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T. Sari, R. Fekih-Salem. Analysis of a model of flocculation in the chemostat. 8ème colloque - Tendances dans les Applications Mathématiques en Tunisie, Algérie et Maroc, May 2017, Hammamet, Tunisia. pp.75-80. hal-01766009

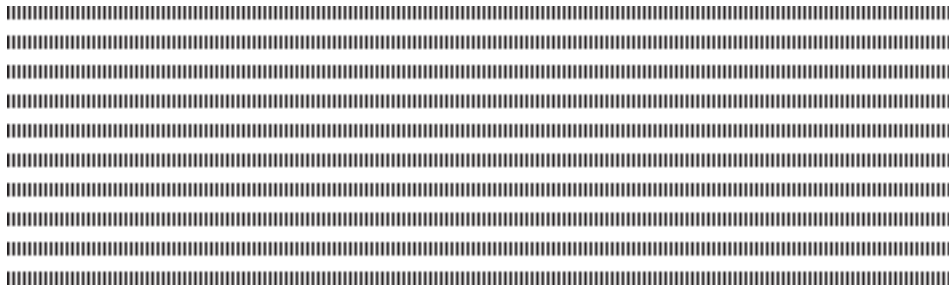
HAL Id: hal-01766009

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Submitted on 13 Apr 2018

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Analysis of a model of flocculation in the chemostat

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ABSTRACT. A model of the chemostat involving planktonic and attached bacteria competing for a single nutrient is considered. We study this flocculation model with monotonic growth rates and same removal rates. We show that this model has at most one positive steady state that is stable as long as it exists where planktonic and attached bacteria can coexist. According to control parameters, the operating diagram illustrates the washout and coexistence regions that depend only on the growth rate of planktonic bacteria. Indeed, flocculation process affects only the density of isolated and attached bacteria at steady state.

RÉSUMÉ. Dans ce travail, on considère un modèle du chimostat incluant une seule espèce composée de bactéries planctoniques et attachées en compétition pour une seule ressource. Nous étudions ce modèle de floculation avec des taux de croissance monotones et le même taux de disparition. Nous montrons que ce modèle admet au plus un équilibre positif qui est stable dès qu'il existe où les bactéries planctoniques et attachées peuvent coexister. Selon les paramètres de contrôle, le diagramme opératoire illustre les régions de lessivage et de coexistence qui dépendent que du taux de croissance des bactéries planctoniques. En effet, le processus de floculation affecte seulement la densité des bactéries isolées et attachées à l'équilibre.

KEYWORDS : Bifurcation, Chemostat, Flocculation, Operating diagram

MOTS-CLÉS : Bifurcation, Chimostat, Floculation, Diagrammes opératoires



1. Introduction

Flocculation is a process wherein microorganisms isolated or planktonic bacteria cluster together to form new flocs and reversibly these flocs can split and liberate isolated bacteria [9]. The attachment of planktonic bacteria could be also on a wall as biofilms [1]. In order to understand these flocculation phenomena and predict the outcome of system, several extensions of the well-known chemostat model [6, 8] have been proposed and studied in the literature by considering two compartments of isolated and attached biomass for each species. This flocculation mechanism can explain the coexistence between species when the most competitive species inhibits its growth by the formation of flocs [3, 4, 6, 7]. Indeed, the flocs consume less substrate than isolated bacteria since they have less access to substrate, given that this access to substrate is proportional to the outside surface of flocs.

In this paper, we consider the flocculation model proposed in [3] where planktonic bacteria of density u can stick with isolated bacteria or flocs of density v to form new flocs, with rate $a(u + v)u$, (a is a positive constant) and that flocs can split and liberate an isolated bacteria, with rate bv (b is a positive constant). With same removal rate, the model take the form

$$\begin{cases} \dot{S} &= D(S_{in} - S) - f(S)u - g(S)v \\ \dot{u} &= [f(S) - D]u - a(u + v)u + bv \\ \dot{v} &= [g(S) - D]v + a(u + v)u - bv \end{cases} \quad (1)$$

where $S(t)$ denotes the concentration of nutrient in the culture at time t ; $u(t)$ and $v(t)$ denote, respectively, the concentration of planktonic and attached bacteria at time t ; $f(S)$ and $g(S)$ represent, respectively, the per-capita growth rates of planktonic and attached bacteria; S_{in} and D denote, respectively, the input concentration of the limiting nutrient and the dilution rate of the chemostat. In [3], model (1), with distinct removal rates, has been studied only in the case where attachment and detachment dynamics are fast compared to growth dynamics. Using singular perturbation methods, the corresponding reduced model is a density-dependent model.

