Maintenance does not affect the stability of a two-tiered microbial 'food chain' *

Tewfik Sari † Jérôme Harmand‡

July 19, 2014

Abstract

Microbial food chains are present in anaerobic digestion where the different reaction steps can be seen as such: the waste products of the organisms on one trophic level (*i.e.* one reaction step) are consumed by organisms of the next trophic level (*i.e.* the next reaction step). In the present paper we study a model of a two-tiered microbial 'food chain' with feedback inhibition, which was recently presented as a stripped version of the anaerobic digestion model ADM1 of the International Water Association (IWA). It is known that in the absence of maintenance (or decay) the microbial 'food chain' is stable while its introduction in a number of models used in ecology may change their qualitative properties. In [7], using a purely numerical approach and ADM1 consensus parameter values, it was shown that the model remains stable when decay terms are added. However, authors could not prove in full generality it remains true for other parameter values. In this paper we prove that introducing decay in the model preserves stability whatever its parameters values are and for a wide range of kinetics.
Keywords: Anaerobic digestion, Syntrophic relationship, Maintenance, Stability

1 Introduction

Anaerobic digestion is a process that converts organic matter into a gaseous mixture composed mainly of methane and carbon dioxide through the action of a complex bacterial ecosystem. It is often used for the treatment of concentrated wastewater or to convert the excess sludge produced in wastewater treatment plants into more stable products [5]. One of its advantages is that the methane produced can be used profitably as a source of energy. It is usually considered that a number of metabolic

*This work was supported by the *Treasure* network, `http://www.treasure.fr`

†*Corresponding author*: `tewfik.sari@irstea.fr`. Irstea, UMR Itap, 361 rue Jean-François Breton, 34196 Montpellier France & Université de Haute Alsace, 4 rue des Frères Lumière, 68093 Mulhourse, France.

‡INRA, UR050, Laboratoire de Biotechnologie de l'Environnement, Avenue des Etangs, Narbonne F-11100, France & Projet Modemic, Inra/Inria, UMR Mistea, 2 place Pierre Viala 34060 Montpellier, France

groups of bacteria are involved sequentially in several conversion steps to finally produce methane and carbon dioxide. Typically, the product of one conversion step is the substrate for the next organism in the chain, each organism consuming the waste product(s) of its predecessor.

The anaerobic digestion model no. 1 (ADM1) of the IWA Task Group for Mathematical Modeling of Anaerobic Digestion Processes [1, 4] is too complex to permit mathematically analysis of its nonlinear dynamics and only numerical investigations are available [2]. In order to make the mathematical analysis possible a model with a two-tiered microbial 'food chain' with feedback inhibition, which encapsulates the essence of methanogenic degradation process was proposed [7]. This model which is presented by Xu *et al.* [7] as a stripped down version of ADM1, considers the syntrophic associations between propionate degraders and methanogens. It includes option for maintenance (or decay). Maintenance is the consumption of energy for all processes other than growth: it is modeled either in adding a negative term on the substrate dynamic without associating it to growth or in considering a decay term on the biomass dynamics. Considering the latter modeling option and according to the Routh-Hurwitz criteria, it was shown that the non-trivial steady state is not necessarily stable. In addition simulation results with the ADM1 consensus values indicate that the positive equilibrium is always stable whenever it exists. For the operators of anaerobic wastewater treatment systems the results of [7] show that the syntrophic associations between propionate degraders and methanogens are inherently stable under realistic environmental conditions. However, the possibility of an unstable positive equilibrium was not excluded for other parameter values and the title of [7], *Maintenance affects the stability of a two-tiered microbial 'food chain'?* leaves unanswered the question of the effects of maintenance from a more general viewpoint. The aim of this paper is to show that for any values of the parameters the positive steady state is stable as long as it exists, that is to say, *maintenance does not affect the stability of the considered two-tiered microbial 'food chain'.*

2 A two-tiered microbial 'food chain' [7]

The model considered in [7] involves a two-tiered microbial 'food chain' with feedback inhibition, consisting of a propionate degrader and a hydrogenotrophic methanogen. The propionate degradation produces hydrogen which inhibits its own growth. Using the notations of ADM1 the model can be written as

$$\left\{\begin{array}{lcl} \dfrac{dS_{pro}}{dt} & = & D\left(S_{pro,in}-S_{pro}\right)-f_0\left(S_{pro},S_{H2}\right)X_{pro} \\ \dfrac{dX_{pro}}{dt} & = & -DX_{pro}+Y_{pro}f_0\left(S_{pro},S_{H2}\right)X_{pro}-k_{dec,pro}X_{pro} \\ \dfrac{dS_{H2}}{dt} & = & -DS_{H2}+0.43\left(1-Y_{pro}\right)f_0\left(S_{pro},S_{H2}\right)X_{pro}-f_1\left(S_{H2}\right)X_{H2} \\ \dfrac{dX_{H2}}{dt} & = & -DX_{H2}+Y_{H2}f_1\left(S_{H2}\right)X_{H2}-k_{dec,H2}X_{H2} \end{array}\right. \tag{1}$$

where S_{pro} and X_{pro} are propionate substrate and biomass concentrations; S_{H2} and X_{H2} are those for hydrogen; Y_{pro} and Y_{H2} are the Yield coefficients and $0.43\left(1-Y_{pro}\right)$

represents the part which goes to hydrogen substrate. Both growth functions take Monod form with an hydrogen inhibition for the first one

$$f_0\left(S_{pro},S_{H2}\right)=\frac{k_{m,pro}S_{pro}}{K_{s,pro}+S_{pro}}\frac{1}{1+\frac{S_{H2}}{K_{I,H2}}},\qquad f_1\left(S_{H2}\right)=\frac{k_{m,H2}S_{H2}}{K_{s,H2}+S_{H2}}\tag{2}$$

