

Exploitative Competition in a Chemostat for Two Complementary Resources

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Abstract. A model of the chemostat involving n species of microorganisms competing for two perfectly complementary, growth-limiting nutrients is considered. A general class of functions is used for nutrient uptake which includes monotone increasing functions. The predicted biological conditions for the survive of one species and coexistence of two species are presented in detail. The results generalize those of Hsu, Cheng, and Hubbell [13] as well as Butler and Wolkowicz [6] where only two species are considered.

Short Title. competition in a chemostat

Keywords. chemostat, competition in chemostat, competitive exclusion principle, coexistence, globally asymptotic behavior

AMS Classification. 92A15, 92A17, 34C15, 34C35

*This research was supported by the Institute for Mathematics and its Applications Postdoctoral Fellowship with funds provided by the National Science Foundation.

1 Introduction

The classical theory of ecological competition is attributed to Lotka [17] and Volterra [32]. It seeks to describe population dynamics without being specific about which limiting resources are and how effectively these limiting resources are utilized by competitors. These models are usually more phenomenological than predictive, as it is difficult to measure the important parameters in the theory without actually growing the species together in competition.

Over the past fifty years or so, a more mechanistic, resource-based theory of ecological competition has been developed (see, e.g. [10], [16], [20], [23], [27], and [28]). This theory considers the dynamics of the resources explicitly as well as the population dynamics of the competing species. In comparison with the classical models, the resource-based models may be less general and more difficult to analyze (see, e.g., [1], [14], and [33]). However, the resource-based models are often more predictive because the parameters can be measured on species alone (see, e.g., Hansen and Hubbell [9]).

The simplest form of resource-based competition occurs in laboratory apparatus, called a chemostat or continuous culture. See the monograph of Smith and Waltman [26] for a description of chemostat in detail and for the general theory of the chemostat. When a species grows on a single limiting nutrient, there is a so called “break-even” concentration of this nutrient at which growth rate just balances removal rate. If there are more than one species competing for the nutrient and the functions for nutrient uptake are monotone increasing or nonmonotone but with certain restrictions, then only the species with lowest break-even concentration survives (see, e.g., [5], [12], [18], [19], [34] and [35]). This is often referred as the “competitive exclusion principle”.

When there are two or more limiting nutrients in the chemostat, it becomes necessary to consider how the nutrients, once consumed, interact to promote growth. Leon and Tumpson [16] and Rapport [22] classify nutrients as perfectly complementary, perfectly substitutable, or imperfectly substitutable. Perfectly complementary nutrients are nutrients of different essential substances which are independently required for growth, such as a carbon source and a nitrogen source for a bacterium. On the other hand, perfectly substitutable nutrients are alternative sources of an essential substance, and represent interdependent requirement for growth, such as two carbon sources for phosphorous. The intermediate case is called imperfectly substitutable.

Chemostat models with two perfectly complementary nutrients have been studied in [2], [6], [13], [16], [22], [24], [25], and [33], and related experiments are described in [2], [24] and [25]. For models with two perfectly substitutable nutrients and two species, see Waltman, Hubble and Hsu [33], Bally and Wolkowicz [3]-[4]. For other related work, see [2], [7], [21] and [29]. In the case in which there are two perfectly complementary nutrients and two species and each competitor's functional response is monotone increasing, Leon and Tumpson [16] find conditions for the existence of a locally asymptotically stable interior steady state and hence conditions for the coexistence of two competitors. Hsu, Cheng, and Hubbell [13], on the other hand, give a complete global analysis of the model with two competitors under the assumption that consumptions of the nutrients follows Michaelis-Menten kinetics, generalized to the two nutrient situation. They give biological conditions based on parameters that predict the outcome of the competition. They conclude that "each of the four outcomes of classical Lotka-Volterra two-species competition theory has multiple mechanistic origins in terms of consumer resource interactions." Their proofs are actually also valid for monotone increasing nutrient uptake functions.

Butler and Wolkowicz [6] give different proofs in the case of monotone increasing response functions and two species. They also study the case in which at least one of the two competitors is inhibited by high concentration of the substrate. They construct examples for which there is a stable periodic solution and examples for which coexistence is possible but surprisingly neither competitors can survive in the absence of its rival.

In this paper, we consider a competition model which describes how n microorganisms compete exploitatively for two perfectly complementary nutrients S and R . We shall say that a species is S -limit (R -limit) if its per capita consumption rate of R (S) is independent of R (S). This paper is organized as follows. In the next section, we present a model that generalizes the models in Hsu, Cheng and Hubbell [13] and Butler and Wolkowicz [6] by allowing more species. In this model we assume a general class of response functions for nutrient uptake, which includes monotone increasing functions. Section 3 deals with existence and local stability of steady states. In section 4, we provide global stability analysis of steady states for the reduced system, which is derived from the “conservation principle”. Section 5 presents global stability results for the steady states of the full system as well as biological discussions. We conclude the paper with a discussion section which consists of a summary of results and comments.

2 The Model

We study the following model of n species of microorganisms competing for two perfectly complementary nutrients in a chemostat:

$$\begin{aligned}
S'(t) &= (S^0 - S(t))D - \sum_{i=1}^n \frac{x_i(t)}{y_{S_i}} f_i(S(t), R(t)), \\
R'(t) &= (R^0 - R(t))D - \sum_{i=1}^n \frac{x_i(t)}{y_{R_i}} f_i(S(t), R(t)), \\
x'_i(t) &= x_i(t)(f_i(S(t), R(t)) - D), \quad i = 1, 2, \dots, n,
\end{aligned} \tag{2. 1}$$

where $S(0) \geq 0$ and $x_i(0) > 0$, $i = 1, 2, \dots, n$, and

$$f_i(S(t), R(t)) = \min(p_i(S(t)), q_i(R(t))), \quad i = 1, 2, \dots, n.$$

In model (2.1), $S(t)$ and $R(t)$ denote the concentrations of the two nonreproducing, perfectly complementary nutrients at time t , and $x_i(t)$ denotes the density of the i th population of microorganisms at time t ; $p_i(S(t))$ ($q_i(R(t))$) represents the per-capita growth rate of the i th population when nutrient S is limiting (nutrient R is limiting), and so $f_i(S(t), R(t))$ is the function that represents the rate of conversion of nutrient to biomass for the i th population. We take the minimum here because the resources are perfectly complementary. We assume that growth rates adjust instantaneously to change in the nutrient concentration. $f_i(S, R)/y_{S_i}$ ($f_i(S, R)/y_{R_i}$) represents the uptake rate of nutrient S (nutrient R) of the i th population; and so y_{S_i} and y_{R_i} are growth yield constants. If only one feed bottle is used in the chemostat, then S^0 and R^0 denote, the concentrations of the growth limiting nutrients S and R respectively in the feed bottle, and D denotes the flow rate of the chemostat. Here we assume that the growth vessel is well stirred, so that nutrients and microorganisms are removed in proportion to their concentrations. We also assume that individual death rates of populations are insignificant compared to the flow rate D .

If two separate feed bottles are used, with each containing only one nutrient, and input from each feed bottle to the growth vessel at different rates, say rate D_S from the bottle containing nutrient S , and rate D_R from the bottle containing nutrient R ,

then $D = D_S + D_R$, $S^0 = (\bar{S}^0 D_S)/(D_S + D_R)$, and $R^0 = (\bar{R}^0 D_R)/(D_S + D_R)$, where \bar{S}^0 and \bar{R}^0 represent the concentrations of nutrients S and R , respectively, in each separate bottle.

