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# ASYMPTOTIC BEHAVIOR OF A CHEMOSTAT MODEL WITH CONSTANT RECYCLE SLUDGE CONCENTRATION

M. AMINE HAMRA, KARIM YADI

**ABSTRACT.** In this work, we study a several species aerobic chemostat model with constant recycle sludge concentration in continuous culture. We reduce the number of parameters by considering a dimensionless model. First, the existence of a global positive uniform attractor for the model with different removal rates is proved using the theory of dissipative dynamical systems. Hence, we investigate the asymptotic behavior of the model under small perturbations using methods of singular perturbation theory and we prove that, in the case of two species in competition, the unique equilibrium which is positive is globally asymptotically stable. Finally, we establish the link between the open problem of the chemostat with different removal rates and monotone functional responses, and our model when two species compete on the same nutrient. We give some numerical simulations to illustrate the results.

## 1. INTRODUCTION

The Chemostat with sludge recycle process (or an activated sludge process) is a biological treatment used for reducing dissolved organic matter from waste-water, and consists of two units, an aeration basin and a clarifier. First, influent is introduced into the aerated tank, in which pollutants are degraded by microorganisms. After a required period of aeration and agitation in the aeration tank, biomass flows to the secondary clarifier, where it is separated into thickened biomass and treated waste-water by gravity sedimentation. A portion of this settled biomass, described as activated sludge is recycled back rapidly into the aeration tank to maintain the desired concentration of organisms in the reactor, see Fig.1.1.  $Q$  is the influent flow rate, (volume/time);  $r$  as subscript, denotes recycle ratio;  $S_0, S$  respectively denote concentration of substrate in influent and aeration basin;  $x_i^0, x_i, x_i^r$  respectively denote concentration of the  $i$ -th species of microorganism in influent, aeration basin and sludge recirculation stream (mass/volume).

Many mathematical models used to describe the behavior of the activated sludge process are available in the literature. In this paper we choose a simplified model

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proposed by [1] and presented later in detailed works by [9, 10, 5]. Another interesting study of the activated sludge processes can be found in [15]. Our purpose being a mathematical study and a discussion on an open problem, we did not consider the more recent and complicated activated sludge models as defined for example in [4]. The model considered in this study expresses the bio-degradation of one pollutant (substrate) by  $n$ -species of microorganisms in a mixed continuous culture.

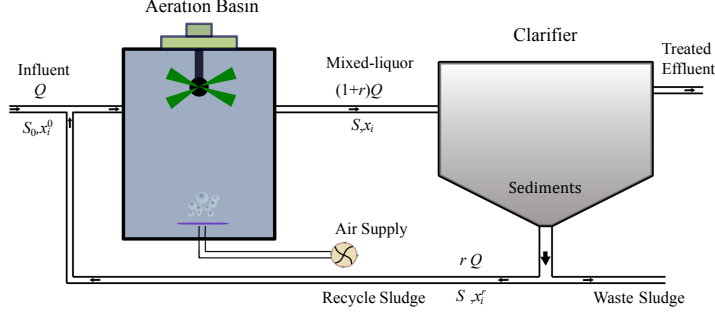


FIGURE 1.1. Mass balance of the Chemostat with sludge recycle

The chemostat with sludge recycle model for  $n$ -species of microorganisms in continuous culture is described by the following system of differential equations :

$$(1.1) \quad \begin{cases} \dot{S} = D(S_0 + rS) - D(1+r)S - \sum_{i=1}^n \frac{1}{Y_i} f_i(S) x_i, \\ \dot{x}_i = D(x_i^0 + r x_i^r) - D(1+r)x_i + (f_i(S) - k_i) x_i, \quad i = \overline{1, n} \end{cases}$$

where  $D = Q/V$  is the dilution rate,  $V$  being the volume of the aeration basin;  $Y_i$  the growth yield coefficient (mass of the organism produced per unit mass of the substrate consumed);  $k_i$  the specific decay-rate constants or removal rates;  $f_i/Y_i$  is the uptake or consumption function, proportional to the growth function  $f_i$ . As usual,  $f_i : \mathbb{R}_+ \rightarrow \mathbb{R}_+$  is such that :

- $f_i$  is continuously differentiable and monotone increasing,
- $f_i(0) = 0$ .

The usual monotonic growth function is the Monod (Holling type II) consumption function [7]

$$\mu(S) = \frac{\mu_{\max} S}{k_S + S},$$

where  $\mu_{\max}$  is the maximum specific growth-rate constant, and  $k_S$  is the Michaelis-Menten constant.

The system of equations 1.1 can be written in the following form

$$\begin{aligned} \left(\frac{\dot{S}}{S_0}\right) &= D\left(1 - \frac{S}{S_0}\right) - \sum_{i=1}^n \frac{1}{Y_i} f_i\left(\frac{S}{S_0} S_0\right) \frac{x_i}{S_0} \\ \left(\frac{\dot{x}_i}{S_0}\right) &= \frac{D(x_i^0 + r x_i^r)}{S_0} + \left[f_i\left(\frac{S}{S_0} S_0\right) - (D(1+r) + k_i)\right] \frac{x_i}{S_0} \end{aligned}$$

Let us introduce, for convenience, the following dimensionless quantities :

$$h_i = \frac{D(x_i^0 + r x_i^r)}{S_0}, \quad k_i \leftarrow k_i + (1+r)D, \quad S \leftarrow S/S_0, \quad x_i \leftarrow x_i/S_0,$$

and replace  $f_i(S_0 S)$  by  $f_i(S)$  (in this change we use the dimensionless  $S$ ). This change of variables and parameters allows us to rewrite (1.1) as:

$$(1.2) \quad \begin{cases} \dot{S} = D(1-S) - \sum_{i=1}^n \frac{1}{Y_i} f_i(S) x_i \\ \dot{x}_i = h_i + (f_i(S) - k_i) x_i \end{cases} \quad i = \overline{1, n}$$