Here apart from the two operating (or control) parameters, which are the inflowing propionate concentration $S_{pro,in}$ and the dilution rate D, that can vary, all others have biological meanings and are fixed depending on the organisms and substrate considered, see [7], Table 1. After applying the following rescaling of substrate and biomass concentrations

$$s_0=\frac{S_{pro}}{K_{s,pro}},\quad x_0=\frac{X_{pro}}{K_{s,pro}Y_{H2}},\quad s_1=\frac{S_{H2}}{K_{s,H2}},\quad x_1=\frac{X_{H2}}{K_{s,H2}Y_{H2}}\tag{3}$$

and for time and operating parameters

$$\tau=k_{m,pro}Y_{pro}t,\quad \alpha=\frac{D}{k_{m,pro}Y_{pro}},\quad u_f=\frac{S_{pro,in}}{K_{s,pro}}\tag{4}$$

we have the following dimensionless system

$$\left\{\begin{array}{lcl}\dfrac{ds_0}{d\tau}&=&\alpha(u_f-s_0)-\mu_0(s_0,s_1)x_0\\ \dfrac{dx_0}{d\tau}&=&-\alpha x_0+\mu_0(s_0,s_1)x_0-Ax_0\\ \dfrac{ds_1}{d\tau}&=&-\alpha s_1+\omega\mu_0(s_0,s_1)x_0-\mu_1(s_1)x_1\\ \dfrac{dx_1}{d\tau}&=&-\alpha x_1+\mu_1(s_1)x_1-Bx_1\end{array}\right.\tag{5}$$

where

$$\mu_0\left(s_0,s_1\right)=\frac{s_0}{1+s_0}\frac{1}{1+\frac{s_1}{K_I}},\qquad \mu_1\left(s_1\right)=\frac{\phi s_1}{1+s_1}\tag{6}$$

and A, B, ω, ϕ and K_I are constant which are calculated explicitly with respect to the biological parameters of the original model (1), see [7] for the details.

The aim of [7] was to to study the stability of the steady states of the model (5) while varying the two operating (or control) parameters u_f and α. The system (5) can have at most three steady state: a trivial solution where both populations are washed out (SS0: $x_0=0$, $x_1=0$), a solution where x_1 is washed out while x_0 survives (SS1: $x_0>0$, $x_1=0$) and a positive solution where both populations survive (SS2: $x_0>0$, $x_1>0$). The local stability of each steady state was tested by linearization around the steady state values of the variables.

The basic results of the analysis of [7] are: for any pair of values of operating parameters, at most one steady state is stable. When one of the decay effect is not taken into account, i.e. $A=0$ or $B=0$ in (5), there is always one and only one steady state which is stable and SS2 is stable as long as it exists. When both decay effects are taken into account, i.e. $A>0$ and $B>0$ in (5), the authors were note able to check all the Routh-Hurwitz criteria for SS2. They claimed that SS2 can be unstable when it exists and they established numerically that with the ADM1 parameters values, SS2 is stable as long as it exists. However they did not give any values for the biological parameters for which, under some operating parameters, SS2 becomes unstable. Actually, we prove in this paper that, for all values of the parameters, and for a general class of growth functions, as long as they keep the signs of their derivatives, the positive SS is stable whenever it exits, which actually gives an answer for the title of [7].

3 The model

Since we want to study the model (1) with general growth functions, we will first use the following simplified notations in this model

$$S_0 = S_{pro}, \quad S_0^{in} = S_{pro,in}, \quad S_1 = S_{H2}, \quad X_0 = X_{pro}, \quad X_1 = X_{H2}$$

$$Y_0 = Y_{pro}, \quad Y_1 = Y_{H2}, \quad Y_2 = 0.43\,(1 - Y_{pro})\,, \quad A = k_{dec,pro}, \quad B = k_{dec,H2}$$

We obtain the following system

$$\left\{\begin{array}{rcl} \dfrac{dS_0}{dt} & = & D\,(S_0^{in} - S_0) - f_0\,(S_0, S_1)\,X_0 \\ \dfrac{dX_0}{dt} & = & -DX_0 + Y_0 f_0\,(S_0, S_1)\,X_0 - AX_0 \\ \dfrac{dS_1}{dt} & = & -DS_1 + Y_2 f_0\,(S_0, S_1)\,X_0 - f_1\,(S_1)\,X_1 \\ \dfrac{dX_1}{dt} & = & -DX_1 + Y_1 f_1\,(S_1)\,X_1 - BX_1 \end{array}\right. \tag{7}$$

Notice that we do not assume any specific analytical expression for the growth functions and inhibition (2). Our analysis will use only the following general assumptions on the growth functions $f_0\,(S_0, S_1)$ and $f_1\,(S_1)$:

A1 For all $S_0 > 0$ and $S_1 \geq 0$, $f_0\,(S_0, S_1) > 0$ and $f_0\,(0, S_1) = 0$.

