

COEXISTENCE STATE OF A REACTION-DIFFUSION SYSTEM

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ABSTRACT. Taking the spatial diffusion into account, we consider a reaction-diffusion system that models three species on a growth-limiting, nonreproducing resources in an unstirred chemostat. Sufficient conditions for the existence of a positive solution are determined. The main techniques is the Leray-Schauder degree theory.

1. INTRODUCTION

The chemostat is a laboratory apparatus used for the continuous culture of microorganisms. It can be used to study competition between different populations of microorganisms, and has the advantage that the parameters are readily measurable. Experimental verification of the match between theory and experiment in the chemostat can be found in [7]. For a general discussion of competition, see [6, 11], while a detailed mathematical description of competition in the chemostat can be found in [12].

In article [2], a mathematical analysis is given to a competition model in a well-mixed chemostat with the equation the

$$\begin{aligned} S' &= (S^0 - S)D - \frac{m_1 S}{a_1 + S} \frac{u_1}{\eta_1} - \frac{m_2 S}{a_2 + S} \frac{u_2}{\eta_2}, \\ u_1' &= u_1 \left(\frac{m_1 S}{a_1 + S} - D - \gamma u_3 \right), \\ u_2' &= u_2 \left((1 - k(u_1, u_2)) \frac{m_2 S}{a_2 + S} - D \right), \\ u_3' &= k(u_1, u_2) \frac{m_2 S u_2}{a_2 + S} - D u_3, \end{aligned} \tag{1.1}$$

where $S(t)$ denotes the nutrient concentration at time t , $u_1(t)$ is the density of the sensitive microorganism at time t , $u_2(t)$ is the density of the toxin-producing organism at time t , and $u_3(t)$ is the concentration of the toxicant at time t , which is lethal to the microorganism $u_1(t)$. $S^{(0)}$ is the input concentration of nutrient, D is the washout rate, m_i are the maximal growth rates, a_i are the Michaelis-Menten constants and η_i , $i = 1, 2$ are the yield constants. $S^{(0)}$ and D are under the

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control of the experimenter, and the other parameters are a function of the organism selected. The function $k(u_1, u_2)$ represents the fraction of potential growth devoted to producing the toxin and we assume that it is smooth. System (1.1) with constant k is studied in [8] and it is noted that system (1.1) is asymptotic to the standard chemostat when $k \equiv 0$. The introduction of $k(u_1, u_2)$ requires that a bacterium has the ability to sense the current state of its habitat and the presence of other bacteria. The interaction between the allelopathic agent and the sensitive microorganism has been taken to be mass action form, $-\gamma u_3 u_1$. This is common modelling when an interaction depends on the two concentrations.

In the current paper, taking the spatial diffusion into account, we remove the well-stirred hypothesis in system (1.1), and thus are led to consider the following reaction-diffusion (rescaled) system

$$\begin{aligned} d_0 \Delta S - m_1 u_1 f_1(S) - m_2 u_2 f_2(S) &= 0, & x \in \Omega \\ d_1 \Delta u_1 + m_1 u_1 f_1(S) - \gamma u_1 u_3 &= 0, \\ d_2 \Delta u_2 + m_2 (1 - k) u_2 f_2(S) &= 0, \\ d_3 \Delta u_3 + m_2 k u_2 f_2(S) &= 0, \end{aligned} \tag{1.2}$$

subject to boundary conditions

$$\begin{aligned} \frac{\partial S}{\partial n} + b(x)S &= S^0(x), & x \in \partial\Omega, \\ \frac{\partial u_i}{\partial n} + b(x)u_i &= 0 \quad (i = 1, 2, 3), \end{aligned} \tag{1.3}$$

where Ω is a bounded domain in R^N ($N \geq 1$) with smooth boundary $\partial\Omega$, and $\frac{\partial}{\partial n}$ denotes the outward normal derivative, $0 < k < 1$. $f_i(S) = \frac{S}{a_i + S}$ ($i = 1, 2$), $b(x)$ and $S^0(x)$ are continuous on $\partial\Omega$, and $b(x), S^0(x) \geq 0, \neq 0$, on $\partial\Omega$. d_0 is the diffusive coefficient for the nutrient S , d_i ($i = 1, 2, 3$) are the random motility coefficient of the microbial population u_i , respectively.

Since only nonnegative solutions (S, u_1, u_2, u_3) are of biological interest, we redefine $\hat{f}_i(S)$ ($i = 1, 2$) for $S < 0$ as follows:

$$\hat{f}_i(S) = \begin{cases} f_i(S), & S \geq 0, \\ \arctan(\frac{2S}{a_i} + 1) - \frac{\pi}{4}, & S < 0. \end{cases}$$

It is easily seen that $\hat{f}_i(S) \in C^1(R)$.

The organization of this paper is as follows. In section 2, we obtain the existence and uniqueness of nonnegative semi-trivial solutions by the principle eigenvalue problem and the maximum principle. In section 3, the existence of the positive solution of (1.2)–(1.3) is obtained by making use of the theory of Leray-Schauder degree [14].

2. THE SEMI-TRIVIAL SOLUTION

In this section, we shall consider the semi-trivial solutions of (1.2)–(1.3). To this end, we first investigate the following problem

$$\begin{aligned} \Delta S &= 0, & x \in \Omega, \\ \frac{\partial S}{\partial n} + b(x)S &= S^0(x), & x \in \partial\Omega, \end{aligned} \tag{2.1}$$

Lemma 2.1. *There exists a unique positive solution $S^*(x)$.*

The proof can be seen in [13, 15], and is omitted here.

