Competition and coexistence in the chemostat*

Tewfik Sari†

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Contents

1 Introduction

The aim of this course is to describe the mathematical model of competition in the chemostat and to study various mechanisms of coexistence of species. Basically, the chemostat consists of a nutrient input, pumped at a constant rate into a well-mixed culture vessel. The culture vessel contains the microorganisms that are growing and competing for the nutrient. Volume is kept constant by pumping the mixed contents out at the same rate. when only one species is present in the chemostat, the model is written

$$\left\{\begin{array}{rcl}\dot{S} &=& D(S_{in}-S)-\dfrac{q(S)}{Y}x\\ \dot{x} &=& \left[q(S)-D_1\right]x,\end{array}\right. \tag{1}$$

where x, denotes the concentration of the species, S is the nutrient (substrate) concentration and Y denotes the yields coefficients; S_{in} and D denote, respectively, the concentration of substrate in the feed bottle and the dilution rate of the chemostat; $q(S)$ represents the growth rate of the species and is assumed to be an increasing function. The parameter D_1 is not necessarily equal to D and can be interpreted as the sum of the dilution rate D and the natural death rate of the species: $D_1 = D + a$, where $a \geqslant 0$. The case $D_1 \leqslant D$ is considered also in the literature. This case has the following biological interpretation : $D_1 = \alpha D$, where $\alpha \in [0, 1]$ is a parameter allowing us to decouple the HRT (Hydraulic Retention Time) and the SRT (Solid Retention Time) [7].

The model (1), occupies a central place in mathematical ecology, see [69] for review. It is well known that for (1) have the washout steady state

$$\mathcal{E}_0 = (S_{in}, 0)$$

where $S = S_{in}$ and $x = 0$, where the species is extinct, and can have a positive steady state

$$\mathcal{E}_1 = (\lambda, x),$$

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[†] Irstea, UMR ITAP, Montpellier, France and Université de Haute Alsace, LMIA, Mulhouse, France

where

$$S = \lambda \text{ is a solution of equation } q(S) = D_1, \text{ and } x = \frac{D}{D_1}(S_{in} - \lambda).$$

This steady state is meaningful only if $\lambda < S_{in}$ and is globally asymptotically stable as long as it exists.

When several species of microorganisms are growing and competing for the nutrient, the interactions of microbial species which are competing for a single nutrient is described by the following model

$$\left\{ \begin{array}{rcll} \dot{S} & = & D(S_{in} - S) - \displaystyle\sum_{i=1}^{n} \frac{q_i(S)}{Y_i} x_i & \\ \dot{x}_i & = & [q_i(S) - D_i]\, x_i, & i = 1, \ldots, n \end{array} \right. \tag{2}$$

where x_i, $i = 1, \ldots, n$, denotes the concentration of species i, S is the nutrient (substrate) concentration and Y_i, $i = 1, \ldots, n$, denotes the yields coefficients; S_{in} and D denote, respectively, the concentration of substrate in the feed bottle and the dilution rate of the chemostat; for $i = 1, \ldots, n$, $q_i(S)$ represents the growth rate of species i and is assumed to be an increasing function. The parameters D_i are not necessarily equal to D.

It is well known [69] that for (2) only one species can survive at steady state. Actually at a steady state of (2) we must have

$$[q_i(S) - D_i]\, x_i = 0, \qquad i = 1, \ldots, n.$$

If the species x_i and x_j, with $i \neq j$, are present at a steady state then

$$q_i(S) = D_i \text{ and } q_j(S) = D_j \text{ with } i \neq j$$

are two equations in the single variable S and, in general, cannot have a solution. Hence, in general, besides the washout steady state

$$\mathcal{E}_0 = (S_{in}, 0, \cdots, 0)$$

where $S = S_{in}$ and $x_i = 0$, $i = 1, \ldots, n$, that is all species are extinct, generically, model (2) can only have the steady states

$$\mathcal{E}_1 = (\lambda_1, x_1, 0, \cdots, 0), \quad \mathcal{E}_2 = (\lambda_2, 0, x_2, 0, \cdots, 0), \cdots, \mathcal{E}_n = (\lambda_n, 0, \cdots, 0, x_n),$$

where

$$S = \lambda_i \text{ is a solution of equation } q_i(S) = D_i, \quad x_i = \frac{D}{D_i}(S_{in} - \lambda_i) \text{ and } x_j = 0 \text{ for } j \neq i$$

that is all species except one, namely x_i, go to extinction at steady state $\mathcal{E}_i$. This steady state is meaningful if and only if $\lambda_i < S_{in}$.

The λ_i are called *break-even concentrations*. If the species are labeled such that $\lambda_1 < \lambda_i$ for all $i > 1$, it is well known that the steady state $\mathcal{E}_1$ is locally asymptotically stable and all other steady states $\mathcal{E}_0$ and $\mathcal{E}_i$, $i > 1$, are unstable [69]. Hence, at steady state, only the species with the lowest break-even concentration survives, this is the species which consumes less substrate to attain its steady state. One of the main results for (2) is known as the Competitive Exclusion Principle (CEP), after Hardin [33]. This result states that, under certain conditions, the locally stable steady state $\mathcal{E}_1$ is in fact globally attractive, see Section 2 for precise results.. The CEP was established by several authors under various hypothesis: Hsu et al. [39] showed the global asymptotic stability of $\mathcal{E}_1$ in the case of Michaelis–Menten (or Monod) kinetics [56] and the same removal rates D_i, Hsu [37] extended the study of [39] with different removal rates by using a Lyapunov–LaSalle argument, Wolkowicz and Lu [76] extended the result of [37] to growth functions which are not necessarily increasing functions of the substrate S. The reader may consult [48, 50, 66] for a more thorough account on the contributions of diverse authors.

Although this theoretical prediction has been corroborated by the experiences of Hansen and Hubell [32], the biodiversity found in nature as well as in waste-water treatment processes and biological reactors seems to contradict the CEP. For example, in aquatic ecosystems, several phytoplankton species competing for some resources can coexist [43, 67]. The biodiversity is also found in biological reactors with a mixture including at least two competitors for one resource, see [36, 68]. This has triggered a lot of mathematical research aimed to extend model (2) to bring theory and observations in better accordance.

In Section 2 we will discuss the so-called Competitive Exclusion Principle. Different mechanisms of coexistence which were proposed in the literature are the flocculation [21, 19, 30, 31], that will be considered in Section 3 and the intra and interspecific competition [1, 47, 23, 77] and the density-dependence of growth functions [20, 51, 52, 53, 54, 35], that will be studied in Section 4. Notice that flocculation can serve as a biological motivation for density-dependent growth functions. Several other mathematical models [11, 17, 25, 29, 45, 49, 41, 40, 9, 42, 60, 64, 65] have attempted to understand the coexistence by adding another substrate (product) in the chemostat. We will not consider these mechanisms of coexistence in this course.

2 Competitive exclusion in the chemostat

The aim of this section is to show that under certain conditions the Competitive Exclusion Principle (CEP) holds for the following competition for a single resource model

$$\begin{array}{rcll} S' & = & D[S_{in}-S]-\sum_{j=1}^{n} p_j(S)x_j, & \\ x_i' & = & [q_i(S)-D_i]x_i, & i=1\cdots n, \end{array} \tag{3}$$

where $S(t)$ and $x_i(t)$, $i=1\cdots n$, denote respectively the nutrient concentration and the concentration of the ith competing species at time t. The input concentration S_{in} and the removal rates D and D_i are assumed to be constant. The uptake rate $p_i(S)$ satisfies

$$p_i(0)=0 \text{ and } p_i(S)>0 \text{ for } S>0. \tag{4}$$

The growth rate $q_i(S)$ satisfies

$$q_i(0)=0 \text{ and } q_i(S)>0 \text{ for } S>0. \tag{5}$$

The functions $y_i(S)$, defined by

$$y_i(S)=\frac{q_i(S)}{p_i(S)}, \qquad i=1\cdots n, \tag{6}$$

are the growth yields. The model (3) was considered by Arino, Pilyugin and Wolkowicz [4] as an extension of the classical chemostat model (2), where $p_i(S)=\frac{q_i(S)}{Y_i}$, for which the yields $y_i(S)=Y_i$ are constant. The smallest positive value of the concentration substrate $S=\lambda_i$ defined by the condition $q_i(S)=D_i$, where the growth $q_i(S)$ of x_i is balanced by the removal rate D_i is called the *break-even concentration* for the ith species.

Let us denote $f_i(S)=q_i(S)-D_i$, then (3) reduces to the model

$$\begin{array}{rcll} S' & = & D(S_{in}-S)-\sum_{j=1}^{n} p_j(S)x_j & \\ x_i' & = & f_i(S)x_i, & i=1\cdots n, \end{array} \tag{7}$$

considered by Fiedler and Hsu [26]. The growth rate $f_i(S)$ satisfies

$$f_i(S)<0 \text{ for } 0\le S<\lambda_i \text{ and } f_i(\lambda_i)=0, \tag{8}$$

where λ_i are the break-even concentrations.

Let us prove first that we can we assume that $D=1$ and $S_{in}=1$ in (7). Indeed, under the change of variables

$$\overline{S}=\frac{S}{S_{in}}, \qquad \overline{t}=Dt, \qquad \overline{p}_i(\overline{S})=\frac{p_i(S_{in}\overline{S})}{S_{in}D}, \qquad \overline{f}_i(\overline{S})=\frac{f_i(S_{in}\overline{S})}{D},$$

equations (7) take the form

$$\begin{array}{rcccll} \frac{d\overline{S}}{d\overline{t}} & = & \frac{1}{S_{in}D}\frac{dS}{dt} & = & 1-\overline{S}-\sum_{j=1}^{n}\overline{p}_j(\overline{S})x_j, & \\ \frac{dx_i}{d\overline{t}} & = & \frac{1}{D}\frac{dx_i}{dt} & = & \overline{f}_i(\overline{S})x_i, & i=1\cdots n. \end{array}$$

Dropping the bars, one obtains (9). Recall that $f_i(0)<0$, so that the concentration of the species x_i is decreasing when the concentration of nutrient is too small. The smallest positive zero $S=\lambda_i$ of f_i is the break-even concentration of the ith species x_i. We adopt the convention $\lambda_i=\infty$ if $f_i(S)<0$ for all $S>0$.

Therefore, without loss of generality, we assume that $D=1$ and $S_{in}=1$ in (7). The system becomes

$$\begin{array}{rcll} S' & = & 1-S-\sum_{j=1}^{n} p_j(S)x_j, & \\ x_i' & = & f_i(S)x_i, & i=1\cdots n. \end{array} \tag{9}$$

Coexistence of the n species is a fundamental question on the model (9) of competition for a single resource. Looking for coexistence at positive equilibria we have to solve equations $f_i(S)=0$ simultaneously for all $i=1\cdots n$.

In general, for $n \geq 2$, these equations cannot be solved for the same value of S. Thus, generically, (9) can have the following equilibria: the washout equilibrium

$$E_0 = (1, 0, \cdots, 0), \tag{10}$$

where all species go extinct, and equilibria E_i, $i = 1 \cdots n$, where all components of E_i vanish, except for the first and the $(i+1)$th, which are

$$S = S^*, \qquad x_i = \frac{1 - S^*}{p_i(S^*)},$$

where $S^* \in]0, 1[$ satisfies $f_i(S^*) = 0$. Hence, at any equilibrium point E_i, all but one species go extinct.

Since $f(\lambda_i) = 0$, the break-even concentration $S^* = \lambda_i$ gives rise to an equilibrium point E_i for the system, if and only if $\lambda_i < 1$. A well-known open-problem in the theory of the chemostat is to prove the global asymptotic stability of the equilibrium point E_i with the lowest break-even concentration. If this equilibrium is globally asymptotically stable (GAS), then the CEP holds: only one species survives, namely the species which makes optimal use of the resource. The reader is referred to [71], for complements and details on the CEP. Most of the results on the CEP for (3) and (2) have been based on Lyapunov functions [5, 37, 50, 62, 66, 76, 78] . For a survey of constructing Lyapunov functions in the chemostat, the reader is referred to [38]. We simply recall here that Hsu [37] proved the CEP for the Monod case of (2), when the growth functions are

$$q_i(S) = \frac{a_i S}{b_i + S}, \tag{11}$$

and Wolkowicz and Lu [76] extended the result of [37] to (2) with more general growth functions.

Instead of a Lyapunov function approach, Fiedler and Hsu [26] applied a multi-dimensional Bendixon-Dulac criterion to exclude periodic solutions. Under some technical conditions on the functions f_i and p_i they proved that (9) does not possess positive non-stationary periodic orbits. In [62, 66, 63], it is shown that both Lyapunov functions used by Hsu [37] and Wolkowicz and Lu [76] can be extended to the variable yields case model (3) or (9).

A necessary condition to avoid washout of the species, and global convergence towards the washout equilibrium E_0 defined by (10), is that $\lambda_i < 1$ for at least one species. Assume that the species are labeled so that $0 < \lambda_1 < 1$. Then

$$E_1^* = (\lambda_1, x_1^*, 0, \cdots, 0), \tag{12}$$

where $x_1 = x_1^* = P_1(\lambda_1)$ is an equilibrium. Here

$$P_1(S) = \frac{1 - S}{p_1(S)}. \tag{13}$$

Using linearization of (9) about E_1^* one proves that:

Lemma 1. *The equilibrium (12) is locally exponentially stable if and only if* $f_1'(\lambda_1) > 0$ *and* $P_1'(\lambda_1) < 0$.

