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GLOBAL DYNAMICS OF THE CHEMOSTAT WITH DIFFERENT REMOVAL RATES AND VARIABLE YIELDS

TEWFIK SARI* AND FREDERIC MAZENC†

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. We construct a Lyapunov function which reduces to the Lyapunov function which where considered by S. B. Hsu [SIAM J. Appl. Math., 34 (1978), pp. 760-763] in the Monod case where the response functions are of Michaelis-Menten type and the yields are constant. Various applications are given including constant, linear and quadratic yields.

Key words. chemostat, competitive exclusion principle, Lyapunov function, global asymptotic stability, variable yield model

AMS subject classifications. 92A15, 92A17, 34C15, 34C35

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:

$$(1.1) \quad \begin{aligned} S'(t) &= D[S^0 - S(t)] - \sum_{i=1}^n \frac{p_i(S(t))}{y_i(S(t))} x_i(t) \\ x'_i(t) &= [p_i(S(t)) - D_i] x_i(t), \quad i = 1 \cdots n, \end{aligned}$$

where $S(0) \geq 0$ and $x_i(0) > 0$, $i = 1 \cdots n$ and S^0 , D and D_i are positive constants. Let

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

In these equations, $S(t)$ denotes the concentration of the substrate at time t ; $x_i(t)$ denotes the concentration of the i th population of microorganisms at time t ; $f_i(S)$ represents the uptake rate of substrate of the i th population; $p_i(S)$ represents the per-capita growth rate of the i th population and so $y_i(S)$ 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 i th population. We make the following assumptions on the functions p_i and y_i :

- $p_i, y_i : \mathbf{R}_+ \rightarrow \mathbf{R}_+$ are continuous,
- $p_i(0) = 0$ and for all $S > 0$, $p_i(S) > 0$,
- for all $S \geq 0$, $y_i(S) > 0$.

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] (see also [13], Section 2.5), we make the following assumptions on

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the form of the response functions p_i : there exist positive extended real numbers λ_i and μ_i with $\lambda_i \leq \mu_i \leq +\infty$ such that

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

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 [10] when the response functions are of Michaelis-Menten form,

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

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 discovered by Hsu is

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

where

$$c_i = \frac{1}{Y_i} \frac{a_i}{a_i - D_i}, \quad i = 1 \cdots n, \quad \text{and} \quad x_1^* = DY_1 \frac{S^0 - \lambda_1}{D_1}.$$

Armstrong and McGehee [2] proved that the CEP is true for arbitrary monotone response functions when, for $i = 1$ to n , $D = D_i$ and the yields are constant. Butler and Wolkowicz [3] extended the result in [2] for non-monotone response functions. Wolkowicz and Lu [14] extended the results of [3] by allowing different removal rates D_i . They considered the functions

$$g_i(S) = \frac{p_i(S) p_1(S) - D_1 S^0 - \lambda_1}{D_1 p_i(S) - D_i S^0 - S}, \quad i = 2 \cdots n$$

and proved that if $\lambda_1 < S^0 < \mu_1$ and it is possible to find positive constants α_i such that

$$(1.4) \quad \max_{0 < S < \lambda_1} g_i(S) \leq \alpha_i \leq \min_{\lambda_i < S < \rho_i} g_i(S), \quad \text{where } \rho_i = \min\{S^0, \mu_i\},$$

for all $i \geq 2$ for which $S^0 > \lambda_i$, then the CEP holds: only the species x_1 survives. These authors identified a large class of response functions, including many prototypes of response functions often found in the literature, where such α_i in (1.4) can always be found. Despite the fact that criterion (1.4) is not satisfied by all response functions, the work of Wolkowicz and Lu [14] represents a major step in the extension of the result of Hsu [4] to general growth functions.

Wolkowicz and Xia [15] extended the result of [4] to general monotone response functions and constant yields, provided the differences between the removal rates D_i

are sufficiently small. Li [8] extended the result of [14] by allowing a more general condition which includes (1.4) as a special case and extended [15] by providing less restrictive bounds on the differences on the removal rates D_i and by allowing non-monotone response functions.

The variable yield case was considered, for $n = 1$ and $n = 2$ by Pilyugin and Waltman [11], with a particular interest to linear and quadratic yields, and by Huang, Zhu and Chang [6]. In [6, 11], the authors were more interested in the existence of limit cycles than in the global asymptotic stability of the equilibrium. The model (1.1), with variable yields, was considered by Arino, Pilyugin and Wolkowicz [1]. In the case $n = 1$, these authors gave sufficient conditions for the global asymptotic stability of the positive equilibrium (see Example 2 below). For biological motivations concerning the dependance of the yields on the substrat, the reader is referred to [1, 11] and the references therein.

The Lyapunov function V_{WL} discovered by Wolkowicz and Lu [14] and further adapted by Li [8] is

$$(1.5) \quad V_{WL} = \int_{\lambda_1}^S \frac{(p_1(\sigma) - D_1)(S^0 - \lambda_1)}{D_1(S^0 - \sigma)} d\sigma + \frac{1}{Y_1} \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi} d\xi + \sum_{i=2}^n \frac{\alpha_i}{Y_i} x_i.$$

Notice that, in the case where the response functions are of Michaelis-Menten form (1.2), the Wolkowicz and Lu Lyapunov function (1.5) does not reduce to the Hsu Lyapunov function (1.3). Indeed, the second and last terms of these functions are the same, but the first terms are not the same. Actually, it is believed (see, for instance, the introduction of [14]) that the Lyapunov function of Hsu works only for Michaelis-Menten or Lotka-Volterra response functions.