A2 For all $S_1 > 0$, $f_1\,(S_1) > 0$ and $f_1(0) = 0$.

A3 For all $S_0 > 0$ and $S_1 > 0$, $\dfrac{\partial f_0}{\partial S_0}\,(S_0, S_1) > 0$ and $\dfrac{\partial f_0}{\partial S_1}\,(S_0, S_1) < 0$.

A4 For all $S_1 > 0$, $\dfrac{df_1}{dS_1}\,(S_1) > 0$.

Hypothesis **A1** signifies that no growth can take place for species X_0 without the substrate S_0. Hypothesis **A1** means that the intermediate product S_1 is necessary for the growth of species X_1. Hypothesis **A3** means that the growth rate of species X_0 increases with the substrate S_0 but it is self-inhibited by the intermediate product S_1. Hypothesis **A4** means that the growth of species X_1 increases with intermediate product S_1 produced by species X_0. Note that this defines a syntrophic relationship between the two species.

The dimensionless rescaling (3,4) of [7] uses the biological parameters $K_{s,pro}$, $K_{s,H2}$ and $k_{m,pro}$ in the growth functions (2). Since we deal with general growth functions, we cannot benefit from this dimensionless rescaling. However, to ease the mathematical analysis of the system, we can rescale system (7) using the following change of variables adapted from [6]:

$$s_0 = Y_2 S_0, \quad x_0 = \frac{Y_2}{Y_0} X_0, \quad s_1 = S_1, \quad x_1 = \frac{1}{Y_1} X_1, \quad s_0^{in} = Y_2 S_0^{in}$$

We obtain the following system

$$\begin{cases} \dfrac{ds_0}{dt} &= D(s_0^{in} - s_0) - \mu_0(s_0, s_1)x_0 \\ \dfrac{dx_0}{dt} &= -Dx_0 + \mu_0(s_0, s_1)x_0 - Ax_0 \\ \dfrac{ds_1}{dt} &= -Ds_1 + \mu_0(s_0, s_1)x_0 - \mu_1(s_1)x_1 \\ \dfrac{dx_1}{dt} &= -Dx_1 + \mu_1(s_1)x_1 - Bx_1 \end{cases} \tag{8}$$

where μ_0 and μ_1 are defined by

$$\mu_0(s_0, s_1) = Y_0 f_0\left(\frac{1}{Y_2}s_0, s_1\right) \quad \text{and} \quad \mu_1(s_2) = Y_1 f_1(s_1) \tag{9}$$

This system has the same structure as the model (5) of [7] except that it runs for the original time t and that the coefficient ω of Xu's model is equal to 1 in our model (8). Moreover the functions μ_0 and μ_1 do not follow Monod kinetics (6), but are general functions with their own properties. Since the functions f_0 and f_1 satisfy hypotheses **A1**–**A3**, it follows from (9) that functions μ_0 and μ_1 satisfy :

H1 For all $s_0 > 0$ and $s_1 \geq 0$, $\mu_0(s_0, s_1) > 0$ and $\mu_0(0, s_1) = 0$.

H2 For all $s_1 > 0$, $\mu_1(S_1) > 0$ and $\mu_1(0) = 0$.

H3 For all $s_0 > 0$ and $s_1 > 0$, $\dfrac{\partial \mu_0}{\partial s_0}(s_0, s_1) > 0$ and $\dfrac{\partial \mu_0}{\partial s_1}(s_0, s_1) < 0$.

H4 For all $s_1 > 0$, $\dfrac{d\mu_1}{ds_1}(s_1) > 0$.

It should be noticed that the model (8) was studied in [3, 6] in the case where maintenance effects are not taken into account, i.e. $A = 0$ and $B = 0$. We can easily prove that that for every non-negative initial conditions, the solution of system (8) has non-negative components and is positively bounded and thus is defined for every positive t.

4 Steady state and stability analysis

A steady state of (8) is a solution of the following nonlinear algebraic system obtained from (8) by setting the right-hand sides equal to zero:

$$D(s_0^{in} - s_0) - \mu_0(s_0, s_1)x_0 = 0 \tag{10}$$

$$-Dx_0 + \mu_0(s_0, s_1)x_0 - Ax_0 = 0 \tag{11}$$

$$-Ds_1 + \mu_0(s_0, s_1)x_0 - \mu_1(s_1)x_1 = 0 \tag{12}$$

$$-Dx_1 + \mu_1(s_1)x_1 - Bx_1 = 0 \tag{13}$$

A steady state exists (or is said to be 'meaningful' [7]) if and only if all its components are non-negative. From equation (11) we deduce that

$$x_0 = 0 \quad \text{or} \quad \mu_0(s_0, s_1) = D + A \tag{14}$$

and from equation (13) we deduce that

$$x_1 = 0 \quad \text{or} \quad \mu_1(s_1) = D + B \tag{15}$$

The case $x_0 = 0$ and $x_1 \neq 0$ is excluded. Indeed, as a consequence of (15), $\mu_1(s_1) = D + b$ and, as a consequence of (12), $Ds_1 + (D+B)x_1 = 0$. Thus $s_1 = -\frac{D+B}{D}x_1 < 0$, which is impossible. Therefore three cases must be distinguished

SS0: $x_0 = 0$, $x_1 = 0$ where both species are washed out.

