

# HETEROCLINIC CYCLES IN THE CHEMOSTAT MODELS AND THE WINNERLESS COMPETITION PRINCIPLE

SZE-BI HSU AND LIH-ING W. ROEGER

ABSTRACT. We consider a chemostat model of  $n$  species of microorganisms competing for  $k$  essential, growth-limiting nutrients. Sufficient conditions for the model to possess stable heteroclinic cycles in the limit sets in this model are given. We construct stable heteroclinic cycles that connect the equilibria in the following manner:  $E_1 \rightarrow E_2 \rightarrow E_3 \rightarrow \dots \rightarrow E_n \rightarrow E_1$  in which  $E_i$ 's are the one-species equilibria. Therefore the competition among the  $n$  species for  $k$  resources is a winnerless competition. Our results show that three essential nutrients may support any finite number of species and competitive exclusion principle does not hold in the model.

## 1. INTRODUCTION

The chemostat model is a basic model in ecology that describes when two or more populations compete for the same resources, such as a common food supply or a growth-limiting nutrient. It can represent the competition in a simple lake, or as a model of wastewater treatment process [17]. The general chemostat model for  $n$  species competing for  $k$  growth-limiting nutrients is as the following [9, 10, 11]:

$$\begin{aligned}
 (1) \quad & N_i'(t) = N_i(t)(\mu_i(R_1, R_2, \dots, R_k) - D), \\
 & R_j'(t) = D(R_j^0 - R_j(t)) - \sum_{i=1}^n c_{ji}\mu_i(R_1, R_2, \dots, R_k)N_i, \\
 & N_i(0) > 0, R_j(0) \geq 0, \quad i = 1, 2, \dots, n, \quad j = 1, 2, \dots, k.
 \end{aligned}$$

$N_i(t)$  denotes the density of species  $i$  at time  $t$ , and  $R_j(t)$  denotes the concentration of nutrient  $j$  at time  $t$ ;  $\mu_i(R_1, \dots, R_k)$  is the specific growth rate of species  $i$  as a function of the nutrients  $R_i$ 's;  $D$  is the flow rate of the chemostat;  $R_j^0$  is the supply concentration of nutrient  $j$ ; and  $c_{ji}$  is the content of nutrient  $j$  in species  $i$ . The individual death rates of populations are assumed to be insignificant compared to the flow rate  $D$ , i.e., the maximal growth rate of each species,  $r_i$ , exceeds the washout rate  $D$  since otherwise it cannot survive. According to Liebig's "Law of the minimum", the specific growth rate of species  $i$  is determined by the nutrient that is the most limiting, that is

$$(2) \quad \mu_i(R_1, R_2, \dots, R_k) = \min(f_{1i}(R_1), f_{2i}(R_2), \dots, f_{ki}(R_k)),$$

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where  $f_{ji}(R_j)$  is the growth rate of the species  $i$  when nutrient  $R_j$  is limiting. The function  $f_{ji} : \mathbb{R}_+ \rightarrow \mathbb{R}_+$  is assumed to be continuously differentiable and satisfies:

$$f_{ji}(0) = 0 \text{ and } f'_{ji}(R) > 0 \text{ for } R > 0.$$

For example, we may choose

$$(3) \quad f_{ji}(R_j) = \frac{r_i R_j}{K_{ji} + R_j}, \quad i = 1, 2, \dots, n, \quad j = 1, 2, \dots, k,$$

which is called the Monod or Michaelis-Menten kinetics for resource up-take.

For each species  $i$  and each resource  $j$ , there is a break-even concentration  $\lambda_{ji}$  defined as

$$f_{ji}(\lambda_{ji}) = D.$$

The break-even concentration  $\lambda_{ji}$  is the subsistence concentration of each resource when species  $i$  is growth-limited by resource  $j$  alone. By the definition of function  $f_{ji}$ , we then have  $f_{ji}(x) < D$  if  $x < \lambda_{ji}$ ; and  $f_{ji}(x) > D$  if  $x > \lambda_{ji}$ . In the numerical example we show later, we assume Monod or Michaelis-Menten kinetics for resource up-take. Then the break-even concentration of species  $i$  on resource  $R_j$  is

$$\lambda_{ji} = f_{ji}^{-1}(D) = \frac{DK_{ji}}{r_i - D}.$$

For model (1), if we form the linear combinations of the variables, we obtain the following equation

$$\frac{d}{dt} \left( R_j(t) + \sum_{i=1}^n c_{ji} N_i(t) \right) = D \left( R_j^0 - R_j(t) - \sum_{i=1}^n c_{ji} N_i(t) \right).$$

Solving this leads to

$$R_j(t) + \sum_{i=1}^n c_{ji} N_i(t) = R_j^0 + O(\exp(-Dt)).$$

Therefore, the polygonal set

$$\{(R_1, \dots, R_k, N_1, \dots, N_n) \in \mathbb{R}_+^{k+n} : R_j + \sum_{i=1}^n c_{ji} N_i = R_j^0, \quad j = 1, \dots, k\}$$

is an invariant and global attracting set for (1). The restriction of (1) to the polygonal set is given by

$$(4) \quad N'_i(t) = N_i(t) [\mu_i(N_1, N_2, \dots, N_n) - D],$$

where

$$\begin{aligned} & \mu_i(N_1, N_2, \dots, N_n) \\ &= \mu_i \left( R_1^0 - \sum_{j=1}^n c_{1j} N_j(t), R_2^0 - \sum_{j=1}^n c_{2j} N_j(t), \dots, R_k^0 - \sum_{j=1}^n c_{kj} N_j(t) \right) \end{aligned}$$

on the set

$$\Gamma = \{(N_1, N_2, \dots, N_n) \in \mathbb{R}_+^n : \sum_{i=1}^n c_{ji} N_i \leq R_j^0, \quad j = 1, \dots, k\}.$$

The resources may be easily recovered from the equations

$$R_j(t) = R_j^0 - \sum_{i=1}^n c_{ji} N_i(t), \quad j = 1, \dots, k.$$

Huisman and Weissing [9, 10, 11] had used the consumer-resource model (1) to explain biodiversity. They showed by numerical simulations that three or more resources can generate sustained oscillations or even chaotic dynamics of species abundances. For three resources, there are periodic oscillations and the results are verified by Li [12]. When there are five species, chaotic dynamics may occur. Moreover, they showed that three resources can support nine species and five resources can support twelve species. Competitive exclusion principle states that at most  $k$  species coexist in the competition for  $k$  resources. Based on the observation by Huisman and Weissing, the competitive exclusion principle no longer holds for three or more resources in the consumer-resource model (1).

In this manuscript, we find the conditions for the existence of stable heteroclinic cycles of model (1) and use this to extend Huisman and Weissing's results so that three resources can support any finite species in the way that all species coexist in the form of stable heteroclinic cycle. A heteroclinic contour consists of finitely many saddle equilibria and finitely many heteroclinic orbits connecting these equilibria. The significance of stable heteroclinic cycle is two-fold. First, it is a potential limit set for the dynamics of the system. Second, it is possible to envision the bifurcation of a very long-period periodic orbit from such a cycle [13].

