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A MODEL OF TWO COMPETITORS IN A CHEMOSTAT WITH AN EXTERNAL INHIBITOR*

MOHAMED DELLAL [‡][†], MUSTAPHA LAKRIB[‡], AND TEWFIK SARI[§]

Abstract. A model of two microbial species in a chemostat competing for a single resource in the presence of an external inhibitor is considered. This model was previously considered only in the case where the growth rate functions and the absorption rate of inhibitor are Michaelis-Menten or Monod kinetics. In this paper, we consider the general case of monotonic functions. Through the three operating parameters of the system represented by the dilution rate and the input concentrations of the substrate and the inhibitor, we give necessary and sufficient conditions for the existence and stability of all equilibria. By means of operating diagrams, we describe the asymptotic behavior of the model with respect to those operating parameters. Some examples are given to illustrate the mathematical results corresponding to cases where the growth rates are of Monod or Holling types.

Key words. Chemostat, competition, inhibitor, stability, operating diagram

AMS subject classifications. 34C80, 34D20, 34D23, 92B05

1. Introduction. The chemostat is an important laboratory apparatus used for the continuous culture of micro-organisms. Competition for single and multiple resources, evolution of resource acquisition, and competition among micro-organisms have been investigated in ecology and biology using chemostats [13, 23, 24, 32]. A detailed mathematical description of competition in the chemostat may be found in [12, 29].

The basic chemostat model predicts that coexistence of two or more microbial populations competing for a single non-reproducing nutrient is not possible. Only the species with the lowest ‘break-even’ concentration survives, this is the species which consumes less substrate to attain its steady state [15]. This result, known as the Competitive Exclusion Principle [11], was established under various hypotheses [4, 14, 26, 36]. The reader may consult [7, 22, 27] for a thorough account on the contributions of diverse authors.

Although this theoretical prediction has been corroborated by the experiences of Hansen and Hubbell [10], the biodiversity found in nature as well as in wastewater treatment processes and biological reactors are exceptions to this principle. Several authors [2, 3, 6, 16, 17, 18, 19, 21, 33] studied the inhibition as a factor in the maintenance of the diversity of microbial ecosystems: Can the production of internal inhibitors or the introduction of external inhibitors induce the stable coexistence of competitors in a chemostat-like environment?

In this paper we consider the model introduced by Lenski and Hattingh [21]. In this model, two species compete for a single limiting resource in presence of an external inhibitor, like a pesticide or an antibiotic, to which one species is sensitive and the other is resistant. Moreover, the resistant species is able to detoxify the environment, that is to remove the inhibitor from the environment. For some values

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of the dilution rate, the sensitive species has the lowest break-even concentration and wins the competition in absence of the inhibitor. The presence of the inhibitor allows the coexistence of both species. The complete mathematical analysis of the model in [21] was provided by Hsu and Waltman [18]. Due to the importance of this phenomenon which promotes the stable coexistence of two species competing for a single resource, the results of [18] were discussed in the text book [29] and in the review paper [20]. The aim of this work is to revisit the results of [18, 20, 21, 29] and to discuss several important questions that were unanswered in these works.

The approach in [21] was to fix the biological parameters of the model, together with the dilution rate of the chemostat, and discuss the behavior of the model with respect to the input concentrations of the limiting nutrient and inhibitor, which are operating parameters of the model. Therefore these authors established the ‘operating diagram’ of the model: seven possible outcomes were shown, corresponding to seven regions of the operating diagram. Without detoxification, the competitive exclusion principle holds, see [21], Fig. 1(a). With detoxification two regions of stable coexistence of both species appear, see [21], Fig. 1(b). Using the Routh-Hurwitz theorem on local stability of the coexistence equilibrium, these authors emphasized on the fact that the coexistence equilibrium may be unstable. They gave conditions on the biological parameters for which the coexistence equilibrium becomes unstable. However they did not depicted the region of the operating parameters in which this behavior holds.

The approach in [18, 20, 29] was more mathematical. The authors rescaled the biological and operating parameters of the model, creating a ‘standard’ environment in which the operating parameters are fixed to the value 1. This rescaling is often used in the mathematical literature on the chemostat [29]. The authors established global results and shown that when the coexistence equilibrium is unstable then the model can have an attracting limit cycle. The theory developed in this standard environment potentially permits to present the operating diagrams of the model. However the operating diagram was not presented in [18, 20, 29]. Our main contribution is to present the operating diagram and to give its properties with respect of the biological parameters. The parameter space of the model is ten dimensional: seven biological parameters and three operating parameters. Exploring all of it is not possible. Our approach to handle this question is to split the question in two intermediary questions. First we fix the biological parameters and present the operating diagram. Second we explore how the operating diagram varies when the biological parameters are changed. The problem is reduced to the determination of the sign of a set of five real valued functions of the dilution rate.

The operating diagram has the operating parameters as its coordinates and the various regions defined in it correspond to qualitatively different dynamics. This bifurcation diagram which determines the effect of the operating parameters, that are controlled by the operator and which are the dilution rate and the input concentrations, is very useful to understand the model from both the mathematical and biological points of view, and is often constructed in the mathematical and biological literature [1, 5, 8, 9, 25, 28, 30, 31, 34, 35].

As it was noticed in [18], the results are probably valid for general monotone growth function, not only for specific Monod growth functions as in [21]. Actually, it is more easy and convenient to develop the theory for a general model. In this paper we extend [18, 20, 29] by considering general growth functions and by describing the operating diagram. We extend also [21] by describing theoretically the various regions of the operating diagram. In particular we show that for the biological parameters

in [21], for all values of the three operating parameters the coexistence equilibrium is stable whenever it exists and we clarify the question of the destabilisation of the coexistence equilibrium that was considered in [21] only through numerical exploration.

The organization of this paper is as follows. In Section 2, we present the model and some properties of its solutions. In Section 3, we discuss the existence and the local asymptotic stability of equilibria. In Section 4, we discuss global results. In Section 5, we present the operating diagrams. In Section 6, we consider examples and we give numerical simulations. A discussion follows in Section 7.

2. Mathematical model. The model of the chemostat with external inhibitor [18, 20, 21, 29] we consider here is of the form

$$(1) \quad \begin{cases} S' &= (S^0 - S)D - f(p)f_1(S)\frac{x}{\gamma_1} - f_2(S)\frac{y}{\gamma_2}, \\ x' &= [f(p)f_1(S) - D]x, \\ y' &= [f_2(S) - D]y, \\ p' &= (p^0 - p)D - g(p)y, \end{cases}$$

with $S(0) \geq 0$, $x(0) > 0$, $y(0) > 0$ and $p(0) \geq 0$. $S(t)$ denotes the concentration of the substrate at time t ; $x(t)$, $y(t)$ are the concentrations of the competitors at time t and $p(t)$ is the concentration of the external inhibitor. $S^0 > 0$ is the input concentration of the nutrient, $D > 0$ is the dilution rate of the chemostat and $p^0 > 0$ is the input concentration of the inhibitor, all of which are assumed to be constant and are under the control of the experimenter. The parameters $\gamma_i > 0$, $i = 1, 2$, are the growth yield coefficients. The function f represents the degree of inhibition of p on the growth rate of x . The so-called functional responses f_i , $i = 1, 2$, represent the specific growth rates of the competitors and the function g represents the absorption rate of the external inhibitor relative to y . The global analysis of the model (1) was considered by Hsu and Waltman [18] when

$$(2) \quad f(p) = e^{-\mu p}, \quad f_1(S) = \frac{m_1 S}{K_1 + S}, \quad f_2(S) = \frac{m_2 S}{K_2 + S}, \quad g(p) = \frac{\delta p}{K + p},$$

where μ , m_i , K_i , $i = 1, 2$, δ and K are some positive constant parameters. Here, except the three variable operating (or control) parameters, which are the input of the inhibitor p^0 , the dilution rate D and the inflowing substrate S^0 , all the other parameters are biological parameters which depend on the organisms, substrate and inhibitor considered.

In this paper, we consider the general model (1) without restricting ourselves to the special case of function f , Monod functions of growth rates of the competitors f_i and of absorption rate of inhibitor g given in (2). We suppose only that f , f_i , $i = 1, 2$, and g in system (1) are C^1 -functions satisfying the following conditions:

- (H1) $f(0) = 1$, $f(p) \geq 0$ and $f'(p) < 0$ for all $p > 0$.
- (H2) For $i = 1, 2$, $f_i(0) = 0$ and $f'_i(S) > 0$ for all $S \geq 0$.
- (H3) $g(0) = 0$ and $g'(p) > 0$ for all $p \geq 0$.

Following [18, 20], without loss of generality, the operating parameters p^0 , D and S^0 together with the yields γ_1 and γ_2 can be fixed to 1. This is done by the following scaling of the dependent variables, and time:

$$(3) \quad \hat{S} = \frac{S}{S^0}, \quad \hat{x} = \frac{x}{S^0 \gamma_1}, \quad \hat{y} = \frac{y}{S^0 \gamma_2}, \quad \hat{p} = \frac{p}{p^0}, \quad \hat{t} = Dt,$$

and the following notations

$$(4) \quad \hat{f}(\hat{p}) = f(p^0 \hat{p}), \quad \hat{g}(\hat{p}) = \frac{S^0 \gamma_2}{p^0 D} g(p^0 \hat{p}), \quad \hat{f}_i(\hat{S}) = \frac{1}{D} f_i(S^0 \hat{S}), \quad i = 1, 2.$$

Note that the functions \hat{f} , \hat{g} and \hat{f}_i , $i = 1, 2$, satisfy assumptions (H1), (H2) and (H3). Then, making the changes (3), (4) and dropping all the hats, model (1) is written in the simplified non-dimensional form

$$(5) \quad \begin{cases} S' &= 1 - S - f(p)f_1(S)x - f_2(S)y, \\ x' &= [f(p)f_1(S) - 1]x, \\ y' &= [f_2(S) - 1]y, \\ p' &= 1 - p - g(p)y, \end{cases}$$

where f , g and f_i , $i = 1, 2$, satisfy assumptions (H1), (H2) and (H3). This is the system we will analyze here.

The proof of the following result is standard and hence omitted.

PROPOSITION 2.1. *For non-negative initial conditions, all solutions of system (5) are bounded and remain non-negative for all $t > 0$. Moreover, the compact set*

$$\Omega = \{(S, x, y, p) \in \mathbb{R}^4 : S \geq 0, x \geq 0, y \geq 0, 0 \leq p \leq 1, S + x + y = 1\}$$

is positively invariant and is a global attractor for system (5).

3. Existence and local stability of equilibria. Hereafter we use the following conditions and notations: for functions f , f_i , $i = 1, 2$, and g in (5), conditions (H1) to (H3) hold. When equations $f_1(S) = 1$, $f_2(S) = 1$ and $f_1(S) = 1/f(1)$ have solutions, they are unique and then we define the break-even concentrations as:

$$(6) \quad \lambda_1 = f_1^{-1}(1), \quad \lambda_2 = f_2^{-1}(1), \quad \lambda^+ = f_1^{-1}\left(\frac{1}{f(1)}\right).$$

Otherwise, we put $\lambda_1 = +\infty$, $\lambda_2 = +\infty$ and $\lambda^+ = +\infty$. We define the function W by

$$W(p) = \frac{1-p}{g(p)}, \quad \text{for } p \in (0, 1].$$

Using (H3), for all $p \in (0, 1)$ we have $W(p) > 0$, $W'(p) < 0$ and $\lim_{p \rightarrow 0} W(p) = +\infty$. Therefore, when $\lambda_2 < 1$, equation $W(p) = 1 - \lambda_2$ admits a unique solution that we denote p^* :

$$(7) \quad W(p^*) = 1 - \lambda_2.$$

We have $0 < p^* < 1$, see Fig. 1(b).

