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Tewfik Sari

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GLOBAL DYNAMICS OF THE CHEMOSTAT WITH VARIABLE YIELDS

TEWFIK SARI

Abstract. In this paper, we consider a competition model between n species in a chemostat including both monotone and non-monotone response functions, distinct removal rates and variable yields. We show that only the species with the lowest break-even concentration survives, provided that additional technical conditions on the growth functions and yields are satisfied. LaSalle's extension theorem of the Lyapunov stability theory is the main tool.

1. Introduction

In this paper we study the global dynamics of the following model of the chemostat in which n populations of microorganisms compete for a single growth-limiting substrate:

$$\begin{aligned} S'(t) &= D[S^0 - S(t)] - \textstyle\sum_{i=1}^n f_i(S(t))x_i(t) \\ x_i'(t) &= [p_i(S(t)) - D_i]x_i(t), \qquad\qquad i = 1 \cdots n, \end{aligned} \tag{1.1}$$

where $S(0) \geq 0$ and $x_i(0) > 0$, $i = 1 \cdots n$ and S^0, D and D_i are positive constants. In these equations, $S(t)$ denotes the concentration of the substrate at time t; $x_i(t)$ denotes the concentration of the ith population of microorganisms at time t; $f_i(S)$ represents the uptake rate of substrate of the ith population; $p_i(S)$ represents the per-capita growth rate of the ith population and so the function $y_i(S)$ defined by

$$y_i(S) = \frac{p_i(S)}{f_i(S)}$$

is the growth yield; S^0 and D denote, respectively, the concentration of substrate in the feed bottle and the flow rate of the chemostat; each D_i represents the removal rate of the ith population. We make the following assumptions on the functions p_i and f_i:

- $p_i, f_i : \boldsymbol{R}_+ \to \boldsymbol{R}_+$ are continuous,
- $p_i(0) = f_i(0) = 0$ and for all $S > 0$, $p_i(S) > 0$ and $f_i(S) > 0$,

For general background on model (1.1), in the constant yield case $y_i(S) = Y_i$, the reader is referred to the monograph of Smith and Waltman [13]. Following Butler and Wolkowicz [3], we make the following assumptions on the form of the response functions p_i: there exist positive extended real numbers λ_i and μ_i with

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$\lambda_i \leq \mu_i \leq +\infty$ such that

$$\begin{array}{lll} p_i(S) < D_i & \text{if} & S \notin [\lambda_i, \mu_i] \\ p_i(S) > D_i & \text{if} & S \in]\lambda_i, \mu_i[. \end{array}$$

Hence there are at most two values of S, $S = \lambda_i$ and $S = \mu_i$, called the break-even concentrations, satisfying the equation $p_i(S) = D_i$. We adopt the convention $\mu_i = \infty$ if this equation has only one solution and $\lambda_i = \infty$ if it has no solution.

The global analysis of this model was considered by Hsu, Hubbell and Waltman [5], in the Monod case [9] when the response functions are of Michaelis-Menten form,

$$p_i(S) = \frac{a_i S}{b_i + S}, \tag{1.2}$$

and the yields are constant $y_i(S) = Y_i$, and $D_i = D$ for $i = 1 \cdots n$. The authors showed that only the species with the lowest break-even concentration survives. Thus the competitive exclusion principle (CEP) holds: only one species survives, namely the species which makes optimal use of the resources. Hsu [4] applied a Lyapunov-LaSalle argument to give a simple and elegant proof of the result in [5] for the case of different removal rates D_i. The Lyapunov function V_H used by Hsu is

$$V_H = \int_{\lambda_1}^{S} \frac{\sigma - \lambda_1}{\sigma} d\sigma + c_1 \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi} d\xi + \sum_{i=2}^{n} c_i x_i, \tag{1.3}$$

where

$$c_i = \frac{1}{Y_i} \frac{a_i}{a_i - D_i}, \quad i = 1 \cdots n, \quad \text{and} \quad x_1^* = D Y_1 \frac{S^0 - \lambda_1}{D_1}.$$

CEP has been proved under a variety of hypothesis [2, 3, 8, 14, 15]. For a survey on the contribution of each paper the reader may consult the introduction of the papers [7, 8, 12]. The variable yield case was considered, for $n = 1$ and $n = 2$ by Pilyugin and Waltman [10], with a particular interest to linear and quadratic yields, and by Huang, Zhu and Chang [6]. The model (1.1) was considered by Arino, Pilyugin and Wolkowicz [1] and Sari and Mazenc [12].

