Heteroclinic cycles in the chemostat models and the winnerless competition principle

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A B S T R A C T

Winnerless competition principle (WLC) is a type of competition that does not have a winner; all species take turns (or switch) to win. In the phase space, it appears as a stable heteroclinic contour connecting single-species equilibria. In ecology, May and Leonard [R.M. May, W.J. Leonard, Nonlinear aspects of competition between three species, SIAM J. Appl. Math. 29 (1975) 243–253] were the first to discover the behavior in their famous paper that the competition of three species experiences a special type of WLC competition, the rock-paper-scissors competition. Recently, WLC concepts are used for the design in neural network dynamics. In this manuscript, it is shown that WLC can also appear in the chemostat model. We consider a chemostat model of n species of microorganisms competing for k essential and growth-limiting nutrients. Sufficient conditions for a stable heteroclinic cycle connecting single-species equilibria in the limit sets are given. The heteroclinic cycle can be constructed so that the equilibria are connected in the following order: $E_1 \to E_2 \to E_3 \to \cdots \to E_n \to E_1$ in which E_i's are the ith species equilibria. This heteroclinic cycle describes the rock-paper-scissors winnerless competition; all of the n species take turns to win, there is no final winner.

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1. Introduction

Winnerless competition principle (WLC) is a type of competition without a winner; all species take turns (or switch) to win. Recently, WLC concepts are used for the design in neural dynamics and neural network computations [1,2,4,12, 14,16,17]. The main point of this principle is the transformation of the spatial inputs into outputs based on the intrinsic "switching" dynamics of the neural system. The geometrical image of the sequence of the switching in the phase space is a stable heteroclinic contour (or cycle).

A heteroclinic cycle consists of finite saddle equilibria and finite heteroclinic orbits that connect these equilibria. A winnerless competition cycle is a heteroclinic cycle that connects only one-species equilibria. The most famous one is the May–Leonard competition models [3,13] in ecology,

$$x'_1 = x_1(1 - x_1 - \alpha_1 x_2 - \beta_1 x_3),$$
$$x'_2 = x_2(1 - \beta_2 x_1 - x_2 - \alpha_2 x_3),$$
$$x'_3 = x_3(1 - \alpha_3 x_1 - \beta_3 x_2 - x_3),$$

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where $0 < \alpha_i < 1 < \beta_i$ for all $i = 1, 2, 3$. For the symmetric case studied by May and Leonard when $\alpha_i = \alpha$, $\beta_i = \beta$, $i = 1, 2, 3$, and $\alpha + \beta > 2$ the solutions of the system asymptotically moves closer and closer to an orbit, a heteroclinic contour, joining the equilibria $(1, 0, 0)$, $(0, 1, 0)$, and $(0, 0, 1)$. Let $A_i = 1 - \alpha_i$ and $B_i = \beta_i - 1$, $i = 1, 2, 3$. Chi et al. [3] showed that in the asymmetric case when $A_1 A_2 A_3 < B_1 B_2 B_3$, the heteroclinic contour is stable and is a WLC phenomena. WLC can also appear in a chemostat model.

Chemostat model is a mathematical model in ecology describing two or more populations competing for the same resources, such as growth-limiting nutrients. It may represent competition in a simple lake, or as a model of waste water treatment process [15]. The general chemostat model for n species competing for k growth-limiting nutrients is as the following [6–8]:

$$N_i'(t) = N_i(t)\big(\mu_i(R_1, R_2, \ldots, R_k) - D\big),$$

$$R_j'(t) = D\big(R_j^0 - R_j(t)\big) - \sum_{i=1}^{n} c_{ji}\mu_i(R_1, R_2, \ldots, R_k)N_i,$$

$$N_i(0) > 0, \qquad R_j(0) \geqslant 0, \quad i = 1, 2, \ldots, n, \ j = 1, 2, \ldots, k. \tag{1}$$

$N_i(t)$ denotes the density of species i at time t; $R_j(t)$ denotes the concentration of nutrient j at time t; $\mu_i(R_1, \ldots, R_k)$ 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

$$\mu_i(R_1, R_2, \ldots, R_k) = \min\big(f_{1i}(R_1), f_{2i}(R_2), \ldots, f_{ki}(R_k)\big), \tag{2}$$

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

$$f_{ji}(0) = 0 \quad \text{and} \quad f_{ji}'(x) > 0 \quad \text{for } x > 0.$$

For example, we may choose the Monod or Michaelis–Menten kinetics for resource up-takes:

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

For species i and resource j, there is a break-even concentration λ_{ji} defined as

