$, one can conclude that (iii) is impossible.

Suppose (ii) holds. Then we can find a sequence of points $(d_2^{(n)}, S_n, u_n, v_n)\in(0, f_2(1))\times\mathbf{X}_0$ with $S_n, u_n, v_n > 0$ on $[0,1]$, which converges to $(\bar{d}_2, S_{d_1}, u_{d_1}, 0)$ in $(0,+\infty)\times\mathbf{X}$. It follows from the equation for v_n, we have

$$-d_2^{(n)} = \lambda_1(-f_2(S_n),\nu_2)\to\lambda_1(-f_2(S_{d_1}),\nu_2) = -\hat{d}_2.$$

Hence, $\bar{d}_2 = \hat{d}_2$, a contradiction. Thus (ii) can not occur.

It follows from Lemma 2.5 that for $d_1 \in [\delta, f_1(1))$ and $d_2 \in [\delta, f_2(1))$, we have $0 < S \le 1, \|u\|_\infty + \|v\|_\infty \le C$. By L^p estimate and Sobolev embedding theorem, we can deduce that $\|S\|_{C^1}, \|u\|_{C^1}, \|v\|_{C^1}$ are bounded. So for $0 < d_1 < f_1(1)$ fixed, Γ is bounded in $[\delta, f_2(1)) \times \mathbf{X}_0$. Thus (i) implies that the global bifurcation branch Γ must meet the boundary of $[\delta, f_2(1)) \times \mathbf{X}_0$. Thus $\Gamma - \{(\hat{d}_2, S_{d_1}, u_{d_1}, 0)\} \not\subseteq \mathbf{X}_0$ or Γ contains a point $(d_2, \bar{S}, \bar{u}, \bar{v}) \in [\delta, f_2(1)) \times \mathbf{X}_0$ with $d_2 = \delta$ or $d_2 = f_2(1)$.

Suppose there exist $d_2^{(n)} \to 0+$ and positive solution (S_n, u_n, v_n) of (7)-(8) with $d_2 = d_2^{(n)}$. It follows from the equations for u_n and v_n respectively that

$$-d_1 = \lambda_1(-f_1(S_n), \nu_1) \text{ and } -d_2^{(n)} = \lambda_1(-f_2(S_n), \nu_2). \tag{27}$$

Since $0 \le S_n \le 1$, we can assume $S_n \to h(x)$ weakly in $L^2(0,1)$, where $0 \le h(x) \le 1$. Letting $n \to \infty$ in (27), we obtain $-d_1 = \lambda_1(-f_1(h(x)), \nu_1)$ and $0 = \lambda_1(-f_2(h(x)), \nu_2)$, which implies $h(x) = 0$ a.e. in $(0,1)$, and $d_1 = 0$, a contradiction.

Suppose there exist $d_2^{(n)} \to f_2(1)-$ and positive solution (S_n, u_n, v_n) of (22) with $d_2 = d_2^{(n)}$. Then (27) still holds, and we may still assume $S_n \to h(x)$ weakly in $L^2(0,1)$, where $0 \le h(x) \le 1$. Letting $n \to \infty$ in (27), we obtain $-d_1 = \lambda_1(-f_1(h(x)), \nu_1)$ and $\lambda_1(-f_2(h(x)), \nu_2) = -f_2(1)$. Meanwhile, $-f_2(1) = \lambda_1(-f_2(1), \nu_2) \le \lambda_1(-f_2(h(x)), \nu_2)$. Moreover, the equality holds if and only if $h(x) = 1$ a.e. in (0, 1). This implies $\lambda_1(-f_1(h(x)), \nu_1) = -f_1(1)$, and $d_1 = -\lambda_1(-f_1(h(x)), \nu_1) = f_1(1)$, a contradiction.

Suppose $\Gamma - \{(\hat{d}_2, S_{d_1}, u_{d_1}, 0)\} \not\subseteq \mathbf{X}_0$. Then we can find a sequence of points

$$(d_2^{(n)}, S_n, u_n, v_n) \in \Gamma \cap \mathbf{X}_0 \text{ with } S_n, u_n, v_n > 0 \text{ on } [0,1],$$

