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A model of flocculation in the chemostat

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ABSTRACT. In this work, we study a flocculation model with a single resource and a single species which is present in two forms: isolated bacteria and attached bacteria. With monotonic growth rates and distinct removal rates, we show that this model presents a rich behavior with multiplicity of positive equilibria and bi-stability. Whereas, this bi-stability could occur in the classical chemostat model only with a non-monotonic growth rate.

RÉSUMÉ. Dans ce travail, nous étudions un modèle de floculation avec une seule ressource et une seule espèce qui se présente sous deux formes: des bactéries isolées et en flocs. Avec des taux de croissance monotones et des taux de prélèvement distincts, nous montrons que ce modèle présente un comportement très riche avec multiplicité des équilibres positifs et bi-stabilité. Cependant, dans le modèle classique du chémostat, cette bi-stabilité ne peut se produire qu'avec un taux de croissance non monotone.

KEYWORDS : Bifurcation, Bi-stability, Chemostat, Flocculation

MOTS-CLÉS : Bifurcation, Bi-stabilité, Chémostat, Floculation

1. Introduction

Flocculation is a process wherein microorganisms isolated or planktonic bacteria cluster together to form a flocs and reversibly this flocs can split and liberate isolated bacteria [10]. The attachment of planktonic bacteria could be also on a wall as biofilms [1]. This flocculation mechanism can explain the coexistence between species when the most competitive species inhibits its growth by the formation of flocs [3, 6]. Indeed, the flocs consume less substrate than isolated bacteria since they have less access to the substrate, given that this access to the substrate is proportional to the outside surface of the floc.

In order to understand and predict these flocculation phenomena, several extensions of the well-known chemostat model [9] have been proposed and studied in the literature by considering two compartments of isolated and attached biomass for each species [3]. For instance, Pilyugin and Waltman [8] have treated a model of wall growth where the attachment and detachment rates are constant, and the population on the wall does not wash out of the chemostat. The Freter model [5] describes a microbial population constituted of planktonic cells in the fluid and adherent cells on the surface. Their model was studied by Jones et al. [7], assuming that the planktonic bacteria are attracted to the wall at a rate proportional to planktonic cell density and the fraction of unoccupied colonization sites on the wall. More recently, the competition model of two species for a single substrate has been studied by Haegeman and Rapaport [6], assuming that only the most competitive species inhibits its growth by the formation of flocs. The study of [6] has been extended by [2] and [4].

In this paper, we study the model of flocculation considered in [3], where the isolated bacteria can stick with isolated bacteria or flocs to form new flocs. We do not assume as in [3] that attachment and detachment dynamics are fast compared to the growth of bacteria. The paper is organized as follows. In Section 2, we present the model of flocculation proposed in [3]. In Section 3, we study the existence and the local stability of the equilibria of system (1) for non-negative attachment and detachment rates. In Section 4, numerical simulations are presented with realistic growth functions (of Monod type) and the conclusion is drawn in the last Section 5. Most of the proofs are reported in the Appendix A.

2. Mathematical model

In this paper, we consider the model of flocculation proposed in [3]

$$\left\{\begin{array}{lcl} \dot{S} & = & D(S_{in}-S)-\mu_u(S)u-\mu_v(S)v \\ \dot{u} & = & [\mu_u(S)-D_u]u-a(u+v)u+bv \\ \dot{v} & = & [\mu_v(S)-D_v]v+a(u+v)u-bv \end{array}\right. \tag{1}$$

where $S(t)$ denotes the concentration of the substrate at time t; $u(t)$ and $v(t)$ denote, respectively, the concentration of planktonic and attached bacteria at time t; $\mu_u(S)$ and $\mu_v(S)$ represent, respectively, the per-capita growth rates of planktonic and attached bacteria; S_{in} and D denote, respectively, the concentration of the substrate in the feed device and the dilution rate of the chemostat; D_u and D_v represent, respectively, the removal rates of planktonic and attached bacteria such that $D_v \leqslant D_u \leqslant D$.

We assume that the planktonic bacteria can stick with the isolated bacteria or the flocs to form a new flocs, with rate $a(u+v)$, where a is a non-negative constant, and that the flocs can split and liberate an isolated bacteria, with rate b, where b is a non-negative constant. We add the following assumptions on the growth rates:

H1: The functions $\mu_u(\cdot)$ and $\mu_v(\cdot)$ are increasing for all $S > 0$ and satisfy $\mu_u(0) = \mu_v(0) = 0$.

Since the bacteria in flocs have less access to the substrate, given that this access to the substrate is proportional to the outside surface of the floc, we assume that the bacteria in flocs consume less substrate than isolated bacteria:

H2: $\mu_u(S) > \mu_v(S)$ for all $S > 0$.