Before we go into details, we introduce the theorem we will apply. The following theorem states the conditions of existence and stability of heteroclinic contours for the canonical Lotka-Volterra model

$$(5) \quad \dot{a}_i = a_i \left[ 1 - \left( a_i + \sum_{j \neq i}^N \rho_{ij} a_j \right) \right], \quad i = 1, 2, \dots, n.$$

This theorem will be generalized to model (1). For the Lotka-Volterra model (5), let's denote by  $A_i$  the equilibrium with only species  $i$  exists, i.e.  $A_i = (0, 0, \dots, 0, 1, 0, \dots, 0)$ . Assume that there is a heteroclinic orbit  $\Gamma_i$  connecting the points  $A_i$  and  $A_{i+1}$ ,  $i = 1, 2, \dots, n$  and  $A_{n+1} = A_1$ . The following result tells us that the contour or the heteroclinic cycle  $\Gamma = \cup_{i=1}^n \Gamma_i \cup A_i$  can be an attractor.

**THEOREM 1.** [2, Afraimovich et al.] *For the Lotka-Volterra competition system (5), assume that for  $i = 1, 2, \dots, n$ ,*

$$(6) \quad \begin{aligned} & \rho_{ki} > 1, \text{ for } k \neq i+1, \text{ and } \rho_{i+1,i} < 1, \\ & \rho_{i,i+1} < 2, \\ & \rho_{k,i+1} < \rho_{i,i+1}, \text{ for } k \neq i, i+2, \\ & \nu = \prod_{i=1}^n \left( -\frac{1 - \rho_{i,i+1}}{1 - \rho_{i+1,i}} \right) > 1. \end{aligned}$$

(here  $i+1 = 1$  if  $i = n$ ). Then there is a neighborhood  $U$  of the contour  $\Gamma$  such that for any initial condition  $a^0 = (a_1^0, a_2^0, \dots, a_n^0)$  in  $U$  with  $a_i^0 > 0$ , one has  $\text{dist}(a(t), \Gamma) \rightarrow 0$  as  $t \rightarrow \infty$  where  $a(t)$  is the orbit going through  $a^0$ .

The assumptions in Theorem 1 utilized eigenvalues of the Jacobian matrices at  $A_i$  for  $i = 1, 2, \dots, n$ . The results can also be applied to the resource-consumer system (1) and its limiting equations (4). For system (1), consider the limiting equations (4). Denote by  $E_i$  the equilibrium with only species  $i$  exists, i.e.

$E_i = (0, 0, \dots, 0, N_i^*, 0, \dots, 0)$ . Then the eigenvalues of the Jacobian matrix evaluated at  $E_i$  are

$$(7) \quad \sigma_{ij} = \begin{cases} \mu_j(E_i) - D, & \text{for } j \neq i, \\ N_i^* \frac{\partial \mu_i(E_i)}{\partial N_i}, & \text{for } j = i. \end{cases}$$

Note that  $\sigma_{ii}$  is always less than zero. Assume that there is a heteroclinic orbit  $\Gamma_i$  connecting the points  $E_i$  and  $E_{i+1}$ ,  $i = 1, 2, \dots, n$  and  $E_{n+1} = E_1$ . Following Theorem 1, the following result tells us that the contour  $\Gamma = \cup_{i=1}^n \Gamma_i \cup E_i$  can be an attractor for the consumer-resource model (1).

**Corollary 1.** *For the resource-consumer competition system (1), assume that for  $i = 1, 2, \dots, n$*

$$(8a) \quad \sigma_{ik} < 0, \text{ for } k \neq i + 1, \text{ and } \sigma_{i,i+1} > 0,$$

$$(8b) \quad \sigma_{i+1,k} < \sigma_{i+1,i}, \text{ for } k \neq i, i + 2,$$

$$(8c) \quad \nu = \prod_{i=1}^n \left( -\frac{\sigma_{i+1,i}}{\sigma_{i,i+1}} \right) > 1.$$

(here  $i + 1 = 1$  if  $i = n$ ). Then there is a neighborhood  $U$  of the contour  $\Gamma$  such that for any initial condition  $a^0 = (a_1^0, a_2^0, \dots, a_n^0)$  in  $U$  with  $a_i^0 > 0$ , one has  $\text{dist}(a(t), \Gamma) \rightarrow 0$  as  $t \rightarrow \infty$  where  $a(t)$  is the orbit going through  $a^0$ .

We will apply Corollary 1 to construct more concrete heteroclinic cycles for the resource-consumer chemostat model (1). This manuscript is organized as follows. In Section 2, the three resources three-species case is reviewed and studied. We show in details how we construct a heteroclinic cycle by embedding the break-even concentrations into the system. In Section 3, We show that the heteroclinic cycle for two-resource  $n$ -species case cannot exist. Three resources and more and  $n$  species case is presented in Section 4. In Section 5, discussion and possible further work are presented.

## 2. THREE RESOURCES AND THREE SPECIES

For the consumer-resource model (1), when there are three resources and three species,  $n = k = 3$ , Li [12] had done an extended study on the special case when the break-even concentrations of the three species  $N_1, N_2$ , and  $N_3$  related to the three resources  $S, R$ , and  $Q$  satisfy the following condition:

$$(9) \quad \begin{aligned} \lambda_{S3} &< \lambda_{S2} < \lambda_{S1} < S^0, \\ \lambda_{R1} &< \lambda_{R3} < \lambda_{R2} < R^0, \\ \lambda_{Q2} &< \lambda_{Q1} < \lambda_{Q3} < Q^0, \end{aligned}$$

where  $N_1$  is limited by  $Q$ ,  $N_2$  is limited by  $S$ , and  $N_3$  is limited by  $R$ . The hypothesis (9) also tell us that among all three species  $N_3$  is the strongest competitor for resource  $S$  and is the weakest competitor for resource  $Q$ ;  $N_2$  is the strongest competitor for resource  $Q$  and the weakest competitor for resource  $R$ ; and  $N_1$  is the strongest competitor for resource  $R$  and the weakest competitor for resource  $S$ . Hence, the competition for resources is in a cyclic fashion.

Let the saddle value  $\nu$  be defined as

$$(10) \quad \nu = -\frac{\sigma_{13}\sigma_{21}\sigma_{32}}{\sigma_{31}\sigma_{12}\sigma_{23}}.$$

Li [12] had proved the following results.