In this paper we generalize [14] by allowing variable yields and we generalize [1] by allowing multi species. We further extend [12] by providing less restrictive assumptions on the system. For biological motivations concerning the dependance of the yields on the substrate, the reader is refeered to [1, 10] and the references therein.

2. Analysis of the model

It is known (see Theorem 4.1 [1]) that the non-negative cone is invariant under the flow of (1.1) and all solutions are defined and remain bounded for all $t \geq 0$. System (1.1) can have many equilibria: the washout equilibrium $E_0 = (S^0, 0, \cdots, 0)$, which is locally exponentially stable if and only if for all $i = 1 \cdots n$, $S^0 \notin [\lambda_i, \mu_i]$ and the equilibria E_i^* and E_i^{**} where all component of E_i^* and E_i^{**} vanish except for the first and the $(i+1)$th, which are

$$S = \lambda_i, \qquad x_i = x_i^* := F_i(\lambda_i), \qquad \text{for } E_i^*$$

and

$$S = \mu_i, \qquad x_i = x_i^{**} := F_i(\mu_i), \qquad \text{for } E_i^{**}$$

respectively, where

$$F_i(S) = D\frac{S^0 - S}{f_i(S)}.$$

The equilibrium E_i^* lies in the non-negative cone if and only if $\lambda_i \leq S^0$. If $\lambda_i < \lambda_j$ for all $i \neq j$ and $F_i'(\lambda_i) < 0$ then it is locally exponentially stable. It coalesces with E_0 when $\lambda_i = S^0$. The equilibrium E_i^{**} lies in the non-negative cone if and only if $\mu_i \leq S^0$ and is locally exponentially unstable if it exists. Its coalesces with E_0 when $\mu_i = S^0$. Besides these equilibria, the system (1.1) can have a continuous set of non-isolated equilibria in the non-generic cases where two or more of the break-even concentrations are equal. In what follows we assume, that

$$\lambda_1 < \lambda_2 \leq \cdots \leq \lambda_n, \qquad \text{and} \qquad \lambda_1 < S^0 < \mu_1. \tag{2.1}$$

Hence E_0 is locally exponentially unstable and the equilibrium E_1^* lies in the non-negative cone. It is locally exponentially stable if and only if

$$F_1'(\lambda_1) < 0 \Longleftrightarrow f_1(\lambda_1) + f_1'(\lambda_1)(S^0 - \lambda_1) > 0. \tag{2.2}$$

We consider the global asymptotic stability of E_1^*.

Before presenting the results, we need the following lemma,

Lemma 2.1. *The solutions $S(t)$, $x_i(t)$, $i = 1 \cdots n$ of (1.1) with positive initial conditions are positive and bounded, and if $\lambda_i < S^0 < \mu_i$ for some $i = 1 \cdots n$, then $S(t) < S^0$ for all sufficiently large t.*

Proof. The proof is similar to the proof of Lemma 2.1 in [14] obtained for the model (1.1) in the case where the yields are constant. □

Theorem 2.2. *Assume that*

(1) $\lambda_1 < \lambda_2 \leq \cdots \leq \lambda_n$, *and* $\lambda_1 < S^0 < \mu_1$.
(2) *There exist constants $\alpha_i > 0$ for each $i \geq 2$ satisfying $\lambda_i < S^0$ such that*

$$\max_{0<S<\lambda_1} g_i(S) \leq \alpha_i \leq \min_{\lambda_i<S<\rho_i} g_i(S), \qquad i \geq 2. \tag{2.3}$$

where

$$g_i(S) = \frac{f_i(S)}{f_1(\lambda_1)} \frac{p_1(S) - D_1}{p_i(S) - D_i} \frac{S^0 - \lambda_1}{S^0 - S}. \tag{2.4}$$