Let $\varphi_u(S)$ and $\varphi_v(S)$ be the functions defined by

$$\varphi_u(S) = \mu_u(S) - D_u \quad \text{and} \quad \varphi_v(S) = \mu_v(S) - D_v.$$

When equations $\mu_u(S) = D_u$, $\mu_v(S) = D_v$ and $\varphi_v(S) = b$ have solutions, they are unique and we define the usual *break-even concentrations*

$$\lambda_u = \mu_u^{-1}(D_u), \quad \lambda_v = \mu_v^{-1}(D_v) \quad \text{and} \quad \lambda_b = \varphi_v^{-1}(b).$$

Otherwise, we put $\lambda_u = +\infty$ or $\lambda_v = +\infty$ or $\lambda_b = +\infty$. We have the following result:

Proposition 2.1 *For any non-negative initial condition, the solutions of system (1) remain non-negative and bounded for all* $t \geqslant 0$. *The set*

$$\Omega = \left\{ (S, u, v) \in \mathbb{R}_+^3 : S + u + v \leqslant \frac{D}{D_v} S_{in} \right\}$$

is positively invariant and is a global attractor for (1).

3. Analysis of the model

3.1. Existence of equilibria

In the following, we propose to study the existence of equilibria of (1). We use the following definitions

$$I = \begin{cases}]\lambda_u, \lambda_v[& \text{if} \quad \lambda_u < \lambda_v \\ ]\lambda_v, \min(\lambda_b, \lambda_u)[& \text{if} \quad \lambda_v < \lambda_u. \end{cases}$$

$$U(S) = \frac{D(S_{in} - S)\varphi_v(S)}{D_u\varphi_v(S) - D_v\varphi_u(S)} \quad \text{and} \quad V(S) = \frac{D(S_{in} - S)\varphi_u(S)}{D_v\varphi_u(S) - D_u\varphi_v(S)}.$$

$$H(S) = \frac{\varphi_u(S)(\varphi_v(S) - b)[D_u\varphi_v(S) - D_v\varphi_u(S)]}{a[\varphi_v(S) - \varphi_u(S)]\varphi_v(S)}. \tag{2}$$

Lemma 3.1 *The system (1), with* $a > 0$ *and* $b > 0$, *admits the following equilibria:*

– *The washout,* $E_0 = (S_{in}, 0, 0)$, *which always exists.*

– *A positive equilibrium,* $E^* = (S^*, u^*, v^*)$ *for each* S^* *solution of the equation*

$$D(S_{in} - S) = H(S), \tag{3}$$

$u^* = U(S^*)$ *and* $v^* = V(S^*)$, *which exists if and only if* $S^* \in I$.

The case $a = b = 0$ is simply the classical model of competition of two microbial species for which the competitive exclusion principle takes place [9].In this case, the system (1) has an equilibrium of extinction of v, $E_u = (\lambda_u, u^*, 0)$, which exists if and only if $\lambda_u < S_{in}$ and an equilibrium of extinction of u, $E_v = (\lambda_v, 0, v^*)$, which exists if and only if $\lambda_v < S_{in}$ with

$$u^* = U(\lambda_u) = \frac{D}{D_u}(S_{in} - \lambda_u) \quad \text{and} \quad v^* = V(\lambda_v) = \frac{D}{D_v}(S_{in} - \lambda_v).$$

In the following, we study the existence of positive equilibria of (1). Each solution of the equation (3) belonging to the interval I gives rise to a positive equilibrium of system. Note that

$$H'(S) = \frac{\mu_u'(\varphi_v - b)\varphi_v F + \mu_v' \varphi_u G}{a(\varphi_v - \varphi_u)^2 \varphi_v^2} \tag{4}$$

where

$$\begin{array}{rcl} F & = & [D_u\varphi_v^2 - 2D_v\varphi_u\varphi_v + D_v\varphi_u^2] > 0 \\ G & = & [bD_u\varphi_v^2 + (D_v - D_u)\varphi_u\varphi_v^2 + bD_v(\varphi_u^2 - 2\varphi_u\varphi_v)] \end{array} \tag{5}$$

In the case $\lambda_u < \lambda_v$, the sign of $H'(S)$ can be positive or negative for $S \in I$ (see Fig. 1). In the case $\lambda_v < \lambda_u$, one has $H'(S) < 0$ on $I =]\lambda_v, \min(\lambda_b, \lambda_u)[$. Therefore, the function $H(\cdot)$ is decreasing on I, but equation (3) can have many solutions (see Figs. 2 and 3).