**THEOREM 2.** ([12]) *Consider the consumer-resource model (1) when  $n = k = 3$  and its three resources  $S$ ,  $R$ , and  $Q$ . If the break-even concentrations satisfy (9) and the saddle value  $\nu < 1$ , then the heteroclinic cycle  $E_1(Q) \rightarrow E_2(S) \rightarrow E_3(R) \rightarrow E_1$  is unstable and there exists a (stable) periodic solution.*

The notation  $E_1(Q) \rightarrow E_2(S) \rightarrow E_3(R) \rightarrow E_1$  will be used throughout the whole manuscript. It expresses that the heteroclinic cycle is in the order of  $E_1 \rightarrow E_2 \rightarrow E_3 \rightarrow E_1$ . By adding the resources in the notation, e.g.,  $E_1(Q)$ ,  $E_2(S)$ , and  $E_3(R)$ , we simply add extra information for this cycle that  $N_1$  is limited by resource  $Q$  near the equilibrium  $E_1$ ,  $N_2$  is limited by resource  $S$  near the equilibrium  $E_2$ , and  $N_3$  is limited by resource  $R$  near the equilibrium  $E_3$ .

By Corollary 1, we obtain stable condition for the heteroclinic cycle. The results follow.

**Corollary 2.** *Consider the consumer-resource model (1) when  $n = k = 3$  and its three resources  $S$ ,  $R$ , and  $Q$ . If the break-even concentrations satisfy (9) and the saddle value  $\nu > 1$ , and furthermore, if*

$$(11) \quad \begin{aligned} \sigma_{ik} &< 0, \text{ for } k \neq i + 1, \text{ and } \sigma_{i,i+1} > 0, \\ \sigma_{i+1,k} &< \sigma_{i+1,i}, \text{ for } k \neq i, i + 2, \end{aligned}$$

(here  $i + 1 = 1$  if  $i = 3$ ) then the heteroclinic cycle  $E_1(Q) \rightarrow E_2(S) \rightarrow E_3(R) \rightarrow E_1$  is (locally) stable.

There are other ways to produce heteroclinic cycles or periodic solutions. For example, if the break-even concentrations satisfy the following conditions:

$$(12) \quad \begin{aligned} \lambda_{S1} &< \lambda_{S2} < \lambda_{S3}, \\ \lambda_{R1} &< \lambda_{R3} < \lambda_{R2}, \\ \lambda_{Q2} &< \lambda_{Q3} < \lambda_{Q1}, \end{aligned}$$

then we maybe able to find the following heteroclinic cycle

$$E_1(Q) \rightarrow E_2(R) \rightarrow E_3(R) \rightarrow E_1$$

and a periodic solution depending on the saddle value  $\nu$ . In addition, we found that if the break-even concentrations for resource  $S$  stay fixed in the order  $\lambda_{S1} < \lambda_{S2} < \lambda_{S3}$ , then there are possibly 36 ways to have heteroclinic cycle in the following order  $E_1 \rightarrow E_2 \rightarrow E_3 \rightarrow E_1$ .

Figure 1 shows an example of a heteroclinic cycle among three species.

### 3. THREE RESOURCES AND FOUR SPECIES

When there are three resources and four species,  $k = 3$  and  $n = 4$ , it is possible to have this heteroclinic cycle  $E_1 \rightarrow E_2 \rightarrow E_3 \rightarrow E_4 \rightarrow E_1$ . There are many different ways depending on the limiting resources on each species. We may embed the break-even concentrations of the fourth species into the known order (9). By doing this, we are able to find at least 14 cases in which the stable heteroclinic loop  $E_1 \rightarrow E_2 \rightarrow E_3 \rightarrow E_4 \rightarrow E_1$  exists. In the following theorem we give one example that the embedding method will work when the order of the break-even concentrations for the first three species follow the one in the previous section, (9); and the break-even concentrations for species four,  $\lambda_{S4}$ ,  $\lambda_{R4}$ , and  $\lambda_{Q4}$ , are

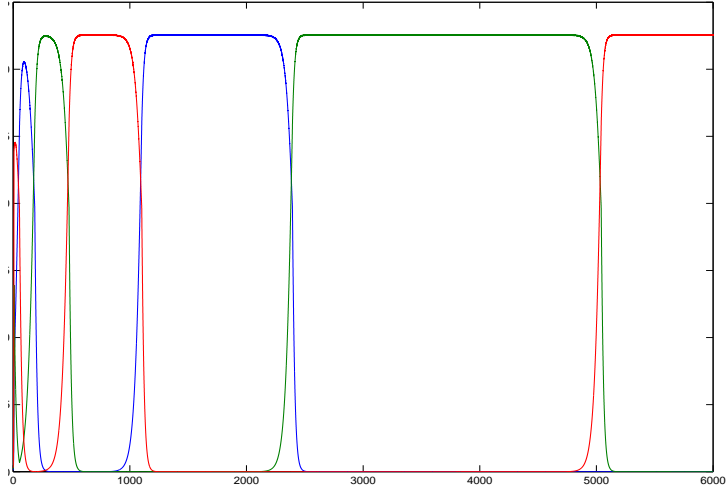


FIGURE 1. A heteroclinic cycle among three species.

embedded into the the previous order. The resulting stable heteroclinic cycle is stated in the following theorem.

**THEOREM 3.** *For the case of three resources  $S$ ,  $R$ , and  $Q$  and four species, if the break-even concentrations of the four species on the three resources satisfy the following:*

$$(13) \quad \begin{aligned} \lambda_{S3} &< \lambda_{S2} < \boxed{\lambda_{S4}} < \lambda_{S1}, \\ \boxed{\lambda_{R4}} &< \lambda_{R1} < \lambda_{R3} < \lambda_{R2}, \\ \lambda_{Q2} &< \lambda_{Q1} < \boxed{\lambda_{Q4}} < \lambda_{Q3}. \end{aligned}$$

*Then the assumption (8a) in Corollary can be satisfied. Furthermore, if the eigenvalues defined as in (7) satisfy (8b) and (8c), i.e.,*

$$\sigma_{13} < \sigma_{14}, \quad \sigma_{24} < \sigma_{21}, \quad \sigma_{31} < \sigma_{32}, \quad \text{and} \quad \sigma_{42} < \sigma_{43}$$

*and*

$$\nu = \frac{\sigma_{21}\sigma_{32}\sigma_{43}\sigma_{14}}{\sigma_{12}\sigma_{23}\sigma_{34}\sigma_{41}} > 1.$$

*then we have a stable heteroclinic loop in the following order*

$$E_1(Q) \rightarrow E_2(S) \rightarrow E_3(R) \rightarrow E_4(Q) \rightarrow E_1.$$

Figure 2 shows an example of a heteroclinic cycle among four species.

*Proof.* We will apply Corollary 1 in our proof. We show that if assumption (13) is satisfied, then all conditions in Corollary 1, (8a), (8b), and (8c) are also satisfied so that a stable heteroclinic orbit  $E_1 \rightarrow E_2 \rightarrow E_3 \rightarrow E_4 \rightarrow E_1$  exists.