We consider the global asymptotic stability of E_1^*. The main result is

Theorem 1. *Assume that (4) and (8) hold. Assume that* $\lambda_1 < 1$ *and for all* $0 < S < 1$,

$$(S - \lambda_1) f_1(S) > 0, \ \textit{for } S \neq \lambda_1, \tag{14}$$

$$(S - \lambda_1)(P_1(S) - P_1(\lambda_1)) < 0, \ \textit{for } S \neq \lambda_1, \tag{15}$$

where $P_1(S)$ *is defined by (13). Assume that there exist constants* $\alpha_i > 0$ *for each* $i \geq 2$ *satisfying* $\lambda_i < 1$*, such that for all* $0 < S < 1$,

$$f_1(S) p_i(S) > \alpha_i f_i(S)(1 - S). \tag{16}$$

Then the equilibrium E_1^* *is GAS for (9) with respect to the interior of the positive cone.*

The proof of this result can be obtained by using an extension of Lyapunov function of Wolkowicz and Lu [76], see Section 2.1, or by using an extension of the Lyapunov function of Hsu [37], see Section 2.2. For details and complements the reader is refered to [63].

Notice that the following property holds.

Lemma 2. *The conditions* $\lambda_1 < 1$ *and (16) imply that* $\lambda_1 < \lambda_i$ *for all* $i \geq 2$.

Proof. Assume that there exists $i \geq 2$ such that $\lambda_i < \lambda_1$. Then, there exists $S \leq \lambda_1$ such that $f_i(S) > 0$. Hence, since $S \leq \lambda_1 < 1$, $f_i(S)(1-S) > 0$. On the other hand, using (8), $f_1(S) \leq 0$. Hence, the inequality (16) is violated. ☐

This lemma shows that the winning species x_1 of Theorem 1 has the lowest break-even concentration, in accordance with the CEP for models of competition for a single resource [71]. We recall that the smallest positive zero $S = \lambda_i$ of f_i is the break-even concentration of the ith species x_i. We adopt the convention $\lambda_i = \infty$ if $f_i(S) < 0$ for all $S > 0$. We have the following results.

Lemma 3. *The non-negative cone is invariant under the flow of (9) and all solutions are defined and remain bounded for all* $t \geq 0$.

Lemma 4. *If for some species* x_i*, the inequality* $(S - \lambda_i) f_i(S) > 0$ *is satisfied for all* $0 < S < 1$, $S \neq \lambda_i$*, then* $S(t) < 1$ *for all sufficiently large* t *and all initial condition .*

Lemma 5. *For all solutions of (9), if* $\lambda_i \geq 1$ *then* $x_i(t) \to 0$ *as* $t \to \infty$.

2.1 Extension of the Lyapunov function of Wolkowicz and Lu

The Lyapunov function used by Wolkowicz and Lu [76] in the constant yields case (2) is

$$V_{WL} = \frac{S_{in} - \lambda_1}{D_1} \int_{\lambda_1}^{S} \frac{q_1(\sigma) - D_1}{S_{in} - \sigma} d\sigma + \frac{1}{Y_1} \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi} d\xi + \sum_{i=2}^{n} \frac{c_i}{Y_i} x_i. \tag{17}$$

with suitable constant $c_i > 0$. Using the notations in (9), and since S_{in} was rescaled to 1, the function in the first integral of (17) is simply equal to $\frac{f_1(\sigma)}{1-\sigma}$. Multiplying (17) by the constant $\frac{D_1}{1-\lambda_1} = \frac{Y_1}{x_1^*}$, gives the following function

$$V = \int_{\lambda_1}^{S} \frac{f_1(\sigma)}{1-\sigma} d\sigma + \frac{1}{x_1^*} \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi} d\xi + \sum_{i=2}^{n} \alpha_i x_i, \tag{18}$$

where α_i are constants to be determined. This is a Lyapunov function for (9) which permits to prove Theorem 1 as shown below.

Proof. (*Theorem 1*) From Lemmas 4 and 5 it follows that there is no loss of generality to assume that $\lambda_i < 1$ for $i = 1 \cdots n$ and to restrict our attention to $0 < S < 1$. Consider the function $V = V(S, x_1, \cdots, x_n)$ given by (18) where α_i are positive constants satisfying (16). The function V is continuously differentiable for $0 < S < 1$ and $x_i > 0$ and positive except at point E_1^*. The derivative of V along the trajectories of (9) is

$$V' = \frac{f_1(S)}{1-S} S' + \frac{x_1 - x_1^*}{x_1^* x_1} x_1' + \sum_{i=2}^{n} \alpha_i x_i'.$$

Since $x_1^* = P_1(\lambda_1)$ and using (9), V' is written

$$V' = \frac{f_1(S)}{1-S} \left[1 - S - \sum_{i=1}^{n} p_i(S) x_i \right] + \frac{1}{P_1(\lambda_1)} [x_1 - P_1(\lambda_1)] f_1(S) + \sum_{i=2}^{n} \alpha_i f_i(S) x_i.$$

The terms $\frac{f_1(S)}{1-S}(1-S)$ and $-\frac{1}{P_1(\lambda_1)} P_1(\lambda_1) f_1(S)$ are canceled. Hence, using (13),

$$V' = x_1 f_1(S) \left[\frac{1}{P_1(\lambda_1)} - \frac{1}{P_1(S)} \right] + \sum_{i=2}^{n} x_i \frac{\alpha_i f_i(S)(1-S) - f_1(S) p_i(S)}{1-S}.$$

Using (14) and (15), the first term of the above sum is non-positive for $0 < S < 1$ and equals 0 if and only if $S = \lambda_1$ or $x_1 = 0$. Using (16), the second term is non-positive for $0 < S < 1$ and equals 0 if and only if $x_i = 0$ for $i = 2 \cdots n$. 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 $i = 2 \cdots n$. Using the Krasovskii-LaSalle extension theorem, the ω-limit set of the trajectory is E_1^*. ☐

Theorem 1 has a special case [66] when the function f_i has at most two positive zeros λ_i and μ_i, with $\lambda_i \leq \mu_i \leq +\infty$, such that

$$f_i(S) < 0 \text{ if } S \notin [\lambda_i, \mu_i], \text{ and } f_i(S) > 0 \text{ if } S \in]\lambda_i, \mu_i[, \tag{19}$$

with the convention that $\mu_i = \infty$ if equation $f_i(S) = 0$ has only one solution and $\lambda_i = \infty$ if it has no solution. This class of functions corresponds to the case when $f_i(S) = q_i(S) - D_i$ and

$$q_i(S) < D_i \text{ if } S \notin [\lambda_i, \mu_i], \text{ and } q_i(S) > D_i \text{ if } S \in]\lambda_i, \mu_i[.$$

It was often considered in the literature [10, 50, 76, 78]. For this class of systems the main result [66] is

Corollary 1 (Theorem 2.1 in [62]). *Assume that (4), (8) and (19) hold. Assume that*

$$\lambda_1 < \lambda_2 \leq \cdots \leq \lambda_n, \text{ and } \lambda_1 < 1 < \mu_1, \tag{20}$$

$$(S - \lambda_1)(P_1(S) - P_1(\lambda_1)) < 0, \text{ for } S \neq \lambda_1, \tag{21}$$

where $P_1(S)$ is defined by (13). Assume that there exist constants $c_i > 0$ for each $i \geq 2$ satisfying $\lambda_i < 1$, such that

$$\max_{0<S<\lambda_1} h_i(S) < c_i < \min_{\lambda_i<S<\rho_i} h_i(S), \tag{22}$$

where $h_i(S) = \frac{1-\lambda_1}{p_1(\lambda_1)} \frac{f_1(S)p_i(S)}{f_i(S)(1-S)}$ and $\rho_i = \min(\mu_i, 1)$. Then the equilibrium E_1^* is GAS for (9) with respect to the interior of the positive cone.

Proof. Assume that (20), (21) and (22) hold. Let us prove that (14), (15) and (16) hold. First, note that (21) is the same as (15), and condition $\lambda_1 < 1 < \mu_1$ in (20) is equivalent to (14). If $\lambda_1 < S < \lambda_i$ then $f_i(S) < 0$ and $f_1(S) > 0$ so that (16) is satisfied for any choice of $\alpha_i > 0$. Similarly if $\mu_i < 1$ and $\mu_i < S < 1$ then $f_i(S) < 0$ and $f_1(S) > 0$ so that (16) is satisfied for any choice of $\alpha_i > 0$. On the other hand, if $0 < S < \lambda_1$ then $f_i(S) < 0$ and, using $h_i(S) < c_i$ in (22),

$$f_1(S)p_i(S) > c_i \frac{p_1(\lambda_1)}{1 - \lambda_1} f_i(S)(1 - S).$$

Finally, if $\lambda_i < S < \rho_i$, then $f_i(S) > 0$ and, using $h_i(S) > c_i$ in (22),

$$f_1(S)p_i(S) > c_i \frac{p_1(\lambda_1)}{1 - \lambda_1} f_i(S)(1 - S).$$

Thus (16) is satisfied for $\alpha_i = c_i \frac{p_1(\lambda_1)}{1-\lambda_1}$. The result follows from Theorem 1. □

Condition (14) means that $S = \lambda_1$ is the only zero of the growth function $f_1(S)$ for $0 < S < 1$. Condition (15) means that $S = \lambda_1$ is the only zero of the function $P_1(S)$ given by (13), for $0 < S < 1$. The technical condition (16) is trivially satisfied in the single species $n = 1$. Following [66, 76] we give now a graphical interpretation of (16). For each $i \geq 2$ such that $\lambda_i < 1$, consider the function

$$g_i(S) = \frac{f_i(S)}{f_1(S)} \frac{1 - S}{p_i(S)}. \tag{23}$$

The functions g_i is defined on $(0, \lambda_1) \cup (\lambda_1, 1]$. It tends to $\pm\infty$ when S tends λ_1. Notice that the function h_i in Corollary 1 is simply a multiple of the reciprocal of g_i. We use g_i instead of h_i, since the zeros of f_i on $[0, 1]$ are not known as for the class of functions f_i considered in Corollary 1. Since $f_1(S) < 0$ over $[0, \lambda_1)$ and $f_1(S) > 0$ over $[\lambda_i, 1]$, the condition (16) is equivalent to

$$\min_{0<S<\lambda_1} g_i(S) > \frac{1}{\alpha_i} > \max_{\lambda_i<S<1} g_i(S). \tag{24}$$

For more details and the graphical depictions of the conditions, the reader is referred to [63]

2.2 Extension of the Lyapunov function of Hsu

The Lyapunov function V_H used by Hsu [37] in the Monod case of (2), where the growth functions are of the form (11), is

$$V_H = \int_{\lambda_1}^{S} \frac{\sigma - \lambda_1}{\sigma} d\sigma + c_1 \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi} d\xi + \sum_{i=2}^{n} c_i x_i, \tag{25}$$

with constants

$$c_i = \frac{1}{Y_i} \frac{a_i}{a_i - D_i}, \quad i = \cdots n, \quad \text{and } \lambda_1 = \frac{b_1 D_1}{a_1 - D_1}.$$

It is readily checked that the function in the first integral of (25) is given by $\frac{S-\lambda_1}{S} = c_1 \frac{f_1(S)}{p_1(S)}$, where

$$f_1(S) = \frac{a_1 S}{b_1 + S} - D_1, \qquad p_1(S) = \frac{1}{Y_1} \frac{a_1 S}{b_1 + S}.$$

Hence, multiplying (25) by the constant $1/c_1$ gives the following function

$$V = \int_{\lambda_1}^{S} \frac{f_1(\sigma)}{p_1(\sigma)} d\sigma + \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi} d\xi + \sum_{i=2}^{n} c_i x_i. \tag{26}$$

where the constants c_i/c_1 in the last sum are simply denoted by c_i to avoid unnecessary new notations. Under some technical conditions, this function is a Lyapunov function for (9) and permits to obtain the global asymptotic stability of the equilibrium point E_1^* as stated in the following result.

Theorem 2. *Assume that (4) and (8) hold. Assume that* $\lambda_1 < 1$ *and for all* $0 < S < 1$,

$$(S - \lambda_1) f_1(S) > 0, \text{ for } S \neq \lambda_1, \tag{27}$$

$$(S - \lambda_1)(P_1(S) - P_1(\lambda_1)) < 0, \text{ for } S \neq \lambda_1, \tag{28}$$

where $P_1(S)$ *is defined by (13). Assume that there exist constants* $c_i > 0$ *for each* $i \geq 2$ *satisfying* $\lambda_i < 1$, *such that for all* $0 < S < 1$,

$$f_1(S) p_i(S) > c_i f_i(S) p_1(S). \tag{29}$$

Then the equilibrium E_1^* *is GAS for (9) with respect to the interior of the positive cone.*

Proof. From Lemmas 4 and 5 it follows that there is no loss of generality to assume that $\lambda_i < 1$ for $i = 1 \cdots n$ and to restrict our attention to $0 < S < 1$. Consider the function $V = V(S, x_1, \cdots, x_n)$ given by (26) where c_i are positive constants satisfying (29). The function V is continuously differentiable in the positive cone and positive except at point E_1^*, where it is equal to 0. The derivative of V along the trajectories of (9) is

$$V' = \frac{f_1(S)}{p_1(S)} S' + \frac{x_1 - x_1^*}{x_1} x_1' + \sum_{i=2}^{n} c_i x_i'.$$

Since $x_1^* = P_1(\lambda_1)$ and, using (9), V' is written

$$V' = \frac{f_1(S)}{p_1(S)} \left[1 - S - \sum_{i=1}^{n} p_i(S) x_i \right] + [x_1 - P_1(\lambda_1)] f_1(S) + \sum_{i=2}^{n} c_i f_i(S) x_i.$$

The terms $-\frac{f_1(S)}{p_1(S)} p_1(S) x_1$ and $x_1 f_1(S)$ are canceled. Therefore, using (13),

$$V' = f_1(S) \left[P_1(S) - P_1(\lambda_1) \right] + \sum_{i=2}^{n} x_i \frac{c_i f_i(S) p_1(S) - f_1(S) p_i(S)}{p_1(S)}.$$

Using (27) and (28), the first term of the above sum is non-positive for $0 < S < 1$ and equals 0 if and only if $S = \lambda_1$. Using (29), the second term is non-positive for $0 < S < 1$ and equals 0 if and only if $x_i = 0$ for $i = 2 \cdots n$. Hence $V' \leq 0$ and $V' = 0$ if and only if $S = \lambda_1$ and $x_i = 0$ for $i = 2 \cdots n$. By the Krasovskii-LaSalle extension theorem, the ω-limit set of the trajectory is E_1^*. □

We have the following property.