This article is organized as follows : first, in Section 2, it is proved that the model (1.2) has a unique equilibrium point which is positive and that the solutions are positively bounded (dissipativity). In Section 3, we show that in the case of a single type of microorganisms the equilibrium is globally asymptotically stable and then we establish in the higher dimensional case a uniform persistence result. We conjecture that this persistence is realized around the equilibrium. Section 4 is devoted to our model written as a slow and fast system in order to make use of reduction technics within the singular perturbation theory. It is proved that, for  $n = 2$ , the unique equilibrium point is globally asymptotically stable (note that for  $n = 3$  we indicate how to obtain the local attractivity). The relationship between stability and singular perturbation theory can be derived from the geometrical point of view (Fenichel's theory [2]) or the 'topological' one [14]. Finally, it is remarkable that when we set in the model (1.1) the input biomass  $x_i^0 = 0$  and the recycle ratio  $r = 0$  the parameter  $h_i$  vanishes. Hence, the obtained dimensionless model (1.2) with  $h_i = 0$  is nothing else than the chemostat model with different removal rates and general monotone growth functions [12, Chapter 2, Sec. 4]. It is well known that the asymptotic behavior of such a model is still an open problem, for which it is conjectured that the species with the smallest break-even concentration wins the competition and the others go extinct. It is the Competitive Exclusion Principle. Note that the problem have been solved for the case of Monod growth function and different removal rates [6]. In Section 5, the link between the two problems is examined, at least for  $n = 2$ , and it is explained that the two conjectures are equivalent. For the singularly perturbed system modelizing the chemostat model with different removal rates and general monotone growth functions and derived from the singularly perturbed model studied in Section 4, we could prove that the Competitive Exclusion Principle holds.

## 2. THE EQUILIBRIUM POINT AND THE DISSIPATIVITY

**Definition 1.** A dynamical system  $\dot{y} = f(y)$  defined in a domain  $\Omega$  is said to be dissipative if trajectories are asymptotically uniformly bounded in positive time, in other words, if there exists a positive real number  $R$  such that all solutions  $y(t)$  with  $y(t) \in \Omega$  for all  $t > 0$  satisfy  $\limsup_{t \rightarrow \infty} \|y(t)\| < R$ .

Define the family of the so-called **break-even concentrations**

$$\{\lambda_i : k_i = f_i(\lambda_i)\}_{i=\overline{1, n}}$$

elements of which are ordered as follows  $\lambda_1 < \lambda_2 \leq \dots \leq \lambda_n$ .

**Proposition 2.** *The system (1.2) admits a unique positive fixed point.*

*Proof.* The equilibrium points are solutions of

$$(2.1) \quad \begin{cases} D(1-S) - \sum_{i=1}^n \frac{1}{Y_i} f_i(S) x_i = 0 \\ h_i + (f_i(S) - k_i) x_i = 0, \quad i = \overline{1, n} \end{cases}$$

In view of positivity of the equilibria, one should have, from the second equation of (2.1),

$$\begin{aligned} x_i = \frac{h_i}{k_i - f_i(S)} > 0 \quad i = \overline{1, n} &\iff f_i(S) < k_i \quad i = \overline{1, n} \\ &\iff f_i(S) < f_i(\lambda_i) \quad i = \overline{1, n} \\ &\iff S < \lambda_i \quad i = \overline{1, n} \text{ (} f_i \text{ is injective for all } i = \overline{1, n} \text{)} \\ &\iff S < \lambda_1. \end{aligned}$$

Denote by  $(S^*, x_1^*, \dots, x_n^*)$  such an equilibrium if it exists. Summing the equations of the system (2.1) at this point, we get

$$(2.2) \quad D(1-S^*) + \sum_{i=1}^n \frac{h_i}{Y_i} - \sum_{i=1}^n \frac{k_i}{Y_i} x_i^* = 0.$$

From (2.2), we have

$$D(1-S^*) + \sum_{i=1}^n \frac{h_i}{Y_i} - \sum_{i=1}^n \frac{h_i k_i / Y_i}{k_i - f_i(S^*)} = 0.$$

Let  $g(S) := D(1-S) + \sum_{i=1}^n \frac{h_i}{Y_i} - \sum_{i=1}^n \frac{h_i k_i / Y_i}{k_i - f_i(S)}$ . It is clear that  $g'(S) \leq 0$ ,  $g(0) = D$  and  $\lim_{S \rightarrow \lambda_1} g(S) = -\infty$ , then there exists a unique  $S^* \in (0, \lambda_1)$  such that  $g(S^*) = 0$ .

Hence, the system (1.2) admits a unique equilibrium point with positive coordinates, designated hereafter by  $(S^*, x_1^*, \dots, x_n^*)$ .  $\square$

**Proposition 3.** *The domain  $\Omega = \{(S, x_1, \dots, x_n) \in \mathbb{R}^{n+1}; S > 0, x_i > 0 \text{ for } i = \overline{1, n}\}$  is positively invariant with respect to the system (1.2). Moreover, the system (1.2) is dissipative.*

*Proof.* Let  $(S, x_1, \dots, x_n)$  a point of the boundary of  $\Omega$ . First, if  $S = 0$  then, according to (1.2),  $\dot{S} = D > 0$  and if  $x_i = 0$  for some  $i$ ,  $\dot{x}_i = h_i > 0$ . Hence the open set  $\Omega$  is positively invariant for the considered system. Now, let

$$\tilde{D} = \min\{D, k_1, k_2, \dots, k_n\}, \quad z = \sum_{i=1}^n \frac{x_i}{Y_i} + S, \quad \hat{D} = (D + \sum_{i=1}^n \frac{h_i}{Y_i}) / \tilde{D}.$$

