On a Mathematical Model Arising from Competition of Phytoplankton Species for a Single Nutrient with Internal Storage: Steady State Analysis

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Abstract

In this paper we construct a mathematical model of two microbial populations competing for a single-limited nutrient with internal storage in an unstirred chemostat. First we establish the existence and uniqueness of steady-state solutions for the single population. The conditions for the coexistence of steady states are determined. Techniques include the maximum principle, theory of bifurcation and degree theory in cones.

Keywords. Chemostat; Maximum principle; Global bifurcation; Coexistence; Degree theory.

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1 Introduction and the Model

The chemostat is a piece of laboratory apparatus which plays an important role in microbiology. It is used as a model of a simple lake, in the commercial production of microorganisms and as a model for waste water treatment. The basic chemostat consists of three vessels. The first vessel, the feed bottle, contains all of the needed nutrient for growth in abundance except one which is limiting. The

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nutrient is pumped at a constant rate into the second, called the culture vessel or bio-reactor. The culture vessel whose volume is constant contains microorganisms which compete for nutrient. The content of the culture vessel are pumped at the same constant rate into the third vessel, called the overflow vessel. It is assumed that the culture vessel is well mixed and that all other significant parameters (e.g. pH, temperature, etc.) affecting growth are kept constant. Since the output is continuous, the chemostat is often referred to as a "continuous culture" in contrast with the more common "batch culture."

Let the constants $S^{(0)}$ and D be the input concentration and dilution rate respectively. If $S(t)$ is the nutrient concentration at time t and $u_1(t)$, $u_2(t)$ are the concentration of competing populations, the model is given below [17]

$$\begin{cases} \frac{dS}{dt} = (S^{(0)} - S)D - \frac{1}{y_1} f_1(S)u_1 - \frac{1}{y_2} f_2(S)u_2, & \\ \frac{du_i}{dt} = (f_i(S) - D)u_i, & i = 1, 2, \\ S(0) > 0,\ u_i(0) > 0,\ f_i(S) = \frac{m_i S}{k_i + S}, & i = 1, 2, \end{cases} \tag{1.1}$$

where m_i, k_i, y_i are the maximal growth rate, the Michaelis-Menten(or half saturation) constant and yield constant of i-th population respectively. The mathematical analysis [15, 17] shows the competitive exclusion principle holds, i.e., only one of the populations u_i survives.

In phytoplankton ecology, it has long been known that the yield constant y_i is not a fixed constant. It can vary depending on the growth rate of i-th population. This led Droop [4] to formulate the following internal storage model:

$$\begin{cases} \frac{dS}{dt} = (S^{(0)} - S)D - f_1(S, Q_1)u_1 - f_2(S, Q_2)u_2, & \\ \frac{du_i}{dt} = (\mu_i(Q_i) - D)u_i, & i = 1, 2, \\ \frac{dQ_i}{dt} = f_i(S, Q_i) - \mu_i(Q_i)Q_i, & i = 1, 2 \\ S(0) \geq 0,\ u_i(0) \geq 0,\ Q_i(0) \geq Q_{\min,i}, & i = 1, 2. \end{cases} \tag{1.2}$$

For i=1,2, $Q_i(t)$ represents the average amount of stored nutrient per cell of i-th population at time t, $\mu_i(Q_i)$ is the growth rate of species i as a function of cell quota Q_i, $f_i(S, Q_i)$ is the per capital nutrient uptake rate, per cell of species i as a function of nutrient concentration S and cell quota Q_i, $Q_{\min,i}$ denotes the threshold cell quota below which no growth of species i occurs.

The growth rate $\mu_i(Q_i)$ takes the forms [1, 2, 4]:

$$\begin{aligned} \mu_i(Q_i) &= \mu_{i\infty}\left(1 - \frac{Q_{\min,i}}{Q_i}\right), \\ \mu_i(Q_i) &= \mu_{i\infty}\frac{(Q_i - Q_{\min,i})_+}{K_i + (Q_i - Q_{\min,i})_+}, \end{aligned} \tag{1.3}$$

where $(Q_i - Q_{\min,i})_+$ is the positive part of $(Q_i - Q_{\min,i})$ and $\mu_{i\infty}$ is the maximal growth rate of the species.

According to Grover [13], the uptake rate $f_i(S, Q_i)$ takes the form:

$$\begin{aligned} f_i(S, Q_i) &= \rho_i(Q_i)\frac{S}{k_i + S}, \\ \rho_i(Q_i) &= \rho^{\text{high}}_{\max,i} - (\rho^{\text{high}}_{\max,i} - \rho^{\text{low}}_{\max,i})\frac{Q_i - Q_{\min,i}}{Q_{\max,i} - Q_{\min,i}}, \end{aligned} \tag{1.4}$$

where $Q_{\min,i} \le Q_i \le Q_{\max,i}$. Cunningham and Nisbet [1, 2] took $\rho_i(Q_i)$ to be a constant.

Motivated by these examples, we assume that $\mu_i(Q_i)$ is defined and continuously differentiable for $Q_i \ge Q_{\min,i} > 0$ and satisfies

(H1) $\quad \mu_i(Q_i) \ge 0,\ \mu_i'(Q_i) > 0$ and is continuous for $Q_i \ge Q_{\min,i},\ \mu_i(Q_{\min,i}) = 0.$

We assume that $f_i(S, Q_i)$ is continuously differentiable for $S > 0$ and $Q_i \ge Q_{\min,i}$ and satisfies

(H2) $$f_i(0, Q_i) = 0,\ \frac{\partial f_i}{\partial S} > 0,\ \frac{\partial f_i}{\partial Q_i} \le 0.$$

In particular, $f_i(S, Q_i) > 0$ when $S > 0$.

Let $U_i = u_i Q_i$ be the total amount of stored nutrient at time t for the species i, $i = 1, 2$. Then we have the conservation property:

$$S + U_1 + U_2 = S^{(0)} + O(e^{-Dt}) \text{ as } t \to \infty. \tag{1.5}$$

In [24, 25], Smith and Waltman use the method of monotone dynamical system to prove the competitive exclusion principle also holds for internal storage model.

Since coexistence of competing species is obvious in the nature, a candidate for an explanation is to remove the "well-mixed" hypothesis. In [18] a system of reaction-diffusion equation is constructed as follows:

$$\begin{cases} S_t = dS_{xx} - \frac{1}{y_1} f_1(S)u_1 - \frac{1}{y_2} f_2(S)u_2, & x \in (0,1),\ t > 0, \\ (u_i)_t = d(u_i)_{xx} + f_i(S)u_i, & x \in (0,1),\ t > 0,\ i = 1,2, \\ f_i(S) = \frac{m_i S}{k_i + S}, & i = 1,2, \end{cases} \tag{1.6}$$

with boundary conditions

$$\begin{cases} S_x(0,t) = -S^{(0)},\ S_x(1,t) + \gamma S(1,t) = 0, & t > 0, \\ (u_i)_x(0,t) = 0,\ (u_i)_x(1,t) + \gamma u_i(1,t) = 0, & t > 0,\ i = 1,2, \end{cases} \tag{1.7}$$

and initial conditions

$$\begin{cases} S(x,0) = S^0(x) \geq 0, \\ u_i(x,0) = u_i^0(x) \geq 0,\ u_i^0(x) \not\equiv 0, \quad i = 1,2. \end{cases} \tag{1.8}$$

In (1.6) we assume that nutrient S and microbial species u_i has the same diffusion coefficient d. The constant γ in (1.7) represents the washout rate. The constants $m_i,\ y_i,\ k_i,\ i = 1,2$ and $S^{(0)}$ have the same biological meaning as those in (1.1). The authors in [18] use the general persistence theorem to show that if we remove the "well-mixed" hypothesis, it can lead to coexistence of competing populations in contrast to the competitive exclusion that holds in the basic model (1.1).

In this paper, we assume that the species u_1 and u_2 diffuse while the internal storage Q_1 and Q_2 depend only on the uptake rate and consumption rate as in the well-mixed case. Thus, we consider the following system of an unstirred chemostat model:

$$\begin{cases} S_t = DS_{xx} - f_1(S,Q_1)u_1 - f_2(S,Q_2)u_2, & x \in (0,1),\ t > 0, \\ (u_i)_t = d_i(u_i)_{xx} + \mu_i(Q_i)u_i, & x \in (0,1),\ t > 0,\ i = 1,2, \\ (Q_i)_t = f_i(S,Q_i) - \mu_i(Q_i)Q_i, & x \in (0,1),\ t > 0,\ i = 1,2, \end{cases} \tag{1.9}$$

with boundary conditions

$$\begin{cases} S_x(0,t) = -S^{(0)},\ S_x(1,t) + \gamma S(1,t) = 0, & t > 0, \\ (u_i)_x(0,t) = 0,\ (u_i)_x(1,t) + \gamma u_i(1,t) = 0, & t > 0,\ i = 1,2, \end{cases} \tag{1.10}$$

and initial conditions

$$\begin{cases} S(x,0) = S^0(x) \geq 0, \\ u_i(x,0) = u_i^0(x) \geq 0,\ u_i^0(x) \not\equiv 0, \quad i = 1,2, \\ Q_i(x,0) = Q_i^0(x) \geq Q_{\mathrm{min,i}}, \quad i = 1,2, \end{cases} \tag{1.11}$$

where $S(x,t)$ represents a nutrient density measured in units of mass per unit length; $u_1(x,t)$ and $u_2(x,t)$ are the number of cells per unit length. In (1.9)-(1.11) we assume that nutrient S and microbial species u_1 and u_2 have the different diffusion coefficients D, d_1 and d_2 respectively. We note that $Q_i(x,t)$ denotes the instored nutrient per cell per unit length. The initial conditions $Q_i^0(x)$ satisfy $Q_i^0(x) \geq Q_{\mathrm{min,i}}$, for $i = 1,2$. The nutrient uptake rates $f_i(S, Q_i)$ satisfy (H2) and the growth rate $\mu_i(Q_i)$ satisfies (H1). The other parameters have the same biological meaning as those in (1.6)-(1.8). The dynamics of (1.9)-(1.11) is not easy to obtain, thus we will concentrate on the existence of positive steady state solutions.

The rests of this paper are organized as follows. In section two, we state some important lemmas which are the main tools in this paper. In section three, we use the bifurcation theorem to establish the results about the growth and extinction of a single population. In section four, the coexistence steady state solutions will be shown by calculation of fixed point indices. Section five is the discussion section.

2 Preliminaries

Bifurcation phenomena occur frequently in solving nonlinear equations. Here we consider an equation

$$F(\lambda, u) = 0, \tag{2.1}$$

where $F : R \times X \to Y$ is a nonlinear differentiable map and X, Y are Banach spaces. From the implicit function theorem, a necessary condition for bifurcation at (λ_0, u_0) is that

$$F_u(\lambda_0, u_0) \text{ is not invertible.} \tag{2.2}$$

When (2.2) holds, we call (λ_0, u_0) a degenerate solution of $F(\lambda, u) = 0$. If there is a branch of trivial solutions $u = u_0$ for all λ, then nontrivial solutions can bifurcate from the trivial branch at a degenerate solution. In the following we state the theorem of bifurcation from a simple eigenvalue by Crandall and Rabinowitz [3].

Let (F1) and (F2) hold where

(F1) $\dim N(F_u(\lambda_0, u_0)) = \operatorname{codim} R(F_u(\lambda_0, u_0)) = 1$, and $N(F_u(\lambda_0, u_0)) = span\{w_0\}$,

where $N(F_u)$ and $R(F_u)$ are the null space and the range of linear operator F_u, and

(F2) The partial derivative $F_{\lambda u}$ is continuous and $F_{\lambda u}(\lambda_0, u_0)[w_0] \notin R(F_u(\lambda_0, u_0))$.

