Direct Interference on Competition in a Chemostat

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Abstract　This paper studies the global dynamics of competition in chemostat in which two populations of microorganisms compete exploitatively for a single, essential, nonreproducing, growth-limiting substrate and there is a direct interference between competitors. In order to understand the differences in the effects of intraspecific and interspecific interference, the both cases are considered respectively.

Key words　Population dynamics ecology　chemostat　competition　interference　interspecific　intraspecific　principal of competitive exclusion

1　The Model

The chemostat is a very important laboratory device for the study of microbial population dynamics under nutrient limitation. See, for example[1], for a detailed description of the chemostat. In this paper we study the global dynamics of competition in chemostat in which two populations of microorganisms compete exploitatively for a single, essential, nonreproducing, growth-limiting substrate. Direct interference between competitors, both interspecific and intraspecific, is permitted.

$$\dot{S} = (S^0 - S)D - x_1 \frac{p_1(S)}{y_1} - x_2 \frac{p_2(s)}{y_2},$$

$$\dot{x}_1 = x_1(-D_1 + p_1(S) - q_{11}(x_1) - q_{12}(x_2)),$$

$$\dot{x}_2 = x_2(-D_2) + p_2(S) - q_{21}(x_1) - q_{22}(x_2)) \tag{1.1}$$

$$S(0) \geq 0, x_i(0) \geq 0, i = 1, 2.$$

where $S(0) \geq 0, x_i \geq 0, i = 1, 2$ and S^0, D, D_i, and y_i are positive constants.

In these equations, as in Wolkowicz and Lu[2], assuming for convenience that the volume of the culture vessel is one cubic unit, $S(t)$ denotes the concentration of the substrate at time t; $x_i(t)$ denotes the concentration of the ith population of microorganisms at time t; S^0 denotes the concentration of substrate in the feed bottle; $p_i(S(t))/y_i$ denotes the uptake rate of substrate of the ith population. We assume that $p_i(S)$ represents the per-capita growth rate of the ith population so that y_i is a growth yield constant. $q_{ii}(x_i)$, describes intraspecific interference and $q_{ij}(x_j)$, $i \neq j$, describes the effect of interspecific interference by population j on population i. D denotes the input rate from the feed bottle containing the substrate and the washout rate of substrate, microorganisms, and byproducts from the growth chamber. Each $D_i = D + \varepsilon_i$, where $\varepsilon_i > 0$ can be in-

terpreted as the species specific death rate of species x_i. The analysis of the model requires only that $D_i > 0$ and so $\varepsilon_i \leq 0$ is also allowed. This leaves the D_i open to other interpretations.

In order to understand the differences in the effects of intraspecific and interspecific interference on the dynamics of the populations we consider two special cases of model (1.1). In the case that no interspesific interference, only intraspecific interference, is permitted, that is $q_{ij}(x_j) \equiv 0$, $i \neq j$, the model becomes:

$$\dot{S} = (S^0 - S)D - x_1 \frac{p_1(S)}{y_1} - x_2 \frac{p_2(S)}{y_2},$$
$$\dot{x}_1 = x_1(-D_1 + p_1(S) - q_{11}(x_1)),$$
$$\dot{x}_2 = x_2(-D_2 + p_2(S) - q_{22}(x_2)),$$
$$S(0) \geq 0, x_i(0) \geq 0, i = 1, 2. \tag{1.2}$$

In the case that no intraspecific interference, only interspecific interference, is permitted, that is $q_{ii}(x_i) \equiv 0$, the model becomes:

$$\dot{S} = (S^0 - S)D - x_1 \frac{p_1(S)}{y_1} - x_2 \frac{p_2(S)}{y_2},$$
$$\dot{x}_1 = x_1(-D_1 + p_1(S) - q_{12}(x_2)),$$
$$\dot{x}_2 = x_2(-D_2 + p_2(S) - q_{21}(x_1)),$$
$$S(0) \geq 0, x_i(0) > 0, i = 1, 2. \tag{1.3}$$

We make the following assumptions on the form of the response functions:

$$p_i, q_{ii}, q_{ij} : R_+ \to R_+, \tag{1.4}$$

$$p_i, q_{ii}, q_{ij} \text{ are continuously differentiable} \tag{1.5}$$

$$p_i(0) = 0, q_{ii}(0) = 0, q_{ij}(0) = 0, \tag{1.6}$$

$$p_i'(S) > 0, \text{ for all } S > 0, \tag{1.7}$$

$$q_{ii}'(x) \geq 0, \text{ and } q_{ij}'(x) \geq 0, \text{ for all } x > 0. \tag{1.8}$$

