

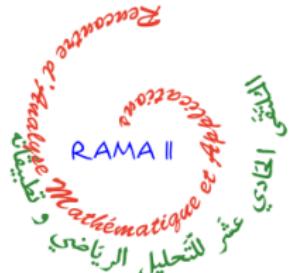
Competition et coexistence dans le chemostat

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Onzième Rencontre d'Analyse Mathématique et Applications
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TREASURE

TREASURE, for **Treatment and Sustainable Reuse of Effluents in semiarid climates**, is a scientific Euro-Mediterranean research network associating research labs and researchers from Southern Europe and Northern Africa countries about biological wastewater treatment plants and microbial ecosystems. At its origins, in 2006, the involved partners only consisted of academics from France, Algeria, Italy and Tunisia. Today the principal partners are located in Kenitra, Montpellier, Narbonne, Sfax, Tlemcen and Tunis.

- Jérôme Harmand, DR, INRA, Narbonne
- <https://www6.inra.fr/treasure/>
- PHC Tassili, Toubkal, Utique





Treasure Network

15 defended PHD: Fatima Zahra Tani (Montpellier, 2019), Mohamed Dellal (Sidi Bel Abbes, 2019), Bachir Bar (Tlemcen, 2019), Mokhlès Kouas (Narbonne-Gabes, 2018), Nesrine Kalboussi (Tunis, 2018), Maha Hmissi (Sfax, 2018), Zineb Khedim (Tlemcen, 2018), Yessmine Daoud (Montpellier-Tunis, 2017), Walid Bouhafs (Tunis, 2016), Sonia Hassam (Tlemcen, 2015), Amel Ghouali (Montpellier-Tlemcen, 2015), Amine Charfi (Tunis, 2014), Radhouane Fekih Salem (Montpellier-Tunis, 2013), Boumediene Benyahia (Tlemcen-Montpellier, 2012), Miled El Hajji (Montpellier, 2010).

10 on going PHD : Benaissa Dekhici (Tlemcen), Manel Dali Youcef (Montpellier), Kenza Boumaza (Montpellier), Farouk Aichouche (Narbonne), Emna Krichen (Montpelier), Mohamed Hanaki (Kenitra), Bochra Belhadji (Ghardaia), Tahani Mtar (Tunis), Sarra Nouaoura (Tunis), Hayat Berhoune (Tlemcen).

15 Seminars since 2006: Tunis, Hammamet, Montpellier, Narbonne, Tlemcen, Marrakech.

Summary

- ① Competition of species in the chemostat
- ② Flocculation (PhD of R. Fekih-Salem)
- ③ Density dependent growth functions (PhD of R. Fekih-Salem)
- ④ Inhibitors (PhDs of M. Dellal and B. Bar)
- ⑤ Commensalism (PhD of B. Benyahia)
- ⑥ Mutualism, Syntrophy (PhDs of M. El Hajji and Y. Daoud)
- ⑦ Other mechanisms of coexistence

Summary

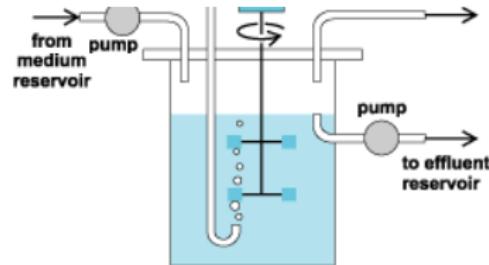
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Chemostat: $S \xrightarrow{\mu(\cdot)} X$

$$\begin{cases} \dot{S} = D(S^{in} - S) - k\mu(S)X \\ \dot{X} = -DX + \mu(S)X \end{cases}$$

- S : concentration of substrate
- X : concentration of bacteria
- S^{in} : input concentration of substrate
- $D = Q/V$: Dilution rate
- k : stoichiometric coefficient
- $\mu(\cdot)$: specific growth functions



Stability analysis (Monod)

$$\begin{cases} \dot{s} = D(s_{in} - s) - k\mu(s)x \\ \dot{x} = (\mu(s) - D)x \end{cases}$$

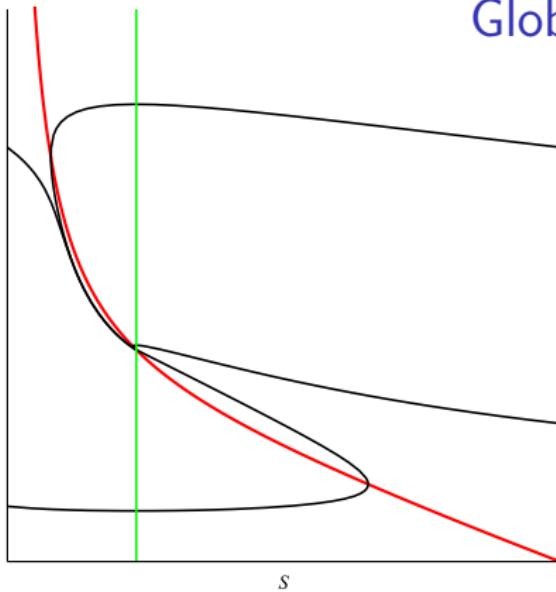
- $\mu(s)$ is increasing. Example: the Monod function

$$\mu(s) = \frac{\mu_{max}s}{K + s}$$

- : Break-even concentration $\lambda(D) = \mu^{-1}(D)$
- $E_0 = (s_{in}, 0)$: washout
- $E_1 = (s^*, x^*)$, where $s^* = \lambda(D)$ and $x^* = (s_{in} - s^*)/k$