Our aim in this paper is to extend the Lyapunov function (1.3) of Hsu [4] to the chemostat with a more general class of response functions and variable yields. Our Lyapunov function is given by

$$(1.6) \quad V = \int_{\lambda_1}^S \frac{p_1(\sigma) - D_1}{f_1(\sigma)} d\sigma + \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi} d\xi + \sum_{i=2}^n \alpha_i x_i$$

where α_i , $i = 2 \dots n$ are positive constants to be determined. We identify a class of response functions, including Lotka-Volterra and Michaelis-Menten growth functions, where our Lyapunov function works. The criterion (1.4) is also needed in our approach, but the functions g_i are not defined as in [14].

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 $E_0 = (S^0, 0, \dots, 0)$, which is locally exponentially stable if and only if for all $i = 1 \dots n$, $S^0 \notin [\lambda_i, \mu_i]$ 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

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

and

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

respectively, where

$$(2.1) \quad F_i(S) = D \frac{S^0 - S}{f_i(S)}.$$

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 collapses 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 collapses 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

$$(2.2) \quad \lambda_1 < \lambda_2 \leq \dots \leq \lambda_n, \quad \text{and} \quad \lambda_1 < S^0 < \mu_1.$$

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

$$(2.3) \quad F'_1(\lambda_1) < 0 \iff f_1(\lambda_1) + f'_1(\lambda_1)(S^0 - \lambda_1) > 0.$$

We consider the global asymptotic stability of E_1^* .

Before presenting the results, we need the following lemma,

LEMMA 2.1. *The solutions $S(t)$, $x_i(t)$, $i = 1 \dots n$ of (1.1) with positive initial conditions are positive and bounded, and if $\lambda_i < S^0 < \mu_i$ for some $i = 1 \dots n$, 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. \square

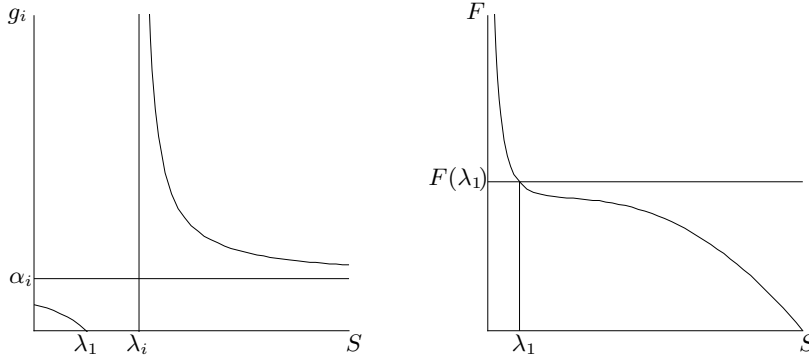


FIG. 2.1. Graphical depictions of conditions (2.5) and (2.6).

Consider the functions

$$(2.4) \quad g_i(S) = \frac{f_i(S) p_1(S) - D_1}{f_1(S) p_i(S) - D_i}.$$

Since (2.2) holds, the functions $g_i(S)$, with $i \geq 2$, are negative if $\lambda_1 < S < \lambda_i$ and are positive if $0 \leq S < \lambda_1$ or $\lambda_i < S < \rho_i$ where $\rho_i = \min\{S^0, \mu_i\}$. We assume that there exist positive real numbers α_i such that (see Fig. 2.1, left)

$$(2.5) \quad \max_{0 < S < \lambda_1} g_i(S) \leq \alpha_i \leq \min_{\lambda_i < S < \rho_i} g_i(S), \quad i \geq 2.$$

In the case where $\lambda_i \geq S^0$, condition (2.5) reduces simply to the condition that $g_i(S)$ is bounded from above on the interval $]0, \lambda_1[$. Notice that this condition cannot be satisfied in the case where, for some index i we have

$$\lim_{S \rightarrow 0} \frac{p_i(S)}{p_1(S)} = +\infty.$$

Let $F(S) = F_1(S)$, where F_1 is defined in (2.1), with $i = 1$. We add the following assumption (see Fig. 2.1, right)

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

The 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 (2.3) of local exponential stability of E_1^* . We have the following result.

THEOREM 2.2. *Consider the system (1.1). Suppose that conditions (2.2) and (2.6) are satisfied and condition (2.5) is satisfied for each $i \geq 2$. Then the equilibrium E_1^* is globally asymptotically stable 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 $V = V(S, x_1, \dots, x_n)$ given by (1.6), where α_i are the positive constants satisfying (2.5). The function V is continuously differentiable in the positive cone and positive except at the point E_1^* . The derivative of V along the trajectories of (1.1) is given by

$$\begin{aligned} V' &= \frac{p_1(S) - D_1}{f_1(S)} \left[D(S^0 - S) - \sum_{i=1}^n x_i f_i(S) \right] + (x_1 - x_1^*) [p_1(S) - D_1] \\ &\quad + \sum_{i=2}^n \alpha_i (p_i(S) - D_i) x_i \\ &= [p_1(S) - D_1] \left[D \frac{S^0 - S}{f_1(S)} - x_1^* \right] \\ &\quad + \sum_{i=2}^n \left[\alpha_i (p_i(S) - D_i) - (p_1(S) - D_1) \frac{f_i(S)}{f_1(S)} \right] x_i \\ &= [p_1(S) - D_1] [F(S) - x_1^*] + \sum_{i=2}^n [p_i(S) - D_i] [\alpha_i - g_i(S)] x_i, \end{aligned}$$

where $g_i(S)$ and $F(S)$ are given by (2.4) and (2.1) respectively. First, note that, using (2.2) 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 $S = \lambda_1$. 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 (2.5), $g_i(S) \leq \alpha_i$ 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 (2.5). Hence $V' \leq 0$ and $V' = 0$ if and only if $x_i = 0$ for $i = 1 \dots n$ or $S = \lambda_1$ and $x_i = 0$ for $i = 2 \dots n$. By LaSalle's Theorem, the ω -limit set of the trajectory is E_1^* . \square

Let us show that Theorem 2.2 applies in two important classical cases.