Lemma 2.1. *[3, 23] Let U be a neighborhood of (λ_0, u_0) in $R \times X$, and let $F : U \to Y$ be a twice continuously differentiable mapping. Assume that $F(\lambda, u_0) = 0$ for $(\lambda, u_0) \in U$. At (λ_0, u_0), F satisfies (F1) and (F2). Let Z be any complement of $span\{w_0\}$ in X. Then the solution set of (2.1) near (λ_0, u_0) consists precisely of the curves $u = u_0$ and $\{(\lambda(s), u(s)) : s \in I = (-\epsilon, \epsilon)\}$, where $\lambda : I \to R$, $z : I \to Z$ are C^1 functions such that $u(s) = u_0 + sw_0 + sz(s)$, $\lambda(0) = \lambda_0$, $z(0) = 0$ and*

$$\lambda'(0) = -\frac{\langle F_{uu}(\lambda_0, u_0)[w_0][w_0], l\rangle}{2\langle F_{\lambda u}(\lambda_0, u_0)[w_0], l\rangle}, \tag{2.3}$$

where l is a linear functional on Y satisfying $N(l) = R(F_u(\lambda_0, u_0))$.

In order to discuss the existence of positive steady-state solution for (1.9)-(1.11), we need the following well-known results.

Lemma 2.2. *[12, 19] Let $q(x) \in C(\bar{\Omega})$, $q(x) > 0$ on $\bar{\Omega}$ in the eigenvalue problem*

$$\begin{cases} \triangle\varphi + \lambda q(x)\varphi = 0, & x \in \Omega, \\ \frac{\partial\varphi}{\partial n} + \gamma(x)\varphi = 0, & x \in \partial\Omega. \end{cases}$$

Then all the eigenvalues of the above eigenvalue problem can be listed in order

$$0 < \lambda_1(q(x)) < \lambda_2(q(x)) \leq ... \to \infty$$

with the corresponding eigenfunction φ_1, φ_2,..., where φ_1 can be chosen to be positive on $\bar{\Omega}$, that is $\varphi_1 > 0$ on $\bar{\Omega}$ and the principal eigenvalue $\lambda_1(q(x))$ is simple. Moreover, the comparison principle holds: $\lambda_j(q_1(x)) \leq \lambda_j(q_2(x))$ for $j \geq 1$ if $q_1(x) \geq q_2(x)$ on $\bar{\Omega}$ and the strict inequality holds if $q_1(x) \not\equiv q_2(x)$.

Lemma 2.3. *[22] Let $q(x) \in C(\bar{\Omega})$, $\eta_1(q(x))$ be the principal eigenvalue of eigenvalue problem*

$$\begin{cases} -d\triangle\varphi + q(x)\varphi = \eta\varphi, & x \in \Omega, \\ \frac{\partial\varphi}{\partial n} + \gamma(x)\varphi = 0, & x \in \partial\Omega. \end{cases}$$

Then $\eta_1(q(x))$ depends continuously on $q(x)$ and that $q_1(x) \le q_2(x)$, $q_1 \not\equiv q_2$ imply $\eta_1(q_1(x)) < \eta_1(q_2(x))$.

Lemma 2.4. *[26] Let $q(x) \in C(\bar{\Omega})$, $q(x) + p > 0$ on $\bar{\Omega}$ with $p > 0$, and η_1 be the principal eigenvalue of eigenvalue problem*

$$\begin{cases} -d\triangle\varphi - q(x)\varphi = \eta\varphi, & x \in \Omega, \\ \frac{\partial\varphi}{\partial n} + \gamma(x)\varphi = 0, & x \in \partial\Omega. \end{cases}$$

If $\eta_1 > 0$(or $\eta_1 < 0$), then the eigenvalue problem with eigenvalue α

$$\begin{cases} -d\triangle\varphi + p\varphi = \alpha(q(x) + p)\varphi, & x \in \Omega, \\ \frac{\partial\varphi}{\partial n} + \gamma(x)\varphi = 0, & x \in \partial\Omega \end{cases}$$

has no eigenvalues smaller than or equal to 1 (or has eigenvalues smaller than 1).

The following lemmas can be found in [5, 6] and are special cases of Theorem2.1 and 2.2 in [21]:

Lemma 2.5. *[5, 6, 21] 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) $\mathrm{index}_W(F, \theta) = 1$ *if $r(A_0) < 1$ where $r(A_0)$ is the spectral radius of A_0;*

(ii) $\mathrm{index}_W(F, \theta) = 0$ *if A_0 has no nonzero fixed point in W and A_0 has eigenvalue greater than 1*

Lemma 2.6. *[7] Let E_1 and E_2 be ordered Banach spaces with positive cones W_1 and W_2, respectively, $E = E_1 \oplus E_2$ and $W = W_1 \oplus W_2$. Let D be an open set in W containing 0 and $A_i : \bar{D} \to W_i$ be completely continuous operators, $i = 1, 2$. Denote by (u, v) a general element in W with $u \in W_1$ and $v \in W_2$ and $A(u, v) =$*

$(A_1(u,v), A_2(u,v))$, $W_2(\varepsilon) = \{v \in W_2 \mid \| v \|_{E_2} < \varepsilon\}$. *Suppose* $U \subset W_1 \cap D$ *is relatively open and bounded, and* $A_1(u,0) \neq u$ *for* $u \in \partial U$, $A_2(u,0) = 0$ *for* $u \in \bar{U}$. *Suppose* $A_2 : D \to W_2$ *extends to a continuously differentiable mapping of a neighborhood of* D *into* E_2, $W_2 - W_2$ *is dense in* E_2 *and* $G = \{u \in U \mid u = A_1(u,0)\}$. *Then the following conclusions are true:*

(i) $\deg_W(I - A, U \times W_2(\varepsilon), 0) = 0$ *for* $\varepsilon > 0$ *is small if for any* $u \in G$, *the spectral radius* $r(A_2'(u,0) \mid_{W_2}) > 1$ *and 1 is not an eigenvalue of* $A_2'(u,0) \mid_{W_2}$ *corresponding to a positive eigenvector;*

(ii) $\deg_W(I - A, U \times W_2(\varepsilon), 0) = \deg_{W_1}(I - A_1 \mid_{W_1}, U, 0)$ *for* $\varepsilon > 0$ *small if for any* $u \in G$, *the spectral radius* $r(A_2'(u,0) \mid_{W_2}) < 1$.

3 Steady State Solution for Single Population Model

Consider the single population model corresponding to (1.9)-(1.11)

$$\begin{cases} S_t = DS_{xx} - f(S,Q)u, & x \in (0,1),\ t > 0, \\ u_t = du_{xx} + \mu(Q)u, & x \in (0,1),\ t > 0, \\ Q_t = f(S,Q) - \mu(Q)Q, & x \in (0,1),\ t > 0, \end{cases} \tag{3.1}$$

with boundary conditions

$$\begin{cases} S_x(0,t) = -S^{(0)},\ S_x(1,t) + \gamma S(1,t) = 0, & t > 0, \\ u_x(0,t) = 0,\ u_x(1,t) + \gamma u(1,t) = 0, & t > 0, \end{cases} \tag{3.2}$$

and initial conditions

$$\begin{cases} S(x,0) = S^0(x) \geq 0, \\ u(x,0) = u^0(x) \geq 0,\ u^0(x) \not\equiv 0, \\ Q(x,0) = Q^0(x) \geq Q_{\min}. \end{cases} \tag{3.3}$$

The steady state solutions for (3.1)-(3.3) satisfy the following system elliptic equations

$$\begin{cases} DS_{xx} - f(S,Q)u = 0, & x \in (0,1), \\ du_{xx} + \mu(Q)u = 0, & x \in (0,1), \\ f(S,Q) - \mu(Q)Q = 0, & x \in (0,1), \end{cases} \tag{3.4}$$

with boundary conditions

$$\begin{cases} S_x(0) = -S^{(0)},\ S_x(1) + \gamma S(1) = 0, \\ u_x(0) = 0,\ u_x(1) + \gamma u(1) = 0. \end{cases} \tag{3.5}$$

From (H1) and (H2), we assume that $Q(S)$ is the unique solution of

$$f(S,Q) - \mu(Q)Q = 0 \text{ provided that } S > 0. \tag{3.6}$$

Then the system (3.4)-(3.5) becomes

$$\begin{cases} DS_{xx} - f(S,Q(S))u = 0, & x \in (0,1), \\ du_{xx} + \mu(Q(S))u = 0, & x \in (0,1), \end{cases} \tag{3.7}$$

with boundary conditions (3.5). We note that $S(x) = z(x)$, $u = 0$ is the trivial solution of (3.7), where $z(x) = S^{(0)}(\frac{1+\gamma}{\gamma} - x)$.

Remark 3.1. *Differentiate both sides of the equation* (3.6) *with respect to* S*, it follows that*

$$[\frac{\partial f}{\partial S}(S,Q(S)) + \frac{\partial f}{\partial Q}(S,Q(S))\frac{dQ(S)}{dS}] - [\mu'(Q(S))\frac{dQ(S)}{dS}Q(S) + \mu(Q(S))\frac{dQ(S)}{dS}] = 0,$$

that is,

$$\frac{dQ(S)}{dS} = \frac{\frac{\partial f}{\partial S}(S,Q(S))}{\mu'(Q(S))Q(S) + \mu(Q(S)) - \frac{\partial f}{\partial Q}(S,Q(S))}. \tag{3.8}$$

From the equality

$$\frac{d}{dS}f(S,Q(S)) = \frac{\partial f}{\partial S}(S,Q(S)) + \frac{\partial f}{\partial Q}(S,Q(S))\frac{dQ(S)}{dS}$$

and (3.8)*, it follows that*

$$\frac{d}{dS}f(S,Q(S)) = \frac{\partial f}{\partial S}(S,Q(S)) + \frac{\partial f}{\partial Q}(S,Q(S))\frac{\frac{\partial f}{\partial S}(S,Q(S))}{\mu'(Q(S))Q(S)+\mu(Q(S))-\frac{\partial f}{\partial Q}(S,Q(S))}$$
$$= \frac{\partial f}{\partial S}(S,Q(S))\left[\frac{\mu'(Q(S))Q(S)+\mu(Q(S))}{\mu'(Q(S))Q(S)+\mu(Q(S))-\frac{\partial f}{\partial Q}(S,Q(S))}\right]. \tag{3.9}$$

From (H1), (H2), (3.8) *and* (3.9)*, we conclude that*

$$\frac{dQ(S)}{dS} > 0, \ \frac{d}{dS}\mu(Q(S)) > 0, \ \frac{d}{dS}f(S,Q(S)) > 0. \tag{3.10}$$

Thus the functions $Q(S)$, $\mu(Q(S))$ and $f(S,Q(S))$ are increasing in S.

Since only nonnegative solution $S(x)$ and $u(x)$ are meaningful and in order to give a priori estimate for (3.7), we need to extend the functions $f(S,Q)$, $\mu(Q)$ in a natural way as follows

$$\tilde{f}(S,Q) = \begin{cases} f(S,Q) & \text{for } S \geq 0,\ Q \geq Q_{\min}, \\ -f(\mid S \mid, Q) & \text{for } S < 0,\ Q \geq Q_{\min}, \\ f(S,Q_{\min}) & \text{for } S > 0,\ Q < Q_{\min}, \\ -f(\mid S \mid, Q_{\min}) & \text{for } S < 0,\ Q < Q_{\min}, \end{cases} \tag{3.11}$$

and

$$\tilde{\mu}(Q) = \begin{cases} \mu(Q) & \text{for } Q \geq Q_{\min}, \\ \mu'(Q_{\min})(Q - Q_{\min}) & \text{for } Q < Q_{\min}. \end{cases} \tag{3.12}$$

It is easy to see that $\tilde{\mu}'(Q) > 0$ for all Q. We will denote $\tilde{f}(S,Q)$ and $\tilde{\mu}(Q)$ by $f(S,Q)$ and $\mu(Q)$ respectively for the sake of convenience.