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

The break-even concentration λ_{ji} is the subsistence concentration of the resource when species i is growth-limited by resource j alone. By definition of the function f_{ji}, we 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-takes. Then the break-even concentration of species i on resource R_j becomes

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

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

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

Therefore, the polygonal set

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

is an invariant and globally attracting set for model (1). On the polygonal set, model (1) is given as

$$N_i'(t) = N_i(t)\big[\mu_i(N_1, N_2, \ldots, N_n) - D\big], \tag{4}$$

where

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

on the set

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

Then the resources can be easily recovered from the equations

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

Huisman and Weissing [6–8] explained biodiversity by using the consumer-resource model (1). Their numerical simulation results showed that three or more resources can generate sustained oscillations or chaotic dynamics of species abundance. For three resources, there are periodic oscillations among three species [9] and among four species [11] and the rigorous mathematical verification was given. When there are five species, chaotic dynamics may occur. Moreover, they showed that three resources can support up to nine species and five resources up to twelve species. Competitive exclusion principle states that at most k species coexist in the competition for k resources. Base on their observation of model (1), the competitive exclusion principle no longer holds when there are more than two resources.

In this manuscript, we present the existence conditions for a stable heteroclinic cycle and therefore a WLC. We state a theorem that helps us to verify the results. The following theorem states the existence and stability conditions of heteroclinic cycles for the Lotka–Volterra competition system

$$a_i'(t) = a_i(t)\left(1 - \sum_{j=1}^n \rho_{ij}a_j(t)\right), \quad i = 1, 2, \ldots, n, \tag{5}$$

where $\rho_{ij} > 0$ for $i, j = 1, \ldots, n$, $i \neq j$ and $\rho_{ii} = 1$ for $i = 1, \ldots, n$. Denote by A_i the equilibrium with only species i exists, i.e., $A_i = (0, \ldots, 0, 1, 0, \ldots, 0)$. The eigenvalues of the Jacobian matrix at A_i are $1 - \rho_{ji}$ for all $j \neq i$ and $1 - 2\rho_{ii} = -1$. Assume that there is a heteroclinic orbit Γ_i connecting the points A_i and A_{i+1}, $i = 1, 2, \ldots, n$, and $A_{n+1} \equiv A_1$. The following results show that the contour or the heteroclinic cycle $\Gamma = \bigcup_{i=1}^n \Gamma_i \cup A_i$ can be an attractor.

Theorem 1. *(See Afraimovich et al. [1].) For the Lotka–Volterra competition system* (5), *assume that for $i = 1, 2, \ldots, n$,*

$$1 - \rho_{ki} < 0, \quad \text{for } k \neq i+1, \quad \text{and} \quad 1 - \rho_{i+1,i} > 0,$$

$$1 - \rho_{i,i+1} > -1 = 1 - 2\rho_{i+1,i+1},$$

$$1 - \rho_{i,i+1} > 1 - \rho_{k,i+1}, \quad \text{for } k \neq i, i+2, \quad \text{and}$$

$$\nu = \prod_{i=1}^n \left(-\frac{1 - \rho_{i,i+1}}{1 - \rho_{i+1,i}}\right) > 1. \tag{6}$$

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

The value of ν is called the saddle value. The conditions in Theorem 1 are obtained by linearizing the system at the equilibria A_i's for all $i = 1, 2, \ldots, n$ and finding the eigenvalues of each Jacobian matrix at A_i. Hence, the results can be applied to the resource-consumer system (1) and its limiting equations (4).

Consider the limiting equations (4). Denote by E_i the equilibrium with only species i exists, i.e., $E_i = (0, \ldots, 0, N_i^*, 0, \ldots, 0)$. The eigenvalues of the Jacobian matrix at E_i are

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

Note that σ_{ii}, $i = 1, 2, \ldots, n$, is always less than zero. For a fixed i, assume that $\sigma_{ik} < 0$, for $k \neq i+1$ and $\sigma_{i,i+1} > 0$. Then the equilibrium E_i has only one-dimension unstable manifold. An intersection of hyper-planes, $P_{2i} = \bigcap_{j=1, \ j\neq i, i+1}^n \{N_j = 0\}$, is a two-dimensional invariant manifold containing points E_i and E_{i+1} such that E_i is a saddle point on P_{2i} and E_{i+1} is a stable node on P_{2i}. System (4) on P_{2i} has the form:

$$N'_i = N_i\big(\mu_i(R_1, R_2, \ldots, R_k) - D\big),$$
$$N'_{i+1} = N_{i+1}\big(\mu_{i+1}(R_1, R_2, \ldots, R_k) - D\big). \tag{8}$$

The functions μ_i's are defined as in (2). Because of the structure of the function μ_i, without loss of generality, we may assume in (8) there are two limiting resources only. Hsu et al. [5] showed that system (8) behaves just like the two-dimensional Lotka–Volterra system. When $\sigma_{ik} < 0$, for $k \neq i+1$ and $\sigma_{i,i+1} > 0$, there is no equilibrium in P_{2i} where $N_i > 0$ and $N_{i+1} > 0$, and the separatrix Γ_i of the saddle point E_i must go to the attractor E_{i+1}.