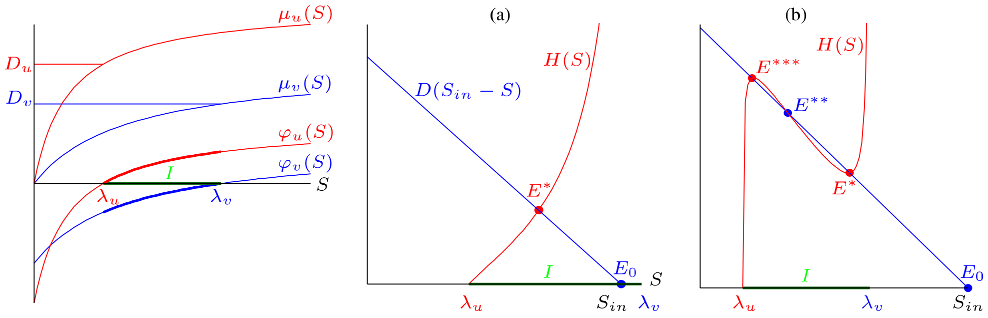

Figure 1. *The case $\lambda_u < \min(\lambda_v, S_{in})$: (a) Existence of unique positive equilibrium. (b) Existence of three positive equilibria.*

Therefore, the equation (3) may have several solutions whose number is generically odd in the case $\lambda_u < \lambda_v$ or $\lambda_v < \lambda_u < S_{in}$ (see Figs. 1 and 3 (b-c)) and even in the case $\lambda_v < S_{in} < \lambda_u$ (see Figs. 2 and 3 (a)). In all figures, we choose the color red to represent the locally exponentially stable equilibria and blue to represent the unstable equilibria. We will show the asymptotic behavior of the equilibria in section 3.2.

In the case $\lambda_u < \lambda_v$, the function $H(\cdot)$ is defined and positive on the interval $I =]\lambda_u, \lambda_v[$ since $\varphi_u(S) > 0$ and $\varphi_v(S) < 0$ for all $S \in]\lambda_u, \lambda_v[$. Moreover, it vanishes at λ_u and tends to infinity as S tends to λ_v. Hence, we have the following result:

Proposition 3.1 *If $\lambda_u < \min(\lambda_v, S_{in})$, then there exists at least one positive equilibrium. Generically, there is an odd number of positive equilibria. If $S_{in} \leqslant \lambda_u < \lambda_v$, then there is no positive equilibrium.*

In the second case $\lambda_v < \lambda_u$, the function $H(\cdot)$ is defined and positive on the interval $I =]\lambda_v, \min(\lambda_u, \lambda_b)[$ since $\varphi_u(S) < 0$ and $0 < \varphi_v(S) < b$ for all $S \in]\lambda_v, \min(\lambda_u, \lambda_b)[$. Moreover, it vanishes for $S = \min(\lambda_u, \lambda_b)$ and tends to infinity as S tends to λ_v. Hence, we have the following result:

Proposition 3.2 *If $\lambda_v < \min(\lambda_u, \lambda_b) < S_{in}$, then there exists at least one positive equilibrium. Generically, one has an odd number of positive equilibria. If $S_{in} < \min(\lambda_u, \lambda_b)$, then the system has generically no positive equilibrium or an even number of positive equilibria.*

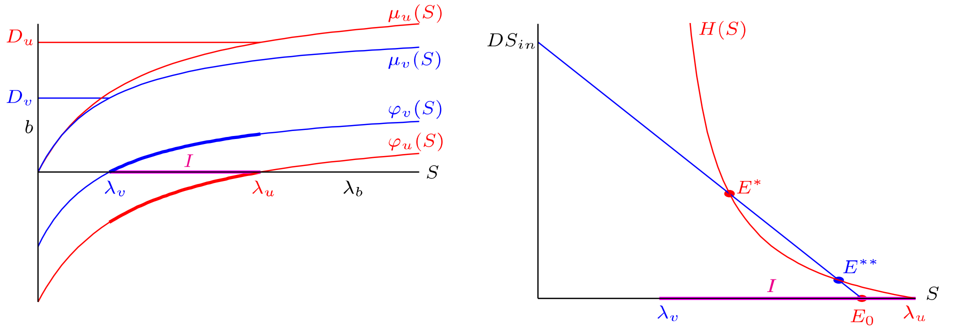

Figure 2. *The case $\lambda_v < \lambda_u < \lambda_b$: Existence of two positive equilibria and bistability for $S_{in} < \min(\lambda_u, \lambda_b)$.*

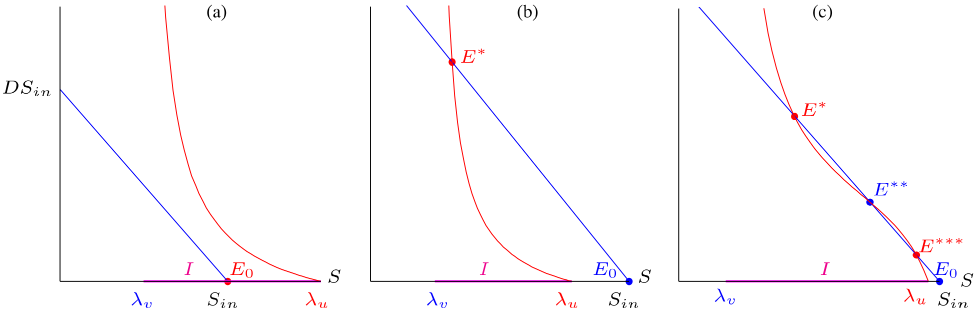

Figure 3. *The case $S_{in} < \min(\lambda_u, \lambda_b)$: There is no positive equilibria (a). The case $S_{in} > \min(\lambda_u, \lambda_b)$: Existence of one (b) or three (c) positive equilibria.*