From the maximum principle, the nonnegative solution (S, u_1, u_2, u_3) of system (1.2)–(1.3) satisfies

$$d_0S + d_1u_1 + d_2u_2 + d_3u_3 \leq d_0S^*(x), \quad x \in \Omega.$$

Let $\lambda_i > 0$ ($i = 1, 2$) be the principal eigenvalue of the problem

$$\begin{aligned} d_i\Delta\phi + \lambda f_i(S^*)\phi &= 0, & x \in \Omega, \\ \frac{\partial\phi}{\partial n} + b(x)\phi &= 0, & x \in \partial\Omega, \end{aligned} \tag{2.2}$$

with the corresponding eigenfunction $\phi_i > 0$ ($i = 1, 2$).

Theorem 2.2. *If $m_1 > \lambda_1$, then (1.2)–(1.3) admits a unique semi-trivial solution $(S_1, \bar{u}_1, 0, 0)$ with $d_0S_1 + d_1\bar{u}_1 = d_0S^*$, $S_1 > 0$, $\bar{u}_1 > 0$.*

Proof. Taking $u_2 \equiv 0, u_3 \equiv 0$, system (1.2)–(1.3) is reduced to the system

$$\begin{aligned} d_0\Delta S - m_1u_1f_1(S) &= 0, & x \in \Omega, \\ d_1\Delta u_1 + m_1u_1f_1(S) &= 0, \\ \frac{\partial S}{\partial n} + b(x)S &= S_0(x), & x \in \partial\Omega, \\ \frac{\partial u_1}{\partial n} + b(x)u_1 &= 0. \end{aligned} \tag{2.3}$$

Let $Z = d_0S + d_1u_1$, then Z satisfies

$$\begin{aligned} \Delta Z &= 0, & x \in \Omega, \\ \frac{\partial Z}{\partial n} + b(x)Z &= d_0S_0(x), & x \in \partial\Omega, \end{aligned} \tag{2.4}$$

from Lemma 2.1, (2.4) have a unique positive solution S^* , it satisfies $d_0S + d_1u_1 = d_0S^*$. Thus u_1 satisfies

$$\begin{aligned} d_1\Delta u_1 + m_1u_1f_1\left(\frac{d_0S^* - d_1u_1}{d_0}\right) &= 0, & x \in \Omega, \\ \frac{\partial u_1}{\partial n} + b(x)u_1 &= 0, & x \in \partial\Omega, \end{aligned} \tag{2.5}$$

Arguing exactly as [13, lemma 3.2], (2.5) have a unique positive solution \bar{u}_1 . Thus we complete the proof of the theorem. \square

Similar to the proof of [13, Lemma 3.2], we can also show that the system

$$\begin{aligned} d_2\Delta\psi + m_2(1-k)\psi f_2\left(S^* - \frac{d_2\psi}{d_0}\right) &= 0, & x \in \Omega, \\ \frac{\partial\psi}{\partial n} + b(x)\psi &= 0, & x \in \partial\Omega \end{aligned} \tag{2.6}$$

has a unique positive solution $\psi < \frac{d_0}{d_2}S^*$ if $m_2 > \frac{\lambda_2}{1-k}$.

Theorem 2.3. *If $m_2 > \frac{\lambda_2}{1-k}$, then system (1.2)–(1.3) admits a unique semi-trivial solution $(S_2, 0, \bar{u}_2, \bar{u}_3)$ with $d_0S_2 + d_2\bar{u}_2 + d_3\bar{u}_3 = d_0S^*$, $S_2 > 0$, $\bar{u}_2 > 0$, $\bar{u}_3 > 0$.*

Proof. We take $u_1 \equiv 0$ and thus reduce (1.2)–(1.3) to the system

$$\begin{aligned} d_0 \Delta S - m_2 u_2 f_2(S) &= 0, & x \in \Omega \\ d_2 \Delta u_2 + m_2(1-k)u_2 f_2(S) &= 0, \\ d_3 \Delta u_3 + m_2 k u_2 f_2(S) &= 0, \\ \frac{\partial S}{\partial n} + b(x)S &= S^0(x), & x \in \partial\Omega, \\ \frac{\partial u_i}{\partial n} + b(x)u_i &= 0 \quad (i = 2, 3), \end{aligned} \tag{2.7}$$

Let $z = d_0 S + d_2 u_2 + d_3 u_3$, then $\frac{z}{d_0}$ satisfies (2.1), and thus $z = d_0 S^*(x)$. Substituting it into (2.7), we get the reduced boundary-value problem

$$\begin{aligned} d_2 \Delta u_2 + m_2(1-k)u_2 f_2\left(S^* - \frac{d_2 u_2 + d_3 u_3}{d_0}\right) &= 0, & x \in \Omega, \\ d_3 \Delta u_3 + m_2 k u_2 f_2\left(S^* - \frac{d_2 u_2 + d_3 u_3}{d_0}\right) &= 0, \\ \frac{\partial u_i}{\partial n} + b(x)u_i &= 0 \quad (i = 2, 3), & x \in \partial\Omega. \end{aligned} \tag{2.8}$$

It is easy to check that $((1-k)\psi, \frac{d_2}{d_3}k\psi)$ is exactly a positive solution of (2.8).

Let (u_2, u_3) be the positive solution of (2.8), and $w = d_2 k u_2 - d_3(1-k)u_3$, then w satisfies

$$\begin{aligned} \Delta w &= 0, & x \in \Omega, \\ \frac{\partial w}{\partial n} + b(x)w &= 0, & x \in \partial\Omega. \end{aligned}$$

By the maximum principle, we get $w = 0$ and $d_2 k u_2 = d_3(1-k)u_3$.

