COMPETITIVE EXCLUSION OF MICROBIAL SPECIES FOR A SINGLE-NUTRIENT WITH INTERNAL STORAGE[*]

SZE-BI HSU[†] AND TING-HAO HSU[†]

Abstract. We study a chemostat model that describes competition between n microbial species for a single-limited resource based on storage. The model incorporates internal resource storage variables that serve the direct connection between species growth and external resource availability. Mathematical analysis for the global dynamics of the model is carried out by using the fluctuating method. It is shown that competitive exclusion principle holds for the limiting system of the model. The species with the smallest ambient nutrient concentration wins the competition. We extend the result of competitive exclusion in the paper [SW1] from two species to n species.

Key words. chemostat, single-limited resource, competition, competitive exclusion, fluctuating lemma

AMS subject classifications. 92A15

1. Introduction. One of the basic hypotheses in the mathematical modeling of competition of microorganisms for a single-limited nutrient in a continuous culture ([HHW],[T],[FS],[AM],[SW2]), is that the rate of consumption of nutrient and the rate of growth of organism are directly proportional ([M]): (Rate of growth of organism)= y (rate of consumption of nutrient), y is called the yield constant and is determined over a finite period of time by

$$y = \frac{\text{weight of organism formed}}{\text{weight of the nutrient used}}.$$

In phytoplankton ecology, it has long been known that the yield can varies depend on the growth rate([D], [G1], [G2], [CN1], [CN2]). Droop[D] is the first one to give a variable yield model, or so called "internal storage" model. He proposed the ideas that organism consumes the nutrient and converts the nutrient into internal storage (cell quota). When the internal storage is below the minimum cell quota, organism ceases to grow. If the cell quota is above the minimum cell quota, then the growth rate increases with cell quota. Furthermore the nutrient uptake rate increases with nutrient concentration and decreases with cell quota. The model of growth with one limiting nutrient incorporating these relations has been tested in both constant and fluctuating environments ([G3], [SC]). Thus the variable yield models are well supported experimentally.

In [SW1], the authors studied the competition between two species competing for a single-limited resource with internal storage. They applied the method of monotone dynamical system [S] to show that competitive exclusion principle holds. When the number of species is greater than two, the method of monotione dynamical system no longer works. In this paper we shall rigorously prove that the competitive exclusion principle also hold for the competition between n microbial species, $n \geq 2$ for a single-limited resource with internal storage. The result is similar to that of the classical simple chemostat model [HHW]: the species with smallest ambient nutrient concentration wins the competition.

In the section two, we present the mathematical model and state the main results. In the section three we give the proof of the main theorem. The main tools in the proof are: the conservation principle, which allows the reduction of $(2n+1)$-dimensional system of ordinary differential equations to $(2n)$-dimensional one; fluctuating method [HHG, WX], which provides tools to determine the global behavior of the $(2n)$-dimensional reduced system; and finally, results on asymptotically autonomous system due to Thieme [Th], which show that the $(2n+1)$-dimensional system and the reduced $(2n)$-dimensional system have the same global asymptotic behavior. In the section 4, we discuss the update mathematical models of microorganisms competing for multiple nutrients in phytoplankton ecology. Several open problems are presented for future research.

2. The model and main result. The model of n species, $n \geq 2$, competing for a single-limited resource with internal storage in a chemostat, takes the form

$$
\begin{aligned}
S'(t) &= (S^{(0)} - S(t))D - \sum_{i=1}^{n} x_i(t) f_i(S(t), Q_i(t)), \\
x_i'(t) &= [\mu_i(Q_i(t)) - D] x_i(t),
\end{aligned}
$$

(2.1)
$$
\begin{aligned}
Q_i'(t) &= f_i(S(t), Q_i(t)) - \mu_i(Q_i(t)) Q_i(t), \\
S(0) &\geq 0, \ x_i(0) > 0, \ Q_i(0) \geq Q_{\min,i}, \quad i = 1, 2, \cdots, n.
\end{aligned}
$$

Here $S(t)$ denotes the concentration of external limiting resource in the chemostat at time t, $x_i(t)$ denotes the concentration of species i at time t, $Q_i(t)$ represents the average amount of stored nutrient per cell of species i 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 capita uptake rate of species i as a function of resource concentration S and cell quota Q_i, $S^{(0)}$ is the input concentration, D is the dilution rate of the chemostat, $Q_{\min,i}$ denotes the threshold cell quota below which no growth of species i occurs. The growth $\mu_i(Q_i)$ takes the following forms [D, G1, G2, CN1, CN2]

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

where $Q_{\min,i}$ is the minimum cell quota necessary to allow cell division and $(Q_i - Q_{\min,i})_+$ 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 [G2],

$$
\begin{aligned}
f_i(S, Q_i) &= \rho_i(Q_i) \frac{S}{a_i + S}, \\
\rho_i(Q_i) &= \rho_{\max}^{\text{high}} - (\rho_{\max}^{\text{high}} - \rho_{\max}^{\text{low}}) \frac{Q_i - Q_{\min,i}}{Q_{\max,i} - Q_{\min,i}},
\end{aligned}
$$

where $Q_{\min,i} \leq Q_i \leq Q_{\max,i}$. Cunningham and Nisbet [CN1, CN2] and Klausmeier and et [KL, KLL] took $\rho_i(Q_i)$ to be a constant.

Motivated by these examples, we assumed that $\mu_i(Q_i)$ is defined and continuously differentiable for $Q_i \geq P_i > 0$ and satisfies

(2.2) $\mu_i(Q_i) \geq 0$, $\mu_i'(Q_i) > 0$ and continuous for $Q_i \geq P_i$, $\mu_i(P_i) = 0$.