If equation $f_1(S) = 1/f(p^*)$ has a solution, it is unique and then we set

$$(8) \quad \lambda^- = f_1^{-1}\left(\frac{1}{f(p^*)}\right).$$

Otherwise, we let $\lambda^- = +\infty$. Since f is decreasing we have $0 < f(1) < f(p^*) < 1$. Therefore $1/f(1) > 1/f(p^*)$ and, since f_1 is increasing, the numbers λ_1 , λ^+ and λ^- are related as follows, see Fig. 1(a):

$$(9) \quad \lambda_1 < \lambda^- < \lambda^+.$$

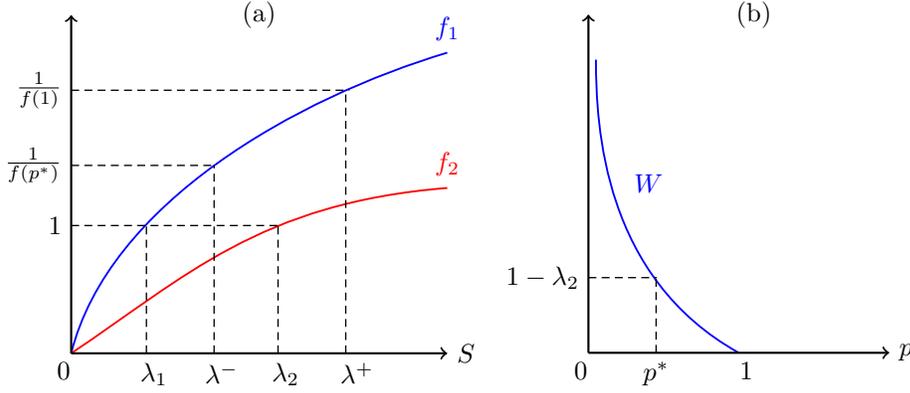


FIG. 1. Illustrative graphs of functions (a): f_1 and f_2 and definitions of break-even concentrations λ_1 , λ^- , λ^+ and λ_2 ; (b): W with the unique positive solution p^* of equation $W(p) = 1 - \lambda_2$, when $\lambda_2 < 1$.

3.1. Existence of equilibria. The existence of equilibria of system (5) is stated by the following result:

PROPOSITION 3.1. Assume that (H1), (H2) and (H3) are satisfied. System (5) has the following equilibria:

- The washout equilibrium $E_0 = (1, 0, 0, 1)$, that always exists.
- The equilibrium $E_1 = (\lambda^+, 1 - \lambda^+, 0, 1)$ of extinction of species y , where λ^+ is given by (6). This equilibrium exists if and only if $\lambda^+ < 1$.
- The equilibrium $E_2 = (\lambda_2, 0, 1 - \lambda_2, p^*)$ of extinction of species x , where λ_2 and p^* are given by (6) and (7), respectively. This equilibrium exists if and only if $\lambda_2 < 1$.
- The coexistence equilibrium $E_c = (\lambda_2, x_c, y_c, p_c)$, where λ_2 is given by (6) and p_c , y_c and x_c are given by

$$(10) \quad p_c = f^{-1}\left(\frac{1}{f_1(\lambda_2)}\right), \quad y_c = W(p_c), \quad x_c = 1 - \lambda_2 - y_c.$$

This equilibrium exists if and only if $\lambda_2 < 1$ and $\lambda^- < \lambda_2 < \lambda^+$, where λ^+ and λ^- are given by (6) and (8), respectively.

Proof. The steady states of (5) are the solutions of the set of equations

$$(11) \quad \begin{cases} 0 &= 1 - S - f(p)f_1(S)x - f_2(S)y, \\ 0 &= [f(p)f_1(S) - 1]x, \\ 0 &= [f_2(S) - 1]y, \\ 0 &= 1 - p - g(p)y. \end{cases}$$

Therefore, besides the washout equilibrium $E_0 = (1, 0, 0, 1)$ where both populations are extinct, that always exists, (5) has the following types of equilibria:

- $E_1 = (S_1, x_1, 0, p_1)$, where second population is extinct and $x_1 > 0$.
- $E_2 = (S_2, 0, y_2, p_2)$, where first population is extinct and $y_2 > 0$.
- $E_c = (S_c, x_c, y_c, p_c)$, where both populations survive: $x_c > 0$, $y_c > 0$.

The components $S = S_1$, $x = x_1$ and $p = p_1$ of the boundary equilibrium E_1 are

the solutions of (11) with $x > 0$ and $y = 0$, that is $p_1 = 1$ and

$$(12) \quad 1 - S_1 = f(p_1)f_1(S_1)x_1,$$

$$(13) \quad f(p_1)f_1(S_1) = 1.$$

Therefore, from (13) we have $f_1(S_1) = \frac{1}{f(1)}$, that is $S_1 = \lambda^+$, where λ^+ is given by (6). Then, using (12) we deduce that $x_1 = 1 - \lambda^+$. This equilibrium exists if and only if $x_1 > 0$, that is $\lambda^+ < 1$.

The components $S = S_2$, $y = y_2$ and $p = p_2$ of the boundary equilibrium E_2 are the solutions of (11) with $x = 0$ and $y > 0$. Hence, $f_2(S_2) = 1$, that is $S_2 = \lambda_2$, where λ_2 is given by (6) and

$$(14) \quad 1 - S_2 = f_2(S_2)y_2,$$

$$(15) \quad 1 - p_2 = g(p_2)y_2.$$

From (14) we have $y_2 = 1 - \lambda_2$. Then, using (15) we deduce that $W(p_2) = 1 - \lambda_2$, that is $p_2 = p^*$, where p^* is given by (7). This equilibrium exists if and only if $y_2 > 0$ and $p_2 > 0$, that is $\lambda_2 < 1$.

The components of $E_c = (S_c, x_c, y_c, p_c)$, a positive equilibrium of (5), are the solutions of (11) with $x > 0$ and $y > 0$. Hence, $f_2(S_c) = 1$, that is $S_c = \lambda_2$, where λ_2 is given by (6) and

$$(16) \quad 1 - S_c = f(p_c)f_1(S_c)x_c + f_2(S_c)y_c,$$

$$(17) \quad f(p_c)f_1(S_c) = 1,$$

$$(18) \quad 1 - p_c = g(p_c)y_c.$$

From (17) we have $f(p_c) = \frac{1}{f_1(\lambda_2)}$, from (18) we have $y_c = W(p_c)$ and from (16) we have $x_c = 1 - \lambda_2 - y_c$. Therefore p_c , y_c and x_c are given by (10). Hence, a positive equilibrium E_c of system (5), if it exists, is unique. Let us study the condition of existence of E_c . We first note that

$$(19) \quad x_c + y_c = 1 - \lambda_2 > 0 \iff \lambda_2 < 1.$$

Moreover, we have $y_c > 0$ if and only if $0 < p_c < 1$. Using the fact that f is decreasing and $f(0) = 1$ (hypothesis (H1)) we have

$$(20) \quad y_c > 0 \iff 0 < p_c < 1 \iff f(1) < f(p_c) < 1.$$

Now, by (6) and (10) we have

$$1 = \frac{1}{f_1(\lambda_1)}, \quad f(1) = \frac{1}{f_1(\lambda^+)}, \quad f(p_c) = \frac{1}{f_1(\lambda_2)},$$

so that, by using the fact that f_1 is increasing (hypothesis (H2)), we obtain from (20)

$$(21) \quad y_c > 0 \iff f_1(\lambda_1) < f_1(\lambda_2) < f_1(\lambda^+) \iff \lambda_1 < \lambda_2 < \lambda^+.$$

On the other hand, by (7), (8) and (10) we have, respectively

$$W(p^*) = 1 - \lambda_2, \quad f(p^*) = \frac{1}{f_1(\lambda^-)}, \quad W(p_c) = y_c, \quad f(p_c) = \frac{1}{f_1(\lambda_2)}.$$

Hence, using the facts that W and f are decreasing, and f_1 is increasing, we have

$$(22) \quad \begin{aligned} x_c > 0 &\iff y_c < 1 - \lambda_2 &\iff W(p_c) < W(p^*) \\ &\iff p_c > p^* &\iff f(p_c) < f(p^*) \\ &\iff f_1(\lambda_2) > f_1(\lambda^-) &\iff \lambda_2 > \lambda^-. \end{aligned}$$

Taking into account (9), from (19), (21) and (22), we conclude finally that E_c exists if and only if $\lambda^- < \lambda_2 < \min(\lambda^+, 1)$. \square

3.2. Local asymptotic stability of equilibria. For the study of the stability of equilibria it is convenient to use the change of variable

$$\Sigma = 1 - S - x - y$$

in system (5) that reveals the cascade structure of the system. Since $\Sigma' = -\Sigma$, the system (5) may then be replaced by

$$(23) \quad \begin{cases} \Sigma' &= -\Sigma, \\ x' &= [f(p)f_1(1 - \Sigma - x - y) - 1]x, \\ y' &= [f_2(1 - \Sigma - x - y) - 1]y, \\ p' &= 1 - p - g(p)y. \end{cases}$$

The Jacobian matrix for the linearization of (23) at an equilibrium point $E^* = (0, x^*, y^*, p^*)$ takes the triangular form

$$J = \begin{bmatrix} -1 & 0 \\ A & M \end{bmatrix},$$

where M is the square matrix

$$(24) \quad M = \begin{bmatrix} m_{11} & m_{12} & m_{13} \\ m_{21} & m_{22} & 0 \\ 0 & m_{32} & m_{33} \end{bmatrix},$$

with

$$\begin{aligned} m_{11} &= f(p^*)f_1(1 - x^* - y^*) - 1 - x^*f'(p^*)f_1'(1 - x^* - y^*), \\ m_{12} &= -x^*f'(p^*)f_1'(1 - x^* - y^*), \quad m_{13} = x^*f'(p^*)f_1(1 - x^* - y^*), \\ m_{21} &= -y^*f_2'(1 - x^* - y^*), \quad m_{22} = f_2(1 - x^* - y^*) - 1 - y^*f_2'(1 - x^* - y^*), \\ m_{32} &= -g(p^*), \quad m_{33} = -1 - y^*g'(p^*). \end{aligned}$$

Therefore, the eigenvalues of J are -1, together with the eigenvalues of matrix M . Hence the equilibrium point E^* is locally exponentially stable (LES) if and only if the eigenvalues of M are of negative real parts. The local stability of equilibria of system (5) is given by the following result.

PROPOSITION 3.2. *Assume that (H1), (H2) and (H3) are satisfied. The stability of equilibria of (5) is as follows:*

- *The equilibrium E_0 is LES if and only if $\lambda^+ > 1$ and $\lambda_2 > 1$.*
- *The equilibrium E_1 , if it exists, has at least three dimensional stable manifolds and is LES if and only if $\lambda^+ < \lambda_2$.*
- *The equilibrium E_2 , if it exists, has at least three dimensional stable manifolds and is LES if and only if $\lambda_2 < \lambda^-$.*

- The equilibrium E_c , if it exists, is LES if and only if

$$(25) \quad (A + B)(A + B + C)C > BEF,$$

where $A > 0$, $B > 0$, $C > 0$, $E > 0$ and $F > 0$ and are defined by:

$$(26) \quad \begin{aligned} A &= f(p_c)f_1'(\lambda_2)x_c, & B &= f_2'(\lambda_2)y_c, & C &= 1 + g'(p_c)y_c, \\ E &= g(p_c), & F &= -f'(p_c)f_1(\lambda_2)x_c. \end{aligned}$$

Proof. At washout equilibrium E_0 , the matrix M defined by (24) is

$$M_0 = \begin{bmatrix} f(1)f_1(1) - 1 & 0 & 0 \\ 0 & f_2(1) - 1 & 0 \\ 0 & -g(1) & -1 \end{bmatrix}.$$

The eigenvalues of M_0 are: -1 , $f(1)f_1(1) - 1$ and $f_2(1) - 1$. Then, the equilibrium E_0 is LES if and only if $f(1)f_1(1) < 1$ and $f_2(1) < 1$, or equivalently, $\lambda^+ > 1$ and $\lambda_2 > 1$.

Suppose that the equilibrium E_1 exists, that is $\lambda^+ < 1$. At E_1 the matrix M defined by (24) is

$$M_1 = \begin{bmatrix} -(1 - \lambda^+)f(1)f_1'(\lambda^+) & 0 & (1 - \lambda^+)f'(1)f_1(\lambda^+) \\ 0 & f_2(\lambda^+) - 1 & 0 \\ 0 & -g(1) & -1 \end{bmatrix}.$$

The eigenvalues of M_1 are: -1 , $-(1 - \lambda^+)f(1)f_1'(\lambda^+) < 0$ and $f_2(\lambda^+) - 1$. Since E_1 has three negative eigenvalues, it has at least three dimensional stable manifolds. Moreover, E_1 is LES if and only if $f_2(\lambda^+) < 1$, or equivalently, $\lambda^+ < \lambda_2$.