Substituting $d_2 k u_2 = d_3(1-k)u_3$ into (2.8), we have

$$\begin{aligned} d_2 \Delta u_2 + m_2(1-k)u_2 f_2\left(S^* - \frac{d_2 u_2}{d_0(1-k)}\right) &= 0, \\ \frac{\partial u_2}{\partial n} + b(x)u_2 &= 0. \end{aligned}$$

Then by the uniqueness of the positive solution of (2.6), it follows that $u_2 = (1-k)\psi$ and thus $u_3 = \frac{d_2}{d_3}k\psi$. The proof is complete. \square

At this position, we can get the following result which implies that $m_1 > \lambda_1, m_2 > \frac{\lambda_2}{1-k}$ is necessary to the existence of coexistence states of system (1.2)–(1.3).

Theorem 2.4. *If $m_1 \leq \lambda_1$ or $m_2 \leq \frac{\lambda_2}{1-k}$ are satisfied, then the nonnegative solution (S, u_1, u_2, u_3) of system (1.2)–(1.3) satisfies $u_1 = 0$ or $u_2 = u_3 = 0$.*

The proof is omitted here and the reader may refer to [9, 10, 13]. Therefore we suppose $m_1 > \lambda_1, m_2 > \frac{\lambda_2}{1-k}$ in what follows.

3. COEXISTENCE STATE

In this section, following some ideas of Dung and Smith [5], we shall determine the sufficient conditions for the existence of positive solutions of (1.2)–(1.3) by the theory of Leray-Schauder degree. Now we state some results about Leray-Schauder degree, which appeared in [1, 14].

Theorem 3.1. *Let X be a retract of some Banach space E , let U be an open subset of X , and let $A : \bar{U} \rightarrow X$ be a compact map. Suppose that $x_0 \in U$ is a fixed point of A , and suppose that there exists a positive number ρ such that $x_0 + \rho B \subset U$, where B denotes the open unit ball of E . Finally, suppose that A is differentiable at x_0 , such that 1 is not an eigenvalue of the derivative $A'(x_0)$. Then x_0 is an isolated fixed point of A , and*

$$\text{index}(x_0, A) = \deg(I - A, B, 0) = \deg(I - A'(x_0), \bar{B}, 0) = (-1)^m,$$

where m is the sum of the multiplicities of all the eigenvalues of $A'(x_0)$ which are greater than one.

For every $\rho > 0$, we denote by P_ρ the positive part of ρB , that is $P_\rho = \rho B \cap P = \rho B^+$.

Lemma 3.2. *Let $A : \bar{P}_\rho \rightarrow P$ be a compact map such that $A(0) = 0$. Suppose that A has a right derivative $A'_+(0)$ at zero such that 1 is not an eigenvalue of $A'_+(0)$ to a positive eigenvector. Then there exists a constant $\sigma \in (0, \sigma_0]$,*

- (i) $\text{index}(P_\rho, A) = \deg(I - A, P_\rho, 0) = 1$ if $A'_+(0)$ has no positive eigenvector to an eigenvalue greater than one;
- (ii) $\text{index}(P_\rho, A) = 0$ if $A'_+(0)$ possesses a positive eigenvector to an eigenvalue greater than one.

Let

$$C_0(\bar{\Omega}) = \left\{ \phi \in C(\bar{\Omega}) : \frac{\partial \phi}{\partial n} + b(x)\phi = 0 \quad \text{on } \partial\Omega \right\}$$

$$K = \{ \phi \in C_0(\bar{\Omega}) : \phi \geq 0 \quad \text{in } \Omega \},$$

then $C_0(\bar{\Omega})$ is a Banach space and K is a positive cone in $C_0(\bar{\Omega})$. We define

$$E = C_0(\bar{\Omega}) \times C_0(\bar{\Omega}) \times C_0(\bar{\Omega}) \times C_0(\bar{\Omega}), \quad E_+ = K \times K \times K \times K.$$

Let $s(x) = S^*(x) - S(x)$, then system (1.2)–(1.3) becomes

$$\begin{aligned} d_0 \Delta s + m_1 u_1 f_1(S^* - s) + m_2 u_2 f_2(S^* - s) &= 0, & x \in \Omega, \\ d_1 \Delta u_1 + m_1 u_1 f_1(S^* - s) - \gamma u_1 u_3 &= 0, \\ d_2 \Delta u_2 + m_2 (1 - k) u_2 f_2(S^* - s) &= 0, \\ d_3 \Delta u_3 + m_2 k u_2 f_2(S^* - s) &= 0, & (3.1) \\ \frac{\partial s}{\partial n} + b(x)s &= 0, & x \in \partial\Omega, \\ \frac{\partial u_i}{\partial n} + b(x)u_i &= 0 \quad (i = 1, 2, 3). \end{aligned}$$

Since $S(x) \geq 0$, the nonnegative solution of (3.1) satisfies $s(x) \leq S^*(x)$. Define $A : E_+ \rightarrow E$ by

$$\begin{aligned} A(s, u_1, u_2, u_3) = & \left((-d_0 \Delta)^{-1} (m_1 u_1 f_1(S^* - s) + m_2 u_2 f_2(S^* - s)), \right. \\ & (-d_1 \Delta)^{-1} (m_1 u_1 f_1(S^* - s) - \gamma u_1 u_3), \\ & (-d_2 \Delta)^{-1} (m_2 (1 - k) u_2 f_2(S^* - s)), \\ & \left. (-d_3 \Delta)^{-1} (m_2 k u_2 f_2(S^* - s)) \right) \end{aligned}$$

for $(s, u_1, u_2, u_3) \in E_+$, then it is observed that A is a compact operator and every nonnegative solution of (1.2)–(1.3) corresponds to the fixed point of the operator A on the cone E_+ .