(3) *The function*

$$F(S) = \frac{f_1(S)}{S^0 - S}. \tag{2.5}$$

satisfies

$$F(S) < F(\lambda_1) \text{ if } S \in]0, \lambda_1[, \qquad F(S) > F(\lambda_1) \text{ if } S \in]\lambda_1, S^0[. \tag{2.6}$$

Then the equilibrium E_1^* is globally asymptotically stable for system (1.1) with respect to the interior of the positive cone.

Proof. From Lemma 2.1 it follows that there is no loss of generality in restricting our attention to $0 \leq S < S^0$. Consider the function $V = V(S, x_1, \cdots, x_n)$ as follows

$$V = \int_{\lambda_1}^{S} \frac{(p_1(\sigma) - D_1)(S^0 - \lambda_1)}{f_1(\lambda_1)(S^0 - \sigma)} d\sigma + \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi} d\xi + \sum_{i=2}^{n} \alpha_i x_i \tag{2.7}$$

where α_i are the positive constants satisfying (2.3). The function V is continuously differentiable for $0 < S < S^0$ and $x_i > 0$ and positive except at the point E_1^*. The derivative of V along the trajectories of (1.1) is given by

$$V' = x_1[p_1(S) - D_1]\frac{F(\lambda_1) - F(S)}{F(\lambda_1)} + \sum_{i=2}^{n} x_i h_i(S)$$

where

$$h_i(S) = [p_i(S) - D_i][\alpha_i - g_i(S)]$$

and $g_i(S)$ and $F(S)$ are given by (2.4) and (2.5) respectively. First, note that, using (2.1) and (2.6), the first term of the above sum is always non-positive for $0 < S < S^0$ and equals 0 for $S \in]0, S^0[$ if and only if $S = \lambda_1$ or $x_1 = 0$. If $S \in [\lambda_1, \lambda_i]$ then $p_i(S) < D_i$ and $p_1(S) > D_1$ so that $g_i(S) < 0 < \alpha_i$ for any choice of $\alpha_i > 0$. Similarly if $\mu_i < S^0$ and $S \in [\mu_i, S^0]$ then $p_i(S) < D_i$ and $p_1(S) > D_1$ so that $g_i(S) < 0 < \alpha_i$ for any choice of $\alpha_i > 0$. On the other hand, if $S \in [0, \lambda_1]$ then $p_i(S) < D_i$ and, using (2.3), $g_i(S) \leq \alpha_i$ so that $h_i(S) < 0$. Finally, if $S \in [\lambda_i, \rho_i]$ then $p_i(S) > D_i$ and $g_i(S) \geq \alpha_i$ so that $h_i(S) < 0$. Thus $h_i(S) < 0$ for every $S \in]0, S^0[$, provided that the numbers α_i satisfy (2.3). Hence $V' \leq 0$ and $V' = 0$ if and only if $x_i = 0$ for $i = 1 \cdots n$ or $S = \lambda_1$ and $x_i = 0$ for $i = 2 \cdots n$. We use LaSalle theorem (the details are as in the proof of Theorem 2.3 in [14]), the ω-limit set of the trajectory is E_1^*. □

Condition (2.6) is satisfied in the particular case where $F'(S) > 0$ for $0 < S < S^0$. For $S = \lambda_1$ we obtain the condition (2.2) of local exponential stability of E_1^*.

3. Applications

In this section we show how Theorem 2.2 extends results in [1, 12, 14].