In both examples above, $P_i = Q_{\min,i}$. We assume that $f_i(S, Q_i)$ is continuous differentiable for $S > 0$ and $Q_i \geq P_i$ and satisfies

$$(2.3) \qquad f_i(0, Q_i) = 0, \ \frac{\partial f_i}{\partial S} > 0, \ \frac{\partial f_i}{\partial Q_i} \leq 0.$$

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

From (2.2) and (2.3), it follows that $Q_i' \geq 0$ if $Q_i = P_i$ and the interval of Q_i values $[P_i, \infty)$ is positively invariant under the dynamics of (2.1). Therefore we assume the initial values satisfy

$$(2.4) \qquad x_i(0) > 0, \ Q_i(0) \geq P_i, \ S(0) \geq 0, \ i = 1, 2, \cdots, n.$$

Assume the equilibrium E takes the form

$$E = (S, x_1, Q_1, \cdots, x_n, Q_n).$$

Then we have the following steady states:

    (i) The washout steady state

$$E_0 = (S^{(0)}, 0, Q_1^0, 0, Q_2^0, \cdots, 0, Q_n^0)$$

always exists. Here Q_i^0 is the unique solution of

$$(2.5) \qquad f_i(S^{(0)}, Q_i) - Q_i \mu_i(Q_i) = 0.$$

    (ii)

$$
\begin{aligned}
E_1 &= (\lambda_1, x_1^*, Q_1^*, 0, \hat{Q}_2^1, 0, \hat{Q}_3^1, \cdots, 0, \hat{Q}_n^1), \\
E_2 &= (\lambda_2, 0, \hat{Q}_1^2, x_2^*, Q_2^*, 0, \hat{Q}_3^2, \cdots, 0, \hat{Q}_n^2), \\
&\ \ \vdots \\
E_n &= (\lambda_n, 0, \hat{Q}_1^n, 0, \hat{Q}_2^n, \cdots, 0, \hat{Q}_{n-1}^n, x_n^*, Q_n^*).
\end{aligned}
$$

The equilibrium E_i corresponds to the presence of i-th population and the absence of the others. The parameter $\lambda_i, Q_i^*, x_i^*, \hat{Q}_j^i, j \neq i$ satisfy

$$(2.6) \qquad \mu_i(Q_i^*) = D,$$
$$(2.7) \qquad f_i(\lambda_i, Q_i^*) = \mu_i(Q_i^*)Q_i^* = DQ_i^*,$$
$$(2.8) \qquad x_i^* = \frac{(S^{(0)} - \lambda_i)D}{f_i(\lambda_i, Q_i^*)} = \frac{S^{(0)} - \lambda_i}{Q_i^*},$$
$$(2.9) \qquad f_j(\lambda_j, \hat{Q}_j^i) = \mu_j(\hat{Q}_j^i)\hat{Q}_j^i, \quad j \neq i.$$

The steady state E_i exists if and only if the equation $\mu_i(Q_i) = D$ has a unique solution Q_i^* and

$$f_i(S^{(0)}, Q_i^*) > DQ_i^*.$$

LEMMA 2.1. *The solutions $S(t), x_1(t), Q_1(t), \cdots, x_n(t), Q_n(t)$ of system (2.1) are positive and bounded for all $t \geq 0$. Furthermore,*

$$(2.10) \qquad S(t) + \sum_{i=1}^n Q_i(t)x_i(t) = S^{(0)} + O(e^{-Dt}), \ t \to \infty.$$

and there exists $\gamma_i > P_i$, $t_0 > 0$ such that $Q_i(t) \geq \gamma_i$ for all $t \geq t_0$ for $i = 1, 2, \ldots, n$.

The above lemma is a statement that system (2.1) is as "well-behaved" as one intuits from the biological problem. (2.10) is the conservation principle. Therefore all solutions of (2.1) asymptotically approach

$$(2.11) \qquad S(t) + \sum_{i=1}^{n} Q_i(t)x_i(t) = S^{(0)},$$

as $t \to \infty$. Consequently, as a first step in the analysis of (2.1) we consider the restriction of (2.1) to the exponentially attracting invariant subset given by (2.11). Dropping S from (2.1) and letting $U_i = Q_i x_i$, $1 \leq i \leq n$, we obtain the following system

$$U_i'(t) = f_i\left(S^{(0)} - \sum_{i=1}^{n} U_i(t),\ Q_i(t)\right) \frac{U_i(t)}{Q_i(t)} - DU_i(t),$$

$$(2.12) \qquad Q_i'(t) = f_i\left(S^{(0)} - \sum_{i=1}^{n} U_i(t),\ Q_i(t)\right) - \mu_i(Q_i(t))Q_i(t),$$

$$U_i(0) > 0,\ Q_i(0) \geq P_i, \quad 1 \leq i \leq n,\ \sum_{i=1}^{n} U_i(0) \leq S^{(0)}.$$

We note that $U_i(t)$ is the total amount of stored nutrient of i-th species at time t. In the next section, we shall study the reduced limiting system (2.12). The relevant domain for (2.12) is

$$(2.13) \qquad \Omega = \left\{ (U_1, Q_1, \cdots, U_n, Q_n) \in \mathbb{R}^{2n} : \begin{array}{l} \sum_{i=1}^{n} U_i \leq S^{(0)},\ U_k \geq 0, \\ Q_k \geq P_k,\ k = 1, 2, \cdots, n \end{array} \right\},$$

which is positively invariant under (2.12).

LEMMA 2.2. *Let $(S(t), x_1(t), Q_1(t), \ldots, x_n(t), Q_n(t))$ be the sytem of (2.1). For $1 \leq i \leq n$. If either one of the following cases holds,*
    (i) *$\mu_i(Q_i) < D$ for all $Q_i \in [P_i, \infty)$;*
    (ii) *(2.6) holds with $f_i(S, Q_i^*) < \mu_i(Q_i^*)Q_i^*$ for all $S \in [0, S^{(0)}]$;*
    (iii) *(2.6) and (2.7) hold with $S^{(0)} < \lambda_i$;*
then

$$\lim_{t \to \infty} x_i(t) = 0.$$

In the first two case, we denote $\lambda_i = +\infty$.

This lemma states that if the maximal growth rate of the i-th organism is less than the dilution rate D or the input concentration $S^{(0)}$ is too small, the i-th organism will die out as time becomes large. Note that the resulting behavior is competition independent.

Our basic hypothesis is

$$0 < \lambda_1 < \lambda_2 \leq \cdots \leq \lambda_n,$$
$$(H_n)$$
$$\lambda_1 < S^{(0)}.$$

For an equilibrium $E = (S, x_1, Q_1, \cdots, x_n, Q_n)$ of system (2.1), we denote

$$\hat{E} = (U_1, Q_1, \cdots, U_n, Q_n),$$

the corresponding equilibrium of system (2.12).