Clearly, $e_0 = (0, 0, 0, 0)$, $e_1 = (S^* - S_1, \bar{u}_1, 0, 0)$, $e_2 = (S^* - S_2, 0, \bar{u}_2, \bar{u}_3)$ are fixed points of compact operator A .

Let $\lambda'_i(q)$ ($i = 1, 2$) be the principal eigenvalue of

$$-d_i \Delta \omega + q(x)\omega = \lambda \omega,$$

with $q(x) \in C(\bar{\Omega})$. It is well known [4] that $\lambda'_i(q)$ depends continuously on q , and $q_1 \leq q_2, q_1 \not\equiv q_2$ implies $\lambda'_i(q_1) < \lambda'_i(q_2)$. From [1, Theorem 4.3, 4.4 and 4.5], $\lambda'_1(-m_1 f_1(S^*)) < 0, \lambda'_2(-m_2(1-k)f_2(S^*)) < 0$ is equivalent to $m_1 > \lambda_1, m_2 > \frac{\lambda_2}{(1-k)}$, respectively.

Lemma 3.3. $\text{index}(e_0, A) = 0$.

Proof. Let $A'(e_0)$ be the derivative of A at e_0 . If $\lambda > 0$ is an eigenvalue of $A'(e_0)$ corresponding to the eigenfunction $(s, u_1, u_2, u_3)^T \in E_+$. Then

$$\begin{aligned} d_0 \Delta s + \frac{1}{\lambda} (m_1 u_1 f_1(S^*) + m_2 u_2 f_2(S^*)) &= 0, \quad x \in \Omega \\ d_1 \Delta u_1 + \frac{1}{\lambda} m_1 u_1 f_1(S^*) &= 0, \\ d_2 \Delta u_2 + \frac{1}{\lambda} m_2 (1-k) u_2 f_2(S^*) &= 0, \\ d_3 \Delta u_3 + \frac{1}{\lambda} m_2 k u_2 f_2(S^*) &= 0, \end{aligned}$$

with homogeneous boundary conditions. From $\lambda'_1(-m_1 f_1(S^*)) < 0$ and $\lambda'_2(-m_2(1-k)f_2(S^*)) < 0$, we have $\lambda \neq 1$. From (2.2) and $m_1 > \lambda_1$, it follows that

$$d_1 \Delta \phi_1 + \frac{1}{\lambda_0} m_1 \phi_1 f_1(S^*) = 0$$

with $\lambda_0 = \frac{m_1}{\lambda_1} > 1$. Then

$$\begin{aligned} A'(e_0)((-d_0 \Delta)^{-1} \frac{1}{\lambda_0} m_1 \phi_1 f_1(S^*), \phi_1, 0, 0)^T \\ = \lambda_0 ((-d_0 \Delta)^{-1} \frac{1}{\lambda_0} m_1 \phi_1 f_1(S^*), \phi_1, 0, 0)^T. \end{aligned}$$

Thus from Lemma 3.2, it follows that $\text{index}(e_0, A) = 0$. □

Lemma 3.4. *There exists a constant $R > 0$ such that $\deg(I - A, P_R, 0) = 1$, where $P_R = \{U \in E_+ : \|s\| < R, \|u_i\| < R\} (i = 1, 2, 3)$.*

Proof. For $t \in [0, 1]$, $(s, u_1, u_2, u_3) = tA(s, u_1, u_2, u_3)$ and $(s, u_1, u_2, u_3) \in E_+$ implies

$$\begin{aligned} d_0 \Delta s + t m_1 u_1 f_1(S^* - s) + t m_2 u_2 f_2(S^* - s) &= 0, \quad x \in \Omega, \\ d_1 \Delta u_1 + t m_1 u_1 f_1(S^* - s) - t \gamma u_1 u_3 &= 0, \\ d_2 \Delta u_2 + t m_2 (1-k) u_2 f_2(S^* - s) &= 0, \\ d_3 \Delta u_3 + t m_2 k u_2 f_2(S^* - s) &= 0, \tag{3.2} \\ \frac{\partial s}{\partial n} + b(x)s &= 0, \quad x \in \partial \Omega, \\ \frac{\partial u_i}{\partial n} + b(x)u_i &= 0 (i = 1, 2, 3). \end{aligned}$$

We claim that $s \leq S^*$. Otherwise, if $g(x) = s(x) - S^*(x)$ attains its maximum at some point $x_0 \in \bar{\Omega}$, then $g(x_0) > 0$ and $g(x)$ satisfies

$$d_0\Delta g + tm_1u_1f_1(-g) + tm_2u_2f_2(-g) = 0.$$

Now if $u_1 = 0$ and $u_2 = 0$ or $t = 0$, then from the first equation in (3.2), it follows $s \equiv 0$ and thus $s \leq S^*$ holds. So we assume that $t > 0$ and $u_1 \neq 0$ or $u_2 \neq 0$. By the maximum principle, $u_1 > 0$ or $u_2 > 0$.