The model (1) has been studied in [6]. For the more general case where removal rates are distinct the reader is referred to [2]. In Section 2, we present the results of [6] and we recall some of the results of [2]. In Section 3, we give the operating diagram of (1). The operating diagram is a bifurcation diagram that describes the system behavior when the two control parameters S_{in} and D vary, and all biological parameters are fixed. The operating diagram has not been considered in [2, 6].

We assume the following hypothesis:

- (H1) $f(0) = g(0) = 0$ and $f'(S) > 0$ and $g'(S) > 0$ for all $S > 0$.
- (H2) $f(S) > g(S)$ for all $S > 0$.

Hypothesis (H1) means that the growth can take place if and only if the substrate is present. In addition, the growth rates of isolated and attached bacteria increase with the concentration of substrate. Hypothesis (H2) means that the bacteria in flocs consume less substrate than isolated bacteria, this means that a lower specific growth rate. Note that system (1) is well defined: its solutions remain non-negative and positively bounded for any non-negative initial condition. In the following, we shall use for convenience the abbreviation LES for Locally Exponentially Stable steady states.

2. Steady state and stability analysis

From (H1), when equations $f(S) = D$ and $g(S) = D$ have solutions, they are unique and we define the usual *break-even concentrations*

$$\lambda_u = f^{-1}(D) \quad \text{and} \quad \lambda_v = g^{-1}(D).$$

In this case, from (H2), one has $\lambda_u < \lambda_v$. Otherwise, $f(S) = D$ or $g(S) = D$ have no solution, we put $\lambda_u = \infty$ or $\lambda_v = \infty$. The steady states of (1) are given by solving equations $\dot{S} = 0$, $\dot{u} = 0$ and $\dot{v} = 0$. From equation $\dot{u} = 0$, if $u = 0$, it follows that $v = 0$. From equation $\dot{v} = 0$, if $v = 0$, then $u = 0$. Hence, we cannot have a steady state of extinction only of planktonic or attached bacteria. Therefore, besides the washout steady state

$$E_0 = (S_{in}, 0, 0)$$

where both planktonic or attached bacteria are extinct, the system can have a positive steady state of coexistence

$$E_1 = (S^*, u^*, v^*)$$

where $S^* > 0$, $u^* > 0$ and $v^* > 0$. We define the following functions:

$$U(S) = \frac{\varphi(S)(\psi(S) - b)}{a[\psi(S) - \varphi(S)]}, \quad V(S) = \frac{\varphi^2(S)(\psi(S) - b)}{a[\varphi(S) - \psi(S)]\psi(S)}, \quad H(S) = D \frac{\varphi(S)(\psi(S) - b)}{a\psi(S)},$$

where

$$\varphi(S) = f(S) - D, \quad \psi(S) = g(S) - D.$$

From $\varphi(S) > 0$ and $\psi(S) < 0$ on $I =]\lambda_u, \lambda_v[$, we deduce that functions $U(\cdot)$, $V(\cdot)$ and

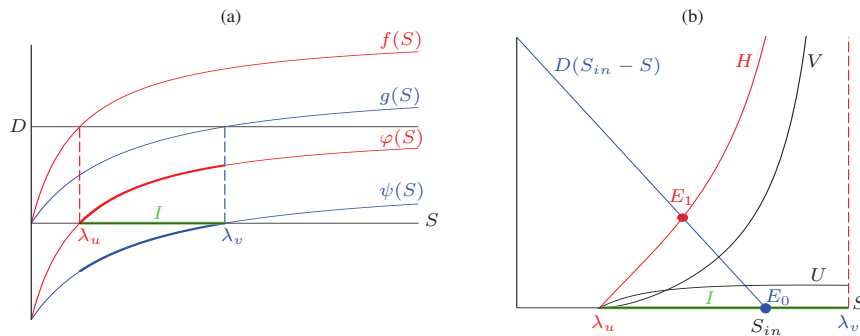


Figure 1: (a) Definition of the interval $I =]\lambda_u, \lambda_v[$. (b) The graphs of functions H , U and V and H showing the existence of a unique positive steady state. Red color is used for LES steady states and blue color for unstable steady states.