SS1: $x_0 > 0$, $x_1 = 0$, where species x_1 is washed out while x_0 survives.

SS2: $x_0 > 0$, $x_1 > 0$, where both species survives.

For the description of the steady states and their stability, we need the following notations. Since the function $s_1 \mapsto \mu_1(s_1)$ is increasing, it has an inverse function $y \mapsto M_1(y)$, so that

$$s_1 = M_1(y) \Longleftrightarrow y = \mu_1(s_1) \text{ for all } s_1 \text{ and } y \tag{16}$$

Let s_1 be fixed. Since the function $s_0 \mapsto \mu_0(s_0, s_1)$ is increasing, it has an inverse function $y \mapsto M_0(y, s_1)$, so that

$$s_0 = M_0(y, s_1) \Longleftrightarrow y = \mu_0(s_0, s_1) \text{ for all } s_0,\ s_1 \text{ and } y \tag{17}$$

We define the functions

$$F_0(D) = M_0(D + A, 0), \quad F_1(D) = M_1(D + B) + M_0(D + A, M_0(D + B)) \tag{18}$$

Notice that $F_1(D) > F_0(D)$ for all $D \geq 0$, as long as they are both defined with the exception $F_1(0) = F_0(0)$, which holds if and only if $A = B = 0$. Now, we can describe the steady states of (8).

Proposition 1. *Assume that assumptions* **H1**-**H4** *hold. Then (8) has at most three steady states:*

- *SS0=*$(s_0 = s_0^{in}, x_0 = 0, s_1 = 0, x_1 = 0)$
  It always exists. It is stable if and only if $s_0^{in} < F_0(D)$.

Steady state	Existence condition	Stability condition
SS0	Always exists	$s_0^{in} < F_0(D)$
SS1	$s_0^{in} > F_0(D)$	$s_0^{in} < F_1(D)$
SS2	$s_0^{in} > F_1(D)$	Always Stable

Table 1: Existence and local stability of steady states.

- *SS1*$=\left(s_0, x_0 = \frac{D\left(s_0^{in}-s_0\right)}{D+A}, s_1 = s_0^{in} - s_0, x_1 = 0\right)$
  where s_0 *is the solution of equation* $\mu_0(s_0, s_0^{in} - s_0) = D + A$*. It exists if and only if* $s_0^{in} > F_0(D)$*. It is stable if and only if* $s_0^{in} < F_1(D)$*.*
- *SS2*$=\left(s_0, x_0 = \frac{D\left(s_0^{in}-s_0\right)}{D+A}, s_1, x_1 = \frac{D\left(s_0^{in}-s_0-s_1\right)}{D+B}\right)$
  where $s_1 = M_1(B + D)$ *and* $s_0 = M_0\left(D + A, M_1(B + D)\right)$*. It exists if and only if* $s_0^{in} > s_0 + s_1 = F_2(D)$*. It is stable if it exists.*

The proof is given in Appendix A.

Notice that SS1 exists as soon as SS0 becomes unstable and SS2 exists as soon as SS1 becomes unstable. One concludes that for any value of the operating parameters, there is always one, and only one, steady state which is stable. The results are summarized in Table 1. When decay effects are not taken into account, i.e. $A = 0$ and $B = 0$, the system can be reduced to a planar system and global stability results can be obtained, see [3] and [6], Section 5.1: for any pair of operating parameters, there is always one, and only one, steady state which is globally asymptotically stable.

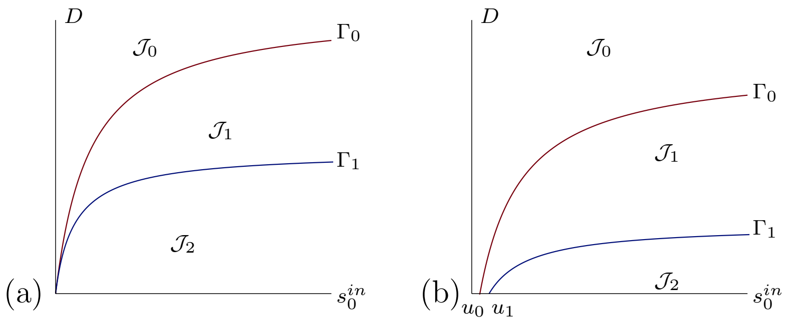

Figure 1: Operating diagram without (a) and with (b) maintenance effects.

5 Operating diagram

The operating diagram shows how the system behaves when we vary the two control parameters S_0^{in} and D. Let $F_0(D)$ and $F_1(D)$ be the functions defined by (18). The curve Γ_0 of equation $s_0^{in} = F_0(D)$ is the border which makes SS0 unstable and at the same time SS1 exists (the red curve on Fig. 1). The curve Γ_1 of equation

Condition	Region	SS0	SS1	SS2
$s_0^{in} < F_0(D)$	$(s_0^{in}, D) \in \mathcal{J}_0$	S		
$F_0(D) < s_0^{in} < F_1(D)$	$(s_0^{in}, D) \in \mathcal{J}_1$	U	S	
$F_1(D) < s_0^{in}$	$(s_0^{in}, D) \in \mathcal{J}_2$	U	U	S

Table 2: Existence and local stability of steady states. The letter S (resp. U) means stable (resp. unstable). No letter means that the steady state does not exist.