LEMMA 2.3. *Let* (H_n) *hold, then the equilibrium* $\hat{E}_1$ *is locally asymptotically stable and the rest of equilibria* $\hat{E}_0, \hat{E}_2, \cdots, \hat{E}_n$ *are saddles if they exist. Furthermore if* $S^{(0)} > \lambda_i$, $i = 1, 2, \ldots, n$ *then the stable manifolds of* $\hat{E}_0$ *and* $\hat{E}_k$, $k = 2, 3, \ldots, n$ *are*

$$M^+(\hat{E}_0) = \{(0, Q_1, 0, Q_2, \ldots, 0, Q_n) : P_i < Q_i, \ i = 1, 2, \ldots, n\},$$

and

$$M^+(\hat{E}_k) = \left\{ (0, Q_1, \ldots, 0, Q_{k-1}, U_k, Q_k, \ldots, U_n, Q_n) : \begin{array}{l} P_i < Q_i, \ i = 1, 2, \ldots, n \\ U_i > 0, \ i = k, k+1, \ldots, n \end{array} \right\}.$$

The following is our main theorem.

THEOREM 2.4. *Let* (H_n) *hold. The solution of* (2.1) *satisfies*

$$\lim_{t \to \infty} (S(t), x_1(t), Q_1(t), x_2(t), Q_2(t), \cdots, x_n(t), Q_n(t)) = E_1$$
$$= (\lambda_1, x_1^*, Q_1^*, 0, \hat{Q}_2^1, 0, \hat{Q}_3^1, \cdots, 0, \hat{Q}_n^1).$$

where Q_1^*, λ_1, x_1^*, $\hat{Q}_j^1$, $j = 2, 3, \ldots, n$ *satisfy*

$$\mu_1(Q_1^*) = D,$$
$$f_1(\lambda_1, Q_1^*) = DQ_1^*,$$
$$x_1^* = \frac{S^{(0)} - \lambda_1}{Q_1^*},$$
$$f_j(\lambda_1, \hat{Q}_j^1) = \mu_j(\hat{Q}_j^1)\hat{Q}_j^1, \ j = 2, \ldots, n.$$

This theorem states that under the hypothesis (H_n) only one species survives, the one with the lowest value of λ_i and gives the limiting nutrient concentrations.

3. Proofs.

From differential inequality [H2], the proof of the following Lemma 3.1 is easy and we omit it.

LEMMA 3.1. *Let* $x : \mathbb{R}_+ \to [a, \infty)$, $y : \mathbb{R}_+ \to [b, \infty)$ *and* $g : [a, \infty) \times [b, \infty) \to \mathbb{R}$ *be continuously differentiable and satisfy*

$$x'(t) \leq g(x(t), y(t)), \ t \geq 0.$$

Suppose

$$\frac{\partial g}{\partial x}(x, y) < 0, \ \frac{\partial g}{\partial y}(x, y) > 0,$$

and suppose that for each $y \in [b, \infty)$ *there exists a unique solution* $x^* = x^*(y) \in [a, \infty)$ *of* $g(x, y) = 0$. *If* $\limsup_{t \to \infty} y(t) \leq \alpha$, *then*

$$\limsup_{t \to \infty} x(t) \leq x^*(\alpha).$$

Proof of Lemma 2.1. From (2.2), (2.3), (2.4), it is easy to verify that the solutions $S(t), Q_i(t), x_i(t), 1 \le i \le n$, are positive for all $t \ge 0$. The first equation of (2.1) gives

$$S' \le (S^{(0)} - S)D,$$

then obviously we have

(3.1) $$\limsup_{t \to \infty} S(t) \le S^{(0)}.$$

For $i = 1, 2, \cdots, n$, consider the differential equation of Q_i in (2.1) :

$$Q_i' = f_i(S, Q_i) - \mu_i(Q_i)Q_i.$$

From (2.2), (2.3), (3.1) and Lemma 3.1 it follows that

(3.2) $$\limsup_{t \to \infty} Q_i(t) \le Q_i^0,$$

where $Q_i^0 > P_i$ is defined in (2.5).

Let $T = S + \sum_{i=1}^n Q_i x_i$. Then T satisfies

$$T' = (S^{(0)} - T)D.$$

Therefore

(3.3) $$T = S^{(0)} + O(e^{-Dt}) \text{ as } t \to \infty.$$

Thus the conservation principle (2.10) holds.

Next we show that there exists $\gamma_i > P_i$ and $t_0 > 0$ such that $Q_i(t) \ge \gamma_i$ for $t \ge t_0$. First we show $S(t)$ is bounded below by a constant $\gamma > 0$. Let $U_i = x_i Q_i$. Rewrite first equation in (2.1) as

$$S' + \left(D + \sum_{i=1}^n \frac{U_i}{Q_i} \frac{f_i(S, Q_i)}{S} \right) S = S^{(0)} D,$$

Then from (3.3), (2.3) it follows that

$$S' + \left[D + S^{(0)} \left(\max_{1 \le i \le n} \frac{1}{P_i} \right) \cdot \max_{\substack{1 \le i \le n \\ 0 \le S \le S^{(0)}}} \frac{\partial f_i}{\partial S}(S, P_i) \right] S \ge S^{(0)} D,$$

Then there exists $\gamma > 0$ such that $S(t) \ge \gamma$, $t \ge t_0$.

From (2.1), we have

$$Q_i' = f_i(S, Q_i) - \mu_i(Q_i)Q_i \ge f_i(\gamma, Q_i) - \mu(Q_i)Q_i.$$

Then it follows that $Q_i(t) \ge \gamma_i$ for $t \ge t_0$, where γ_i satisfies

$$f_i(\gamma, \gamma_i) = \mu(\gamma_i)\gamma_i, \ \gamma_i > P_i.$$

For each $1 \le i \le n$, we have

$$x_i(t) = U_i(t)/Q_i(t) \le T(t)/P_i \le (S^{(0)} + \varepsilon)/P_i, \text{ for } t \text{ large}.$$

Consequently the solution

$$(S(t), x_1(t), Q_1(t), \cdots, x_n(t), Q_n(t))$$

is bounded for $t \geq 0$.   □

   Proof of Lemma 2.2. Suppose case (i) holds. Then

(3.4) $\mu_i(Q_i^0) < D,$

where Q_i^0 is defined in (2.5). In case (ii) or (iii), we have

$$f_i(S^{(0)}, Q_i^*) < \mu_i(Q_i^*)Q_i^*.$$

Since $g_i(Q) = f_i(S^{(0)}, Q) - \mu_i(Q)Q$ is strictly decreasing in Q, from (2.5) it follows that $Q_i^* > Q_i^0$. Thus from (2.2) we obtain (3.4) again.