$H(\cdot)$ are positive on I (see Figure 1). Moreover, $H(\lambda_u) = U(\lambda_u) = V(\lambda_u) = 0$ and $H(\cdot)$, $V(\cdot)$ tend to infinity as S tends to λ_v (see Figure 1(b)).

Straightforward computations, see [2, 6], show that the positive steady state is $E_1 = (S^*, u^*, v^*)$ where S^* is the solution of equation

$$D(S_{in} - S^*) = H(S^*), \quad (2)$$

and $u^* = U(S^*)$, $v^* = V(S^*)$.

Proposition 1. Assume that assumptions (H1)-(H2) hold. Then system (1) has at most two steady states:

The washout $E_0 = (S_{in}, 0, 0)$, that always exists. It is LES if and only if $f(S_{in}) < D$.

The positive steady state, $E_1 = (S^*, u^*, v^*)$, that exists if and only if $f(S_{in}) > D$. If it exists, it is unique and LES.

Proof. The stability of E_0 is easy to obtain. For the existence and uniqueness of E_1 , straightforward computations show that the function H is increasing. Therefore E_1 exists, and is unique, if and only if $S_{in} > \lambda_u$ which is equivalent to $f(S_{in}) > D$. Since $z = S + u + v$ satisfies $\dot{z} = D(S_{in} - z)$, it tends to S_{in} . Therefore, (1) is reduced to the two dimensional system

$$\begin{cases} \frac{du}{dt} = \varphi(S_{in} - u - v)u - a(u + v)u + bv \\ \frac{dv}{dt} = \psi(S_{in} - u - v)v + a(u + v)u - bv. \end{cases}$$

The Jacobian matrix at (u^*, v^*) is

$$J^* = \begin{bmatrix} -u^*\varphi'(s^*) + \varphi(s^*) - a(2u^* + v^*) & -u^*\varphi'(s^*) - au^* + b \\ -v^*\psi'(s^*) + a(2u^* + v^*) & -v^*\psi'(s^*) + \psi(s^*) + au^* - b \end{bmatrix}.$$

Straightforward calculations show that

$$\text{Tr} J^* = -u^*\varphi'(s^*) - v^*\psi'(s^*) - b\frac{v^*}{u^*} - a\frac{(u^* + v^*)u^*}{v^*} < 0,$$

$$\text{Det} J^* = Au^*\varphi'(s^*) + Bv^*\psi'(s^*) + C,$$

where

$$A = a\frac{(u^* + v^*)^2}{v^*} > 0, \quad B = b\frac{u^* + v^*}{u^*} > 0, \quad C = -\varphi(s^*)(\psi(s^*) - b) > 0.$$

Therefore E_1 is LES if it exists. See [6] for more details. \square

In the case where removal rates are distinct, the function H is not necessarily increasing, nor we have necessarily $\lambda_u < \lambda_v$, so that equation (2) can have multiple solutions. Therefore, the system can have multiple positive steady states [2]. In [2] it is shown that a positive steady state is LES if and only if $H'(S^*) > -D$. Therefore, the result of Prop. 1 is a particular case of the results in [2]. The Table in Figure 2 summarizes existence and local stability of steady states given in the previous proposition. The letter S (resp. U) means stable (resp. unstable). Absence of letter means that the corresponding equilibrium does not exist.

3. Operating diagram

The operating diagram describes the system behavior when the control parameters S_{in} and D vary. All others parameters are known and can be measurable because they depend on properties of the micro-organisms and substrate introduced in the chemostat. Let Γ be the curve of equation $f(S_{in}) = D$ that separates the operating plane (S_{in}, D) in two regions, labeled as \mathcal{I}_0 and \mathcal{I}_1 . The transition from the region \mathcal{I}_0 to the region \mathcal{I}_1 by the curve Γ corresponds to a transcritical bifurcation making the steady state E_0 unstable