If $x_0 \in \Omega$, then $\Delta g(x_0) \leq 0$. However, $g(x_0) > 0$ implies

$$d_0\Delta g(x_0) = tm_1u_1(x_0)f_1(-g(x_0)) - tm_2u_2(x_0)f_2(-g(x_0)) > 0,$$

a contradiction. Hence $x_0 \in \partial\Omega$ and thus $\frac{\partial g}{\partial n}|_{x_0} > 0$ by the maximum principle. On the other hand, $\frac{\partial g}{\partial n}|_{x_0} + b(x_0)g(x_0) = -S^0(x_0) \leq 0$ implies that $\frac{\partial g}{\partial n}|_{x_0} \leq 0$, a contradiction. Therefore $s \leq S^*$ on $\bar{\Omega}$. Let $\hat{S} = S^* - s$, then system (3.2) becomes

$$d_0\Delta\hat{S} - tm_1u_1f_1(\hat{S}) - tm_2u_2f_2(\hat{S}) = 0, \quad x \in \Omega,$$

$$d_1\Delta u_1 + tm_1u_1f_1(\hat{S}) - t\gamma u_1u_3 = 0,$$

$$d_2\Delta u_2 + tm_2(1 - k)u_2f_2(\hat{S}) = 0,$$

$$d_3\Delta u_3 + tm_2ku_2f_2(\hat{S}) = 0,$$

$$\frac{\partial\hat{S}}{\partial n} + b(x)\hat{S} = S^0(x), \quad x \in \partial\Omega,$$

$$\frac{\partial u_i}{\partial n} + b(x)u_i = 0 (i = 1, 2, 3),$$

It follows that $d_0\hat{S} + d_1u_1 + d_2u_2 + d_3u_3 \leq d_0S^*$. Hence $u_i \leq \frac{d_0S^*}{d_i} (i = 1, 2, 3)$. Let $M = \max\{1, \frac{d_0}{d_1}, \frac{d_0}{d_2}, \frac{d_0}{d_3}\}$, $R = M \max_{x \in \bar{\Omega}} S^*(x)$, Then $U = (s, u_1, u_2, u_3) \notin \partial P_R$. By the homotopy invariance of the degree, we obtain

$$\deg(I - A, P_R, 0) = \deg(I, P_R, 0) = 1.$$

□

Lemma 3.5. *Suppose $\lambda'_2(-m_2(1 - k)f_2(S_1)) < 0$, then $\text{index}(e_1, A) = 0$.*

Proof. Consider problem (3.1) in the form

$$\begin{aligned} d_0\Delta s + m_1u_1f_1(S^* - s) + tm_2u_2f_2(S^* - s) &= 0, \quad x \in \Omega \\ d_1\Delta u_1 + m_1u_1f_1(S^* - s) - t\gamma u_1u_3 &= 0, \\ d_2\Delta u_2 + m_2(1 - k)u_2f_2(S^* - s) &= 0, \\ d_3\Delta u_3 + m_2ku_2f_2(S^* - s) &= 0, \\ \frac{\partial s}{\partial n} + b(x)s &= 0, \quad x \in \partial\Omega, \\ \frac{\partial u_i}{\partial n} + b(x)u_i &= 0 (i = 1, 2, 3), \end{aligned} \tag{3.3}$$

where the parameter $t = 1$.

Here we regard $t \in [0, 1]$ as the homotopy parameter and hence equivalent fixed point problem can be denoted by $U = H(t, U)$. It is obvious that $H(1, U) = A(U)$.

We assume that $A(U) = U$ has no one positive solution in $P_R \setminus \bar{P}_r (r \ll 1)$, otherwise there are nothing to do.

Choose a neighborhood $Q = V \times W$ of e_1 in $P_R \setminus \overline{P_r}$, where V is a neighborhood $(S^* - S_1, \bar{u}_1)$ in $C_0(\bar{\Omega}) \times C_0(\bar{\Omega})$, and W is a small neighborhood of $(0, 0)$ in $C_0(\bar{\Omega}) \times C_0(\bar{\Omega})$.

If $H(0, U) = U$ has a solution $U = (s, u_1, u_2, u_3) \in \partial Q$, which implies $u_1 \neq 0$, then $(s, u_1) = (S^* - S_1, \bar{u}_1)$ by Theorem 2.2. If $u_2 = 0$, then $U = e_1$, but $e_1 \notin \partial Q$. Therefore $u_2 > 0$ and thus we have a contradiction to $\lambda'_2(-m_2(1-k)f_2(S_1)) < 0$.

If there exists $t \in (0, 1]$ such that $H(t, U) = U$ has a solution $U = (s, u_1, u_2, u_3) \in \partial Q$, then $u_2 \neq 0$. Since once $u_2 \equiv 0$, then $U = e_1$ contradicting $U \in \partial Q$. Therefore $u_2 > 0$, and thus (s, u_1, tu_2, tu_3) is a positive fixed point of A contradicting our assumption.

By the homotopy invariance of Leray-Schauder degree

$$\text{index}(e_1, A) = \text{index}(e_1, H(1, \cdot)) = \text{index}(e_1, H(0, \cdot)).$$

Now consider the boundary-value problem with parameter $t \in [0, 1]$

$$\begin{aligned} d_0 \Delta s + m_1 u_1 f_1(S^* - s) &= 0, & x \in \Omega, \\ d_1 \Delta u_1 + m_1 u_1 f_1(S^* - s) &= 0, \\ d_2 \Delta u_2 + m_2(1-k)u_2 f_2(tS_1 + (1-t)(S^* - s)) &= 0, \\ d_3 \Delta u_3 + m_2 k u_2 f_2(tS_1 + (1-t)(S^* - s)) &= 0, \\ \frac{\partial s}{\partial n} + b(x)s &= 0, & x \in \partial\Omega, \\ \frac{\partial u_i}{\partial n} + b(x)u_i &= 0 \quad (i = 1, 2, 3). \end{aligned} \tag{3.4}$$