$s_0^{in} = F_1(D)$ is the border which makes SS1 unstable and at the same time SS2 exists (the blue curve on Fig. 1). The curves Γ_0 and Γ_1 separate the operating plane (s_0^{in}, D) in three regions, as shown in Fig. 1, labeled $\mathcal{J}_0$, $\mathcal{J}_1$ and $\mathcal{J}_2$. The results of Prop. 1 are summarized in Table 2 which shows the existence and stability of the steady states SS0, SS1 and SS2 in the regions $\mathcal{J}_0$, $\mathcal{J}_1$ and $\mathcal{J}_2$ of the operating diagram.

The values u_0 and u_1 plotted on the figure are obtained as follows:

$$u_0 = F_0(0) = M(A, 0), \qquad u_1 = F_1(0) = \beta + M(A, \beta), \text{ where } \beta = M_1(B)$$

If $A \geq \sup_{s_0>0} \mu_0(s_0, 0)$, $F_0(0)$ is not defined and we let $u_0 = +\infty$. In this case the regions $\mathcal{J}_1$ and $\mathcal{J}_2$ are empty. If $B < \sup_{s_1>0} \mu_1(s_1)$ or $A \geq \sup_{s_0>0} \mu_0(s_0 - \beta, \beta)$, $F_1(0)$ is not defined and we let $u_1 = +\infty$. In this case the region $\mathcal{J}_2$ is empty. When maintenance effects are not taken into consideration (i.e. $A = B = 0$), then $u_0 = u_1 = 0$ and we have

$$F_0(D) = M(D, 0), \qquad F_1(D) = M_1(D) + M_0(D, M_1(D))$$

6 An example

We illustrate our results for the two-tiered microbial 'food chain' (1)-(2) considered in Section 2: we consider our general model (8) with Monod growth function

$$\mu_0(s_0, s_1) = \frac{m_0 s_0}{K_0 + s_0} \frac{1}{1 + s_1/K_i}, \qquad \mu_1(s_1) = \frac{m_1 s_1}{K_1 + s_1} \tag{19}$$

In this case the inverse functions $M_1(y)$ and $y \mapsto M_0(y, s_1)$ of the functions $\mu_1(s_1)$ and $s_0 \mapsto \mu_0(s_0, s_1)$ can be calculated explicitly:

$$M_1(y) = \frac{K_1 y}{m_1 - y}, \qquad M_0(y, s_1) = \frac{K_0 y}{\frac{m_0}{1+s_1/K_i} - y}$$

Therefore, the functions $F_1(D)$ and $F_2(D)$ defined by (18) are given explicitly by

$$F_0(D) = \frac{K_0(D + A)}{m_1 - D - A}, \quad F_1(D) = \frac{K_1(D + B)}{m_1 - D - B} + \frac{K_0(D + A)}{\frac{m_0}{1+\frac{K_1(D+B)}{(m_1-D-B)K_i}} - D - A} \tag{20}$$

On the other hand, the solution s_0 of equation $\mu_0(s_0, s_0^{in} - s_0) = D + A$ which is used in SS1 is simply the positive solution of the quadratic equation

$$m_0 s_0 = (D + A)(K_0 + s_0)\left(1 + \frac{s_0^{in} - s_0}{K_i}\right) \tag{21}$$

As a corollary of Proposition 1 we have the following result.

Proposition 2. *Let $F_0(D)$ and $F_1(D)$ be defined by (20). The system (8-19) has at most three steady states*

- *SS0=$(s_0 = s_0^{in}, x_0 = 0, s_1 = 0, x_1 = 0)$*
  It always exists. It is stable if and only if $s_0^{in} < F_0(D)$.
- *SS1=$\left(s_0, x_0 = \frac{D\left(s_0^{in} - s_0\right)}{D+A}, s_1 = s_0^{in} - s_0, x_1 = 0\right)$*
  where s_0 is the positive solution of the quadratic equation (21). It exists if and only if $s_0^{in} > F_0(D)$. If it exists then it is stable if and only if $s_0^{in} < F_1(D)$.
- *SS2=$\left(s_0, x_0 = \frac{D\left(s_0^{in} - s_0\right)}{D+A}, s_1, x_1 = \frac{D\left(s_0^{in} - s_0 - s_1\right)}{D+B}\right)$*
  where
  $$s_1 = \frac{K_1(D + B)}{m_1 - D - B}, \qquad s_0 = \frac{K_0(D + A)}{\frac{m_0}{1 + \frac{K_1(D+B)}{(m_1 - D - B)K_i}} - D - A}$$
  It exists if and only if $s_0^{in} > s_0 + s_1 = F_1(D)$. It is stable if it exists.

Using the rescaling (9) and the biological parameters in (2) we obtain

$$m_0 = Y_0 k_{m,pro}, \quad K_0 = Y_2 K_{s,pro}, \quad K_i = K_{I,H2}, \quad m_1 = Y_1 k_{m,H2}, \quad K_1 = K_{s,H2} \tag{22}$$

For the numerical simulations we will use the nominal values of Table 3 obtained from Table 1 of [7] by using the formulas (22). For these values of the parameters,

Parameters	Units	Nominal Value
m_0	d^{-1}	0.52
K_0	kg COD/m^3	0.124
m_1	d^{-1}	2.10
K_1	kg COD/m^3	$2.5\ 10^{-5}$
K_i	kg COD/m^3	$3.5\ 10^{-6}$
A	d^{-1}	0.02
B	d^{-1}	0.02

Table 3: Nominal parameters values.

the values u_0 and u_1 are very small, see Fig. 2. Notice that the scaling on the two coordinates in Fig. 2 are different from those of Fig. 2 of [7], since the authors used the dimensionless rescaling (4).