From the system (1.2), we have

$$\begin{aligned} \sum_{i=1}^n \frac{\dot{x}_i}{Y_i} + \dot{S} &= D(1-S) + \sum_{i=1}^n \left( \frac{h_i}{Y_i} - \frac{k_i}{Y_i} x_i \right) \\ &\leq D + \sum_{i=1}^n \frac{h_i}{Y_i} - \tilde{D} \left( \sum_{i=1}^n \frac{x_i}{Y_i} + S \right). \end{aligned}$$

Hence,  $z(t) \leq \hat{D} + z(0) \exp(-\tilde{D}t)$  for all  $t \geq 0$ , which implies that  $\limsup_{t \rightarrow \infty} z(t) \leq \hat{D}$ . Then, given any  $\epsilon > 0$  we can choose a certain  $T \geq 0$ , such that  $z(t) = \sum_{i=1}^n \frac{x_i(t)}{Y_i} +$

$S(t) \leq \hat{D} + \epsilon$ ,  $t \geq T$ . Since each term of the sum is positive the boundedness of the solutions now follows immediately. In other words, the system is dissipative.  $\square$

### 3. UNIFORM PERSISTENCE RESULTS

Let us first show that in the case of a single type of microorganisms the unique equilibrium is globally asymptotically stable (Theorem 4 below). In this case the system (1.1) is given by:

$$(3.1) \quad \begin{cases} \dot{S} = D(1 - S) - \frac{1}{Y} f(S)x \\ \dot{x} = h + (f(S) - k_d)x \end{cases}$$

Note that,  $(S^*, x^*) = (S^*, \frac{h}{k_d - f(S^*)})$  is the unique positive fixed point of (3.1).

**Theorem 4.** *The unique positive fixed point of the system (3.1) is globally asymptotically stable.*

*Proof.* The linearization of (3.1) around  $(S^*, x^*)$  yields the Jacobian matrix:

$$J_{(S^*, x^*)} = \begin{pmatrix} -D - \frac{1}{Y} f'(S^*)x^* & -\frac{1}{Y} f(S^*) \\ f'(S^*)x^* & -h/x^* \end{pmatrix}$$

Hence,  $\text{trace}(J_{(S^*, x^*)}) = -(D + \frac{1}{Y} f'(S^*)x^* + h/x^*) < 0$ , and  $\det(J_{(S^*, x^*)}) > 0$ . Then, the equilibrium point  $(S^*, x^*)$  is locally asymptotically stable for the system (3.1).

Since  $x(t) > 0$  for all  $t \geq 0$ , there exists  $\eta : \mathbb{R}_+ \rightarrow \mathbb{R}$  such that  $x(t) = \exp(\eta(t))$ .

We get a system which is topologically equivalent to (3.1)

$$\begin{cases} \dot{S} = D(1 - S) - \frac{1}{Y} f(S) \exp(\eta(t)) =: g_1(S, \eta) \\ \dot{\eta} = h \exp(-\eta(t)) + f(S) - k_d =: g_2(S, \eta) \end{cases}$$

Then

$$\frac{\partial g_1}{\partial S}(S, \eta) + \frac{\partial g_2}{\partial \eta}(S, \eta) = -D - \frac{1}{Y} f'(S) \exp(\eta(t)) - h \exp(-\eta(t)) < 0.$$

Since the topological equivalence preserves the periodicity of trajectories, the Bendixson's criterion implies that there are no periodic orbits. Applying the Poincaré-Bendixson's Theorem, the  $\omega$ -limit set of trajectories of (3.1) must be the unique equilibrium  $(S^*, \frac{h}{k_d - f(S^*)})$  defined by  $D(1 - S^*) - \frac{h}{Y} - \frac{h k_d / Y}{k_d - f(S^*)} = 0$ .  $\square$

Now, in the presence of many species, we propose to show that the system (1.2) is uniformly persistent and we recall hereafter this notion.

**Definition 5.** The system

$$\begin{cases} \dot{y}_i = g_i(y_1, y_2, \dots, y_n) \\ y_i(0) = y_i^0 > 0 \quad i = \overline{1, n}, \end{cases}$$

is said to be **uniformly persistent** if  $\exists \kappa > 0$  ( $\kappa$  is independent of initial conditions) such that for all solutions we have  $\liminf_{t \rightarrow \infty} y_i(t) > \kappa$ .

**Definition 6.** A bounded closed set  $\mathfrak{A} \subset \Omega$  is called a **global attractor** for a dynamical system  $\dot{y} = f(y)$  defined in  $\Omega$ , if  $\mathfrak{A}$  is positively invariant and attracts all trajectories starting in bounded sets. In other words, for any bounded set  $B \subset \Omega$ ,

$$\lim_{t \rightarrow \infty} \sup_{a \in \mathfrak{A}} \inf_{y_0 \in B} \|y(t, y_0) - a\| = 0.$$

**Theorem 7.** *The system (1.2) is uniformly persistent in the domain  $\Omega$  and possesses a compact global attractor in  $\Omega$ .*

*Proof.* From (1.2) we have

$$\begin{aligned}\dot{x}_i &= h_i + (f_i(S) - k_i)x_i \\ &\geq h_i - k_i x_i,\end{aligned}$$

therefore

$$\forall t \geq 0, x_i(t) \geq (x_i(0) - \frac{h_i}{k_i}) \exp(-k_i t) + \frac{h_i}{k_i},$$

which yields

$$\liminf_{t \rightarrow \infty} x_i(t) \geq \frac{h_i}{k_i} > 0.$$

From the previous proposition we have  $x_i(t) \leq Y_i(\hat{D} + \epsilon_z)$  for all  $t \geq T$ , and by the Mean Value Theorem, there exists a point  $\theta_i$  in  $(0, \hat{D} + \epsilon_z)$  such that  $f_i(S) \leq f'_i(\theta_i)S$  for all  $i = \overline{1, n}$ , then from (1.2), we have,

$$\begin{aligned}\dot{S} &= D(1 - S) - \sum_{i=1}^n \frac{1}{Y_i} f_i(S) x_i \\ &\geq D(1 - S) - S(\hat{D} + \epsilon_z) \sum_{i=1}^n f'_i(\theta_i) \\ &= D - [D + (\hat{D} + \epsilon_z) \sum_{i=1}^n f'_i(\theta_i)] S.\end{aligned}$$