We will see that $\mu(Q(z(x))) > 0$ on [0,1] by Lemma 3.1. From Lemma 2.2, we denote $\lambda_1 > 0$ to be the principal(least) eigenvalue of the problem

$$\begin{cases} \psi_1''(x) + \lambda_1 \mu(Q(z(x)))\psi_1(x) = 0, & x \in (0,1), \\ \psi_1'(0) = \psi_1'(1) + \gamma\psi_1(1) = 0, \end{cases} \tag{3.13}$$

with the corresponding positive eigenfunction $\psi_1(x)$ uniquely determined by the normalization $\max_{[0,1]}\psi_1(x) = 1$. Some simple properties for non-negative solutions of (3.7) are given as follows.

Lemma 3.1. *Suppose (S, u) is a non-negative solution of* (3.7) *with $S(x) \not\equiv 0$ and $u(x) \not\equiv 0$. Then*

(1) $u(x) > 0,\ 0 < S(x) < z(x)$ on [0,1];

(2) $Q(S) > Q_{\min}$ on [0,1], where $Q(S)$ satisfies (3.6);

(3) $0 < d < \frac{1}{\lambda_1}$.

Proof. Firstly, we prove the positivity for u. Let $c(x) := \mu(Q(S(x)))$. We rewrite $c(x) = c^+(x) - c^-(x)$, where $c^+(x)$, $c^-(x)$ are the positive and negative part of $c(x)$ respectively. Hence, the second equation of (3.7) becomes

$$du'' - c^-(x)u = -c^+(x)u \le 0 \text{ for all } x\ \in (0,1).$$

Suppose that $u(x_0) = 0$, for some $x_0 \in [0,1]$. If $x_0 \in (0,1)$, by the strong maximum principle, one has that $u \equiv 0$, a contradiction. If $x_0 = 0$, by the Hopf boundary lemma, one has $u'(0) > 0$, this contradicts (3.5). Similarly, $x_0 = 1$ is impossible. Thus, $u > 0$ on [0,1].

We claim that $S > 0$ on $[0,1]$. The first equation of (3.7) can be rewritten as

$$DS'' - [u \int_0^1 \frac{df(\tau S, Q(\tau S))}{d(\tau S)} d\tau] S = 0 \le 0, \quad x \in (0,1).$$

Suppose that $\inf\limits_{0 \le x \le 1} S(x) := S(x_0) < 0$, for some $x_0 \in [0,1]$. If $x_0 \in (0,1)$, by the strong maximum principle, one has that $S(x) \equiv S(x_0) < 0$, a contradiction. If $x_0 = 0$, by the Hopf boundary lemma, one has $S'(0) > 0$, this contradicts (3.5). Similarly, $x_0 = 1$ is impossible. Thus, $S > 0$ on [0,1].

Now we are in a position to show that $S \le z$ on [0,1]. Let $y(x) = z(x) - S(x)$. Then

$$\begin{cases} Dy'' + f(z(x) - y(x), Q(z(x) - y(x)))u = 0, & x \in (0,1), \\ y'(0) = 0,\ y'(1) + \gamma y(1) = 0, \end{cases} \tag{3.14}$$

Assume $\inf\limits_{0 \le x \le 1} y(x) = y(x_0) < 0$, for some $x_0 \in [0,1]$. If $x_0 \in (0,1)$, one has $y''(x_0) \ge 0$. On the other hand, by (3.14)

$$Dy''(x_0) = -f(z(x_0) - y(x_0), Q(z(x_0) - y(x_0)))u(x_0) < 0,$$

which leads to a contradiction. If $x_0 = 0$, one has that $y(0) < 0$, $y'(0) = 0$, $y''(0) < 0$, and $y(0) = \inf\limits_{0 \le x \le 1} y(x)$, which is impossible. If $x_0 = 1$, one has $y'(1) \le 0$, and it follows that $y'(1) + \gamma y(1) < 0$. This contradicts to the boundary condition $y'(1) + \gamma y(1) = 0$. Therefore, $S \leq z$ on [0,1].

Furthermore, $y(x) = z(x) - S(x) > 0$ on $[0, 1]$. In fact, from the following equality

$$\frac{\partial}{\partial \tau}(f(z(x) - \tau y, Q(z(x) - \tau y))) = \frac{\partial f}{\partial S}(z(x) - \tau y, Q(z(x) - \tau y))(-y)$$
$$+\frac{\partial f}{\partial Q}(z(x) - \tau y, Q(z(x) - \tau y))Q'(z(x) - \tau y)(-y), \tag{3.15}$$

one has that,

$$f(z(x) - y, Q(z(x) - y)) - f(z(x), Q(z(x))) = \int_0^1 \frac{\partial f}{\partial S}(z(x) - \tau y, Q(z(x) - \tau y))(-y)d\tau$$
$$+\int_0^1 \frac{\partial f}{\partial Q}(z(x) - \tau y, Q(z(x) - \tau y))Q'(z(x) - \tau y)(-y)d\tau. \tag{3.16}$$

Using (3.16), one shall rewrite (3.14) as

$$Dy'' - u[\int_0^1 \frac{\partial f}{\partial S}(z(x) - \tau y, Q(z(x) - \tau y))d\tau]y = -uf(z(x), Q(z(x)))$$
$$+u[\int_0^1 \frac{\partial f}{\partial Q}(z(x) - \tau y, Q(z(x) - \tau y))Q'(z(x) - \tau y)d\tau]y, \tag{3.17}$$

that is,

$$\begin{cases} Dy'' - u[\int_0^1 \frac{\partial f}{\partial S}(z(x) - \tau y, Q(z(x) - \tau y))d\tau]y \leq 0, \quad x \in (0, 1), \\ y'(0) = 0, \ y'(1) + \gamma y(1) = 0. \end{cases} \tag{3.18}$$

Suppose $y(\hat{x}) = 0$, for some $\hat{x} \in [0, 1]$. If $\hat{x} \in (0, 1)$, then by the strong maximum principle, one has that $y \equiv 0$, a contradiction. If $\hat{x} = 0$, by the Hopf boundary lemma, one has $y'(0) > 0$, this is a contradiction. Similarly, $\hat{x} = 1$ is impossible. Hence, $S < z$ on $[0, 1]$.

From (3.6), $\mu(Q(S))Q(S) = f(S, Q(S)) > 0$, hence $Q(S) > Q_{\min}$ on [0,1].

Suppose that $\frac{1}{d} \leq \lambda_1$, that is $d\lambda_1 \geq 1$. By the second equation in (3.7), we have that $-du'' + [-\mu(Q(S))]u = 0$. From part(1) of Lemma 3.1, $u > 0$ on $[0, 1]$. Thus, $\eta_1(-\mu(Q(S))) = 0$ by Lemma 2.3. Similarly, using (3.13), one has that

$\eta_1(-d\lambda_1\mu(Q(z(x)))) = 0$. Since $Q(S)$ is strictly increasing in S (by (3.10)) and $S(x) < z(x)$ on $[0, 1]$, it implies that

$$0 = \eta_1(-\mu(Q(S))) > \eta_1(-d\lambda_1\mu(Q(z(x)))) = 0,$$

which is a contradiction. Therefore, one must have $\frac{1}{d} > \lambda_1$. If $d = 0$, it follows from (3.7) that $u \equiv 0$ on $[0, 1]$, which is a contradiction. □

The proof of Theorem 3.1 relies on the following a priori estimates for (3.7).

Lemma 3.2. *Suppose that $D > 0$ is fixed and $[m, M]$ is any compact subinterval of $(0, \frac{1}{\lambda_1})$. For any $d \in [m, M] \subset (0, \frac{1}{\lambda_1})$, there exists a positive constant C depending on $[m, M]$ and independent of d such that any positive solution $\{(S(x), u(x))\}$ of (3.7) satisfies $\| S \|_\infty + \| u \|_\infty < C$.*

Proof. Suppose that the conclusion of Lemma 3.2 is not true. Then we can find a sequence $d_n \in [m, M] \subset (0, \frac{1}{\lambda_1})$ and a sequence of positive function pairs $\{(S_n, u_n)\}$ satisfying

$$\begin{cases} DS_n'' - f(S_n, Q(S_n))u_n = 0, & x \in (0, 1), \\ d_n u_n'' + \mu(Q(S_n))u_n = 0, & x \in (0, 1), \end{cases} \tag{3.19}$$

with boundary conditions (3.5) such that $\| S_n \|_\infty + \| u_n \|_\infty \to \infty$ as $n \to \infty$. One can use the similar arguments as in Lemma 3.1 to show that $S_n(x) < z(x)$ and $Q(S_n) > Q_{\min}$ on $[0, 1]$ and then it follows that $\| u_n \|_\infty \to \infty$ as $n \to \infty$. Denote $\hat{u}_n = \frac{u_n}{\|u_n\|_\infty}$. Then $\hat{u}_n$ satisfies $\| \hat{u}_n \|_\infty = 1$ and

$$\begin{cases} -\hat{u}_n'' = \frac{1}{d_n}\mu(Q(S_n))\hat{u}_n, \ x \in (0, 1), \\ \hat{u}_n'(0) = 0, \ \hat{u}_n'(1) + \gamma\hat{u}_n(1) = 0. \end{cases} \tag{3.20}$$

Therefore $\{\hat{u}_n''\}$ and $\{\hat{u}_n\}$ are both bounded sequence in $L^\infty([0, 1])$. By standard L^p theory of elliptic equations, $\{\hat{u}_n\}$ are bounded in $W^{2,p}([0, 1])$ for any $p > 1$, and hence, by the Sobolev imbedding theorem, it is precompact in $C^1([0, 1])$. By passing to a subsequence, we may assume that $\hat{u}_n \to \hat{u}$ in $C^1([0, 1])$.

Since $\{d_n\}$ is bounded above, we may assume that $d_n \to d_0$ and $d_0 \in [m, M] \subset (0, \frac{1}{\lambda_1})$. Since $\{\mu(Q(S_n))\}$ is a bounded sequence in $L^\infty([0, 1])$, by passing to a subsequence, we may assume that $\mu(Q(S_n)) \to g$ weakly in $L^2([0, 1])$ (see pp. 640

in [11]). We note that $0 \le g \le \mu(Q(z(x)))$ in [0,1] since each $\mu(Q(S_n))$ has this property. It is now easily seen that $\hat{u}$ is a weak solution of

$$\begin{cases} -\hat{u}'' = \frac{1}{d_0} g\hat{u}, \quad x \in (0,1), \\ \hat{u}'(0) = 0, \ \hat{u}'(1) + \gamma \hat{u}(1) = 0, \end{cases} \tag{3.21}$$

and $\hat{u} \ge 0$, $\| \hat{u} \|_\infty = 1$. Since $g\hat{u} \in L^\infty([0,1])$, we can apply the strong maximum principle for weak solutions (e.g. Theorem 8.19 in [14]) to conclude that $\hat{u} > 0$ on $[0,1]$.