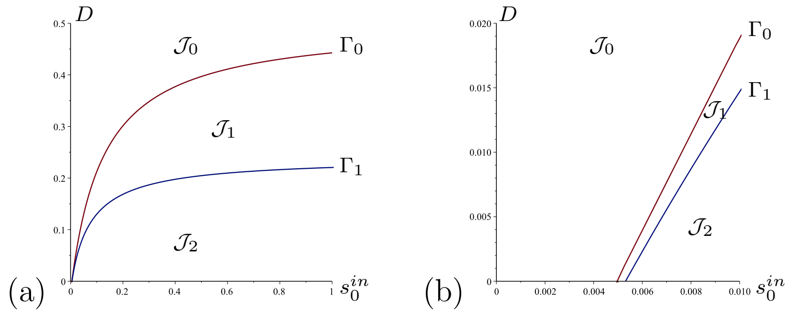

Figure 2: Operating diagram of the model (8)-(19). (a) The model was parametrized with the ADM1 consensus values listed in Table 3. (b) A zoom showing the values $u_0 = 49.6\,10^{-4}$, $u_1 = 53.1\,10^{-4}$.

7 Discussion

Following [7], we considered a two-tiered food chain with feedback inhibition, which is a generalized model describing the syntrophic interaction of a propionate degrader and a hydrogenotropic methagogen. In the absence of maintenance [7] proved that their two-tiered food chain is always stable, but suggested that when maintenance is included in the model the two-tiered generalized food chain is not necessarily stable. However, using the consensus parameters of ADM1 and numerical simulations, they have shown that the model of the methanogenic two-tiered propionate-hydrogen food chain is always stable. They noticed that direct application of symbolic analysis programs, such as Maple or Mathematica, turned out fruitless. In this work we have generalized the model of the two-tiered food chain of [7] by considered generic growth functions and we established the stability of the generalized model with maintenance terms.

In this two-tiered 'food chain', the first species x_0 uses the substrate s_0 for its growth and produces a substrate s_1 consumed by the second species x_1 for its growth. The substrate s_1 produced by the first species inhibits its own growth, that is, the growth function $\mu_0(s_0, s_1)$ is decreasing with respect to s_1. In practice, the second species is also inhibited by the excess of the first substrate. Thus it is interesting to consider the case where the second species is inhibited by the substrate s_0, that is in considering that $\mu_1(s_0, s_1)$ also depends on s_0 and is decreasing with respect to s_0. It has been recently shown in [6] that the introduction of this last inhibiting relationship in the model completely changes the model properties while maintenance was not considered. In particular, the modified model exhibits multiplicity of positive steady state. However it should be stressed that these results were very general: whether this instability occurs for realistic environmental conditions or not is under investigation.

A Steady states

We give the proof of Prop. 1. A steady state (s_0, x_0, s_1, x_1) of (8) is a solution of the set of algebraic equations (10-13). The local stability of each steady state depends on the sign of the real parts of the eigenvalues of the corresponding Jacobian matrix for the system (8). This is the matrix of the partial derivatives of the right hand side with respect to the state variables evaluated at the given steady state (s_0, x_0, s_1, x_1), that is

$$J = \begin{bmatrix} -D - Ex_0 & -\mu_0 & Fx_0 & 0 \\ Ex_0 & \mu_0 - D - A & -Fx_0 & 0 \\ Ex_0 & \mu_0 & -D - Fx_0 - Gx_1 & -\mu_1 \\ 0 & 0 & Gx_1 & \mu_1 - D - B \end{bmatrix} \quad (23)$$

where

$$E = \frac{\partial \mu_0}{\partial s_0}(s_0, s_1) > 0, \quad F = -\frac{\partial \mu_0}{\partial s_1}(s_0, s_1) > 0, \quad G = \frac{d\mu_1}{ds_1}(s_1) > 0$$

The eigenvalues of J are the roots of its characteristic polynomial $\det(J - \lambda I)$. Notice that we have used the opposite sign for the partial derivative $F = -\frac{\partial \mu_0}{\partial s_1}(s_0, s_1)$, so that all constants involved in the computations become positive, which will simplify the analysis of the characteristic polynomial of J.

SS0: $x_0 = 0$, $x_1 = 0$. As a result of (10) and (12), $s_0 = s_0^{in}$ and $s_1 = 0$. SS0 always exists. Evaluated at SS0, the Jacobian matrix (23) becomes

$$J = \begin{bmatrix} -D & -\mu_0(s_0^{in}, 0) & 0 & 0 \\ 0 & \mu_0(s_0^{in}, 0) - D - A & 0 & 0 \\ 0 & \mu_0(s_0^{in}, 0) & -D & 0 \\ 0 & 0 & 0 & -D - B \end{bmatrix}$$

Its eigenvalues are $\lambda_1 = \mu_0(s_0^{in}, 0) - D - A$, $\lambda_2 = -D - B$ and $\lambda_3 = \lambda_4 = -D$. For being stable we need $\lambda_1 < 0$. Therefore SS0 is unstable if and only if

$$\mu_0(s_0^{in}, 0) > D + A \quad (24)$$

that is $s_0^{in} > M_0(D + A, 0) = F_0(D)$.