We make the following assumptions on functions p_i and q_i :

$$p_i, q_i : R_+ \rightarrow R_+; \quad (2. 2)$$

$$p_i, q_i \text{ are continuously differentiable,} \quad (2. 3)$$

$$p_i(0) = 0, \quad q_i(0) = 0, \quad (2. 4)$$

and there exist positive extended real numbers λ_{S_i} and λ_{R_i} such that

$$\begin{aligned} p_i(S) < D & \text{ for } S \in (0, \lambda_{S_i}) \quad \text{and} \quad p_i(S) > D & \text{ for } S \in (\lambda_{S_i}, +\infty), \\ q_i(R) < D & \text{ for } R \in (0, \lambda_{R_i}) \quad \text{and} \quad q_i(R) > D & \text{ for } R \in (\lambda_{R_i}, +\infty). \end{aligned} \quad (2. 5)$$

Thus λ_{S_i} and λ_{R_i} are the break-even concentrations for nutrient S and R respectively, when the nutrient is limiting. In the case where $p_i(S) < D$ ($q_i(R) < D$) for all $S > 0$ ($R > 0$), then we regard $\lambda_{S_i} = +\infty$ ($\lambda_{R_i} = +\infty$).

We make the following generic assumptions:

$$\begin{aligned} \text{If } \lambda_{S_i} \text{ (} \lambda_{R_i} \text{) is finite, then} \\ p'_i(\lambda_{S_i}) \neq 0 \text{ (} q'_i(\lambda_{R_i}) \neq 0 \text{).} \end{aligned} \quad (2. 6)$$

Note that p_i and q_i need not to be increasing. Due to the assumption (2.3), the functions $f_i(S, R)$ satisfy a Lipschitz condition in S and R on any compact subset of $R_+ \times R_+$, and therefore we have uniqueness of initial-value problems and continuous dependence on initial conditions and parameters for the system (2.1).

If we assume that

$$p'_i(S) > 0 \quad \text{for all } S > 0 \quad \text{and} \quad q'_i(R) > 0 \quad \text{for all } R > 0, \quad (2. 7)$$

and that there are only two species, then (2.1) is precisely model III of Leon and Tumpson [16] adapted to the chemostat, as well as the model studied by Butler and

Wolkowicz [6] in the noninhibitory kinetics case. If we further assume that the p_i and q_i , satisfy Michaelis-Menten dynamics, it is the model studied by Hsu, Cheng and Hubbell [13]. By means of linear analysis, Leon and Tumpson [16] provided local analysis of steady states, and pointed out that the necessary and sufficient conditions for coexistence of two species at a locally asymptotically stable steady equilibrium “are that each species must at equilibrium consume engaged fraction of the net rate of supply of its limiting resource than of the net rate of supply of its competitor’s limiting resource”. Hsu, Cheng and Hubbell [13], and Butler and Wolkowicz [6], on the other hand, did a complete global analysis of the model.

Following Hsu et al. [13], we define

$$C_i = y_{S_i}/y_{R_i}, \quad i = 1, 2, \dots, n. \quad (2. 8)$$

The parameter C_i represents the fixed yield ration for species i growing on R and S , since the units of $1/y_{S_i}$ are (units of S consumed)/(units of population i produced).

Let

$$T_i = \frac{R^0 - \lambda_{R_i}}{S^0 - \lambda_{S_i}}, \quad i = 1, 2, \dots, n, \quad (2. 9)$$

and

$$T_{ij} = \frac{R^0 - \lambda_{R_i}}{S^0 - \lambda_{S_j}}, \quad i = 1, 2, \dots, n. \quad (2. 10)$$

The parameter T_i represents the ratio in which nutrients S and R are externally regenerated under steady-state consumption pressure from the population i in the absence of its competitors. By comparing T_i and C_i one can determine population i is S -limited or R -limited. If $T_i > C_i$, population i is S -limited because S is regenerating at a steady-state rate slower than R with respect to the required consumption ratio of population i . Similarly $T_i < C_i$ implies that population i is R -limited.

T_{ij} represents the ratio of the steady state regeneration rate of R when x_i is

alone to that of S when x_j is alone.

To avoid steady states for which the associated Jacobian matrix of the linearization has any real root equal to zero, if the parameters are finite, we assume that

$$\begin{aligned} \lambda_{S_i} \text{ and } \lambda_{S_j} \text{ are distinct from each other and from } S^0 \\ \lambda_{R_i} \text{ and } \lambda_{S_j} \text{ are distinct from each other and from } R^0, \end{aligned} \quad (2.11)$$

and

$$T_{ij} \text{ is distinct from } C_i \text{ and } C_j. \quad (2.12)$$

To ensure that the critical points are all isolated we assume that there are i and j , $i \neq j$, such that

$$C_i \neq C_j. \quad (2.13)$$

We further assume that

$$T_i \neq C_j \quad (2.14)$$

which ensure that if $(\bar{S}, \bar{R}, \bar{x}_1, \dots, \bar{x}_n)$ is a critical point, then $p_i(\bar{S}) \neq q_i(\bar{R})$ for $i = 1, 2, \dots, n$.

We assume the equations are numbered such that

$$\lambda_{S_1} < \lambda_{S_2} < \lambda_{S_3} < \dots < \lambda_{S_n}. \quad (2.15)$$

This assumption will help us save space in describing various outcomes of the chemostat without loss of generality. Here we do not make any assumption on the order of $\lambda_{R_1}, \lambda_{R_2}, \dots, \lambda_{R_n}$.

We now state some preliminary results for system (2.1). It is easy to see that solutions of (2.1) are positive and bounded. Adding S equation and all x_i equations, and adding R equation and all x_i equations, we obtain the following two equations respectively.

$$\frac{d}{dt} \left\{ S(t) + \sum_{i=1}^n \frac{x_i(t)}{y_{S_i}} \right\} = D \left\{ S^0 - S(t) - \sum_{i=1}^n \frac{x_i(t)}{y_{S_i}} \right\},$$

and

$$\frac{d}{dt}\left\{R(t) + \sum_{i=1}^n \frac{x_i(t)}{y_{R_i}}\right\} = D\left\{R^0 - R(t) - \sum_{i=1}^n \frac{x_i(t)}{y_{R_i}}\right\}.$$

Solving the above two equations leads to

$$\lim_{t \rightarrow \infty} \left(S(t) + \sum_{i=1}^n \frac{x_i(t)}{y_{S_i}}\right) = S^0, \quad (2.16)$$

and

$$\lim_{t \rightarrow \infty} \left(R(t) + \sum_{i=1}^n \frac{x_i(t)}{y_{R_i}}\right) = R^0. \quad (2.17)$$

(2.16) or (2.17) is often referred as the ‘‘conservation principle’’, which allows us to reduce (2.1) to a lower dimensional system.

The polygonal set

$$M = \left\{(S, R, x_1, \dots, x_n) \in \mathbb{R}^4_+ : S + \sum_{i=1}^n \frac{x_i}{y_{S_i}} = S^0, \text{ and } R + \sum_{i=1}^n \frac{x_i}{y_{R_i}} = R^0\right\} \quad (2.18)$$

is a global attractor for (2.1). System (2.1) restricted to M is given by

$$\begin{aligned} x'_i(t) &= x_i(t) \left(f_i\left(S^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{R_i}}, R^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{R_i}} - D_i\right), \right. \\ x_i(0) &> 0, \quad i = 1, 2, \dots, \\ \sum_{i=1}^n \frac{x_i(t)}{y_{S_i}} &\leq S^0, \quad \sum_{i=1}^n \frac{x_i(t)}{y_{R_i}} \leq R^0, \end{aligned} \quad (2.19)$$

coupled with

$$S(t) = S^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{R_i}}, \quad R(t) = R^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{R_i}}. \quad (2.20)$$

System (2.19) is referred as the limit or reduced system of (2.1). The global analysis will proceed on the reduced system (2.19) on set M . Since every trajectory is asymptotic to its omega limit set, knowledge of the globally asymptotic behavior of system (2.19) on set M is essential for determining the globally asymptotic behavior of (2.1). See Corollary 4.3 of Thieme [30] for general results returning to the original system from the associated limit system. Roughly speaking, that corollary says that

if all steady states of a reduced system are isolated and not cyclically chained to each other, then every solution of the full system converges to a steady state.