Each of the single-species equilibria  $E_1 = (N_1^*, 0, 0, 0)$ ,  $E_2 = (0, N_2^*, 0, 0)$ ,  $E_3 = (0, 0, N_3^*, 0)$ , and  $E_4 = (0, 0, 0, N_4^*)$  must have only one-dimensional unstable manifold. In other words, there is only one positive eigenvalue for each Jacobian matrix

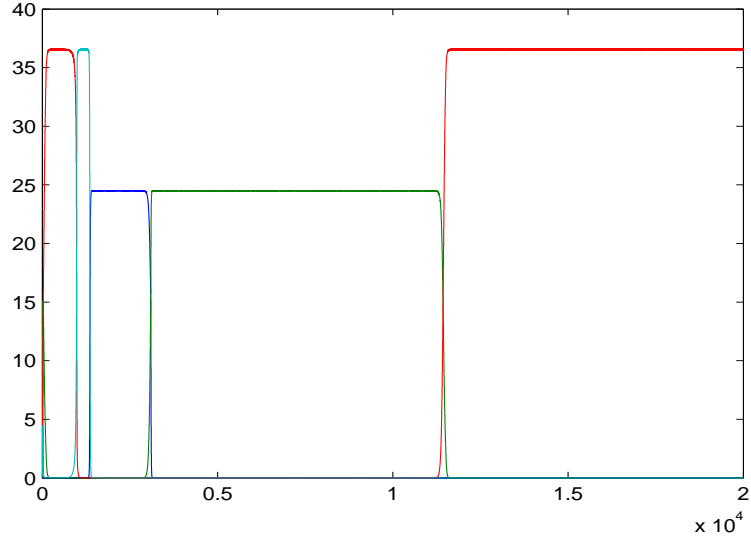


FIGURE 2. A heteroclinic cycle among four species.

evaluated at  $E_1$ ,  $E_2$ ,  $E_3$ , or  $E_4$ . The eigenvalues  $\sigma_{ij}$  of each equilibrium are defined as in (7). They must satisfy  $\sigma_{12} > 0$ ,  $\sigma_{23} > 0$ ,  $\sigma_{34} > 0$ , and  $\sigma_{41} > 0$ , and  $\sigma_{ij} < 0$  for  $ij \neq 12, 23, 34$ , and  $41$ .

If  $E_1 = (N_1^*, 0, 0, 0)$  is a steady state at which  $N_1$  is limited by  $Q$ , then the  $Q$  value at  $E_1$  is

$$(14) \quad Q_1^* = \lambda_{Q1}.$$

Then  $N_1^*$  can be found to be

$$N_1^* = (Q^0 - \lambda_{Q1})/c_{Q1}$$

and the other two corresponding nutrient values are

$$S_1^* = S^0 - c_{S1}N_1^* \text{ and } R_1^* = R^0 - c_{R1}N_1^*.$$

In order for  $E_1$  to be a steady state, i.e.,  $\mu_1(S_1^*, R_1^*, Q_1^*) - D = 0$ , we need to have

$$(15) \quad S_1^* > \lambda_{S1} \text{ and } R_1^* > \lambda_{R1}.$$

The Jacobian matrix of (1) when  $k = 3$  and  $n = 4$  at  $E_1$  is given by

$$J(E_1) = \begin{pmatrix} -N_1^* f'_{Q1} c_{Q1} & -N_1^* f'_{Q1} c_{Q2} & -N_1^* f'_{Q1} c_{Q3} & -N_1^* f'_{Q1} c_{Q4} \\ 0 & \sigma_{12} & 0 & 0 \\ 0 & 0 & \sigma_{13} & 0 \\ 0 & 0 & 0 & \sigma_{14} \end{pmatrix},$$

where  $f'_{Q1} = f'_{Q1}(Q_1^*)$  and

$$\sigma_{1j} = \mu_j(S_1^*, R_1^*, Q_1^*) - D = \min(f_{Sj}(S_1^*), f_{Rj}(R_1^*), f_{Qj}(Q_1^*)) - D, \quad j = 2, 3, 4.$$

We would like to have  $\sigma_{12} > 0$ ,  $\sigma_{13} < 0$ , and  $\sigma_{14} < 0$ . In order for  $\sigma_{12} > 0$ , we need to have

$$(16) \quad S_1^* > \lambda_{S2}, R_1^* > \lambda_{R2}, \text{ and } Q_1^* > \lambda_{Q2};$$

for  $\sigma_{13} < 0$ , we need to have

$$(17) \quad S_1^* < \lambda_{S3}, R_1^* < \lambda_{R3}, \text{ or } Q_1^* < \lambda_{Q3};$$

and for  $\sigma_{14} < 0$ , we need to have

$$(18) \quad S_1^* < \lambda_{S4}, R_1^* < \lambda_{R4}, \text{ or } Q_1^* < \lambda_{Q4}.$$

Neither conditions (14)–(18) contradict the assumption (13). We may also conclude from (14)–(18) that

$$S_1^* > \lambda_{S1} \quad \text{and} \quad R_1^* > \lambda_{R2}.$$

That is

$$(19) \quad \frac{S^0 - \lambda_{S1}}{Q^0 - \lambda_{Q1}} > \frac{c_{S1}}{c_{Q1}} \quad \text{and} \quad \frac{R^0 - \lambda_{R2}}{Q^0 - \lambda_{Q1}} > \frac{c_{R1}}{c_{Q1}}.$$

We also obtain that

$$\sigma_{13} = f_{Q3}(Q_1^*) - D \quad \text{and} \quad \sigma_{14} = f_{Q4}(Q_1^*) - D.$$

If  $E_2 = (0, N_2^*, 0, 0)$  is a steady state at which  $N_2$  is limited by  $S$ , then  $S$  value at  $E_2$  is

$$(20) \quad S_2^* = \lambda_{S2}.$$

Then  $N_2^*$  can be found to be

$$N_2^* = (S^0 - \lambda_{S2})/c_{S2}$$

and the other two corresponding nutrient values are

$$R_2^* = R^0 - c_{R2}N_2^* \quad \text{and} \quad Q_2^* = Q^0 - c_{Q2}N_2^*.$$

In order for  $E_2$  to be a steady state, i.e.,  $\mu_2(S_2^*, R_2^*, Q_2^*) - D = 0$ , we need to have

$$(21) \quad R_2^* > \lambda_{R2} \quad \text{and} \quad Q_2^* > \lambda_{Q2}.$$

The Jacobian matrix of (1) when  $k = 3$  and  $n = 4$  at  $E_2$  is given by

$$J(E_2) = \begin{pmatrix} \sigma_{21} & 0 & 0 & 0 \\ -N_2^* f'_{S2} c_{S1} & -N_2^* f'_{S2} c_{S2} & -N_2^* f'_{S2} c_{S3} & -N_2^* f'_{S2} c_{S4} \\ 0 & 0 & \sigma_{23} & 0 \\ 0 & 0 & 0 & \sigma_{24} \end{pmatrix},$$

where  $f'_{S2} = f'_{S2}(S_2^*)$  and

$$\sigma_{2j} = \mu_j(S_2^*, R_2^*, Q_2^*) - D = \min(f_{Sj}(S_2^*), f_{Rj}(R_2^*), f_{Qj}(Q_2^*)) - D, \quad j = 1, 3, 4.$$