Lemma 6. *The conditions* $\lambda_1 < 1$ *and* (29) *imply that* $\lambda_1 < \lambda_i$ *for all* $i \geq 2$.

Proof. If $f_i(S) > 0$ for some $S \leq \lambda_1$, then $f_1(S) \leq 0$, so that the inequality (29) is violated. □

This lemma shows that the winning species x_1 in Theorem 2 has the lowest break-even concentration. Actually Theorem 2 is a consequence of Theorem 1.

Proposition 1. *Theorem 2 is a corollary of Theorem 1.*

Proof. Assume that (27), (28) and (29) hold. Notice that (27) is the same as (14) and (28) is the same as (15). Let us prove that (16) holds. If $f_i(S) < 0$ and $f_1(S) > 0$ (which occurs if $\lambda_1 < S < \lambda_i$ and may occur also for $\lambda_i < S < 1$), then (16) holds for any choice of $\alpha_i > 0$. If $0 < S < \lambda_1$ then, by (28), $P_1(S) > P_1(\lambda_1)$ and, since $f_i(S) < 0$, $\frac{f_i(S)}{P_1(S)} > \frac{f_i(S)}{P_1(\lambda_1)}$. Finally, if $\lambda_i < S < 1$ and $f_i(S) > 0$ then, by (28), $P_1(S) < P_1(\lambda_1)$, and hence, $\frac{f_i(S)}{P_1(S)} > \frac{f_i(S)}{P_1(\lambda_1)}$. Therefore, in both cases $\lambda_i < S < 1$ and $0 < S < \lambda_1$,

$$\frac{f_i(S)}{P_1(S)} > \frac{f_i(S)}{P_1(\lambda_1)}.$$

Thus, using (29),

$$f_1(S)p_i(S) > c_i f_i(S)p_1(S) = c_i\frac{f_i(S)}{P_1(S)}(1-S) > c_i\frac{f_i(S)}{P_1(\lambda_1)}(1-S).$$

Thus, (16) holds for $\alpha_i = \frac{c_i}{P_1(\lambda_1)}$. Hence, (28) and (29) imply (16). □

Theorem 2 recovers the classical case Monod case [37]. Indeed, consider the particular case of (2), when the growth functions $q_i(S)$ are given by (11). System (2), with $D = 1$ and $S_{in} = 1$, takes the form

$$\begin{aligned} S' &= 1 - S - \sum_{j=1}^{n} \frac{a_j S}{b_j + S}\frac{x_j}{Y_j}, \\ x_i' &= \left[\frac{a_i S}{b_i + S} - D_i\right] x_i, \qquad\qquad i = 1\cdots n. \end{aligned} \tag{30}$$

We consider the case where, for all $i = 1\cdots n$, $a_i > D_i$. The break-even concentrations are

$$\lambda_i = \frac{b_i D_i}{a_i - D_i}. \tag{31}$$

Corollary 2 (Theorem 3.3 in [37])**.** *Assume that*

$$\lambda_1 < \lambda_2 \leq \cdots \leq \lambda_n, \qquad \lambda_1 < 1. \tag{32}$$

Then the equilibrium E_1^* *is GAS for* (30) *with respect to the interior of the positive cone.*

Proof. Assume that (32) holds. Let us prove that (27), (28) and (29) hold. Since $f_1(S) = q_1(S) - D_1$ is increasing, the function $f_1(S)$ changes sign only at $S = \lambda_1$ and hence, (27) is satisfied. Since

$$P_1(S) = Y_1(1-S)\frac{b_1 + S}{a_1 S} \qquad \text{and} \qquad P_1'(S) = -Y_1\frac{S^2 + b_1}{a_1 S^2} < 0,$$

the function $P_1(S)$ changes sign only at $S = \lambda_1$ and hence (28) is satisfied. Condition (29) is

$$\frac{(a_1 - D_1)S - b_1 D_1}{b_1 + S}\frac{1}{Y_i}\frac{a_i S}{b_i + S} > c_i\frac{(a_i - D_i)S - b_i D_i}{b_i + S}\frac{1}{Y_1}\frac{a_1 S}{b_1 + S}, \qquad i \geq 2.$$

After simplification by $\frac{S}{(b_1+S)(b_i+S)}$, this condition is equivalent to

$$(a_1 - D_1)\frac{a_i}{Y_i}(S - \lambda_1) > c_i(a_i - D_i)\frac{a_1}{Y_1}(S - \lambda_i) \qquad i \geq 2, \tag{33}$$

which is satisfied for $c_i = \frac{(a_1 - D_1)a_i Y_1}{(a_i - D_i)a_1 Y_i}$. Indeed, for this choice of the constants c_i, (33) is simply

$$S - \lambda_1 > S - \lambda_i \Longleftrightarrow \lambda_1 < \lambda_i, \qquad i \geq 2,$$

which is the same as (32). Thus (29) is satisfied. The global asymptotic stability of E_1^* follows from Theorem 2. □

2.3 Monod growth functions and linear yields

Models with linear yields were biologically motivated by [2, 13, 14] who noticed the existence of limit cycles for some values of the parameters. The rigorous mathematical study was given in [58]. Consider the particular case of (2), where the growth functions $q_i(S)$ are given by (11), and the yields $y_i(S) = q_i(S)/p_i(S)$ are linear

$$y_i(S) = Y_i(1 + c_i S)$$

where $Y_i > 0$ and $c_i \geq 0$. System (2), with $D = 1$ and $S_{in} = 1$, takes the form

$$\begin{aligned} S' &= 1 - S - \sum_{j=1}^{n} \frac{a_j S}{b_j + S} \frac{x_j}{Y_j(1 + c_j S)}, \\ x_i' &= \left[\frac{a_i S}{b_i + S} - D_i\right] x_i, \qquad\qquad i = 1 \cdots n. \end{aligned} \tag{34}$$

The break-even concentrations λ_i are given by (31). In this section we give analytical conditions on the parameters of (34) so that conditions (14), (15) and (16) are satisfied and Theorem 1 can be applied.

We need the following technical result.

Lemma 7. *The function* $Q(S) = \frac{(1-S)(b+S)(1+cS)}{S}$ *is decreasing over* $[0, 1]$ *if and only if*

$$[c(1 - b) - 1]^3 \leq 27bc^2.$$

This condition is equivalent to either $b \geq 1$ *or* $b < 1$ *and* $c \leq c_{crit}(b)$*, where* $c_{crit}(b)$ *is the positive zero of* $[c(1 - b) - 1]^3 = 27bc^2$*.*

Proof. Since

$$Q'(S) = -\frac{2cS^3 + (1 + c(b - 1))\, S^2 + b}{S^2}, \quad Q''(S) = -\frac{2\left(b - cS^3\right)}{S^2},$$

the function $Q(S)$ has an inflexion point for $S = (b/c)^{\frac{1}{3}}$. The function $Q(S)$ is nonincreasing over $[0, 1]$ if and only if its derivative at the inflexion point is nonpositive, that is, $P'\left((b/c)^{\frac{1}{3}}\right) \leq 0$. Straightforward computations show that this condition is equivalent to $[c(1 - b) - 1]^3 \leq 27bc^2$. If $b \geq 1$ then the first term of the inequality is negative and hence the inequality if satisfied for all $c \geq 0$. If $b < 1$, then the inequality is satisfied if and only if $c \leq c_{crit}(b)$. □

The expression of $c_{crit}(b)$ can be obtained by Cardan formulas. Notice that $c_{crit}(0) = 1$ and $c_{crit}(b)$ is increasing with b.

Theorem 3. *Assume that*

$$\lambda_1 < \lambda_2 \leq \cdots \leq \lambda_n, \qquad \lambda_1 < 1, \tag{35}$$

$$\text{either } b_1 \geq 1 \text{ or for each } i \geq 1 \text{ satisfying } \lambda_i < 1,\ c_i \leq c_{crit}(b_1). \tag{36}$$

Then the equilibrium E_1^* *is GAS for (34) with respect to the interior of the positive cone.*

Proof. Let us prove that (14), (15) and (24) hold. The Monod function $f_1(S)$ is increasing. Hence, (14) holds. The function $P_1(S)$ is

$$P_1(S) = \frac{(1 - S)(b_1 + S)(1 + c_1 S)}{S}.$$

By Lemma 7, it is decreasing if and only if either $b_1 \geq 1$ or $b_1 < 1$ and $c_1 \leq c_{crit}(b_1)$. Hence, (15) holds. For each $i \geq 2$, the function $g_i(S)$ defined by (23) is

$$g_i(S) = \frac{f_i(S)}{f_1(S)} \frac{1 - S}{p_i(S)} = \frac{Y_i}{a_i} \frac{a_i - D_i}{a_1 - D_1} \frac{S - \lambda_i}{S - \lambda_1} Q_i(S)$$

where $Q_i(S) = \frac{(1-S)(b_1+S)(1+c_i S)}{S}$. Assume that (36) holds. By Lemma 7, the function $Q_i(S)$ is decreasing. Therefore,

$$\min_{0<S\leq\lambda_1} Q_i(S) = Q_i(\lambda_1) > Q_i(\lambda_i) = \max_{\lambda_i \leq S < 1} Q_i(S).$$

Since $\lambda_1 < \lambda_i$, the function $S \mapsto \frac{S-\lambda_i}{S-\lambda_1}$ is increasing. Therefore,

$$\min_{0<S\leq\lambda_1} \frac{S-\lambda_i}{S-\lambda_1} = \frac{\lambda_i}{\lambda_1} > 1 > \frac{1-\lambda_i}{1-\lambda_1} = \max_{\lambda_i\leq S<1} \frac{S-\lambda_i}{S-\lambda_1}.$$

Thus,

$$\min_{0<S<\lambda_1} g_i(S) \geq \frac{Y_i}{a_i}\frac{a_i-D_i}{a_1-D_1} \min_{0<S<\lambda_1} \frac{S-\lambda_i}{S-\lambda_1} \min_{0<S<\lambda_1} Q_i(S) > \frac{Y_i}{a_i}\frac{a_i-D_i}{a_1-D_1}Q_i(\lambda_1),$$

and

$$\max_{\lambda_i<S<1} g_i(S) \leq \frac{Y_i}{a_i}\frac{a_i-D_i}{a_1-D_1} \max_{\lambda_i<S<1} \frac{S-\lambda_i}{S-\lambda_1} \max_{\lambda_i<S<1} Q_i(S) < \frac{Y_i}{a_i}\frac{a_i-D_i}{a_1-D_1}Q(\lambda_i).$$

Hence (24) holds. The result follows from Theorem 1. □

Theorem 3 extends Corollary 2 which corresponds to the case where the yields are constant. Indeed, (35) is the same as (32) and, for constant yields, $c_i = 0$, so that the conditions (36) in Theorem 3 are satisfied. Notice that (36) is a sufficient and not necessary condition for the existence of a gap between the minimum of $g_i(S)$ over $(0, \lambda_1)$ and its maximum over $[\lambda_i, 1]$.

3 Flocculation

Flocculation is a physical and chemical process in which the isolated or planktonic bacteria naturally aggregate, reversibly, to one another to form macroscopic flocs. This mechanism of attachment could be to a wall like biofilms [12, 44] or simply a formation of flocs or aggregates [72]. Jones et al. [46] studied the Freter model of biofilm formation (that represents the functioning of intestine) where the parameter values used for the simulations have been chosen from the experimental data of Freter et al. [27, 28].

In this section, we consider a flocculation mechanism and show how it can lead also to oscillations and non intuitive phenomena of the dynamics. In [30], the effect of flocculation on the growth dynamics was analyzed with an arbitrary number of bacteria in flocs. Haegeman and Rapaport [31] proposed a competition model of two microbial species on a single nutrient with monotonic increasing uptake functions, where attached bacteria or flocs of bacteria do not grow and are subject to the same dilution rate than isolated biomass. Assuming that the most competitive species inhibits its growth by the formation of flocs, they could explain the coexistence between two species. An extension of this model was studied in [24] without neglecting the substrate consumption of attached bacteria, but assuming that they consume less substrate than the isolated bacteria, since the bacteria at the surface of flocs have easier access to the substrate than the bacteria inside the flocs. More recently, Fekih-Salem et al. [19] proposed a model of flocculation of n species that generalizes several models [70, 57, 46] that have been considered in the literature. Assuming that the flocculation and deflocculation dynamics are fast compared to the growth dynamics, Haegeman and Rapaport [31] could build a density-dependent model with the same dilution rate that is studied in [51, 54]. Moreover, the study of a flocculation model [19] with different dilution rates leads also to density-dependent dilution rates for the overall biomass [19], which is a new feature. In [21], the flocculation model proposed in [31] is revisited by considering a substrate inhibition on the growth of the planktonic bacteria.

In order to generalize the flocculation modelling in the literature, we consider the following flocculation model where the three first equations have been introduced in [19]:

$$\left\{\begin{array}{lcl} \dot{S} & = & D(S_{in}-S) - f(S)u - g(S)v - f_2(S)x_2 \\ \dot{u} & = & (f(S)-D_0)u - \alpha(\cdot)u + \beta(\cdot)v \\ \dot{v} & = & (g(S)-D_1)v + \alpha(\cdot)u - \beta(\cdot)v \\ \dot{x}_2 & = & (f_2(S)-D_2)x_2 \end{array}\right. \tag{37}$$

where $u(t)$ and $v(t)$ denote, respectively, the concentrations of isolated and attached bacteria of the first species at time t; $f(\cdot)$ and $g(\cdot)$ represent, respectively, the per-capita growth rates of the isolated and attached bacteria; D_0, D_1 and D_2 represent, respectively, the removal rates of isolated and attached bacteria of the first species, and of the second species; $\alpha(\cdot)u$ and $\beta(\cdot)v$, denote, respectively, the flocculation and deflocculation rates.