Example 1 (The Monod case). Consider the particular case where the growth functions are given by (1.2) and the yields are constant. The equations take the form

$$(2.7) \quad \begin{aligned} S' &= D(S^0 - S) - \sum_{i=1}^n \frac{a_i S}{b_i + S} \frac{x_i}{Y_i} \\ x_i' &= \left[\frac{a_i S}{b_i + S} - D_i \right] x_i, \quad i = 1 \dots n. \end{aligned}$$

We consider the case where, for all $i = 1 \dots n$, $a_i > D_i$. In that case:

$$\lambda_i = \frac{b_i D_i}{a_i - D_i}, \quad \mu_i = \infty, \quad g_i(S) = w_i \frac{S - \lambda_1}{S - \lambda_i}, \quad \text{where} \quad w_i = \frac{a_i Y_1 (a_1 - D_1)}{a_1 Y_i (a_i - D_i)}.$$

Since the function $h_i(S) = \frac{S-\lambda_i}{S-\lambda_i}$ is decreasing on $[0, \lambda_1]$ and on $]\lambda_i, +\infty[$ and admits 1 as an horizontal asymptote, we have (see Figure 2.2, right)

$$(2.8) \quad \max_{0 < S < \lambda_1} h_i(S) = h_i(0) < 1 < h_i(\rho_i) = \min_{\lambda_i < S < \rho_i} h_i(S).$$

Thus the conditions (2.5) are satisfied with $\alpha_i = w_i$. Since

$$F(S) = Y_1 D(S^0 - S) \frac{b_1 + S}{a_1 S} \quad \text{and} \quad F'(S) = -Y_1 D \frac{S^2 + b_1 S^0}{a_1 S^2},$$

the first derivative of the function $F(S)$ is negative. Hence, condition (2.6) is satisfied. The global stability of the equilibrium E_1^* follows from Theorem 2.2. This was the main result of [4] (see also [13], Section 2.4). In this case the Lyapunov function (1.6) is simply

$$V = \frac{a_1 - D_1}{a_1 Y_1} V_H$$

where V_H is the Lyapunov function (1.3) discovered by Hsu [4]. Hence, our Lyapunov function (1.6) reduces to the Hsu Lyapunov function in the case of Michaelis-Menten response functions and constant yields.

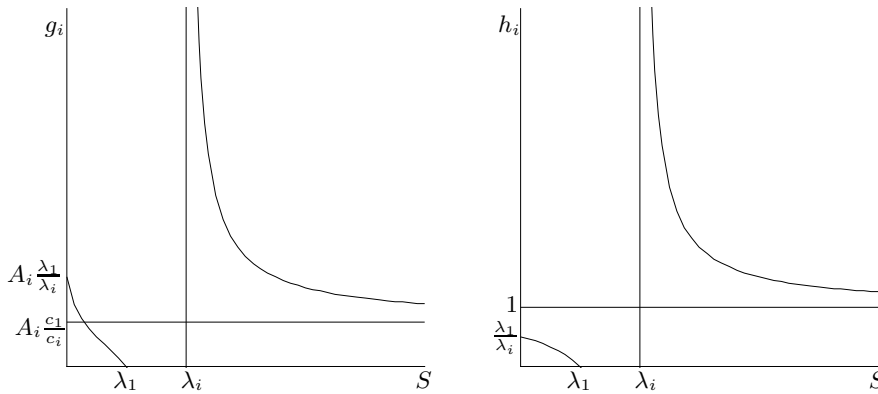


FIG. 2.2. On the left, the graph of the function $g_i(S)$ for $p_i(S) = \frac{a_i S}{b_i + S}$ and $y_i(S) = Y_i(1 + c_i S)$. On the right the graph of the function $h_i(S) = \frac{S-\lambda_1}{S-\lambda_i}$.

Example 2 (One species). In the case $n = 1$ the equations take the form

$$(2.9) \quad \begin{aligned} S' &= D(S^0 - S) - x_1 f_1(S) \\ x_1' &= [p_1(S) - D_1]x_1 \end{aligned}$$

If $\lambda_1 < S^0 < \mu_1$ and condition (2.6) is satisfied then the equilibrium $E_1^* = (\lambda_1, x_1^*)$, where $x_1^* = D \frac{S^0 - \lambda_1}{f_1(\lambda_1)}$ is globally asymptotically stable with respect to the interior of the positive quadrant. This results follows from Theorem 2.2 since in the case where $n = 1$ the condition (2.5) is satisfied. The global asymptotic stability of E_1^* was obtained by Arino, Pilyugin and Wolkowicz [1]. These authors used the following Lyapunov function

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

They proved (see [1], Theorem 2.11) that if

$$(2.10) \quad 1 - \frac{f_1(S)(S^0 - \lambda_1)}{f_1(\lambda_1)(S^0 - S)}$$

has exactly one sign change for $S \in (0, S^0)$ then E_1^* is globally asymptotically stable. Condition (2.10) is equivalent to (2.6). Notice that the Lyapunov function we obtain is not proportional to their function.

3. Applications. In this section we show how Theorem 2.2 can be fruitfully used to analyze the stability properties of systems whose yield functions depend on the variable S .

3.1. Michaelis-Menten growth functions and linear or quadratic yields.

Consider the particular case where the growth functions are given by (1.2) and the yields are linear

$$(3.1) \quad y_i(S) = Y_i(1 + c_i S)$$

or quadratic

$$(3.2) \quad y_i(S) = Y_i(1 + c_i S^2).$$

where $Y_i > 0$ and $c_i \geq 0$.