3 Steady States and Their Local Stability

The washout steady state for (2.1) is denoted by $E_0 = (S^0, R^0, 0, \dots, 0)$. There are $2n$ possible steady states involving one species each. Let $E_{S_k} = (\lambda_{S_k}, r_k, 0, \dots, 0, \bar{x}_k, 0, \dots, 0)$ denote the steady state involving only species x_k when x_k is S -limited, where $r_k = R^0 - C_k(S^0 - \lambda_{S_k})$ and $\bar{x}_k = (S^0 - \lambda_{S_k})y_{S_k}$. Let $E_{R_k} = (s_k, \lambda_{R_k}, \dots, 0, \bar{x}_k, 0, \dots, 0)$ denote the steady state involving only species x_k when x_k is R -limited, where $s_k = S^0 - (R^0 - \lambda_{R_k})/C_k$ and $\bar{x}_k = (R^0 - \lambda_{R_k})y_{R_k}$. There are $n(n-1)/2$ steady states involving coexistence of two species, say species k and l , denoted by $E_{kl} = (\lambda_{S_l}, \lambda_{R_k}, 0, \dots, 0, \bar{x}_k, 0, \dots, 0, \bar{x}_l, 0, \dots, 0)$ where

$$\begin{aligned}\bar{x}_k &= y_{S_k} y_{R_k} \frac{y_{S_l}(S^0 - \lambda_{S_l}) - y_{R_l}(R^0 - \lambda_{R_k})}{y_{S_l} y_{R_k} - y_{S_k} y_{R_l}}, \\ \bar{x}_l &= y_{S_l} y_{R_l} \frac{y_{R_k}(R^0 - \lambda_{R_k}) - y_{S_k}(S^0 - \lambda_{S_l})}{y_{S_l} y_{R_k} - y_{S_k} y_{R_l}},\end{aligned}\tag{3. 1}$$

and $k, l = 1, 2, \dots, n$. Due to (2.15), $k < l$ is necessary for every component of E_{kl} to be nonnegative. There is no any other type steady states. We summarize notation for the possible steady states in Table 1.

We now discuss the existence of the steady states. The washout steady state E_0 always exists. For E_{S_k} to exist, we must have $q(R^0 - C_k(S^0 - \lambda_{S_k})) > D$ which is equivalent to $R^0 - C_k(S^0 - \lambda_{S_k}) > \lambda_{R_k}$ or $T_k > C_k$. Similarly, E_{R_k} exists if $T_k < C_k$. In other words, E_{S_k} exists if the species k is S -limited, and E_{R_k} exists if the species k is R -limited. E_{kl} exists if

$$\begin{aligned}R^0 - \frac{\bar{x}_k}{y_{R_k}} - \frac{\bar{x}_l}{y_{R_l}} &= \lambda_{R_k}, \\ S^0 - \frac{\bar{x}_l}{y_{S_l}} - \frac{\bar{x}_k}{y_{S_k}} &= \lambda_{S_l},\end{aligned}\tag{3. 2}$$

$$p_k(\lambda_{S_l}) > D,\tag{3. 3}$$

$$q_l(\lambda_{R_k}) > D.\tag{3. 4}$$

Symbol	Steady state
E_0	$= (S^0, R^0, 0, \dots, 0)$
E_{S_k}	$= (\lambda_{S_k}, r_k, 0, \dots, 0, \bar{x}_k, 0, \dots, 0)$ where $r_k = R^0 - C_k(S^0 - \lambda_{S_k})$ and $\bar{x}_k = (S^0 - \lambda_{S_k})y_{S_k}$
E_{R_k}	$= (s_k, \lambda_{R_k}, 0, \dots, 0, \bar{x}_k, 0, \dots, 0)$ where $s_k = S^0 - (R^0 - \lambda_{R_k})/C_k$ and $\bar{x}_k = (R^0 - \lambda_{R_k})y_{R_k}$
E_{kl}	$= (\lambda_{S_l}, \lambda_{R_k}, 0, \dots, 0, \bar{x}_k, 0, \dots, 0, \bar{x}_l, 0, \dots, 0)$ where $\bar{x}_k = y_{S_k}y_{R_k} \frac{y_{S_l}(S^0 - \lambda_{S_l}) - y_{R_l}(R^0 - \lambda_{R_k})}{y_{S_l}y_{R_k} - y_{S_k}y_{R_l}}$ $\bar{x}_l = y_{S_l}y_{R_l} \frac{y_{R_k}(R^0 - \lambda_{R_k}) - y_{S_k}(S^0 - \lambda_{S_l})}{y_{S_l}y_{R_k} - y_{S_k}y_{R_l}}$

Table 1: Notation for the Steady States

(3.2) yields (3.1). In order for E_{kl} to exist, we must have $\bar{x}_k > 0$ and $\bar{x}_l > 0$ which lead to $C_k < T_{kl} < C_l$ or $C_k > T_{kl} > C_l$. By (2.15), (3.3) is automatically true. (3.4) holds if and only if $\lambda_{R_l} < \lambda_{R_k}$.

In Table 2, we summarize criteria that ensure that these steady states lie in the nonnegative cone, as well as criteria that guarantee their local asymptotic stability. The linear analysis for local stability of steady states is standard and can be found in Appendix 1.

4 Global Analysis of the Reduced System

The global stability of the steady states for the reduced system (2.19) is studied in this section. The steady states for the reduced system (2.19) are denoted by

$$F_0 = (0, 0, \dots, 0)$$

$$F_{S_k} = (0, \dots, 0, \bar{x}_k, 0, \dots, 0) \text{ where } \bar{x}_k = (S^0 - \lambda_{S_k})y_{S_k}$$

$$F_{R_k} = (0, \dots, 0, \bar{x}_k, 0, \dots, 0) \text{ where } \bar{x}_k = (R^0 - \lambda_{R_k})y_{R_k}$$

$$F_{kl} = (0, \dots, 0, \bar{x}_k, 0, \dots, \bar{x}_l, 0, \dots, 0)$$

Steady state	Criteria for existence	Criteria for asymptotic stability
E_0	always exists	$\lambda_{S_i} > S^0$ or $\lambda_{R_i} > R^0$ for $i = 1, \dots, n$
E_{S_k}	$\lambda_{S_k} < S^0$, $\lambda_{R_k} < R^0$ and $T_k > C_k$	$T_{ik} < C_k$ for $1 \leq i < k$
E_{R_k}	$\lambda_{S_k} < R^0$, $\lambda_{R_k} < R^0$ and $T_k < C_k$	$\lambda_{R_k} < \lambda_{R_i}$ or $T_{ki} > C_k$ for $1 \leq i \leq n$ and $i \neq k$
E_{kl}	$k < l$, $\lambda_{R_l} < \lambda_{R_k} < R^0$ and $\left(\begin{array}{c} C_k < T_{kl} < C_l \\ \text{or} \\ C_k > T_{kl} > C_l \end{array} \right)$	$C_k > C_l$, and $\lambda_{R_k} < \lambda_{R_i}$ for $1 \leq i < l$ and $i \neq k$

Table 2: Summary of Local Stability

where

$$\bar{x}_k = y_{S_k} y_{R_k} \frac{y_{S_l}(S^0 - \lambda_{S_l}) - y_{R_l}(R^0 - \lambda_{R_l})}{y_{S_l} y_{R_k} - y_{S_k} y_{R_l}},$$

$$\bar{x}_l = y_{S_l} y_{R_l} \frac{y_{R_k}(R^0 - \lambda_{R_k}) - y_{S_k}(S^0 - \lambda_{S_l})}{y_{S_l} y_{R_k} - y_{S_k} y_{R_l}}$$

$$k, l = 1, 2, \dots, n, \quad k < l.$$

F_0 , F_{S_k} , F_{R_k} and F_{kl} correspond to E_0 , E_{S_k} , E_{R_k} and E_{kl} respectively.