Suppose that the equilibrium E_2 exists, that is $\lambda_2 < 1$. At E_2 the matrix M defined by (24) is

$$M_2 = \begin{bmatrix} f(p^*)f_1(\lambda_2) - 1 & 0 & 0 \\ -(1 - \lambda_2)f_2'(\lambda_2) & -(1 - \lambda_2)f_2'(\lambda_2) & 0 \\ 0 & -g(p^*) & -1 - (1 - \lambda_2)g'(p^*) \end{bmatrix}.$$

The eigenvalues of M_2 are: $f(p^*)f_1(\lambda_2) - 1$, $-(1 - \lambda_2)f_2'(\lambda_2) < 0$ and $-1 - (1 - \lambda_2)g'(p^*) < 0$. Since E_2 has three negative eigenvalues, it has at least three dimensional stable manifolds. Moreover, E_2 is LES if and only if $f(p^*)f_1(\lambda_2) < 1$, or equivalently, $\lambda_2 < \lambda^-$.

At E_c , the matrix M defined by (24) takes the form

$$M_c = \begin{bmatrix} -A & -A & -F \\ -B & -B & 0 \\ 0 & -E & -C \end{bmatrix},$$

where A , B , C , E and F are defined by (26). Obviously $A > 0$, $B > 0$, $C > 0$, $E > 0$ and $F > 0$. The characteristic polynomial of M_c is given by

$$\lambda^3 + B_1\lambda^2 + B_2\lambda + B_3 = 0,$$

with $B_1 = A + B + C$, $B_2 = C(A + B)$ and $B_3 = BEF$. Since $B_1 > 0$, $B_2 > 0$ and $B_3 > 0$, by the Routh-Hurwitz criterion, E_c is LES if and only if $B_1B_2 > B_3$ that is to say (25) holds. \square

We summarize the results on existence and local stability of equilibria of (5), given by Propositions 3.1 and 3.2, in Table 1 below. We observe that E_0 is LES if and only if E_1 and E_2 do not exist, and E_c exists if and only if E_2 exists and is unstable, and E_1 , if it exists, is also unstable. One concludes that there is one and only one equilibrium which is stable.

Equilibria	Existence	Local exponential stability
E_0	Always	$\lambda^+ > 1$ and $\lambda_2 > 1$
E_1	$\lambda^+ < 1$	$\lambda^+ < \lambda_2$
E_2	$\lambda_2 < 1$	$\lambda_2 < \lambda^-$
E_c	$\lambda^- < \lambda_2 < \min(\lambda^+, 1)$	$(A + B)(A + B + C)C > BEF$

TABLE 1

Existence and local asymptotic stability of equilibria of system (5). Note that there is a typo in Table 2 of [20]: the condition $\lambda_1 > 1$ of stability of E_0 should be replaced by $\lambda^+ > 1$.

4. Global asymptotic stability of equilibria. In this section we discuss the results of [18, 29] on the global asymptotic stability of equilibria of (5) obtained in the case where the growth functions are given by (2). The results of these authors can be extended without added difficulty to the general case where it is simply assumed that f , f_1 , f_2 and g satisfy hypotheses (H1), (H2) and (H3).

THEOREM 4.1.

- If $\lambda^+ > 1$ and $\lambda_2 > 1$, then the washout equilibrium E_0 of system (5) exists and is globally asymptotically stable.
- If $\lambda^+ < 1$ and $\lambda^+ < \lambda_2$, then the boundary equilibrium E_1 of system (5) exists and is globally asymptotically stable with respect to solutions with $x(0) > 0$.
- If $\lambda_2 < 1$ and $\lambda_2 < \lambda^-$, then the boundary equilibrium E_2 of system (5) exists and is globally asymptotically stable with respect to solutions with $y(0) > 0$.

Proof. The proof of Item 1 is similar to the proof of Proposition 3.1 in [18] or in [29]. The proof of Item 2 is similar to the proof of Theorem 5.5 in [18] or Theorem 5.1 in [29]. The proof of Item 3 is similar to the proof of Theorem 5.4 in [18] or Theorem 5.2 in [29]. \square

As it is shown in Table 1, when $\lambda^- < \lambda_2 < \lambda^+$, the positive equilibrium E_c exists. The result below shows then that the ω -limit set of every solution of system (5) for which $x(0) > 0$ and $y(0) > 0$ remains at a positive distance away from the boundary of \mathbb{R}_+^4 .

THEOREM 4.2. Let the positive equilibrium E_c exist and let $(S(t), x(t), y(t), p(t))$ be a solution of system (5) with $x(0) > 0$ and $y(0) > 0$. Then

$$\liminf_{t \rightarrow \infty} x(t) > 0 \quad \text{and} \quad \liminf_{t \rightarrow \infty} y(t) > 0.$$

The ω -limit set of every solution of system (5), with $x(0) > 0$ and $y(0) > 0$, lies interior to the positive cone.

Proof. The proof is similar to the proof of Theorem 6.1 in [18] or Theorem 7.1 in [29]. \square

From a biological point of view, Theorem 4.2 guarantees the coexistence of both species x and y when E_c exists. However, it does not give the global asymptotic behavior. To study the global asymptotic behavior of system (5) when E_c exists, we

need a supplementary condition on the following limiting system, obtained by putting $\Sigma = 0$ in system (23):

$$(27) \quad \begin{cases} x' &= [f(p)f_1(1-x-y) - 1]x \\ y' &= [f_2(1-x-y) - 1]y \\ p' &= 1 - p - g(p)y \end{cases}$$

THEOREM 4.3. *Suppose that system (27) has no limit cycles. Then the positive equilibrium E_c is globally asymptotically stable with respect to solutions with positive initial conditions.*

Proof. The proof is similar to the proof of Theorem 6.2 in [18] or Theorem 7.2 in [29]. \square

5. Operating diagrams. In this section we give our main result which is the discussion of the existence and stability of equilibria of (1) with respect of the operating parameters D , p^0 and S^0 . We assume that f , g and f_1 , f_2 are fixed, and without loss of generality we can assume that the yields are equal to 1 ($\gamma_1 = \gamma_2 = 1$). So, we consider the system

$$(28) \quad \begin{cases} S' &= (S^0 - S)D - f(p)f_1(S)x - f_2(S)y, \\ x' &= [f(p)f_1(S) - D]x, \\ y' &= [f_2(S) - D]y, \\ p' &= (p^0 - p)D - g(p)y. \end{cases}$$

5.1. Existence and stability of equilibria with respect of operating parameters. To emphasize the dependence of the equilibria of (28) with respect to the operating parameters, we rewrite our previous results, obtained for the non dimensional system (5).

Using the inverse functions $f_1^{-1} : I_1 \rightarrow \mathbb{R}^+$ and $f_2^{-1} : I_2 \rightarrow \mathbb{R}^+$ where

$$I_1 = [0, f_1(+\infty)), \quad I_2 = [0, f_2(+\infty)),$$

which are increasing, we define the break-even concentrations as

$$(29) \quad \lambda_1(D) = f_1^{-1}(D), \quad \lambda_2(D) = f_2^{-1}(D), \quad \lambda^+(D, p^0) = f_1^{-1}\left(\frac{D}{f(p^0)}\right),$$

which are the solutions of equations $f_1(S) = D$, $f_2(S) = D$ and $f_1(S) = D/f(p^0)$, respectively. Note that λ_1 is defined on I_1 , λ_2 is defined on I_2 and λ^+ is defined for (D, p^0) such that $p^0 \geq 0$ and $D/f(p^0) \in I_1$.

We define the function W by

$$W(p, D, p^0) = \frac{(p^0 - p)D}{g(p)}, \quad \text{for } p \in (0, p^0].$$

Note that W is defined for (p, D, p^0) such that $p \geq 0$, $D \geq 0$ and $0 < p \leq p^0$. Note also that $\frac{\partial W}{\partial p} < 0$. Therefore, when $\lambda_2 < S^0$, equation $W(p, D, p^0) = S^0 - \lambda_2$ has a unique solution denoted by $p^* = p^*(D, p^0, S^0)$

$$(30) \quad W(p^*, D, p^0) = S^0 - \lambda_2.$$

If equation $f_1(S) = D/f(p^*)$ has a solution, it is unique and then we set

$$(31) \quad \lambda^-(D, p^0, S^0) = f_1^{-1}\left(\frac{D}{f(p^*)}\right).$$

We define

$$(32) \quad p_c(D) = f^{-1} \left(\frac{D}{f_1(\lambda_2(D))} \right).$$

Note that $p_c(D)$ is defined for $D \in I_c$ where

$$(33) \quad I_c = \{D \in I_1 \cap I_2 : \lambda_1(D) < \lambda_2(D)\}.$$

For simplicity we assume that equation $f_1(S) = f_2(S)$ has at most one positive solution $S = \bar{S} > 0$, which is the case when $f_1(S)$ and $f_2(S)$ are Monod functions. The case of multiple intersections can be treated similarly. We have

- $I_c = \emptyset$ if $f_1(S) < f_2(S)$ for all $S > 0$.
- $I_c = (\bar{D}, f_2(+\infty))$, if $f_1(S) < f_2(S)$ for $0 < S < \bar{S}$ and $f_1(S) > f_2(S)$ for $S > \bar{S}$, see Fig. 2(a).
- $I_c = (0, \bar{D})$, if $f_1(S) > f_2(S)$ for $0 < S < \bar{S}$ and $f_1(S) < f_2(S)$ for $S > \bar{S}$, see Fig. 2(b).
- $I_c = (0, f_2(+\infty))$ if $f_1(S) > f_2(S)$ for all $S > 0$.

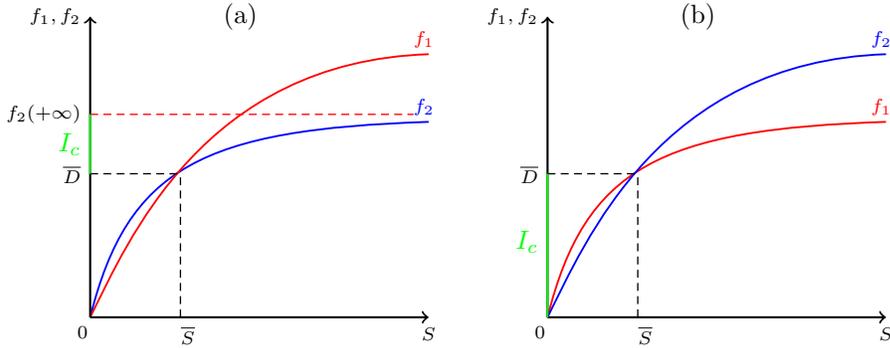


FIG. 2. Graphs of f_1 (in red) and f_2 (in blue) when equation $f_1(S) = f_2(S)$ has a positive solution $S = \bar{S}$ and graphical depiction of I_c . (a): $I_c = (\bar{D}, f_2(+\infty))$. (b): $I_c = (0, \bar{D})$ where $\bar{D} = f_1(\bar{S}) = f_2(\bar{S})$.

We define

$$(34) \quad y_c(D, p^0) = W(p_c(D), D, p^0), \quad x_c(D, p^0, S^0) = S^0 - \lambda_2(D) - y_c(D, p^0).$$

Note that y_c is defined for $(D, p^0) \in J_c$, where

$$(35) \quad J_c = \{(D, p^0) \in I_c \times \mathbb{R}^+ : 0 < p_c(D) < p^0\},$$

with I_c defined by (33). Note that x_c is defined for $(D, p^0, S^0) \in \mathcal{D}_c$ where

$$(36) \quad \mathcal{D}_c = \{(D, p^0, S^0) \in J_c \times \mathbb{R}^+ : S^0 > \lambda_2(D) + y_c(D, p^0)\},$$

with J_c defined by (35).

To avoid cumbersome notations, and when there is no risk of confusion, we will omit to mention the operating parameters D , p^0 and S^0 in λ_2 , λ^+ , λ^- , p^* , p_c , y_c and x_c . Straightforward computations, similar to those used in the proofs of Propositions 3.1 and 3.2 show that the following result holds.

PROPOSITION 5.1. Assume that (H1), (H2) and (H3) are satisfied. Let λ_2 , λ^+ and λ^- be defined by (29) and (31), respectively. Let p^* be defined by (30). Let p_c , x_c and y_c be defined by (32) and (34), respectively. System (28) has the following equilibria:

- The washout equilibrium $E_0 = (S^0, 0, 0, p^0)$.
- The boundary equilibrium $E_1 = (\lambda^+, S^0 - \lambda^+, 0, p^0)$ of extinction of species y .
- The boundary equilibrium $E_2 = (\lambda_2, 0, S^0 - \lambda_2, p^*)$ of extinction of species x .
- The positive equilibrium $E_c = (\lambda_2, x_c, y_c, p_c)$ of coexistence of the species.