Then it follows by comparison that

$$\liminf_{t \rightarrow \infty} S(t) \geq \frac{D}{D + (\hat{D} + \epsilon_z) \sum_{i=1}^n f'_i(\theta_i)} > 0.$$

Hence, the system is uniformly persistent. Since it also dissipative, there exists a global attractor in  $\Omega$ .  $\square$

Note that uniform persistence together with dissipativity is called permanence. Numerous numerical simulations (see Figs. 3.1, 3.2) encourage us to state that :

**Conjecture 8.** *The unique positive fixed point  $(S^*, x_1^*, x_2^*, \dots, x_n^*)$  of (1.2) is globally asymptotically stable in  $\mathbb{R}_+^{n+1}$ .*

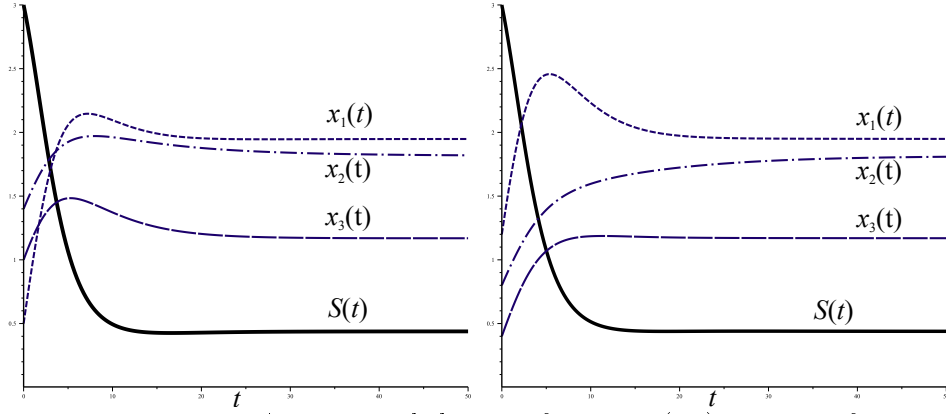


FIGURE 3.1. Asymptotic behavior of system (1.2) in case of three types of microorganisms. Here,  $f_1(S) = \frac{\mu_{\max}^1 S}{k_S^1 + S}$ ,  $f_2(S) = \frac{\mu_{\max}^2 S}{k_S^2 + S}$ ,  $f_3(S) = \frac{\mu_{\max}^3 S}{k_S^3 + S}$ ,  $k_S^1 = 50$ ,  $k_S^2 = 45$ ,  $k_S^3 = 40$ ,  $\mu_{\max}^1 = 2$ ,  $\mu_{\max}^2 = 3$ ,  $\mu_{\max}^3 = 4$ ,  $Y_1 = 0.5$ ,  $Y_2 = 0.4 = Y_3$ ,  $k_1 = 0.1$ ,  $k_2 = 0.2$ ,  $k_3 = 0.5$ ,  $D = 0.2$ ,  $h_1 = 0.15$ ,  $h_2 = 0.2$ ,  $h_3 = 0.5$ .

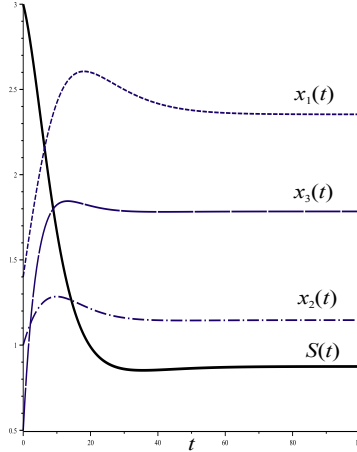


FIGURE 3.2. Asymptotic behavior of system (1.2) in case of three types of microorganisms with  $f_1(S) = \frac{1}{10} \ln(1 + \frac{S}{2})$ ,  $f_2(S) = \frac{1}{10} \ln(1 + \frac{S}{3})$ ,  $f_3(S) = \frac{1}{10} \ln(1 + \frac{S}{4})$ ,  $Y_1 = 0.5$ ,  $Y_2 = 0.4 = Y_3$ ,  $k_1 = 0.1$ ,  $k_2 = 0.2$ ,  $k_3 = 0.5$ ,  $D = 0.2$ ,  $h_1 = 0.15$ ,  $h_2 = 0.2$ ,  $h_3 = 0.5$ .

The example simulated in Fig 3.2 is just a mathematical illustration of the conjecture, and the growth functions has no biological meaning, but emphasize the fact that they are monotone increasing. We are not able until now to confirm this result, an we propose to examine a special case in the following section.