COROLLARY 3.1. *Consider the system (1.1) where the growth functions are given by (1.2) and the yields are given by (3.1) or (3.2). Suppose that conditions (2.2) and (2.6) are satisfied and the conditions*

$$(3.3) \quad c_i \lambda_1 \leq c_1 \lambda_i$$

are satisfied for each $i \geq 2$ satisfying $\lambda_i < S^0$. Then the equilibrium E_1^ is globally asymptotically stable with respect to the interior of the positive cone.*

Proof. For linear yields (3.1) we have

$$g_i(S) = A_i \frac{1 + c_1 S}{1 + c_i S} \frac{S - \lambda_1}{S - \lambda_i}, \quad \text{where} \quad A_i = \frac{a_i Y_1 (a_1 - D_1)}{a_1 Y_i (a_i - D_i)}.$$

Thus

$$g'_i(S) = A_i \frac{c_1 - c_i}{(1 + c_i S)^2} \frac{S - \lambda_1}{S - \lambda_i} + A_i \frac{1 + c_1 S}{1 + c_i S} \frac{\lambda_1 - \lambda_i}{(S - \lambda_i)^2}.$$

Two cases can be distinguished. If $c_1 < c_i$ then $g'_i(S) < 0$ for all $0 \leq S \leq \lambda_1$ and $S > \lambda_i$. Hence (see Fig. 2.2, left)

$$\max_{0 < S < \lambda_1} g_i(S) = g_i(0) = A_i \frac{\lambda_1}{\lambda_i}$$

and

$$\min_{\lambda_i < S < S^0} g_i(S) = g_i(S^0) > g_i(+\infty) = A_i \frac{c_1}{c_i}.$$

Under condition (3.3) there exists α_i satisfying (2.5). If $c_1 \geq c_i$ then the function

$$w_i(S) = A_i \frac{1 + c_1 S}{1 + c_i S}$$

is non-decreasing over $[0, +\infty[$. Thus

$$\max_{0 < S < \lambda_1} w_i(S) \leq \min_{\lambda_i < S < \rho_i} w_i(S).$$

Since (2.8) the functions $g_i(S) = w_i(S)h_i(S)$ satisfy (2.5). The result follows by Theorem 2.2. For quadratic yields (3.2) we have

$$g_i(S) = A_i \frac{1 + c_1 S^2}{1 + c_i S^2} \frac{S - \lambda_1}{S - \lambda_i}, \quad \text{where} \quad A_i = \frac{a_i Y_1 (a_1 - D_1)}{a_1 Y_i (a_i - D_i)}.$$

Thus

$$g'_i(S) = A_i \frac{2(c_1 - c_i)S}{(1 + c_i S^2)^2} \frac{S - \lambda_1}{S - \lambda_i} + A_i \frac{1 + c_1 S^2}{1 + c_i S^2} \frac{\lambda_1 - \lambda_i}{(S - \lambda_i)^2}.$$

Next, the proof is *mutatis mutandis* the same as the proof given above for the case of linear yields (3.1). \square

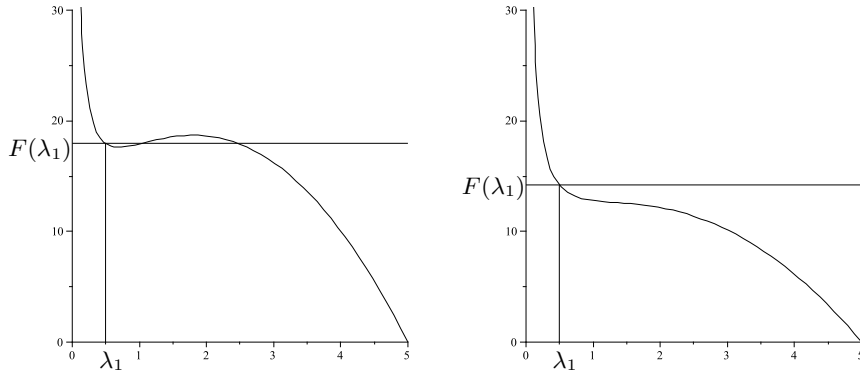


FIG. 3.1. The graph of the function $F(S)$ for $p_1(S) = \frac{a_1 S}{b_1 + S}$ (where $a_1 = 2.1/1.1$, $b_1 = 0.5/1.1$ and $\lambda_1 = 0.5$) and $y_1(S) = Y_1(1 + c_1 S)$. On the left the case $c_1 = 1.8$ for which the condition (2.6) is not satisfied. On the right, the case $c_1 = 1$ for which the condition (2.6) is satisfied.

Remark. This result contains as a particular case the result of Hsu [4] which corresponds to the case where the yields are constant. Indeed, for constant yields $c_i = 0$ and condition (3.3) is satisfied. When $c_1 > 0$, and the yield $y_1(S)$ is linear, the function $F(S)$ is given by

$$F(S) = DY_1 \frac{S^0 - S}{a_1 S} (b_1 + S)(1 + c_1 S).$$

Since this function is not monotone in general on the interval $]0, S^0[$, it is not easy to give a condition on the parameters for which (2.6) holds. However, the graphical depiction of condition (2.6) is very simple as shown in Fig. 3.1.