Denote $\hat{v}_n = \frac{S_n}{\|u_n\|_\infty}$. From (3.5) and the first equation of (3.19), $\hat{v}_n$ satisfies

$$\begin{cases} D\hat{v}_n'' = f(S_n, Q(S_n))\hat{u}_n, \ x \in (0,1), \\ \hat{v}_n'(0) = h_n, \ \hat{v}_n'(1) + \gamma \hat{v}_n(1) = 0, \end{cases} \tag{3.22}$$

where $h_n = -\frac{S^{(0)}}{\|u_n\|_\infty}$ and $\{h_n\}$ satisfies $h_n \to 0$. Note that $\{\hat{v}_n''\}$ and $\{\hat{v}_n\}$ are both bounded sequence in $L^\infty([0,1])$. By standard L^p theory of elliptic equations, $\{\hat{v}_n\}$ are bounded in $W^{2,p}([0,1])$ for any $p > 1$, and hence, by the Sobolev imbedding theorem, it is precompact in $C^1([0,1])$. By passing to a subsequence, we may assume that $\hat{v}_n \to \hat{v}$ in $C^1([0,1])$.

Since $\{f(S_n, Q(S_n))\}$ is a bounded sequence in $L^\infty([0,1])$, by passing to a subsequence, we may assume that $f(S_n, Q(S_n)) \to \tilde{f}$ weakly in $L^2([0,1])$ (see pp. 640 in [11]). We note that $\tilde{f} \ge 0$ in [0,1] since each $f(S_n, Q(S_n))$ has this property. It is now easily seen that $\hat{v}$ is a weak solution of

$$\begin{cases} D\hat{v}'' = \tilde{f}\hat{u}, \ x \in (0,1), \\ \hat{v}'(0) = 0, \ \hat{v}'(1) + \gamma \hat{v}(1) = 0. \end{cases} \tag{3.23}$$

Since $\hat{v}_n := \frac{S_n}{\|u_n\|_\infty} \to 0$ in $L^\infty([0,1])$ and $\hat{v}_n \to \hat{v}$ in $C^1([0,1])$, it follows that $\hat{v} \equiv 0$ in $[0,1]$. Thus $\tilde{f} \equiv 0$ in $[0,1]$.

Since $\{S_n\}$ is a bounded sequence in $L^\infty([0,1])$, it follows that $Q(S_n)$ is also a bounded sequence in $L^\infty([0,1])$, by passing to a subsequence, we may assume that $Q(S_n) \to \tilde{Q} \ge Q_{\min}$ weakly in $L^2([0,1])$ (see pp. 640 in [11]). From (3.6), it follows that

$$f(S_n, Q(S_n)) = \mu(Q(S_n))Q(S_n). \tag{3.24}$$

Thus $\tilde{f} \equiv g\tilde{Q}$ in $[0,1]$, that is, $g \equiv 0$ in $[0,1]$. Substitute $g \equiv 0$ into (3.21), it follows that $\hat{u} \equiv 0$ on $[0,1]$, which is a contradiction. $\square$

Let $\lambda = \frac{1}{d}$ in (3.7) and regard λ as a bifurcation parameter. We will show that a local branch bifurcates from the branch of trivial solutions $S = z(x)$, $u = 0$. Let $T = z(x) - S$. Then (3.7) become

$$\begin{cases} DT_{xx} + f(z(x) - T, Q(z(x) - T))u = 0, & x \in (0,1), \\ u_{xx} + \lambda\mu(Q(z(x) - T))u = 0, & x \in (0,1), \end{cases} \tag{3.25}$$

with boundary conditions

$$\begin{cases} T_x(0) = 0,\ T_x(1) + \gamma T(1) = 0 \\ u_x(0) = 0,\ u_x(1) + \gamma u(1) = 0. \end{cases} \tag{3.26}$$

For $p > 1$, let $X = \{u \in W^{2,p}([0,1]) : u'(0) = 0,\ u'(1) + \gamma u(1) = 0\}$, and $Y = L^p([0,1])$. Define $F : \mathbf{R} \times X \times X \to Y \times Y$ by

$$F(\lambda, T, u) = \begin{pmatrix} DT'' + f(z(x) - T, Q(z(x) - T))u \\ u'' + \lambda\mu(Q(z(x) - T))u \end{pmatrix},$$

where $\lambda = \frac{1}{d}$.

We consider the bifurcation at $(\lambda, T, u) = (\lambda_1, 0, 0)$. From calculations,

$$F_{(T,u)}(\lambda, T, u)[\phi, \psi] = \begin{pmatrix} D\phi'' + a(T)(x)u\phi + f(z(x) - T, Q(z(x) - T))\psi \\ \psi'' + \lambda b(T)(x)u\phi + \lambda\mu(Q(z(x) - T))\psi \end{pmatrix},$$

where $a(T)(x) = \frac{\partial}{\partial T}[f(z(x) - T, Q(z(x) - T))]$, $b(T)(x) = \frac{\partial}{\partial T}[\mu(Q(z(x) - T))]$. Furthermore,

$$F_\lambda(\lambda, T, u) = \begin{pmatrix} 0 \\ \mu(Q(z(x) - T))u \end{pmatrix},$$

$$F_{\lambda,(T,u)}(\lambda, T, u)[\phi, \psi] = \begin{pmatrix} 0 \\ b(T)(x)u\phi + \mu(Q(z(x) - T))\psi \end{pmatrix},$$

$$F_{(T,u),(T,u)}(\lambda, T, u)[\phi, \psi]^2 = \begin{pmatrix} a'(T)(x)u\phi^2 + 2a(T)(x)\phi\psi \\ \lambda b'(T)(x)u\phi^2 + 2\lambda b(T)(x)\phi\psi \end{pmatrix}.$$

At $(\lambda, T, u) = (\lambda_1, 0, 0)$, it is easy to verify that the kernel $N(F_{(T,u)}(\lambda_1, 0, 0)) = span\{(\phi_1, \psi_1)\}$, where ψ_1 is the eigenfunction of (3.13) and ϕ_1 satisfies $D\phi_1'' = -f(z(x), Q(z(x))\psi_1 < 0$. By the maximum principle, we have that $\phi_1 > 0$ on $[0, 1]$. Next, we will show that the range $R(F_{(T,u)}(\lambda_1, 0, 0)) = \{(f, g) \in Y^2 : \int_0^1 g(x)\psi_1(x)dx = 0\}$. In fact,

$$F_{(T,u)}(\lambda_1, 0, 0)[\phi, \psi] = \begin{pmatrix} D\phi'' + f(z(x), Q(z(x)))\psi \\ \psi'' + \lambda_1 \mu(Q(z(x)))\psi \end{pmatrix},$$

thus $(f, g) \in R(F_{(T,u)}(\lambda_1, 0, 0))$ if and only if $f = D\phi'' + f(z(x), Q(z(x)))\psi$ and $g = \psi'' + \lambda_1 \mu(Q(z(x)))\psi$. It follows that $\int_0^1 g(x)\psi_1(x)dx = \int_0^1 (\psi_1(x)\psi'' + \lambda_1 \mu(Q(z(x)))\psi_1(x)\psi)dx$. From (3.13),

$$\int_0^1 g(x)\psi_1(x)dx = \int_0^1 (\psi_1(x)\psi'' - \psi_1''\psi)dx,$$

therefore $\int_0^1 g(x)\psi_1(x)dx = 0$ by integration by parts and the boundary conditions of ψ and ψ_1. Since $F_{\lambda,(T,u)}(\lambda_1, 0, 0)[\phi_1, \psi_1] = [0\ \mu(Q(z(x)))\psi_1]^T$ and $\int_0^1 \mu(Q(z(x)))\psi_1^2(x)dx > 0$, we have that $F_{\lambda,(T,u)}(\lambda_1, 0, 0)[\phi_1, \psi_1] \notin R(F_{(T,u)}(\lambda_1, 0, 0))$. Thus we can apply Lemma 2.1 to conclude that the set of positive solutions to (3.7) near $(\lambda_1, z(x), 0)$ is a smooth curve

$$\Gamma = \{(\lambda(t), z(x) - T_1(t), u_1(t)) : t \in (0, \delta)\} \tag{3.27}$$

with $T_1(t) = t\phi_1(x) + o(t)$, $u_1(t) = t\psi_1(x) + o(t)$. Moreover, $\lambda'(0)$ can be calculated by Lemma 2.1(see also Refs. [8]-[10] and [23]):

$$\lambda'(0) = -\frac{\langle F_{(T,u),(T,u)}(\lambda_1, 0, 0)[\phi_1, \psi_1]^2, l\rangle}{2\langle F_{\lambda,(T,u)}(\lambda_1, 0, 0)[\phi_1, \psi_1], l\rangle}, \tag{3.28}$$

where l is a linear functional on Y^2 defined as $\langle [f, g], l\rangle = \int_0^1 g(x)\psi_1(x)dx$. Since

$$F_{\lambda,(T,u)}(\lambda_1, 0, 0)[\phi_1, \psi_1] = [0\ \mu(Q(z(x)))\psi_1]^T$$

and the second component of $F_{(T,u),(T,u)}(\lambda_1, 0, 0)[\phi_1, \psi_1]^2$ takes the form

$$-2\lambda_1 \mu'(Q(z(x)))Q'(z(x))\phi_1\psi_1.$$

Thus,

$$\lambda'(0) = \frac{\int_0^1 \lambda_1 \mu'(Q(z(x)))Q'(z(x))\phi_1(x)\psi_1^2(x)dx}{\int_0^1 \mu(Q(z(x)))\psi_1^2(x)dx} > 0. \tag{3.29}$$

Lemma 3.3. *The system* (3.7) *has at most one positive solution.*

Due to the a priori estimates for (3.7) (see Lemma 3.2) and a standard global bifurcation consideration, as in ([16], p.1135), we have the following theorem:

Theorem 3.1. (1) *If* $\frac{1}{d} := \lambda \leq \lambda_1$, *then the trivial solution* $(z(x), 0)$ *of* (3.7) *is the unique nonnegative solution ;*

(2) *If* $\frac{1}{d} := \lambda > \lambda_1$, *then there exists a unique solution (S(x),u(x)) of* (3.7) *with* $S(x) > 0$, $u(x) > 0$ *for* $0 \leq x \leq 1$.

Using the similar method in [16], we can establish the uniqueness of nonnegative solutions to (3.7). Before we prove the uniqueness in Theorem 3.1, we present the following lemmas.

Lemma 3.4. *Suppose* (S_1, u_1), (S_2, u_2) *are nonnegative solutions of* (3.7) *with* $S_1 \geq S_2$. *Then* $S_1 \equiv S_2$, $u_1 \equiv u_2$ on [0,1].

Proof. Suppose $S_1 \geq S_2$ and $u_1 \not\equiv u_2$. Let $w = \frac{u_2}{u_1}$. Then from (3.7), w satisfies

$$\begin{cases} dw'' + 2d(\frac{u_1'}{u_1})w' + [\mu(Q(S_2)) - \mu(Q(S_1))]w = 0, & x \in (0,1), \\ w'(0) = 0, \quad w'(1) = 0. \end{cases} \tag{3.30}$$

From (3.10), $\mu(Q(S))$ is increasing in S, hence $\mu(Q(S_2)) - \mu(Q(S_1)) \leq 0$ on [0,1]. By the maximum principle [20], it follows that w is a positive constant. From (3.30), it deduces that $S_1 \equiv S_2$ on [0,1]. From the first equation of (3.7), we have that $u_1 \equiv u_2$ on [0,1].

Lemma 3.5. *Suppose* (S_1, u_1), (S_2, u_2) *are nonnegative solutions of* (3.7) *with* $S_1 \not\equiv S_2$. *Then the curve* $y = S_1(x)$ *crosses the curve* $y = S_2(x)$ *a finite number of times* on [0,1].