## 4. THE SINGULARLY PERTURBED CASE

Classical methods of reduction are based on the conservation principle, which plays an important role to reduce higher dimensional system to a simple limiting system using separation theorems [12]. But our system (1.2) does not have the conservation property, which causes the difficulty. Stability of the system (1.2) can be achieved in some specific cases which are biologically plausible. In this subsection we want to reduce the stability analysis of the system (1.2) with the use of singular perturbation methods. Indeed, biologically it is reasonable to take  $Y_i = \epsilon \bar{Y}_i$  and  $\bar{D} = \epsilon D$  with  $0 < \epsilon \ll 1$  because in higher dilution rates, the yield values are considered small [13, P.72]. In a culture of three species of microorganisms this leads to a system given by

$$(4.1) \quad \begin{cases} \epsilon \dot{S} = \bar{D}(1 - S) - \sum_{i=1}^3 \frac{1}{\bar{Y}_i} f_i(S) x_i =: G(S, x_1, x_2, x_3), \\ \dot{x}_i = h_i + (f_i(S) - k_i) x_i, \end{cases} \quad i = \overline{1, 3}.$$

By Proposition 2, this system possesses a unique positive fixed point

$$X_\epsilon^* = (S^*(\epsilon), x_1^*(\epsilon), x_2^*(\epsilon), x_3^*(\epsilon))$$

which, actually, does not depend on  $\epsilon$  in this case. Taking  $\epsilon = 0$  in the above system, the resulting equation is

$$(4.2) \quad \begin{cases} 0 = \bar{D}(1 - S) - \sum_{i=1}^3 \frac{1}{\bar{Y}_i} f_i(S) x_i = G(S, x_1, x_2, x_3), \\ \dot{x}_i = h_i + (f_i(S) - k_i) x_i, \end{cases} \quad i = \overline{1, 3}.$$

The partial derivative  $G_S$  is  $-\bar{D} - \sum_{i=1}^3 \frac{1}{\bar{Y}_i} f'_i(S) x_i < 0$  for all  $(S, x_1, x_2, x_3) \in \mathbb{R}_+^4$ .

So the Implicit Function Theorem asserts the existence of a  $C^1$  function  $S = \psi(x_1, x_2, x_3)$  defined in  $\mathbb{R}_+^3$ , such that

$$(4.3) \quad G(\psi, x_1, x_2, x_3) = 0.$$

The Fenichel's First Theorem [8, 2] ensures the existence of a slow invariant attractive manifold  $\mathcal{M}_\epsilon = \{(S, x_1, x_2, x_3) \in \mathbb{R}_+^4, S = \psi_\epsilon(x_1, x_2, x_3)\}$  for the perturbed system that is  $O(\epsilon)$  close to the critical manifold  $\mathcal{M}_0 = \{(S, x_1, x_2, x_3) \in \mathbb{R}_+^4, S = \psi(x_1, x_2, x_3)\}$ . On  $\mathcal{M}_\epsilon$  the slow dynamics decouples from the fast dynamics and then we can restrict the study to the regular perturbed problem

$$(4.4) \quad \dot{x}_i = h_i + (f_i(\psi_\epsilon) - k_i) x_i, \quad i = \overline{1, 3}.$$

Setting  $\epsilon = 0$  in (4.4), we obtain a three-dimensional competitive system

$$(4.5) \quad \dot{x}_i = h_i + (f_i(\psi) - k_i) x_i, \quad i = \overline{1, 3}.$$

We know that this system admits a positive fixed point  $(x_1^*, x_2^*, x_3^*)$  such that  $S^* = \psi(x_1^*, x_2^*, x_3^*)$ .

Now, if we differentiate the equation (4.3) implicitly with respect to  $x_1, x_2$ , and  $x_3$ , we obtain

$$\psi_{x_j} = \frac{\partial \psi}{\partial x_j} = - \frac{\frac{1}{\bar{Y}_j} f_j(S)}{\bar{D} + \sum_{i=1}^3 \frac{1}{\bar{Y}_i} f'_i(S) x_i} \leq 0, \quad j = 1, 2, 3.$$

The Jacobian matrix of (4.5) at the equilibrium  $(x_1^*, x_2^*, x_3^*)$  is given by

$$J_{(x_1^*, x_2^*, x_3^*)} = - \begin{pmatrix} a_{11} + \alpha_1 & a_{12} & a_{13} \\ a_{21} & a_{22} + \alpha_2 & a_{23} \\ a_{31} & a_{32} & a_{33} + \alpha_3 \end{pmatrix},$$

where

$$a_{ij} = -f'_i(S^*)x_i^*\psi_{x_j}(x_1^*, x_2^*, x_3^*) > 0 \text{ and } \alpha_i = \frac{h_i}{x_i^*}.$$

First, notice that  $a_{ij}a_{mn} = a_{in}a_{mj}$  (in particular,  $a_{ij}a_{ji} = a_{ii}a_{jj}$ ). The characteristic polynomial of the above Jacobian is

$$p(\lambda) = \lambda^3 + b_1\lambda^2 + b_2\lambda + b_3,$$

where,

$$b_1 = a_{11} + a_{22} + a_{33} + \alpha_1 + \alpha_2 + \alpha_3,$$

$$b_2 = \alpha_1(\alpha_2 + \alpha_3 + a_{22} + a_{33}) + \alpha_2(\alpha_3 + a_{11} + a_{33}) + \alpha_3(a_{11} + a_{22}),$$

$$b_3 = \alpha_1\alpha_2(\alpha_3 + a_{33}) + \alpha_3(\alpha_1a_{22} + \alpha_2a_{11}).$$

By the Routh-Hurwitz Criterion [3], the roots of  $p(\lambda)$  have negative real parts if and only if all Hurwitz determinants are positive. Here,  $b_1$  and  $b_3$  are positive, and

$$\begin{vmatrix} b_1 & 1 \\ b_3 & b_2 \end{vmatrix} = (\alpha_3a_{22} + \alpha_2a_{33} + \alpha_1\alpha_3)(b_1 - \alpha_1) + \alpha_3a_{11}(b_1 - \alpha_2) \\ + b_1(\alpha_1(\alpha_2 + a_{22} + a_{33}) + \alpha_2(\alpha_3 + a_{11})) > 0.$$

Then, the equilibrium point  $(x_1^*, x_2^*, x_3^*)$  is locally asymptotically stable for the system (4.5), and so is the corresponding equilibrium point  $X_\epsilon^* = (S^*, x_1^*, x_2^*, x_3^*)$  for the whole system (4.1) according to Fenichel's theory.