   To complete the proof, it remains to show that the inequality (3.4) implies that $\lim_{t\to\infty} x_i(t) = 0$. Let $\eta = (D - \mu_i(Q_i^0))/2$. Since $\mu_i(Q_i)$ is increasing in Q_i, there exists $\delta > 0$ such that

$$\mu_i(Q_i) \leq \mu_i(Q_i^0) + \eta = D - \eta \quad \text{whenever } Q_i \leq Q_i^0 + \delta.$$

By (3.2) there exists $t_\delta > 0$ such that

$$Q_i(t) < Q_i^0 + \delta \text{ for all } t \geq T_\delta > 0.$$

It follows that

$$
\begin{aligned}
x_i(t) &= x_i(T_\delta) \exp\left(\int_{T_\delta}^t (\mu_i(Q_i(\tau)) - D)\, d\tau \right) \\
&\leq x_i(T_\delta)e^{-\eta(t-T_\delta)} \to 0 \text{ as } t \to \infty. \quad \square
\end{aligned}
$$

   Proof of Lemma 2.3. Assume the equilibrium $\hat{E}$ takes of the form

$$\hat{E} = (U_1, Q_1, \cdots, U_n, Q_n).$$

Let the variational matrix evaluated at $\hat{E}$ be $J(\hat{E}) = (a_{ij})_{i,j=1}^{2n}$.

   Let $\hat{E} = \hat{E}_0$. Then it is easy to verify that the eigenvalues of $J(\hat{E}_0)$ are $a_{11}, a_{22}, \ldots, a_{2n,2n}$, where

$$a_{2i-1,2i-1} = \mu_i(Q_i^0) - D,$$

(3.5) $a_{2i,2i} = \dfrac{\partial f_i}{\partial Q_i}(S^{(0)}, Q_i^0) - \mu_i'(Q_i^0)Q_i^0 - \mu_i(Q_i^0) < 0, \ i = 1, 2, \ldots n.$

From (2.3), (2.5), (2.7) we have $S^{(0)} > \lambda_i$ if and only if $Q_i^0 > Q_i^*$. Therefore

$$a_{1,1} > \mu_1(Q_1^*) - D = 0,$$

and consequently $\hat{E}_0$ is unstable. Furthermore it is a saddle since (3.5) holds. It is easy to verify that if $S^{(0)} > \lambda_i$, $i = 1, 2, \ldots, n$ then $a_{2i-1,2i-1} > 0$, $i = 1, 2, \ldots, n$ and $\hat{E}_0$ is a saddle point with n-dimensional stable manifold

$$M^+(\hat{E}_0) = \{(0, Q_1, 0, Q_2, \ldots, 0, Q_n) : P_i < Q_i, \ i = 1, 2, \ldots, n\}.$$

Let $\hat{E} = \hat{E}_k$, $1 \le k \le n$. Then for $i \ne k$,

$$a_{2i-1,2i-1} = \mu_i(\hat{Q}_i^k) - D,$$
$$a_{2i,2i} = \frac{\partial f_i}{\partial Q_i}(\lambda_k, \hat{Q}_i^k) - \hat{Q}_i^k \mu_i'(\hat{Q}_i^k) - \mu_i(\hat{Q}_i^k) < 0.$$

It is easy to verify that the set of eigenvalues of $J(\hat{E}_k)$ is the union of

$$\{a_{2i-1,2i-1}, a_{2i,2i} : 1 \le i \le n, i \ne k\},$$

and the set of eigenvalues of M_k where

$$M_k = \begin{pmatrix} -\frac{\partial f_k}{\partial S} x_k^* & -f_k(\lambda_k, Q_k^*) \frac{x_k^*}{Q_k^*} + \frac{\partial f_k}{\partial Q_k} x_k^* \\ -\frac{\partial f_k}{\partial S} & \frac{\partial f_k}{\partial Q_k} - \mu_k' Q_k^* - \mu_k \end{pmatrix}.$$

Since

$$\mathrm{trace}(M_k) = -\frac{\partial f_k}{\partial S} x_k^* + \frac{\partial f_k}{\partial Q_k} - \mu_k' Q_k^* - \mu_k < 0,$$
$$\det(M_k) = \frac{\partial f_k}{\partial S} x_k^* \mu_k' Q_k^* > 0,$$

the eigenvalues of M_k have negative real part.

Consider $\hat{E} = \hat{E}_1$. The assumption (H_n) implies that

(3.6) $$\hat{Q}_i^1 < Q_i^*, \quad i = 2, \cdots, n.$$

Therefore from (3.6) it follows that

$$a_{2i-1,2i-1} = \mu_i(\hat{Q}_i^1) - D < \mu_i(Q_i^*) - D = 0, \quad i = 2, \cdots, n,$$

and consequently $\hat{E}_1$ is locally asymptotically stable.

Consider $\hat{E} = \hat{E}_k$, $k \in \{2, \ldots, n\}$. The assumption (H_n) implies that $\lambda_1 < \lambda_k$. Then from (2.3) we have

$$f_1(\lambda_1, \hat{Q}_1^k) < f_1(\lambda_k, \hat{Q}_1^k) = \mu_1(\hat{Q}_1^k)\hat{Q}_1^k,$$
$$f_1(\lambda_1, \hat{Q}_1^k) - \mu_1(\hat{Q}_1^k)\hat{Q}_1^k < 0 = f_1(\lambda_1, Q_1^*) - \mu_1(\hat{Q}_1^*)Q_1^*.$$