3.2. Pilyugin-Waltman's example. This system was given in [11] as a model of the competition in the chemostat exhibiting limit cycles. The existence of the limit cycles is a consequence of the variable yield in the model. The model takes the form

$$(3.4) \quad \begin{aligned} S' &= 1 - S - \frac{2S}{0.7+S} \frac{x_1}{1+cS^3} - \frac{m_2 S}{6.5+S} \frac{x_2}{120} \\ x_1' &= \left[\frac{2S}{0.7+S} - 1 \right] x_1 \\ x_2' &= \left[\frac{m_2 S}{6.5+S} - 1 \right] x_2. \end{aligned}$$

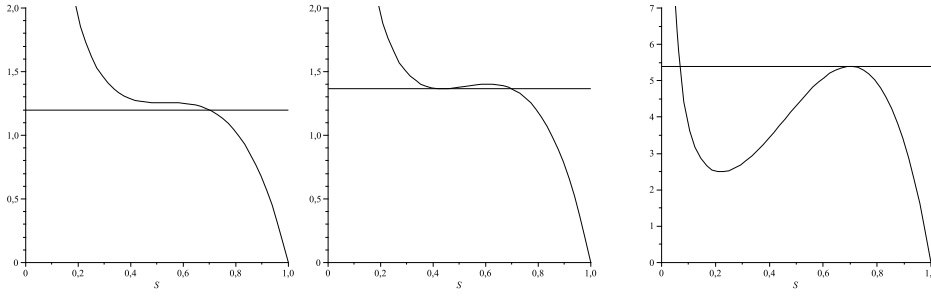


FIG. 3.2. The graph of the function $F(S)$ for $p_1(S) = 2S/(0.7 + S)$ and $y_1(S) = 1 + cS^3$ in the cases $c = c_0$ (left), $c = c_1$ (middle) and $c = c_2$ (right).

In their study Pilyugin and Waltman [11] fixed $c = 50$ and considered m_2 as a bifurcation parameter. They shown that for $m_2 \geq 9.85$ the system exhibits sustained oscillations. In this section we fix $m_2 = 10$ and we consider $c \geq 0$ as a bifurcation parameter. In this case we have

$$\lambda_1 = \frac{0.7}{2-1} = 0.7, \quad \lambda_2 = \frac{6.5}{10-1} \approx 0.72, \quad F(S) = \frac{(1-S)(0.7+S)(1+cS^3)}{2S}.$$

Straightforward computations lead to the formula

$$F'(\lambda_1) = \frac{49}{2000}c - \frac{17}{14}.$$

Hence $F'(\lambda_1) > 0$ if and only if $c > 2$ where $c_2 = \frac{17000}{343} \approx 49.562682$.

An analysis of the behavior of the function $F(S)$ shows (see Fig. 3.2) that there exist two bifurcation values c_0 and c_1 , $0 < c_0 < c_1 < c_2$, such that the function $F(S)$ is decreasing on $]0, S_0[$ if and only if $0 \leq c \leq c_0$ and the function $F(S)$ has two extrema $S_1, S_2 \in]0, \lambda_1[$ satisfying $F(S_1) < F(\lambda_1) < F(S_2)$ if and only if $c \in]c_1, c_2[$. The numerical values of c_0 and c_1 are $c_0 \approx 8.743009$ and $c_1 \approx 10.350424$.

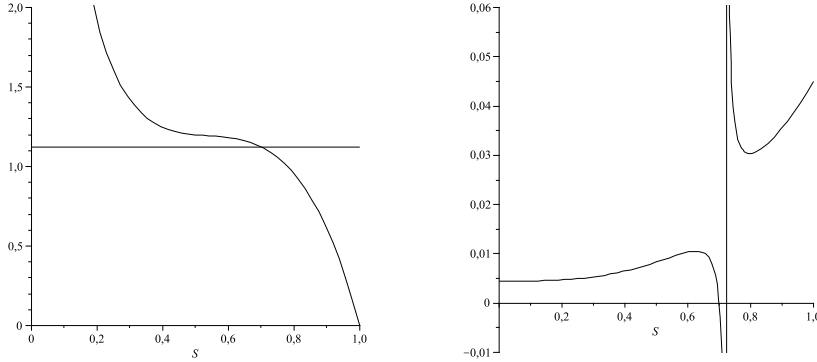


FIG. 3.3. Graphical verification of assumptions (2.5) and (2.6) for (3.4) with $c = 8$ and $m_2 = 10$. On the left, the graph of the function $F(S)$. On the right the graph of the function $g_2(S)$.

COROLLARY 3.2. *The equilibrium E_1^* is locally exponentially unstable if and only if $c > c_2$. If $0 \leq c < c_1$ then the equilibrium E_1^* is globally asymptotically stable.*

Proof. Since $\lambda_1 < \lambda_2$ and $F'(\lambda_1) > 0$ if and only if $c > c_2$ the condition (2.3) of local exponential stability of the equilibrium E_1^* holds if and only if $c > c_2$. The condition (2.6) is satisfied if and only if $0 \leq c < c_1$ (see Fig. 3.3, left). The function $g_2(S)$ is defined by

$$g_2(S) = \frac{1 + cS^3}{216} \frac{S - \lambda_1}{S - \lambda_2}.$$

For $c \geq 0$, the function $S \mapsto 1 + cS^3$ is non-decreasing. Since $h_2(S) = \frac{S - \lambda_1}{S - \lambda_2}$ satisfies (2.8), the condition (2.5) with $i = 2$ holds (see Fig. 3.3, right), and the result follows from Theorem 2.2. \square

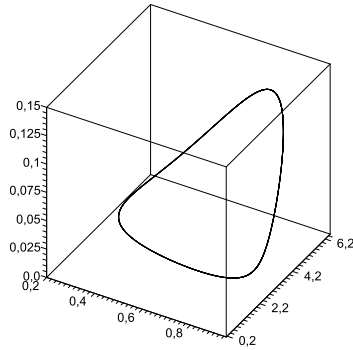


FIG. 3.4. The numerical limit cycle of (3.4) with $c = 8$ and $m_2 = 10$. It was computed with initial conditions $S(0) = 4$, $x_1(0) = 2$, $x_2(0) = 0.1$. The figure shows the plot of this the trajectory $(S(t), x_1(t), x_2(t))$ for $2000 \leq t \leq 2100$.