Table 1 summarizes the modelling assumptions and describes the flocculation and deflocculation rates used in the literature.

Modelling assumptions	Flocculation and deflocculation rates	References
$D_i = D,\ i = 0,1,\ x_2 = 0$	$\alpha(\cdot) = a(1-W)$, $\beta(\cdot) = b + g(S)(1 - G(W))$	Jones et al. [46]
$D_i = D,\ i = 0,1,\ x_2 = 0$	$\alpha(\cdot) = \alpha(S),\ \ \beta(\cdot) = \beta(S)$	Tang et al. [70]
$D_0 \neq D,\ D_1 = 0,\ x_2 = 0$	$\alpha(\cdot) = a,\ \ \beta(\cdot) = b$	Pilyugin and Waltman [57]
$D_i = D,\ i = 0,1,2,\ g(S) = 0$	$\alpha(\cdot) = au,\ \ \beta(\cdot) = b$	Haegeman and Rapaport [31]
$D_i = D,\ i = 0,1,2$	$\alpha(\cdot) = au,\ \ \beta(\cdot) = b$	Fekih-Salem et al. [24]
$D_i \neq D,\ i = 0,1,\ x_2 = 0$	$\alpha(\cdot) = \alpha(S,v,u)$, $\beta(\cdot) = \beta(S,u,v)$	Fekih-Salem et al. [19]
$D_i = D,\ i = 0,1,\ f$ non monotone	$\alpha(\cdot) = au,\ \ \beta(\cdot) = b$	Fekih-Salem et al. [21]

Table 1: Modelling assumptions and the description of flocculation and deflocculation rates. All growth rates are monotonic increasing except in the last line where a substrate inhibition on the growth of the planktonic bacteria is taken into consideration (f non monotone). Note that $W = v/v_{\max}$ where $v_{\max}$ denotes the maximum areal biomass density of adherent bacteria and $G(\cdot)$ is a decreasing function. The terms a and b are positive constants.

3.1 Fast attachment and detachment dynamics

Literature reports flocculation time scales of the order of 1 to 10 min [16, 74] to be compared with bacterial growth times of 1 h to 1 day, and with retention times of a few hours to a few days. Thus, considering that attachment and detachment processes may be fast compared to biological time, it is shown in [31] that the reduced dynamics of such systems amounts to have a single biomass compartment for each strain but with a density dependent growth rate. This justifies the consideration of density dependent growth functions in the chemostat model, as already introduced in the literature in the field of mathematical ecology [3] or waste-water process engineering [34]. In can be shown [19] that when attachment and detachment rates are fast one can build a reduced model without distinction between isolated and attached bacteria, but the resulting growth rate is density-dependent as well as the dilution rate, due to the fact that attached and isolated bacteria have different removal rates. In the present section we consider this reduction.

The general model for the flocculation is

$$\left\{\begin{array}{lcl} \dot{S} & = & D(S_{in} - S) - f(S)u - g(S)v \\ \dot{u} & = & (f(S) - D_0)u - A(S,v,u)u + B(S,u,v)v \\ \dot{v} & = & (g(S) - D_1)v + A(S,v,u)u - B(S,u,v)v \end{array}\right. .$$

If we assume that the dynamics of attachment and detachment is much faster than the growth of the species, one can write

$$A(S,x,\varepsilon) = \frac{\alpha(S,u,v)}{\varepsilon}, \qquad B(S,x,\varepsilon) = \frac{\beta(S,u,v)}{\varepsilon}$$

where ε is expected to be a small non-negative number. The model becomes

$$\left\{\begin{array}{lcl} \dot{S} & = & D(S_{in} - S) - f(S)u - g(S)v \\ \dot{u} & = & (f(S) - D_0)u - \dfrac{\alpha(S,u,v)}{\varepsilon}u + \dfrac{\beta(S,u,v)}{\varepsilon}v \\ \dot{v} & = & (g(S) - D_1)v + \dfrac{\alpha(S,u,v)}{\varepsilon}u - \dfrac{\beta(S,u,v)}{\varepsilon}v \end{array}\right. \tag{38}$$

Notice that the dynamics of the total biomass $x = u + v$ is given by the equation

$$\dot{x} = (f(S) - D_0)u + (g(S) - D_1)v.$$

Thus, u and v are fast variables, while S and x are slow ones. In the variables (S,x,p), where $p = u/x$ is the proportion of u in x, since $u = px$ and $v = (1-p)x$, (38) is written

$$\left\{\begin{array}{lcl} \dot{S} & = & D(S_{in} - S) - f(S)px - g(S)(1-p)x \\ \dot{x} & = & (f(S) - D_0)px + (g(S) - D_1)(1-p)x \\ \dot{p} & = & p(1-p)\left[(f(S) - D_0) - (g(S) - D_1)\right] - \dfrac{\alpha(S,px,(1-p)x)}{\varepsilon}p + \dfrac{\beta(S,px,(1-p)x)}{\varepsilon}(1-p) \end{array}\right. \tag{39}$$

At time scale $\tau = t/\varepsilon$ we have:

$$\left\{\begin{array}{lcl} S' &=& \varepsilon\left(D(S_{in}-S)-f(S)px-g(S)(1-p)x\right) \\ x' &=& \varepsilon\left((f(S)-D_0)px+(g(S)-D_1)(1-p)x)\right) \\ p' &=& \varepsilon p(1-p)\left[(f(S)-D_0)-(g(S)-D_1)\right]-\alpha(S,px,(1-p)x)p+\beta(S,px,(1-p)x)(1-p) \end{array}\right. \tag{40}$$

where the prime denotes the derivative with respect to τ :

$$S' = \varepsilon\dot{S}, \qquad x' = \varepsilon\dot{x}, \qquad p' = \varepsilon\dot{p}$$

Therefore, the fast equation, obtained by letting $\varepsilon = 0$ is

$$p' = -\alpha(S,px,(1-p)x)p + \beta(S,px,(1-p)x)(1-p)$$

where S and x are considered as constant parameters ($S' = 0$, $x' = 0$). This equation can be written

$$p' = F(S,x,p) \tag{41}$$

where

$$F(S,x,p) = \beta(S,px,(1-p)x) - \left(\alpha(S,px,(1-p)x)+\beta(S,px,(1-p)x)\right)p$$

The slow manifold which is the set of steady states of the fast equation is given by equatuion

$$F(S,x,p) = 0 \tag{42}$$

We have the following result

Proposition 2. *Assume that for all $S \geq 0$, $u \geq 0$ and $p \in [0,1]$ we have*

$$\frac{\partial F}{\partial p} < 0 \tag{43}$$

Then there exists a function

$$(S \geq 0, x \geq 0) \mapsto p(S,x) \in (0,1]$$

such that

$$p(S,0) = \frac{\beta(S,0,0)}{\alpha(S,0,0)+\beta(S,0,0)}$$

and $p = p(S,x)$ is a steady state of (41), that is to say

$$F(S,x,p(S,x)) = 0 \text{ for all } S \geq 0 \text{ and } x \geq 0. \tag{44}$$

Moreover $p = p(S,x)$ is a locally exponentially stable steady state of (41). This steady state is globally attractive.

Proof. Let $S \geq 0$ and $x \geq 0$ be fixed. Using (43) we see that the function

$$p \in [0,1] \mapsto F(S,x,p) \in \mathbb{R}$$

is decreasing. We have

$$F(S,x,0) = \beta(S,0,x) > 0, \qquad F(S,x,1) = -\alpha(S,x,0) \leq 0$$

Therefore, by the intermediate value theorem, for all $S \geq 0$ and $x \geq 0$, there exists a unique $p \in (0,1]$, denoted by $p = p(S,x)$, such that

$$F(S,x,p(S,x)) = 0, \text{ for all } S \geq 0 \text{ and } x \geq 0$$

Hence (44) holds. If $x = 0$ then

$$G(S,0,p(S,0)) = \beta(S,0,0) - \left(\alpha(S,0,0)+\beta(S,0,0)\right)p(S,0) = 0$$

Hence

$$p(S,0) = \frac{\beta(S,0,0)}{\alpha(S,0,0)+\beta(S,0,0)}$$

Since

$$\frac{\partial F}{\partial p} < 0, \text{ for all } S \geq 0 \text{ and } x \geq 0$$

$p = p(S,x)$ is a locally exponentially stable steady state of (41). Since $p = p(S,x)$ is the unique steady state the attractivity is global. □

Using the Tikhonov theory we can consider the reduced model, obtained by replacing in the equations of S and x the fast variable p by $p = p(S,x)$. This reduced system is

$$\left\{ \begin{array}{l} \dot{S} = D(S_{in} - S) - \mu(S,x)x \\ \dot{x} = (\mu(S,x) - d(S,x))\,x \end{array} \right. \tag{45}$$

where

$$\mu(S,x) = p(S,x)f(S) + (1 - p(S,x))g(S),$$
$$d(S,x) = p(S,x)D_0 + (1 - p(S,x))D_1.$$

As a consequence of the Tikhonov's theorem [55, 73, 75] we have the following result

Theorem 4. *Let* $(S(t,\varepsilon), u(t,\varepsilon), v(t,\varepsilon))$ *be the solution of (38) with initial condition* (S_0, u_0, v_0) *satisfying* $S_0 \geq 0$, $u_0 \geq 0$, *and* $v_0 \geq 0$. *Let* $(\overline{S}(t), \overline{x}(t))$ *be the solution of the reduced problem (45) with initial conditions*

$$\overline{S}(0) = S_0, \quad \overline{x}(t) = u_0 + v_0.$$

Then as $\varepsilon \to 0$,

$$S(t,\varepsilon) = \overline{S}(t) + o(1), \qquad x(t,\varepsilon) = \overline{x}(t) + o(1) \tag{46}$$

uniformly for $t \in [0,T]$, *and*

$$u(t,\varepsilon) = \overline{x}(t)p\left(\overline{S}(t),\overline{x}(t)\right) + o(1), \qquad v(t,\varepsilon) = \overline{x}(t)\left(1 - p\left(\overline{S}(t),\overline{x}(t)\right)\right) + o(1) \tag{47}$$

uniformly for $t \in [t_0, T]$, *where* $0 < t_0 < T$ *are arbitrary but fixed and independent of* ε. *If the solution* $(\overline{S}(t),\overline{x}(t))$ *of the reduced problem converges to an asymptotically stable equilibrium, then we can put* $T = +\infty$ *in the the approximations (46) and (47) given.*

Remark 1. Notice that

$$\frac{\partial F}{\partial p} = \left(\frac{\partial \beta}{\partial u} - \frac{\partial \beta}{\partial v}\right) x(1-p) - \left(\frac{\partial \alpha}{\partial u} - \frac{\partial \alpha}{\partial v}\right) xp - (\alpha(S, xp, x(1-p)) + \beta(S, xp, x(1-p)))$$

If $\alpha \geq 0$ and $\beta > 0$, then a sufficient condition for (43) to hold is

$$\frac{\partial \beta}{\partial u} \leq \frac{\partial \beta}{\partial v}, \text{ and } \frac{\partial \alpha}{\partial u} \geq \frac{\partial \alpha}{\partial v} \tag{48}$$

In the following cases considered in the literature,

$$\alpha(S,u,v) = \alpha(S), \qquad \beta(S,u,v) = \beta(S)$$
$$\alpha(S,u,v) = a, \qquad \beta(S,u,v) = b$$
$$\alpha(S,u,v) = au, \qquad \beta(S,u,v) = b$$
$$\alpha(S,u,v) = a(u+v), \qquad \beta(S,u,v) = b$$

the conditions (48) are satisfied.

3.2 Flocculation with several species

We assume that n species are competing on a same limiting resource, and that each species is present in two forms: isolated bacteria, of density u_i, and bacteria in flocks, of density v_i, for $i = 1 \cdots n$. We assume that isolated bacteria can stick with isolated bacteria with flocks to form new flocks, with rate $\alpha_i(\cdot)u_i$. We assume also that flocks can split and liberate isolated bacteria with rate $\beta_i(\cdot)v_i$.

$$u_i \xrightarrow{\alpha_i(\cdot)u_i} v_i, \qquad u_i \xleftarrow{\beta_i(\cdot)v_i} v_i\ .$$

Then the equations are

$$\left\{ \begin{array}{l} \dot{S} = D(S_{in} - S) - \displaystyle\sum_{i=1}^{n}(f_i(S)u_i + g_i(S)v_i) \\ \dot{u}_i = (f_i(S) - D_{0i})u_i - \alpha_i(\cdot)u_i + \beta_i(\cdot)v_i, \quad 1 \leqslant i \leqslant n \\ \dot{v}_i = (g_i(S) - D_{1i})v_i + \alpha_i(\cdot)u_i - \beta_i(\cdot)v_i \end{array} \right. \tag{49}$$

The dynamics of the total biomass densities $x_i = u_i + v_i$ of the species i is

$$\dot{x_i} = f_i(S)u_i + g_i(S)v_i - D_{0i}u_i - D_{1i}v_i \ .$$

We consider here the case where

$$\alpha_i(\cdot) = \sum_{j=1}^{n} A_{ij}x_j, \qquad \beta_i(\cdot) = B_i$$

where A_{ij} and B_i are non-negative constants.

Remark 2. By letting the functions $\alpha_i(\cdot)$ depending on x_j with $j \neq i$, we implicitly consider that flocks or aggregates can incorporate individuals of different species.
The removal rate D_{1i} has to be interpreted as the sum of the removal rate of the aggregates and the mortality rate of each species i in its attached form.