There exist uniquely defined positive extended real numbers λ_i, such that

$$p_i(\lambda_i) = D_i \tag{1.9}$$

In the case that $p_i(S) < D_i$ for all $S > 0$, then $\lambda_i = \infty$. When at least one λ_i is finite, we assume that

$$\lambda_1 < \lambda_2 \tag{1.10}$$

Finally, we introduce the following notation.

$$\lim_{x \to \infty} q_{ij}(x) = \eta_{ij} \quad i, j = 1, 2 \tag{1.11}$$

When the η_{ij} are finite, this indicates that the corresponding response function, q_{ij} saturates. However, $\eta_{ij} = \infty$ is not excluded, so that the results hold as well for unbounded response functions.

1.1 Preliminary results

By proofs similar to the ones used to prove lemma 2.1 and 2.2 in Wolkowicz and Lu[2], the following can be shown.

Lemma 1.1 (1) The solutions $S(t)$, $x_i(t)$, $i = 1, 2$ of models (1.1), (1.2), and (1.3) remain nonnegative and bounded for all $t > 0$.

(2) If $S(t) \geq S^0$ for all $t > 0$, then $S(t) \to S^0$ and $x_i(t) \to 0$ as $t \to \infty$.

(3) If $S(t) < S^0$ for some $t > 0$, then $S(t) < S^0$ for all $t > 0$.

(4) If $\lambda_1 < S^0$, then $S(t) < S^0$ for all sufficiently large t.

(5) If $\lambda_i \geq S^0$, $i = 1$ or 2, then $x_i(t) \to 0$ as $t \to \infty$.

1.2 The washout equilibrium, E_{S^0}

First, note that the washout equilibrium, $E_{S^0} = (S^0, 0, 0)$, is always a solution.

Theorem 1.2 If $S^0 \leq \lambda_1$, then E_{S^0} is globally asymptotically stable. If $S^0 > \lambda_1$, then E_{S^0} is unstable and the stable manifold of E_{S^0} is the set

$$M^+(E_{S^0}) = \{(S, x_1, x_2) : x_1 = 0 \text{ and } x_2 > 0\} \text{ if } \lambda_2 \geq S^0. \tag{1.12}$$

$$M^+(E_{S^0}) = \{(S, x_1, x_2) : x_1 = 0 \text{ and } x_2 = 0\} \text{ if } \lambda_2 < S^0. \tag{1.13}$$

Proof The global stability follows immediately from part 5. of Lemma 1.1.

The instability follows immediately if one linearizes about the equilibrium. One finds the eigenvalues of the variational matrix are:

$$- D \text{ and } - D_i + p_i(S^0), \quad i = 1, 2.$$

This also gives the dimension of the stable manifold of $M^+(E_{S^0})$. The definition of $M^+(E_{S^0})$, follows from the invariance of each of the faces where $x_i = 0$.

2 Intraspecific Competition-Model (1.2)

For this model we make the technical assumptions

$$q'_{ii}(x) > 0 \text{ for all } x > 0. \tag{2.1}$$

$$\eta_{ii} > - D_i + p_i(S^0). \tag{2.2}$$

2.1 Existence of equilibrium solutions-model (1.2)

Recall (from Section 1.2) that the washout equilibrium, $E_{S^0} = (S^0, 0, 0)$, is always a solution. There exists a planar equilibrium of the form $E_{\hat{S}_1} = (\hat{S}_1, \hat{x}_1, 0)$, with $\hat{x}_1 > 0$ if and only if $\lambda_1 < S^0$. If it exists, it is unique and $\lambda_1 < \hat{S}_1 < S^0$. Similarly, there exists a planar equilibrium of the form $E_{\hat{S}_2} = (\hat{S}_2, 0, \hat{x}_2)$, with $\hat{x}_2 > 0$ if and only if $\lambda_2 < S^0$. If it exists it is also unique, and $\lambda_2 < \hat{S}_2 < S^0$. In both cases,

$$\hat{x}_i = \frac{y_i(S^0 - \hat{S}_i)D}{p_i(\hat{S}_i)},$$

where $\hat{S}_i$ must satisfy

$$q_{ii}\left(\frac{y_i(S^0 - \hat{S}_i)D}{p_i(\hat{S}_i)}\right) = - D_i + p_i(\hat{S}_i).$$

That each planar equilibrium solution is uniquely defined follows easily from the technical assumption (2.2), the monotonicity assumptions on p_i and q_{ii} and the fact that the right hand side of the above equation is a decreasing function of $\hat{S}_i$ for $\lambda_i < \hat{S}_i < S^0$.