Note that the criteria given in Table 2 also work for the steady states of the reduced system (2.19). Table 2 shows that multiple locally stable steady states may exist. Therefore additional conditions may be needed to ensure the globally asymptotic stability of a steady state.

We shall proceed global analysis for the reduced system (2.19) by taking the Linapunv function approach. The following notation is needed for our analysis.

$$\Delta_{S_k} = \left\{ x : \sum_{i=1}^n \frac{x_i}{y_{S_i}} = S^0 - \lambda_{S_k} \right\},$$

$$B_{S_k} = \left\{ x : \sum_{i=1}^n \frac{x_i}{y_{S_i}} < S^0 - \lambda_{S_k} \right\},$$

$$C_{S_k} = \left\{ x : \sum_{i=1}^n \frac{x_i}{y_{S_i}} > S^0 - \lambda_{S_k} \right\},$$

$$\Delta_{R_k} = \left\{ x : \sum_{i=1}^n \frac{x_i}{y_{R_i}} = R^0 - \lambda_{R_k} \right\},$$

$$B_{R_k} = \left\{ x : \sum_{i=1}^n \frac{x_i}{y_{R_i}} < R^0 - \lambda_{R_k} \right\},$$

$$C_{R_k} = \left\{ x : \sum_{i=1}^n \frac{x_i}{y_{R_i}} > R^0 - \lambda_{R_k} \right\}.$$

Lemma 4.1. Let $x(t) = (x_1(t), \dots, x_n(t))$ be a solution of (2.19). If for some i , $\lambda_{S_i} > S^0$ or $\lambda_{R_i} > R^0$, then

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

for the same i .

Proof. It follows from (2.19) that there exists a $\alpha_i > 0$ such that for large t

$$f_i(S(t), R(t)) - D < -\alpha_i$$

and therefore for large t

$$x_i'(t) \leq -\alpha_i x_i(t)$$

which leads to $\lim_{t \rightarrow \infty} x_i(t) = 0$. This completes the proof.

The following theorem follows immediately from Lemma 4.1.

Theorem 4.1. If $\lambda_{S_i} > S^0$ or $\lambda_{R_i} > R^0$ for $1 \leq i \leq n$, then F_0 is a global attractor for system (2.19).

Theorem 4.2. Let $\lambda_{S_k} < S^0$ and $T_k > C_k$ for some k , $1 \leq k \leq n$. Assume that

- (i) for each j with $1 \leq j < k$, either $\lambda_{R_j} > R^0$ or $T_{jk} < C_i$ for $1 \leq i \leq n$;
- (ii) for each j with $j \leq n$, $j \neq k$, one of the following is true: (1) $\lambda_{S_j} > S^0$; (2) either $\lambda_{R_k} < \lambda_{R_j}$ or $T_{kj} > C_i$ for $1 \leq i \leq n$.

Then F_{S_k} is a global attractor for (2.19).

Proof. Let $x(t)$ be a solution of system (2.19) for which $x_k(0) > 0$. Divide the

relevant portion of the positive cone into three disjoint regions: Δ_{S_k} , B_{S_k} , and C_{S_k} .

For $x \in (\Delta_{S_k} \cup C_{S_k}) \setminus F_{S_k}$, $S^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{S_i}} \leq \lambda_{S_k} < \lambda_{S_j}$ for $j > k$. It follows that

$$f_k(S^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{S_i}}, R^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{R_i}}) - D \leq 0$$

and for $j > k$

$$f_j(S^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{S_i}}, R^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{R_i}}) - D < 0.$$

On the other hand, condition (i) ensures that for $x \in (\Delta_{S_k} \cup C_{S_k}) \setminus F_{S_k}$ and $1 \leq j < k$,

$R^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{R_i}} < \lambda_{R_j}$ and thus

$$f_j(S^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{S_i}}, R^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{R_i}}) - D < 0.$$

Therefore, for $x \in (\Delta_{S_k} \cup C_{S_k}) \setminus F_{S_k}$,

$$\left(\sum_{i=1}^n \frac{x_i(t)}{y_{S_i}}\right)' = \sum_{i=1}^n \frac{x_i(t)}{y_{S_i}} [f_i(S^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{S_i}}, R^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{R_i}}) - D] < 0.$$

It follows immediately that if $x \in \Delta_{S_k} \setminus F_{S_k}$ for some t , then $x(s) \in B_{S_k}$ for $s > t$. In particular, once a solution enters B_{S_k} , it can never get out. So we only need consider solutions remaining in B_{S_k} or C_{S_k} for all $t \geq 0$.

Suppose that a solution $x(t)$ stays in C_{S_k} for $t \geq 0$ for which $x_k(0) > 0$. The previous calculation shows that if $V(x) = \sum_{i=1}^n x_i/y_{S_i}$ in C_{S_k} , then $\dot{V}(x) < 0$. One can see that $\dot{V}(x) = 0$ for $x \in \Delta_{S_k} \cup C_{S_k}$, the closure of C_{S_k} , if and only if $x \in \Delta_{S_k}$. On the other hand the invariant set for $V(x)$ in Δ_{S_k} is F_{S_k} . By the LaSalle corollary, $x(t)$ converges to F_{S_k} .

Next we consider a solution $x(t)$ which belongs to B_{S_k} for $t \geq 0$ for which $x_k(0) > 0$. Divide the relevant portion of the positive cone into three disjoint regions: Δ_{R_k} , B_{R_k} , and C_{R_k} . Note that for $x \in (\Delta_{R_k} \cup C_{R_k})$, $\lambda_{R_k} < \lambda_{R_j}$ implies $R^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{R_i}} < \lambda_{R_j}$, and $\lambda_{S_j} > S^0$ or $T_{kj} > C_i$ for all $1 \leq i \leq n$ implies that

$S^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{S_i}} < \lambda_{S_j}$. Therefore condition (ii) ensures that for $x \in \Delta_{R_k} \cup C_{R_k} \setminus F_{R_k}$,

$$\frac{d}{dt} \left(\sum_{i=1}^n \frac{x_i(t)}{y_{R_i}} \right) < 0.$$

It follows that if $x \in \Delta_{R_k} \setminus F_{R_k}$ for t , then $x(s) \in B_{R_k}$ for $s > t$. Particularly, if a solution enters B_{R_k} , it will stay there.