Therefore, for the full system (1) and its limiting equations (4), there is a heteroclinic orbit Γ_i connecting the points E_i and E_{i+1}, $i = 1, 2, \ldots, n$, and $E_{n+1} = E_1$. We have similar results for model (1) for the heteroclinic contour $\Gamma = \bigcup_{i=1}^n \Gamma_i \cup E_i$ following Theorem 1.

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

$$\sigma_{ik} < 0, \quad \text{for } k \neq i+1, \quad \text{and} \quad \sigma_{i,i+1} > 0, \tag{9a}$$

$$\sigma_{i+1,i} > \sigma_{i+1,i+1}, \tag{9b}$$

$$\sigma_{i+1,i} > \sigma_{i+1,k}, \quad \text{for } k \neq i, i+2, \tag{9c}$$

$$\nu = \prod_{i=1}^n \left(-\frac{\sigma_{i+1,i}}{\sigma_{i,i+1}}\right) > 1. \tag{9d}$$

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

Corollary 1 is used to construct a locally stable heteroclinic cycle for model (1). This manuscript is organized as follows. In Section 2, the three-resource–three-species case is reviewed and studied. Three-resource–four-species is studied in Section 3. In Section 4, we show that the heteroclinic cycles for the two-resource–n-species case does not exist. Three and more resources and n species case is presented in Section 5. In Section 6, discussion and possible further work are presented.

2. Three resources and three species

For the consumer-resource model (1), when $n = k = 3$, Li [9] studied 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 satisfying the following:

$$\lambda_{S3} < \lambda_{S2} < \lambda_{S1} < S^0,$$
$$\lambda_{R1} < \lambda_{R3} < \lambda_{R2} < R^0,$$
$$\lambda_{Q2} < \lambda_{Q1} < \lambda_{Q3} < Q^0, \tag{10}$$

where N_1 is limited by Q, N_2 is limited by S, and N_3 is limited by R. The hypothesis (10) says that among all three species N_3 is the strongest competitor for resource S and is the weakest for resource Q; N_2 is the strongest for resource Q and the weakest for resource R; and N_1 is the strongest for resource R and the weakest for resource S. Hence, the competition for resources is in cyclic fashion. The saddle value ν for the system is

$$\nu = -\frac{\sigma_{13}\sigma_{21}\sigma_{32}}{\sigma_{31}\sigma_{12}\sigma_{23}}. \tag{11}$$

Li [9] had proved the following results.

Theorem 2. *(See [9].) Consider the consumer-resource model* (1) *when $n = k = 3$ and its three resources S, R, and Q. If the break-even concentrations satisfy* (10) *and the saddle value $\nu < 1$, then the heteroclinic cycle $E_1(Q) \to E_2(S) \to E_3(R) \to E_1$ is unstable and there exists a stable periodic solution.*

The notation $E_1(Q) \to E_2(S) \to E_3(R) \to E_1$ will be used throughout the manuscript. It represents the heteroclinic cycle in the order $E_1 \to E_2 \to E_3 \to E_1$. The notation $E_1(Q)$ denotes that the first species N_1 is limited by the resource Q near the equilibrium E_1. By Corollary 1, we obtain stable condition for a heteroclinic cycle.

Theorem 3. *Consider the consumer-resource model* (1) *when $n = k = 3$ and its three resources S, R, and Q. Assume the break-even concentrations satisfy* (10) *and the saddle value $\nu > 1$. Furthermore, if*
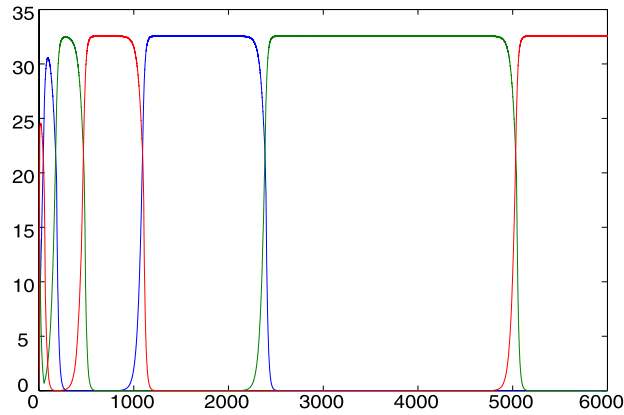
Fig. 1. A stable heteroclinic cycle for model (1) when $n = k = 3$.