The conditions of existence and stability of these equilibria are given in the following table:

Equilibria	Existence	Local exponential stability
E_0	Always	$\lambda^+ > S^0$ & $\lambda_2 > S^0$
E_1	$\lambda^+ < S^0$	$\lambda^+ < \lambda_2$
E_2	$\lambda_2 < S^0$	$\lambda_2 < \lambda^-$
E_c	$\lambda^- < \lambda_2 < \min(\lambda^+, S^0)$	$(A + B)(A + B + C)C > BEF$

where $A = A(D, p^0, S^0)$, $B = B(D, p^0)$, $C = C(D, p^0)$, $E = E(D)$, $F = F(D, p^0, S^0)$ are defined by

$$(37) \quad \begin{aligned} A(D, p^0, S^0) &= \alpha(D)x_c(D, p^0, S^0), & B(D, p^0) &= \beta(D)y_c(D, p^0), \\ C(D, p^0) &= D + \gamma(D)y_c(D, p^0), & E(D) &= g(p_c(D)), \\ F(D, p^0, S^0) &= \phi(D)x_c(D, p^0, S^0). \end{aligned}$$

Here $\alpha(D)$, $\beta(D)$, $\gamma(D)$ and $\phi(D)$ are given by

$$(38) \quad \alpha = f(p_c)f_1'(\lambda_2), \quad \beta = f_2'(\lambda_2), \quad \gamma = g'(p_c), \quad \phi = -f'(p_c)f_1(\lambda_2).$$

In what follows, our aim is to express the conditions of existence and stability of the equilibria in Proposition 5.1 with respect of the operating parameters D , p^0 and S^0 . For this purpose, we need the following definitions. We let

$$(39) \quad F_1(D, p^0) = f(p^0)f_1(f_2^{-1}(D)).$$

Note that F_1 is defined on $I_2 \times \mathbb{R}^+$. We have the following result.

LEMMA 5.2. The following equivalences hold:

$$p_c(D) < p^0 \iff D > F_1(D, p^0) \iff \lambda_2(D) < \lambda^+(D, p^0).$$

Proof. Using (29), hypothesis (H2) and the definition (39), we have

$$\begin{aligned} \lambda^+ < \lambda_2 &\iff f_1^{-1}\left(\frac{D}{f(p^0)}\right) < f_2^{-1}(D) \iff \frac{D}{f(p^0)} < f_1(f_2^{-1}(D)) \\ &\iff D < f(p^0)f_1(f_2^{-1}(D)) \iff D < F_1(D, p^0). \end{aligned}$$

On the other hand, using (29), (32) and hypotheses (H1) and (H2), we have

$$\begin{aligned} p_c(D) < p^0 &\iff f^{-1}\left(\frac{D}{f_1(\lambda_2)}\right) < f^{-1}\left(\frac{D}{f_1(\lambda^+)}\right) \iff \frac{D}{f_1(\lambda_2)} > \frac{D}{f_1(\lambda^+)} \\ &\iff f_1(\lambda_2) < f_1(\lambda^+) \iff \lambda_2 < \lambda^+. \end{aligned}$$

This completes the proof of the lemma. \square

We let

$$(40) \quad F_2(D, p^0) = f_2^{-1}(D) + W(p_c(D), D, p^0).$$

Note that F_2 is defined for $(D, p^0) \in J_c$, where J_c is given by (35). Therefore, using Lemma 5.2, we have

$$J_c = \{(D, p^0) : D \in I_c, D > F_1(D, p^0)\}.$$

If we assume that equation $f(p^0)f_1(S) = f_2(S)$ has at most one positive solution $S = \bar{S}(p^0) > 0$, which is the case when $f_1(S)$ and $f_2(S)$ are Monod functions, then the function F_2 is defined for all $(D, p^0) \in I_c \times \mathbb{R}^+$ such that $\bar{D}(p^0) < D < f_2(+\infty)$, if $f(p^0)f_1(S) > f_2(S)$ for $0 < S < \bar{S}(p^0)$, or $0 < D < \bar{D}(p^0)$, if $f(p^0)f_1(S) < f_2(S)$ for $0 < S < \bar{S}(p^0)$. Here $\bar{D}(p^0) = f_2(\bar{S}(p^0))$. We have the following result.

LEMMA 5.3. *The following equivalences hold:*

$$p_c(D) > p^*(D, p^0, S^0) \iff S^0 > F_2(D, p^0) \iff \lambda_2(D) > \lambda^-(D, p^0, S^0).$$

Proof. Using (31) and (32), together with hypotheses (H1) and (H2), we have

$$(41) \quad \begin{aligned} \lambda_2 > \lambda^- &\iff f_1(\lambda_2) > f_1(\lambda^-) \iff \frac{D}{f(p_c)} > \frac{D}{f(p^*)} \\ &\iff f(p_c) < f(p^*) \iff p_c > p^*. \end{aligned}$$

Using the fact that $\frac{\partial W}{\partial p} < 0$ and (30), we have

$$(42) \quad p_c > p^* \iff W(p_c, D, p^0) < W(p^*, D, p^0) \iff W(p_c(D), D, p^0) < S^0 - \lambda_2.$$

Therefore, from (42), together with $\lambda_2 = f_2^{-1}(D)$ and the definition (40) of F_2 , we deduce that $p_c > p^*$ is equivalent to $S^0 > F_2(D, p^0)$. \square

We define also the function

$$(43) \quad F_3(D, p^0, S^0) = (A + B)(A + B + C)C - BEF,$$

where A, B, C, E and F are defined by (37). Note that F_3 is defined for $(D, p^0, S^0) \in \mathcal{D}_c$, where \mathcal{D}_c is given by (36). Therefore, using Lemmas 5.2 and 5.3, we have

$$\mathcal{D}_c = \{(D, p^0, S^0) : D \in I_c, D > F_1(D, p^0), S^0 > F_2(D, p^0)\}.$$

Using these notations, we have the following description of existence and stability of the equilibria of (28).

THEOREM 5.4. *Assume that the hypotheses and notations of Proposition 5.1 hold. The conditions of existence and stability of equilibria of (28) can be expressed with respect to the operating parameters D, p^0 and S^0 as follows:*

Equilibria	Existence	Local exponential stability
E_0	Always	$D > \max(f(p^0)f_1(S^0), f_2(S^0))$
E_1	$D < f(p^0)f_1(S^0)$	$D < F_1(D, p^0)$
E_2	$D < f_2(S^0)$	$S^0 < F_2(D, p^0)$
E_c	$D > F_1(D, p^0)$ & $S^0 > F_2(D, p^0)$	$F_3(D, p^0, S^0) > 0$

where $F_1(D, p^0)$, $F_2(D, p^0)$ and $F_3(D, p^0, S^0)$ are defined by (39), (40) and (43), respectively.

Proof. Using (29) and hypothesis (H2), the condition $\lambda^+ > S^0$ and $\lambda_2 > S^0$ of stability of E_0 in Proposition 5.1 is equivalent to $D > f(p^0)f_1(S^0)$ and $D > f_2(S^0)$. Similarly, the condition $\lambda^+ < S^0$ [resp. $\lambda_2 < S^0$] of existence of E_1 [resp. E_2] in Proposition 5.1 is equivalent to $D < f(p^0)f_1(S^0)$ [resp. $D < f_2(S^0)$].

We consider now the stability of E_1 and E_2 . Using Lemma 5.2, the condition $\lambda^+ < \lambda_2$ of stability of E_1 in Proposition 5.1 is equivalent to $D < F_1(D, p^0)$. On the other hand, using Lemma 5.3, the condition $\lambda_2 < \lambda^-$ of stability of E_2 in Proposition 5.1 is equivalent to $S^0 < F_2(D, p^0)$.

Let us consider now the existence and stability of E_c . Using Lemmas 5.2 and 5.3, we see that the condition $\lambda^- < \lambda_2 < \lambda^+$ of existence of E_c in Proposition 5.1 is equivalent to $D > F_1(D, p^0)$ and $S^0 > F_2(D, p^0)$. Finally, using the definition (43) of the function F_3 , the condition of stability of E_c in Proposition 5.1 is equivalent to $F_3(S^0, D, p^0) > 0$. \square

5.2. Necessary and sufficient conditions for instability of E_c . We give now the necessary and sufficient conditions on the operating parameters D , p^0 and S^0 such that the positive equilibrium E_c is unstable, that is we discuss the sign of $F_3(D, p^0, S^0)$. We have

$$(44) \quad F_3 = a_2x_c^2 + a_1x_c + a_0.$$

The coefficients $a_2 = a_2(D, p^0)$, $a_1 = a_1(D, p^0)$ and $a_0 = a_0(D, p^0)$ of this polynomial are given by

$$(45) \quad a_2 = \alpha^2C, \quad a_1 = \alpha(2B + C)C - \phi BE, \quad a_0 = B(B + C)C,$$

where B , C , E are defined by (37) and α , ϕ are given by (38). Hence, F_3 given by (44), appears as a second order polynomial in x_c whose coefficients are depending only on D and p^0 and not on S^0 . Let $\Delta = \Delta(D, p^0)$ be the discriminant of F_3 :

$$(46) \quad \Delta = a_1^2 - 4a_0a_2.$$

The roots of F_3 ,

$$(47) \quad x_1(D, p^0) = \frac{-a_1 - \sqrt{\Delta}}{2a_2} \quad \text{and} \quad x_2(D, p^0) = \frac{-a_1 + \sqrt{\Delta}}{2a_2},$$

exist and are positive if and only if

$$(48) \quad a_1(D, p^0) < 0 \quad \text{and} \quad \Delta(D, p^0) > 0.$$

We define the following functions

$$(49) \quad F_4(D, p^0) = F_2(D, p^0) + x_1(D, p^0), \quad F_5(D, p^0) = F_2(D, p^0) + x_2(D, p^0),$$

where $F_2(D, p^0)$ is given by (40) and $x_1(D, p^0)$, $x_2(D, p^0)$ are given by (47).

We give now necessary and sufficient conditions on the operating parameters D and p^0 such that (48) hold. We have

$$(50) \quad a_1 = b_2y_c^2 + b_1y_c + b_0,$$

where the coefficients $b_i = b_i(D)$ are given by

$$(51) \quad b_2 = \alpha\gamma(2\beta + \gamma), \quad b_1 = 2\alpha D(\beta + \gamma) - \beta E\phi, \quad b_0 = \alpha D^2,$$

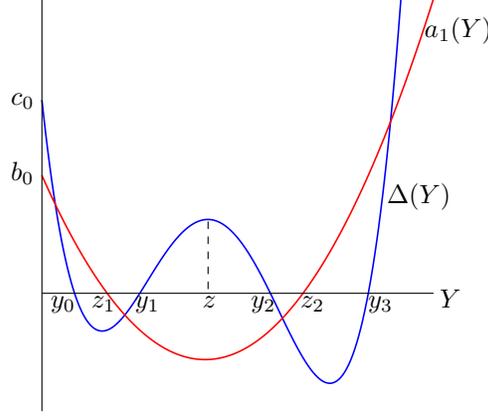


FIG. 3. The graphs of $a_1(Y)$ and $\Delta(Y)$, showing the relative positions of the roots $y_i = y_i(D)$, $i = 0 \cdots 3$, of $\Delta(Y)$ with respect to the roots $z_1 = z_1(D)$ and $z_2 = z_2(D)$ of $a_1(Y)$, when $a_1(z) < 0$ and $\Delta(z) > 0$ where $z = z(D)$ is the local maximum of $\Delta(Y)$.

with E , α , β , γ and ϕ defined by (37) and (38), respectively. We have

$$(52) \quad \Delta = c_4 y_c^4 + c_3 y_c^3 + c_2 y_c^2 + c_1 y_c + c_0,$$

where the coefficients $c_i = c_i(D)$ are given by

$$\begin{aligned} c_4 &= \alpha^2 \gamma^4, & c_3 &= 4\alpha^2 D \gamma^3 - 2\alpha\beta\gamma E \phi(2\beta + \gamma), \\ c_2 &= 6\alpha^2 D^2 \gamma^2 + \beta^2 E^2 \phi^2 - 4\alpha\beta(\beta + \gamma) D E \phi, \\ c_1 &= 4\alpha^2 \gamma D^3 - 2\alpha\beta D^2 E \phi, & c_0 &= \alpha^2 D^4, \end{aligned}$$

with E , α , β , γ and ϕ defined by (37) and (38), respectively. Hence, a_1 given by (50) and Δ given by (52), appear as a second order polynomial and a fourth order polynomial in y_c , respectively, whose coefficients are depending only on D and not on p^0 nor S^0 . For the convenience of the notations we denote by

$$a_1(Y) = b_2 Y^2 + b_1 Y + b_0, \quad \Delta(Y) = c_4 Y^4 + c_3 Y^3 + c_2 Y^2 + c_1 Y + c_0,$$

the polynomials (50) and (52). Notice first that, since $b_2 > 0$, we have $a_1(Y) < 0$ if and only if $z_1(D) < Y < z_2(D)$ where $z_1(D)$ and $z_2(D)$ are the positive real roots of $a_1(Y)$. This condition holds if and only if $b_1(D) < 0$ and $\Delta_1(D) > 0$ where $\Delta = \Delta_1(D)$ is the discriminant of the polynomial a_1 :

$$(53) \quad \Delta_1 = b_1^2 - 4b_0b_2.$$

If this discriminant is positive, the roots $z_1(D)$ and $z_2(D)$ are given by

$$(54) \quad z_1(D) = \frac{-b_1 - \sqrt{\Delta_1}}{2b_2} \quad \text{and} \quad z_2(D) = \frac{-b_1 + \sqrt{\Delta_1}}{2b_2}.$$