In fixed point form, system (3.4) becomes $G(t, U) = U$. If $G(t, U) = U$ for some $t \in [0, 1]$ and $U = (s, u_1, u_2, u_3) \in \partial Q$, then obviously $(s, u_1) = (S^* - S_1, \bar{u}_1)$, and so $u_2 \equiv 0$ by $\lambda'_2(-m_2(1-k)f_2(S_1)) < 0$. Thus $U = e_1$ contradicting $e_1 \notin \partial Q$. Again, by the homotopy invariance of Leray-Schauder degree,

$$\text{index}(e_1, A) = \text{index}(e_1, H(0, \cdot)) = \text{index}(e_1, G(0, \cdot)) = \text{index}(e_1, G(1, \cdot)).$$

However, $G(1, \cdot)$ can be view as the product of two maps G_1 on V and G_2 on W , which are associated with the boundary value problems

$$\begin{aligned} d_0 \Delta s + m_1 u_1 f_1(S^* - s) &= 0, \\ d_1 \Delta u_1 + m_1 u_1 f_1(S^* - s) &= 0, \end{aligned}$$

and

$$\begin{aligned} d_2 \Delta u_2 + m_2(1-k)u_2 f_2(S_1) &= 0, \\ d_3 \Delta u_3 + m_2 k u_2 f_2(S_1) &= 0, \end{aligned}$$

with homogeneous boundary conditions, respectively.

Now, by the uniqueness of $(S^* - S_1, \bar{u}_1)$ and $m_1 > \lambda_1$,

$$\text{deg}(G_1, V, (0, 0)) = \text{index}((S^* - S_1, \bar{u}_1), G_1) = 1.$$

Furthermore from $\lambda'_2(-m_2(1-k)f_2(S_1)) < 0$, it follows

$$\text{deg}(G_2, W, (0, 0)) = \text{index}((0, 0), G_2).$$

In fact, if $\lambda > 0$ is an eigenvalue of $G'_2(0, 0) = G_2$ corresponding to the eigenfunction $(u_2, u_3)^T \in W$, then

$$\begin{aligned} d_2\Delta u_2 + \frac{1}{\lambda}m_2(1 - k)u_2f_2(S_1) &= 0, \\ d_3\Delta u_3 + \frac{1}{\lambda}m_2ku_2f_2(S_1) &= 0. \end{aligned}$$

By $\lambda'_2(-m_2(1 - k)f_2(S_1)) < 0$, $\lambda \neq 1$. Therefore there exists $\lambda > 1$ and $u_2 > 0$ the corresponding eigenfunction such that

$$d_2\Delta u_2 + \frac{1}{\lambda}m_2(1 - k)u_2f_2(S_1) = 0.$$

Thus $G'_2(0, 0)(u_2, (-d_3\Delta)^{-1}(\frac{1}{\lambda}m_2kf_2(S_1)))^T = \lambda(u_2, (-d_3\Delta)^{-1}(\frac{1}{\lambda}m_2kf_2(S_1)))^T$. It follows from Lemma 3.2 that $\text{index}((0, 0), G_2) = 0$.

By the product theorem of Leray-Schauder degree [14, Theorem 13.F]

$$\text{index}(e_1, A) = \text{deg}(G_1, V, (0, 0)) \text{deg}(G_2, W, (0, 0)) = 0.$$

□

Lemma 3.6. *Suppose $\lambda'_1(-m_1f_1(S_2) + \gamma\bar{u}_3) < 0$, then $\text{index}(e_2, A) = 0$.*

Proof. Consider (3.1) in the form

$$\begin{aligned} d_0\Delta s + tm_1u_1f_1(S^* - s) + m_2u_2f_2(S^* - s) &= 0, \quad x \in \Omega \\ d_1\Delta u_1 + m_1u_1f_1(S^* - s) - \gamma u_1u_3 &= 0, \\ d_2\Delta u_2 + m_2(1 - k)u_2f_2(S^* - s) &= 0, \\ d_3\Delta u_3 + m_2ku_2f_2(S^* - s) &= 0, \tag{3.5} \\ \frac{\partial s}{\partial n} + b(x)s &= 0, \quad x \in \partial\Omega, \\ \frac{\partial u_i}{\partial n} + b(x)u_i &= 0 \quad (i = 1, 2, 3). \end{aligned}$$

with the parameter $t = 1$.

Here we regard $t \in [0, 1]$ as the homotopy parameter and hence equivalent fixed point problem can be denoted by $U = H(t, U)$. It is obvious that $H(1, U) = A(U)$.

We assume that $A(U) = U$ has no one positive solution in $P_R \setminus \bar{P}_r$ ($r \ll 1$), otherwise there are nothing to do.

Choose a neighborhood $Q = V \times W$ of e_2 in $P_R \setminus \bar{P}_r$, where V is a neighborhood $(S^* - S_2, \bar{u}_2, \bar{u}_3)$ in $C_0(\bar{\Omega}) \times C_0(\bar{\Omega}) \times C_0(\bar{\Omega})$, and W is a small neighborhood of (0) in $C_0(\bar{\Omega})$.

If $H(0, U) = U$ has a solution $U = (s, u_1, u_2, u_3) \in \partial Q$, which implies $u_2 \neq 0$, then $(s, u_2, u_3) = (S^* - S_2, \bar{u}_2, \bar{u}_3)$ by Theorem 2.3. If $u_1 = 0$, then $U = e_2$, but $e_2 \notin \partial Q$. Therefore $u_1 > 0$ and thus we have a contradiction to $\lambda'_1(-m_1f_1(S_2) + \gamma\bar{u}_3) < 0$.