which converges to $(\bar{d}_2, \bar{S}, \bar{u}, \bar{v}) \in (\Gamma - \{(\hat{d}_2, S_{d_1}, u_{d_1}, 0)\}) \cap \partial\mathbf{X}_0$ in $(0, +\infty) \times \mathbf{X}$. Clearly, $\bar{S} > 0$ on [0, 1]. Hence, $(\bar{S}, \bar{u}, \bar{v}) \in \partial\mathbf{X}_0$ means either $\bar{u} \ge 0, \bar{u}(x_0) = 0$ for some point $x_0 \in [0,1]$ or $\bar{v} \ge 0, \bar{v}(x_0) = 0$ for some point $x_0 \in [0,1]$. By the maximum principle, we have $\bar{u} \equiv 0$ if $\bar{u}(x_0) = 0$ for some point $x_0 \in [0,1]$. Similarly, we can show $\bar{v} \equiv 0$ for the other case. Hence, we obtain the following three alternatives: (a)$(\bar{S}, \bar{u}, \bar{v}) \equiv (1,0,0)$; (b)$(\bar{S}, \bar{u}, \bar{v}) \equiv (S_{d_1}, u_{d_1}, 0)$; (c)$(\bar{S}, \bar{u}, \bar{v}) \equiv (S_{d_2}, 0, v_{d_2})$.

If $(d_2^{(n)}, S_n, u_n, v_n) \to (\bar{d}_2, 1, 0, 0)$, then $d_1 = -\lambda_1(-f_1(S_n), \nu_1) \to f_1(1)$, contradicting $d_1 \in (\delta, f_1(1) - \delta)$. If $(d_2^{(n)}, S_n, u_n, v_n) \to (\bar{d}_2, S_{d_1}, u_{d_1}, 0)$, one can find that $-d_2^{(n)} = \lambda_1(-f_2(S_n), \nu_2) \to \lambda_1(-f_2(S_{d_1}), \nu_2) = -\hat{d}_2$, which implies $\bar{d}_2 = \hat{d}_2$, a contradiction. Thus (c) necessarily happens and the global bifurcation Γ must meet the semi-trivial branch $\Gamma_v = \{(d_2, S_{d_2}(x), 0, v_{d_2}(x)) : 0 < d_2 < f_2(1)\}$ at some point $(d_2, S_{d_2}(x), 0, v_{d_2}(x))$, that is, $\Gamma \cap \Gamma_v = \{(d_2, S_{d_2}(x), 0, v_{d_2}(x))\}$. Hence there exists a sequence $(d_2^{(n)}, S_n, u_n, v_n) \to (d_2, S_{d_2}(x), 0, v_{d_2}(x))$. By the equation for u_n, we have $d_1 = -\lambda_1(-f_1(S_n), \nu_1)$. Taking the limit, we get $d_1 = -\lambda_1(-f_1(S_{d_2}), \nu_1)$. It follows from Lemma 3.5 that there exists a $\tilde{d}_2 \in [\delta, f_2(1))$ such that $d_1 = -\lambda_1(-f_1(S_{\tilde{d}_2}), \nu_1) = \hat{d}_1(\tilde{d}_2)$. The proof is completed. □

5. **Discussion.** The purpose of this section is to present some numerical results on the coexistence region which complement the analytic results of the previous sections. It follows from Theorem 4.1 that (7)-(8) has a positive solution if d_2 lies between $\hat{d}_2$ and $\tilde{d}_2$, where $\hat{d}_2 = \hat{d}_2(d_1) = -\lambda_1(-f_2(S_{d_1}), \nu_2)$ and $\tilde{d}_2$ is determined by $\hat{d}_1(\tilde{d}_2) = -\lambda_1(-f_1(S_{\tilde{d}_2}), \nu_1) = d_1$. Hence, the length $|\hat{d}_2 - \tilde{d}_2|$ can describe the coexistence region roughly.

To this end, we first introduce an indirect numerical method to determine the eigenvalues $\hat{d}_2$ and $\tilde{d}_2$. The main idea comes from [1, 22]. To determine $\hat{d}_2$, we consider the system

$$\begin{array}{ll} S_t = (D_0(x)S_x)_x - \alpha_1 f_1(S)u, & x \in (0,1), t > 0, \\ u_t = (D(x)u_x - \nu_1(x)u)_x + (f_1(S) - d_1)u, & x \in (0,1), t > 0, \\ v_t = (D(x)v_x - \nu_2(x)v)_x + (f_2(S) - d_2)v, & x \in (0,1), t > 0 \end{array} \tag{28}$$