$$\sigma_{12} > 0, \qquad \sigma_{23} > 0, \qquad \sigma_{31} > 0,$$
$$\sigma_{11} < \sigma_{13} < 0,$$
$$\sigma_{22} < \sigma_{21} < 0,$$
$$\sigma_{33} < \sigma_{32} < 0, \tag{12}$$

then the heteroclinic cycle $E_1(Q) \to E_2(S) \to E_3(R) \to E_1$ is locally stable.

For the system when $n = k = 3$, there are other ways to produce heteroclinic cycles or periodic solutions. For example, if the break-even concentrations satisfy the following conditions:

$$\lambda_{S1} < \lambda_{S2} < \lambda_{S3},$$
$$\lambda_{R1} < \lambda_{R3} < \lambda_{R2},$$
$$\lambda_{Q2} < \lambda_{Q3} < \lambda_{Q1},$$

then we maybe able to find the following heteroclinic cycle

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

and a periodic solution depending on the saddle value ν. In addition, 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 $E_1 \to E_2 \to E_3 \to E_1$. Fig. 1 shows a heteroclinic cycle of model (1) when $n = k = 3$.

3. Three resources and four species

When there are three resources and four species, $k = 3$ and $n = 4$, we can construct a heteroclinic cycle in this order: $E_1 \to E_2 \to E_3 \to E_4 \to E_1$. There are many ways to do it depending on the limiting resources of each species. The following theorem presents one stable heteroclinic cycle in the model.

Theorem 4. *For the case of three resources S, R, and Q and four species, assume the break-even concentrations satisfy the following*:

$$\lambda_{S3} < \lambda_{S2} < \lambda_{S4} < \lambda_{S1},$$
$$\lambda_{R4} < \lambda_{R1} < \lambda_{R3} < \lambda_{R2},$$
$$\lambda_{Q2} < \lambda_{Q1} < \lambda_{Q4} < \lambda_{Q3}. \tag{13}$$

Then the assumption (9a) *in Corollary 1 is satisfied. Furthermore, if the eigenvalues* (7) *satisfy* (9b), (9c), *and* (9d), *i.e.,*

$$\sigma_{21} > \sigma_{22}, \qquad \sigma_{21} > \sigma_{24},$$
$$\sigma_{32} > \sigma_{33}, \qquad \sigma_{32} > \sigma_{31},$$
$$\sigma_{43} > \sigma_{44}, \qquad \sigma_{43} > \sigma_{42},$$
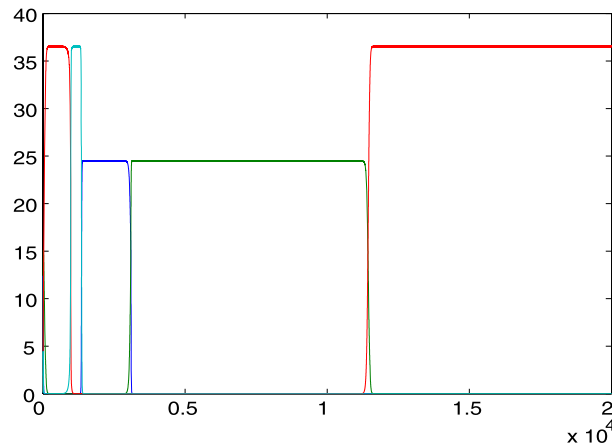$$\sigma_{14} > \sigma_{11}, \qquad \sigma_{14} > \sigma_{13}, \tag{14}$$

Fig. 2. A stable heteroclinic cycle among four species for system (1).

and

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

then there exists a stable heteroclinic cycle in the following order

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

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

Proof. There are four 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 $E_4 = (0, 0, 0, N_4^*)$. The eigenvalues σ_{ij} of the Jacobian matrix at E_i are defined as in (7). Under the condition that N_1, N_2, N_3, and N_4 are limited by resources Q, S, R, and Q respectively, we find the resource values at each equilibrium that satisfy (13) such that assumption (9a) is satisfied, i.e., $\sigma_{12} > 0$, $\sigma_{23} > 0$, $\sigma_{34} > 0$, and $\sigma_{41} > 0$, and $\sigma_{ij} < 0$ for $ij \neq 12, 23, 34$, and 41.