For the study of the sign of $\Delta(Y)$ we use the following facts. Since $a_1(z_1(D)) = a_1(z_2(D)) = 0$, from $\Delta = a_1^2 - 4a_0a_2$ we deduce that

$$\Delta(z_1(D)) < 0 \quad \text{and} \quad \Delta(z_2(D)) < 0.$$

Therefore, from $\Delta(0) = c_0 > 0$ and $\Delta(+\infty) = +\infty$ it is deduced that the polynomial $\Delta(Y)$ has at least two roots

$$y_0(D) \in (0, z_1(D)) \text{ and } y_3(D) \in (z_2(D), +\infty).$$

The condition (48) is satisfied if and only if $\Delta(Y)$ takes positive values on the interval $(z_1(D), z_2(D))$ on which $a_1(Y) < 0$, see Fig. 3. If this condition holds then $\Delta(Y)$ has necessarily three extremal points, that is to say, its polynomial derivative,

$$\Delta'(Y) = 4c_4Y^3 + 3c_3Y^2 + 2c_2Y + c_1,$$

has three real roots. A necessarily and sufficient condition for this is that the discriminant of the polynomial $\Delta'(Y)$ is positive. Let us denote by $\Delta_2 = \Delta_2(D)$ this discriminant to emphasize its dependence on the sole operating parameter D :

$$(55) \quad \Delta_2 = -27d_0^2d_3^2 + 18d_0d_1d_2d_3 - 4d_0d_2^3 - 4d_1^3d_3 + d_1^2d_2^2,$$

where $d_3 = 4c_4$, $d_2 = 3c_3$, $d_1 = 2c_2$ and $d_0 = c_1$. If $\Delta_2(D) > 0$ then $\Delta'(Y)$ has three real roots $z_b(D)$, $z(D)$ and $z_\#(D)$ such that $z_b(D) < z(D) < z_\#(D)$. Thus

$$(56) \quad z(D) \text{ is the middle root of } \Delta'(Y).$$

If $a_1(z(D)) < 0$ and $\Delta(z(D)) > 0$ then the polynomial $\Delta(Y)$ has two supplementary real roots $y_1(D) \in (z_1(D), z(D))$ and $y_2(D) \in (z(D), z_2(D))$, see Fig. 3. Thus $y_1(D)$ and $y_2(D)$ are defined by

$$(57) \quad \Delta(y_1(D)) = \Delta(y_2(D)) = 0 \text{ and } z_1(D) < y_1(D) < y_2(D) < z_2(D).$$

Therefore (48) holds only if $D \in I_3$, where I_3 is the subset of I_c defined by

$$(58) \quad I_3 = \{D \in I_c : b_1(D) < 0, \Delta_1(D) > 0, \Delta_2(D) > 0, a_1(z(D)) < 0, \Delta(z(D)) > 0\},$$

where I_c is defined by (33), b_1 is given by (51), Δ_1 is given by (53), Δ_2 is given by (55), a_1 is given by (45), Δ is given by (46) and $z(D)$ is given by (56). If $D \in I_3$ then $\Delta(Y) > 0$ and $a_1(Y) < 0$ if and only if $y_1(D) < Y < y_2(D)$. We define the following functions

$$(59) \quad F_6(D) = p_c(D) + \frac{1}{D}y_1(D)g(p_c(D)), \quad F_7(D) = p_c(D) + \frac{1}{D}y_2(D)g(p_c(D)),$$

where $p_c(D)$ is defined by (32) and $y_1(D)$, $y_2(D)$ are given by (57). We can determine the sign of F_3 , that is the stability of E_c , as stated in the following result.

THEOREM 5.5. *The positive equilibrium E_c is unstable only if the subset I_3 of I_c given by (58) is non empty. If this condition holds then E_c is unstable if and only if the three following conditions are satisfied by the operating parameters D , p^0 and S^0 :*

1. $D \in I_3$,
2. $F_6(D) < p^0 < F_7(D)$ where $F_6(D)$ and $F_7(D)$ are given by (59),
3. $F_4(D, p^0) < S^0 < F_5(D, p^0)$ where $F_4(D, p^0)$ and $F_5(D, p^0)$ are given by (49).

Proof. If $\Delta > 0$, the roots of $F_3 = 0$ are $x_1(D, p^0)$ and $x_2(D, p^0)$. Their product is equal to $\frac{a_0}{a_2}$ which is positive. Therefore, the roots exist and are positive if and only if (48) holds. The roots $z_1(D)$ and $z_2(D)$ of $a_1(Y)$, given by (54), exist and are positive if and only if $b_1(D) < 0$ and $\Delta_1(D) > 0$ which are the two first conditions in the definition of I_3 (58). Now, $\Delta(Y)$ takes positive values between $z_1(D)$ and $z_2(D)$

if and only if the three last conditions in (58) hold. Let $y_1(D)$ and $y_2(D)$ be the roots of $\Delta(Y)$ defined by (57), that is such that $z_1(D) < y_1(D) < y_2(D) < z_2(D)$. One has $a_1 < 0$ and $\Delta > 0$ if and only if

$$(60) \quad y_1(D) < y_c < y_2(D).$$

Using (34), we have

$$y_c(D, p^0) = D \frac{p^0 - p_c(D)}{g(p_c(D))}.$$

Therefore, (60) is equivalent to the condition 2 in the theorem. On the other hand $F_3 < 0$ if and only if x_c is between the roots, that is,

$$(61) \quad x_1(D, p^0) < x_c < x_2(D, p^0),$$

where $x_1(D, p^0)$ and $x_2(D, p^0)$ are defined by (47). Using (34) and (40) we have $x_c = S^0 - F_2(D, p^0)$. Therefore, (61) is equivalent to the condition 3 in the theorem. \square

5.3. Operating diagram. The effect of the operating conditions on the asymptotic behavior of the system can be summarized with the aid of the operating diagram. The operating diagram has the operating parameters D , S^0 and p^0 as its coordinates and the various regions defined in it correspond to qualitatively different dynamics. It is not easy to represent the regions of existence and stability of the equilibria in the three dimensional space of the operating parameters D , p^0 and S^0 . For this reason we will fix the operating parameter D and show the regions of existence and stability in the operating plane (p^0, S^0) , see Fig. 4 and Fig. 5(b). The boundaries of the regions in the operating diagram are locations where bifurcations occur. In order to construct the operating diagram of the system one must compute these boundaries. These boundaries are defined by formulas (62), (63), (64), (65) and (66) below.

Boundary	Equation in (p^0, S^0) , with D fixed
Γ_1	Graph of $S^0 = f_1^{-1} \left(\frac{D}{f(p^0)} \right)$
Γ_2	Horizontal line $S^0 = \lambda_2(D)$
Γ_3	Vertical line $p^0 = p_c(D)$ and $S^0 > \lambda_2(D)$
Γ_4	Oblique line $S^0 = \frac{D(p^0 - p_c(D))}{g(p_c(D))} + \lambda_2(D)$ and $p^0 > p_c(D)$
Γ_5	Graphs of $S^0 = F_4(D, p^0)$ or $S^0 = F_5(D, p^0)$

TABLE 2
Boundaries of the regions in the operating diagram.

The surface Γ_1 defined by

$$(62) \quad \Gamma_1 := \{(D, p^0, S^0) : D = f(p^0)f_1(S^0)\}$$

is the border to which E_1 exists. The surface Γ_2 defined by

$$(63) \quad \Gamma_2 := \{(D, p^0, S^0) : D = f_2(S^0)\}$$

is the border to which E_2 exists. The surface Γ_3 defined by

$$(64) \quad \Gamma_3 := \{(D, p^0, S^0) : D = F_1(D, p^0), D < f(p^0)f_1(S^0)\}$$

is the border to which E_1 is stable. The surface Γ_4 defined by

$$(65) \quad \Gamma_4 := \{(D, p^0, S^0) : S^0 = F_2(D, p^0), D < f_2(S^0)\}$$

is the border to which E_2 is stable. The surfaces Γ_3 and Γ_4 are the border to which E_c exists. The surface Γ_5 defined by

$$(66) \quad \Gamma_5 := \{(D, p^0, S^0) : F_3(D, p^0, S^0) = 0\}$$

is the border to which E_c is unstable.

Table 2 gives the descriptions of these boundaries in the operating plane (p^0, S^0) , where $D > 0$ is fixed. The curves Γ_i , $i = 1, 2, 3, 4$, intersect at point (p^0, S^0) where $p^0 = p_c(D)$ and $S^0 = \lambda_2(D)$, see Fig. 4 and Fig. 5(b). We have the following result.

PROPOSITION 5.6. *Assume that the tangent of Γ_1 at point (p_c, λ_2) is under Γ_4 , see Fig. 4(b). Then $b_1(D) > 0$ for all D , and hence E_c is LES whenever it exists.*

Proof. Let D be fixed and let $F(p^0) = f_1^{-1}\left(\frac{D}{f(p^0)}\right)$. The curve Γ_1 is the graph of the function $S^0 = F(p^0)$. Using $f_1(\lambda_2) f(p_c) = D$, we get that the slope $F'(p_c)$ of the tangent of Γ_1 at point (p_c, λ_2) is given by

$$F'(p_c) = \frac{1}{f_1'\left(f_1^{-1}\left(\frac{D}{f(p_c)}\right)\right)} \frac{-Df'(p_c)}{f^2(p_c)} = \frac{1}{f_1'(\lambda_2)} \frac{-f'(p_c)f_1(\lambda_2)}{f(p_c)}.$$

Since the slope of the straight-line Γ_4 is $D/g(p_c)$, the condition $F'(p_c) < D/g(p_c)$ is equivalent to

$$Df_1'(\lambda_2) f(p_c) + f'(p_c)f_1(\lambda_2) g(p_c) > 0.$$

Straightforward computations show that

$$b_1(D) = f_2'(\lambda_2) M + Df(p_c)f_1'(\lambda_2) [f_2'(\lambda_2) + 2g'(p_c)],$$

where $M = Df_1'(\lambda_2) f(p_c) + f'(p_c)f_1(\lambda_2) g(p_c) > 0$. Hence $b_1(D) > 0$ for all $D \in I_c$. \square

Assume that the condition in Proposition 5.6 holds. Since Γ_1 has a vertical asymptote, it intersects the straight-line Γ_4 at least at one second point, different from (p_c, λ_2) , see Fig. 4(b). For simplicity, we assume that there is only one such intersection point, which is the case for instance if Γ_1 is convex. An example exhibiting a non convex curve Γ_1 will be examined in Section 6.5. A sufficient condition for convexity of Γ_1 ($F'' \geq 0$) is given in the following result.

LEMMA 5.7. *Assume that $f_1'' \leq 0$ and $(1/f)'' \geq 0$ then $F'' \geq 0$.*

Proof. From $F(p) = f_1^{-1}\left(\frac{D}{f(p)}\right)$ we deduce that $F'(p) = \frac{D}{f_1'(F(p))} \left(\frac{1}{f(p)}\right)'$. Since $\left(\frac{1}{f(p)}\right)' = \frac{-f'(p)}{f^2(p)} > 0$, we have $F'(p) > 0$. Therefore

$$F''(p) = \frac{-Df_1''(F(p)) F'(p)}{[f_1'(F(p))]^2} \left(\frac{1}{f(p)}\right)' + \frac{D}{f_1'(F(p))} \left(\frac{1}{f(p)}\right)''.$$

Since $f_1'' \leq 0$, $F' > 0$, $\left(\frac{1}{f(p)}\right)' > 0$ and $\left(\frac{1}{f(p)}\right)'' \geq 0$ we have $F'' \geq 0$. \square

Therefore, the curves Γ_i , $i = 1..4$, separate the operating space (D, p^0, S^0) into at most seven regions, as illustrated by Fig. 4(b), labeled I, II, III, IV, V, VI and VII. Some

of these regions may be empty as shown on Fig. 4(a,c). Some of them may be not connected, as shown in Section 6.5, where region VII has two connected components, see Fig. 13(a).