Moreover, we assume that the dynamics of flocculation and detachment are fast compared with the dynamics of the growth of bacteria, that is

$$A_{ij} = \frac{a_{ij}}{\varepsilon}, \quad B_i = \frac{b_i}{\varepsilon} \ .$$

In the variables S, x_i, u_i, the system is written

$$\left\{\begin{array}{rcl} \dot{S} & = & D(S_{in} - S) - \displaystyle\sum_{i=1}^{n}[f_i(S)u_i + g_i(S)(x_i - u_i)] \\ \dot{x_i} & = & f_i(S)u_i + g_i(S)(x_i - u_i) - D_{0i}u_i - D_{1i}(x_i - u_i), \quad i = 1 \cdots n \\ \dot{u}_i & = & (f_i(S) - D_{0i})u_i - \dfrac{1}{\varepsilon}\displaystyle\sum_{j=1}^{n} a_{ij}x_ju_i + \dfrac{b_i}{\varepsilon}(x_i - u_i) \end{array}\right. \tag{50}$$

This is a slow/fast system with the variables S, x_i are slow and the variables u_i fast. The fast equations are

$$u_i' = -\sum_{j=1}^{n} a_{ij}x_ju_i + b_i(x_i - u_i), \quad i = 1 \cdots n \tag{51}$$

where x_i are considered as parameters. The slow manifold (or quasi steady-state) is given by

$$u_i = \frac{b_ix_i}{b_i + \displaystyle\sum_{j=1}^{n} a_{ij}x_j}, \quad i = 1 \cdots n \ . \tag{52}$$

Since one has $\sum_{j=1}^{n} a_{ij}x_j > 0$, for $i = 1 \cdots n$, this slow manifold is globally asymptotically stable for (51). Thus, the Tikhonov's Theorem [55, 73, 75] applies and asserts that, after a fast transition toward the slow manifold, the solutions are approximated by a solution of the reduced equation, which is obtained by replacing the fast variables u_i in (50) by the quasi steady states (52). One obtains the following reduced model

$$\left\{\begin{array}{l} \dot{S} = D(S_{in} - S) - \displaystyle\sum_{i=1}^{n} \mu_i(S, x)x_i \\ \dot{x}_i = (\mu_i(S, x) - d_i(x))\, x_i, \quad i = 1 \cdots n \end{array}\right. \tag{53}$$

where

$$\mu_i(S, x) = f_i(S)p_i(x) + g_i(S)(1 - p_i(x)), \quad d_i(x) = D_{0i}p_i(x) + D_{1i}(1 - p_i(x)), \qquad i = 1, \cdots, n \tag{54}$$

with

$$p_i(x) = \frac{b_i}{b_i + \displaystyle\sum_{j=1}^{n} a_{ij}x_j}, \qquad x = (x_1, \cdots, x_n). \tag{55}$$

Hence, we have shown the following result

Theorem 5. *Let $(S(t,\varepsilon), u_1(t,\varepsilon), v_1(t,\varepsilon), \cdots, u_n(t,\varepsilon), v_n(t,\varepsilon))$ be the solution of (49) with initial conditions $S(0) \geqslant 0$ and $u_i(0) > 0$, $v_i(0) \geqslant 0$, for $1 \leqslant i \leqslant n$. Let $\left(\overline{S}(t), \overline{x}_1(t), \cdots, \overline{x}_n(t)\right)$ be the solution of the reduced problem (53) with initial conditions*

$$\overline{S}(0) = S(0), \qquad \overline{x}_i(t) = u_i(0) + v_i(0), \quad 1 \leqslant i \leqslant n.$$

Then as $\varepsilon \to 0$

$$S(t,\varepsilon) = \overline{S}(t) + o(1), \qquad x_i(t,\varepsilon) = \overline{x}_i(t) + o(1), \quad 1 \leqslant i \leqslant n$$

uniformly for $t \in [0,T]$, and for all $1 \leqslant i \leqslant n$, as $\varepsilon \to 0$

$$u_i(t,\varepsilon) = \frac{b_i \overline{x}_i(t)}{b_i + \sum_{j=1}^n a_{ij}\overline{x}_j(t)} + o(1), \quad v_i(t,\varepsilon) = \frac{\left(\sum_{j=1}^n a_{ij}\overline{x}_j(t)\right)\overline{x}_i(t)}{b_i + \sum_{j=1}^n a_{ij}\overline{x}_j(t)} + o(1)$$

uniformly for $t \in [t_0, T]$, where $T > t_0 > 0$ are arbitrarily fixed. If the solution of the reduced problem tends to an asymptotically stable equilibrium, then we can put $T = +\infty$ in the approximations given above.

Since the planktonic bacteria have a better access to the substrate than the bacteria in flocks one assumes $f_i(S) > g_i(S)$. Notice that one has $\frac{\partial p_i}{\partial x_j} < 0$ for any i, j. Hence

$$\frac{\partial \mu_i}{\partial x_j} = (f_i(S) - g_i(S))\frac{\partial p_i}{\partial x_j} < 0$$

with

$$\frac{\partial \mu_i}{\partial S} = f_i'(S)p_i(x) + g_i'(S)(1 - p_i(x)) > 0\ .$$

As for the one species case this approach give a motivation to density dependent growth function models, that may lead to species coexistence, as discussed in the following section.

4 Density-dependent growth functions

In this section, we will consider models with density-dependent growth functions. The general model is the following extension of (2)

$$\left\{\begin{array}{rcll} \dot{S} & = & D(S_{in} - S) - \sum_{i=1}^n \mu_i(S, x_1, \ldots, x_n)x_i & \\ \dot{x}_i & = & [\mu_i(S, x_1, \ldots, x_n) - D_i]\, x_i, & i = 1, \ldots, n \end{array}\right. \tag{56}$$

where the growth function $\mu_i(S, x_1, \ldots, x_n)$ can depend now not only on the substrate S but also on the species concentrations x_i, $i = 1, \ldots, n$. The function μ_i is assumed to be increasing in the variable S and decreasing in each variable x_j. This model was considered in a series of paper by Lobry et al. [20, 51, 52, 53, 54, 35]. Now, for (56) it is possible to have a coexistence steady state since at steady state we must have

$$[\mu_i(S, x_1, \ldots, x_n) - D_i]\, x_i = 0, \qquad i = 1, \ldots, n.$$

If all x_i are positive then

$$\mu_i(S, x_1, \ldots, x_n) = D_i, \qquad i = 1, \ldots, n$$

is a set of n equations with n variables x_i which could have a positive solution $x_i = X_i(S)$, $i = 1, \ldots, n$. Replacing x_i by $X_i(S)$ in the first equation leads the following equation in the single variable S

$$D(S_{in} - S) - \sum_{i=1}^n D_i X_i(S) = 0.$$

Solving this equation gives S and then the possibility of a positive steady state.

4.1 No interspecific competition : the steady-state characteristic

In [54] the authors considered the case where $\mu_i(S,x_i)$ depends only on the concentration of species i. They introduced the concept of *steady-state characteristic* for each species and showed how to use it to give sufficient conditions for coexistence and to determine the asymptotic behavior of the system. Global results were also obtained when $D_i = D$ for all species [53]. In [19] it is shown that the method of steady-state characteristic is still applicable in the case where both the growth rate $\mu_i(S,x_i)$ and the removal rate $D_i = d_i(x_i)$ of each species depend on the density of the same species. In [1] it is shown that the method of steady-state characteristic permits a quite comprehensive analysis of the model considered in [47], where the growth rate $\mu_i(S)$ depends only on S but the removal rate of x_i is of the form $D_i + a_i x_i$. The term $a_i x_i$ corresponds to the so-called crowding effect.

We consider the model

$$\left\{\begin{array}{lcll} \dot{S} & = & D(S_{in}-S) - \displaystyle\sum_{i=1}^{n} \mu_i(S,x_i)x_i & \\ \dot{x}_i & = & [\mu_i(S,x_i) - d_i(x_i)]x_i & i = 1,\cdots,n \end{array}\right. \tag{57}$$

This model was studied in [51], in the case when $d_i(x_i) = D$. We assume that

H5: $\mu_i(0,x_i) = 0$ and $\mu_i(S,x_i) \geqslant 0$ for all $S > 0$ and all $x_i \geqslant 0$.

H6: $\dfrac{\partial \mu_i}{\partial S} > 0$ and $\dfrac{\partial \mu_i}{\partial x_i} < 0$ for all $S > 0$ and all $x_i \geqslant 0$.

H7: $d_i(0) = D_{0i}$, $d_i(+\infty) = D_{1i} < D_{0i} \leqslant D$, $d_i(x_i) > 0$, $d_i'(x_i) < 0$ and $[x_i d_i(x_i)]' > 0$ for all $x_i \geqslant 0$.

Let us denote by

$$f_i(S) = \mu_i(S,0) \quad \text{and} \quad g_i(S) = \mu_i(S,+\infty).$$

The functions $f_i(.)$ and $g_i(.)$ are increasing and positive for all $S > 0$. If equations $f_i(S) = D_{0i}$ and $g_i(S) = D_{1i}$ have solutions, one let

$$\lambda_{0i} = f_i^{-1}(D_{0i}) \quad \text{and} \quad \lambda_{1i} = g_i^{-1}(D_{1i})$$

otherwise one let $\lambda_{ki} = +\infty$, $k = 0,1$. As for the case of one species (see Assumption **H3**), we add the following assumption

H8: $\lambda_{0i} < \lambda_{1i}$ for $i = 1 \cdots n$. For all $S \in]\lambda_{0i}, \lambda_{1i}[$ and $x_i \geqslant 0$, one has $d_i'(x_i) > \frac{\partial \mu_i}{\partial x_i}(S,x_i)$.

If the inequality $\lambda_{0i} < \lambda_{1i}$ is reversed for some $i = 1 \cdots n$, then the situation is much more difficult and will be studied in the future. Denote

$$\tilde{\lambda}_0 = \max\{\lambda_{0i}; \quad i = 1,\cdots,n\} \quad \text{and} \quad \tilde{\lambda}_1 = \min\{\lambda_{1i}; \quad i = 1,\cdots,n\}.$$

We assume that

H9: $\tilde{\lambda}_0 < \min(\tilde{\lambda}_1, S_{in})$.

We consider here the existence of a positive equilibrium. The equilibria of (57) are solutions of the set of equations

$$\left\{\begin{array}{l} D(S_{in}-S) = \displaystyle\sum_{i=1}^{n} \mu_i(S,x_i)x_i \\ \mu_i(S,x_i) = d_i(x_i) \quad \text{or} \quad x_i = 0 \qquad i = 1,\cdots,n. \end{array}\right. \tag{58}$$

Thus we have to solve the equations

$$\mu_i(S,x_i) = d_i(x_i).$$

Since **H6**, by the implicit function theorem, this equation gives a function $S = \phi_i(x_i)$ defined for all $x_i \geqslant 0$, such that $\phi_i(0) = \lambda_{0i}$, $\phi_i(+\infty) = \lambda_{1i}$ and

$$\phi_i'(x_i) = \frac{d_i'(x_i) - \dfrac{\partial \mu_i}{\partial x_i}(S,x_i)}{\dfrac{\partial \mu_i}{\partial S}(S,x_i)} > 0.$$

The sign of $\phi'(\cdot)$ is given by assumptions **H8**. We define the function $X_i : S \mapsto X_i(S)$ on $[0, \lambda_{1i}[$ by

$$\begin{array}{rcl} X_i : [0, \quad \lambda_{1i}[& \longrightarrow & \mathbb{R}_+ \\ S & \longrightarrow & X_i(S) = \begin{cases} 0 & \text{if} \quad 0 \leqslant S \leqslant \lambda_{0i} \\ x_i = \phi_i^{-1}(S) & \text{if} \quad \lambda_{0i} \leqslant S < \lambda_{1i}. \end{cases} \end{array}$$

Let $h_i(S) = \mu_i(S, X_i(S))X_i(S)$. Since $X_i(\cdot)$ is increasing over $[\lambda_{0i}, \lambda_{1i}[$, so is $h_i(\cdot)$ over this interval. Indeed, one has

$$h_i'(S) = \left(\frac{\partial \mu_i}{\partial S} + \frac{\partial \mu_i}{\partial x_i} X_i'(S) \right) X_i(S) + \mu_i\left(S, X_i(S)\right) X_i'(S).$$

Moreover, for $S \in]\lambda_{0i}, \lambda_{1i}[$, $\mu_i\left(S, X_i(S)\right) = d_i(X_i(S))$ and

$$X_i'(S) = \frac{\dfrac{\partial \mu_i}{\partial S}(S, X_i(S))}{d_i'(X_i(S)) - \dfrac{\partial \mu_i}{\partial x_i}(S, X_i(S))} > 0.$$

Then

$$h_i'(S) = \left[d_i'\left(X_i(S)\right) X_i(S) + d_i\left(X_i(S)\right)\right] X_i'(S), \quad \text{for} \quad S \in]\lambda_{0i}, \lambda_{1i}[.$$

Using **H7**,

$$[d_i(x_i)x_i]' = d_i'(x_i)x_i + d_i(x_i) > 0, \quad \text{for} \quad x_i \geqslant 0.$$

Hence the sign of $h_i'(S)$ is the same as the sign of $X_i'(S)$, that is, $h_i(\cdot)$ is increasing over $[\lambda_{0i}, \lambda_{1i}[$, (see Fig. 1).

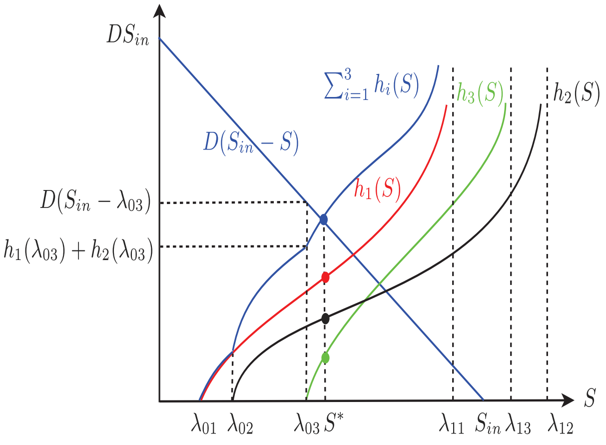

Figure 1: The steady state characteristics gives the necessary and sufficient condition of existence of the positive equilibrium of (57) for $n = 3$.