We would like to have  $\sigma_{21} < 0$ ,  $\sigma_{23} > 0$ , and  $\sigma_{24} < 0$ . In order for  $\sigma_{21} < 0$ , we need to have

$$(22) \quad S_2^* < \lambda_{S1}, R_2^* < \lambda_{R1}, \text{ or } Q_2^* < \lambda_{Q1};$$

for  $\sigma_{23} > 0$ , we need to have

$$(23) \quad S_2^* > \lambda_{S3}, R_2^* > \lambda_{R3}, \text{ and } Q_2^* > \lambda_{Q3};$$

and for  $\sigma_{24} < 0$ , we need to have

$$(24) \quad S_2^* < \lambda_{S4}, R_2^* < \lambda_{R4}, \text{ or } Q_2^* < \lambda_{Q4}.$$

Neither conditions (20)–(24) contradict the assumption (13). We may also conclude from (20)–(24) that

$$R_2^* > \lambda_{R3} \quad \text{and} \quad Q_2^* > \lambda_{Q3}.$$

That is

$$(25) \quad \frac{R^0 - \lambda_{R3}}{S^0 - \lambda_{S2}} > \frac{c_{R2}}{c_{S2}} \quad \text{and} \quad \frac{Q^0 - \lambda_{Q3}}{S^0 - \lambda_{S2}} > \frac{c_{Q2}}{c_{S2}}.$$

We also obtain that

$$\sigma_{21} = f_{S1}(S_2^*) - D \quad \text{and} \quad \sigma_{24} = f_{S4}(S_2^*) - D.$$

If  $E_3 = (0, 0, N_3^*, 0)$  is a steady state at which  $N_3$  is limited by  $R$ , then the  $R$  value at  $E_3$  is

$$(26) \quad R_3^* = \lambda_{R3}.$$

Then  $N_3^*$  can be found to be

$$N_3^* = (R^0 - \lambda_{R3})/c_{R3}$$

and the other two corresponding nutrient values are

$$S_3^* = S^0 - c_{S3}N_3^* \quad \text{and} \quad Q_3^* = Q^0 - c_{Q3}N_3^*.$$

In order for  $E_3$  to be a steady state, i.e.,  $\mu_3(S_3^*, R_3^*, Q_3^*) - D = 0$ , we need to have

$$(27) \quad S_3^* > \lambda_{S3} \quad \text{and} \quad Q_3^* > \lambda_{Q3}.$$

The Jacobian matrix of (1) when  $k = 3$  and  $n = 4$  at  $E_3$  is given by

$$J(E_3) = \begin{pmatrix} \sigma_{31} & 0 & 0 & 0 \\ 0 & \sigma_{32} & 0 & 0 \\ -N_3^* f'_{R3} c_{R1} & -N_3^* f'_{R3} c_{R2} & -N_3^* f'_{R3} c_{R3} & -N_3^* f'_{R3} c_{R4} \\ 0 & 0 & 0 & \sigma_{34} \end{pmatrix},$$

where  $f'_{R3} = f'_{R3}(R_3^*)$  and

$$\sigma_{3j} = \mu_j(S_3^*, R_3^*, Q_3^*) - D = \min(f_{Sj}(S_3^*), f_{Rj}(R_3^*), f_{Qj}(Q_3^*)) - D, \quad j = 1, 2, 4.$$

We would like to have  $\sigma_{31} < 0$ ,  $\sigma_{32} < 0$ , and  $\sigma_{34} > 0$ . In order for  $\sigma_{31} < 0$ , we need to have

$$(28) \quad S_3^* < \lambda_{S1}, R_3^* < \lambda_{R1}, \quad \text{or} \quad Q_3^* < \lambda_{Q1};$$

for  $\sigma_{32} < 0$ , we need to have

$$(29) \quad S_3^* < \lambda_{S2}, R_3^* < \lambda_{R2}, \quad \text{or} \quad Q_3^* < \lambda_{Q2};$$

and for  $\sigma_{34} > 0$ , we need to have

$$(30) \quad S_3^* > \lambda_{S4}, R_3^* > \lambda_{R4}, \quad \text{and} \quad Q_3^* > \lambda_{Q4}.$$

Neither conditions (26)–(30) contradict the assumption (13). We may also conclude from (26)–(30) that

$$\lambda_{S1} > S_3^* > \lambda_{S4} \quad \text{and} \quad Q_3^* > \lambda_{Q3}.$$

That is

$$(31) \quad \frac{S^0 - \lambda_{S1}}{R^0 - \lambda_{R3}} < \frac{c_{S3}}{c_{R3}} < \frac{S^0 - \lambda_{S4}}{R^0 - \lambda_{R3}} \quad \text{and} \quad \frac{Q^0 - \lambda_{Q3}}{R^0 - \lambda_{R3}} > \frac{c_{Q3}}{c_{R3}}.$$

We also obtain

$$\sigma_{31} = f_{S1}(S_3^*) - D \quad \text{and} \quad \sigma_{32} = f_{R2}(R_3^*) - D.$$

If  $E_4 = (0, 0, 0, N_4^*)$  is a steady state at which  $N_4$  is limited by  $Q$ , then the  $Q$  value at  $E_4$  is

$$(32) \quad Q_4^* = \lambda_{Q4}.$$

Then  $N_4^*$  can be found to be

$$N_4^* = (Q^0 - \lambda_{Q4})/c_{Q4}$$

and the other two corresponding nutrient values are

$$S_4^* = S^0 - c_{S4}N_4^* \text{ and } R_4^* = R^0 - c_{R4}N_4^*.$$

In order for  $E_4$  to be a steady state, i.e.,  $\mu_4(S_4^*, R_4^*, Q_4^*) - D = 0$ , we need to have

$$(33) \quad S_4^* > \lambda_{S4} \text{ and } R_4^* > \lambda_{R4}.$$

The Jacobian matrix of (1) when  $k = 3$  and  $n = 4$  at  $E_4$  is given by

$$J(E_4) = \begin{pmatrix} \sigma_{41} & 0 & 0 \\ 0 & \sigma_{42} & 0 \\ 0 & 0 & \sigma_{43} \\ -N_4^* f'_{Q4} c_{Q1} & -N_4^* f'_{Q4} c_{Q2} & -N_4^* f'_{Q4} c_{Q3} & -N_4^* f'_{Q4} c_{Q4} \end{pmatrix},$$

where  $f'_{Q4} = f'_{Q4}(Q_4^*)$  and

$$\sigma_{4j} = \mu_j(S_4^*, R_4^*, Q_4^*) - D = \min(f_{Sj}(S_4^*), f_{Rj}(R_4^*), f_{Qj}(Q_4^*)) - D, \quad j = 1, 2, 3.$$

We would like to have  $\sigma_{41} > 0$ ,  $\sigma_{42} < 0$ , and  $\sigma_{43} < 0$ . In order for  $\sigma_{41} > 0$ , we need to have

$$(34) \quad S_4^* > \lambda_{S1}, R_4^* > \lambda_{R1}, \text{ and } Q_4^* > \lambda_{Q1};$$

for  $\sigma_{42} < 0$ , we need to have

$$(35) \quad S_4^* < \lambda_{S2}, R_4^* < \lambda_{R2}, \text{ or } Q_4^* < \lambda_{Q2};$$

and for  $\sigma_{43} < 0$ , we need to have

$$(36) \quad S_4^* < \lambda_{S3}, R_4^* < \lambda_{R3}, \text{ or } Q_4^* < \lambda_{Q3}.$$