Suppose a solution $x(t)$ remains in C_{R_k} for $t \geq 0$ for which $x_k(0) > 0$. Since for each $j \neq k$, either λ_{R_j} is strictly greater than λ_{R_k} or T_{k_j} is strictly greater than C_i for $1 \leq i \leq n$, there is $\alpha_j > 0$ such that $x'_j(t) \leq -\alpha_j x_j(t)$. This shows

$$\lim_{t \rightarrow \infty} x_j(t) = 0 \quad \text{for } j \neq k. \quad (4.1)$$

Recall that $x(t)$ also belongs to B_{S_k} . Then it follows from (4.1) that

$$x'_k(t) = x_k(t) \left(f_k \left(S^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{S_i}}, R^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{R_i}} \right) - D \right) < 0 \quad (4.2)$$

eventually. Therefore $\lim_{t \rightarrow \infty} x_k(t)$ exists. Let $V(x) = x_k$, then $\dot{V} < 0$. By the LaSalle corollary, the limit value \bar{x}_k of x_k is determined by

$$\bar{x}_k \left(f_k \left(S^0 - \frac{\bar{x}_k}{y_{S_k}}, R^0 - \frac{\bar{x}_k}{y_{R_k}} \right) - D \right) = 0.$$

Then $\bar{x}_k = 0$ or $\bar{x}_k = y_{R_k}(R^0 - \lambda_{R_k})$ or $\bar{x}_k = y_{S_k}(S^0 - \lambda_{S_k})$. By (4.1), $T_k > C_k$ and $x \in B_{S_k}$, we see that $\bar{x}_k = y_{S_k}(S^0 - \lambda_{S_k})$ is impossible. $\bar{x}_k = 0$ is also impossible.

Otherwise as $t \rightarrow \infty$,

$$f_k \left(S^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{S_i}}, R^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{R_i}} \right) - D \rightarrow f_k(S^0, R^0) - D > 0$$

which leads to $x_k(t) \rightarrow \infty$ as $t \rightarrow \infty$, a contradiction. If $\bar{x}_k = y_{R_k}(R^0 - \lambda_{R_k})$, then as $t \rightarrow \infty$,

$$f_k \left(S^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{S_i}}, R^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{R_i}} \right) - D \rightarrow f_k \left(S^0 - \frac{R^0 - \lambda_{R_k}}{C_k}, \lambda_{R_k} \right) - D < 0$$

that leads to $\lim_{t \rightarrow \infty} x_k(t) = 0$, a contraction. Therefore $x(t)$ can not remain in both C_{R_k} and B_{S_k} .

Finally, we consider a solution $x(t)$ which belongs to B_{R_k} as well as B_{S_k} for $t \geq 0$ for which $x_k(0) > 0$. For such a solution,

$$\begin{aligned} x'_k(t) &= x_k(t) \left(f_k \left(S^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{S_i}}, R^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{R_i}} \right) - D \right) \\ &> x_k(t) \left(f_k(\lambda_{S_k}, R^0 - C_k(S^0 - \lambda_{S_k})) - D \right) > 0. \end{aligned} \quad (4.3)$$

So $\lim_{t \rightarrow \infty} x_k(t)$ exists and $\lim_{t \rightarrow \infty} x_k(t) > 0$. Obviously, if $V(x) = -x_k$ in $B_{S_k} \cap B_{R_k}$ then $\dot{V}(x) < 0$. Further, $\dot{V}(x) = 0$ for $x \in B_{S_k} \cap B_{R_k} \cup \Delta_{S_k} \cup \Delta_{R_k}$ if and only if $x \in \Delta_{S_k}$ or $x \in \Delta_{R_k}$ or $x \in B_{S_k} \cap B_{R_k}$ and $x_k = 0$. By the LaSalle corollary, the solution $x(t)$ converges to the largest invariant set in $\{x \in B_{S_k} \cap B_{R_k} \cup \Delta_{S_k} \cup \Delta_{R_k} : \dot{V}(x) = 0\}$. For our solution, obviously the omega limit set belongs to $\Delta_{S_k} \cup \Delta_{R_k}$ since x_k increases along $x(t)$. The only invariant subset of $\Delta_{S_k} \cup \Delta_{R_k}$ is $F_{S_k} \cup F_{R_k}$; so necessarily $x(t) \rightarrow F_{S_k} \cup F_{R_k}$ as $t \rightarrow \infty$. On the other hand, at F_{R_k}

$$x'_k = (R^0 - \lambda_{R_k}) y_{R_k} \left(f_k \left(S^0 - \frac{R^0 - \lambda_{R_k}}{C_k}, \lambda_{R_k} \right) - D \right) < 0.$$

This indicates that F_{R_k} can not be an omega limit point for $x(t)$. Therefore, $x(t)$ converges to F_{S_k} . The proof is complete.

Theorem 4.3. Let $\lambda_{S_k} < S^0$, $\lambda_{R_k} < R^0$ and $T_k < C_k$ for some k , $1 \leq k \leq n$.

Assume that

(i) for $j \neq k$, one of the follow is true: (1) $\lambda_{R_k} < \lambda_{R_j}$; (2) either $\lambda_{S_j} > S^0$ or $T_{kj} > C_i$ for $1 \leq i \leq n$;

(ii) for $1 \leq j < k$, $T_{jk} < C_i$ for $1 \leq i \leq n$.

Then F_{R_k} is a global attractor.

Proof. The proof of this theorem is similar to that of theorem 1. We only describe the outline of the proof here and omit the details.

Let $x(t)$ be a solution for which $x_k(0) > 0$. If $x \in (\Delta_{R_k} \cup C_{R_k}) \setminus F_{R_k}$, then condition (i) implies that either $R^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{R_i}} < \lambda_{R_j}$, or $S^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{S_i}} < \lambda_{S_j}$ if $\lambda_{S_j} < S^0$. It follows that if $x \in \Delta_{R_k} \setminus F_{R_k}$ for some t , then $x(s) \in B_{R_k}$ for $s > t$. Therefore if a solution enters B_{R_k} , it can never get out. So we only need consider solutions remaining in B_{R_k} or C_{R_k} for all $t \geq 0$.

Suppose that a solution stays in C_{R_k} for all $t \geq 0$, using $V(x) = \sum_{i=1}^n x_i/y_{R_i}$ in C_{S_k} and the LaSalle corollary, one can show that any solution remaining in C_{S_k} for $t \geq 0$ converges to F_{R_k} .

Next we consider a solution $x(t)$ which belongs to B_{S_k} for $t \geq 0$ for which $x_k(0) > 0$. Condition (ii) implies that if $x \in (\Delta_{S_k} \cup C_{S_k})$, then $R^0 - \sum_{i=1}^n \frac{x_i}{y_{S_i}} < \lambda_{S_j}$ for $j > k$, and $S^0 - \sum_{i=1}^n \frac{x_i}{y_{R_i}} < \lambda_{R_j}$ for $j < k$. Therefore

$$\frac{d}{dt} \left(\sum_{i=1}^n \frac{x_i(t)}{y_{S_i}} \right) < 0.$$

It follows that if $x \in \Delta_{S_k}$ for t , then $x(s) \in B_{S_k}$ for $s > t$. In particular, if a solution enters B_{R_k} , it will never get out. Further, one can show that $x(t)$ can not remain in both C_{R_k} and B_{S_k} . Finally if $x(t)$ belongs to B_{R_k} as well as B_{S_k} for $t \geq 0$ for which $x_k(0) > 0$. Using $V(x) = -x_k$ in $B_{S_k} \cap B_{R_k}$ and the LaSalle corollary, one can show $x(t)$ converges to F_{R_k} , which completes the proof.

As we see from Table 2, F_{kl} is locally asymptotic stable if and only if $\lambda_{R_i} > \lambda_{R_k} > \lambda_{R_l}$ for $i < l$, $i \neq k$ as well as $C_k > T_{kl} > C_l$. In this case, we arrange $\lambda_{R_1}, \lambda_{R_2}, \dots, \lambda_{R_l}$ in the order

$$\lambda_{R_l} < \lambda_{R_k} < \lambda_{R_{k_1}} < \lambda_{R_{k_2}} < \dots < \lambda_{R_{k_{l-2}}}. \quad (4.4)$$

Next we discuss the global stability of F_{kl} . We will need the global stability result of F_{12} when there are only two species in the chemostat. As we mentioned earlier, the proofs given in Hsu et. al [13] are valid for monotone increasing nutrient

uptake functions. As a matter of fact, they are also valid for functions satisfying (2.15). In particular, the proof for Theorem 5.6 (iii) in [13] regarding the coexistence of two species is valid for the following lemma.