Let $E_1 = (N_1^*, 0, 0, 0)$ be a steady state at which N_1 is limited by Q. Then since $\mu_1(S_1^*, R_1^*, Q_1^*) - D = 0$, at E_1 we have

$$Q_1^* = \lambda_{Q1}, \qquad S_1^* > \lambda_{S1}, \quad \text{and} \quad R_1^* > \lambda_{R1}. \tag{15}$$

N_1^*, S_1^*, and R_1^* can be found to be

$$N_1^* = \left(Q^0 - \lambda_{Q1}\right)/c_{Q1}, \qquad S_1^* = S^0 - c_{S1}N_1^* \quad \text{and} \quad R_1^* = R^0 - c_{R1}N_1^*.$$

The Jacobian matrix at E_1 is

$$\begin{pmatrix} -c_{Q1}N_1^*f_{Q1}'(Q_1^*) & -c_{Q2}N_1^*f_{Q1}'(Q_1^*) & -c_{Q3}N_1^*f_{Q1}'(Q_1^*) & -c_{Q4}N_1^*f_{Q1}'(Q_1^*) \\ 0 & \sigma_{12} & 0 & 0 \\ 0 & 0 & \sigma_{13} & 0 \\ 0 & 0 & 0 & \sigma_{14} \end{pmatrix},$$

where

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

The conditions that satisfy $\sigma_{12} > 0$, $\sigma_{13} < 0$, and $\sigma_{14} < 0$ are

$$\begin{aligned} S_1^* &> \lambda_{S2}, \qquad R_1^* > \lambda_{R2}, \quad \text{and} \quad Q_1^* > \lambda_{Q2}; \\ S_1^* &< \lambda_{S3}, \qquad R_1^* < \lambda_{R3}, \quad \text{or} \quad Q_1^* < \lambda_{Q3}; \\ S_1^* &< \lambda_{S4}, \qquad R_1^* < \lambda_{R4}, \quad \text{or} \quad Q_1^* < \lambda_{Q4}. \end{aligned} \tag{16}$$

These three inequalities (16) do not contradict the break-even concentration relations (13). The above four inequalities, (15) and (16), can be simplified to

$$Q_1^* = \lambda_{Q1}, \qquad S_1^* > \lambda_{S1}, \quad \text{and} \quad R_1^* > \lambda_{R2}. \tag{17}$$

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

$$Q_2^* > \lambda_{Q2}, \qquad S_2^* = \lambda_{S2}, \quad \text{and} \quad R_2^* > \lambda_{R2}, \tag{18}$$

so that $\mu_2(S_2^*, R_2^*, Q_2^*) - D = 0$. Then N_2^*, R_2^*, and Q_2^* can be found to be

$$N_2^* = (S^0 - \lambda_{S2})/c_{S2}, \qquad R_2^* = R^0 - c_{R2}N_2^* \quad \text{and} \quad Q_2^* = Q^0 - c_{Q2}N_2^*.$$

The Jacobian matrix at E_2 is

$$\begin{pmatrix} \sigma_{21} & 0 & 0 & 0 \\ -c_{S1}N_2^* f_{S2}'(S_2^*) & -c_{S2}N_2^* f_{S2}'(S_2^*) & -c_{S3}N_2^* f_{S2}'(S_2^*) & -c_{S4}N_2^* f_{S2}'(S_2^*) \\ 0 & 0 & \sigma_{23} & 0 \\ 0 & 0 & 0 & \sigma_{24} \end{pmatrix},$$

where

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

The conditions that satisfy $\sigma_{21} < 0$, $\sigma_{23} > 0$, and $\sigma_{24} < 0$ are

$$\begin{aligned} S_2^* &< \lambda_{S1}, & R_2^* &< \lambda_{R1}, & \text{or} \quad Q_2^* &< \lambda_{Q1}; \\ S_2^* &> \lambda_{S3}, & R_2^* &> \lambda_{R3}, & \text{and} \quad Q_2^* &> \lambda_{Q3}; \\ S_2^* &< \lambda_{S4}, & R_2^* &< \lambda_{R4}, & \text{or} \quad Q_2^* &< \lambda_{Q4}. \end{aligned} \tag{19}$$

These inequalities (19) do not contradict (13). These statements (18) and (19) can be simplified to

$$S_2^* = \lambda_{S2}, \qquad R_2^* > \lambda_{R3}, \quad \text{and} \quad Q_2^* > \lambda_{Q3}. \tag{20}$$