There exists a coexistence equilibrium, if and only if $\lambda_1 < S^0$, $\lambda_2 < S^0$, and $\hat{S}_1 > \lambda_2$. When it exists it is denoted, $E_{\tilde{S}} = (\tilde{S}, \tilde{x}_1, \tilde{x}_2)$ where $\tilde{x}_i > 0$. It can be shown that when it exists, it is unique and $\lambda_2 < \tilde{S} < \tilde{S}_1$.

To see this, first note that the components of any coexistence equilibrium must satisfy,

$$(S^0 - S)D - x_1 \frac{p_1(S)}{y_1} - x_2 \frac{p_2(S)}{y_2} = 0, \tag{2.3}$$

$$-D_1 + p_1(S) - q_{11}(x_1) = 0, \tag{2.4}$$

$$-D_2 + p_2(S) - q_{22}(x_2) = 0. \tag{2.5}$$

Lemma 2.1 The following are equivalent.

(1) There exists a unique coexistence equilibrium, $E_{\hat{S}}$.

(2) $\hat{S}_1 > \lambda_2$.

(3) There exist $x_{\lambda_2} > 0$ satisfying

$$(S^0 - \lambda_2)D - x_{\lambda_2} \frac{p_1(\lambda_2)}{y_1} > 0, \tag{2.6}$$

and

$$-D_1 + p_1(\lambda_2) - q_{11}(x_{\lambda_2}) = 0 \tag{2.7}$$

Proof (a) $(2.\Rightarrow 3.)$ If $\hat{S}_1 > \lambda_2$, then since by definition

$$-D_1 + p_1(\hat{S}_1) - q_{11}(\hat{x}_1) = 0 \tag{2.8}$$

in order for (2.7) to hold, $x_{\lambda_2} < \hat{x}_1$. Therefore,

$$0 = (S^0 - \hat{S}_1)D - \hat{x}_1 \frac{p_1(\hat{S}_1)}{y_1} \leq (S^0 - \lambda_2)D - x_{\lambda_2} \frac{p_1(\lambda_2)}{y_1}$$

and so (2.6) holds.

(b) $(3.\Rightarrow 2.)$ If $\hat{S}_1 \leq \lambda_2$, in order for (2.7) to hold, $\hat{x}_1 \leq x_{\lambda_2}$. But

$$0 = (S^0 - \hat{S}_1)D - \hat{x}_1 \frac{p_1(\hat{S}_1)}{y_1} \geq (S^0 - \lambda_2)D - x_{\lambda_2} \frac{p_1(\lambda_2)}{y_1}$$

and so (2.6) cannot hold. Therefore, (2.6) and (2.7) imply that $\hat{S}_1 > \lambda_2$.

(c) $(1.\Rightarrow 3.)$ Suppose $E_{\hat{S}}$ exists, but (3) does not. Therefore, if (2.7) holds, then (2.6) cannot hold by part (b) of this proof. In order for (2.5) to hold for some $\hat{x}_2 > 0$, clearly $\bar{S} > \lambda_2$. Increasing S from λ_2 to $\tilde{S}$ in (2.4) and (2.5) forces x_1 to increase from x_{λ_2} and x_2 to increase from 0, forcing the left hand side of (2.3) to be negative, contradicting the existence of $E_{\hat{S}}$.

(d) $(3.\Rightarrow 1.)$ Consider the curve $(R, x_1(R), x_2(R))$, $\lambda_2 \leq R \leq S^0$ satisfying (2.4) and (2.5). If $R = \lambda_2$, then $x_1(R) = x_{\lambda_2}$ and $x_2(R) = 0$, and from (3) it follows that the left hand side of (2.3) evaluated at $S = R, x_1 = x_1(R)$, and $x_2 = x_2(R)$, is strictly positive.

On the other hand, if $R = \hat{S}_1 > \lambda_2$, (by part (b)) then $x_1(R) = \hat{x}_1$ and $x_2(R) > 0$, and so the left hand side of (2.3) evaluated at $S = R, x_1 = x_1(R)$, and $x_2 = x_2(R)$, is strictly negative.