Proof. From Lemma 3.4, the curve $y = S_1(x)$ must cross the curve $y = S_2(x)$ on [0,1]. Suppose the curve $y = S_1(x)$ crosses the curve $y = S_2(x)$ an infinite number of times on [0,1]. Then there exists $\{x_n\}_{n=1}^{\infty}$ such that $S_1(x_n) = S_2(x_n)$ and there exists $a \in [0,1]$ such that $x_n \to a$ as $n \to \infty$. Obviously, $S_1(a) = S_2(a)$. Let $T(x) = S_1(x) - S_2(x)$, $x \in [0,1]$. For any neighborhood of a, the curve $y = S_1(x)$ crosses the curve $y = S_2(x)$ an infinite number of times, thus the Taylor expansion of $T(x)$ at a yields $T'(a) = 0$, $T''(a) = 0$, $T'''(a) = 0$. That is $S_1'(a) = S_2'(a)$, $S_1''(a) = S_2''(a)$, $S_1'''(a) = S_2'''(a)$. From (3.7), we have that $u_1(a) = u_2(a)$, $u_1'(a) = u_2'(a)$, $u_1''(a) = u_2''(a)$. By the uniqueness of the solution of the ordinary differential equations (3.7) yields $S_1 \equiv S_2$, $u_1 \equiv u_2$ on [0,1]. We get a contradiction, thus the proof is complete.

Proof of Theorem 3.1(uniqueness).

Suppose that $(S_1(x), u_1(x))$, $(S_2(x), u_2(x))$ are two nonnegative solutions of (3.7) with $S_1 \not\equiv S_2$ and $\frac{1}{d} := \lambda \geq \lambda_1$. By Lemma 3.1, $S_1(x), S_2(x)$, $u_1(x), u_2(x)$ are positive on [0,1]. From Lemma 3.4, Lemma 3.5, the curve $y = S_1(x)$ crosses the curve $y = S_2(x)$ a finite number of times on [0,1]. Let $x_0 = 0$, $x_{n+1} = 1$ and x_1, x_2, ..., x_n be the points where two curves cross each other.

Without loss of generality, we may assume $S_1 \geq S_2$ on $[x_k, x_{k+1}]$, where $0 \leq k \leq n$, k is even, and $S_2 \geq S_1$ on $[x_k, x_{k+1}]$, where $0 \leq k \leq n$, k is odd. In order to obtain a contradiction, we discuss two cases.

Case1. $u_1(0) \leq u_2(0)$. Let $w = \frac{u_2}{u_1}$ on $0 \leq x \leq x_1$. Then from (3.7), w satisfies

$$\begin{cases} dw'' + 2d(\frac{u_1'}{u_1})w' + [\mu(Q(S_2)) - \mu(Q(S_1))]w = 0, \quad x \in (0, x_1), \\ w'(0) = 0. \end{cases} \tag{3.31}$$

It is not hard to show that $w''(0) \geq 0$. Then the maximum principle yields $u_2(x) > u_1(x)$ for all $0 < x \leq x_1$. We claim $y = u_2(x)$ must cross $y = u_1(x)$ at some point $c_1 \in (x_1, x_2)$. If not, then $u_2 \geq u_1$, $S_2 \geq S_1$ on $[x_1, x_2]$. Since $S_2(x_2) = S_1(x_2)$, $S_2'(x_1) \geq S_1'(x_1)$, $S_2(x_1) = S_1(x_1)$ and (3.10), it follows that

$$\begin{aligned} S_1(x_2) = S_2(x_2) &= S_2(x_1) + (x_2 - x_1)S_2'(x_1) + \frac{1}{D}\int_{x_1}^{x_2}\int_{x_1}^{t} f(S_2(\tau), Q(S_2(\tau)))u_2(\tau)d\tau dt \\ &> S_1(x_1) + (x_2 - x_1)S_1'(x_1) + \frac{1}{D}\int_{x_1}^{x_2}\int_{x_1}^{t} f(S_1(\tau), Q(S_1(\tau)))u_1(\tau)d\tau dt \\ &= S_1(x_2). \end{aligned}$$

This is a contradiction. Similarly, let $\hat{w} = \frac{u_1}{u_2}$ on $c_1 \leq x \leq x_2$. Then from (3.7), $\hat{w}$ satisfies

$$\begin{cases} d\hat{w}'' + 2d(\frac{u_2'}{u_2})\hat{w}' + [\mu(Q(S_1)) - \mu(Q(S_2))]\hat{w} = 0, \quad x \in (c_1, x_2), \\ \hat{w}(c_1) = 1. \end{cases} \tag{3.32}$$

Then the maximum principle yields $u_1(x) > u_2(x)$ for all $c_1 < x \leq x_2$.

Repeating the arguments shows that there exist c_2,...,c_n, $x_i < c_i < x_{i+1}$, i =1,2,...,n such that $u_1(c_i) = u_2(c_i)$, i =1,...,n. Moreover, $u_1 \geq u_2$ on $[c_i, c_{i+1}]$ where i is odd, and $u_2 \geq u_1$ on $[c_i, c_{i+1}]$ where i is even. If $S_1 \geq S_2$ on $[x_n, 1]$ then $u_2 \geq u_1$ on $[c_n, 1]$. Consider $w = \frac{u_2}{u_1}$ on $c_n \leq x \leq 1$. Then from (3.7), w satisfies

$$\begin{cases} w'' + 2d(\frac{u_1'}{u_1})w' + [\mu(Q(S_2)) - \mu(Q(S_1))]w = 0, \quad x \in (c_n, 1), \\ w'(1) = 0. \end{cases} \tag{3.33}$$

Then the maximum principle yields the maximum of w occurs at $x = 1$, but it contradicts to the boundary condition $w'(1) = 0$. If $S_2 \geq S_1$ on $[x_n, 1]$ then $u_1 \geq u_2$ on $[c_n, 1]$. Similarly, consider $\hat{w} = \frac{u_1}{u_2}$ on $c_n \leq x \leq 1$. Then from (3.7), $\hat{w}$ satisfies

$$\begin{cases} d\hat{w}'' + 2d(\frac{u_2'}{u_2})\hat{w}' + [\mu(Q(S_1)) - \mu(Q(S_2))]\hat{w} = 0, \quad x \in (c_n, 1), \\ \hat{w}'(1) = 0. \end{cases} \tag{3.34}$$

Then the maximum principle yields the maximum of $\hat{w}$ occurs at $x = 1$, but it contradicts to the boundary condition $\hat{w}'(1) = 0$.

Case2. $u_2(0) < u_1(0)$.

We claim $y = u_1(x)$ must cross $y = u_2(x)$ at some point $c_0 \in (0, x_1)$. If not, then $u_1 \geq u_2$, $S_1 \geq S_2$ on $[0, x_1]$. Since $S_1(0) \geq S_2(0)$, $S_1'(0) = S_2'(0) = -S^{(0)}$ and (3.10), it follows that

$$\begin{aligned} S_2(x_1) = S_1(x_1) &= S_1(0) + \frac{1}{D}\int_0^{x_1}\int_0^t f(S_1(\tau), Q(S_1(\tau)))u_1(\tau)d\tau dt \\ &> S_2(0) + \frac{1}{D}\int_0^{x_1}\int_0^t f(S_2(\tau), Q(S_2(\tau)))u_2(\tau)d\tau dt \\ &= S_2(x_1). \end{aligned}$$

This is a contradiction. Using the similar arguments as in Case1, there exist $\bar{c}_1$,...,$\bar{c}_n$, $x_i < \bar{c}_i < x_{i+1}$, i =1,2,...,n such that $u_1(\bar{c}_i) = u_2(\bar{c}_i)$ and $y = u_1(x)$, $y = u_2(x)$ cross each other at $\bar{c}_i$. Applying the same arguments as in Case1 we obtain a contradiction.

Thus we complete our proof.

4 Steady State Solutions for the Two Species Model

Consider the steady-state solution for (1.9)-(1.11)

$$\begin{cases} DS_{xx} - f_1(S, Q_1(S))u_1 - f_2(S, Q_2(S))u_2 = 0, & x \in (0,1), \\ d_i(u_i)_{xx} + \mu_i(Q_i(S))u_i = 0, & x \in (0,1),\ i = 1,2, \end{cases} \tag{4.1}$$

with boundary conditions

$$\begin{cases} S_x(0) = -S^{(0)},\ S_x(1) + \gamma S(1) = 0, \\ (u_i)_x(0) = 0,\ (u_i)_x(1) + \gamma u_i(1) = 0, \quad i = 1,2, \end{cases} \tag{4.2}$$

where $Q_i(S)$ satisfy

$$f_i(S, Q_i(S)) - \mu_i(Q_i(S))Q_i(S) = 0, \quad i = 1,2. \tag{4.3}$$

Clearly, we are interested only in nonnegative solutions. We have a trivial nonnegative solution $(S(x), u_1(x), u_2(x)) = (z(x), 0, 0)$ for (4.1)-(4.2). Other nonnegative solutions can be classified by two types:

(1) nonnegative solutions with exactly one components identically zero $(\hat{S}(x), \hat{u}_1(x), 0)$, $(\tilde{S}(x), 0, \tilde{u}_2(x))$;

(2) nonnegative solutions with no component identically zero.

4.1 Existence and Local Stability for semi-trivial solution

In this subsection, we first give conditions to ensure the existence of semi-trivial solutions.

Suppose that σ_i is the principal eigenvalue of the problem

$$\begin{cases} \phi_i''(x) + \sigma_i \mu_i(Q_i(z(x)))\phi_i(x) = 0, & x \in (0,1),\ i = 1,2, \\ \phi_i'(0) = \phi_i'(1) + \gamma\phi_i(1) = 0, & i = 1,2, \end{cases} \tag{4.4}$$

with the corresponding positive eigenfunction $\phi_i(x)$ uniquely determined by the normalization $\max_{[0,1]}\phi_i(x) = 1$.

The following a priori estimates for (4.1)-(4.2) are crucial to the proofs of coexistence results.

Lemma 4.1. *Suppose* (S, u_1, u_2) *is a nonnegative solution of* (4.1)-(4.2) *with* $S(x) \neq 0$ *and* $u_i(x) \not\equiv 0$, $i = 1, 2$. *Then*

(1) $u_i(x) > 0,\ 0 < S(x) < z(x)$ on [0,1];

(2) $Q_i(S) \geq Q_{\min,i}$ on [0,1], where $Q_i(S)$ satisfies (4.3);

(3) $0 < d_i < \frac{1}{\sigma_i}$.

Proof. The proofs are similar to the proof as in Lemma 3.1 and we omit it. □

Lemma 4.2. *Suppose that* $D > 0$ *is fixed and* $[m_i, M_i]$ *is any compact subinterval of* $(0, \frac{1}{\sigma_i})$, $i = 1, 2$. *For* $d_i \in [m_i, M_i] \subset (0, \frac{1}{\sigma_i})$, *there exists a positive constant* C *independent of* d_1 *and* d_2 *such that any positive solution* $\{(S(x), u_1(x), u_2(x))\}$ *of* (4.1)-(4.2) *satisfies* $\| S \|_\infty + \| u_1 \|_\infty + \| u_2 \|_\infty < C$.

Proof. The proofs are similar to the proof as in Lemma 3.2 and we omit it. □

Setting $u_2 = 0$ in (4.1), then

$$\begin{cases} DS_{xx} - f_1(S, Q_1(S))u_1 = 0, & x \in (0, 1), \\ d_1(u_1)_{xx} + \mu_1(Q_1(S))u_1 = 0, & x \in (0, 1), \end{cases} \tag{4.5}$$

with boundary conditions

$$\begin{cases} S_x(0) = -S^{(0)},\ S_x(1) + \gamma S(1, t) = 0, \\ (u_1)_x(0) = 0,\ (u_1)_x(1) + \gamma u_1(1) = 0, \end{cases}$$

It follows by Theorem 3.1 that there exists a unique semi-trivial solution $(\hat{S}(x), \hat{u}_1(x), 0)$ for (4.1)-(4.2) if $\frac{1}{d_1} > \sigma_1$. From (4.3), $Q_i(\hat{S})$ satisfies

$$f_i(\hat{S}, Q_i(\hat{S})) - \mu_i(Q_i(\hat{S}))Q_i(\hat{S}) = 0.$$

Thus $(S, u_1, Q_1, u_2, Q_2) = (\hat{S}, \hat{u}_1, Q_1(\hat{S}), 0, Q_2(\hat{S}))$ is a steady-state solution for (1.9)-(1.11) if $\frac{1}{d_1} > \sigma_1$.