Thus

$$Q_1^* < \hat{Q}_1^k.$$

Therefore

$$a_{1,1} = \mu_1(\hat{Q}_1^k) - D > \mu_1(Q_1^*) - D = 0,$$

and consequently $\hat{E}_k$ is unstable. Furthermore from (3.5) it is a saddle . Similarly it is easy to verify that if $S^{(0)} > \lambda_i$, $i = 1, 2, \ldots, n$, then $a_{2i-1,2i-1} > 0$, $i = 1, 2, \ldots, k-1$ and $\hat{E}_k$ is a saddle point with $(2n + 1 - k)$-dimensional stable manifold. From the results of ([SW1]) and induction on n, it follows that

$$M^+(\hat{E}_k) = \left\{ (0, Q_1, \ldots, 0, Q_{k-1}, U_k, Q_k, \ldots, U_n, Q_n) : \begin{array}{l} P_i < Q_i, \\ i = 1, 2, \ldots, n \end{array} \right\}. \qquad \square$$

We note now the following lemma

LEMMA 3.2. ([C]) Let $f(t) \in C^2[t_0, \infty)$. If $f(t) \to$ constant and $|f''(t)|$ is bounded for $t \geq t_0$, then

$$\lim_{t \to \infty} f'(t) = 0.$$

The following is so called the "fluctuating lemma" which will be used to prove our main result.

LEMMA 3.3. ([HHG]) Let $f : \mathbb{R}_+ \to \mathbb{R}$ be a differentiable function. If

$$\liminf_{t \to \infty} f(t) < \limsup_{t \to \infty} f(t),$$

then there are sequence $\{t_m\} \nearrow \infty$ and $\{\tau_m\} \nearrow \infty$ such that for all m

$$f'(t_m) = 0, \quad f(t_m) \to \limsup_{t \to \infty} f(t) \ as \ m \to \infty,$$
$$f'(\tau_m) = 0, \quad f(\tau_m) \to \liminf_{t \to \infty} f(t) \ as \ m \to \infty.$$

Now we prove our main result of this paper

LEMMA 3.4. Let $S(t) = S^{(0)} - \sum_{i=1}^n U_i(t)$. Consider the solution

$$(U_1(t), Q_1(t), \cdots, U_n(t), Q_n(t))$$

of the reduced system (2.12) with initial conditions $U_i(0) > 0, Q_i(0) \geq P_i$, $1 \leq i \leq n$, $S(0) \geq 0$. Suppose $\lim_{t \to \infty} S(t)$ does not exist, then $\limsup_{t \to \infty} S(t) \leq \lambda_j$ for some $j \in \{1, 2, \cdots, n\}$.

Proof. Since $\lim_{t \to \infty} S(t)$ does not exist, it follows that

$$\liminf_{t \to \infty} S(t) < \limsup_{t \to \infty} S(t).$$

From Lemma 3.3, there exists $\{t_m\} \nearrow \infty$ such that

(3.7) $\qquad S'(t_m) = 0 \quad$ and $\quad S(t_m) \to \limsup_{t \to \infty} S(t)$ as $m \to \infty$.

Since

$$S'(t) = -(U_1'(t) + \ldots + U_n'(t)),$$

for each t_m there exists $j_m \in \{1, 2, \cdots, n\}$ such that

$$U_{j_m}'(t_m) \leq 0, \quad m = 1, 2, \cdots.$$

We may choose a subsequence $\{\bar{t}_m\}$ of $\{t_m\}$ such that

$$U_j'(\bar{t}_m) \leq 0,$$

for some $j \in \{1, 2, \cdots, n\}$ and for all m. Thus without loss of generality we may assume

$$U_j'(t_m) \leq 0,$$

for some $j \in \{1, 2, \cdots, n\}$ and for all m. Thus

$$f_j(S(t_m), Q_j(t_m)) \leq DQ_j(t_m).$$

Let $\gamma_S = \limsup_{t \to \infty} S(t)$ and $\gamma_Q = \limsup_{t \to \infty} Q(t)$. Let $\{\tilde{t}_m\}$ be a subsequence of $\{t_m\}$ such that $\lim_{m \to \infty} Q_j(\tilde{t}_m) = \bar{Q}_j$. Then $\bar{Q}_j \leq \limsup_{t \to \infty} Q(t) = \gamma_Q$, and from above inequality we have $f_j(\gamma_S, \bar{Q}_j) \leq D\bar{Q}_j$. Since $f_j(\gamma_S, Q_j) - DQ_j$ is strictly decreasing in Q_j, then $f_j(\gamma_S, \gamma_Q) - D\gamma_Q < f_j(\gamma_S, \bar{Q}_j) - D\bar{Q}_j \leq 0$. Thus we have

(3.8) $$f_j(\gamma_S, \gamma_Q) < D\gamma_Q.$$

Consider the differential equation of Q_j in (2.1) :

(3.9) $$Q_j' = f_j(S, Q_j) - \mu_j(Q_j)Q_j.$$

From (3.1), (2.3) and Lemma 3.1 it follows that

(3.10) $$\gamma_Q = \limsup_{t \to \infty} Q_j(t) \leq K^{(0)},$$

where

(3.11) $$f_j(S^{(0)}, K^{(0)}) - \mu_j(K^{(0)})K^{(0)} = 0.$$

If $\lambda_j > S^0$, from (3.1) the assertion of the lemma holds. Thus we assume $\lambda_j \leq S^0$. From (2.3) and (3.11) it follows that

$$f_j(\lambda_j, K^{(0)}) - \mu_j(K^{(0)})K^{(0)} \leq 0.$$

Compare the above inequality with (2.7) :

(3.12) $$f_j(\lambda_j, Q_j^*) - \mu_j(Q_j^*)Q_j^* = 0.$$

From (2.2), (2.3), (3.11), (3.12) it follows that

(3.13) $$K^{(0)} \geq Q_j^*.$$

Let $L^{(1)}$ satisfy

(3.14) $$f_j(L^{(1)}, K^{(0)}) - DK^{(0)} = 0.$$

Then from (2.3), (3.10) we have

$$0 = f_j(L^{(1)}, K^{(0)}) - DK^{(0)} \leq f_j(L^{(1)}, \gamma_Q) - D\gamma_Q.$$