Proposition 3.3 *Let $E^* = (S^*, u^*, v^*)$ and $E^{**} = (S^{**}, u^{**}, v^{**})$ be two positive equilibria of (1) such that $S^* < S^{**}$.*

1) If $\lambda_u < \lambda_v$, then $u^* > u^{**}$ and $v^* < v^{**}$, this means that the equilibrium E^* promotes isolated biomass u and E^{**} promotes biomass in flocs v.

2) If $\lambda_v < \lambda_u$, then $u^* > u^{**}$ and $v^* > v^{**}$, this means that the equilibrium E^* promotes simultaneously two biomass u and v.

Proposition 3.4 *The system (1) with $a = 0$, $b > 0$, admits at most three equilibria:*

– The washout, $E_0 = (S_{in}, 0, 0)$, which always exists.

– The equilibrium of extinction of v, $E_u = (\lambda_u, u^*, 0)$ with $u^* = U(\lambda_u)$, which exists if and only if $\lambda_u < S_{in}$.

– The positive equilibrium, $E^* = (S^*, u^*, v^*)$ with $S^* = \lambda_b$, $u^* = U(\lambda_b)$ and $v^* = V(\lambda_b)$, which exists if and only if $\lambda_v < \lambda_b < \lambda_u$ and $\lambda_b < S_{in}$.

Proposition 3.5 *The system (1), with $a > 0$ and $b = 0$, admits the following equilibria:*

– The washout, $E_0 = (S_{in}, 0, 0)$, which always exists.

– The equilibrium of extinction of u, $E_v = (\lambda_v, 0, v^*)$ with $v^* = V(\lambda_v)$, which exists if and only if $\lambda_v < S_{in}$.

– The positive equilibrium $E^* = (S^*, u^*, v^*)$*, with* S^* *solution of the equation* $D(S_{in} - S) = H(S)$*,* $u^* = U(S^*)$ *and* $v^* = V(S^*)$ *which exists if and only if* $\lambda_u < S^* < \lambda_v$ *and* $S^* < S_{in}$*.*

3.2. Stability of equilibria

We study in the following the local stability of the washout equilibrium of (1).

Proposition 3.6 E_0 *is locally exponentially stable if and only if* $S_{in} < \lambda_u$ *and* $S_{in} < \lambda_b$*.*

In the following, we study the local asymptotic behavior of the positive equilibria of (1).

Proposition 3.7 *Let* $E^* = (S^*, u^*, v^*)$ *be a positive equilibrium with* $a > 0$ *and* $b > 0$*.*

1) The case $\lambda_u < \lambda_v$*:* E^* *is locally exponentially stable if* $H'(S^*) > -D$ *and is unstable if* $H'(S^*) < -D$*.*

2) The case $\lambda_v < \lambda_u$*:* E^* *is locally exponentially stable if* $H'(S^*) < -D$ *and is unstable if* $H'(S^*) > -D$*.*

Table 1 summarizes the previous results:

Equilibria	Existence condition	Stability condition
E_0	Always exists	$S_{in} < \min(\lambda_u, \lambda_b)$
E^*	(3) has solution $S^* \in I$	Case $\lambda_u < \lambda_v$: $H'(S^*) > -D$ Case $\lambda_u > \lambda_v$: $H'(S^*) < -D$

Table 1. *Existence and local stability of equilibria in system (1).*

The proofs of the following results are given in [2].

Proposition 3.8 *In the case* $a = 0$ *and* $b > 0$*:*

– E_u *is locally exponentially stable if and only if* $\lambda_u < \lambda_b$*.*

– Whenever E^* *exists, it is locally exponentially stable.*

Similarly to proofs of Props. 3.7 and 3.8 (see [2]), we obtain the following results:

Proposition 3.9 *In the case* $a > 0$ *and* $b = 0$*:*

– E_v *is locally exponentially stable if and only if* $S_{in} > \lambda_v + \frac{1}{D}H(\lambda_v)$*.*

– The positive equilibrium $E^* = (S^*, u^*, v^*)$ *is locally exponentially stable if* $H'(S^*) > -D$ *and is unstable if* $H'(S^*) < -D$*.*