SS1: $x_0 \neq 0$, $x_1 = 0$. As a consequence of (14) $\mu_0(s_0, s_1) = D + A$. As a result of (10) and (12)

$$D(s_0^{in} - s_0) = \mu_0(s_0, s_1)x_0 \quad \text{and} \quad Ds_1 = \mu_0(s_0, s_1)x_0$$

Hence $x_0 = \frac{D\left(s_0^{in} - s_0\right)}{D+A}$ and $D(s_0^{in} - s_0) = Ds_1$, so that $s_0 + s_1 = s_0^{in}$. Therefore s_0 is a solution of equation

$$\mu_0(s_0, s_0^{in} - s_0) = D + A \quad (25)$$

SS1 exists if and only if this equation has a solution in the interval $(0, s_0^{in})$. The function $s_0 \mapsto \psi(s_0) = \mu_0(s_0, s_0^{in} - s_0)$ is increasing since its derivative $\frac{d\psi}{ds_0} = \frac{\partial \mu_0}{\partial s_0} - \frac{\partial \mu_0}{\partial s_1} >$ is positive. Using $\psi(0) = 0$ and $\psi(s_0^{in}) = \mu(s_0^{in}, 0)$ we conclude that equation (25) has a solution in the interval $(0, s_0^{in})$ if and only if $\psi(s_0^{in}) = \mu(s_0^{in}, 0) > D + A$, that is to say condition (24) holds. The condition of existence of SS1 is then

equivalent to the condition of instability of SS0.
Evaluated at SS1, the Jacobian matrix (23) becomes

$$J = \begin{bmatrix} -D-Ex_0 & -D-A & Fx_0 & 0 \\ Ex_0 & 0 & -Fx_0 & 0 \\ Ex_0 & -D-A & -D-Fx_0 & -\mu_1 \\ 0 & 0 & 0 & \mu_1 - D - B \end{bmatrix}$$

Its characteristic polynomial is

$$\det(J-\lambda I) = (\lambda-\mu_1+D+B)(\lambda+D)\left(\lambda^2 + [D+(E+F)x_0]\,\lambda + (D+A)(E+F)x_0\right)$$

Its eigenvalues are $\lambda_1 = \mu_1 - D - B$, $\lambda_2 = -D$ and λ_3 and λ_4 are the roots of the following quadratic equation

$$\lambda^2 + [D+(E+F)x_0]\,\lambda + (D+A)(E+F)x_0 = 0$$

Since $\lambda_3\lambda_4 = (D+A)(E+F)x_0 > 0$ and $\lambda_3+\lambda_4 = -\left[D+(E+F)x_0\right] < 0$, the real parts of λ_3 and λ_4 are negative. So for being stable it must be $\lambda_1 < 0$. Therefore SS1 is stable if and only if

$$\mu_1(s_0^{in} - s_0) < D + B, \text{ where } s_0 \text{ is the solution of (25)} \tag{26}$$

Since the function $s_1 \mapsto \mu_1(s_1)$ is increasing, we have the following equivalence

$$\mu_1(s_0^{in} - s - 0) < D + B \Longleftrightarrow s_0 < s_0^{in} - M_1(D+B)$$

Since the function $s_0 \mapsto \psi(s_0) = \mu_0\left(s_0, s_0^{in} - s_0\right)$ is decreasing, we deduce that $\psi\left(s_0\right) > \psi\left(s_0^{in} - M_1(D+B)\right)$. Since s_0 be the solution of (25),

$$\psi((s_0) = \mu_0\left(s_0, s_0^{in} - s_0\right) = D + A$$

Therefore, the condition (26) of stability of SS1 is equivalent to

$$D + A < \mu_0\left(s_0^{in} - M_1(D+B), M_1(D+B)\right)$$

that is $s_0^{in} - M_1(D+B) < M_0\left(D+A, M_1(D+B)\right)$ which is equivalent to

$$s_0^{in} < M_1(D+A,0) + M_0\left(D+A, M_1(D+B)\right) = F_1(D)$$

SS2: $x_0 \neq 0$, $x_1 \neq 0$. As a consequence of (14) and (15) s_0 and s_1 are solutions of the set of equations

$$\mu_0(s_0, s_1) = D + A, \qquad \mu_1(s_1) = D + B$$

Using (16) we obtain $s_1 = M_1(D+B)$ and s_0 is a solution of equation

$$\mu_0\left(s_0, M_1(D+B)\right) = D + A \tag{27}$$

Using (17) we obtain $s_0 = M_0\left(D+A, M_1(D+B)\right)$. As a result of (10) and (12)

$$x_0 = \frac{D\left(s_0^{in} - s_0\right)}{D+A}, \qquad x_1 = \frac{D\left(s_0^{in} - s_0 - s_1\right)}{D+B}$$

SS2 exists if and only if $s_0^{in} > s_0 + s_1$, that is

$$s_0^{in} > M_1(D+B) + M_0\left(D+A, M_1(D+B)\right) = F_1(D)$$

Evaluated at SS2, the Jacobian matrix (23) becomes

$$J = \begin{bmatrix} -D-Ex_0 & -D-A & Fx_0 & 0 \\ Ex_0 & 0 & -Fx_0 & 0 \\ Ex_0 & D+A & -D-Fx_0-Gx_1 & -D-B \\ 0 & 0 & Gx_1 & 0 \end{bmatrix}$$