From (2.3), (3.8), it follows that

$$f_j(L^{(1)}, \gamma_Q) \geq D\gamma_Q \geq f_j(\gamma_S, \gamma_Q),$$

(3.15) $$\gamma_S \leq L^{(1)}.$$

Since $K^{(0)} \geq Q_j^*$, from (3.14) and (2.3) it follows that

$$f_j(L^{(1)}, Q_j^*) - DQ_j^* \geq 0.$$

From (3.12) we have

$$L^{(1)} \geq \lambda_j.$$

On the other hand, the inequality $K^{(0)} \geq Q_j^*$ implies that

$$f_j(L^{(1)}, K^{(0)}) = DK^{(0)} = \mu_j(Q_j^*)K^{(0)} \leq \mu_j(K^{(0)})K^{(0)} = f_j(S^{(0)}, K^{(0)}).$$

Thus we have

(3.16) $$S^{(0)} \geq L^{(1)} \geq \lambda_j.$$

By (3.9), (3.15) and Lemma 3.1, we have

(3.17) $$\limsup_{t \to \infty} Q_j(t) \leq K^{(1)},$$

where

(3.18) $$f_j(L^{(1)}, K^{(1)}) = \mu_j(K^{(1)})K^{(1)}.$$

Since $\lambda_j \leq L^{(1)}$, it follows that

$$f_j(\lambda_j, K^{(1)}) - \mu_j(K^{(1)})K^{(1)} \leq 0.$$

By (3.12), we have

$$K^{(1)} \geq Q_j^*.$$

Since $S^{(0)} \geq L^{(1)}$, from (3.11), (3.16), (3.18) it follows that

(3.19) $$K^{(0)} \geq K^{(1)} \geq Q_j^*.$$

Inductively we construct two sequences $\{L^{(m)}\}_{m=1}^{\infty}$ and $\{K^{(m)}\}_{m=1}^{\infty}$ satisfying

$$S^{(0)} \geq L^{(1)} \geq L^{(2)} \geq \ldots \geq \lambda_j,$$
$$K^{(0)} \geq K^{(1)} \geq K^{(2)} \geq \ldots \geq Q_j^*,$$

and for any $m = 1, 2, \cdots,$

(3.20) $$\limsup_{t \to \infty} S(t) \leq L^{(m)},$$
$$\limsup_{t \to \infty} Q_j(t) \leq K^{(m)},$$

(3.21) $$f_j(L^{(m+1)}, K^{(m)}) = DK^{(m)},$$
$$f_j(L^{(m)}, K^{(m)}) = \mu_j(K^{(m)})K^{(m)}.$$

Let $L = \lim_{m \to \infty} L^{(m)}$ and $K = \lim_{m \to \infty} K^{(m)}$. Then from (3.21) it follow that

$$f_j(L, K) = DK,$$
$$f_j(L, K) = \mu_j(K)K.$$

Thus $K = Q_j^*$ and $L = \lambda_j$. By (3.20) it follows that

$$\limsup_{t \to \infty} S(t) \leq \lambda_j,$$
$$\limsup_{t \to \infty} Q_j(t) \leq Q_j^*.$$

Hence we complete the proof of Lemma 3.4. $\square$

THEOREM 3.5. *Let* $(\mathrm{H_n})$ *hold. Then the solution*

$$(U_1(t), Q_1(t), \cdots, U_n(t), Q_n(t))$$

of the reduced system (2.12) *in the relevant domain* Ω *(See* (2.13)*) satisfies*

(3.22) $$\lim_{t \to \infty} (U_1(t), Q_1(t), \cdots, U_n(t), Q_n(t)) = \hat{E}_1 = (U_1^*, Q_1^*, 0, \hat{Q}_2^1, \cdots, 0, \hat{Q}_n^1).$$

Proof. Let $S(t) = S^{(0)} - \sum_{i=1}^n U_i(t)$. If $\lim_{t \to \infty} S(t)$ exists, we claim that $\lim_{t \to \infty} S(t) = \lambda_1$. Let $\lim_{t \to \infty} S(t) = c$.

If $c > \lambda_1$ then for $\varepsilon > 0$ small there exists $T_\varepsilon > 0$ such that

$$Q_1' > f_1(\lambda_1 + \varepsilon, Q_1) - \mu_1(Q_1)Q_1, \text{ for } t \geq \mathrm{T}_\varepsilon.$$

Thus $Q_1(t) \geq Q_1^* + \eta$, $\eta > 0$ small, $t \geq T_\varepsilon$. Hence

$$\frac{x_1'}{x_1} = \mu_1(Q_1) - D \geq \mu_1(Q_1^* + \eta) - D > 0.$$

Then $x_1(t)$ is unbounded for $t \geq T_\varepsilon$. This is a contradiction to Lemma 2.1.

If $c < \lambda_1$ then for $2 \leq i \leq n$, by the differential equation of Q_i in (2.1) and Lemma 3.1, we have $\limsup_{t \to \infty} Q_1(t) < Q_1^*$ and $\limsup_{t \to \infty} Q_i(t) < \hat{Q}_i^1$ for $2 \leq i \leq n$. Hence from (3.6) $\lim_{t \to \infty} x_i(t) = 0$, $1 \leq i \leq n$ and $\lim_{t \to \infty} S(t) = S^{(0)} < \lambda_1$. This is a contradiction to $(\mathrm{H_n})$.

Obviously from Lemma 3.2, $\lim_{t \to \infty} S(t) = \lambda_1$ implies

$$\lim_{t \to \infty} Q_i(t) = \hat{Q}_i^1, \ \lim_{t \to \infty} x_i(t) = 0, \ 2 \leq i \leq n;$$
$$\lim_{t \to \infty} Q_1(t) = Q_1^*, \ \lim_{t \to \infty} x_1(t) = x_1^*.$$

Thus the trajectory $(U_1(t), Q_1(t), \cdots, U_n(t), Q_n(t))$ tends to $\hat{E}_1$ as $t \to \infty$.