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

$$R_3^* = \lambda_{R3}, \qquad S_3^* > \lambda_{S3}, \quad \text{and} \quad Q_3^* > \lambda_{Q3}. \tag{21}$$

The conditions for $\sigma_{31} < 0$, $\sigma_{32} < 0$, and $\sigma_{34} > 0$ are

$$\begin{aligned} S_3^* &< \lambda_{S1}, & R_3^* &< \lambda_{R1}, & \text{or} \quad Q_3^* &< \lambda_{Q1}; \\ S_3^* &< \lambda_{S2}, & R_3^* &< \lambda_{R2}, & \text{or} \quad Q_3^* &< \lambda_{Q2}; \\ S_3^* &> \lambda_{S4}, & R_3^* &> \lambda_{R4}, & \text{and} \quad Q_3^* &> \lambda_{Q4}. \end{aligned} \tag{22}$$

They can be simplified to

$$R_3^* = \lambda_{R3}, \qquad \lambda_{S1} > S_3^* > \lambda_{S4}, \quad \text{and} \quad Q_3^* > \lambda_{Q3}. \tag{23}$$

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

$$Q_4^* = \lambda_{Q4}, \qquad S_4^* > \lambda_{S4}, \quad \text{and} \quad R_4^* > \lambda_{R4}. \tag{24}$$

The conditions for $\sigma_{41} > 0$, $\sigma_{42} < 0$, and $\sigma_{43} < 0$ are

$$\begin{aligned} S_4^* &> \lambda_{S1}, & R_4^* &> \lambda_{R1}, & \text{and} \quad Q_4^* &> \lambda_{Q1}; \\ S_4^* &< \lambda_{S2}, & R_4^* &< \lambda_{R2}, & \text{or} \quad Q_4^* &< \lambda_{Q2}; \\ S_4^* &< \lambda_{S3}, & R_4^* &< \lambda_{R3}, & \text{or} \quad Q_4^* &< \lambda_{Q3}. \end{aligned} \tag{25}$$

They can be simplified to

$$Q_4^* = \lambda_{Q4}, \qquad S_4^* > \lambda_{S1} \quad \text{and} \quad \lambda_{R2} > R_4^* > \lambda_{R1}. \tag{26}$$

That is, we may find appropriate parameters that satisfy (17), (20), (23), and (26) such that assumption (9a) is satisfied. The proof is complete. $\quad\square$

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] showed that the competition outcomes are similar to the Lotka–Volterra two-species competition models. When there are more than two species, Li and Smith [10] 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:

$$\begin{aligned} \lambda_{S1} &< \lambda_{S2} < \lambda_{S3} < \cdots < \lambda_{Sn}, \\ \lambda_{Rn} &< \lambda_{R,n-1} < \cdots < \lambda_{R2} < \lambda_{R1}. \end{aligned} \tag{27}$$

Additional results are obtained for the two-resource–n-species case in the following theorem.

Theorem 5. *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* (27). *Then there exists no heteroclinic cycle.*

Proof. We prove by contradiction that the assumption (9a) in Corollary 1 can never be satisfied.

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 Γ_{ij} denote the heteroclinic orbit connecting the two points E_i and E_j. We prove that the heteroclinic orbits $\Gamma_{12}, \Gamma_{23}, \ldots$, and $\Gamma_{n-2,n-1}$ can be found, but Γ_{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 $\Gamma_{k,k+1}$, $k = 1, 2, \ldots, n-1$, then species k must be limited by resource R; (ii) there is no heteroclinic orbit Γ_{km} where $k+1 < m \leqslant n$; and (iii) there is no heteroclinic orbit Γ_{n1}.

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

Since there is a heteroclinic orbit $\Gamma_{k,k+1}$, we have $\sigma_{k,k+1} > 0$ and $\sigma_{k,j} < 0$ for all $j \neq k+1$. If N_k is limited by resource S, then at E_k, $S_k^* = \lambda_{S,k}$ and $R_k^* > \lambda_{R,k}$. Since the heteroclinic orbit $\Gamma_{k,k+1}$ connects E_k to E_{k+1}, the $k+1$st eigenvalue $\sigma_{k,k+1}$ of the Jacobian matrix 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 (27) 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

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

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 $\sigma_{k,k+2} < 0$, $\sigma_{k,k+3} < 0$, $\ldots$, 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 $k+1 < m \leqslant n$.

Suppose there is one, then $\sigma_{k,m} > 0$ and $\sigma_{k,k+1} < 0$. If N_k is S-limited, then at E_k we have $S_k^* = \lambda_{S,k}$ 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 (27) 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 (27).