Reducing R from $\hat{S}_1$, also decreases $x_1(R)$ and $x_2(R)$ in order to continue satisfing (2.4) and (2.5), thus increasing the left hand side of (2.3). By continuity and the monotonicity of p_i and q_{11}, there exists a unique $\bar{S}$ satisfying $\lambda_2 < \bar{S} < \hat{S}_1$ so that for $R = \bar{S}, x_1(R) = \tilde{x}_1$, and $x_2(R) = \tilde{x}_2$, (2.3)~(2.5) are satisfied.

2.2 Stability of equilibrium solutions-model (1.2)

The stability of the washout equilibrium was already considered in the Section 1.2. Next we consider the stability of the single species survival equilibria.

Theorem 2.2 (1) Assume that $E_{\hat{S}_1}$ exists, that is $\lambda_1 < S^0$. If $\hat{S}_1 < \lambda_2$, then $E_{\hat{S}_1}$ is locally

asymptotically satble. If $S_1 > \lambda_2$, then E_{S_1} is unstable.

(2) Whenever E_{S_2} exists, that is $\lambda_2 < S^0$, E_{S_2} is unstable.

(3) In the absence of a competitor, each planar equilibrium E_{S_1} is globally asymptotically stable provided $\lambda_i < S^0$.

(4) If $\lambda_1 < S^0 < \lambda_2$, then E_{S_1} is globally asymptotically stable with respect to all solutions with $x_1(0) > 0$.

(5) Assume that $\lambda_2 < S^0$. Define

$$g(S) = \frac{p_2(S)(-p_1(S_1) + p_1(S))(S^0 - S_1)}{p_1(S_1)(-D_2 + p_2(S))(S^0 - S)}.$$

If it is possible to find a constant $a > 0$, satisfying

$$\max_{0 < S < S_1} g(S) \leq a \leq \min_{\lambda_2 < S < S^0} g(S), \tag{2.9}$$

and if $S_1 < \lambda_2$, then E_{S_1} is globally asymptotically stable with respect to all solutions with $x_1(0) > 0$. For example, for any response functions $p_i(S)$ of the following forms:

(a) Lotka-Volterra: $p_i(S) = r_i S$ where r_i is a positive constant,

(b) Michaelis-Menten: $p_i(S) = \dfrac{c_i S}{a_i + S}$ where c_i and a_i are positive constants.

(c) Sigmoidal: $p_i(S) = \dfrac{m_i S^2}{(a_i + S)(b_i + S)}$ where m_i, a_i and b_i are positive constants.

it is always possible to satisfy (2.9).

Proof (1) The characteristic polynomial associated with the variational matrix about the equilibrium solution E_{S_1} is:

$$(-D_2 + p_2(S_1) - \gamma)\Big[\gamma^2 + \gamma(D + \bar{x}_1 \frac{p_1'(S_1)}{y_1} + \bar{x}_1 q'_{11}(\bar{x}_1))$$

$$+ \bar{x}_1 q'_{11}(\bar{x}_1)(D + \bar{x}_1 \frac{p_1'(S_1)}{y_1}) + \bar{x}_1 \frac{p_1'(S_1) p_1(S_1)}{y_1}\Big].$$

It follows from assumptions $(1.4) - (1.8)$ that all of the coefficients of the quadratic are positive and so by the Routh-Hurwicz condition at least two eigenvalues always have negative real parts. The remaining eigenvalue is $-D_2 + p_2(S_1)$.

(2) The characteristic polynomial associated with the variational matrix about the equilibrium solution E_{S_2} is identical with the polynomial given in part 1, provided all subscripts 1 and 2 are interchanged. Since $S_2 > \lambda_2 > \lambda_1$, the result follows, that is there is always 1 real positive eigenvale and the other 2 eigenvalues have negative real parts.