Its characteristic polynomial is

$$\det(J - \lambda I) = \lambda^4 + f_1\lambda^3 + f_2\lambda^2 + f_3\lambda + f_4$$

where

$$f_1 = Gx_1 + (E+F)x_0 + 2D > 0$$

$$f_2 = EGx_0x_1 + (2D+A)(E+F)x_0 + (2D+B)Gx_1 + D^2 > 0$$

$$f_3 = (2D+A+B)EGx_0x_1 + D(D+A)(E+F)x_0 + D(D+B)Gx_1 > 0$$

$$f_4 = (D+A)(D+B)EGx_0x_1 > 0$$

Since the quantity $E+F$ occurs so often in the computations, we use the notation $H = E+F$. Straightforward calculations show that

$$f_1f_2 - f_3 = 2D^3 + \alpha_2D^2 + \alpha_1D + \alpha_0$$

where

$$\alpha_2 = 4(Hx_0 + Gx_1), \qquad \alpha_1 = AHx_0 + 2(Hx_0+Gx_1)^2 + BGx_1$$

$$\alpha_0 = EGHx_0^2x_1 + EG^2x_0x_1^2 + AH^2x_0^2 + (A+B)FGx_0x_1 + BG^2x_1^2$$

Thus $f_1f_2 - f_3 > 0$. On the other hand we have

$$f_1f_2f_3 - f_1^2f_4 - f_3^2 = \beta_5D^5 + \beta_4D^4 + \beta_3D^3 + \beta_2D^2 + \beta_1D + \beta_0$$

where

$$\beta_5 = 2Hx_0 + 2Gx_1, \qquad \beta_4 = 4(Hx_0+Gx_1)^2 + 2AHx_0 + 2BGx_1$$

$$\begin{aligned}\beta_3 &= 2(Hx_0+Gx_1)^3 + 4EGHx_0^2x_1 + 4EG^2x_0x_1^2 \\ &\quad +5AH^2x_0^2 + (A+B)(3E+5F)Gx_0x_1 + 5BG^2x_1^2\end{aligned}$$

$$\begin{aligned}\beta_2 &= 4EGH^2x_0^3x_1 + 8EG^2Hx_0^2x_1^2 + 4EG^3x_0x_1^3 \\ &\quad +3AH^3x_0^3 + (AE+2BE+6AH+3BF)GHx_0^2x_1 \\ &\quad +(2AE+BE+3AF+6BH)G^2x_0x_1^2 + 3BG^3x_1^3 \\ &\quad +A^2F(F+2E)x_0^2 + (AEx_0 - BGx_1)^2 + 2ABGFx_0x_1\end{aligned}$$

$$\begin{aligned}
\beta_1 &= 2E^2G^2Hx_0^3x_1^2 + 2E^2G^3x_0^2x_1^3 + (4A+B)EGH^2x_0^3x_1 \\
&+(A+B)(3E+5F)EG^2x_0^2x_1^2 + (A+4B)EG^3x_0x_1^3 \\
&+A^2(3E^2+3EF+F^2)Fx_0^3 + A(2AE+AF+2BF)GFx_0^2x_1 \\
&+(Ex_0+Gx_1)(AEx_0-BGx_1)^2 + (2AB+B^2)G^2Fx_0x_1^2
\end{aligned}$$

$$\begin{aligned}
\beta_0 &= (A+B)E^2G^2Hx_0^3x_1^2 + (A+B)E^2G^3x_0^2x_1^3 + A^2(2E+F)EFGx_0^3x_1 \\
&+(A^2+B^2)EFG^2x_0^2x_1^2 + (AEx_0-BGx_1)^2EGx_0x_1
\end{aligned}$$

Thus $f_1f_2f_3 - f_1^2f_4 - f_3^2 > 0$. Therefore the Routh-Hurwitz criteria are satisfied. SS3 is stable as long as it exists.

References

[1] D.J. Batstone, J. Keller, I. Angelidaki, S.V. Kalyuzhnyi, S.G. Pavlostathis, A. Rozzi, W.T.M Sanders, H. Siegrist, V.A. Vavilin. The Iwa Anaerobic Digestion Model No 1 (ADM1). Water Sci. Technol. 45 (2002), 65–73.

[2] A. Bornhöft, R. Hanke-Rauschenbach, K. Sundmacher. Steady-state analysis of the Anaerobic Digestion Model No. 1 (ADM1). Nonlinear Dynamics, 73 (2013), 535–549.

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

[4] IWA Task Group for Mathematical Modeling of Anaerobic Digestion Processes. Anaerobic Digestion Model No.1 (ADM1). Scientific and Technical Report No. 13 (2002), IWA Publishing, London.

[5] I. Ramirez, E.I.P. Volcke, R. Rajinikanth, J.P. Steyer, Modeling microbial diversity in anaerobic digestion through an extended adm1 model. Water Res. 43 (2009), 27872800.

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

[7] A. Xu, J. Dolfing, T.P. Curtis, G. Montague, E. Martin, 2011. Maintenance affects the stability of a two-tiered microbial 'food chain'? Journal of Theoretical Biology 276, 35-41.