3.1. One species.

In the case $n = 1$ the equations take the form

$$\begin{aligned} S' &= D(S^0 - S) - x_1 f_1(S) \\ x_1' &= [p_1(S) - D_1]x_1 \end{aligned} \tag{3.1}$$

Corollary 3.1. *If $\lambda_1 < S^0 < \mu_1$ and $1 - \frac{f_1(S)(S^0-\lambda_1)}{f_1(\lambda_1)(S^0-S)}$ has exactly one sign change for $S \in (0, S^0)$ then E_1^* is globally asymptotically stable with respect to the interior of the positive quadrant.*

Proof. The result follows from Theorem 2.2 since the hypothesis on the change of sign is is equivalent to (2.6). In the case when $n = 1$ the condition (2.3) is obviously satisfied. □

Corollary 3.1 was obtained by Arino, Pilyugin and Wolkowicz (see [1], Theorem 2.11). These authors used the following Lyapunov function

$$V_{APW} = \int_{\lambda_1}^{S} \frac{(p_1(\sigma) - D_1)(S^0 - \lambda_1)}{f_1(\lambda_1)(S^0 - \sigma)} d\sigma + \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi} d\xi.$$

Notice that the Lyapunov function (2.7) we use reduces to the function V_{APW} in the case when $n = 1$.

3.2. **Constant yields.** In the case when the yields are constant, $y_i(S) = Y_i$, the equations take the form

$$\begin{aligned} S' &= D[S^0 - S] - \textstyle\sum_{i=1}^n \frac{p_i(S)}{Y_i} x_i \\ x_i' &= [p_i(S) - D_i]x_i, \qquad\qquad i = 1 \cdots n, \end{aligned} \tag{3.2}$$

Corollary 3.2. *Assume that*

(1) $\lambda_1 < \lambda_2 \leq \cdots \leq \lambda_n$, *and* $\lambda_1 < S^0 < \mu_1$.
(2) *There exist constants* $\alpha_i > 0$ *for each* $i \geq 2$ *satisfying* $\lambda_i < S^0$ *such that*

$$\max_{0<S<\lambda_1} g_i^{WL}(S) \leq \alpha_i \leq \min_{\lambda_i<S<\rho_i} g_i^{WL}(S), \qquad i \geq 2. \tag{3.3}$$

where

$$g_i^{WL}(S) = \frac{p_i(S)}{D_1} \frac{p_1(S) - D_1}{p_i(S) - D_i} \frac{S^0 - \lambda_1}{S^0 - S}. \tag{3.4}$$

Then the equilibrium E_1^* *is globally asymptotically stable for system (3.2) with respect to the interior of the positive cone.*

Proof. In the case when the yields are constant, we have

$$g_i(S) = \frac{Y_1}{Y_i} g_i^{WL}(S).$$

Hence the conditions (3.3) imply the conditions (2.3) with constants α_i replaced by $\alpha_i Y_1/Y_i$. On the other hand $F(S) = \frac{p_1(S)}{(S^0-S)Y_1}$. Thus, assumption (2.6) follows from hypothesis $\lambda_1 < S^0 < \mu_1$. The result follows from Theorem 2.2. □

Corollary 3.2 was obtained by Wolkowicz and Lu (see [14], Theorem 2.3). These authors used the following Lyapunov function

$$V_{WL} = \int_{\lambda_1}^{S} \frac{(p_1(\sigma) - D_1)(S^0 - \lambda_1)}{D_1(S^0 - \sigma)} d\sigma + \frac{1}{Y_1} \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi} d\xi + \sum_{i=2}^{n} \frac{\alpha_i}{Y_i} x_i.$$

Notice that the Lyapunov function (2.7) we use satisfies $V = Y_1 V_{WL}$ in the case when the yields are constant.

3.3. **Variable yields.** In [12], another Lyapunov function is proposed in the case when the yields are variable, leading to the following result.

Corollary 3.3. *Assume that*

(1) $\lambda_1 < \lambda_2 \leq \cdots \leq \lambda_n$, *and* $\lambda_1 < S^0 < \mu_1$.
(2) *There exist constants* $\alpha_i > 0$ *for each* $i \geq 2$ *such that*

$$\max_{0<S<\lambda_1} g_i^{SM}(S) \leq \alpha_i \leq \min_{\lambda_i<S<\rho_i} g_i^{SM}(S), \qquad i \geq 2. \tag{3.5}$$

where

$$g_i^{SM}(S) = \frac{f_i(S)}{f_1(S)} \frac{p_1(S) - D_1}{p_i(S) - D_i}. \tag{3.6}$$