Lemma 4.2. Let $n = 2$ in (2.19). If $\lambda_{R_2} < \lambda_{R_1} < R^0$ and $C_1 > T_{12} > C_2$, then F_{12} is a global attractor.

We are now ready to state the following theorem.

Theorem 4.4. Assume that

- (i) $\lambda_{R_i} > \lambda_{R_k} > \lambda_{R_l}$ for $i < l$, $i \neq k$, $C_k > T_{kl} > C_l$, and λ_{R_1} through λ_{R_l} are arranged as in (4.4);
- (ii) for all $l < m \leq n$, one of the following is true: (1) either $\lambda_{S_m} > S^0$ or $\lambda_{R_m} > R^0$;
- (2) either $\lambda_{R_m} > \lambda_{R_h}$ or $T_{hm} > C_i$ for $1 \leq h \leq m$ and $1 \leq i \leq n$;
- (iii) either $\lambda_{R_m} > R^0$ or $T_{k_m k_h} \leq C_i$ for $1 < m \leq l - 2$, $1 \leq h \leq m$, and $1 \leq i \leq n$.

Then F_{kl} is a global attractor.

Proof. Without loss of generality, assume that $n > l$. We show that $x_n(t) \rightarrow 0$ as $t \rightarrow \infty$. This is obvious if either $\lambda_{S_n} > S^0$ or $\lambda_{R_n} > R^0$. Next we assume that $\lambda_{S_n} < S^0$ and $\lambda_{R_n} < R^0$. Observe that condition (ii) shows that for $x \in \Delta_{S_n} \setminus F_{S_n}$, $R^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{R_i}} > \lambda_{R_i}$ for $1 \leq i \leq n$. This indicates that for $x \in \Delta_{S_n} \setminus F_n$,

$$\left(\sum_{i=1}^n \frac{x_i(t)}{y_{S_i}} \right)' = \sum_{i=1}^n \frac{x_i(t)}{y_{S_i}} \left[f_i \left(S^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{S_i}}, R^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{R_i}} \right) - D \right] > 0.$$

It follows immediately that if $x \in \Delta_{S_n} \setminus F_n$ for some t , then $x(s) \in C_{S_n}$ for $s > t$. In particular, once a solution enters C_{S_n} , it can never get out. So we only need consider solutions remaining in B_{S_n} or C_{S_n} for all $t \geq 0$.

Suppose that a solution $x(t)$ stays in C_{S_n} for all $t \geq 0$. Then

$$x'_n(t) = x_n(t) \left(f_n \left(S^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{S_i}}, R^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{R_i}} \right) - D \right) < 0. \quad (4.5)$$

Let $V(x) = x_n$ in C_{S_n} then $\dot{V}(x) < 0$. It is easy to see that $\dot{V}(x) = 0$ for $x \in \Delta_{S_n} \cup C_{S_n}$, the closure of C_{S_n} , if and only if either $x_n = 0$ or $x \in \Delta_{S_n}$. Since the largest invariant set in Δ_{S_n} is F_{S_n} , applying the LaSalle corollary yields $x(t) \rightarrow x_0 \cup F_{S_n}$ as $t \rightarrow \infty$, where x_0 takes the form

$$x_0 = (x_1, x_2, \dots, x_{n-1}, 0)$$

with $x_i \geq 0$ for $1 \leq i \leq n-1$. On the other hand, $x'_l > 0$ at F_{S_n} , which indicates F_{S_n} can not be in the omega limit set of $x(t)$. Therefore x_0 is the omega limit set and we have $x_n(t) \rightarrow 0$ as $t \rightarrow \infty$.

Suppose that a solution $x(t)$ remains in B_{S_n} for all $t \geq 0$. Then

$$x'_n(t) = x_n(t) \left(f_n \left(S^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{S_i}}, R^0 - \sum_{i=1}^n \frac{x_i(t)}{y_{R_i}} \right) - D \right) > 0.$$

Let $V(x) = x_n$ in C_{B_n} then $\dot{V}(x) < 0$. It is easy to see that $\dot{V}(x) = 0$ for $x \in \Delta_{S_n} \cup B_{S_n}$ if and only if either $x_n = 0$ or $x \in \Delta_{S_n}$. Since the largest invariant set in Δ_{S_n} is F_{S_n} and $x_n(t)$ increases along the orbit of $x(t)$, applying the LaSalle corollary yields $x(t)$ converges to F_{S_n} . However, that $x(t)$ converges to F_{S_n} implies $x_k(t) \rightarrow \infty$ as $t \rightarrow \infty$, a contradiction. Therefore $x(t)$ can not stay in B_{S_n} .

Next we consider the limit system of (2.19), which consists of x_i equation for $1 \leq i \leq n-1$ with $x_n = 0$. Similar discussion shows if $n-1 > l$ then $x_{n-1} \rightarrow 0$ as $t \rightarrow \infty$. In general, one can show that if $m > l$ then $x_m(t) \rightarrow 0$ as $t \rightarrow \infty$ for the reduced system that consists of x_i equation for $1 \leq i \leq m$ with $x_{m+1} = x_{m+2} = \dots = 0$.

By using similar argument and condition (iii), one can show that if $k_{l-2} \geq k_m \geq k_1$ then $x_{k_m}(t)$ converges to 0 in the reduced system consisting of x_k , x_l , and x_{k_i} equations for $1 \leq i \leq m$ with $x_{k_{m+1}} = \dots = x_{k_{l-2}} = 0$.

Therefore under condition (i), (ii) and (iii), the limiting system of (2.19) is given

by

$$\begin{aligned}
x'_k(t) &= x_k(t) \left(f_k \left(S^0 - \frac{x_k(t)}{y_{S_k}} - \frac{x_l(t)}{y_{S_l}}, R^0 - \frac{x_k(t)}{y_{R_k}} - \frac{x_k(t)}{y_{R_k}} \right) - D \right), \\
x'_l(t) &= x_l(t) \left(f_l \left(S^0 - \frac{x_k(t)}{y_{S_k}} - \frac{x_l(t)}{y_{S_l}}, R^0 - \frac{x_k(t)}{y_{R_k}} - \frac{x_k(t)}{y_{R_k}} \right) - D \right), \\
x_k(0) &> 0, \quad x_l(0) > 0.
\end{aligned} \tag{4.6}$$

In view of Lemma 4.2, $x_0 = (\bar{x}_k, \bar{x}_l)$ is a global attractor for (4.6). Note that all steady states for both system (2.19) and (4.6) are hyperbolic and hence isolated. It is clear that every solution of (4.6) converges to a steady state and therefore there are no homoclinic orbit or chains of steady states for (4.6). By Corollary 4.3 of Thieme [30], every solution of (2.19) converges to one of the steady states of (2.19). On the other hand, applying the persistence theory of Thieme [31] shows that every solution of (2.19) is bounded away from any plane x_i - x_j different that x_k - x_j plane. It follows that every solution of (2.19) converges to F_{kl} . This completes the proof.

5 Global Analysis of (2.1)

We now use the results of asymptotically autonomous systems to show the connection between the dynamics for system (2.19) and system (2.1). By applying Corollary 4.3 of Thieme [30], we can obtain global stability of steady states for (2.1) from the results for (2.19) given in the previous section. In fact, conditions in each of Theorem 4.1-4.4 also guarantee the global stability of the corresponding steady state for system (2.1). The proofs for the theorems in this section are basically the same as the last part of the proof of Theorem 3.4 in spirit, so we omit them here.