4. Simulations

In the case where the growth rates are Monod-type, the equation $D(S_{in} - S) = H(S)$ is equivalent to a polynomial equation of fifth degree. Therefore, there is at most five solutions of this equation. The positive equilibria correspond to solutions which are in the interval I. We succeeded in finding parameters sets with 3 solutions at most in this interval. The following Monod-type growth rates are considered where all parameter values used are given in Table 2.

$$\mu_u(S) = \frac{m_1 S}{K_1 + S} \quad \text{and} \quad \mu_v(S) = \frac{m_2 S}{K_2 + S}.$$

Fig. 4 illustrates the case $\lambda_u < \lambda_v < S_{in}$ with three positive equilibria

$$E^* \simeq (3.06, 12.11, 157.46),\ E^{**} \simeq (5.17, 8.53, 524.30),\ E^{***} \simeq (8.81, 2.64, 1086.32).$$

The numerical simulations show the bi-stability with two basins of attraction, one toward E^* and the other toward E^{***} which are stable nodes. These two basins are separated by the stable manifold of a saddle point E^{**}. As it was proved in Prop. 3.3, u is promoted at E^* and v is promoted at E^{***}.

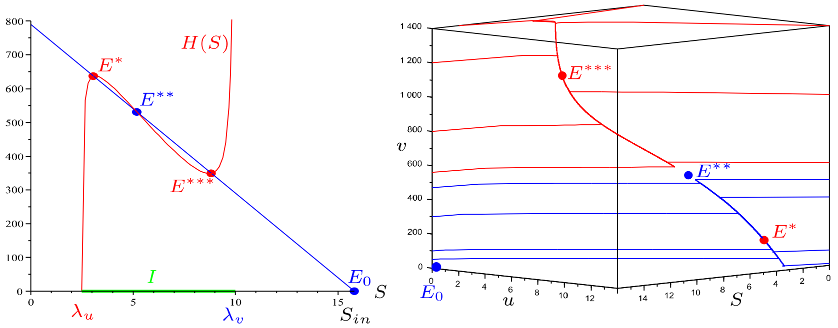

Figure 4. *The case $\lambda_u < \lambda_v < S_{in}$: Three positive equilibria and bi-stability.*

Fig. 5 illustrates the case $S_{in} > \lambda_u > \lambda_v$ with three positive equilibria

$$E^* \simeq (3.31, 2.23, 27.08),\ E^{**} \simeq (3.98, 1.67, 4.12),\ E^{***} \simeq (4.39, 0.63, 0.24).$$

The numerical simulations show the bi-stability of E^* and E^{***} which are stable nodes. The two basins of attraction are separated by the stable manifold of a saddle point E^{**}. As it was proved in Prop. 3.3, u and v are both promoted at E^*.

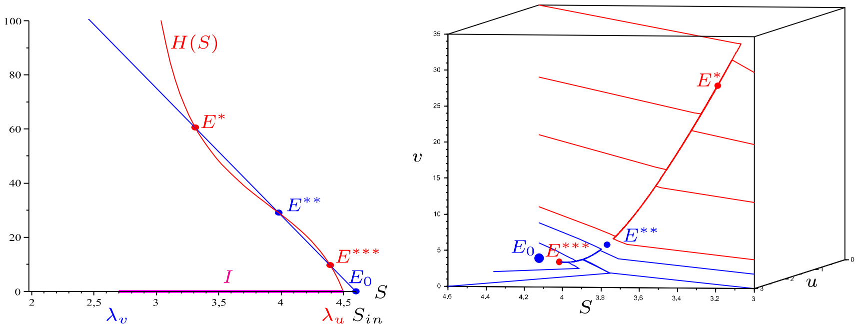

Figure 5. *The case $\lambda_v < \lambda_u < S_{in}$: Existence of three positive equilibria and bi-stability.*

5. Conclusion

In this work, we have considered a model of the chemostat with a single growth-limiting resource and one species that is present in two forms: isolated and aggregated bacteria. We have assumed that the growth rates are increasing and the dilution rates are distinct. Without assuming that attachment and detachment dynamics are faster than the growth dynamics of planktonic and attached biomass, the qualitative behavior of three order model (1) is analyzed. We have shown the multiplicity of positive equilibria with the possibility of bi-stability of two positive equilibria which can promote the planktonic and/or aggregated biomass. Whereas, the bi-stability could occur in the classical chemostat model only when the growth rate is non monotonic. The simulations illustrate the mathematical results demonstrated.