Similarly, if $\frac{1}{d_2} > \sigma_2$ there exists a unique semi-trivial solution $(\tilde{S}(x), 0, \tilde{u}_2(x))$ for (4.1)-(4.2), where $Q_i(\tilde{S})$ satisfies

$$f_i(\tilde{S}, Q_i(\tilde{S})) - \mu_i(Q_i(\tilde{S}))Q_i(\tilde{S}) = 0.$$

Thus $(S, u_1, Q_1, u_2, Q_2) = (\tilde{S}, 0, Q_1(\tilde{S}), \tilde{u}_2, Q_2(\tilde{S}))$ is a steady-state solution for (1.9)-(1.11) if $\frac{1}{d_2} > \sigma_2$.

In order to discuss the local stability for semi-trivial solution, we define the following two principal eigenvalues $\hat{\sigma}_1$ and $\hat{\sigma}_2$. Suppose that $\hat{\sigma}_1$ is the principal eigenvalue of the problem

$$\begin{cases} \psi''(x) + \hat{\sigma}_1 \mu_1(Q_1(\tilde{S}))\psi(x) = 0, \quad x \in (0,1), \\ \psi'(0) = \psi'(1) + \gamma\psi(1) = 0, \end{cases} \tag{4.6}$$

with the corresponding positive eigenfunction $\psi(x)$ uniquely determined by the normalization $\max_{[0,1]}\psi(x) = 1$. Similarly, suppose that $\hat{\sigma}_2$ is the principal eigenvalue of the problem

$$\begin{cases} \phi''(x) + \hat{\sigma}_2 \mu_2(Q_2(\hat{S}))\phi(x) = 0, \quad x \in (0,1), \\ \phi'(0) = \phi'(1) + \gamma\phi(1) = 0, \end{cases} \tag{4.7}$$

with the corresponding positive eigenfunction $\phi(x)$ uniquely determined by the normalization $\max_{[0,1]}\phi(x) = 1$. By Lemma 2.2, it is easy to see that $\hat{\sigma}_1 > \sigma_1$ and $\hat{\sigma}_2 > \sigma_2$ because $\mu_1(Q_1(z(x))) > \mu_1(Q_1(\tilde{S}))$ and $\mu_2(Q_2(z(x))) > \mu_2(Q_2(\hat{S}))$.

We discuss the stability of $\hat{E}$, where $\hat{E} = (\hat{S}, \hat{u}_1, Q_1(\hat{S}), 0, Q_2(\hat{S}))$. For this purpose, noting that $\hat{Q}_1 = Q_1(\hat{S})$, $\hat{Q}_2 = Q_2(\hat{S})$, we consider the linearized eigenvalue problem for the system (1.9)-(1.11) about the steady state $\hat{E}$:

$$\begin{cases} DS_{xx} - [\frac{\partial f_1(\hat{S},\hat{Q}_1)}{\partial S}\hat{u}_1]S - f_1(\hat{S},\hat{Q}_1)u_1 - [\frac{\partial f_1(\hat{S},\hat{Q}_1)}{\partial Q_1}\hat{u}_1]Q_1 - f_2(\hat{S},\hat{Q}_2)u_2 = -\lambda S, \\ d_1 u_{1xx} + \mu_1(\hat{Q}_1)u_1 + [\mu_1'(\hat{Q}_1)\hat{u}_1]Q_1 = -\lambda u_1, \ x \in (0,1), \ t > 0, \\ [\frac{\partial f_1(\hat{S},\hat{Q}_1)}{\partial S}]S + [\frac{\partial f_1(\hat{S},\hat{Q}_1)}{\partial Q_1} - \mu_1'(\hat{Q}_1)\hat{Q}_1 - \mu_1(\hat{Q}_1)]Q_1 = -\lambda Q_1, \\ d_2 u_{2xx} + \mu_2(\hat{Q}_2)u_2 = -\lambda u_2, \\ [\frac{\partial f_2(\hat{S},\hat{Q}_2)}{\partial S}]S + [\frac{\partial f_2(\hat{S},\hat{Q}_2)}{\partial Q_2} - \mu_1'(\hat{Q}_2)\hat{Q}_2 - \mu_2(\hat{Q}_2)]Q_2 = -\lambda Q_2, \end{cases} \tag{4.8}$$

with boundary conditions

$$\begin{cases} S_x(0,t) = 0, \ S_x(1,t) + \gamma S(1,t) = 0, \\ u_{ix}(0,t) = 0, \ u_{ix}(1,t) + \gamma u_i(1,t) = 0, \quad i = 1,2. \end{cases} \tag{4.9}$$

Let η_1 be the principal eigenvalue of the problem

$$\begin{cases} -d_2\phi''(x) + [-\mu_2(Q_2(\hat{S}))]\phi(x) = \eta\phi(x), \quad x \in (0,1), \\ \phi'(0) = \phi'(1) + \gamma\phi(1) = 0. \end{cases} \tag{4.10}$$

From Lemma 2.3 it is easy to see that $\frac{1}{d_2} > \hat{\sigma}_2$ if and only if $\eta_1 < 0$. Since $u_2 = \phi(x) > 0$ and $-\lambda = -\eta_1 > 0$ satisfy the fourth equation in (4.8), we conclude that the semi-trivial solution $(\hat{S}, \hat{u}_1, Q_1(\hat{S}), 0, Q_2(\hat{S}))$ is unstable provided that $\frac{1}{d_2} > \hat{\sigma}_2$.

Similarly, we can also conclude that the semi-trivial solution $(\tilde{S}, 0, Q_1(\tilde{S}), \tilde{u}_2, Q_2(\tilde{S}))$ is unstable provided that $\frac{1}{d_1} > \hat{\sigma}_1$.

Remark 4.1. *Summarizing the above discussion, we have the following results.*

(i) *If* $\frac{1}{d_1} > \sigma_1$, *then* $(\hat{S}, \hat{u}_1, Q_1(\hat{S}), 0, Q_2(\hat{S}))$ *exists uniquely.*

(ii) *If* $\frac{1}{d_2} > \sigma_2$, *then* $(\tilde{S}, 0, Q_1(\tilde{S}), \tilde{u}_2, Q_2(\tilde{S}))$ *exists uniquely.*

(iii) *If* $\frac{1}{d_1} > \sigma_1$ *and* $\frac{1}{d_2} > \hat{\sigma}_2$, *then* $(\hat{S}, \hat{u}_1, Q_1(\hat{S}), 0, Q_2(\hat{S}))$ *is unstable.*

(iv) *If* $\frac{1}{d_1} > \hat{\sigma}_1$ *and* $\frac{1}{d_2} > \sigma_2$, *then* $(\tilde{S}, 0, Q_1(\tilde{S}), \tilde{u}_2, Q_2(\tilde{S}))$ *is unstable.*

In the next subsection, we will use the degree theory in cones to show that if $\frac{1}{d_1} > \hat{\sigma}_1$, $\frac{1}{d_2} > \hat{\sigma}_2$ then there exists at least one positive steady-state solution for (1.9)-(1.11), or equivalently, there exists at least one positive solution for (4.1)-(4.2).

4.2 Existence of Positive Solutions

In this subsection, we will show that if $\frac{1}{d_1} > \hat{\sigma}_1$, $\frac{1}{d_2} > \hat{\sigma}_2$ then there exists at least one positive solution for (4.1)-(4.2) by the method of degree theory.

Let $T = z(x) - S$. Then (4.1)-(4.2) becomes

$$\begin{cases} DT_{xx} + f_1(z(x) - T, Q_1(z(x) - T))u_1 + f_2(z(x) - T, Q_2(z(x) - T))u_2 = 0, & x \in (0,1), \\ d_1(u_1)_{xx} + \mu_1(Q_1(z(x) - T))u_1 = 0, & x \in (0,1), \\ d_2(u_2)_{xx} + \mu_2(Q_2(z(x) - T))u_2 = 0, & x \in (0,1), \end{cases} \tag{4.11}$$

with boundary conditions

$$\begin{cases} T_x(0) = 0,\ T_x(1) + \gamma T(1,t) = 0, \\ (u_i)_x(0) = 0,\ (u_i)_x(1) + \gamma u_i(1) = 0, \quad i = 1, 2. \end{cases} \tag{4.12}$$

Note that we have a trivial nonnegative solution $(T(x), u_1(x), u_2(x)) = (0, 0, 0)$ for (4.11)-(4.12). Other nonnegative solutions of (4.11)-(4.12) can be classified by two types:

(1) Two nonnegative solutions with exactly one component identically zero, $(\hat{T}(x), \hat{u}_1(x), 0)$, $(\tilde{T}(x), 0, \tilde{u}_2(x))$, where $\hat{T}(x) = z(x) - \hat{S}(x)$, $\tilde{T}(x) = z(x) - \tilde{S}(x)$;

(2) nonnegative solutions with no components identically zero.

Let $C^1_B([0,1]) = \{y \in C^1([0,1]) \mid y'(0) = 0, \quad y'(1) + \gamma y(1) = 0\}$ and $E = C^1_B([0,1]) \oplus C^1_B([0,1]) \oplus C^1_B([0,1])$. For a large positive constant M and $\tau \in [0,1]$, consider system

$$\begin{cases} (-D\frac{d^2}{dx^2} + M)T = MT + \tau f_1(z(x) - T, Q_1(z(x) - T))u_1 + \tau f_2(z(x) - T, Q_2(z(x) - T))u_2, \\ (-d_1\frac{d^2}{dx^2} + M)u_1 = Mu_1 + \tau\mu_1(Q_1(z(x) - T))u_1, \ x \in (0,1), \\ (-d_2\frac{d^2}{dx^2} + M)u_2 = \ Mu_2 + \tau\mu_2(Q_2(z(x) - T))u_2, \end{cases} \tag{4.13}$$

with boundary conditions

$$\begin{cases} T_x(0) = 0, \ T_x(1) + \gamma T(1,t) = 0, \\ (u_i)_x(0) = 0, \ (u_i)_x(1) + \gamma u_i(1) = 0, \quad i = 1,2. \end{cases} \tag{4.14}$$

Assume (T, u_1, u_2) is a nonnegative solution of (4.13)-(4.14). Then one can use a similar argument as in Lemma 4.1 and Lemma 4.2 to show that $T(x)$, $u_1(x)$ and $u_2(x)$ are bounded functions on $[0,1]$ for all $\tau \in [0,1]$. Hence, there exists positive numbers P, P_1 and P_2 such that $T(x) \le P$, $u_1(x) \le P_1$ and $u_2(x) \le P_2$ on $[0,1]$ for all $\tau \in [0,1]$.

Let

$$K_B([0,1]) = \{u \in C^1_B([0,1]) \mid u(x) \ge 0, \quad x \in [0,1]\},$$

$$W = \{(T, u_1, u_2) \in E \mid T(x) \ge 0, \ u_1(x) \ge 0, \ u_2(x) \ge 0, \quad x \in [0,1]\},$$

$$\Delta = \{(T, u_1, u_2) \in E \mid T(x) \le P + 1, \ u_1(x) \le P_1 + 1, \ u_2(x) \le P_2 + 1, \quad x \in [0,1]\},$$

$$\Sigma = \mathrm{int}(\Delta) \cap W.$$

Then $W = K_B([0,1]) \oplus K_B([0,1]) \oplus K_B([0,1])$ is a cone of E and Σ is a bounded open set in W.