Theorem 5.1. If $\lambda_{S_i} > S^0$ or $\lambda_{R_i} > R^0$ for $1 \leq i \leq n$, then E_0 is a global attractor for system (2.1).

Theorem 5.1 states that if both input nutrient concentrations are inadequate for all species, then the species will be washed out from the chemostat.

The rest of this section deals with the case that input nutrient concentrations are

adequate for at least one species. The next theorem provides conditions for species x_k to be the only survivor in the chemostat when x_k is S -limited. Before stating the theorem, we clarify the conditions in Theorem 4.2. Condition (i) in Theorem 4.2 implies that for $1 \leq j < k$, $T_j < C_j$ if $\lambda_{R_j} < R^0$. On the other hand, condition (ii) in Theorem 4.2 implies that for $j \neq k$, $T_j > C_j$ if $\lambda_{S_j} < S^0$ and $\lambda_{R_k} > \lambda_{R_j}$. To avoid conflicts, for $1 \leq j < k$, $\lambda_{R_k} < \lambda_{R_j}$ is necessary if $\lambda_{S_j} < S^0$. The modified conditions are presented in the following theorem.

Theorem 5.2. Let $\lambda_{S_k} < S^0$ and $T_k > C_k$ for some k , $1 \leq k \leq n$. Assume that

- (i) for each j , $1 \leq j < k$, one of the following is true: (1) $\lambda_{R_j} > R^0$; (2) $\lambda_{R_k} < \lambda_{R_j}$ and $T_{jk} < C_i$ for $1 \leq i \leq n$;
- (ii) for each j , $k < j \leq n$, one of the following is true: (1) $\lambda_{S_j} > S^0$; (2) either $\lambda_{R_k} < \lambda_{R_j}$ or $T_{kj} > C_i$ for $1 \leq i \leq n$.

Then E_{S_k} is a global attractor for (2.1).

This theorem indicates, in the case of adequate input concentrations, for $1 \leq j < k$, x_j is R -limited (i.e., $T_j < C_j$), and for $k < j \leq n$ x_j is S -limited (i.e., $T_j > C_j$). But, since species x_k has the lowest break-even concentration for resource R among x_1, \dots, x_k , and species x_k has the lowest break-even concentration for resource S among x_k, \dots, x_n , species x_k always wins. Note that in this case x_k is S -limited. The next theorem gives conditions for species x_k to be the only survivor when x_k is R -limited. The conditions of Theorem 4.3 are modified, as indicated in the following theorem.

Theorem 5.3. Let $\lambda_{S_k} < S^0$, $\lambda_{R_k} < R^0$ and $T_k < C_k$ for some k , $1 \leq k \leq n$. Assume that

- (i) for each j , $1 \leq j < k$, $\lambda_{R_k} < \lambda_{R_j}$ and $T_{jk} < C_i$ for $1 \leq i \leq n$;
- (ii) for each j , $k < j \leq n$, one of the following is true: (1) $\lambda_{R_k} < \lambda_{R_j}$; (2) either

$\lambda_{S_j} > S^0$ or $T_{kj} > C_i$ for $1 \leq i \leq n$.

Then E_{R_k} is a global attractor.

The biological meaning of this theorem is the same as that of Theorem 5.2 except that x_k is R -limited.

We would like to point out that the conditions in Theorem 5.2-5.3 are necessary if there are only two species in the chemostat. See [6] and [13] for details. The following corollary of Theorem 5.2-5.3 states that if one species has the lowest break-even concentrations for both nutrients S and R , then that species will survive and its rivals will not.

Corollary 5.1. Assume that $\lambda_{S_1} < S^0$, $\lambda_{R_1} < R^0$, and

$$\lambda_{R_1} < \lambda_{R_i} \text{ for } 2 \leq i \leq n. \quad (5.1)$$

If $T_k > C_k$ ($T_k < C_k$), then E_{S_1} (E_{R_1}) is a global attractor for system (2.1).

This corollary can be viewed as an extension of the “competitive exclusion principle” for the chemostat with one limiting nutrient.

The next theorem presents conditions for E_{kl} to be a global attractor.

Theorem 5.4 Assume that

- (i) $\lambda_{R_i} > \lambda_{R_k} > \lambda_{R_l}$ for $i < l$, $i \neq k$ and $C_k > T_{kl} > C_l$, and λ_{R_1} through λ_{R_l} are arranged as in (4.4);
- (ii) for all $l < m \leq n$, one of the following is true: (1) either $\lambda_{S_m} > S^0$ or $\lambda_{R_m} > R^0$;
- (2) either $\lambda_{R_m} > \lambda_{R_h}$ or $T_{hm} > C_i$ for $1 \leq h \leq m$ and $1 \leq i \leq n$;
- (iii) either $\lambda_{R_m} > R^0$ or $T_{k_m k_h} \leq C_i$ for $1 \leq m \leq l - 2$, $1 \leq h \leq m$, and $1 \leq i \leq n$.

Then E_{kl} is a global attractor for (2.1).

Condition (i) in Theorem 5.4 shows that λ_{R_l} is smallest and λ_{R_k} is the second

smallest among λ_{R_1} through λ_{R_l} , x_k is R -limited, and x_l is S -limited. Condition (ii) implies that for $l < j \leq n$, x_j is S -limited, and condition (iii) implies that for $1 \leq j < l$, $j \neq k$, x_j is R -limited. Therefore x_k and x_l win and others die out. On the other hand, species x_k (x_l) has the lower break-even concentration for nutrient R (S) than species x_l (x_k). Coexistence of x_k and x_l occurs because each species has the lower break-even concentration for that resource which, at the two-species steady state mixture of nutrients, limits the growth of the other.

6 Discussion

In this paper we considered a model of n species of microorganisms competing for two perfectly complementary, growth-limiting nutrients in a chemostat. We assumed a general class of response functions for nutrient uptake which include monotone increasing functions. We generalized the results in Hsu, Cheng and Hubbell [13] and in Butler and Wolkowicz [13] by allowing more species.

The difficulty we faced was that the reduced system is no longer a two dimensional system, and we therefore had to examine a high dimensional system. The Liapunov function approach we took turned out successful. The key idea was to divide the positive cone into several appropriate disjoint sets, on each of which the dynamics of the model can be determined analytically. Very simple Liapunov functions were used to capture the global stability of steady states.

The analysis in previous sections provided conditions which ensure the the survive of one species and coexistence of two species. All conditions are sharp if there are only two species involved in the chemostat. Our results for adequate input concentrations indicate that based on the assumption (2.15), in order for x_k to be the only survivor, x_j should be S -limited for $j > k$, and for $j < k$, $\lambda_{R_j} > \lambda_{R_k}$, and x_j

should be R -limited. In order for x_k and x_l to coexist, x_l and x_k should have the two smallest break-even concentrations for nutrient R among λ_{R_1} through λ_{R_l} with $\lambda_{R_k} > \lambda_{R_l}$, for $j < l$, x_j should be R -limited, and for $j > l$, x_j should be S -limited.

When $n > 2$, there is no positive steady state for system (2.1). This implies that all species can not coexist in the sense that they are persistent, i.e., each species always has a positive lower bound. (Otherwise, there would be an interior positive steady state exist due to a result of Hofbauer [11]). So, two perfectly complementary nutrients can not support more than two species. We guess that, in general, every solution of system (2.1) approach to a steady state. For example, if there are multiple locally stable steady states or if all steady states are locally unstable (they are saddle points in this case), we conjecture that every solution approaches a steady state, depending on the initial condition.

Butler and Wolkowicz [6] study the case in which at least one response function for nutrient uptake has two nontrivial break-even concentrations due to that the species is inhibited by high concentration of the substrate, and show oscillation occurs. It would be interesting to investigate this problem when more species are involved in the chemostat.