Fig. 4(a) corresponds to the case without detoxification, that is to say $g(p) = 0$, where regions VI and VII are empty. On the other hand, Fig. 4(c) corresponds to the case where the tangent of Γ_1 at point (p_c, λ_2) is above Γ_4 , where the region V has disappeared.

In the case depicted in Fig. 4(c), E_c is not necessarily stable as in the case depicted in Fig. 4(b). Therefore sub-regions VIII \subset VII and IX \subset VI may occur, on which E_c is unstable, see Fig. 4(d) and Fig. 5(b). We describe below how these regions VIII and IX are constructed. The necessary condition on D for which E_c is unstable is $D \in I_3$, as shown in Theorem 5.5. Assume that I_3 defined by (58) is non empty.

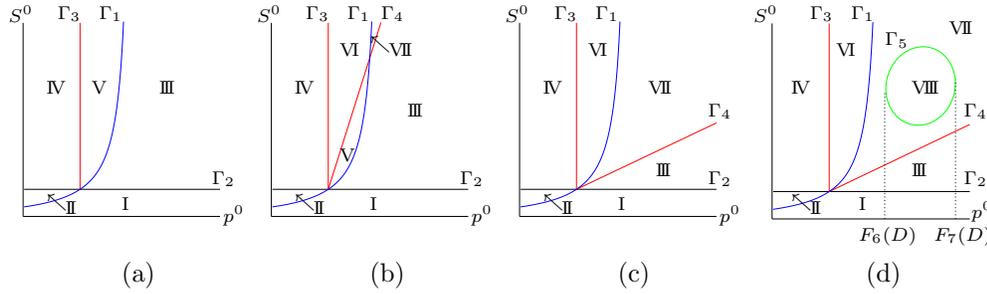


FIG. 4. Illustrative operating diagrams: (a) corresponds to the case without detoxification; in case (b), E_c is stable whenever it exists; in case (c) the stability of E_c does not always occur and a region of instability can appear as shown in case (d).

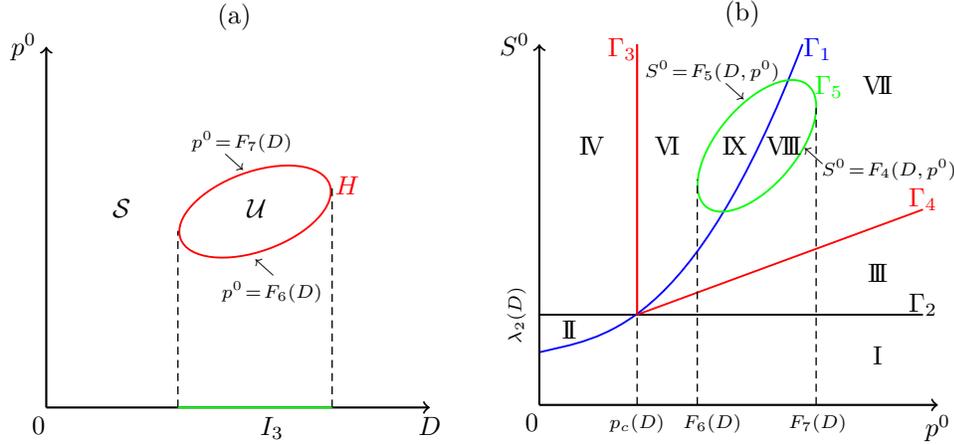


FIG. 5. Illustrative operating diagram for system (28). (a): The subset of (D, p^0) on which (48) holds. (b): The operating plane (p^0, S^0) with D fixed. The parameter D is fixed in the subset I_3 , that is the regions VIII or IX exist.

For simplicity, we assume that I_3 is a sub-interval of I_c , as shown in Fig. 5(a). The curve H of equation

$$(67) \quad H = \{(D, p^0) : a_1(D, p^0) < 0, \Delta(D, p^0) = 0\}$$

separates the operating plane (D, p^0) in two regions: the bounded region \mathcal{U} in which $a_1(D, p^0) < 0$ and $\Delta(D, p^0) > 0$, that is to say the condition (48) holds, and the region \mathcal{S} where this condition does not hold, see Fig. 5(a). Notice that H is simply the union of the graphs of functions $p^0 = F_6(D)$ and $p^0 = F_7(D)$, given by (59), with $D \in I_3$. Let $(D, p^0) \in \mathcal{U}$. Therefore $D \in I_3$ and $F_6(D) < p^0 < F_7(D)$. Hence, according to Theorem 5.5, E_c is unstable if and only if $F_4(D, p^0) < S^0 < F_5(D, p^0)$.

For $D \in I_3$ fixed, equation $F_3(D, p^0, S^0) = 0$ defines a closed curve Γ_5 in the operating plane (p^0, S^0) , see Fig. 4(d) and Fig. 5(b). Notice that Γ_5 is simply the union of the graphs of functions $S^0 = F_4(D, p^0)$ and $S^0 = F_5(D, p^0)$, given by (49), with $D \in I_3$ and $F_6(D) \leq p^0 \leq F_7(D)$. The curve Γ_5 can have no intersection with the curve Γ_1 , as in Fig. 4(d). It defines then a sub-region VIII of region VII. In this case we simply denote by the same letter VII, the complement of VIII in the region VII, see Fig. 4(d). On the other hand, the curve Γ_5 can intersect the curve Γ_1 , as in Fig. 5(b). It defines then two sub-regions VIII \subset VII and IX \subset VI. For simplicity we denote by the same letter VII, the complement of VIII in the region VII and by the same letter VI the complement of IX in the region VI, see Fig. 5(b). With these notations, E_c is unstable in the bounded sub-region VIII \cup IX of existence of E_c , and stable in its complementary region VI \cup VII. The behavior of the system in each of the nine regions I, ..., IX is given by Theorem 5.4. This behavior is summarized in Table 3.

Regions	I	II	III	IV	V	VI	VII	VIII	IX
E_0	S	U	U	U	U	U	U	U	U
E_1		S		S	U	U			U
E_2			S	U	S	U	U	U	U
E_c						S	S	U	U

TABLE 3

Existence and stability of equilibria in the regions of the operating diagrams of Fig. 4, Fig. 5(b), Fig. 7(b), Fig. 8, Fig. 9(b), Fig. 10(b), Fig. 11(b), Fig. 12(b) and Fig. 13. The letter S (resp. U) means stable (resp. unstable) and no letter means that the equilibrium does not exist.

Hsu and Waltman [18] conjectured that for the growth functions given by (2), if E_c and E_1 exist and E_1 is unstable, which occurs in region VI, then E_c is necessarily stable. This means that in this case the sub-region IX cannot exist. All the simulations given in Section 6 show that the region IX never exist for the Monod growth functions given by (2). However we will show that this region can exist for Holling type 3 growth functions (71), as shown in Section 6.5.

In Fig. 5(a) we have assumed that I_3 is a sub-interval of I_c . Actually, if we want to determine I_3 we have to fix the biological parameters of the model, and then we have to plot the graphs of the five functions appearing in the definition (58) of I_3 . Then, we consider the subset on which these functions have the determined sign, see Fig. 6. Therefore the determination of stability of E_c , with respect to the biological and operating parameters, is reduced to the determination of the sign of functions depending only on the dilution rate D . It will be seen in the examples given in Section 6 that I_3 is indeed a sub-interval of the interval $I_c = (D_1, D_2)$, defined by (33), of one of the three forms shown in Table 4

The operating diagrams shown in Fig. 4 and Fig. 5 are given only as illustrative examples, showing that our analysis gives a complete description of the behavior of the system for a large class of growth functions. Notice that for plotting operating diagrams we must choose functions f , f_1 , f_2 , and g in system (28) and fix the values

Case	Interval I_3	Figures
Left	$I_3 = (D_1, D_3)$, where $D_1 < D_3 < D_2$	Fig. 7(a) and Fig. 9(a)
Center	$I_3 = (D_3, D_4)$, where $D_1 < D_3 < D_4 < D_2$	Fig. 10(a) and Fig. 12(a)
Right	$I_3 = (D_3, D_2)$, where $D_1 < D_3 < D_2$	Fig. 11(a)

TABLE 4
Three forms of interval I_3 .

of the biological parameters. We illustrate this in the following section for various examples that have been considered in the literature.

6. Examples. In this section, excepted for Section 6.5, we consider the model (28) with f , f_1 , f_2 , and g given by (2). Let us show the usefulness of our results on the construction of the operating diagram corresponding to various set of biological parameters encountered in the literature, in particular those considered in [18, 21]. Notice that the functions f_1 and f satisfy the conditions in Lemma 5.7. Therefore Γ_1 intersects Γ_4 at most at one point different from $(p_c(D), \lambda_2(D))$.

Parameters	m_1	m_2	K_1	K_2	δ	K	μ	Figures
Case 1	5	6	0.5	3.5	50	0.1	5	Fig. 6 and Fig. 7
Case 2	5	6	0.5	3.5	0.02	0.1	5	Fig. 8(a)
Case 3	0.7	0.7	5	10	1	10	1	Fig. 8(b)
Case 4	0.7	0.7	5	10	1	0.035	1	Fig. 9
Case 5	0.7	0.7	0.4	10	1	10	1	Fig. 10
Case 6	8	3	2.5	1	5	0.01	3	Fig. 11
Case 7	1	0.01	1	1	0.5	0.007	1	Fig. 12 and Fig. 13

TABLE 5
Nominal parameter values.

6.1. Parameter values of Hsu and Waltman [18]. The parameter values used by [18] are given in Table 5, Case 1. The plots of the functions $b_1(D)$, $\Delta_1(D)$, $\Delta_2(D)$, $a_1(z(D))$ and $\Delta(z(D))$, see Fig. 6, show that $I_3 = (0, D_3)$ with $D_3 \approx 2.0578$. According to Theorem 5.5, if $D > D_3$ then E_c is stable whenever it exists. Notice that $D = 1 \in I_3$. The plot of the curve H defined by (67) is shown in Fig. 7(a). The curve H separates the plane (D, p^0) into two regions \mathcal{U} and \mathcal{S} . According to Theorem 5.5, E_c is unstable only if $(D, p^0) \in \mathcal{U}$. Now, we determine the operating diagram (p^0, S^0) for $D = 1 \in I_3$. According to Theorem 5.5, for all $p^0 \in (F_6(1), F_7(1))$, with $F_6(1) \approx 0.4034$ and $F_7(1) \approx 2.108$, we have $(1, p^0) \in \mathcal{U}$ and hence E_c is unstable as soon as $(p^0, S^0) \in \text{VIII}$, see Fig. 7(b). Notice that $(S^0 = 1, p^0 = 1) \in \text{VIII}$ which agrees with the result of [18] in which it was shown that for $D = S^0 = p^0 = 1$, E_c is unstable.

6.2. Sufficient conditions of stability of E_c whenever it exists. As stated in Proposition 5.6, when the tangent of Γ_1 at point (p_c, λ_2) is under Γ_4 , E_c is stable whenever it exists. This case occurs for the parameter values given in Table 5, Case 2, where the parameters are the same as in Case 1, except that δ is lowered from 50 to 0.02. The operating diagram in the plane (p^0, S^0) and $D = 1$ is shown in Fig. 8(a). The region VIII of instability of E_c does not exist as predicted by Proposition 5.6.

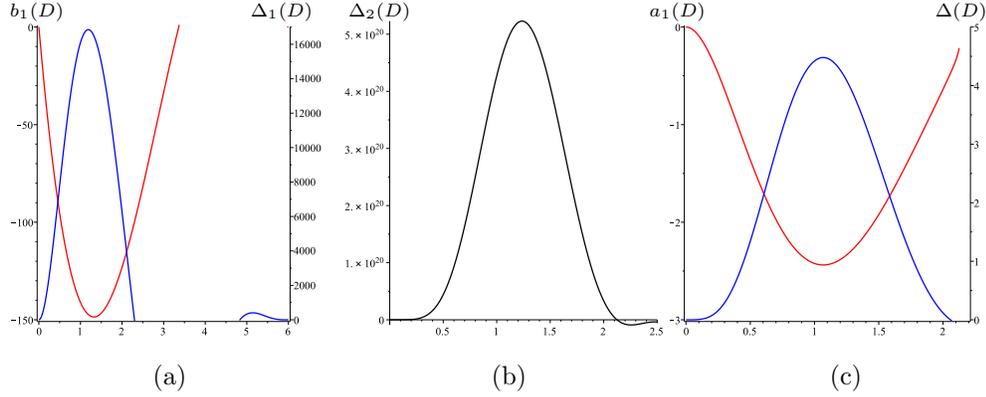


FIG. 6. The numerical plots of (a): $b_1(D)$ (in red) and $\Delta_1(D)$ (in blue); (b): $\Delta_2(D)$; (c): $a_1(z(D))$ (in red) and $\Delta(z(D))$ (in blue). These plots show that the conditions in the definition (58) of I_3 hold for $0 < D < D_3$ with $D_3 \approx 2.0578$. The biological parameters are given in Table 5, Case 1.