For $\tau \in [0,1]$, define $A_\tau : E \to E$ by $A_\tau(T, u_1, u_2) =$

$$\begin{pmatrix} (-D\frac{d^2}{dx^2} + M)^{-1}[MT + \tau f_1(z(x) - T, Q_1(z(x) - T))u_1 + \tau f_2(z(x) - T, Q_2(z(x) - T))u_2] \\ (-d_1\frac{d^2}{dx^2} + M)^{-1}[Mu_1 + \tau\mu_1(Q_1(z(x) - T))u_1] \\ (-d_2\frac{d^2}{dx^2} + M)^{-1}[Mu_2 + \tau\mu_2(Q_2(z(x) - T))u_2] \end{pmatrix}.$$

Let M be sufficiently large such that

$$M+\tau\frac{\partial f_1(z(x)-T,Q_1(z(x)-T))}{\partial T}u_1+\tau\frac{\partial f_2(z(x)-T,Q_2(z(x)-T))}{\partial T}u_2>0,$$

for all $(T,u_1,u_2)\in\Sigma$ and $\tau\in[0,1]$. Clearly, A_τ is compact. Let $A=A_1$. Then $A:\Sigma\to W$ is continuously differentiable. Obviously, (T,u_1,u_2) is a nonnegative solution for (4.11)-(4.12) if and only if $(T,u_1,u_2)\in\Sigma$ is a fixed point of A. Moreover, A_τ has no nonzero fixed points on $\partial\Sigma$. By homotopic invariance of the degree, we obtain $\mathrm{index}_W(A,\Sigma)=\mathrm{index}_W(A_\tau,\Sigma)=\mathrm{index}_W(A_0,\Sigma)$.

Lemma 4.3. *If* $\frac{1}{d_1}>\sigma_1$, $\frac{1}{d_2}\neq\sigma_2$ *or* $\frac{1}{d_1}\neq\sigma_1$, $\frac{1}{d_2}>\sigma_2$, *then* $\mathrm{index}_W(A,(0,0,0))=0$*; If* $\frac{1}{d_1}<\sigma_1$, $\frac{1}{d_2}<\sigma_2$, *then* $\mathrm{index}_W(A,(0,0,0))=1$.

Proof. By calculation,

$$A'(0,0,0)\begin{pmatrix}T\\u_1\\u_2\end{pmatrix}=\begin{pmatrix}(-D\frac{d^2}{dx^2}+M)^{-1}[MT+f_1(z(x),Q_1(z(x)))u_1+f_2(z(x),Q_2(z(x)))u_2]\\(-d_1\frac{d^2}{dx^2}+M)^{-1}[Mu_1+\mu_1(Q_1(z(x)))u_1]\\(-d_2\frac{d^2}{dx^2}+M)^{-1}[Mu_2+\mu_2(Q_2(z(x)))u_2]\end{pmatrix}.$$

Hence, $A'(0,0,0)(T,u_1,u_2)^T=\lambda(T,u_1,u_2)^T$ is equivalent to

$$\begin{cases}-D\frac{d^2}{dx^2}T+MT=\frac{1}{\lambda}[MT+f_1(z(x),Q_1(z(x)))u_1+f_2(z(x),Q_2(z(x)))u_2],\\-d_1\frac{d^2}{dx^2}u_1+Mu_1=\frac{1}{\lambda}[M+\mu_1(Q_1(z(x))]u_1,\ x\in(0,1),\\-d_2\frac{d^2}{dx^2}u_2+Mu_2=\frac{1}{\lambda}[M+\mu_2(Q_2(z(x)))]u_2.\end{cases}\tag{4.15}$$

with the usual boundary conditions. Suppose that $\frac{1}{d_1}>\sigma_1$, $\frac{1}{d_2}\neq\sigma_2$ or $\frac{1}{d_1}\neq\sigma_1$, $\frac{1}{d_2}>\sigma_2$. Since $\sigma_i,\ i=1,2$ satisfy (4.4) and $\frac{1}{d_1}\neq\sigma_1$, $\frac{1}{d_2}\neq\sigma_2$, it follows that 1 is not an eigenvalue of $A'(0,0,0)$. Hence, $(0,0,0)$ is an isolated fixed point. Let $\bar\eta_1$ and $\hat\eta_1$ be the principal eigenvalues of $-d_1\psi''(x)+[-\mu_1(Q_1(z(x)))]\psi(x)=\bar\eta\psi(x)$, $-d_2\psi''(x)+[-\mu_2(Q_2(z(x)))]\psi(x)=\hat\eta\psi(x)$ for $x\in(0,1)$. It follows by Lemma 2.3 that $\bar\eta_1<0$ if $\frac{1}{d_1}>\sigma_1$ and $\hat\eta_1<0$ if $\frac{1}{d_2}>\sigma_2$. Then $A'(0,0,0)$ has an eigenvalue $\lambda>1$ by Lemma 2.4 and that $\mathrm{index}_W(A,(0,0,0))=0$ by Lemma 2.5(ii).

If $\frac{1}{d_1}<\sigma_1$, $\frac{1}{d_2}<\sigma_2$, then by Lemma 2.3, it follows that $\bar\eta_1>0$, $\hat\eta_1>0$. By Lemma 2.4, it follows that all the eigenvalues of $A'(0,0,0)$ are smaller than 1, which ensure that $\mathrm{index}_W(A,(0,0,0))=1$ by Lemma 2.5(i).

Lemma 4.4. $\mathrm{index}_W(A,\Sigma)=1$.

Proof. It is easy to see that A_τ has no nonzero fixed points on $\partial\Sigma$. By homotopic invariance of the topological degree, we obtain $\text{index}_W(A,\Sigma) = \text{index}_W(A_\tau,\Sigma) = \text{index}_W(A_0,\Sigma)$. Since $(0,0,0)$ is the unique nonnegative fixed point of A_0, it follows that $\text{index}_W(A,\Sigma) = \text{index}_W(A_0,(0,0,0))$. By calculations,

$$A_0'(0,0,0)\begin{pmatrix} T \\ u_1 \\ u_2 \end{pmatrix} = \begin{pmatrix} (-D\frac{d^2}{dx^2}+M)^{-1}(MT) \\ (-d_1\frac{d^2}{dx^2}+M)^{-1}(Mu_1) \\ (-d_2\frac{d^2}{dx^2}+M)^{-1}(Mu_2) \end{pmatrix}.$$

Hence, $A_0'(0,0,0)(T,u_1,u_2)^T = \lambda(T,u_1,u_2)^T$ is equivalent to

$$\begin{cases} -D\frac{d^2}{dx^2}T + MT = \frac{1}{\lambda}MT, \\ -d_1\frac{d^2}{dx^2}u_1 + Mu_1 = \frac{1}{\lambda}Mu_1, \quad x\in(0,1), \\ -d_2\frac{d^2}{dx^2}u_2 + Mu_2 = \frac{1}{\lambda}Mu_2, \end{cases} \tag{4.16}$$

with the usual boundary conditions. One can use the similar argument as in Lemma 4.3 to show that all the eigenvalues of $A_0'(0,0,0)$ are smaller than 1, which ensure that $\text{index}_W(A_0,(0,0,0))) = 1$ by Lemma 2.5(i). From the homotopic invariance of the degree, we obtain $\text{index}_W(A,\Sigma) = 1$.

Lemma 4.5. *If* $\frac{1}{d_1} > \sigma_1$, $\frac{1}{d_2} > \hat{\sigma}_2$, *then* $\text{index}_W(A,(\hat{T},\hat{u}_1,0)) = 0$*; If* $\frac{1}{d_1} > \hat{\sigma}_1$, $\frac{1}{d_2} > \sigma_2$, *then* $\text{index}_W(A,(\tilde{T},0,\tilde{u}_2)) = 0$.

Proof. We only consider the case for $(\hat{T},\hat{u}_1,0)$. Similar results hold for $(\tilde{T},0,\tilde{u}_2)$. Let $E_1 = C_B^1([0,1])\oplus C_B^1([0,1])$, $E_2 = C_B^1([0,1])$, $W_1 = K_B([0,1])\oplus K_B([0,1])$, $W_2 = K_B([0,1])$. Then $E = E_1\oplus E_2$ and $W = W_1\oplus W_2$. Let $F_1(T,u_1,u_2) =$

$$\begin{pmatrix} (-D\frac{d^2}{dx^2}+M)^{-1}[MT + f_1(z(x)-T,Q_1(z(x)-T))u_1 + f_2(z(x)-T,Q_2(z(x)-T))u_2] \\ (-d_1\frac{d^2}{dx^2}+M)^{-1}[Mu_1 + \mu_1(Q_1(z(x)-T))u_1] \end{pmatrix},$$

$$F_2(T,u_1,u_2) = (-d_2\frac{d^2}{dx^2}+M)^{-1}[Mu_2 + \mu_2(Q_2(z(x)-T))u_2],$$

and $A = (F_1,F_2)$. By calculation, one obtains

$$F_2'(\hat{T},\hat{u_1},0)\mid_{W_2}(T,u_1,u_2)^T = (-d_2\frac{d^2}{dx^2}+M)^{-1}[Mu_2 + \mu_2(Q_2(\hat{S}))u_2],$$

where $\hat{S} = z(x)-\hat{T}$. Hence, $F_2'(\hat{T},\hat{u_1},0)\mid_{W_2}(T,u_1,u_2)^T = \lambda u_2$ is equivalent to

$$(-d_2\frac{d^2}{dx^2}+M)u_2 = \frac{1}{\lambda}[M + \mu_2(Q_2(\hat{S}))]u_2.$$

If $\frac{1}{d_2} > \hat{\sigma}_2$, then $\eta_1 < 0$ by Lemma 2.3, where η_1 is the principal eigenvalues of (4.10). By Lemma 2.4, it follows that there exists λ satisfies $\frac{1}{\lambda} \in (0, 1)$, that is, $\lambda > 1$. Hence, $r(F_2'(\hat{T}, \hat{u}_1, 0) \mid_{W_2}) > 1$.

From Lemma 2.6(i) and the above discussions, one obtains that $\deg_W(I - A, U \times W_2(\epsilon), (0, 0, 0)) = 0$ if $\frac{1}{d_2} > \hat{\sigma}_2$. Observing that the above degree does not depend on the particular choices of U and ϵ [12], and this degree is precisely the index of $(\hat{T}, \hat{u}_1, 0)$, denoted it by $\text{index}_W(A, (\hat{T}, \hat{u}_1, 0))$. Hence, $\text{index}_W(A, (\hat{T}, \hat{u}_1, 0)) = 0$. Similarly, $\text{index}_W(A, (\tilde{T}, 0, \tilde{u}_2)) = 0$ if $\frac{1}{d_1} > \hat{\sigma}_1$.

Lemma 4.6. *If $\frac{1}{d_1} > \hat{\sigma}_1$, $\frac{1}{d_2} > \hat{\sigma}_2$, then there exist positive solutions to the system (4.11)-(4.12).*

Proof. If $\frac{1}{d_1} > \hat{\sigma}_1$, $\frac{1}{d_2} > \hat{\sigma}_2$, then it follows from Lemma 4.3 and Lemma 4.5 that $\text{index}_W(A, (0, 0, 0))) = 0$, $\text{index}_W(A, (\hat{T}, \hat{u}_1, 0)) = 0$ and index $_W(A, (\tilde{T}, 0, \tilde{u}_2)) = 0$. Suppose A has no positive fixed points in Σ. Then by Lemma 4.4 and the additivity of index,

$$1 = \text{index}_W(A, \Sigma) = \text{index}_W(A, (0, 0, 0)) + \text{index}_W(A, (\hat{T}, \hat{u}_1, 0)) + \text{index}_W(A, (\tilde{T}, 0, \tilde{u}_2)) = 0,$$

which is a contradiction. Thus A has at least one nontrivial fixed point other than $(0, 0, 0)$, $(\hat{T}, \hat{u}_1, 0)$, $(\tilde{T}, 0, \tilde{u}_2)$ in W. In other words, system (4.11)-(4.12) has at least one nonnegative solution different from $(0, 0, 0)$, $(\hat{T}, \hat{u}_1, 0)$, $(\tilde{T}, 0, \tilde{u}_2)$, which is a positive solution.