with boundary conditions (5) and initial conditions (6). Let (S, u, v) be the solution of (28) with boundary conditions (5) and initial conditions (6). Taking initial conditions characterized by a very small density of v_0, we can observe numerically that S and u rapidly approach the equilibrium $(S_{d_1}(x), u_{d_1}(x))$. Hence for large time t, we have $S(x,t) \approx S_{d_1}(x)$. Moreover, lots of simulations on (28) indicate what happens to v depends essentially on the sign of $d_2 - \hat{d}_2$. If $d_2 - \hat{d}_2 > 0$, we observed numerically the exponential decay of the solution v of (28) to very small values; if $d_2 - \hat{d}_2 < 0$, we observed numerically the eventual exponential growth of the solution v of (28) to very large values. In this way, we can numerically approximate $\hat{d}_2$ by observing there is neither exponential decay to very small values nor exponential growth to very large values when changing d_2 in $(0, f_2(1))$ (see Table 1 and Table 2). The numerical approximate values of $\tilde{d}_2$ can be obtained similarly (see Table 1 and Table 2) by investigating the following system

$$\begin{array}{ll} S_t = (D_0(x)S_x)_x - \alpha_2 f_2(S)v, & x \in (0,1), t > 0, \\ u_t = (D(x)u_x - \nu_1(x)u)_x + (f_1(S) - d_1)u, & x \in (0,1), t > 0, \\ v_t = (D(x)v_x - \nu_2(x)v)_x + (f_2(S) - d_2)v, & x \in (0,1), t > 0 \end{array}$$

with boundary conditions (5) and initial conditions (6).

The basic parameters are taken as follows in the numerical simulations: $\alpha_1 = \alpha_2 = 1/10^6, m_1 = 0.4, a_1 = 1, m_2 = 0.3, a_2 = 0.6, S^0 = 100, \beta = 0.05$. The numerical approximations on the coexistence regions convince us that

(1) The nonconstant vertical eddy diffusion coefficients have the benefit of coexistence comparing with the constant vertical eddy diffusion coefficients;

(2) For the nonconstant vertical eddy diffusion coefficients case, the coexistence regions become smaller with the increase of the velocity of cells. However, for the constant vertical eddy diffusion coefficients case, the coexistence regions are almost constant with the increase of the velocity of cells;

(3) The coexistence regions barely change when the parameter a changes, which measures the spatial variation of the vertical eddy diffusion coefficients;

(4) The coexistence regions become larger with the increase of the depth of the water column.

Acknowledgments. The authors would like to give their sincere thanks to the anonymous referees for their valuable suggestions leading to an improvement of the paper.

REFERENCES

[1] M. Ballyk, L. Dung, D. A. Jones and H. L. Smith, Effects of random motility on microbial growth and competition in a flow reactor, *SIAM J. Appl. Math.*, **59** (1998), 573–596.

[2] R. Courant and D. Hilbert, *Methods of Mathematical Physics*, Vol. I, Wiley-Interscience, New York, 1953.

[3] M. G. Crandall and P. H. Rabinowitz, Bifurcation from simple eigenvalues, *J. Functional Analysis*, **8** (1971), 321–340.

Table 1. Take the nonconstant vertical eddy diffusion coefficients $D_0(x) = D(x) = D_m + \frac{D_M - D_m}{1+e^{a(x-L/2)}}$, where $D_M = 10^3, D_m = 10$.

d_1	$\nu_1 = \nu_2$	L	a	$\hat{d}_2$	$\tilde{d}_2$	$\hat{d}_2 - \tilde{d}_2$
0.05	1.2	20	20	0.04563	0.04515	0.00048
0.1	1.2	20	20	0.086113	0.08516	0.000953
0.15	1.2	20	20	0.1247	0.12337	0.00133
0.05	0	20	20	0.043203	0.042666	0.000537
0.1	0	20	20	0.081601	0.08052	0.001081
0.15	0	20	20	0.119162	0.117499	0.001663
0.1	1.2	20	10	0.086018	0.085068	0.000951
0.1	1.2	20	20	0.086113	0.08516	0.000953
0.1	1.2	20	30	0.086141	0.08519	0.000951
0.1	1.2	20	20	0.086113	0.08516	0.000953
0.1	1.2	25	20	0.08594	0.08497	0.00097
0.1	1.2	30	20	0.086061	0.085081	0.00098

Table 2. Take the constant vertical eddy diffusion coefficients $D_0(x) = D(x) = \frac{D_M + D_m}{2}$, which is the average of the function $D_m + \frac{D_M - D_m}{1+e^{a(x-L/2)}}$.

d_1	$\nu_1 = \nu_2$	L	a	$\hat{d}_2$	$\tilde{d}_2$	$\hat{d}_2 - \tilde{d}_2$
0.05	1.2	20	20	0.044175	0.04376	0.000415
0.1	1.2	20	20	0.08537	0.0846235	0.0007465
0.15	1.2	20	20	0.125899	0.124867	0.001032
0.05	0	20	20	0.044134	0.043719	0.000415
0.1	0	20	20	0.085326	0.084578	0.000748
0.15	0	20	20	0.125871	0.124839	0.001032

[4] E. N. Dancer, On the indices of fixed points of mappings in cones and applications, *J. Math. Anal. Appl.*, **91** (1983), 131–151.