The same conclusion can be drawn for the case of a system with two species of microorganisms

$$(4.6) \quad \begin{cases} \epsilon \dot{S} = \bar{D}(1 - S) - \sum_{i=1}^2 \frac{1}{Y_i} f_i(S) x_i, \\ \dot{x}_i = h_i + (f_i(S) - k_i) x_i, \quad i = \overline{1, 2}. \end{cases}$$

Moreover, the Bendixson's criterion applied to the two dimensional reduced system excludes periodic solutions, and the local asymptotic stability of  $(x_1^*, x_2^*)$  is global by the Poincaré-Bendixson Theorem. We summarize these results in the following theorem.

**Theorem 9.** *For  $\epsilon$  sufficiently small, the 4-dimensional singularly perturbed model (4.1) has a unique positive equilibrium point which is locally asymptotically stable and the 3-dimensional singularly perturbed model (4.6) is uniformly persistent around a globally asymptotically equilibrium point.*

We give some numerical simulations which illustrate the robustness of the stability when  $\epsilon \rightarrow 1$ .

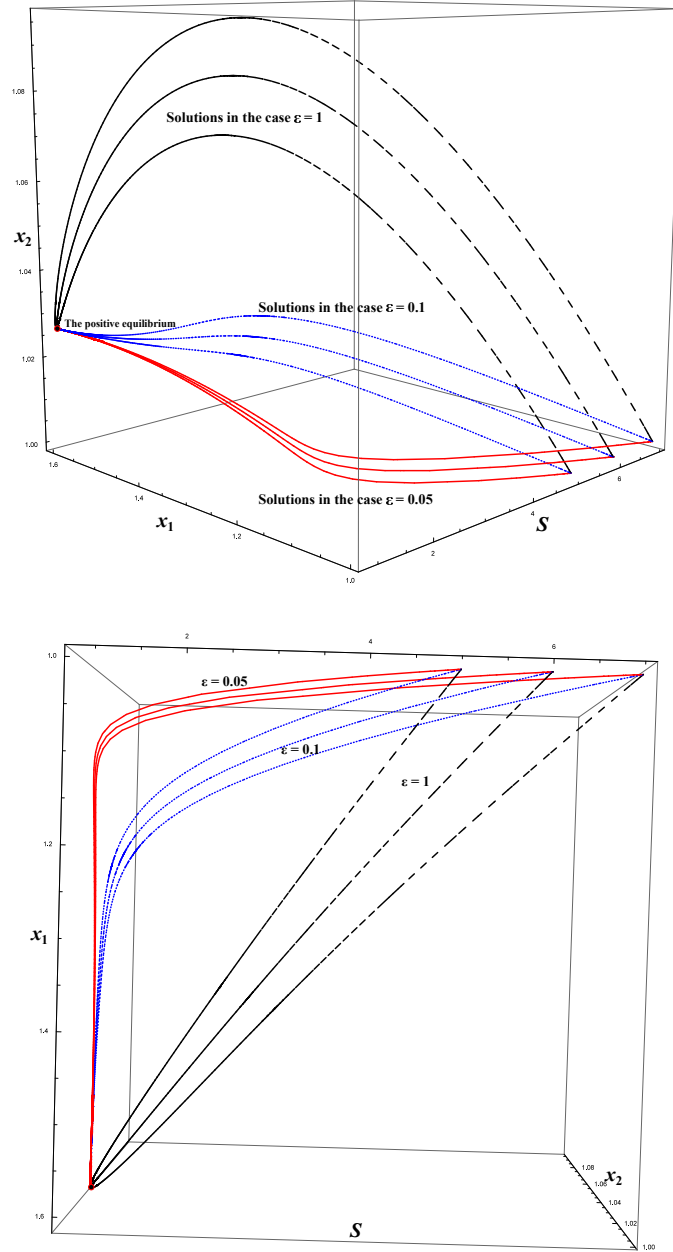


FIGURE 4.1. Two viewpoints of the phase portraits of system (4.6) for the increasing values of  $\epsilon$ , where  $f_1(S) = \frac{\mu_{\max}^1 S}{k_S^1 + S}$ ,  $f_2(S) = \frac{\mu_{\max}^2 S}{k_S^2 + S}$ ,  $k_S^1 = 50$ ,  $k_S^2 = 45$ ,  $\mu_{\max}^1 = 0.3$ ,  $\mu_{\max}^2 = 0.4$ ,  $\bar{Y}_1 = 0.5$ ,  $\bar{Y}_2 = 0.4$ ,  $k_1 = 0.1$ ,  $k_2 = 0.2$ ,  $\bar{D} = 0.15$ ,  $h_1 = 0.15$ ,  $h_2 = 0.2$ . The same interior equilibrium is globally stable. The second figure underlines the disappearance of the boundary layer (fast motion) when  $\epsilon$  increases. In the case  $\epsilon = 0.05$  the solutions converge exponentially fast toward the slow manifold then continues on it slowly.

## 5. THE RELATIONSHIP WITH AN OPEN PROBLEM OF COMPETITIVE EXCLUSION

In this section we study the case  $n = 2$ . For the sake of simplicity, we suppose  $h_i = h$ . Hence we consider the model

$$(5.1) \quad \begin{cases} \dot{S} = D(1 - S) - \sum_{i=1}^2 \frac{1}{Y_i} f_i(S) x_i, \\ \dot{x}_i = h + (f_i(S) - k_i) x_i, \end{cases} \quad i = 1, 2.$$

If we set  $h = 0$  we obtain the simple chemostat model

$$(5.2) \quad \begin{cases} \dot{S} = D(1 - S) - \sum_{i=1}^2 \frac{1}{Y_i} f_i(S) x_i, \\ \dot{x}_i = (f_i(S) - k_i) x_i, \end{cases} \quad i = 1, 2$$

Biologically, this approach could be made independent of the recycle problem by considering the following reasoning : one starts from the model (5.2) for which it is conjectured that the first species wins the competition, and than tries to obtain coexistence with a constant input of some species, namely those who were eliminated. In this case, the  $h_i$ 's could be different. That is exactly what Robledo et al. [11] recently presented by proposing a new chemostat model of competition of  $n$ -species, with constant input of some species and identical removal rates. They made use of reduction and polytopic Lyapunov functions.