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

Suppose there is one, then $\sigma_{n,1} > 0$ and $\sigma_{n,2} < 0$. If N_n is R-limited, then at E_n we have $R_n^* = \lambda_{R,n}$ 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 $E_1(R) \to E_2(R) \to \cdots \to E_{n-1}(R) \to E_n$, but $E_n \to E_1$ is impossible. There is no heteroclinic loop under the assumption (27). $\square$

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 [6–8].

Theorem 6. *Assume the break-even concentrations of three resources S, R, and Q and n species $N_1, N_2, \ldots, N_n$, satisfy the following relations:*

$$\lambda_{S1} < \lambda_{S2} < \lambda_{S3} < \cdots < \lambda_{Sn},$$
$$\lambda_{R1} < \lambda_{Rn} < \lambda_{R2} < \lambda_{R3} < \cdots < \lambda_{R,n-1},$$
$$\lambda_{Q,n-1} < \lambda_{Qn} < \lambda_{Q,n-2} < \cdots < \lambda_{Q2} < \lambda_{Q1}. \tag{28}$$

Then the assumption (9a) *in Corollary* 1 *can be satisfied. Furthermore, if the eigenvalues defined as in* (7) *satisfy* (9b), (9c), *and* (9d), *then we have the following stable heteroclinic cycle:*

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

Proof. We verify the following four cases: (i) $E_k(Q) \to E_{k+1}$, $k = 1, \ldots, n-3$, (ii) $E_{n-2}(Q) \to E_{n-1}$, (iii) $E_{n-1}(R) \to E_n$, and (iv) $E_n(S) \to E_1$, so that the eigenvalues defined in (7) satisfy the assumption (9a).

(i) $E_k(Q) \to E_{k+1}$, $k = 1, \ldots, n-3$. Since N_k is limited by Q, we have $Q_k^* = \lambda_{Qk}$. Let S_k^* and R_k^* satisfy

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

We show that the choices of the S_k^* and R_k^* imply $\sigma_{ki} < 0$ for $i \neq k+1$ and $\sigma_{k,k+1} > 0$. And hence $E_k \to E_{k+1}$.

Since

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

we have $\sigma_{k,k+1} > 0$. Since

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

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

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

we have $\sigma_{ki} < 0$ for $i = k+2, k+3, \ldots, n$.

(ii) $E_{n-2}(Q) \to E_{n-1}$. Since N_{n-2} is limited by Q we have $Q_{n-2}^* = \lambda_{Q,n-2}$. Let S_{n-2}^* and R_{n-2}^* satisfy

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

Since $S_{n-2}^* < \lambda_{Sn}$ we have $\sigma_{n-2,n} < 0$. Since $Q_{n-2}^* = \lambda_{Q,n-2} < \lambda_{Qi}$ for $i = 1, 2, \ldots, n-3$ we have $\sigma_{n-2,i} < 0$. Since $S_{n-2}^* > \lambda_{S,n-1}$, $R_{n-2}^* > \lambda_{R,n-1}$, and $Q_{n-2}^* > \lambda_{Q,n-1}$, we have $\sigma_{n-1,n-2} > 0$.

(iii) $E_{n-1}(R) \to E_n$. Since N_{n-1} is limited by R, $R_{n-1}^* = \lambda_{R,n-1}$. Let S_{n-1}^* and Q_{n-1}^* satisfy

$$\lambda_{Sn} < S_{n-1}^*,$$
$$\lambda_{Qn} < Q_{n-1}^* < \lambda_{Q,n-2}.$$

Since $Q_{n-1}^* < \lambda_{Qi}$ for $i \neq n-1, n$, we have $\sigma_{n-1,i} < 0$. Since $S_{n-1}^* > \lambda_{Sn}$, $Q_{n-1}^* > \lambda_{Qn}$, and $R_{n-1}^* > \lambda_{R,n}$, we have $\sigma_{n-1,n} > 0$.

(iv) $E_n(S) \to E_1$. Since N_n is limited by S so $S_n^* = \lambda_{Sn}$. Let R_n^* and Q_n^* satisfy

$$\lambda_{R1} < R_n^* < \lambda_{R2},$$
$$\lambda_{Q1} < Q_n^*.$$

Since $R_n^* < \lambda_{R2} < \lambda_{R3} < \cdots < \lambda_{R,n-1}$, we have $\sigma_{ni} < 0$ for $n \neq 1, n$. Since $Q_n^* > \lambda_{Q1}$, $R_n^* > \lambda_{R1}$, and $S_n^* > \lambda_{S1}$, we have $\sigma_{n1} > 0$. $\quad\square$