Theorem 4.1. *If $\frac{1}{d_1} > \hat{\sigma}_1$, $\frac{1}{d_2} > \hat{\sigma}_2$, then there exist positive solutions to the system (4.1)-(4.2).*

Proof. From Lemma 4.6, we see that (4.11)-(4.12) has at least one positive solution, say (T^*, u_1^*, u_2^*). Thus, (S^*, u_1^*, u_2^*) is a positive solution for (4.1)-(4.2), where $S^* = z(x) - T^*$.

5 Discussion

We first give an interpretation for the existence of positive steady state solutions. From [18] and (3.13), we have

$$\lambda_1 = \min_{\psi} \frac{\int_0^1 (\psi'(x))^2 dx + \gamma \psi^2(1)}{\int_0^1 \mu(Q(z(x)))\psi^2(x) dx}. \tag{5.1}$$

Assume $\mu(Q)$, $f(S,Q)$ take special forms of (1.3), (1.4) respectively, that is

$$\mu(Q) = \mu_\infty(1 - \frac{Q_{\min}}{Q}), \quad f(S,Q) = \rho\frac{S}{k+S}, \ \rho \text{ is a positive constant.}$$

From (3.6),

$$\mu(Q(z(x))) = \frac{\frac{\rho z(x)}{k+z(x)}}{Q_{\min} + \frac{\rho z(x)}{\mu_\infty(k+z(x))}}.$$

Thus

$$\lambda_1 = \min_{\psi>0} \frac{\int_0^1 (\psi'(x))^2 dx + \gamma\psi^2(1)}{\int_0^1 \frac{\frac{\rho z(x)}{k+z(x)}}{Q_{\min}+\frac{\rho z(x)}{\mu_\infty(k+z(x))}}\psi^2(x)dx}. \tag{5.2}$$

Since $z(x) = S^{(0)}(\frac{1+\gamma}{\gamma} - x)$ and (5.2), it follows that λ_1 is a function of input concentration $S^{(0)}$, the maximal growth rate of the species μ_∞, washout rate γ, the minimum cell quota $Q_{\min}$ and half-saturation constant k. We note that $S^{(0)}$ and γ are the controlling parameters operated by the experimenter; $Q_{\min}$, k and the maximal growth rate μ_∞ are the intrinsic biological characteristics of the species. From (5.2), it follows that

$$\lambda_1 = \lambda_1(S^{(0)}, \mu_\infty, \gamma, Q_{\min}, k)$$

satisfies that λ_1 is strictly increasing in γ, $Q_{\min}$, and k and strictly decreasing in $S^{(0)}$ and μ_∞. Theorem 3.1 states that if the diffusion coefficient d is smaller than $\frac{1}{\lambda_1}$, the critical diffusion coefficient, then the species survives, otherwise, the species goes to extinction. With the diffusion coefficient d fixed, if the minimal cell quota $Q_{\min}$ is smaller ($\frac{1}{d} > \lambda_1 = \lambda_1(Q_{\min})$, $\lambda_1(Q_{\min})$ is strictly increasing in $Q_{\min}$) or the maximal growth rate μ_∞ is larger ($\frac{1}{d} > \lambda_1 = \lambda_1(\mu_\infty)$, $\lambda_1(\mu_\infty)$ is strictly decreasing in μ_∞) or the half saturation constant k is smaller ($\frac{1}{d} > \lambda_1 = \lambda_1(k)$, $\lambda_1(k)$ is strictly increasing in k), then the species survives. Similarly, if the chemostat is operated by increasing the input concentration $S^{(0)}$ ($\frac{1}{d} > \lambda_1 = \lambda_1(S^{(0)})$, $\lambda_1(S^{(0)})$ is strictly decreasing in $S^{(0)}$) or by decreasing the washout rate γ ($\frac{1}{d} > \lambda_1 = \lambda_1(\gamma)$, $\lambda_1(\gamma)$ is strictly increasing in γ), then the species survives.

In summary, we conclude that larger $\mu_{\infty,i}$, $i = 1,2$, larger $S^{(0)}$ or smaller γ, smaller d_i, smaller $Q_{\min,i}$, smaller k_i, $i = 1,2$ benefit the existence of positive steady state solutions for this unstirred chemostat model (1.9)-(1.11).

From Remark 4.1 and Theorem 4.1 it follows that if $(\hat{S}, \hat{u}_1, Q_1(\hat{S}), 0, Q_2(\hat{S}))$, $(\tilde{S}, 0, Q_1(\tilde{S}), \tilde{u}_2, Q_2(\tilde{S}))$ are both unstable for (1.9)-(1.11), then there exists at least

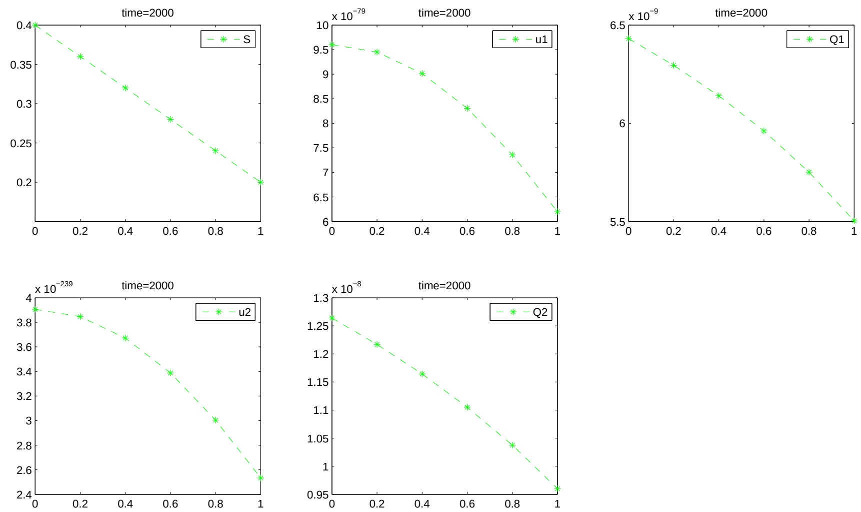

Figure 5.1: Both species go to extinction:$D = 0.25$, $d_1 = 1.6$, $d_2 = 1.1$.

one positive steady state solutions for (1.9)-(1.11). We have the parallel results as in the fixed-yield unstirred chemostat model (1.6)-(1.8) ([18]). It is worth emphasizing that (1.9)-(1.11) can lead to coexistence of competing populations in contrast to the competitive exclusion that holds in the "well-mixed" internal storage model (1.2) ([24]).

In the following numerical simulations for the systems (1.9)-(1.11), we assume that the per-capita growth rate $\mu_i(Q_i)$ takes the form as in the first equation of (1.3), and the per-capita uptake rate $f_i(S, Q_i)$ takes the form as in (1.4), $i = 1, 2$. The parameters(except D, d_1 and d_2) are choosen as follows: $S^{(0)} = 0.2$, $\gamma = 1$, $k_1 = 1$, $k_2 = 1$, $Q_{\min,1} = 3 \times 10^{-9}$, $Q_{\min,2} = 3 \times 10^{-9}$, $Q_{\max,1} = 10^{-8}$, $Q_{\max,2} = 2.95 \times 10^{-8}$, $\mu_{1\infty} = 2.16$, $\mu_{2\infty} = 0.732$, $\rho^{\text{high}}_{\max,1} = 5 \times 10^{-8}$, $\rho^{\text{low}}_{\max,1} = 9 \times 10^{-10}$, $\rho^{\text{high}}_{\max,2} = 3.83 \times 10^{-8}$, $\rho^{\text{low}}_{\max,2} = 9 \times 10^{-10}$. When we change the values of D, d_1 and d_2, we have three outcomes.

In Fig.5.1, we choose $D = 0.25$, $d_1 = 1.6$, $d_2 = 1.1$. Then both species u_1 and u_2 go to extinction. In Fig.5.2, we choose $D = 0.25$, $d_1 = 0.25$, $d_2 = 0.25$. Then species u_1 survives and species u_2 goes to extinction. In Fig.5.3, we choose $D = 0.25$, $d_1 = 0.16$, $d_2 = 0.105$. Then species u_1 and u_2 coexist.

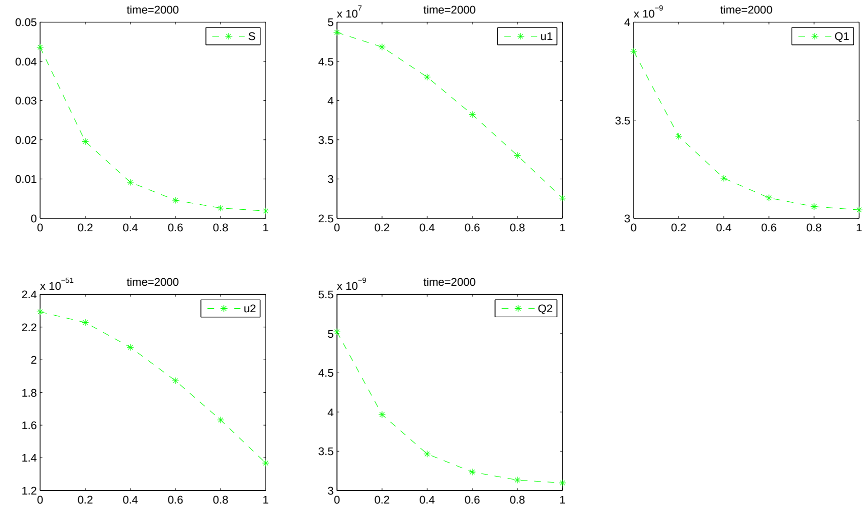

Figure 5.2: Exactly one species exists:$D = 0.25$, $d_1 = 0.25$, $d_2 = 0.25$.

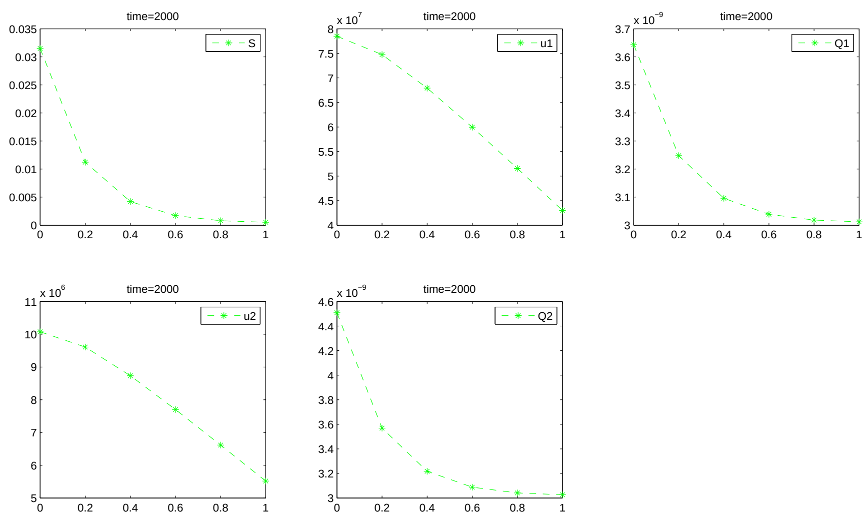

Figure 5.3: Coexistence:$D = 0.25$, $d_1 = 0.16$, $d_2 = 0.105$.

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