A. Proofs

Proof of Prop. 2.1. One has

$$\begin{array}{l} S=0 \ \Rightarrow \ \dot{S}=DS_{in}>0 \ , \\ v=0 \ \Rightarrow \ \dot{v}=au^2 \geqslant 0 \ . \end{array}$$

Hence $S(t) \geqslant 0$ and $v(t) \geqslant 0$ for all $t \geqslant 0$. One has also

$$u=0 \ \Rightarrow \ \dot{u}=bv \geqslant 0 \ ,$$

and then $u(t) \geqslant 0$ for all $t \geqslant 0$. Denote $z=S+u+v$. The sum of the three equations of (1) gives

$$\dot{z}(t) \leqslant D_v \left[\frac{D}{D_v}S_{in}-z(t)\right] .$$

Hence, one has

$$z(t) \leqslant \frac{D}{D_v}S_{in}+(z(0)-\frac{D}{D_v}S_{in})e^{-D_v t} \quad \text{for all} \quad t \geqslant 0. \tag{6}$$

We deduce that

$$z(t) \leqslant \max\left(z(0), \frac{D}{D_v}S_{in}\right) \quad \text{for all} \quad t \geqslant 0.$$

Thus, the solution of (1) is positively bounded and is defined for all $t \geqslant 0$. From (6), it can be deduced that the set Ω is positively invariant and is a global attractor for (1). ■

Proof of Lemma 3.1. We must solve the system

$$\left\{\begin{array}{l} D(S_{in}-S)=\mu_u(S)u+\mu_v(S)v \\ 0=[\mu_u(S)-D_u]u-a(u+v)u+bv \\ 0=[\mu_v(S)-D_v]v+a(u+v)u-bv. \end{array}\right. \tag{7}$$

Making the sum of the second and the third equation of (7), we obtain

$$\varphi_u(S)u+\varphi_v(S)v=0. \tag{8}$$

This equation admits positive solutions u and v if and only if $\varphi_u(S)$ and $\varphi_v(S)$ have opposite signs, i.e. S is between λ_u and λ_v. Therefore, we must seek solutions (S,u,v) of (7) such that S is between λ_u and λ_v. In this case, $\varphi_v(S) \neq 0$ and the equation (8) can be rewritten as

$$v=-\frac{\varphi_u(S)}{\varphi_v(S)}u. \tag{9}$$

If $u=0$, then from the second equation of (7), we deduce $v=0$. If $v=0$, then from the last equation of (7), we deduce $u=0$. Hence we cannot have an equilibria of extinction only of u or only of v. Replacing v by its expression (9) in the second equation of (7), we obtain

$$u = U_1(S) \quad \text{with} \quad U_1(S) = \frac{\varphi_u(S)(\varphi_v(S) - b)}{a[\varphi_v(S) - \varphi_u(S)]}. \tag{10}$$

Note that u defined by (10) is positive if and only if $\lambda_u < S < \lambda_v$ or $\lambda_v < S < \min(\lambda_b, \lambda_u)$, that is to say, if and only if $S \in I$.

Therefore, we must seek the solutions of (7) such that $S \in I$. By replacing u by (10) in (9), we obtain

$$v = V_1(S) \quad \text{with} \quad V_1(S) = -\frac{\varphi_u^2(S)(\varphi_v(S) - b)}{a[\varphi_v(S) - \varphi_u(S)]\varphi_v(S)}. \tag{11}$$

Making the sum of three equations of (7) and replacing u and v by (10) and (11), it follows that S is solution of equation (3). Hence,

$$\frac{\varphi_u(S)(\varphi_v(S) - b)}{a[\varphi_v(S) - \varphi_u(S)]} = \frac{D(S_{in} - S)\varphi_v(S)}{D_u\varphi_v(S) - D_v\varphi_u(S)}.$$

Therefore, (10) and (11) can be rewritten as $u = U(S)$ and $v = V(S)$. ■

Proof of Prop. 3.3. We show that

1) If $\lambda_u < \lambda_v$, then $U(\cdot)$ is decreasing on $I \cap]0, S_{in}[$ and $V_1(\cdot)$ is increasing on I.

2) If $\lambda_v < \lambda_u$, then $U_1(\cdot)$, $V(\cdot)$ and $V_1(\cdot)$ are decreasing on $I \cap]0, S_{in}[$.

Indeed, we have

$$U'(S) = D\frac{-\varphi_v(D_u\varphi_v - D_v\varphi_u) - \mu_v' D_v\varphi_u(S_{in} - S) + \mu_u' D_v\varphi_v(S_{in} - S)}{(D_u\varphi_v - D_v\varphi_u)^2},$$

$$U_1'(S) = \frac{\mu_u'\varphi_v(\varphi_v - b) + \mu_v'\varphi_u(b - \varphi_u)}{a(\varphi_v - \varphi_u)^2}.$$