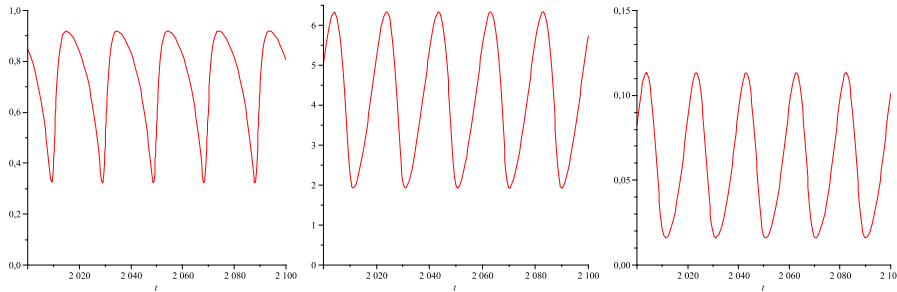


FIG. 3.5. The solution $S(t)$ (on the left), $x_1(t)$ (on the middle) and $x_2(t)$ (on the right) corresponding to the limit cycle shown in Fig. 3.3. The limit cycle is not on the face $x_2 = 0$.

Pilyugin and Waltman shown by numerical simulations that their system exhibits limit cycles in the case where $c = 50$ and $m_2 \geq 9.85$ (see Figs. 3.4 and 3.5 or Fig. 4 in [11]). The example was revisited by Huang, Zhu and Chang [6] who claimed that the limit cycle of the system should remain only on the face $x_2 = 0$ (see [6], Remark 2). We do not agree with this claim. We performed ourselves numerical simulations and actually the limit cycle is contained within the positive cone as shown in Figs. 3.4 and 3.5 and not in the face $x_2 = 0$ as claimed in [6].

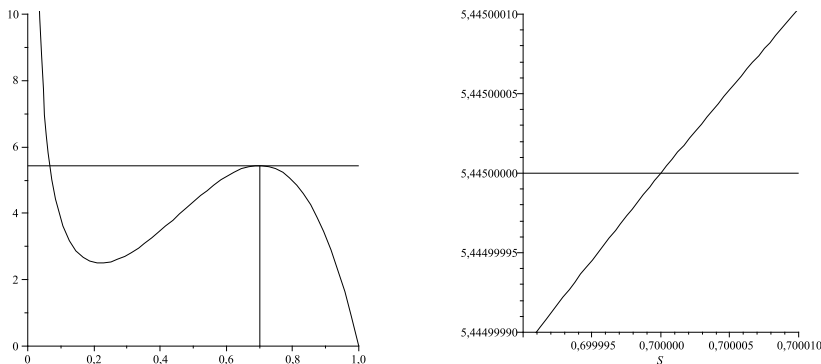


FIG. 3.6. Plot of $F(S)$ for (3.4). The magnification (on the right) of the neighborhood of $\lambda_1 = 0.7$ shows that $F'(\lambda_1) > 0$. Hence the equilibrium is locally exponentially unstable.

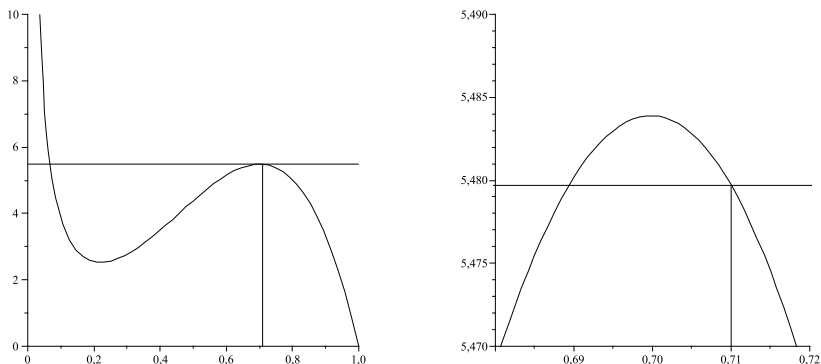


FIG. 3.7. Plot of $F(S)$ for (3.5). The magnification (on the right) of the neighborhood of $\lambda_1 = 0.71$ shows that $F'(\lambda_1) < 0$. Hence the equilibrium is locally exponentially stable. Since condition (2.6) is not satisfied Theorem 2.2 does not apply.

Huang, Zhu and Chang [6] made a simple modification by replacing $2S/(0.7 + S)$ with $2S/(0.71 + S)$ in (3.4) and obtained an example exhibiting competitive exclusion. The model takes the form

$$\begin{aligned}
 (3.5) \quad S' &= 1 - S - \frac{2S}{0.71+S} \frac{x_1}{1+50S^3} - \frac{m_2 S}{6.5+S} \frac{x_2}{120} \\
 x_1' &= \left[\frac{2S}{0.7+S} - 1 \right] x_1 \\
 x_2' &= \left[\frac{m_2 S}{6.5+S} - 1 \right] x_2.
 \end{aligned}$$

It is claimed, without proof, in [6] that the equilibrium E_1^* is globally asymptotically stable. Our criterion (2.6) does not apply (see Fig. 3.7) and we cannot prove the global stability. However an explanation of the high sensitivity when 0.7 is replaced by 0.71 is easy to find. Actually the plots of the function $F(S)$ in the case of (3.4), where $c = 50$ and (3.5) are very similar (see Figs. 3.6 and 3.7, left), but a magnification of the neighborhood of the value $S = \lambda_1$ shows the differences (see Figs. 3.6 and 3.7, right). In (3.4), $F'(\lambda_1) > 0$. Hence the equilibrium E_1^* is locally exponentially unstable. In (3.5), $F'(\lambda_1) < 0$. Hence the equilibrium E_1^* is locally exponentially stable.

3.3. Further applications. In this section we describe a class of response functions $p_i(S)$ and yields $y_i(S)$ for which constants α_i satisfying (2.5) exist and hence Theorem 2.2 can be applied.