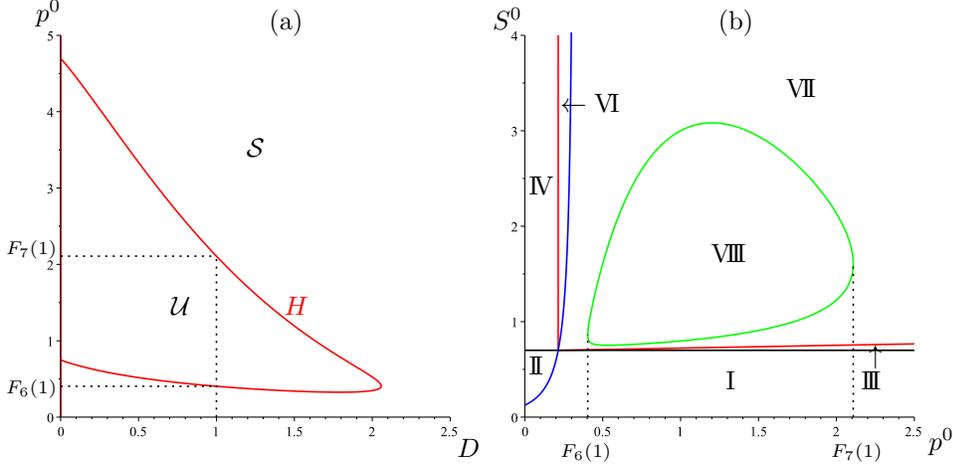


FIG. 7. (a): The subset of (D, p^0) on which (48) holds. (b): The operating diagram (p^0, S^0) for $D = 1$ corresponding to the biological parameters given in Table 5, Case 1.

Let us give now another sufficient condition on the biological parameters such that E_c is stable whenever it exists.

PROPOSITION 6.1. Let $\mu_0 = \frac{2}{\sqrt{K^2+4K}-K} \ln\left(\frac{m_1 K_2}{m_2 K_1}\right)$ and $\mu_1 = 2\frac{m_2 K_1}{m_1 K_2}$. If

$$(68) \quad K_1 < K_2 \text{ and } \mu_0 \leq \mu \leq \mu_1,$$

then $b_1(D) > 0$ for all D , so that E_c is LES whenever it exists.

Proof. Recall that $b_1 = b_1(D)$ is given by (51)

$$b_1 = 2\alpha D(\beta + \gamma) - \beta E\phi,$$

where E is defined by (26) and α, β, γ and ϕ are defined by (38). From $g(p) = \frac{\delta p}{K+p}$ and $g'(p) = \frac{\delta K}{(K+p)^2}$ one has $g(p) \leq g'(p)$ if and only if $(K+p)p \leq K$. Therefore p is

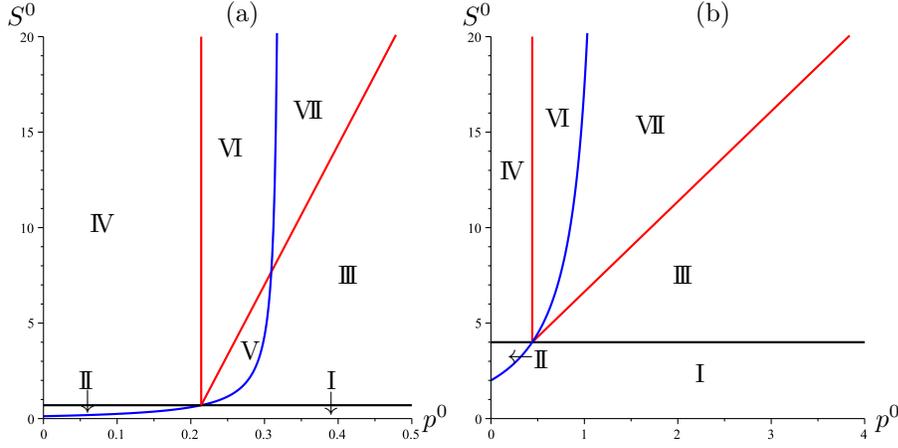


FIG. 8. E_c is LES whenever it exists. (a): The operating diagram (p^0, S^0) for $D = 1$ corresponding to the biological parameters in Table 5, Case 2. (b): The operating diagram (p^0, S^0) for $D = 0.2$ corresponding to the biological parameters in Table 5, Case 3.

between the roots of equation $p^2 + Kp - K = 0$. Since $p \geq 0$ we have

$$(69) \quad g(p) \leq g'(p) \iff 0 \leq p \leq \frac{\sqrt{K^2 + 4K} - K}{2}.$$

Straightforward calculations show that

$$p_c(D) = \frac{1}{\mu} \ln \left(\frac{m_1 K_2}{m_2 K_1 + D(K_2 - K_1)} \right).$$

Since $K_1 < K_2$, p_c is decreasing. Thus, using $\mu \geq \mu_0$, one has

$$p_c(D) < p_c(0) = \frac{1}{\mu} \ln \left(\frac{m_1 K_2}{m_2 K_1} \right) \leq \frac{\sqrt{K^2 + 4K} - K}{2}.$$

Therefore, using (69), one has

$$(70) \quad g(p_c) \leq g'(p_c).$$

Now using (70), (38) and (26) together with $f'(p) = -\mu f(p)$, one has

$$b_1(D) \geq f(p_c(D)) g(p_c(D)) M, \text{ where } M = 2Df'_1(\lambda_2(D)) - \mu f_1(\lambda_2(D))f'_2(\lambda_2(D)).$$

Thus, if $M > 0$ then $b_1(D) > 0$. Straightforward computations show that

$$f_1(\lambda_2(D)) = \frac{m_1 K_2 D}{m_2 K_1 + D(K_2 - K_1)}, \quad f'_1(\lambda_2(D)) = \frac{m_1 K_1 (m_2 - D)^2}{(m_2 K_1 + D(K_2 - K_1))^2},$$

$$f'_2(\lambda_2(D)) = \frac{(m_2 - D)^2}{m_2 K_2}.$$

Hence

$$M = \frac{m_1 D (D - m_2)^2}{m_2 (m_2 K_1 + D(K_2 - K_1))^2} N, \text{ where } N = K_1 m_2 (2 - \mu) + \mu D (K_1 - K_2).$$

Thus M is positive if and only if $N > 0$. Since $p_c(D) > 0$ we have

$$D(K_1 - K_2) > m_2K_1 - m_1K_2,$$

from which we deduce that

$$N > K_1m_2(2 - \mu) + \mu(m_2K_1 - m_1K_2) = 2K_1m_2 - \mu m_1K_2.$$

Hence, from $\mu \leq \mu_1$ one has $N > 0$. Therefore, if (68) holds then $b_1(D) > 0$. \square

6.3. Parameter values of Lenski and Hattingh [21]. Let us give an application of Proposition 6.1, with the parameter values used in [21], given in Table 5, Case 3. These biological parameters satisfy the conditions (68). In this case, we have $\mu_0 \approx 0.76$ and $\mu_1 = 1$. Thus $\mu_0 \leq \mu \leq \mu_1$. According to Proposition 6.1, E_c is stable whenever it exists. Therefore our findings give a justification of the claim of [21], that is, for $D = 0.2$, the coexistence equilibrium E_c is stable whenever it exists. The stability occurs for all values of D , not only for $D = 0.2$. The operating diagram in the plane (p^0, S^0) and $D = 0.2$ is shown in Fig. 8(b). We obtain the same result as [21], Fig. 1(b).

In [21], it was also stated that the instability of E_c can be accomplished in two different ways. First, lowering K_1 can destabilize E_c : the authors claimed that in the limiting case $K_1 = 0$, E_c exists and is unstable when $D = 0.2$, $p^0 = 2.5$ and $S^0 = 20$. Second, lowering K while raising μ may destabilize E_c : the authors claimed that in the limiting case $K = 0$, if $\mu = 10$, then E_c exists and is unstable when $D = 0.2$, $p^0 = 2.5$ and $S^0 = 20$. Let us show how our analysis can clarify this question.

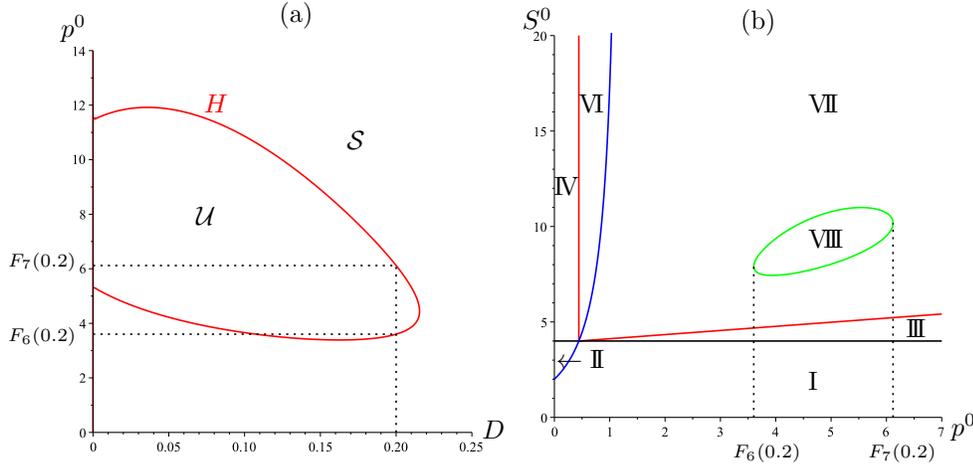


FIG. 9. (a): The subset of (D, p^0) on which (48) holds. (b): The operating diagram (p^0, S^0) for $D = 0.2$. The biological parameters are given in Table 5, Case 4.

It is seen from the inequalities $\mu_0 \leq \mu \leq \mu_1$ in (68) that lowering K_1 will raise μ_0 and diminish μ_1 so that the inequalities $\mu_0 \leq \mu \leq \mu_1$ can be violated, giving hence the possibility of instability. On the other hand lowering K will raise μ_0 , so that the inequality $\mu_0 \leq \mu$ can be violated, giving hence the possibility of instability.

Let us consider the parameter values given in Table 5, Case 4, where the parameters are the same as in Case 3, except that K is lowered from 10 to 0.035. For these parameter values $\mu_0 \approx 4.06$ and $\mu_1 = 1$, thus the inequality $\mu_0 \leq \mu$ is violated.

Indeed, we can see that the instability of E_c can occur. The plots of the functions $b_1(D)$, $\Delta_1(D)$, $\Delta_2(D)$, $a_1(z(D))$ and $\Delta(z(D))$, similar to those presented in Fig. 6, show that $I_3 = (0, D_3)$ with $D_3 \approx 0.2155$. According to Theorem 5.5, if $D > D_3$ then E_c is stable whenever it exists. The plot of the curve H defined by (67) is shown in Fig. 9(a). The curve H separates the plane (D, p^0) into two regions \mathcal{U} and \mathcal{S} . According to Theorem 5.5, E_c is unstable only if $(D, p^0) \in \mathcal{U}$. Now, we determine the operating diagram (p^0, S^0) for $D = 0.2 \in I_3$. According to Theorem 5.5, for all $p^0 \in (F_6(0.2), F_7(0.2))$, with $F_6(0.2) \approx 3.602$ and $F_7(0.2) \approx 6.119$, we have $(0.2, p^0) \in \mathcal{U}$ and hence E_c is unstable as soon as $(p^0, S^0) \in \text{VIII}$, see Fig. 9(b).