Therefore, if $\lambda_u < \lambda_v$, then $U'(S)$ is negative on $I \cap]0, S_{in}[$ and if $\lambda_v < \lambda_u$, then $U_1'(S)$ is negative on I. In addition, we have

$$V'(S) = D\frac{-\varphi_u(D_v\varphi_u - D_u\varphi_v) - \mu_u' D_u\varphi_v(S_{in} - S) + \mu_v' D_u\varphi_u(S_{in} - S)}{(D_v\varphi_u - D_u\varphi_v)^2},$$

$$V_1'(S) = \frac{-\mu_u'[\varphi_u\varphi_v(\varphi_v - b)](2\varphi_v - \varphi_u) + \mu_v'\varphi_u^2(\varphi_v - b)(2\varphi_v - \varphi_u)}{a(\varphi_v - \varphi_u)^2\varphi_v^2}.$$

If $\lambda_u < \lambda_v$, then $V_1'(S)$ is positive on I and if $\lambda_v < \lambda_u$, then $V'(S)$ is negative on $I \cap]0, S_{in}[$ and $V_1'(S)$ is negative on I. Therefore, if $\lambda_u < \lambda_v$, then

$$u^* = U(S^*) > u^{**} = U(S^{**}) \quad \text{and} \quad v^* = V_1(S^*) < v^{**} = V_1(S^{**}).$$

Furthermore, if $\lambda_v < \lambda_u$ then

$$u^* = U_1(S^*) > u^{**} = U_1(S^{**}) \quad \text{and} \quad v^* = V(S^*) > v^{**} = V(S^{**}).$$

■

Proof of Prop. 3.4. When $a = 0$, the system (7) is written as

$$\left\{\begin{array}{l} D(S_{in}-S)=\mu_u(S)u+\mu_v(S)v \\ 0=[\mu_u(S)-D_u]u+bv \\ 0=[\mu_v(S)-D_v]v-bv. \end{array}\right. \tag{12}$$

The third equation of (12) can be rewritten as

$$\varphi_v(S)v-bv=0.$$

If $v=0$, then from the second equation of (12), we deduce $u=0$ or $S=\lambda_u$. If $u=v=0$, then from the first equation, one has $S=S_{in}$. If $v=0$ and $S=\lambda_u$, then from the first equation we deduce

$$u=\frac{D(S_{in}-\lambda_u)}{D_u}=U(\lambda_u)$$

which is positive if and only if $\lambda_u<S_{in}$. If v is nonzero and the equation $\varphi_v(S)=b$ has solution $S=\lambda_b$, then from the second equation of (12), we deduce u is nonzero and

$$\varphi_u(\lambda_b)u+bv=0.$$

This equation admits positive solutions u and v if and only if $\lambda_b<\lambda_u$. Making the sum of the second and the third equation of (12), we obtain the equation (8) which admits positive solutions u and v if and only if λ_b is between λ_u and λ_v. Making the sum of the second and the third equation of (12), the first equation is rewritten as

$$D(S_{in}-\lambda_b)=D_u u+D_v v.$$

Replacing v by its expression (9), we obtain

$$D(S_{in}-\lambda_b)=D_u u-D_v\frac{\varphi_u(\lambda_b)}{\varphi_v(\lambda_b)}u=\frac{D_u\varphi_v(\lambda_b)-D_v\varphi_u(\lambda_b)}{\varphi_v(\lambda_b)}u.$$

Hence $u=U(\lambda_b)$ and from the equation (9), we deduce that $v=V(\lambda_b)$ which are positive if and only if $\lambda_v<\lambda_b<\lambda_u$ and $\lambda_b<S_{in}$. ■

Proof of Prop. 3.5. When $b=0$, the system (7) is written as

$$\left\{\begin{array}{l} D(S_{in}-S)=\mu_u(S)u+\mu_v(S)v \\ 0=(\mu_u(S)-D_u)u-a(u+v)u \\ 0=(\mu_v(S)-D_v)v+a(u+v)u. \end{array}\right. \tag{13}$$

Note that in this case $b=0$, the expression (2) of $H(S)$ is simplified and becomes

$$H(S)=\frac{\varphi_u(S)[D_u\varphi_v(S)-D_v\varphi_u(S)]}{a[\varphi_v(S)-\varphi_u(S)]}. \tag{14}$$

Moreover, $\lambda_b=\lambda_v$. Therefore, the interval I is empty in the case $\lambda_v<\lambda_u$. The second equation of (13) can be rewritten as

$$\varphi_u(S)u-a(u+v)u=0.$$

If $u=0$, from the last equation, we deduce $\varphi_v(S)=0$, means that $S=\lambda_v$ and from the first equation $v=V(\lambda_v)$ which is positive if and only if $\lambda_v<S_{in}$. The previous calculation shows that if u is nonzero then

$$D(S_{in}-S)=D_u u+D_v v=D_u u-D_v\frac{\varphi_u}{\varphi_v}u.$$

Hence $u = U(S)$ and $v = V(S)$ which are positive if and only if $\lambda_u < S < \lambda_v$ with S solution of the equation $D(S_{in} - S) = H(S)$. ■