Consider now the function

$$H(S) = \sum_{i=1}^{n} h_i(S) - D(S_{in} - S).$$

Lemma 8. *Equation* $H(S) = 0$ *admits a unique solution* $S^* \in]0, \tilde{\lambda}_1[$.

Proof. Since $h_i(S) = 0$ for $S \in [0, \lambda_{0i}]$ and $h_i(S)$ is increasing over $[\lambda_{0i}, \lambda_{1i}[$, the function $H(\cdot)$ is increasing over $(0, \tilde{\lambda}_1)$, and

$$H(0) = -DS_{in} < 0 \quad \text{and} \quad \lim_{S \to \tilde{\lambda}_1} H(S) = +\infty.$$

Hence, there exists a unique $S^* \in]0, \tilde{\lambda}_1[$ such that $H(S^*) = 0$. ☐

We have the following result :

Proposition 3. *Assume that* **H5**-**H9** *hold. System (57) has a unique positive equilibrium if and only if*

$$\sum_{i=1}^{n} \mu_i\left(\tilde{\lambda}_0, X_i(\tilde{\lambda}_0)\right) X_i(\tilde{\lambda}_0) < D(S_{in} - \tilde{\lambda}_0). \tag{59}$$

Proof. A positive equilibrium $E^* = (S^*, x_1^*, \cdots, x_n^*)$, must satisfy

$$D(S_{in} - S^*) = \sum_{i=1}^{n} \mu_i(S^*, x_i^*) x_i^* \tag{60}$$

and

$$\mu_i(S^*, x_i^*) = d_i(x_i^*). \tag{61}$$

Equation (61) is equivalent to $x_i^* = X_i(S^*)$. Thus, (60) can be written

$$D(S_{in} - S^*) = \sum_{i=1}^{n} \mu_i(S^*, X_i(S^*)) X_i(S^*) = \sum_{i=1}^{n} h_i(S^*),$$

that is $H(S^*) = 0$. Since $\sum_{i=1}^{n} h_i(S^*) > 0$, then one must have

$$S^* < S_{in} \text{ and } S^* > \tilde{\lambda}_0.$$

Notice that $\tilde{\lambda}_0 < S^* < \tilde{\lambda}_1$ and $S^* < S_{in}$ are satisfied if **H9** holds. Then, since $H(S)$ est increasing over $[0, \tilde{\lambda}_1[$,

$$\tilde{\lambda}_0 < S^* \iff H(\tilde{\lambda}_0) < H(S^*) = 0.$$

Therefore there exists a unique positive equilibrium S^* exactly when $H(\tilde{\lambda}_0) < 0$, which is equivalent to (59). $\square$

We study now the asymptotic behavior of the positive equilibrium. First, we establish the following result :

Lemma 9. *Consider the matrix*

$$A = \begin{bmatrix} -D - \sum_{i=1}^{n} a_i & c_1 & c_2 & \cdots & c_n \\ a_1 & -b_1 & 0 & \cdots & 0 \\ a_2 & 0 & -b_2 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ a_n & 0 & 0 & \cdots & -b_n \end{bmatrix} \tag{62}$$

Assume that $D > 0$ and for $i = 1 \cdots n$, $a_i \geqslant 0$, $b_i > 0$ and $c_i \leqslant b_i$. Then all eigenvalues of A have negative real part.

The proof is given in [19].

Then, we state the following result :

Proposition 4. *If E^* exists, then it is locally exponentially stable.*

Proof. . Since $\mu_i(S^*, x_i^*) = d_i(x_i^*)$, the Jacobian of the system (57) at E^* is of the form (62) where

$$a_i = \frac{\partial \mu_i}{\partial S}(S^*, x_i^*) x_i^* \quad b_i = -\frac{\partial \mu_i}{\partial x_i}(S^*, x_i^*) x_i^* + x_i^* d_i'(x_i^*), \quad c_i = -\frac{\partial \mu_i}{\partial x_i}(S^*, x_i^*) x_i^* - d_i(x_i^*).$$

Since **H6**, $a_i > 0$. Since **H7**, $d_i(x_i^*) + x_i^* d_i'(x_i^*) > 0$, then $-d_i(x_i^*) < x_i^* d_i'(x_i^*)$ and hence $c_i < b_i$. Since **H8**, $b_i > 0$. The result follows from Lemma 9. $\square$

4.2 Intra and interspecific competition

General model (56) was considered in [51] only through numerical simulations. These authors considered a particular situation where the growth functions are of the form

$$\mu_i(S, x_1, \ldots, x_n) = \nu_i \left(S, x_i + \alpha \sum_{j \neq i} x_j \right) \tag{63}$$

where α is a nonnegative parameter which denotes the interspecific competition. They observed that the coexistence which was predicted in [54], when $\alpha = 0$ (only intraspecific competition is present), is still a property of the model when α is small enough but it is no longer the case when α is sufficiently large. The particular case of (56,63) where

$n = 2$ (two species) and $D_1 = D_2 = D$, has been studied theoretically in [18, 22]. In these works, the authors gave theoretical explanations for the phenomenon, which was numerically observed in [51], where the coexistence holds for α small enough while the exclusion of one species occurs for α large enough. Growth functions of form (63) and density dependent yields were considered also in [61].

Actually, we have not at our disposal any general mathematical study of (56). The paper [20] can be considered as the first step towards a mathematical study of (56). In this section we consider the two species model

$$\left\{\begin{array}{lcl} \dot{S} & = & D(S_{in} - S) - \mu_1(S, x_1, x_2)x_1 - \mu_2(S, x_2, x_1)x_2 \\ \dot{x}_1 & = & [\mu_1(S, x_1, x_2) - D_1]x_1 \\ \dot{x}_2 & = & [\mu_2(S, x_2, x_1) - D_2]x_2. \end{array}\right. \tag{64}$$

We make the following assumptions.

(H0) For $i = 1, 2$, $D_i = D + a_i$, where $a_i \geq 0$.

(H1) For $i = 1, 2$, $j = 1, 2$, $i \neq j$, $\mu_i(0, x_i, x_j) = 0$ and $\mu_i(S, x_i, x_j) > 0$ for all $S > 0$, $x_1 \geqslant 0$ and $x_2 \geqslant 0$.

(H2) For $i = 1, 2$, $j = 1, 2$, $i \neq j$, $\frac{\partial \mu_i}{\partial S}(S, x_i, x_j) > 0$, $\frac{\partial \mu_i}{\partial x_i}(S, x_i, x_j) \leqslant 0$ and $\frac{\partial \mu_i}{\partial x_j}(S, x_i, x_j) \leqslant 0$ for all $S > 0$, $x_1 \geqslant 0$ and $x_2 \geqslant 0$.

Condition (H0) means that the dilution rate of the species is the sum of the dilution rate of the chemostat and a specific mortality rate of the species. This condition will be used only in the stability analysis of positive steady states, see Proposition 9 below. Condition (H1) means that the growth can take place if and only if the substrate is present. Condition (H2) means that the growth rate of each species increases with the concentration of substrate and is inhibited by intra- and interspecific competition. We have the following result:

Proposition 5. *For any nonnegative initial condition, the solutions of (64) remain nonnegative and are positively bounded. Moreover, the set*

$$\Omega = \left\{(S, x_1, x_2) \in \mathbb{R}^3_+ : S + x_1 + x_2 \leqslant S_{in}\right\}$$

is positively invariant and is a global attractor for (64).

The proof is given in [20].

The steady states of (64) are the solutions of the set of equations

$$\left\{\begin{array}{lcl} 0 & = & D(S_{in} - S) - \mu_1(S, x_1, x_2)x_1 - \mu_2(S, x_2, x_1)x_2 \\ 0 & = & [\mu_1(S, x_1, x_2) - D_1]x_1 \\ 0 & = & [\mu_2(S, x_2, x_1) - D_2]x_2. \end{array}\right. \tag{65}$$

Therefore, (64) has the following types of steady states:

- $\mathcal{E}_0 = (S_{in}, 0, 0)$, called the washout, where both populations are extinct: $x_1 = x_2 = 0$. This steady state always exists.
- $\mathcal{E}_1 = (\tilde{S}_1, \tilde{x}_1, 0)$, where second population is extinct: $x_2 = 0$ and $\tilde{x}_1 > 0$.
- $\mathcal{E}_2 = (\tilde{S}_2, 0, \tilde{x}_2)$, where first population is extinct: $x_1 = 0$ and $\tilde{x}_2 > 0$.
- $\mathcal{E}^* = (S^*, x_1^*, x_2^*)$, where both populations survive: $x_1^* > 0$, $x_2^* > 0$.

The components $S = \tilde{S}_i$ and $x = \tilde{x}_i$ of a boundary steady state $\mathcal{E}_i$ are the solutions of (65) with $x_i > 0$ and $x_j = 0$, $j \neq i$. Therefore $\tilde{S}_i$ and $\tilde{x}_i$ are the solutions of equations Therefore

$$\tilde{S}_i = S_{in} - \frac{D_i}{D}\tilde{x}_i. \tag{66}$$

and $x_i = \tilde{x}_i$ must be a solution of

$$\mu_i\left(S_{in} - \frac{D_i}{D}x_i, x_i, 0\right) = D_i. \tag{67}$$

$\tilde{S}_i$ is positive if and only if $\tilde{x}_i < DS_{in}/D_i$, that is to say, (67) has a solution in the interval $(0, DS_{in}/D_i)$. From (H1) and (H2) we know that the function

$$x_i \mapsto \mu_i\left(S_{in} - \frac{D_i}{D}x_i, x_i, 0\right) - D_i, \qquad i = 1, 2.$$

is decreasing from $\mu_i(S_{in},0,0)-D_i$ for $x_i=0$, to $\psi_i(DS_{in}/D_i)=-D_i$ for $x_i=DS_{in}/D_i$. Thus, there exists an $x_i=\tilde{x}_i\in(0,DS_{in}/D_i)$ satisfying (67) if and only if

$$\mu_i(S_{in},0,0)>D_i \tag{68}$$

holds. If such an $\tilde{x}_i$ exists then it is unique. Therefore, we obtain the following result which gives the condition of existence of a boundary steady state $\mathcal{E}_i$.

Proposition 6. *Let $\mathcal{E}_i$ be a steady state of (64) with $\tilde{x}_i>0$ and $x_j=0$, $j\neq i$. Then $\tilde{S}_i$ is given by (66) where $x_i=\tilde{x}_i$ is the solution of (67). This steady state exists if and only if (68) holds. If it exists then it is unique.*

The components $S=S^*$, $x_1=x_1^*$ and $x_2=x_2^*$ of a coexistence steady state $\mathcal{E}^*$ must be the solutions of (65) with $x_1>0$ and $x_2>0$. Therefore S^* is given by

$$S^*=S_{in}-\frac{D_1}{D}x_1^*-\frac{D_2}{D}x_2^*. \tag{69}$$

and $(x_1=x_1^*,x_2=x_2^*)$ must be a solution of

$$\begin{cases} f_1(x_1,x_2)=0 \\ f_2(x_1,x_2)=0 \end{cases} \tag{70}$$

where

$$f_i(x_1,x_2):=\mu_i\left(S_{in}-\frac{D_1}{D}x_1-\frac{D_2}{D}x_2,x_i,x_j\right)-D_i, \quad \text{for} \quad i=1,2,\ j=1,2, \quad i\neq j. \tag{71}$$

The functions (71) are defined on the set

$$M=\left\{(x_1,x_2)\in\mathbb{R}_+^2:\frac{D_1}{D}x_1+\frac{D_2}{D}x_2\leqslant S_{in}\right\}. \tag{72}$$

S^* is positive if and only if $\frac{D_1}{D}x_1^*+\frac{D_2}{D}x_2^*<S_{in}$, that is to say, (70) has a solution in the interior M^o of M, defined by (72). To solve (70) in this open M^o, we need the following result:

Lemma 10. *Assume that (68) holds for $i=1,2$ and let $\tilde{x}_i$ be a solution of (67). The equation $f_i(x_1,x_2)=0$ defines a smooth decreasing function*

$$F_i:[0,\tilde{x}_i]\to\mathbb{R}, \quad x_i\mapsto F_i(x_i)$$

such that $F_i(\tilde{x}_i)=0$ and the graph γ_i of F_i lies in M^o. More precisely, $(x_1,F_1(x_1))\in M^o$ [resp. $(F_2(x_2),x_2)\in M^o$] for all $x_i\in(0,\tilde{x}_i)$.

The proof is given in [20].

Remark 3. Notice that $F_i:[0,\tilde{x}_i]\to[0,\bar{x}_j]$, $x_i\mapsto F_i(x_i)$, where $\bar{x}_j=F_i(0)$ is the unique solution of

$$\mu_i\left(S_{in}-\frac{D_j}{D}x_j,0,x_j\right)=D_i. \tag{73}$$

Using the definitions (71) of f_1 and f_2 one sees that $\tilde{x}_1$, $\tilde{x}_2$ which are the solutions of (67) and $\bar{x}_1$, $\bar{x}_2$ which are the solutions of (73) are simply the solutions of the following equations

$$f_1(\tilde{x}_1,0)=0, \quad f_2(0,\tilde{x}_2)=0, \quad f_1(0,\bar{x}_2)=0, \quad f_2(\bar{x}_1,0)=0.$$

These quantities represent the coordinates of the intersections of the curves γ_1 and γ_2 with the coordinates axes. Their relative positions play a major role in the behavior of the system.