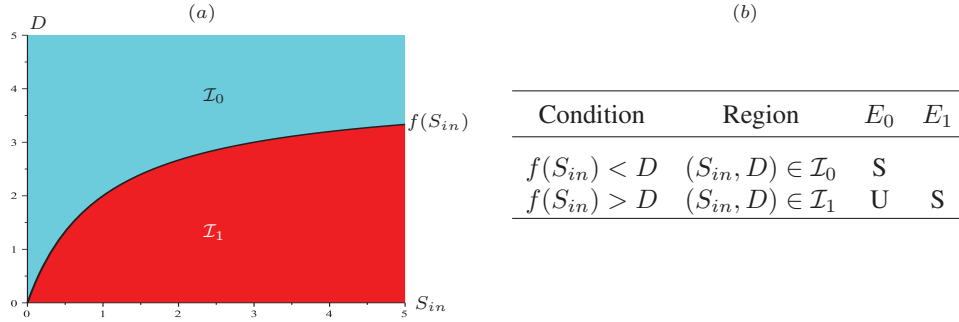


Figure 2: (a): Operating diagrams of model (1). Cyan color represents the region of washout (E_0 is LES) and red color represents the region of coexistence (E_1 is LES). (b): Existence and local stability of steady states according to regions in the operating diagram.

(saddle point) with the appearance of the coexistence steady state E_1 which is LES. The washout and coexistence regions depend only on the growth rate of planktonic bacteria which are more efficient than attached bacteria. The operating diagram is shown in Figure 2.

Figure 3 illustrates the one-parameter bifurcation diagrams of the each component at steady states showing the transcritical bifurcation making the steady state E_0 unstable with the appearance of the positive steady state E_1 which is LES. Moreover, the density of substrate, isolated and attached bacteria at steady state increase as S_{in} varies.

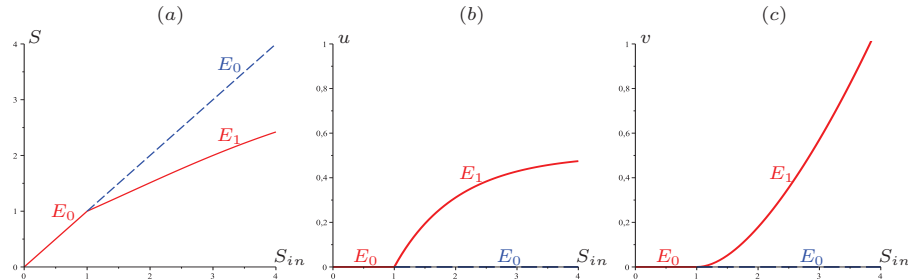


Figure 3: One-parameter bifurcation diagrams of model (1): the components S (a), u (b) and v (c) of each steady state. Parameter values are given in Table 1.

For numerical simulation, the growth functions are of Monod-type, defined by:

$$f(S) = \frac{m_1 S}{K_1 + S} \quad \text{and} \quad g(S) = \frac{m_2 S}{K_2 + S}, \quad (3)$$

where m_i and K_i , $i = 1, 2$, denote, respectively, the maximum growth rates and the Michaelis-Menten (or half-saturation) constants. The parameter values used for the simulations are provided in Table 1.

Parameter	m_1	K_1	m_2	K_2	a	b	D	S_{in}
Figure 2	2.05	1.5	4	0.5	2	1	Variable	Variable
Figure 3								

Table 1: Parameter values used for (1) where the growth rates are given by (3).

4. Discussion

In this work, we have studied a chemostat model with a single resource and one microbial species that is present in two forms: isolated and aggregated bacteria. With monotonic growth rates and same removal rates, the model shows the coexistence of planktonic and attached bacteria. The one-parameter bifurcation diagrams show the emergence of the positive steady state through a transcritical bifurcation with the washout steady state. The operating diagram determines the regions of the operating parameters (input concentration of the nutrient and dilution rate), which depict the asymptotic behavior of the system.

Since the flocs have less access to substrate than planktonic bacteria, the coexistence of these two forms of bacteria depends only on the growth rate of the isolated bacteria. The flocculation and deflocculation dynamics affect only the density of isolated and attached bacteria at steady state and not the coexistence region of the operating parameters. More precisely, the operating condition $f(S_{in}) > D$ of survival of the species is the same as if the species was present only in the form of isolated bacteria. The only difference is that, compared to the case of only isolated bacteria, where at steady state the substrate is λ_u and the total biomass is $S_{in} - \lambda_u$, the consumption of substrate to survive is now larger ($S^* > \lambda_u$) and the total biomass at steady state is lower ($u^* + v^* = S_{in} - S^* < S_{in} - \lambda_u$).

Acknowledgments

We thank the financial support of PHC UTIQUE project No. 13G1120 and of TREASURE euro-Mediterranean research network (<http://www.inra.fr/treasure>).

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