(3) From parts 1. and 2. it follows that in the absence of a competitor, each planar equilibrium is locally asymptotically stable. Consider,

$$\Delta \equiv \oint_\Gamma \mathrm{div}(S, x_i)\mathrm{d}t$$

$$= \oint_\Gamma (-D - \frac{x_i p_i'(S)}{y_i} - D_i + p_i(S) - q_{ii}(x_i) - x_i q'_{ii}(x_i))\mathrm{d}t$$

$$= \oint_{\Gamma} (-D + \frac{x_i p'_i(S)}{y_i} + x_i q'_{ii}(x_i)) + \frac{\dot{x}_i}{x_i}) dt$$

$$= \oint_{\Gamma} - (D + \frac{x_i p'_i(S)}{y_i} + x_i q'_{ii}(x_i)) dt$$

$$< 0.$$

Using the Poincaré criterion[3], any periodic orbit in the plane must be orbitally asymptotically stable and so no planar periodic orbit can exist.

(4) From part 5. of Lemma 1.1 it follows that the x_2 component of any point in the omega limit set of a solution with $x_1(0) > 0$ is identically zero. Using the Butler-McGehee Lemma[1,4], it can be shown that the x_1 component of any point is the omega limit set of a solution with $x_1(0) > 0$ must be positive. From part 3. it follows that E_{S_1} must be in the omega limit set. From part 1., since $\hat{S}_1 < S^0 < \lambda_2$, it follows that E_{S_1} is locally asymptoically stable, and hence is the only point in the omega limit set.

(5) Define the Lyapunov function,

$$V(S, x_1, x_2) = \int_{\hat{S}_1}^{S} \frac{(p_1(\xi) - p_1(\hat{S}_1))(S^0 - \hat{S}_1)}{p_1(\hat{S}_1)(s^0 - \xi)} d\xi + \frac{1}{y_1} \int_{\hat{x}_1}^{x_1} \frac{x - \hat{x}_1}{x} dx + \frac{\alpha}{y_2} x_2.$$

Then

$$\nabla(S, x_1, x_2) = \frac{(p_1(S) - p_1(\hat{S}_1)(S^0 - \hat{S}_1))}{p_1(\hat{S}_1)(S^0 - S)}((S^0 - S)D - \frac{x_1 p_1(S)}{y_1} - \frac{x_2 p_2(S)}{y_2})$$

$$+ \frac{1}{y_1}(x_1 - \hat{x}_1)(-D_1 + p_1(S) - q_{11}(x_1) + p_1(\hat{S}_1) - p_1(\hat{S}_1)$$

$$+ q_{11}(\hat{x}_1) - q_{11}(\hat{x}_1)) + \frac{\alpha}{y_2}x_2(-D_2 + p_2(S) - q_{22}(x_2))$$

$$= (p_1(S) - p_1(\hat{S}_1))\frac{x_1}{y_1}(1 - \frac{(S^0 - \hat{S}_1)p_1(S)}{(S^0 - S)p_1(\hat{S}_1)})$$

$$+ \frac{1}{y_1}(x_1 - \hat{x}_1)(q_{11}(\hat{x}_1) - q_{11}(x_1))$$

$$+ \frac{x_2}{y_2}(\alpha(p_2(S) - D_2 - q_{22}(x_2)) - \frac{p_2(S)(p_1(S) - p_1(\hat{S}_1))(S^0 - \hat{S}_1)}{p_1(\hat{S}_1)(S^0 - S)})$$

$$\leqslant 0,$$

with equality, if and only if $S = \hat{S}_1$ and $x_1 = \hat{x}_1$, $x_2 = 0$ (since $\hat{S}_1 < \lambda_1$). Hence the result follows by the LaSalle extension theorem [5].

Remarks concerning Theorem 2.2

1. This theorem can easily be shown to hold for the analogous model involving n competitors.

2. One can also prove part 3. using the Lyapunov function

$$\int_{\hat{S}_i}^{S} \frac{p_i(S) - p_i(\hat{S}_i)}{p_i(S)} ds + \frac{1}{y_i} \int_{\hat{x}_i}^{x_i} \frac{x_i - \hat{x}_i}{x_i} dx_i. \tag{2.10}$$

3. Part 5. also holds for certain nonmonotone response functions as in Wolkowicz and Lu [2].

4. We conjecture that part 5. is true without assumption.

Next we consider the possibility of coexistence of two competitor populations.

Theorem 2.3 (1) When $E_{\tilde{S}}$ exists, it is locally asymptotically stable.

(2) When $E_{\tilde{S}}$ exists, model (1.2) is uniformly persistent.

Remark We conjecture that whenever $E_{\tilde{S}}$ exists, it is in fact globally asymptotically stable.