If there exists $t \in (0, 1]$ such that $H(t, U) = U$ has a solution $U = (s, u_1, u_2, u_3) \in \partial Q$, then $u_1 \neq 0$. Since once $u_1 \equiv 0$, then $U = e_2$ contradicting $U \in \partial Q$. Therefore $u_1 > 0$, and thus (s, tu_1, u_2, u_3) is a positive fixed point of A contradicting our assumption.

By the homotopy invariance of Leray-Schauder degree

$$\text{index}(e_2, A) = \text{index}(e_2, H(1, \cdot)) = \text{index}(e_2, H(0, \cdot)).$$

Now consider the boundary value problem with parameter $t \in [0, 1]$

$$\begin{aligned}
 d_0 \Delta s + m_2 u_2 f_2(S^* - s) &= 0, \quad x \in \Omega, \\
 d_1 \Delta u_1 + m_1 u_1 f_1(tS_2 + (1-t)(S^* - s)) - \gamma u_1 u_3 &= 0, \\
 d_2 \Delta u_2 + m_2(1-k)u_2 f_2(S^* - s) &= 0, \\
 d_3 \Delta u_3 + m_2 k u_2 f_2(S^* - s) &= 0, \\
 \frac{\partial s}{\partial n} + b(x)s &= 0, \quad x \in \partial\Omega, \\
 \frac{\partial u_i}{\partial n} + b(x)u_i &= 0 \quad (i = 1, 2, 3).
 \end{aligned} \tag{3.6}$$

In fixed point form, system (3.6) becomes $G(t, U) = U$. If $G(t, U) = U$ for some $t \in [0, 1]$ and $U = (s, u_1, u_2, u_3) \in \partial Q$, then obviously $(s, u_2, u_3) = (S^* - S_2, \bar{u}_2, \bar{u}_3)$, and so $u_1 \equiv 0$ by $\lambda'_1(-m_1 f_2(S_1) + \gamma \bar{u}_3) < 0$. Thus $U = e_2$ contradicting $e_2 \notin \partial Q$. Again, by the homotopy invariance of Leray-Schauder degree,

$$\text{index}(e_2, A) = \text{index}(e_2, H(0, \cdot)) = \text{index}(e_2, G(0, \cdot)) = \text{index}(e_2, G(1, \cdot)).$$

Next, consider the boundary value problem with parameter $t \in [0, 1]$

$$\begin{aligned}
 d_0 \Delta s + m_2 u_2 f_2(S^* - s) &= 0, \quad x \in \Omega, \\
 d_1 \Delta u_1 + m_1 u_1 f_1(S_2) - t\gamma u_1 u_3 &= 0, \\
 d_2 \Delta u_2 + m_2(1-k)u_2 f_2(S^* - s) &= 0, \\
 d_3 \Delta u_3 + m_2 k u_2 f_2(S^* - s) &= 0, \\
 \frac{\partial s}{\partial n} + b(x)s &= 0, \quad x \in \partial\Omega, \\
 \frac{\partial u_i}{\partial n} + b(x)u_i &= 0 \quad (i = 1, 2, 3).
 \end{aligned} \tag{3.7}$$

In fixed point form, system (3.7) becomes $K(t, U) = U$. If $K(t, U) = U$ for some $t \in [0, 1]$ and $U = (s, u_1, u_2, u_3) \in \partial Q$, then obviously $(s, u_2, u_3) = (S^* - S_2, \bar{u}_2, \bar{u}_3)$, and so $u_1 \equiv 0$ by $\lambda'_1(-m_1 f_1(S_2) + \gamma \bar{u}_3) < 0$. Thus $U = e_2$ contradicting $e_2 \notin \partial Q$. Again, by the homotopy invariance of Leray-Schauder degree,

$$\text{index}(e_2, A) = \text{index}(e_2, G(1, \cdot)) = \text{index}(e_2, K(1, \cdot)) = \text{index}(e_2, K(0, \cdot)).$$

However, $K(0, \cdot)$ can be view as the product of two maps K_1 on V and K_2 on W , which are associated with the boundary value problems

$$\begin{aligned}
 d_0 \Delta s + m_2 u_2 f_2(S^* - s) &= 0, \\
 d_2 \Delta u_2 + m_2(1-k)u_2 f_2(S^* - s) &= 0, \\
 d_3 \Delta u_3 + m_2 k u_2 f_2(S^* - s) &= 0, \\
 d_1 \Delta u_1 + m_1 u_1 f_1(S_2) &= 0,
 \end{aligned}$$

with homogeneous boundary conditions, respectively.

Now, by the uniqueness of $(S^* - S_2, \bar{u}_2, \bar{u}_3)$ and $m_2 > \lambda_2/(1-k)$,

$$\text{deg}(K_1, V, 0) = \text{index}((S^* - S_2, \bar{u}_2, \bar{u}_3), K_1) = 1.$$

Furthermore from $\lambda'_1(-m_1 f_1(S_2)) < \lambda'_1(-m_1 f_1(S_2) + \gamma \bar{u}_3) < 0$, it follows that

$$\text{deg}(K_2, W, 0) = \text{index}(0, K_2) = 0.$$

In fact, if $\lambda > 0$ is an eigenvalue of $K_2'(0) = K_2$ corresponding to the eigenfunction $u_1 \in W$, then

$$d_1 \Delta u_1 + \frac{1}{\lambda} m_1 u_1 f_1(S_2) = 0.$$

By $\lambda_1'(-m_1 f_1(S_2) + \gamma \bar{u}_3) < 0$, $\lambda \neq 1$. Therefore there exist $\lambda > 1$ and the corresponding eigenfunction $u_1 > 0$ such that

$$d_1 \Delta u_1 + \frac{1}{\lambda} m_1 u_1 f_1(S_2) = 0.$$

It follows from Lemma 3.2 that $\text{index}(0, K_2) = 0$.