The following four cases must be distinguished (see Figures 2 and 3):

$$\text{Case 1: } \bar{x}_1>\tilde{x}_1 \quad \text{and} \quad \bar{x}_2>\tilde{x}_2, \qquad \text{Case 2: } \bar{x}_1<\tilde{x}_1 \quad \text{and} \quad \bar{x}_2<\tilde{x}_2, \tag{74}$$

$$\text{Case 3: } \bar{x}_1<\tilde{x}_1 \quad \text{and} \quad \bar{x}_2>\tilde{x}_2, \qquad \text{Case 4: } \bar{x}_1>\tilde{x}_1 \quad \text{and} \quad \bar{x}_2<\tilde{x}_2. \tag{75}$$

We restrict our attention to the generic situation, where all intersections of curves γ_1 and γ_2 are transverse. We give the following definitions:

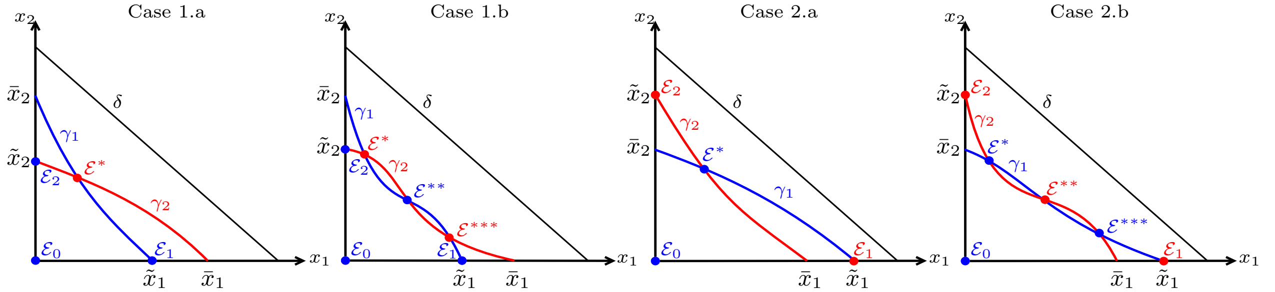
Case 1.a Case 1.b Case 2.a Case 2.b

Figure 2: Case 1 : $\bar{x}_1 > \tilde{x}_1$ and $\bar{x}_2 > \tilde{x}_2$: (a) unique intersection, (b) an odd number of intersections. Case 2 : $\bar{x}_1 < \tilde{x}_1$ and $\bar{x}_2 < \tilde{x}_2$: (a) unique intersection, (b) an odd number of intersections.

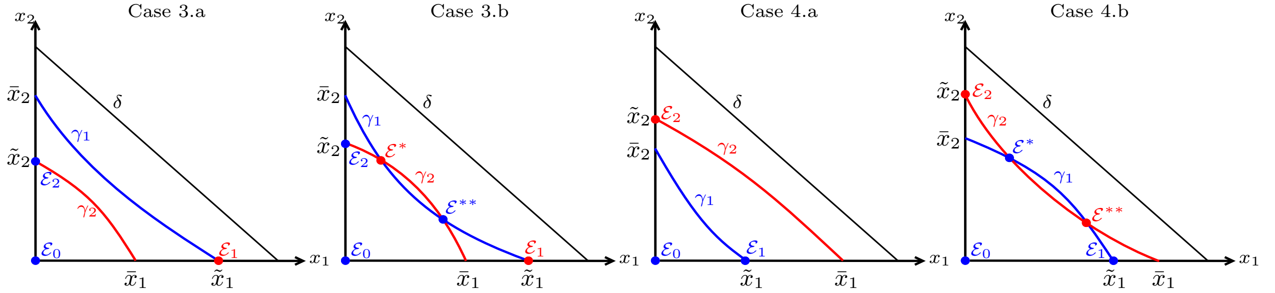
Case 3.a Case 3.b Case 4.a Case 4.b

Figure 3: Case 3 : $\bar{x}_1 < \tilde{x}_1$ and $\bar{x}_2 > \tilde{x}_2$: (a) no intersection, (b) an even number of intersections. Case 4 : $\bar{x}_1 > \tilde{x}_1$ and $\bar{x}_2 < \tilde{x}_2$: (a) no intersection, (b) an even number of intersections.

Definition 1. *A positive steady state $\mathcal{E}^* = (S^*, x_1^*, x_2^*)$ of (64) is said to be blue [resp. red] if and only if, on the right of (x_1^*, x_2^*), the tangent of γ_1 at point (x_1^*, x_2^*) is above [resp. under] the tangent of γ_2 at point (x_1^*, x_2^*).*

The positive steady states are alternatively red and blue and are represented in red and blue colors respectively in Figures 2 and 3. We have the following characterization of red and blue positive steady states.

Lemma 11. *A positive steady state $\mathcal{E}^* = (S^*, x_1^*, x_2^*)$ is blue if and only if $F_1'(x_1^*)\,F_2'(x_2^*) < 1$. It is red if and only if $F_1'(x_1^*)\,F_2'(x_2^*) > 1$.*

Proof. The curves γ_1 and γ_2 are the graphs of the functions $x_1 \mapsto F_1(x_1)$ and $x_1 \mapsto F_2^{-1}(x_1)$, respectively, where F_2^{-1} is the inverse function of F_2. Therefore, the positive steady state is blue if and only if $F_1'(x_1^*) > \left(F_2^{-1}\right)'(x_1^*) = \frac{1}{F_2'(x_2^*)}$. Since $F_2'(x_2^*) < 0$ this condition is equivalent to $F_1'(x_1^*)\,F_2'(x_2^*) < 1$. The same proof holds for red positive steady states. □

We have the following result:

Theorem 6. *Assume that (H0), (H1), (H2) and (68), for $i = 1, 2$ hold.*

1. *Blue positive steady states are unstable. If for all S, x_1, x_2,*

$$\frac{\partial \mu_1}{\partial x_1} < \frac{\partial \mu_1}{\partial x_2} \quad \text{and} \quad \frac{\partial \mu_2}{\partial x_2} < \frac{\partial \mu_2}{\partial x_1} \tag{76}$$

   hold, or $D_1 = D_2 = D$, then red positive steady states are LES, that is to say, positive steady states are alternatively unstable and LES.

2. *If Case 1 holds, the system can have generically an odd number of positive steady states, while $\mathcal{E}_1$ and $\mathcal{E}_2$ are unstable. The positive steady states at the left-hand end and right-hand end are red (see Figure 2, Case 1). If, in addition, for all S, x_1, x_2,*

$$\frac{\partial \mu_1}{\partial x_1} < \frac{D_1}{D_2}\frac{\partial \mu_1}{\partial x_2} \quad \text{and} \quad \frac{\partial \mu_2}{\partial x_2} < \frac{D_2}{D_1}\frac{\partial \mu_2}{\partial x_1} \tag{77}$$

   hold, then the positive steady state is unique (see Figure 2, Case 1.a).

3. *If Case 2 holds, the system can have generically an odd number of positive steady states, while $\mathcal{E}_1$ and $\mathcal{E}_2$ are LES. The positive steady states at the left-hand end and right-hand end are blue (see Figure 2, Case 2). If, in addition, for all S, x_1, x_2,*
$$\frac{\partial \mu_1}{\partial x_1} > \frac{D_1}{D_2}\frac{\partial \mu_1}{\partial x_2} \quad \text{and} \quad \frac{\partial \mu_2}{\partial x_2} > \frac{D_2}{D_1}\frac{\partial \mu_2}{\partial x_1} \tag{78}$$
hold, then $\mathcal{E}^*$ is unique and unstable (see Figure 2, Case 2.a).
4. *If Case 3 [resp. Case 4] holds, then generically the system has no positive steady state or an even number of positive steady states where $\mathcal{E}_1$ is LES [resp. unstable] and $\mathcal{E}_2$ is unstable [resp. LES]. The positive steady state at the right-hand [resp. left-hand] end, if it exists, is blue (see Figure 3). If, in addition, (77) or (78) hold, then the system has no positive steady state (see Figure 3, Case 3.a [resp. Case 4.a]).*

The proof which uses some results given hereafter is postponed until the end of this section.

Remark 4. When $D_1 = D_2 = D$, the stability of positive steady states is completely characterized: a positive steady state is LES if and only if it is red. When D_i are distinct, we do not have at our disposal a necessary and sufficient condition for stability: the complete characterization of local behavior of $\mathcal{E}^*$ remains an open problem. This problem is solved when conditions (76) hold since in this case we know also that a positive steady state is LES if and only if it is red. However, we were not able to find an example where D_i are distinct and (76) does not hold, for which there exists a red positive steady state which is unstable. This question deserves further investigations.

We emphasize on the two following particular situations: Theorem 6 asserts that if Case 2 holds and conditions (78) are satisfied then $\mathcal{E}^*$ exists, is unique and is unstable. It asserts also that if Case 1 holds and both conditions (76) and (77) are satisfied then $\mathcal{E}^*$ exists, is unique and is LES. These properties deserve the biological interpretations given in the following remark.

Remark 5. Since the partial derivatives $\frac{\partial \mu_i}{\partial x_j}$, $i, j = 1, 2$ are nonpositive, conditions (78) are equivalent to

$$0 \leqslant -\frac{\partial \mu_1}{\partial x_1} < \frac{D_1}{D_2}\left(-\frac{\partial \mu_1}{\partial x_2}\right) \quad \text{and} \quad 0 \leqslant -\frac{\partial \mu_2}{\partial x_2} < \frac{D_2}{D_1}\left(-\frac{\partial \mu_2}{\partial x_1}\right)$$

which means that the intraspecific competition in each population of micro-organisms, measured by the partial derivative $\left(-\frac{\partial \mu_i}{\partial x_i}\right)$, is dominated by the interspecific competition, measured by the partial derivative $\left(-\frac{\partial \mu_i}{\partial x_j}\right)$, $i = 1, 2$, $j = 1, 2$, $i \neq j$. If these conditions are satisfied then Theorem 6 asserts that, if the positive steady state exists, it is unique and unstable.
Note also that conditions (76) together with conditions (77) are equivalent to

$$-\frac{\partial \mu_1}{\partial x_1} > \max\left(\frac{D_1}{D_2}, 1\right)\left(-\frac{\partial \mu_1}{\partial x_2}\right) \geqslant 0 \quad \text{and} \quad -\frac{\partial \mu_2}{\partial x_2} > \max\left(\frac{D_2}{D_1}, 1\right)\left(-\frac{\partial \mu_2}{\partial x_1}\right) \geqslant 0.$$

Hence, Theorem 6 asserts that in the case where the intraspecific competition is dominant with respect to interspecific competition then, if the positive steady state exists, it is unique and LES. Note that conditions (76) and (77) cannot hold if $\frac{\partial \mu_1}{\partial x_1} = 0$ or $\frac{\partial \mu_2}{\partial x_2} = 0$. On the other hand, conditions (78) cannot hold if $\frac{\partial \mu_1}{\partial x_2} = 0$ or $\frac{\partial \mu_2}{\partial x_1} = 0$.

In order to show Theorem 6, we need the following three propositions whose proofs are given in [20].

Proposition 7. *If (77) holds then, if Case 1 holds, the positive steady state exists and is unique and, if Case 3 or Case 4 hold, there is no positive steady state. This condition is incompatible with Case 2.*
If (78) holds then, if Case 2 holds, the positive steady state exists and is unique and, if Case 3 or Case 4 hold, there is no positive steady state. This condition is incompatible with Case 1.

Proposition 8. *$\mathcal{E}_0$ is LES if and only if $\mu_i(S_{in}, 0, 0) < D_i$, $i = 1, 2$, that is, $\mathcal{E}_1$ and $\mathcal{E}_2$ do not exist. For $i = 1, 2$, $\mathcal{E}_i$ is LES if and only if $\tilde{x}_i > \bar{x}_i$.*

Proposition 9. *Let $\mathcal{E}^* = (S^*, x_1^*, x_2^*)$ be a positive steady state. Assume that (H0) holds.*

1. *If $F_1'(x_1^*) F_2'(x_2^*) < 1$, then $\mathcal{E}^*$ is unstable.*
2. *If (76) holds or $D_1 = D_2 = D$, then $\mathcal{E}^*$ is LES if and only if $F_1'(x_1^*) F_2'(x_2^*) > 1$.*

Proof of Theorem 6. From item 1 of Proposition 9 and Lemma 11, it follows that blue positive steady states are unstable. From item 2 of Proposition 9 and Lemma 11, if (76) holds or $D_1 = D_2 = D$, then it follows that red positive steady states are LES. This proves item 1 of the theorem.

If Case 1 [resp. Case 2] holds, then there exists at least one positive steady state. Using Proposition 8, we deduce that $\mathcal{E}_1$ and $\mathcal{E}_2$ exist and are unstable [resp. LES]. The steady states at the left-hand end and right-hand end are red [resp. blue], since on the right of the corresponding intersections of curves γ_1 and γ_2, the tangent of γ_1 is under [resp. above] the tangent of γ_2. If (77) [resp. (78)] holds, then using Proposition 7, we deduce that $\mathcal{E}^*$ is the unique positive steady state [resp. and is unstable]. If (77) [resp. (78)] does not hold, then in the generic case, the curves γ_1 and γ_2 can have an odd number of intersections. This proves items 2 and 3 of the theorem.
If Case 3 [resp. Case 4] holds, then generically the curves γ_1 and γ_2 have no intersection or an even number of intersections. From Proposition 8, $\mathcal{E}_1$ is LES [resp. unstable] and $\mathcal{E}_2$ is unstable [resp. LES]. If (77) or (78) hold, then using Proposition 7, we deduce that the system has no positive steady state. The positive steady state at the right-hand [resp. left-hand] end is blue, since on the right of the corresponding intersection of curves γ_1 and γ_2, the tangent of γ_1 is above the tangent of γ_2. This proves item 4 of the theorem. □

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References

[1] N. Abdellatif, R. Fekih-Salem and T. Sari, Competition for a single resource and coexistence of several species in the chemostat, *Math. Biosci. Eng.*, **13** (2016), 631–652.

[2] P. Agrawal, C. Lee, H.C. Lim, and D. Ramkrishna, Theoretical investigations of dynamic behaviour of isothermal continuous stirred tank biological reactors. Chemical Engineering Science, 37, 453–462 (1982).