Neither conditions (32)–(36) contrast to the assumption (13). We may also conclude from (32)–(36) that

$$S_4^* > \lambda_{S1} \quad \text{and} \quad \lambda_{R2} > R_4^* > \lambda_{R1}.$$

That is

$$(37) \quad \frac{S^0 - \lambda_{S1}}{Q^0 - \lambda_{Q4}} > \frac{c_{S4}}{c_{Q4}} \quad \text{and} \quad \frac{R^0 - \lambda_{R1}}{Q^0 - \lambda_{Q4}} > \frac{c_{R4}}{c_{Q4}} > \frac{R^0 - \lambda_{R2}}{Q^0 - \lambda_{Q4}}.$$

We can also obtain that

$$\sigma_{42} = f_{R2}(R_4^*) - D \quad \text{and} \quad \sigma_{43} = f_{Q3}(Q_4^*) - D.$$

So far, the four conditions (19), (25), (31), and (37) verify the first assumption (8a) in Corollary 1. With the further assumptions (8b) and (8c), we can then apply Corollary 1. The proof is complete.  $\square$

4. TWO RESOURCES AND  $n$  SPECIES

For the consumer-resource model (1), when there are two nutrients and two species in a continuous culture, Hsu et al. [5] had shown that the competition outcomes are similar to the Lotka-Volterra two-species competition models. When there are more than two species, Li and Smith [13] showed that competitive exclusion principle holds for the case of 3 species and all of the cases for  $n > 3$  species except for the following case when their break-even concentrations satisfy the following:

$$(38) \quad \begin{aligned} \lambda_{S1} &< \lambda_{S2} < \lambda_{S3} < \cdots < \lambda_{Sn}, \\ \lambda_{Rn} &< \lambda_{R,n-1} < \cdots < \lambda_{R2} < \lambda_{R1}. \end{aligned}$$

We have additional results for the two-resource  $n$ -species case in the following theorem.

**THEOREM 4.** *Consider the limiting system (4) of the chemostat model with  $n$  species competing for two essential nutrients  $S$  and  $R$ . Assume that the break-even concentrations satisfy (38). Then there exists no heteroclinic cycle.*

*Proof.* We only need to show that the assumption (8a) in Corollary 1 cannot be satisfied. The theorem is proved by contradiction.

Suppose there is a heteroclinic cycle connecting all single species equilibria  $E_i$ 's. Without loss of generality we may start the cycle from  $E_1$ . Let  $\Gamma_{ij}$  denote the heteroclinic orbit connecting the two points  $E_i$  and  $E_j$ . We can summarize the proof as follows: the heteroclinic orbits  $\Gamma_{12}, \Gamma_{23}, \dots$ , and  $\Gamma_{n-2,n-1}$  can be found, but  $\Gamma_{n1}$  does not exist. The cycle is broken between  $E_n$  and  $E_1$ . Therefore, there is no heteroclinic cycle.

The proof consists of three parts: (i) if there is a heteroclinic orbit  $\Gamma_{k,k+1}$ ,  $k = 1, 2, \dots, n-1$ , then species  $k$  is limited by resource  $R$ , (ii) there is no heteroclinic orbit  $\Gamma_{km}$  where  $k+1 < m \leq n$ , and (iii) there is no heteroclinic orbit  $\Gamma_{n1}$ .

Claim 1: If there is a heteroclinic orbit  $\Gamma_{k,k+1}$ ,  $k = 1, 2, \dots, n-1$ , then species  $k$  is limited by the resource  $R$ .

If  $N_k$  is limited by  $S$ , then  $S_k^* = \lambda_{S,k}$  and  $R_k^* > \lambda_{R,k}$ . To guarantee the heteroclinic orbit connecting  $E_k$  to  $E_{k+1}$ , the  $k+1$ st eigenvalue  $\sigma_{k,k+1}$  of the Jacobian matrix evaluated at  $E_k$  is positive which implies  $S_k^* > \lambda_{S,k+1}$  and  $R_k^* > \lambda_{R,k+1}$ , a contradiction to the assumption (38) that says  $S_k^* = \lambda_{S,k} < \lambda_{S,k+1}$ . If  $N_k$  is  $R$ -limited, then  $S_k^* > \lambda_{S,k}$  and  $R_k^* = \lambda_{R,k}$ . Since  $\lambda_{R_k^*} < \lambda_{R,k-1} < \lambda_{R,k-2} < \cdots < \lambda_{R2} < \lambda_{R1}$ , we have

$$\sigma_{k,k-1} < 0, \sigma_{k,k-2} < 0, \dots, \sigma_{k,2} < 0, \text{ and } \sigma_{k,1} < 0.$$

$S_k^*$  can be chosen in this way  $\lambda_{S,k+1} < S_k^* < \lambda_{S,k+2} < \lambda_{S,k+3} < \cdots < \lambda_{S,n}$  so that  $\sigma_{k,k+2} < 0$ ,  $\sigma_{k,k+3} < 0, \dots$ , and  $\sigma_{k,n} < 0$ . Since  $S_k^* > \lambda_{S,k+1}$  and  $R_k^* = \lambda_{R,k} > \lambda_{R,k+1}$ , we obtain  $\sigma_{k,k+1} > 0$ .

Claim 2: There is no heteroclinic orbit connecting  $E_k$  to  $E_m$  where  $k+1 < m \leq n$ .

If  $N_k$  is  $S$ -limited, then  $S_k^* = \lambda_{S,k}$  and  $R_k^* > \lambda_{R,k}$ .  $\sigma_{k,m} > 0$  implies  $S_k^* > \lambda_{S,m}$  and  $R_k^* > \lambda_{R,m}$ , a contradiction to (38) which says  $S_k^* = \lambda_{S,k} < \lambda_{S,m}$ . If  $N_k$  is  $R$ -limited, then  $S_k^* > \lambda_{S,k}$  and  $R_k^* = \lambda_{R,k}$ , then  $\sigma_{k,k+1} < 0$  implies  $S_k^* < \lambda_{S,k+1}$  or  $R_k^* < \lambda_{R,k+1}$ , both are impossible due to (38).

Claim 3: There is no heteroclinic orbit connecting  $E_n$  to  $E_1$ .

If  $N_n$  is  $R$ -limited, then  $R_n^* = \lambda_{R,n}$  and  $S_n^* > \lambda_{S,n}$ . If  $\sigma_{n,1} > 0$  then  $S_n^* > \lambda_{S,1}$  and  $R_n^* > \lambda_{R,1}$ , a contradiction. If  $N_n$  is  $S$ -limited, then  $R_n^* > \lambda_{R,n}$  and  $S_n^* = \lambda_{S,n}$ . If  $\sigma_{n,2} < 0$  then  $S_n^* < \lambda_{S,2}$  or  $R_n^* < \lambda_{R,2}$ , a contradiction.