PROPOSITION 3.3. *Suppose that conditions (2.2) and (2.6) are satisfied. For each $i \geq 2$, if $w_i(S)$ satisfies*

$$(3.6) \quad \max_{0 < S < \lambda_1} w_i(S) \leq \min_{\lambda_i < S < \rho_i} w_i(S),$$

where $w_i(S) = g_i(S) \frac{S - \lambda_i}{S - \lambda_1}$, then the equilibrium E_1^* is globally asymptotically stable with respect to the interior of the positive cone.

Proof. Since (3.6) and (2.8) the functions $g_i(S) = w_i(S)h_i(S)$ satisfy (2.5) and hence the result follows by Theorem 2.2. \square

It is convenient to use the notation

$$P_i(S) = \frac{S - \lambda_i}{p_i(S) - D_i} p_i(S).$$

Then

$$(3.7) \quad p_i(S) = \frac{D_i P_i(S)}{P_i(S) + \lambda_i - S}$$

and

$$w_i(S) = \frac{y_1(S) P_i(S)}{y_i(S) P_1(S)}.$$

Remark. Notice that we can take the functions $P_i(S)$ as any functions that are positive for $0 < S \leq S^0$ and satisfy $P_i(0) = 0$ and use formulas (3.7) to define the functions $p_i(S)$ for $i = 1 \dots n$ and $S \in [0, S^0]$. We must impose also

$$P_i(S) > S - \lambda_i, \text{ for all } S \in [0, S^0] \text{ and } i = 1 \dots n.$$

The functions (3.7) satisfy that $p_i(S) < D_i$ for $S \in [0, \lambda_i[$ and $p_i(S) > D_i$ for $S \in]\lambda_i, S^0]$. Thus $\mu_i > S^0$. If we find a class of yield functions $y_i(S)$ such that the conditions (3.6) hold, then we can use Proposition 3.3 to obtain the global asymptotic stability of the equilibrium E_1^* .

As a particular application of Proposition 3.3, we consider the following prototypes of response functions often found in the literature. These functions were considered also by Wolkowicz and Lu [14] who indicated for each combination of them that it is always possible to find appropriate constants α_i satisfying the criterion (1.4).

The Holling type II (Michaelis-Menten or Monod) growth functions

$$p_i(S) = \frac{D_i m_i S}{(m_i - 1)S + \lambda_i}$$

correspond to the choice $P_i(S) = m_i$ and $m_i > 1$. For these functions we have $\mu_i = +\infty$. The case where $m_i = 1$ reduces to the Holling type I (Lotka-Volterra) growth functions $p_i(S) = D_i S / \lambda_i$. For linear yields (3.1) we have

$$w_i(S) = \frac{Y_1 m_i}{Y_i m_1} \frac{1 + c_1 S}{1 + c_i S}.$$

If $c_1 \geq c_i$ then $w_i(S)$ is non-decreasing over $[0, +\infty[$ and hence conditions (3.6) are satisfied. Notice that the condition $c_1 \geq c_i$ implies the condition (3.3) of Corollary 3.1. For quadratic yields (3.2) we have

$$w_i(S) = \frac{Y_1 m_i}{Y_i m_1} \frac{1 + c_1 S^2}{1 + c_i S^2}.$$

If $c_1 \geq c_i$ then $w_i(S)$ is non-decreasing over $[0, +\infty[$ and hence conditions (3.6) are satisfied. Notice that the condition $c_1 \geq c_i$ implies the condition (3.3) of Corollary 3.1.

The Holling type III (or sigmoidal) growth functions

$$(3.8) \quad p_i(S) = \frac{D_i m_i S^2}{(a_i + S)(b_i + S)}, \quad \text{with} \quad m_i = \frac{(a_i + \lambda_i)(b_i + \lambda_i)}{\lambda_i^2}$$

correspond to the choice

$$P_i(S) = \frac{(a_i + \lambda_i)(b_i + \lambda_i)S^2}{(a_i + b_i)\lambda_i S + a_i b_i (S + \lambda_i)}.$$

For these functions we have $\mu_i = +\infty$.

PROPOSITION 3.4. *Consider the system (1.1) where $p_i(S)$ are given by (3.8) and $y_i(S) = Y_i$ are constant. Suppose that conditions (2.2) and (2.6) are satisfied and*

$$(3.9) \quad v_1 u_i \geq u_1 v_i, \quad i \geq 2$$

where $u_i = a_i b_i \lambda_i$ and $v_i = (a_i + b_i)\lambda_i + a_i b_i$. Then the equilibrium E_1^* is globally asymptotically stable with respect to the interior of the positive cone.

Proof. We have

$$w_i(S) = \frac{Y_1}{Y_i} \frac{(a_i + \lambda_i)(b_i + \lambda_i)}{(a_1 + \lambda_1)(b_1 + \lambda_1)} \frac{(a_1 + b_1)\lambda_1 S + a_1 b_1 (S + \lambda_1)}{(a_i + b_i)\lambda_i S + a_i b_i (S + \lambda_i)}.$$

These functions are of the form $w_i(S) = k_i \frac{u_i + v_i S}{u_i + v_i S}$ where the k_i 's are constant. If (3.9) holds then $w_i(S)$ is non-decreasing over $[0, +\infty[$ and hence conditions (3.6) are satisfied. The result follows by Proposition 3.3. \square

For the growth functions (3.8) we can find another class of yield functions for which our result applies. Indeed, for the yields given by

$$y_i(S) = \frac{Y_i}{(a_i + b_i)\lambda_i S + a_i b_i (S + \lambda_i)}$$

the functions

$$w_i(S) = \frac{Y_1}{Y_i} \frac{(a_i + \lambda_i)(b_i + \lambda_i)}{(a_1 + \lambda_1)(b_1 + \lambda_1)}$$

are constant, and hence conditions (3.6) are satisfied. If condition (2.6) holds then the global stability of the equilibrium E_1^* follows from Proposition 3.3.