If $\lim_{t \to \infty} S(t)$ does not exist, then $\limsup_{t \to \infty} S(t) > \liminf_{t \to \infty} S(t)$. From Lemma 3.4, we have $\limsup_{t \to \infty} S(t) \leq \lambda_j$ for some $j \in \{1, 2, \cdots, n\}$. From $(\mathrm{H_n})$, we have

$$\limsup_{t \to \infty} S(t) \leq \lambda_n.$$

Assume (2.6) and (2.7) hold. Consider the differential equation of Q_n in (2.1) :

$$Q_n' = f_n(S, Q_n) - \mu_n(Q_n)Q_n.$$

From Lemma 3.1 it follows that

$$\limsup_{t \to \infty} Q_n(t) \leq \tilde{Q}_n,$$

where $\tilde{Q}_n$ satisfies

$$f_n(\lambda_n, \tilde{Q}_n) = \mu_n(\tilde{Q}_n)\tilde{Q}_n.$$

From (2.7) it follows that $\tilde{Q}_n = Q_n^*$. Thus

(3.23) $$\limsup_{t\to\infty} Q_n(t) \le Q_n^*.$$

Let

$$\kappa_n = \liminf_{t\to\infty} Q_n(t).$$

If $\kappa_n = Q_n^*$, then $\lim_{t\to\infty} Q_n(t) = Q_n^*$. From (3.23) and Lemma 3.2, we have $\lim_{t\to\infty} S(t) = \lambda_n$, which contradicts to the assumption that $\lim_{t\to\infty} S(t)$ does not exist. Hence we have $\kappa_n < Q_n^*$. Let

$$y_0 = (U_1(0), Q_1(0), \cdots, U_n(0), Q_n(0)), \ U_i(0) > 0, \ Q_i(0) \ge P_i(0), \ \text{for } 1 \le i \le n.$$

Next we claim that the ω-limit set $\omega(y_0)$ satisfies

(3.24) $$\omega(y_0) \cap (\{(U_1, Q_1, \cdots, U_n, Q_n) : U_n = 0\} \setminus M) \ne \emptyset,$$

where

$$M := \left(M^+(\hat{E}_0) \bigcup M^+(\hat{E}_2) \bigcup \cdots \bigcup M^+(\hat{E}_n)\right),$$

$M^+(\hat{E})$ denotes the stable manifold of the equilibrium $\hat{E}$. First we prove that

$$\omega(y_0) \setminus M \ne \emptyset.$$

If not, then $\omega(y_0) \subseteq M$. It is easy to show that $\omega(y_0) \ne \{\hat{E}_0\}$. If $\hat{E}_0 \in \omega(y_0)$ then from Bulter-McGhee Lemma [BFW], there exists a point

$$q \in \left(M^+(\hat{E}_0) \setminus \{\hat{E}_0\}\right) \bigcap \omega(y_0).$$

Then the negative orbit $O^-(q) \subseteq \omega(y_0)$. But from Lemma 2.3, $O^-(q)$ is either unbounded or $(0, P_1, 0, P_2, \ldots, 0, P_n) \in O^-(q)$. This contradicts to Lemma 2.1. Assume $\hat{E}_k \in \omega(y_0)$ for some $k \in \{2, \ldots, n\}$. Obviously $\omega(y_0) \ne \{\hat{E}_k\}$. If $\hat{E}_k \in \omega(y_0)$ then from Bulter-McGhee Lemma, there exists a point $q \in \left(M^+(\hat{E}_k) \setminus \{\hat{E}_k\}\right) \bigcap \omega(y_0)$. Then from Lemma 2.3 the negative orbit $O^-(q)$ is unbounded or $\hat{E}_0 \in O^-(q)$ or $(0, P_1, \ldots, 0, P_{k-1}, U_k, P_k, \ldots, U_n, P_n) \in O^-(q)$ for some $U_k, \ldots, U_n$. For any one of three cases, we obtain contradiction.

Since $y_0 \notin M$, we may choose

(3.25) $$\bar{y}_0 = (\bar{U}_1(0), \bar{Q}_1(0), \cdots, \bar{U}_n(0), \bar{Q}_n(0)) \in (\omega(y_0) \setminus M).$$

Consider the solution of (2.12)

$$y(t, \bar{y}_0) = (U_1(t; \bar{y}_0), Q_1(t; \bar{y}_0), \cdots, U_n(t; \bar{y}_0), Q_n(t; \bar{y}_0)).$$

From (3.23) and the positive invariance of $\omega(y_0)$, we have

$$Q_n(t, \bar{y}_0) \le Q_n^*, \quad t \ge 0.$$

Thus

(3.26)
$$\mu_n(Q_n(t; \bar{y}_0)) - D \leq 0, \quad t \geq 0.$$

Let

$$\eta = D - \mu_n \left(\frac{Q_n^* + \kappa_n}{2} \right) > 0,$$

and

$$\Lambda(t) = \left\{ \tau \; : \; 0 \leq \tau \leq t, \; Q_n(\tau; \bar{y}_0) \leq \frac{Q_n^* + \kappa_n}{2} \right\}, \quad t \geq 0.$$

Then

$$\mu_n \left(Q_n(\tau, \bar{y}_0) \right) - D < -\eta, \quad \tau \in \Lambda(t).$$

Since $Q_n'(t; \bar{y}_0)$ is uniformly bounded for $t \in [0, \infty)$, $Q_n(t; \bar{y}_0)$ is uniformly continuous on $[0, \infty)$. Let $\{\tau_m\} \nearrow \infty$ satisfies $Q_n(\tau_m; \bar{y}_0) \to \kappa_n$ as $m \to \infty$. Then given

$$\varepsilon = \frac{Q_n^* + \kappa_n}{2} - \kappa_n > 0,$$

there exists $\delta = \delta(\varepsilon) > 0$ such that

$$|Q_n(\tau; \bar{y}_0) - \kappa_n| < \varepsilon \text{ whenever } |\tau - \tau_m| < \delta.$$

Hence

$$Q_n(\tau; \bar{y}_0) < \kappa_n + \varepsilon = \frac{Q_n^* + \kappa_n}{2} \quad \text{for } -\delta < \tau - \tau_m < \delta,$$

and therefore

$$|\Lambda(t)| \to +\infty \text{ as } t \to \infty.$$

Since

$$x_n'(t; \bar{y}_0) = (\mu_n(Q_n(t; \bar{y}_0)) - D)x_n(t; \bar{y}_0),$$

it follows that

$$x_n(t; \bar{y}_0) = x_n(0; \bar{y}_0) \exp \left(\int_0^t (\mu_n(Q_n(\tau; \bar{y}_0) - D) \, d\tau \right)$$

$$\leq x_n(0; \bar{y}_0) \exp \left(\int_{\Lambda(t)} (\mu_n(Q_n(\tau; \bar{y}_0) - D) \, d\tau \right)$$

$$\leq x_n(0; \bar{y}_0) e^{-\eta|\Lambda(t)|} \to 0 \text{ as } t \to \infty.$$

Therefore

$$\limsup_{t \to \infty} U_n(t; \bar{y}_0) \leq \left(\limsup_{t \to \infty} x_n(t; \bar{y}_0) \right) \left(\limsup_{t \to \infty} Q_n(t; \bar{y}_0) \right)$$

$$\leq \left(\limsup_{t \to \infty} x_n(t; \bar{y}_0) \right) Q_n^* = 0.$$

Hence

$$\omega(\bar{y}_0) \subseteq \{(U_1, Q_1, \cdots, U_n, Q_n) \in \Omega : U_n = 0\}.$$