Let us come back to our problem. First, we would like to understand how equilibria of the model (5.1) transform in the equilibria of (5.2). Regardless the biological meaning, we allow the  $x_i$ -components to be negative. The equilibria of (5.1) and (5.2) are :

Equilibria of (5.1)	Characteristics of the equilibria
$p_1 = (S_1^*, \frac{h}{k_1 - f_1(S_1^*)}, \frac{h}{k_2 - f_2(S_1^*)})$ positive	$S_1^* < \lambda_1 < \lambda_2, S_1^* < 1$
$p_2 = (S_2^*, \frac{h}{k_1 - f_1(S_2^*)}, \frac{h}{k_2 - f_2(S_2^*)})$ not positive	$\lambda_1 < S_2^* < \lambda_2$
$p_3 = (S_3^*, \frac{h}{k_1 - f_1(S_3^*)}, \frac{h}{k_2 - f_2(S_3^*)})$ not positive	$\lambda_1 < \lambda_2 < S_3^*, S_3^* > 1$
Equilibria of (5.2)	
	$q_1 = (\lambda_1, \frac{DY_1}{k_1}(1 - \lambda_1), 0)$
	$q_2 = (\lambda_2, 0, \frac{DY_2}{k_2}(1 - \lambda_2))$
	$q_3 = (1, 0, 0)$

where  $S^*$  is defined by (we omit the subscribes)

$$(5.3) \quad D(1 - S^*) - h \sum_{i=1}^2 \frac{f_i(S^*)/Y_i}{k_i - f_i(S^*)} = 0.$$

The Implicit Function Theorem implies that the equation (5.3) is locally a graph  $S^* = S^*(h)$ . Let us show how the limits  $\lim_{h \rightarrow 0} p_i(h), i = 1, 2, 3$  are related to the equilibria of (5.1).

From (5.3) we have

$$(5.4) \quad h(S^*) = D(S^* - 1)/(g_1(S^*) - g_2(S^*)),$$

where  $g_1(S) = \frac{f_1(S)/Y_1}{f_1(S) - k_1}$  and  $g_2(S) = -\frac{f_2(S)/Y_2}{f_2(S) - k_2}$ .

We plot the graphs of  $g_1(S)$  and  $g_2(S)$  on the same axes for the case of Monod type consumption functions. One can easily check that the graphs of the general functions  $g_1(S)$  and  $g_2(S)$  have globally the same aspect, see Fig.5.1. The intersections occur at  $R \in (\lambda_1, \lambda_2)$  and the sign of  $g_1(S^*) - g_2(S^*)$  is positive when  $S^* \in (\lambda_1, R) \cup (\lambda_2, \infty)$  and negative in  $(0, \lambda_1) \cup (R, \lambda_2)$ .

By implicit differentiation of (5.3) with respect to  $S^*$ , the slope is given by

$$h'(S^*) = \frac{1}{g_1(S^*) - g_2(S^*)} \left( D + h(S^*) \sum_{i=1}^2 \frac{k_i f'_i(S^*)/Y_i}{(f_i(S^*) - k_i)^2} \right).$$

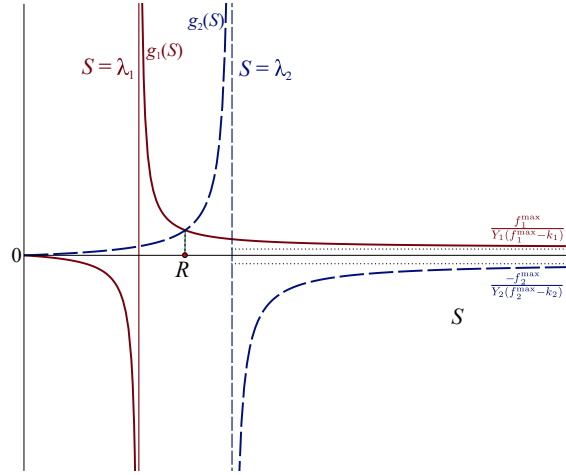


FIGURE 5.1. Sign of  $g_1(S) - g_2(S)$

Domains for which  $h > 0$  and sign of  $h'$ , when  $h > 0$ , can be summarized in the following table :

	$\lambda_1 < \lambda_2 < 1$	$\lambda_1 < 1 < \lambda_2$	$1 < \lambda_1 < \lambda_2$
$S_1^* < \lambda_1 < \lambda_2$ $S_1^* < 1$	$S_1^* < \lambda_1$ $h(S_1^*) \searrow$	$S_1^* < \lambda_1$ $h(S_1^*) \searrow$	$S_1^* < \lambda_1$ $h(S_1^*) \searrow$
$\lambda_1 < S_2^* < \lambda_2$	$\overline{R < S_2^* < \lambda_2}$ $h(S_2^*) \searrow$	$\min(R, 1) < S_2^* < \max(R, 1)$ $h(S_2^*) \searrow$ if $R > 1$ $h(S_2^*) \nearrow$ if $R < 1$	$\overline{R < S_2^* < \lambda_2}$ $h(S_2^*) \searrow$
$\lambda_1 < \lambda_2 < S_3^*$ $S_3^* > 1$	$\overline{S_3^* > 1}$ $h(S_3^*) \nearrow$	$S_3^* > \lambda_2$ $h(S_3^*) \nearrow$	$\overline{S_3^* > \lambda_2}$ $h(S_3^*) \nearrow$

TABLE 1. The over-lined inequalities represent the intervals in which  $h > 0$ . The sign  $\nearrow$  (resp.  $\searrow$ ) denotes increasing (resp. decreasing) functions. The first row of the table indicates the position of  $\lambda_1, \lambda_2$  with respect to 1, and the first column indicates the position of the first components of  $p_1, p_2$  and  $p_3$ .