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

Theorem 7. *If there are $m + 3$ resources $S, R, Q, P_1, \ldots, P_m$, and n species $N_1, N_2, \ldots, N_n$, then under the following conditions*

$$\lambda_{S1} < \lambda_{S2} < \lambda_{S3} < \cdots < \lambda_{Sn},$$
$$\lambda_{R1} < \lambda_{Rn} < \lambda_{R2} < \lambda_{R3} < \cdots < \lambda_{R,n-1},$$
$$\lambda_{Q,n-1} < \lambda_{Qn} < \lambda_{Q,n-2} < \cdots < \lambda_{Q2} < \lambda_{Q1},$$
$$\lambda_{P_j,1} < \lambda_{P_j,2} < \lambda_{P_j,3} < \cdots < \lambda_{P_j,n}, \quad j = 1, 2, \ldots, m. \tag{29}$$

Then the assumption (9a) *in corollary can be satisfied. Furthermore, if the eigenvalues defined as in* (7) *satisfy* (9b), (9c), *and* (9d), *then we have the following stable heteroclinic cycle:*

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

Proof. The proof of this theorem is similar to that of Theorem 6. We verify the following four cases: (i) $E_k(Q) \to E_{k+1}$, $k = 1, \ldots, n-3$, (ii) $E_{n-2}(Q) \to E_{n-1}$, (iii) $E_{n-1}(R) \to E_n$, and (iv) $E_n(S) \to E_1$, so that the eigenvalues defined in (7) satisfy the assumption (9a).

(i) $E_k(Q) \to E_{k+1}$. Since N_k is limited by Q, we have $Q_k^* = \lambda_{Qk}$. Let S_k^*, R_k^*, and $P_{j,k}^*$, $j = 1, \ldots, m$, satisfy

$$\lambda_{S,k+1} < S_k^* < \lambda_{S,k+2},$$
$$\lambda_{R,k+1} < R_k^* < \lambda_{R,k+2},$$
$$\lambda_{P_j,k+1} < P_{j,k}^* < \lambda_{P_j,k+2}. \tag{30}$$

(ii) $E_{n-2}(Q) \to E_{n-1}$. Since N_{n-2} is limited by Q we have $Q_{n-2}^* = \lambda_{Q,n-2}$. Let S_{n-2}^*, R_{n-2}^*, and $P_{j,n-2}^*$, $j = 1, \ldots, m$, satisfy

$$\lambda_{S,n-1} < S^*_{n-2} < \lambda_{Sn},$$
$$\lambda_{R,n-1} < R^*_{n-2},$$
$$\lambda_{P_j,n-1} < P^*_{j,n-2} < \lambda_{P_j,n}. \tag{31}$$

(iii) $E_{n-1}(R) \to E_n$. N_{n-1} is limited by R, so $R^*_{n-1} = \lambda_{R,n-1}$. Let S^*_{n-1}, R^*_{n-1}, and $P^*_{j,n-1}$, $j = 1, \ldots, m$, satisfy

$$\lambda_{Sn} < S^*_{n-1},$$
$$\lambda_{Qn} < Q^*_{n-1} < \lambda_{Q,n-2},$$
$$\lambda_{P_j,n} < P^*_{j,n-1}. \tag{32}$$

(iv) $E_n(S) \to E_1$. Since N_n is limited by S, $S^*_n = \lambda_{Sn}$. Let S^*_n, R^*_n, and $P^*_{j,n}$, $j = 1, \ldots, m$, satisfy

$$\lambda_{Rn} < R^*_n < \lambda_{R2},$$
$$\lambda_{Q1} < Q^*_n,$$
$$\lambda_{P_j,1} < P^*_{j,n}. \tag{33}$$

The four conditions (30)–(33) imply the assumption (9a). The proof is done. □

6. Discussion

In this paper we consider the existence of a stable heteroclinic cycle connecting one-species equilibria for n species competing for k essential resources in a chemostat model. 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. The existence of the heteroclinic cycle may indicate the coexistence state of n species in oscillation form. Li and Smith [10] had conjectured the competitive exclusion principle holds for n species, $n > 2$, competing for two essential resources. In Theorem 5 we proved that there exists no heteroclinic cycle for this case which may give a clue for the future proof of the conjecture. For the case of three essential resources, we construct a stable heteroclinic cycle of four species in Theorem 4, thus we extend the result of the paper [9] from three species to four species. Furthermore in Theorem 6 we prove that for three essential resources we are able to construct a stable heteroclinic cycle for any finite number of species. In fact in Theorem 7, the result can be extended to case of any finite number of species competing for k resources, $k > 3$.

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