Proof of Prop. 3.6. The Jacobian matrix at washout $E_0 = (S_{in}, 0, 0)$, is given by

$$\mathbf{J}_{\mathbf{E_0}} = \begin{bmatrix} -D & -\mu_u(S_{in}) & -\mu_v(S_{in}) \\ 0 & \varphi_u(S_{in}) & b \\ 0 & 0 & \varphi_v(S_{in}) - b \end{bmatrix}.$$

The eigenvalues are $-D, \varphi_u(S_{in})$ and $\varphi_v(S_{in}) - b$. ■

Proof of Prop. 3.7. The Jacobian matrix at a positive equilibrium $E^* = (S^*, u^*, v^*)$ is given by

$$\mathbf{J}_{\mathbf{E}^*} = \begin{bmatrix} -m_{11} & -m_{12} & -m_{13} \\ m_{21} & -m_{22} & a_{23} \\ m_{31} & m_{32} & -m_{33} \end{bmatrix}$$

where $m_{11} = D + \mu_u'(S^*)u^* + \mu_v'(S^*)v^*, \ m_{12} = \mu_u(S^*), \ m_{13} = \mu_v(S^*)$,

$$m_{21} = \mu_u'(S^*)u^*, \quad m_{22} = a(2u^* + v^*) - \varphi_u(S^*), \quad a_{23} = b - au^*,$$

$$m_{31} = \mu_v'(S^*)v^*, \quad m_{32} = a(2u^* + v^*) \quad \text{and} \quad m_{33} = b - au^* - \varphi_v(S^*).$$

From the second equation of (7), we have

$$\begin{aligned} \varphi_u(S^*)u^* - a(u^* + v^*)u^* + bv^* &= \varphi_u(S^*)u^* - a(2u^* + v^*)u^* + a(u^*)^2 + bv^* \\ &= -m_{22}u^* + a(u^*)^2 + bv^* = 0. \end{aligned}$$

Hence $m_{22} = au^* + bv^*/u^* > 0$. From the third equation of (7), we have

$$\varphi_v(S^*)v^* + a(u^* + v^*)u^* - bv^* = -m_{33}v^* + a(u^*)^2 = 0.$$

and therefore,

$$m_{33} = a\frac{(u^*)^2}{v^*} > 0.$$

Thus, all m_{ij} are positive for all $i, j = 1, \ldots, 3$ with $(i, j) \neq (2, 3)$. The characteristic polynomial is given by

$$P(\lambda) = |J_{E^*} - \lambda * I| = c_0\lambda^3 + c_1\lambda^2 + c_2\lambda + c_3,$$

where I is the 3×3 identity matrix, $c_0 = -1$, $c_1 = -(m_{11} + m_{22} + m_{33})$,

$$c_2 = -m_{12}m_{21} - m_{13}m_{31} + m_{32}a_{23} - (m_{11}m_{22} + m_{11}m_{33} + m_{22}m_{33}),$$

$$c_3 = -m_{11}(m_{22}m_{33} - m_{32}a_{23}) - m_{21}(m_{12}m_{33} + m_{32}m_{13}) - m_{31}(m_{12}a_{23} + m_{13}m_{22}).$$

It is clear that $c_0 = -1 < 0$ and, since $m_{ii} > 0, i = 1, \ldots, 3$, we have $c_1 < 0$. It can be shown by long and tedious calculations (see [2]) that

$$c_2 < 0 \text{ and } c_1c_2 - c_0c_3 > 0$$

and that we have the following properties

1) In the case where $\lambda_u < \lambda_v$, we have $c_3 < 0$ if and only if $H'(S^*) > -D$.

2) In the case where $\lambda_v < \lambda_u$, we have $c_3 < 0$ if and only if $H'(S^*) < -D$. The result of stability follows from the Routh-Hurwitz criterion, which asserts that E^* is locally exponentially stable if and only if

$$\begin{cases} c_i < 0, & i = 0, \ldots, 3 \\ c_1 c_2 - c_0 c_3 > 0. \end{cases}$$

This completes the proof. ■

B. Parameters used in numerical simulations

Parameter	m_1	K_1	m_2	K_2	D	D_u	D_v	a	b	S_{in}	λ_u	λ_v
Fig. 4	60	0.5	0.6	20	50	50	0.2	0.01	0.01	15.8	2.5	10
Fig. 5	20	1.5	2	2.7	47	15	1	1.2	3	4.6	4.5	2.7

Table 2. *Parameter values and the corresponding λ_u and λ_v.*

Acknowledgments. The authors wish to thank the financial support of TREASURE euro-Mediterranean research network (https://project.inria.fr/treasure/). This work was partly done in the PhD thesis of the first author within the INRA/INRIA team MODEMIC, with the financial support of the Averroes program, the PHC UTIQUE project No. 13G1120 and the COADVISE project.

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