Proof (1) The characteristic polynomial associated with the variational matrix about the equilibrium solution $E_{\tilde{S}}$ is

$$\gamma^3 + \gamma^2 (D + \sum_{i=1}^{2} (\frac{\bar{x}_i p'_i(\tilde{S})}{y_i} + \bar{x}_i q'_{ii}(\tilde{X}_i))) + \gamma(\bar{x}_1 \bar{x}_2 q'_{11}(\tilde{x}_1) q'_{22}(\bar{x}_2)$$

$$+ \sum_{i=1}^{2} \frac{\bar{x}_i p'_i(\tilde{S} p_i(\tilde{S}))}{y_i} + (D + \sum_{i=1}^{2} \frac{\bar{x}_i p'_i(\tilde{S})}{y_i})(\sum_{i=1}^{2} \bar{x}_i q'_{ii}(\bar{x}_i)))$$

$$+ \bar{x}_1 \bar{x}_2 q'_{11}(\tilde{x}_1) q'_{22}(\bar{x}_2)(D + \sum_{i=1}^{2} \frac{\bar{x}_i p'_i(\tilde{S})}{y_i})$$

$$+ \bar{x}_1 \bar{x}_2 \Big(q'_{11}(\tilde{x}_1) \frac{p'_2(\tilde{S}) p_2(\tilde{S})}{y_2} + q'_{22}(\bar{x}_2) \frac{p'(\tilde{S}) p_1(\tilde{S})}{y_1} \Big) = 0.$$

It follows from (1.4)~(1.8) and (2.1) that all the coefficients of this polynomial are positive. To prove that all the roots have negative real part using the Routh-Hurwicz criteria, it remains only to show that the determinant condition is satisfied. This was done using the symbol manipulation language MAPLE, since the computation is rather tedious.

(2) Note first that when $E_{\tilde{S}}$ exists, both planar equilibria E_{S_i}, $i = 1, 2$ are unstable, since $\tilde{S}_1 > \lambda_2$, in this case (see Lemma 2.1). Each planar equilibrium has a one-dimensional unstable manifold (pointing into the interior of the positive cone) and a two-dimensional stable manifold (in the plane where the competitor is absent). First we show that the system is persistent. Clearly $\liminf_{t \to \infty} S(t) > 0$, since the entire face where $S(t) = 0$ repells into the interior. Suppose for some initial point P in the interior of R_+^3, $\liminf_{t \to \infty} x_1(t) = 0$. Then there exists a point $\bar{P} = (\bar{S}, 0, \bar{x}_2)$ with $\bar{x}_2 > 0$, in the omega limit set of the trajectory through P, $\Omega^+(P)$.

First we show that E_{S^0} is not in the omega limit set of any trajectory initiating in the interior of R_+^3. Note first that by Theorem 1.2 E_{S^0} has the one dimensional stable manifold,

$$M^+(E_{S^0}) = \{(S, x_1, x_2) : x_1 = 0 \text{ and } x_2 = 0\}.$$

Therefore, be the Butler-McGehee Lemma if E_{S^0} is in $\Omega^+(P)$, then since it cannot be the only point in $\Omega^+(P)$, there must be another point in $\Omega^+(P)$ that is also in $M^+(E_{S^0})$. But then the entire trajectory through that point must be in $\Omega^+(P)$. But any such trajectory either becomes unbounded or leaves the nonnegative cone as $t \to \infty$, a contradiction, since by Lemma 1.1 the omega limit set of any trajectory initiating in the nonnegative cone, is a compact subset contained in the nonnegative cone.

If a point of the form $(\bar{S}, 0, \bar{x}_2) \in \Omega^+(P)$, then by part 3. of Lemma 2.2, $E_{S_2} \in \Omega^+(P)$. But by Theorem 1.2

$$M^+(E_{S_2}) = \{(S, x_1, x_2) : x_1 = 0 \text{ and } x_2 > 0\}$$

is two-dimensional and does not interset the interior of R_+^3. Therefore, E_{S_2} is not the only point in $\Omega^+(P)$ and so again by the Butler-McGehee Lemma, there exists a point in $(\Omega^+(P)) \cap M^+$

$(E_{S_2}))\setminus E_{S_2}$. But then the entire trajectory through that point must be in $\Omega^+(P)$. However, if $t \to \infty$, this trajectory leaves the nonnegative cone, becomes unbounded, or converges to E_{S^0}, all impossible. Therefore, $\liminf_{t\to\infty} x_1(t) > 0$. Similarly, $\liminf_{t\to\infty} x_2(t) > 0$. Therefore, if $E_{\bar{S}}$ exists, system (1.1) is persistent. That it is uniformly persistent follows easily from the main theorem in Butler, Freedman, Waltman[6].