Acknowledgment

I would like to thank Professor Wei-Ming Ni for his fruitful discussions.

7 Appendix 1.

In this appendix, we present analysis for local stability of steady states of system (2.1). Since the reduced system (2.19) is more compact, the local stability analysis for its steady states is much easier. On the other hand, the local stability of a steady state of (2.1) is the same as that of the corresponding steady state of (2.19). We shall proceed local stability analysis for the steady states of system (2.19). We investigate the local stability of these steady states by finding the eigenvalues of the associated Jacobian matrices.

The Jacobian matrix of (2.19) takes the form

$$J = \begin{bmatrix} f_1 - D + x_1 \frac{\partial f_1}{\partial x_1} & x_1 \frac{\partial f_1}{\partial x_2} & \cdots & x_1 \frac{\partial f_1}{\partial x_n} \\ x_2 \frac{\partial f_1}{\partial x_2} & f_2 - D + x_2 \frac{\partial f_2}{\partial x_2} & \cdots & x_2 \frac{\partial f_1}{\partial x_n} \\ \vdots & \vdots & \ddots & \vdots \\ x_n \frac{\partial f_n}{\partial x_1} & x_n \frac{\partial f_n}{\partial x_2} & \cdots & f_n - D + \frac{x_n \partial f_n}{\partial x_n} \end{bmatrix}. \quad (7. 1)$$

where

$$f_i = f_i(S, R), \quad i = 1, 2, \dots, n, \quad S = S^0 - \sum_{i=1}^n \frac{x_i}{y_{S_i}} \quad \text{and} \quad R = R^0 - \sum_{i=1}^n \frac{x_i}{y_{R_i}}.$$

At F_0 ,

$$J(F_0) = \begin{bmatrix} f_1(S^0, R^0) - D & 0 & \cdots & 0 \\ 0 & f_2(S^0, R^0) - D & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & f_n(S^0, R^0) - D \end{bmatrix}. \quad (7. 2)$$

The eigenvalues lie on the diagonal. They are all negative if and only if $f_i(S^0, R^0) - D < 0$ for all i , that is either $\lambda_{S_i} < S^0$ or $\lambda_{R_i} < R^0$ for all i .

When F_{S_k} exists, the Jacobin matrix at F_{S_k} is $J(F_{S_k}) =$

$$\begin{bmatrix} f_1 - D & 0 & \cdots & 0 & \cdots & 0 \\ 0 & f_2 - D & \cdots & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots & \ddots & 0 \\ \bar{x}_k \frac{\partial f_k}{\partial x_1} & \bar{x}_k \frac{\partial f_k}{\partial x_2} & \cdots & f_k - D + \bar{x}_k \frac{\partial f_k}{\partial x_k} & \cdots & \bar{x}_k \frac{\partial f_k}{\partial x_n} \\ \vdots & \vdots & \ddots & \vdots & \ddots & 0 \\ 0 & 0 & \cdots & 0 & \cdots & f_n - D \end{bmatrix}. \quad (7.3)$$

Where $f_i = f_i(\lambda_{S_k}, r_k)$ for $i = 1, 2, \dots, n$ and $r_k = R^0 - \frac{\bar{x}_k}{y_{R_k}}$. Note that when F_{S_k} exists, $f_k(\lambda_{S_k}, r_k) - D$ is zero and $\frac{\partial f_k(\lambda_{S_k}, r_k)}{\partial x_k} < 0$. So, The eigenvalues lie on the diagonal. They are all negative if and only if

$$f_i(S_{R_k}, r_k) - D < 0 \quad (7.4)$$

for all $i \neq k$. Due to (2.15), (7.4) holds for $i > k$. If $i < k$, then (7.4) holds if and only if $r_k < \lambda_{R_i}$ or $T_{ik} < C_k$.

When F_{R_k} exists, the Jacobin matrix at F_{R_k} is the same as that at F_{S_k} except f_i being replaced by $f_i(s_k, \lambda_{R_k})$ where $s_k = S^0 - \bar{x}_k/y_{S_k}$, $i = 1, 2, \dots, n$. The eigenvalues are all negative if and only if

$$f_i(s_k, \lambda_{R_k}) - D < 0 \quad (7.5)$$

for all $i \neq k$. (7.5) is equivalent to

$$s_k < \lambda_{S_i} \quad \text{or} \quad \lambda_{R_k} < \lambda_{R_i}$$

or

$$T_{ki} > C_k \quad \text{or} \quad \lambda_{R_k} < \lambda_{R_i}$$

for all $i \neq k$.

When F_{kl} exists, the Jacobin matrix at F_{kl} is $J(F_{S_k}) =$

$$\begin{bmatrix} f_1 - D & 0 & \cdots & 0 & \cdots & 0 & \cdots & 0 \\ 0 & f_2 - D & \cdots & 0 & \cdots & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots & \ddots & \vdots & \ddots & \vdots \\ \bar{x}_k \frac{\partial f_k}{\partial x_1} & \bar{x}_k \frac{\partial f_k}{\partial x_2} & \cdots & f_k - D + \bar{x}_k \frac{\partial f_k}{\partial x_k} & \cdots & \bar{x}_k \frac{\partial f_k}{\partial x_l} & \cdots & \bar{x}_k \frac{\partial f_k}{\partial x_n} \\ \vdots & \vdots & \ddots & \vdots & \ddots & \vdots & \ddots & \vdots \\ \bar{x}_l \frac{\partial f_l}{\partial x_1} & \bar{x}_l \frac{\partial f_l}{\partial x_2} & \cdots & \bar{x}_l \frac{\partial f_l}{\partial x_k} & \cdots & f_l - D + \bar{x}_l \frac{\partial f_l}{\partial x_l} & \cdots & \bar{x}_l \frac{\partial f_l}{\partial x_n} \\ \vdots & \vdots & \ddots & \vdots & \ddots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & 0 & \cdots & 0 & \cdots & f_n - D \end{bmatrix}. \quad (7.6)$$

where $f_i = f_i(\lambda_{S_l}, \lambda_{R_k})$. Note that when F_{kl} exists, $f_k - D = f_l - D = 0$. The eigenvalues of matrix (7.6) consists of

$$f_i(\lambda_{S_l}, \lambda_{R_k}) - D, \quad \text{for } i \neq k, l,$$

and the eigenvalues of

$$\begin{bmatrix} \bar{x}_k \frac{\partial f_k}{\partial x_k} & \bar{x}_k \frac{\partial f_k}{\partial x_l} \\ \bar{x}_l \frac{\partial f_l}{\partial x_k} & \bar{x}_l \frac{\partial f_l}{\partial x_l} \end{bmatrix}. \quad (7.7)$$

Note that at F_{kl} , $\frac{\partial f_k}{\partial x_k} < 0$ and $\frac{\partial f_l}{\partial x_k} < 0$. It follows that the trace of (7.7) is negative and therefore all eigenvalues of (7.7) have negative real parts if and only if

$$\bar{x}_k \bar{x}_l \left(\frac{\partial f_k}{\partial x_k} \frac{\partial f_l}{\partial x_l} - \frac{\partial f_k}{\partial x_l} \frac{\partial f_l}{\partial x_k} \right) > 0$$

which is equivalent to

$$C_k > C_l.$$

On the other hand, due to (2.15), $f_i(\lambda_{S_l}, \lambda_{R_k}) - D < 0$ holds for $i > l$. For $i < l$, it holds if and only if $\lambda_{R_k} < \lambda_{R_i}$. Therefore F_{kl} is locally asymptotically stable if and only if $C_k > C_l$ and $\lambda_{R_k} < \lambda_{R_i}$ for $i < l$ and $i \neq k$.

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