Since $\bar{y}_0 \notin M$ by (3.25), it follows that

$$\omega(\bar{y}_0) \cap (\{(U_1, Q_1, \cdots, U_n, Q_n) \in \Omega : U_n = 0\} \setminus M) \neq \emptyset.$$

By the invariance of ω-limit sets, we have

$$\omega(\bar{y}_0) \subseteq \omega(y_0).$$

It follows that

$$\omega(y_0) \cap (\{(U_1, Q_1, \cdots, U_n, Q_n) \in \Omega : U_n = 0\} \setminus M) \neq \emptyset.$$

Continuing the above arguments, we consider the systems (2.12) with $1 \leq i \leq n-1$. Then from the positive invariance of ω-limit set,

$$\omega(y_0) \cap (\{(U_1, Q_1, \cdots, U_n, Q_n) \in \Omega : U_{n-1} = U_n = 0\} \setminus M) \neq \emptyset.$$

Inductively we have

$$\omega(y_0) \cap (\Gamma \setminus M) \neq \emptyset,$$

where

$$\Gamma = \{(U_1, Q_1, \cdots, U_n, Q_n) \in \Omega : U_2 = U_3 = \cdots = U_n = 0\}.$$

In particular,

$$\omega(y_0) \cap (\Gamma \setminus \{\hat{E}_0\}) \neq \emptyset,$$

It is easy to verify that

$$\omega(\Gamma \setminus \{\hat{E}_0\}) = \{\hat{E}_1\}.$$

Consequently we have

$$\hat{E}_1 \in \omega(y_0).$$

By Lemma 2.3, the assumption (H_n) implies that $\hat{E}_1$ is asymptotically stable. Thus

$$\omega(y_0) = \{\hat{E}_1\}.$$

That is,

$$\lim_{t \to \infty} (U_1(t), Q_1(t), \cdots, U_n(t), Q_n(t)) = \hat{E}_1.$$

The above equality contradicts to the assumption that $\lim_{t \to \infty} S(t)$ does not exist. Thus $\lim_{t \to \infty} S(t)$ exists and we complete the proof of Theorem 3.5. $\square$

Proof of Theorem 2.4. From Lemma 2.1 all solutions of the system (2.1) with initial condition $S(0) > 0, x_i(0) > 0, Q_i(0) \geq P_i$ asymptotically approach

$$S + \sum_{i=1}^{n} U_i = S^{(0)},$$

as $t \to \infty$. Hence the system (2.12) is the reduced limiting system of (2.1). To apply (Theorem 4.2 [Th]), we note that the equilibria of (2.12) are isolated invariant sets of (2.12) and by Theorem 3.5, every solution of (2.12) converges to the equilibrium $\hat{E}_1 = (U_1^*, Q_1^*, 0, \hat{Q}_2^1, \cdots, 0, \hat{Q}_n^1)$. Furthermore, we conclude from ([Th], Theorem 4.2) that every solution of (2.1) converges to the equilibrium

$$E_1 = (\lambda_1, x_1^*, Q_1^*, 0, \hat{Q}_2^1, 0, \hat{Q}_3^1, \cdots, 0, \hat{Q}_n^1). \qquad \square$$

4. Disussion. It is well-known that the competitive exclusion principle holds for microorganisms competing for a single-limited nutrient in a chemostat when the yields of organisms are assumed to be fixed constants ([HHW],[H1]). In phytoplankton ecology, it has long been known that yield is not constant and it can vary depending on the growth rate [D]. This led to the formulation of the variable-yield model, or the internal storage model. In this paper we proved that the competitive exclusion principle also holds for the variable-yield model in case of single-limited nutrient. Mathematically we extend the result of competitive exclusion in [SW1] from two species to arbitary n species. Biologically the internal storage model with one limiting nutrient has been tested successfully in both constant and fluctuating environments ([G3],[SC]). It is more realistic than the constant-yield model.

However organisms require multiple nutrients to live and reproduce. In phytoplankton ecology, there are many studies in the competition of species for multiple nutrients. A. Narang and S. Pilyugin [NP] studied the dynamics of micorbial growth by constructing some new physiological models. In [LC] Legovic and Cruzado proposed an internal storage model of one species consuming multiple complementary nutrients in a continuous culture. Then in [LLSK] Leenheer and et proved the global stability for the above model by the method of monotone dynamical systems. B. Li and Hal Smith [LS1] studied the internal storage model for two species competing for two complementary nutrients. By using the method of monotone dynamical systems, they established the global dynamics of the model. It is shown that basically the model exhibits the familiar Lotka-Volterra alternatives: competitive exclusion, stable coexistence and bi-stability. In phytoplankton ecology, many people studied the competition of organisms for multiple complementary nutrients by using the internal storage model. In [KL] C. Klausmeier and E. Litchman studied the phytoplankton growth and stoichiometry under multiple nutrient limitation. In [KLL] Klausmeier and et. studied the case of two species and two essential nutrients and suggest the experimental tests for the model. In [LKMSF] the authors studied the multiple-nutrient, multiple-group model for phytoplankton communities and listed many biological parameters in the internal storage model.

We conjecture that for internal storage model there are at most two species survive for the case of n organisms competing for two complementary nutrients. We note that even in the classical model of fixed yields, the conjecture is still unsolved [LS2]. It is also interesting to compare the mathematical analysis results of internal storage model to those of the classical constant-yield model in the case of three or more complementary nutrients [PH]. These will be our work in the future.

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