The prototype for a non-monotone response function

$$(3.10) \quad p_i(S) = \frac{D_i m_i S}{(a_i + S)(b_i + S)}, \quad \text{with} \quad m_i = \frac{(a_i + \lambda_i)(b_i + \lambda_i)}{\lambda_i}$$

corresponds to the choice

$$P_i(S) = \frac{(a_i + \lambda_i)(b_i + \lambda_i)}{a_i b_i - \lambda_i S}.$$

For these functions we have $\mu_i = \frac{a_i b_i}{\lambda_i}$.

PROPOSITION 3.5. *Consider the system (1.1) where the functions $p_i(S)$ are given by (3.10) and $y_i(S) = Y_i$ are constant. Suppose that conditions (2.2) and (2.6) are satisfied and*

$$(3.11) \quad \lambda_1 a_i b_i \geq \lambda_i a_1 b_1, \quad S^0 < \mu_i, \quad i \geq 2.$$

Then the equilibrium E_1^ is globally asymptotically stable with respect to the interior of the positive cone.*

Proof. We have

$$w_i(S) = \frac{Y_1}{Y_i} \frac{(a_i + \lambda_i)(b_i + \lambda_i)}{(a_1 + \lambda_1)(b_1 + \lambda_1)} \frac{a_1 b_1 - \lambda_1 S}{a_i b_i - \lambda_i S}.$$

If (3.11) holds then $w_i(S)$ is non-decreasing on $[0, S^0]$ and hence condition (3.6) are satisfied. The result follows by Proposition 3.3. \square

For the growth functions (3.10) we can find another class of yield functions for which our result applies. Indeed, assume that $\mu_i > S^0$, that is $a_i b_i - \lambda_i S^0 > 0$. For the yields given by

$$y_i(S) = \begin{cases} \frac{Y_i}{a_i b_i - \lambda_i S} & \text{if } 0 \leq S \leq S^0, \\ \frac{Y_i}{a_i b_i - \lambda_i S^0} & \text{if } S > S^0, \end{cases}$$

the functions

$$w_i(S) = \frac{Y_1}{Y_i} \frac{(a_i + \lambda_i)(b_i + \lambda_i)}{(a_1 + \lambda_1)(b_1 + \lambda_1)}$$

are constant on $[0, S^0]$, and hence conditions (3.6) are satisfied. If condition (2.6) holds then the global stability of the equilibrium E_1^* follows from Proposition 3.3.

Hereafter we use the remark following Proposition 3.3 to define two new classes of functions, which are not considered in the literature, for which our results apply. A class of monotone response functions of the form (3.7) is obtained with

$$P_i(S) = \alpha_i \left[S + \frac{\alpha S}{1 + \beta S} \right]$$

where $\alpha > 0$, $\beta > 0$ and $\alpha_i \geq 1$. In this case we have

$$p_i(S) = \frac{D_i \alpha_i S (1 + \alpha + \beta S)}{\alpha \alpha_i S + (1 + \beta S)(\alpha_i S - S + \lambda_i)}.$$

For constant yields $y_i(S) = Y_i$ the functions $w_i(S) = \frac{Y_i \alpha_i}{Y_i \alpha_i}$ are constant and hence conditions (3.6) are satisfied. For linear yields (3.1) we have $w_i(S) = \frac{Y_1 \alpha_i}{Y_i \alpha_i} \frac{1 + c_1 S}{1 + c_1 S}$. If $c_1 \geq c_i$ then $w_i(S)$ is non-decreasing and hence conditions (3.6) are satisfied. For quadratic yields (3.2) we have $w_i(S) = \frac{Y_1 \alpha_i}{Y_i \alpha_i} \frac{1 + c_1 S^2}{1 + c_1 S^2}$. If $c_1 \geq c_i$ then $w_i(S)$ is non-decreasing and hence conditions (3.6) are satisfied.

A class of non-monotone response functions of the form (3.7) is obtained with

$$P_i(S) = \alpha_i S^2$$

and $\alpha_i > \frac{1}{4\lambda_i}$. In this case we have

$$p_i(S) = \frac{D_i \alpha_i S^2}{\alpha_i S^2 - S + \lambda_i}.$$

For constant yields $y_i(S) = Y_i$ the functions $w_i(S) = \frac{Y_i \alpha_i}{Y_i \alpha_i}$ are constant and hence conditions (3.6) are satisfied. For linear yields (3.1) we have $w_i(S) = \frac{Y_i \alpha_i (1+c_1 S)}{Y_i \alpha_i (1+c_1 S)}$. If $c_1 \geq c_i$ then $w_i(S)$ is non-decreasing and hence conditions (3.6) are satisfied. For quadratic yields (3.2) we have $w_i(S) = \frac{Y_i \alpha_i (1+c_1 S^2)}{Y_i \alpha_i (1+c_1 S^2)}$. If $c_1 \geq c_i$ then $w_i(S)$ is non-decreasing and hence conditions (3.6) are satisfied.

4. Discussion. In this paper we considered a mathematical model (1.1) of n species of microorganisms in competition 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 $N = \{i : \lambda_i < S^0\}$. Li [8] conjectured that this result can be extended to the case of different removal rates. Under condition (2.2), 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 (2.2) 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 [12] 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 results enlarge the class of growth functions for which the CEP holds. More substantially our results concern also the case of variable yields, for which it is known [1, 6, 11] 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. We extended the result of Hsu [4] to the case of linear or quadratic yields.

Our proof relies on the construction of non-strict Lyapunov functions, i.e. Lyapunov functions whose derivative along the trajectories are non-positive. We conjecture that the strictification techniques of Chapter 5 of [9] can be used to construct strict Lyapunov functions, i.e. Lyapunov functions whose derivative along the trajectories are definite negative, which next can be used to establish some robustness properties. This can be the subject of further research.

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