So far, the possible heteroclinic orbit is  $E_1(R) \rightarrow E_2(R) \rightarrow \cdots \rightarrow E_{n-1}(R) \rightarrow E_n$ , but since  $E_n \rightarrow E_1$  is impossible. We have proved that there is no heteroclinic loop under the assumption (38).  $\square$

### 5. THREE OR MORE RESOURCES AND $n$ SPECIES

The following theorem says that three resources can support any finite number of species, which greatly improve the results by Huisman and Weissing [9, 10, 11].

**THEOREM 5.** *Three resources  $S$ ,  $R$ , and  $Q$  and  $n$  species  $N_1, N_2, \dots, N_n$ .*

$$(39) \quad \begin{aligned} \lambda_{S1} &< \lambda_{S2} < \lambda_{S3} < \cdots < \lambda_{Sn}, \\ \lambda_{R1} &< \lambda_{Rn} < \lambda_{R2} < \lambda_{R3} < \cdots < \lambda_{R,n-1}, \\ \lambda_{Q,n-1} &< \lambda_{Qn} < \lambda_{Q,n-2} < \cdots < \lambda_{Q2} < \lambda_{Q1}, \end{aligned}$$

*Then the assumption (8a) in Corollary 1 can be satisfied. Furthermore, if the eigenvalues defined as in (7) satisfy (8b) and (8c), then we have the following stable heteroclinic loop:*

$$E_1(Q) \rightarrow E_2(Q) \rightarrow \cdots \rightarrow E_{n-2}(Q) \rightarrow E_{n-1}(R) \rightarrow E_n(S) \rightarrow E_1.$$

*Proof.* We only need to verify the following four cases: (i)  $E_k(Q) \rightarrow E_{k+1}$ ,  $k = 1, \dots, n-3$ , (ii)  $E_{n-2}(Q) \rightarrow E_{n-1}$ , (iii)  $E_{n-1}(R) \rightarrow E_n$ , and (iv)  $E_n(S) \rightarrow E_1$ .

(i)  $E_k(Q) \rightarrow E_{k+1}$ : Since  $N_k$  is limited by  $Q$ , we have  $Q_k^* = \lambda_{Qk}$ . Choose  $S_k^*$  and  $R_k^*$  such that

$$\begin{aligned} \lambda_{S,k+1} &< S_k^* < \lambda_{S,k+2}, \\ \lambda_{R,k+1} &< R_k^* < \lambda_{R,k+2}. \end{aligned}$$

The Jacobian matrix evaluated at  $E_k = (0, 0, \dots, N_k^*, 0, \dots, 0)$  has along the diagonal the eigenvalues  $\sigma_{kj}$  for  $j = 1, 2, \dots, n$ . The eigenvalues are defined as in (7).

In order to have  $E_k \rightarrow E_{k+1}$  we need to have  $\sigma_{ki} < 0$  for  $i \neq k+1$  and  $\sigma_{k,k+1} > 0$ . For  $\sigma_{k,k+1} > 0$ , we need to have

$$S_k^* > \lambda_{S,k+1}, \quad R_k^* > \lambda_{R,k+1}, \quad \text{and} \quad Q_k^* > \lambda_{Q,k+1}.$$

This can be done by the way we choose  $S_k^*$ ,  $R_k^*$  and  $Q_k^*$ .

In order to have  $\sigma_{ki} < 0$ ,  $i \neq k, k+1$ , we need

$$S_k^* < \lambda_{Qi} \quad \text{or} \quad R_k^* < \lambda_{Ri} \quad \text{or} \quad Q_k^* < \lambda_{Qi}.$$

Since

$$Q_k^* < \lambda_{Q,k-1} < \lambda_{Q,k-2} < \cdots < \lambda_{Q1},$$

we have  $\sigma_{ki} < 0$  for  $i = 1, 2, \dots, k-1$ . Since

$$S_k^* < \lambda_{S,k+2} < \lambda_{S,k+3} < \cdots < \lambda_{Sn},$$

we have  $\sigma_{ki} < 0$  for  $i = k+2, k+3, \dots, n$ . Then the eigenvalues of the Jacobian matrix at  $E_k$  satisfy  $\sigma_{k,k+1} > 0$  and  $\sigma_{ki} < 0$  for  $i \neq k+1$ .

(ii)  $E_{n-2}(Q) \rightarrow E_{n-1}$ : Since  $N_{n-2}$  is limited by  $Q$  we have  $Q_{n-2}^* = \lambda_{Q,n-2}$ . Choose  $S_{n-2}^*$  and  $R_{n-2}^*$  such that

$$\begin{aligned} \lambda_{S,n-1} &< S_{n-2}^* < \lambda_{Sn}, \\ \lambda_{R,n-1} &< R_{n-2}^*. \end{aligned}$$

Since  $S_{n-2}^* < \lambda_{S_n}$  we have  $\sigma_{n-2,n} < 0$ . Since  $Q_{n-2}^* = \lambda_{Q,n-2} < \lambda_{Q_i}$  for  $i = 1, 2, \dots, n-3$  we have  $\sigma_{n-2,i} < 0$ . Then we have  $\sigma_{n-1,n-2} > 0$  and  $\sigma_{n-2,i} < 0$  for  $i \neq n-1, n-2$ .

(iii)  $E_{n-1}(R) \rightarrow E_n$ :  $N_{n-1}$  is limited by  $R$ , so  $R_{n-1}^* = \lambda_{R,n-1}$ . Choose  $S_{n-1}^*$  and  $Q_{n-1}^*$  such that

$$\begin{aligned}\lambda_{S_n} &< S_{n-1}^*, \\ \lambda_{Q_n} &< Q_{n-1}^* < \lambda_{Q,n-2}.\end{aligned}$$

Since  $Q_{n-1}^* < \lambda_{Q_i}$  for  $i \neq n-1, n$ , we have  $\sigma_{n-1,i} < 0$ . Then we have  $\sigma_{n-1,n} > 0$  and  $\sigma_{n-1,i} < 0$  for  $i \neq n, n-1$ .

(iv)  $E_n(S) \rightarrow E_1$ :  $N_n$  is limited by  $S$  so  $S_n^* = \lambda_{S_n}$ . Choose  $R_n^*$  and  $Q_n^*$  so that

$$\begin{aligned}\lambda_{R_n} &< R_n^* < \lambda_{R_2}, \\ \lambda_{Q_1} &< Q_n^*.\end{aligned}$$

Since  $R_n^* < \lambda_{R_2} < \lambda_{R_3} < \dots < \lambda_{R,n-1}$ , we have  $\sigma_{ni} < 0$  for  $n \neq 1, n$ . Then we have  $\sigma_{n1} > 0$  and  $\sigma_{ni} < 0$  for  $i \neq 1, n$ .  $\square$

The previous results can be extended to  $m+3$  resources and  $n$  species.