(3) *The function* $F(S) = \dfrac{f_1(S)}{S^0 - S}$ *satisfies*

$$F(S) < F(\lambda_1) \text{ if } S \in]0, \lambda_1[, \qquad F(S) > F(\lambda_1) \text{ if } S \in]\lambda_1, S^0[. \tag{3.7}$$

Then the equilibrium E_1^* *is globally asymptotically stable for system (1.1) with respect to the interior of the positive cone.*

Proof. The condition (3.7) is the same as the condition (2.6). On the other hand we have

$$g_i(S) = \frac{S^0 - \lambda_1}{f_1(\lambda_1)} F(S) g_i^{SM}(S).$$

By (3.5) and (3.7) we have (2.3) with appropriate constants α_i. The result follows from Theorem 2.2. □

Corollary 3.3 was obtained by Sari and Mazenc (see [12], Theorem 2.2). These authors used the following Lyapunov function

$$V_{SM} = \int_{\lambda_1}^{S} \frac{p_1(\sigma) - D_1}{f_1(\sigma)} d\sigma + \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi} d\xi + \sum_{i=2}^{n} \alpha_i x_i$$

where α_i, $i = 2 \cdots n$ are positive constants satisfying (3.5). In the case when the response functions are of Michaelis-Menten form (1.2) and the yields are constant the Lyapunov function V_{SM} reduces to the Lyapunov function V_H (1.3) useb by Hsu [4]. Notice that the Lyapunov function (2.7) we use is not proportional to the function V_{SM}.

4. Discussion

In this paper we considered a mathematical model (1.1) of n species of microorganisms in competion in a chemostat for a single resource. The model incorporates both monotone and non-monotone response functions, distinct removal rates and variable yields. We demonstrated that the CEP holds for a large class of growth functions and yields.

Even with constant yields, the problem is not yet completely solved: the CEP holds for a large class of growth functions [2, 3, 4, 8, 14, 15] but an important open question remains: *is the CEP true assuming only that the f_i are monotone with no restriction on the D_i ?* This major open problem remains unresolved after more than thirty years [7]. However, in the case of constant yields numerical simulations of model (1.1) have only displayed competitive exclusion.

In the case where the yields are constant, it is known [3] that the CEP holds provided that $D_i = D$ for all i, the set $Q = \bigcup_{i \in N}]\lambda_i, \mu_i[$ is connected, and $S^0 \in Q$, where $N = \{i : \lambda_i < S^0\}$. Wolkowicz and Lu [14] conjectured that this result can be extented to the case of different removal rates. Under condition (2.1), it is clear that the set Q is connected, and $S^0 \in Q$. The condition $\lambda_1 < \lambda_i$ for $i \neq 1$ can be stated without loss of generality, by labelling the populations such that the index $i = 1$ corresponds to the lowest break-even concentration, but the condition $\lambda_1 < S^0 < \mu_1$ in (2.1) cannot be stated without loss of generality. If $\mu_1 < S^0$, it is not possible to show the CEP by the methods that we used. To the best of our knowledge, in the case of different removal rates and non-monotone response functions, the CEP has been proved only under the assumption $S^0 < \mu_1$ [8, 14, 15]. However, Rapaport and Harmand [11] considered the case of two populations and proposed conditions on the growth functions such that the CEP holds under the condition $\mu_1 < S^0$. It should be interesting to extend their methods to more general cases. We leave this problem for future investigations.

Our result concern also the case of variable yields, for which it is known [1, 6, 10] that more exotic dynamical behaviours, including limit cycles, are possible. Thus

in the case of variable yields, it is of great importance to have criteria ensuring the global convergence to an equilibrium with at most one surviving species.

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Laboratoire de Mathématiques, Informatique et Applications, Université de Haute Alsace, 4 rue des frères Lumière, 68093 Mulhouse, and EPI MERE INRIA-INRA, UMR MISTEA, 2, pl. Viala, 34060 Montpellier, France

E-mail address: Tewfik.Sari@uha.fr