[3] R. Arditi and L.R. Ginzburg, Coupling in predator-prey dynamics: ratio-dependence, *J. Theor. Biol.* 139 (1989) 311–326.

[4] J. Arino, S.S. Pilyugin, G.S.K. Wolkowicz, Considerations on yield, nutrient uptake, cellular growth, and competition in chemostat models. Canadian Applied Mathematics Quarterly, 11, 107–142 (2003).

[5] R.A. Armstrong, R. McGehee, Competitive exclusion, Amer. Natur., 115, 151–170 (1980).

[6] J. R. Beddington, Mutual interference between parasites or predators and its effect on searching efficiency, *J. Anim. Ecol.*, **44** (1975), 331–340.

[7] B. Benyahia, T. Sari, B. Cherki, J. Harmand, Bifurcation and stability analysis of a two step model for monitoring anaerobic digestion processes, J. Process Control 22 (2012) 1008–1019.

[8] R. Borja, C. J. Banks, A. Martin and B. Khalfaoui, Anaerobic digestion of palm oil mill effluent and condensation water waste: an overall kinetic model for methane production and substrate utilization, *Bioprocess. Eng.*, **13** (1995), 87–95.

[9] J. P. Braselton and P. Waltman, A competition model with dynamically allocated inhibitor production. *Math. Biosci.*, **173** (2001), 55–84.

[10] G.J. Butler, G.S.K. Wolkowicz, A mathematical model of the chemostat with a general class of functions describing nutrient uptake, SIAM Journal on Applied Mathematics, 45, 138–151 (1985).

[11] R. S. Cantrell, C. Cosner and S. Ruan, Intraspecific interference and consumer-resource dynamics, *Discrete and Continuous Dynamical Systems-Series B*, **4** (2004), 527–546.

[12] J. Costerton, Overview of microbial biofilms, *J. Indust. Microbiol.* **15** (1995) 137–140.

[13] P.S. Crooke, R.D. Tanner, Hopf bifurcations for a variable yield continuous fermentation model, Int. J. Eng. Sci., 20, 439–443 (1982).

[14] P.S. Crooke, C-J. Wei, and R.D. Tanner, The effect of the specific growth rate and yield expressions on the existence of oscillatory behaviour of continuous fermentation model, Chemical Engineering Communications, 6, 333–347 (1980).

[15] D. L. DeAngelis, R. A. Goldstein and R. V. O'Neill, A model for trophic interaction, *Ecology*, **56** (1975), 881–892.

[16] A. Ding, MJ. Hounslow and CA. Biggs. Population balance modelling of activated sludge flocculation: Investigating the size dependence of aggregation, breakage and collision efficiency. *Chem Eng Sci.* 61 (2006) 63–74.

[17] M. El Hajji, F. Mazenc, J. Harmand, A mathematical study of a syntrophic relationship of a model of anaerobic digestion process, Math. Biosci. Eng. 7 (2010) 641–656.

[18] R. Fekih-Salem, *Modèles mathématiques pour la compétition et la coexistence des espèces microbiennes dans un chémostat*, (Ph.D. thesis), University of Montpellier 2 and University of Tunis el Manar, 2013. https://tel.archives-ouvertes.fr/tel-01018600.

[19] R. Fekih-Salem, J. Harmand, C. Lobry, A. Rapaport and T. Sari, Extensions of the chemostat model with flocculation, *J. Math. Anal. Appl.*, **397** (2013), 292–306.

[20] R. Fekih-Salem, C. Lobry and T. Sari, A density-dependent model of competition for one resource in the chemostat. 2016. <hal-01359078>

[21] R. Fekih-Salem, A. Rapaport and T. Sari, Emergence of coexistence and limit cycles in the chemostat model with flocculation for a general class of functional responses, *Appl. Math. Modell.*, **40** (2016), 7656–7677.

[22] R. Fekih-Salem and T. Sari, Sur la stabilité globale de l'équilibre de coexistence d'un modèle densité-dépendant de compétition pour une ressource, *Proceedings of the 12th African Conference on Research in Computer Science and Applied Mathematics, INRIA* (2014), 19–30.

[23] R. Fekih-Salem, T. Sari and N. Abdellatif, Sur un modèle de compétition et de coexistence dans le chémostat, *ARIMA J.*, **14** (2011), 15–30.

[24] R. Fekih-Salem, T. Sari, A. Rapaport, La floculation et la coexistence dans le chemostat, Proceedings of the 5th conference on Trends in Applied Mathematics in Tunisia, Algeria, Morocco, (2011) 477–483.

[25] H. Fgaier, M. Kalmokoff, T. Ells and H. J. Eberl, An allelopathy based model for the Listeria overgrowth phenomenon, *Math. Biosci.*, **247** (2014), 13–26.

[26] B. Fiedler, S.B. Hsu, Non-periodicity in chemostat equations: a multi-dimensional negative Bendixon-Dulac criterion, J. Math. Biol., 59, 233–253 (2009).

[27] R. Freter, H. Brickner, J. Fekete, M.M. Vickerman, K.E. Carey, Survival and implantation of Escherichia coli in the intestinal tract, Infect. Immun. 39 (1983) 686–703.

[28] R. Freter, H. Brickner, S. Temme, An understanding of colonization resistance of the mammalian large intestine requires mathematical analysis, Microecology and Therapy 16 (1986) 147–155.

[29] J. P. Grover and F. B. Wang, Competition for one nutrient with internal storage and toxin mortality, *Math. Biosci.*, **244** (2013), 82–90.

[30] B. Haegeman, C. Lobry and J. Harmand, Modeling bacteria flocculation as density-dependent growth, *AIChE J.*, **53** (2007), 535–539.

[31] B. Haegeman and A. Rapaport, How flocculation can explain coexistence in the chemostat, *J. Biol. Dyn.*, **2** (2008), 1–13.

[32] S.R. Hansen and S.P. Hubbell, Single-nutrient microbial competition: qualitative agreement between experimental and theoretically forecast outcomes, *Science*, **207** (1980), 1491–1493.

[33] G. Hardin, The competitive exclusion principle, *Science*, **131** (1960), 1292–1297.

[34] J. Harmand and J. J. Godon, Density-dependent kinetics models for a simple description of complex phenomena in macroscopic mass-balance modeling of bioreactors. *Ecological Modelling* 200 (2007) 393–402

[35] J. Harmand, A. Rapaport, D. Dochain and C. Lobry, Microbial ecology and bioprocess control: Opportunities and challenges, *Journal of Process Control*, **18** (2008), 865–875.

[36] J. Heßeler, J.K. Schmidt, U. Reichl and D. Flockerzi, Coexistence in the chemostat as a result of metabolic by-products, *J. Math. Biol.*, **53** (2006), 556–584.

[37] S. B. Hsu, Limiting behavior for competing species, *SIAM J. Appl. Math*, **34** (1978), 760–763.

[38] S.B. Hsu, A survey of constructing Lyapunov functions for mathematical models in population biology, Taiwanese Journal of Mathematics, 9, 151–173 (2005).

[39] S. B. Hsu, S. P. Hubbell and P. Waltman, A mathematical theory for single-nutrient competition in continuous cultures of micro-organisms, *SIAM J. Appl. Math.*, **32** (1977), 366–383.

[40] S. B. Hsu, Y. S. Li and P. Waltman, Competition in the presence of a lethal external inhibitor, *Math. Biosci.*, **167** (2000), 177–199.

[41] S. B. Hsu and P. Waltman, Analysis of a model of two competitors in a chemostat with an external inhibitor, *SIAM J. Appl. Math*, **52** (1992), 528–540.

[42] S. B. Hsu and P. Waltman, A survey of mathematical models of competition with an inhibitor, *Math. Biosci.*, **187** (2004), 53–91.

[43] G. E. Hutchinson, The paradox of the plankton, *Am. Nat.*, **95** (1961), 137–145.

[44] IWA Task Group on Biofilm Modeling, Mathematical modeling of biofilms, IWA publishing, 2006.

[45] L. Imhof and S. Walcher, Exclusion and persistence in deterministic and stochastic chemostat models, *J. Differential Equations*, **217** (2005), 26–53.

[46] D. Jones, H.V. Kojouharov, D. Le, H.L. Smith, The Freter model: A simple model of biofilm formation, *J. Math. Biol.* **47** (2003) 137–152.

[47] P. De Leenheer, D. Angeli and E. D. Sontag, Crowding effects promote coexistence in the chemostat, *J. Math. Anal. Appl.*, **319** (2006), 48–60.

[48] P. De Leenheer, B. Li and H. L. Smith, Competition in the chemostat: Some remarks, *Canadian Applied Mathematics Quarterly*, **11** (2003), 229–248.

[49] R. E. Lenski and S. E. Hattingh, Coexistence of two competitors on one resource and one inhibitor: a chemostat model based on bacteria and antibiotics, *J. Theor. Biol.*, **122** (1986), 83–93.

[50] B. Li, Global asymptotic behavior of the chemostat: general response functions and different removal rates, *SIAM J. Appl. Math.*, **59** (1998), 411–422.

[51] C. Lobry and J. Harmand, A new hypothesis to explain the coexistence of n species in the presence of a single resource, *C. R. Biol.*, **329** (2006), 40–46.

[52] C. Lobry and F. Mazenc, Effect on persistence of intra-specific competition in competition models, *Electron. J. Diff. Eqns.*, **125** (2007), 1–10.

[53] C. Lobry, F. Mazenc and A. Rapaport, Persistence in ecological models of competition for a single resource, *C. R. Acad. Sci. Paris, Ser. I*, **340** (2005), 199–204.

[54] C. Lobry, A. Rapaport and F. Mazenc, Sur un modèle densité-dépendant de compétition pour une ressource, *C. R. Biol.*, **329** (2006), 63–70.

[55] C. Lobry, T. Sari and S. Touhami, On Tikhonov's theorem for convergence of solutions of slow and fast systems. *Electron. J. Diff. Eqns.* 1998 (1998), No. 19, 1-22.

[56] J. Monod, La technique de culture continue. Théorie et applications, *Ann. Inst. Pasteur*, **79** (1950), 390–410.

[57] S. Pilyugin, P. Waltman, The simple chemostat with wall growth, SIAM J. Appl. Math. 59 (1999) 1552–1572.

[58] S.S. Pilyugin, P. Waltman, Multiple limit cycles in the chemostat with variable yields, Mathematical Biosciences, 182, 151–166 (2003).

[59] H. Roques, S. Yue, S. Saipanich and B. Capdeville, Faut-il abandonner le formalisme de Monod pour la modélisation des processus de dépollution par voie biologique?, *Water Res.*, **16** (1982), 839–847.

[60] S. Ruan, A. Ardito, P. Ricciardi and D. L. DeAngelis, Coexistence in competition models with density-dependent mortality, *C. R. Biol.*, **330** (2007), 845–854.

[61] Y. Saito and T. Miki, Species coexistence under resource competition with intraspecific and interspecific direct competition in a chemostat, *Theor. Popul. Biol.*, **78** (2010), 173–182.

[62] T. Sari, A Lyapunov function for the chemostat with variable yields, C. R. Math. Acad. Sci. Paris, 348, (2010), 747–751 .

[63] T. Sari, Competitive Exclusion for Chemostat Equations with Variable Yields, Acta Appl. Math., 123 (1), 2013, 201–219.

[64] T. Sari, M. El Hajji and J. Harmand, The mathematical analysis of a syntrophic relationship between two microbial species in a chemostat, *Math. Biosci. Eng.*, **9** (2012), 627–645.

[65] T. Sari and J. Harmand, A model of a syntrophic relationship between two microbial species in a chemostat including maintenance, *Math. Biosci.*, **275** (2016), 1–9.

[66] T. Sari and F. Mazenc, Global dynamics of the chemostat with different removal rates and variable yields, *Math. Biosci. Eng.*, **8** (2011), 827–840.

[67] M. Scheffer, S. Rinaldi, J. Huisman and F.J. Weissing, Why plankton communities have no equilibrium: solutions to the paradox, *Hydrobiologia*, **491** (2003), 9–18.

[68] J. K. Schmidt, B. König and U. Reichl, Characterization of a three bacteria mixed culture in a chemostat: evaluation and application of a quantitative Terminal-Restriction Fragment Length Polymorphism (T-RFLP) analysis for absolute and species specific cell enumeration, *Biotechnol. Bioeng.*, **96** (2007), 738–756.

[69] H. L. Smith and P. Waltman, *The Theory of the Chemostat: Dynamics of Microbial Competition*, Cambridge University Press, 1995.

[70] B. Tang, A. Sitomer, T. Jackson, Population dynamics and competition in chemostat models with adaptive nutrient uptake, J. Math. Biol. 35 (1997) 453–479.

[71] D. Tilman, Resource Competition and Community Structure. Princeton University Press (1982).

[72] D.N. Thomas, S.J. Judd, N. Fawcett, Flocculation modelling: a review, *Water Res.* **33** (1999) 1579–1592.

[73] A. N. Tikhonov, Systems of differential equations containing small parameters multiplying the derivatives, *Mat. Sb.* 31 (1952) 575-586.

[74] E. Wahlberg, T. Keinath and D. Parker. Influence of activated sludge flocculation time on secondary clarification. *Wat Environ Res.* 66 (1994) 779–786.

[75] W. Wasow, *Asymptotic Expansions for Ordinary Differential Equations*, Krieger, New York (1976).

[76] G. S. K. Wolkowicz and Z. Lu, Global dynamics of a mathematical model of competition in the chemostat: general response functions and differential death rates, *SIAM J. Appl. Math.*, **52** (1992), 222–233.

[77] G. S. K. Wolkowicz and Z. Lu, Direct interference on competition in a chemostat, *J. Biomath*, **13** (1998), 282–291.

[78] G.S.K. Wolkowicz, H. Xia, Global asymptotic behavior of a chemostat model with discrete delays. SIAM Journal on Applied Mathematics, 57, 1019–1043 (1997).