3 Interspecific Competition-Model (1.3)

For this model we make the technical assumptions:

$$q'_{ij}(x) > 0 \text{ for all } x > 0, \tag{3.1}$$

$$\eta_{ij} > -D_i + p_i(S^0). \tag{3.2}$$

3.1 Existence of equilibrium solutions-model (1.3)

Recall (from Section 2.2) that the washout equilibrium, $E_{S^0} = (S^0, 0, 0)$, is always a solution. Next we consider the single species survival equilibria.

There exists a planar equilibrium of the form $E_{S_1} = (\hat{S}_1, \hat{x}_1, 0)$, with $\hat{x}_1 > 0$ if and only if $\lambda_1 < S^0$. If it exists, it is unique and $\hat{S}_1 = \lambda_1$. Similarly, there exists a planar equilibrium of the form $E_{S_2} = (\hat{S}_2, 0, \hat{x}_2)$, with $\hat{x}_2 > 0$ if and only if $\lambda_2 < S^0$. If it exists it is also unique, and $\hat{S}_2 = \lambda_2$. In both cases,

$$\hat{x}_i = \frac{y_i(S^0 - \lambda_i)D}{D_i}.$$

There exists a coexistence equilibrium, if and only if $\lambda_1 < S^0$, $\lambda_2 < S^0$, and

$$-D_1 + p_1(\lambda_2) - q_{12}(\hat{x}_2) < 0. \tag{3.3}$$

When it exists it is denoted, $E_{\bar{S}} = (\bar{S}, \bar{x}_1, \bar{x}_2)$ where $\bar{x}_i > 0$. It can be shown that when it exists, it is unique and $\lambda_2 < \bar{S}$.

To see this, first note that the components of any coexistence equilibrium must satisfy,

$$(S^0 - S)D - x_1\frac{p_1(S)}{y_1} - x_2\frac{p_2(S)}{y_2} = 0, \tag{3.4}$$

$$-D_1 + p_1(S) - q_{12}(x_2) = 0, \tag{3.5}$$

$$-D_2 + p_2(S) - q_{21}(x_1) = 0. \tag{3.6}$$

It follows immediately from (3.6) that $\lambda_2 < \bar{S}$. Since $\lambda_2 < \bar{S}$, it follows from (3.4) that $\bar{x}_2 < \hat{x}_2$. Hence, in order for a coexistence equilibrium to exist, (3.3) must hold.

On the other hand, if (3.3) holds, a coexistence equilibrium exists since increasing S in (3.5) and (3.6) forces x_1 and x_2 to increase in a continuous manner. But (3.4) is a decreasing function of S, x_1 and x_2. At $S = \lambda_2$, in order to satisfy (3.5) and (3.6) $x_1 = 0$ and by (3.3), $x_2 = x' < \hat{x}_2$, so that the left hand side of (3.4) is positive. On the other hand, it $S = S^0$, then the left hand side of (3.4) negative for any choice of $\bar{x}_1$ and $\bar{x}_2$ satisfying (3.5) and (3.6). (Solutions always exists, not necessarily unique, by technical assumption (3.2)). Therefore, there must be some value of $S \in (\lambda_2, S^0)$ with corresponding values of x_1 and x_2 satisfying (3.5) and (3.6) so that (3.4) is also satisfied. Thus there is at least one coexistence equilibrium, $(\bar{S}, \bar{x}_1, \bar{x}_2)$. That it is unique follows since increasing S from $\bar{S}$ also would force $\bar{x}_i$, $i = 1, 2$ to increase and thus (3.

4) would be violated. Similarly, decreasing S from $\bar{S}$ also would force $\bar{x}_i$, $i=1,2$ to decrease and thus (3.4) would again be violated.

3.2 Stability of equilibrium solutions-model (1.3)

The stability of the washout equilibrium was already considered in the Section 2.2. Next we consider the stability of the single species survival equilibria.

Theorem 3.1   (1) Assume that $\lambda_1 < S^0$. E_{S_1} is locally asymptotically stable.