[5] E. N. Dancer, On positive solutions of some pairs of differential equations, *Trans. Amer. Math. Soc.*, **284** (1984), 729–743.

[6] Y. Du and L. F. Mei, On a nonlocal reaction-diffusion-advection equation modelling phytoplankton dynamics, *Nonlinearity*, **24** (2011), 319–349.

[7] J. P. Grover, *Resource Competition*, Chapman and Hall, London, 1997.

[8] S.B. Hsu, Steady states of a system of partial differential equations modeling microbial ecology, *SIAM J. Math. Anal.*, **14** (1983), 1130–1138.

[9] S. B. Hsu and Y. Lou, Single phytoplankton species growth with light and advection in a water column, *SIAM J. Appl. Math.*, **70** (2010), 2942–2974.

[10] S. B. Hsu and P. Waltman, On a system of reaction-diffusion equations arising from competition in an un-stirred chemostat, *SIAM J. Appl. Math.*, **53** (1993), 1026–1044.

[11] J. López-Gómez and R. Parda, Existence and uniqueness of coexistence states for the predator-prey model with diffusion: the scalar case, *Differential Integral Equations*, **6** (1993), 1025–1031.

[12] P. Magal and X.Q. Zhao, Global attractors and steady states for uniformly persistent dynamical systems, *SIAM J. Math Anal.*, **37** (2005), 251–275.

[13] J. P. Mellard, K. Yoshiyama, E. Litchman and C. A. Klausmeier, The vertical distribution of phytoplankton in stratified water columns, *J. Theoret. Biol.*, **269** (2011), 16-30.

[14] H. Nie and J. Wu, Multiplicity results for the unstirred chemostat model with general response functions, *Sci. China Math.*, **56** (2013), 2035–2050.

[15] H. Nie and J. Wu, Positive solutions of a competition model for two resources in the unstirred chemostat, *J. Math. Anal. Appl.*, **355** (2009), 231–242.

[16] H. Nie and J. Wu, Uniqueness and stability for coexistence solutions of the unstirred chemostat model, *Appl. Anal.*, **89** (2010), 1141–1159.

[17] J. P. Shi and X. F. Wang, On global bifurcation for quasilinear elliptic systems on bounded domains, *J. Differential Equations*, **246** (2009), 2788–2812.

[18] H. L. Smith and X. Q. Zhao, Robust persistence for semidynamical systems, *Nonlinear Anal.*, **47** (2001), 6169–6179.

[19] J. Smoller, *Shock Waves and Reaction-Diffusion Equations*, 2^{nd} edition, Springer-Verlag, New York, 1994.

[20] D. Tilman, *Resource Competition and Community Structure*, Princeton University Press, Princeton, 1982.

[21] M. X. Wang, *Nonlinear Elliptic Equations*, Science Press, Beijing, 2010(in Chinese).

[22] J. Wu, H. Nie and G. S. K. Wolkowicz, A mathematical model of competition for two essential resources in the unstirred chemostat, *SIAM J. Appl. Math.*, **65** (2004), 209–229.

[23] J. Wu, H. Nie and G. S. K. Wolkowicz, The effect of inhibitor on the plasmid-bearing and plasmid-free model in the unstirred chemostat, *SIAM J. Math. Anal.*, **38** (2007), 1860–1885.

[24] J. Wu and G. S. K. Wolkowicz, A system of resource-based growth models with two resources in the un-stirred chemostat, *J. Differential Equations*, **172** (2001), 300–332.

[25] K. Yoshiyama and H. Nakajima, Catastrophic transition in vertical distributions of phytoplankton: alternative equilibria in a water column, *J. Theoret. Biol.*, **216** (2002), 397–408.

[26] K. Yoshiyama, J. P. Mellard, E. Litchman and C.A. Klausmeier, Phytoplankton competition for nutrients and light in a stratified water column, *Am. Nat.*, **174** (2009), 190–202.

Received xxxx 20xx; revised xxxx 20xx.

E-mail address: niehua@snnu.edu.cn(correspondence author)
E-mail address: sbhsu@math.nthu.edu.tw
E-mail address: jianhuaw@snnu.edu.cn