The lecture of the columns of Table 1 permits to sketch the graphs of  $h(S^*)$  in the three considered cases. Fig.5.4 could have no biological meaning and is given

for completeness of the study. For our purpose, both Figs.5.2 and 5.3 explains how equilibria of (5.1) tend to those of (5.2) when  $h$  goes to zero positively. For example, when  $\lambda_1 < \lambda_2 < 1$ , the positive equilibrium  $p_1$  of (5.1) goes to the equilibrium  $q_1$  corresponding, in the classical chemostat (5.2), to the species with the smallest break-even concentration. The none positive equilibria  $p_2$  and  $p_3$  tend respectively to  $q_2$ , for which the first species goes extinct, and to the washout equilibrium  $q_3$ . The conclusion is the same when  $\lambda_1 < 1 < \lambda_2$  but  $p_2$  converges to the washout equilibrium and  $p_3$  converges to  $q_2$ . The different limits are summarized in Table 2.

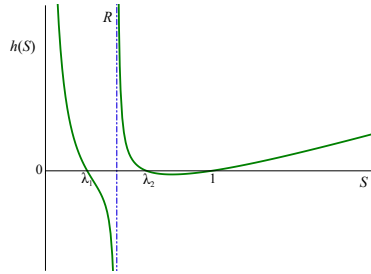


FIGURE 5.2. The graph of  $h(S^*)$  in the case  $\lambda_1 < \lambda_2 < 1$

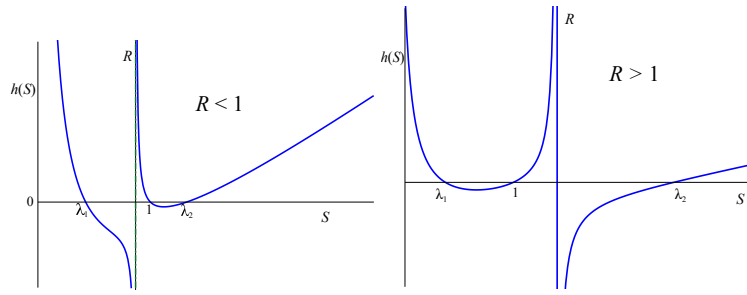


FIGURE 5.3. The graph of  $h(S^*)$  in the case  $\lambda_1 < 1 < \lambda_2$

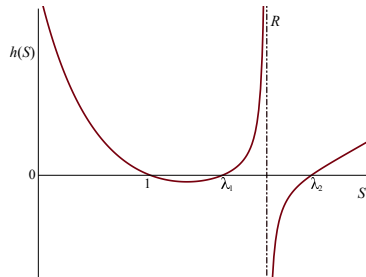


FIGURE 5.4. The graph of  $h(S^*)$  in the case  $1 < \lambda_1 < \lambda_2$

Then,

	$\lambda_1 < \lambda_2 < 1$	$\lambda_1 < 1 < \lambda_2$	$1 < \lambda_1 < \lambda_2$
$p_1(h) \xrightarrow{h \rightarrow 0}$	$q_1$	$q_1$	$q_3$
$p_2(h) \xrightarrow{h \rightarrow 0}$	$q_2$	$q_3$	$q_1$
$p_3(h) \xrightarrow{h \rightarrow 0}$	$q_3$	$q_2$	$q_2$

TABLE 2. The limits of  $p_1$ ,  $p_2$ , and  $p_3$ 

We now can state the following result :

**Theorem 10.** *Suppose that  $\lambda_1 < \lambda_2$  and  $\lambda_1 < 1$ , and consider the positive solutions of the equations (5.1) and (5.2). If  $p_1$  is GAS for the model (5.1) then  $q_1$  is GAS for the model (5.2).*

*Proof.* We explained before how  $p_1 \rightarrow q_1$  when  $h \rightarrow 0^+$ . On the other hand, Figs.5.2 and 5.3 could be considered as bifurcation diagrams for which  $h = 0$ , is clearly not a bifurcation value. Actually, such a value is negative and corresponds to the local minimum of  $h(S)$ . Hence, the limit preserves stability properties. The conclusion comes from the well known fact that the equilibria  $q_2$  and  $q_3$  are unstable in the positive direction so no positive trajectory can converge to one of them.  $\square$

This theorem is equivalent to the open problem mentioned above, at least for  $n = 2$ . Moreover, we can assert, according to Theorem 9 the following competitive exclusion result :

**Theorem 11.** *Suppose that, for  $i = 1, 2$ , the growth functions  $f_i : \mathbb{R}_+ \rightarrow \mathbb{R}_+$  are continuously differentiable and monotone increasing, with  $f_i(0) = 0$ . Consider the singularly perturbed model*

$$(5.5) \quad \begin{cases} \epsilon \dot{S} = D(1 - S) - \sum_{i=1}^2 \frac{1}{Y_i} f_i(S) x_i \\ \dot{x}_i = (f_i(S) - k_i) x_i \end{cases} \quad i = \overline{1, 2}$$

*and suppose that  $\lambda_1 < \lambda_2$  and  $\lambda_1 < 1$ . Then for  $\epsilon$  small enough, every positive solution  $(S(t), x_1(t), x_2(t))$  converges to  $q_1 = (\lambda_1, \frac{DY_1}{k_1}(1 - \lambda_1), 0)$ .*

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