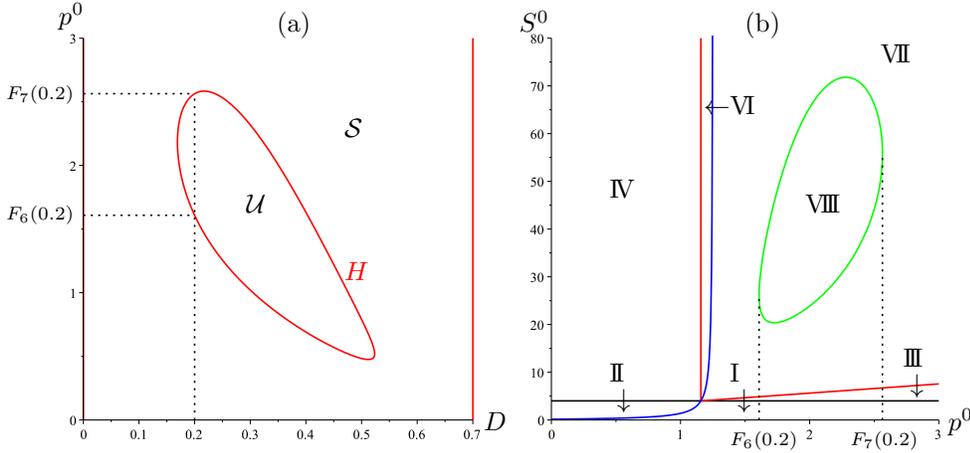


FIG. 10. (a): The subset of (D, p^0) on which (48) holds. (b): The operating diagram (p^0, S^0) for $D = 0.2$. The biological parameters are given in Table 5, Case 5.

Let us consider the parameter values given in Table 5, Case 5, where the parameters are the same as in Case 3, except that K_1 is lowered from 5 to 0.4. For these parameter values $\mu_0 \approx 3.51$ and $\mu_1 = 0.08$, thus the inequalities $\mu_0 \leq \mu \leq \mu_1$ are violated. Indeed, we can see that the instability of E_c can occur. The plots of the functions $b_1(D)$, $\Delta_1(D)$, $\Delta_2(D)$, $a_1(z(D))$ and $\Delta(z(D))$, similar to those presented in Fig. 6, show that $I_3 = (D_3, D_4)$ with $D_3 \approx 0.1691$ and $D_4 \approx 0.5236$. According to Theorem 5.5, if $D < D_3$ or $D > D_4$ then E_c is stable whenever it exists. The plot of the curve H defined by (67) is shown in Fig. 10(a). The curve H separates the plane (D, p^0) into two regions \mathcal{U} and \mathcal{S} . According to Theorem 5.5, E_c is unstable only if $(D, p^0) \in \mathcal{U}$. Now, we determine the operating diagram (p^0, S^0) for $D = 0.2 \in I_3$. According to Theorem 5.5, for all $p^0 \in (F_6(0.2), F_7(0.2))$, with $F_6(0.2) \approx 1.608$ and $F_7(0.2) \approx 2.564$, we have $(0.2, p^0) \in \mathcal{U}$ and hence E_c is unstable as soon as $(p^0, S^0) \in \text{VIII}$, see Fig. 10(b).

6.4. Parameter values corresponding to case ‘Right’ of Table 4. Let us consider the parameter values given in Table 5, Case 6. The plots of the functions $b_1(D)$, $\Delta_1(D)$, $\Delta_2(D)$, $a_1(z(D))$ and $\Delta(z(D))$, similar to those presented in Fig. 6, show that $I_3 = (D_3, m_2)$ with $D_3 \approx 2.1219$. According to Theorem 5.5, if $D < D_3$ then E_c is stable whenever it exists. The plot of the curve H defined by (67) is shown in Fig. 11(a). The curve H separates the plane (D, p^0) into two regions \mathcal{U} and \mathcal{S} . According to Theorem 5.5, E_c is unstable only if $(D, p^0) \in \mathcal{U}$. Now, we determine the operating diagram (p^0, S^0) for $D = 2.2 \in I_3$. According to Theorem 5.5, for

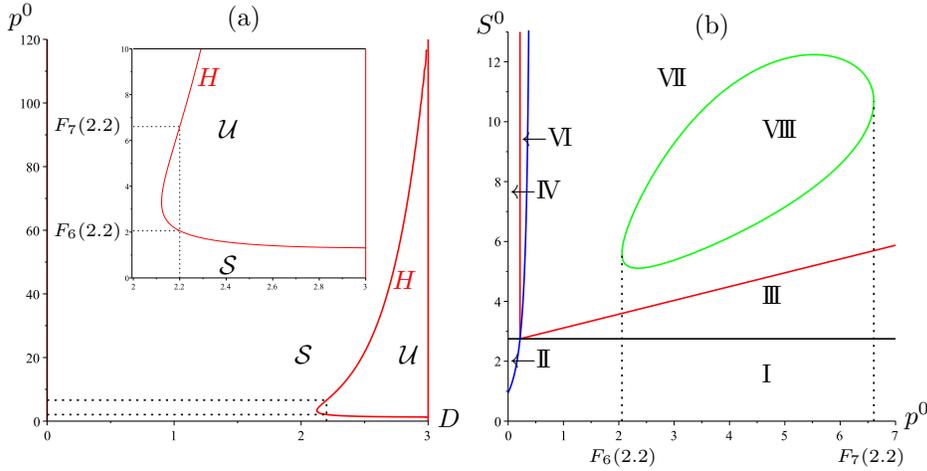


FIG. 11. (a): The subset of (D, p^0) on which (48) holds, with a zoom showing the values $F_6(2.2)$ and $F_7(2.2)$. (b): The operating diagram (p^0, S^0) for $D = 2.2$. The biological parameters are given in Table 5, Case 6.

all $p^0 \in (F_6(2.2), F_7(2.2))$, with $F_6(2.2) \approx 2.0568$ and $F_7(2.2) \approx 6.6073$, we have $(2.2, p^0) \in \mathcal{U}$ and hence E_c is unstable as soon as $(p^0, S^0) \in \text{VIII}$, see Fig. 11(b).

6.5. An example with curve Γ_5 intersecting curve Γ_1 . Let us consider the following growth functions

$$(71) \quad f(p) = \frac{1}{1 + \mu p}, \quad f_1(S) = \frac{m_1 S^2}{K_1^2 + S^2}, \quad f_2(S) = \frac{m_2 S}{K_2 + S}, \quad g(p) = \frac{\delta p}{K + p},$$

with parameter values given in Table 5, Case 7. The plots of the functions $b_1(D)$, $\Delta_1(D)$, $\Delta_2(D)$, $a_1(z(D))$ and $\Delta(z(D))$, similar to those presented in Fig. 6, show that $I_3 = (D_3, D_4)$ with $D_3 \approx 1.43610^{-4}$ and $D_4 \approx 4.90110^{-4}$. According to Theorem 5.5, if $D < D_3$ or $D > D_4$ then E_c is stable whenever it exists. The plot of the curve H defined by (67) is shown in Fig. 12(a). The curve H separates the plane (D, p^0) into two regions \mathcal{U} and \mathcal{S} . According to Theorem 5.5, E_c is unstable only if $(D, p^0) \in \mathcal{U}$. Now, we determine the operating diagram (p^0, S^0) for $D = 0.0003 \in I_3$. Notice that in this example, Γ_5 intersects Γ_1 . Let us denote by VIII and IX the regions delimited by these curves as shown in Fig. 12(b). According to Theorem 5.5, for all $p^0 \in (F_6(0.0003), F_7(0.0003))$, with $F_6(0.0003) \approx 27.05$ and $F_7(0.0003) \approx 594.7$, we have $(0.0003, p^0) \in \mathcal{U}$ and hence E_c is unstable as soon as $(p^0, S^0) \in \text{VIII} \cup \text{IX}$, see Fig. 12(b). Note that the curve Γ_1 is not convex and the region VII is not connected.

7. Discussion. In this work we have generalized the model of competition in the chemostat with an inhibitor [18, 21] by considering generic growth rate functions of competitors and absorption rate of external inhibitor. Our mathematical analysis of the model has revealed 9 possible behaviors. We have first shown the existence of a unique positive equilibrium that may be locally asymptotically stable while all other equilibria are unstable. In a first step, we studied the existence and stability of equilibria of the model with respect to the operating parameters D , p^0 and S^0 , by fixing the biological parameters. Next, we gave the necessary and sufficient conditions on those operating parameters for which the positive equilibrium E_c is unstable. Since the effect of the operating conditions on the dynamic characteristics of the system can

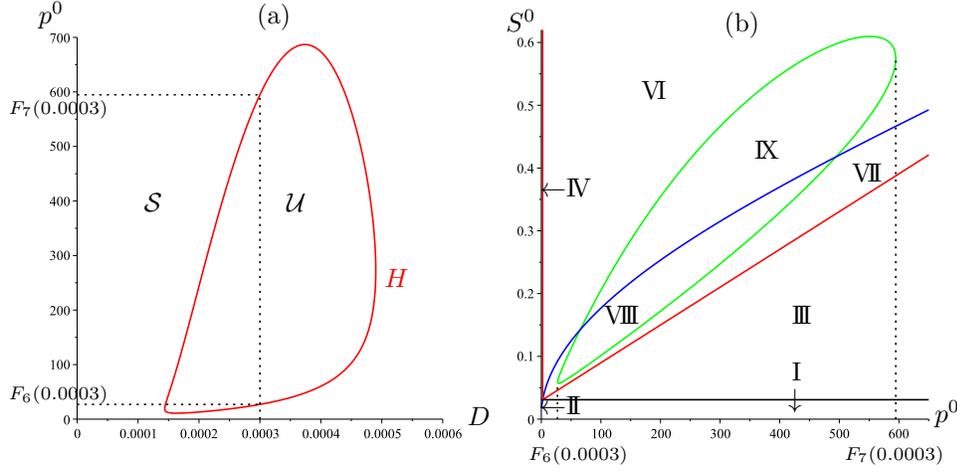


FIG. 12. (a): The subset of (D, p^0) on which (48) holds. (b): The operating diagram (p^0, S^0) for $D = 0.0003$. The biological parameters are given in Table 5, Case 7.

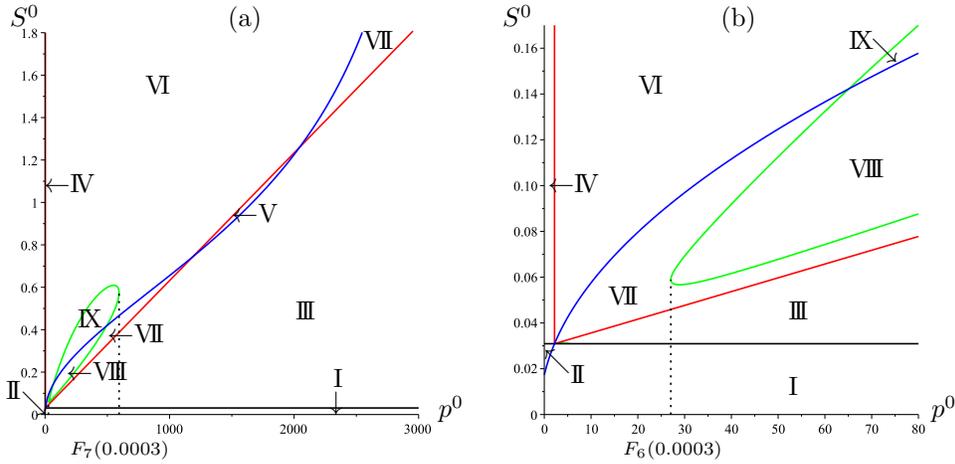


FIG. 13. Supplementary information on the operating diagram shown in Fig. 12. (a): The full operating diagram. (b): A zoom near the origin. The nine regions I, ..., IX are non empty. The region VII is not connected. The growth functions are given by (71) and the biological parameters are given in Table 5, Case 7.

be summarized with the aid of the operating diagram, we considered the one that has the operating parameters D , S^0 and p^0 as its coordinates. As it is not easy to represent the regions of existence and stability of the equilibria in a three dimensional space, we fixed the operating parameter D and showed the regions of existence and stability in the operating plane (p^0, S^0) in which the various outcomes occur.

To maintain the coexistence of species in the chemostat, the ideally parameter values of S^0 and p^0 should be chosen in the region $\text{VI} \cup \text{VII}$, of coexistence but not in the other regions of washout or exclusion of one species. A region $\text{VIII} \cup \text{IX}$ may occur, on which E_c is unstable. The simulations given showed that the region IX never exist for the Monod growth functions which agrees with a Conjecture of Hsu and Waltman [18]. However we showed that this region can exist for Holling type 3

growth functions.

Our main contribution in this work is the determination of the operating diagram and the analysis of its dependence with respect to the biological parameters. As it was noticed by Smith and Waltman, [29], p. 252, the operating diagram is probably the most useful answer for the discussion of the behavior of the model with respect of the parameters. This diagram shows how robust or how extensive is the parameter region where coexistence occurs, where the coexistence equilibrium is stable and where it is unstable.

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