By the product theorem of Leray-Schauder degree [14],

$$\text{index}(e_2, A) = \text{deg}(K_1, V, 0) \text{deg}(K_2, W, 0) = 0.$$

□

Therefore, by the additivity property of the fixed point index and above Lemmas, we have the following result.

Theorem 3.7. *Assume that $\lambda_1'(-m_1 f_1(S_2) + \gamma \bar{u}_3) < 0$ and $\lambda_2'(-m_2(1-k)f_2(S_1)) < 0$, then system (1.2)–(1.3) admits at least one positive solution.*

We note that $\lambda_1'(-m_1 f_1(S_2) + \gamma \bar{u}_3) < 0$ and $\lambda_2'(-m_2(1-k)f_2(S_1)) < 0$ implies $\lambda_1'(-m_1 f_1(S^*)) < 0$ and $\lambda_2'(-m_2(1-k)f_2(S^*)) < 0$ respectively, since $S_1, S_2 \leq S^*$ and the monotonicity of function f_i .

For the other case, we present the following results, whose proofs are very similar to that of Lemmas 3.5, 3.6 and Theorem 3.7.

Lemma 3.8. *Assume that $\lambda_2'(-m_2(1-k)f_2(S_1)) > 0$, then $\text{index}(e_1, A) = 1$.*

Lemma 3.9. *Assume that $\lambda_1'(-m_1 f_1(S_2) + \gamma \bar{u}_3) > 0$, then $\text{index}(e_2, A) = 1$.*

Theorem 3.10. *Assume that $\lambda_1'(-m_1 f_1(S_2) + \gamma \bar{u}_3) > 0$ and that*

$$\lambda_2'(-m_2(1-k)f_2(S_1)) > 0,$$

then (1.2)–(1.3) admits at least one positive solution.

Remark 3.11. (1) If (s, u_1, u_2, u_3) is the positive solution of (1.2)–(1.3), then $u_i \leq \bar{u}_i (i = 1, 2, 3)$ by the maximum principle.

(2) Our results implies that the existence of positive steady states of (1.2)–(1.3) if the semi-trivial nonnegative solutions are stable or unstable simultaneously.

(3) System (1.2)–(1.3) with $\gamma = 0$ is fundamentally more tractable than the general case and rather complete analysis can be done, due to the existence of a “conservation principle” which allows the reduction of system (1.1)–(1.2) to the competition system. In fact, if $\gamma = 0$, then $d_0 S + d_1 u_1 + d_2 u_2 + d_3 u_3 = d_0 S^*$, and thus system (1.2)–(1.3) reduces to the competition system

$$\begin{aligned} d_1 \Delta u_1 + m_1 u_1 f_1\left(S^* - \frac{d_1 u_1 + \frac{d_2}{1-k} u_2}{d_0}\right) &= 0, \quad x \in \Omega, \\ d_2 \Delta u_2 + m_2(1-k) u_2 f_2\left(S^* - \frac{d_1 u_1 + \frac{d_2}{1-k} u_2}{d_0}\right) &= 0, \\ \frac{\partial u_i}{\partial n} + b(x) u_i &= 0 \quad (i = 1, 2), \quad x \in \partial\Omega, \end{aligned} \tag{3.8}$$

noticing $d_2ku_2 = d_3(1-k)u_3$. By the above results, (3.8) has at least one positive coexistence solution (u_1, u_2) if $\lambda'_1(-m_1f_1(S_2)) \cdot \lambda'_2(-m_2(1-k)f_2(S_1)) > 0$. Now we assume that $\lambda'_1(-m_1f_1(S_2)) < 0$ and $\lambda'_2(-m_2(1-k)f_2(S_1)) > 0$.

We define u_1^n to be the unique nonnegative nontrivial solution of

$$d_1\Delta u_1 + m_1u_1f_1\left(S^* - \frac{d_1u_1 + \frac{d_2}{1-k}u_2^{n-1}}{d_0}\right) = 0$$

and u_2^n to be the unique nonnegative nontrivial solution of

$$d_2\Delta u_2 + m_2(1-k)u_2f_2\left(S^* - \frac{d_1u_1^n + \frac{d_2}{1-k}u_2}{d_0}\right) = 0,$$

with $u_2^0 = \bar{u}_2$, respectively. Thus $u_1^1 < u_1^2 < \dots < u_1^n < \dots$ and $u_2^1 > u_2^2 > \dots > u_2^n > \dots$. By arguments in [3], we can conclude that if $\lambda'_1(-m_1f_1(S_2)) < 0$ and $\lambda'_2(-m_2(1-k)f_2(S_1)) > 0$, then system (3.8) has the coexistence solutions if and only if $\lambda'_2(-m_2(1-k)f_2(S^* - \frac{d_1u_1^n}{d_0})) < 0$, for all $n \in N$. A similar result holds for $\lambda'_1(-m_1f_1(S_2)) > 0$ and $\lambda'_2(-m_2(1-k)f_2(S_1)) < 0$.

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