**THEOREM 6.** *If there are  $m+3$  resources  $S, R, Q, P_1, \dots, P_m$ , and  $n$  species  $N_1, N_2, \dots, N_n$ , then under the following conditions*

$$(40) \quad \begin{aligned}\lambda_{S_1} &< \lambda_{S_2} < \lambda_{S_3} < \dots < \lambda_{S_n}, \\ \lambda_{R_1} &< \lambda_{R_n} < \lambda_{R_2} < \lambda_{R_3} < \dots < \lambda_{R,n-1}, \\ \lambda_{Q,n-1} &< \lambda_{Q_n} < \lambda_{Q,n-2} < \dots < \lambda_{Q_2} < \lambda_{Q_1}, \\ \lambda_{P_j,1} &< \lambda_{P_j,2} < \lambda_{P_j,3} < \dots < \lambda_{P_j,n}, j = 1, 2, \dots, m,\end{aligned}$$

*Then the assumption (8a) in Corollary can be satisfied. Furthermore, if the eigenvalues defined as in (7) satisfy (8b) and (8c), then we have the following stable heteroclinic loop:*

$$E_1(Q) \rightarrow E_2(Q) \rightarrow \dots \rightarrow E_{n-2}(Q) \rightarrow E_{n-1}(R) \rightarrow E_n(S) \rightarrow E_1.$$

*Proof.* We only need to verify the following four cases: (i)  $E_k(Q) \rightarrow E_{k+1}$ ,  $k = 1, \dots, n-3$ , (ii)  $E_{n-2}(Q) \rightarrow E_{n-1}$ , (iii)  $E_{n-1}(R) \rightarrow E_n$ , and (iv)  $E_n(S) \rightarrow E_1$ .

(i)  $E_k(Q) \rightarrow E_{k+1}$ : Since  $N_k$  is limited by  $Q$ , we have  $Q_k^* = \lambda_{Q_k}$ . Choose  $S_k^*$ ,  $R_k^*$ , and  $P_{j,k}^*$ ,  $j = 1, \dots, m$  such that

$$\begin{aligned}\lambda_{S,k+1} &< S_k^* < \lambda_{S,k+2}, \\ \lambda_{R,k+1} &< R_k^* < \lambda_{R,k+2}, \\ \lambda_{P_j,k+1} &< P_{j,k}^* < \lambda_{P_j,k+2}.\end{aligned}$$

Similar to the arguments before, the eigenvalues of the Jacobian matrix at  $E_k$  satisfy  $\sigma_{k,k+1} > 0, \sigma_{ki} < 0, i \neq k+1$ .

(ii)  $E_{n-2}(Q) \rightarrow E_{n-1}$ : Since  $N_{n-2}$  is limited by  $Q$  we have  $Q_{n-2}^* = \lambda_{Q,n-2}$ . Choose  $S_{n-2}^*$ ,  $R_{n-2}^*$ , and  $P_{j,n-2}^*$ ,  $j = 1, \dots, m$  such that

$$\begin{aligned}\lambda_{S,n-1} &< S_{n-2}^* < \lambda_{S_n}, \\ \lambda_{R,n-1} &< R_{n-2}^*, \\ \lambda_{P_j,n-1} &< P_{j,n-2}^* < \lambda_{P_j,n}.\end{aligned}$$

Then we have  $\sigma_{n-1,n-2} > 0, \sigma_{n-2,i} < 0, i \neq n-1, n-2$ .

(iii)  $E_{n-1}(R) \rightarrow E_n$ :  $N_{n-1}$  is limited by  $R$ , so  $R_{n-1}^* = \lambda_{R,n-1}$ . Choose  $S_{n-1}^*$ ,  $R_{n-1}^*$ , and  $P_{j,n-1}^*$ ,  $j = 1, \dots, m$  such that they satisfy

$$\begin{aligned}\lambda_{S_n} &< S_{n-1}^*, \\ \lambda_{Q_n} &< Q_{n-1}^* < \lambda_{Q,n-2}, \\ \lambda_{P_{j,n}} &< P_{j,n-1}^*.\end{aligned}$$

Since  $Q_{n-1}^* < \lambda_{Q_i}$  for  $i \neq n-1, n$ , we have  $\sigma_{n-1,i} < 0$ . Then we have  $\sigma_{n-1,n} > 0$ ,  $\sigma_{n-1,i} < 0$ ,  $i \neq n, n-1$ .

(iv)  $E_n(S) \rightarrow E_1$ :  $N_n$  is limited by  $S$ ,  $S_n^* = \lambda_{S_n}$ , and choose  $S_n^*$ ,  $R_n^*$ , and  $P_{j,n}^*$ ,  $j = 1, \dots, m$  satisfying

$$\begin{aligned}\lambda_{R_n} &< R_n^* < \lambda_{R_2}, \\ \lambda_{Q_1} &< Q_n^*, \\ \lambda_{P_{j,1}} &< P_{j,n}^*.\end{aligned}$$

Since  $R_n^* < \lambda_{R_2} < \lambda_{R_3} < \dots < \lambda_{R,n-1}$ , we have  $\sigma_{ni} < 0$  for  $n \neq 1, n$ . Then we have  $\sigma_{n1} > 0$ ,  $\sigma_{ni} < 0$ , for  $i \neq 1, n$ .  $\square$

## 6. DISCUSSION

In this paper we consider the possibility of constructing a stable heteroclinic loop of one-species equilibria for  $n$  species competing for  $k$  essential resources in a chemostat. The significance of the construction is two-fold. First, it is a potential limit set for the dynamics of the system. Second, it is possible to envision the bifurcation of a very long-period periodic orbit from such a cycle. Thus the existence of the loop may indicate the coexistence state of  $n$  species in oscillation form. In [13] Li and Smith conjectured the competitive exclusion principle holds for  $n$  species,  $n > 2$ , competing for two essential resources. In Theorem 4 we prove that there exists no heteroclinic loop for this case. Thus it may give a clue for the future proof of the conjecture. For the case of three essential resources, we construct a stable heteroclinic loop of four species in Theorem 3, thus we extend the result of the paper [12] from three species to four species. Furthermore in Theorem 5 we prove that for three essential resources we are able to construct a stable heteroclinic loop for any finite number of species. Thus our analytic result improves the results of Huisman and Weissing in [9, 10, 11] which are numerical. In fact in Theorem 6, the result can be extended to case of any finite number of species competing for  $k$  resources,  $k > 3$ .

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(S.-B. Hsu) DEPARTMENT OF MATHEMATICS, NATIONAL TSING-HUA UNIVERSITY, HSINCHU 300, TAIWAN

*E-mail address:* sbhsu@math.nthu.edu.tw

(L.-I. W. Roeger) DEPARTMENT OF MATHEMATICS AND STATISTICS, BOX 41042, TEXAS TECH UNIVERSITY, LUBBOCK, TX 79409, TEL: 806-742-2580, FAX: 806-742-1112

*E-mail address:* lih-ing.roeger@ttu.edu