(2) Assume that $\lambda_2 < S^0$. E_{S_2} is locally asymptotically stable if $-D_1 + p_1(\lambda_2) - q_{12}(\hat{x}_2) < 0$ and unstable if $-D_1 + p_1(\lambda_2) - q_{12}(\hat{x}_2) > 0$.

(3) In the absence of a competitor, each planar equilibrium E_{S_i} is globally asymptotically stable provided $\lambda_i < S^0$.

Proof (1) The characteristic polynomial associated with the variational matrix about the equilibrium solution E_{S_1} is:

$$(-D_2 + p_2(\lambda_1) - q_{21}(\bar{x}_1) - \gamma)(\gamma^2 + \gamma(D + \bar{x}_1 \frac{p'_1(S_1)}{y_1}) + \bar{x}_1 \frac{p'_1(\lambda_1)p_1(\lambda_1)}{y_1})$$

Clearly, all of the coefficients of the quadratic are positive and so by the Routh-Hurwicz condition at least two eigenvalues always have negative real parts. The remaining eigenvalue is

$$-D_2 + p_2(\lambda_1) - q_{21}(\bar{x}_1) < 0.$$

(2) The characteristic polynomial associated with the variational matrix about the equilibrium solution E_{S_2} is identical with the polynomial given in part (a) provided all subscripts 1 and 2 are interchanged.

(3) The proof is similar to the proof of part 3. of theorem 2.2.

Remark As in the intraspecific interference case one can also prove this result using Lyapunov function (2.10).

Next we consider the possibility of coexistence of two competitor populations.

Theorem 3.2   1. When $E_{\hat{S}}$ exists, it is unstable.

Proof The characteristic polynomial associated with the variational matrix about the equilibrium solution $E_{\hat{S}}$ is

$$\gamma^3 + \gamma^2(D + \sum_{i=1}^{2}(\frac{\bar{x}_i p'_i(\bar{S})}{y_i}) + \gamma(-\bar{x}_1\bar{x}_2 q'_{12}(\bar{x}_2) q'_{21}(\bar{x}_1)$$

$$+ \sum_{i=1}^{2} \frac{\bar{x}_i p'_i(\bar{S}) p_i(\bar{S})}{y_i} + (\sum_{i=1}^{2}\frac{\bar{x}_i p_i(\bar{S}) p'_i(\bar{S})}{y_i}))$$

$$- (\bar{x}_1\bar{x}_2 q'_{12}(\bar{x}_2) q'_{21}(\bar{x}_1)(D + \sum_{i=1}^{2}\frac{\bar{x}_i p'_i(\bar{S})}{y_i}) + \bar{x}_1\bar{x}_2(q'_{12}(\bar{x}_2)\frac{p'_2(\bar{S}) p_1(\bar{S})}{y_1}$$

$$+ q'_{21}\bar{x}_1 \frac{p'_1(\bar{S}) p_2(\bar{S})}{y_2})) = 0$$

From assumptions (1.4)–(1.8) and (3.1) it follows that the constant term is negative. This implies that the product of the roots is positive. Hence, there exists at least one real positive root. Therefore, $E_{\hat{S}}$ is always unstable.

References

1   Smith H L, Waltman P. The theory of the chemostat, Dynamics of microbial competition. Cambridge University Press, Cambridge, New York, Melbourne(1995)

2   Wolkowicz G S K, Lu Zhiqi. Global dynamics of a mathematical model of competition in the chemostat; general response functions and differential death rate. *SIAM J Appl Math*, 1992, 52(1), 222~233

3   Coppel W A. Stability and asymptotic behavior of differential equations. Boston; D. C. Heath, 1965

4   Freedman H I, Waltman P. Persistence in a model of three interacting-prey populations. *Mathematical Bioscience*, 1984, 68:213 ~231.

5   LaSalle J. Some extensions of Lyapunov's second method. IRE Trans. Circuit, CT~7, 1960; 520~527

6   Butler G, Freedman H, Waltman P. Uniformly Persistent Systems, Proceedings of the American Mathematical Society. 1986, 96; 425~430

7   Armstrong R A, McGehee R. Competitive exclusion. *Am Nat*, 1980, 115; 151~170

8   Butler G J, Wolkowicz G S. A mathematical model of the chemostat with a general class of functions describing nutrient uptake. *SIAM J Appl Math*, 1985, 45; 138~151

9   Butler G J, Wolkowicz G S K. Predator-mediated competition in the chemostat. *J Math Biol*, 1986, 24; 167~191