Steady-state	Existence condition	Stability condition
E_0	Always exists	$\mu(s_{in}) < D$
E_1	$\mu(s_{in}) > D$	GAS if it exists

Global Stability



Isoclines

- $\dot{S} = 0 \implies X = D \frac{S_{in} - S}{k\mu(S)}$ (in red on the figure)
- $\dot{X} = 0 \implies S = S^*$ (in green on the figure)

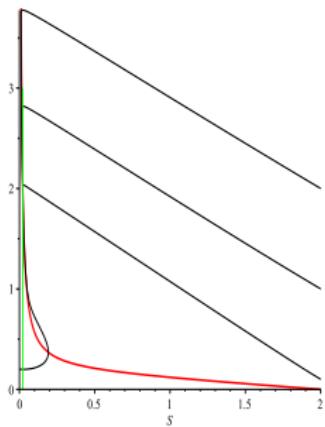
Stability analysis ($D_1 \neq D$)

$$\begin{cases} \dot{s} = D(s_{in} - s) - k\mu(s)x \\ \dot{x} = (\mu(s) - D_1)x \end{cases}$$

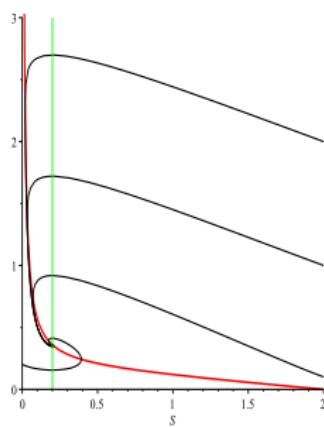
- : Break-even concentration $\lambda(D) = \mu^{-1}(D_1)$
- $E_0 = (s_{in}, 0)$: washout
- $E_1 = (s^*, x^*)$, where $s^* = \lambda(D)$ and $x^* = \frac{D}{D_1}(s_{in} - s^*)/k$

Steady-state	Existence condition	Stability condition
E_0	Always exists	$\mu(s_{in}) < D$
E_1	$\mu(s_{in}) > D$	GAS if it exists

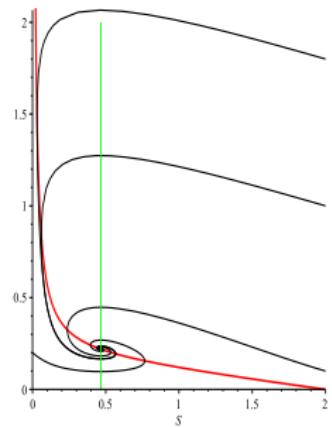
Stables oscillations



$m = 0$



$m = 0.4$



$m = 0.6$

$$\begin{cases} \dot{S} = D(S_{in} - S) - \frac{S}{0.2+S}x \\ \dot{x} = \left(\frac{S}{0.2+S} - m - D \right)x \end{cases}$$

with $D = 0.1$, $S_{in} = 2$

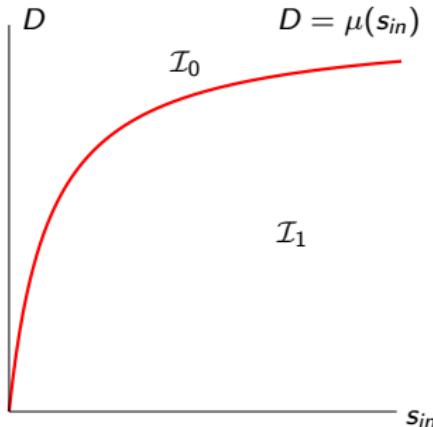
Operating diagram

$$\begin{cases} \dot{s} = D(s_{in} - s) - k\mu(s)x \\ \dot{x} = -Dx + \mu(s)x \end{cases}$$

Apart from the two operating (or control) parameters, which are the inflowing substrate s_{in} and the dilution rate D , that can vary, all others parameters (k , and parameters in $\mu(S)$) have biological meaning and are fixed depending on the organisms and substrate considered.

The operating diagram describes the behaviour of the system with respect to the operating parameters

Operating diagram



region	E_0	E_1
$(s_{in}, D) \in \mathcal{I}_0$	S	
$(s_{in}, D) \in \mathcal{I}_1$	U	S

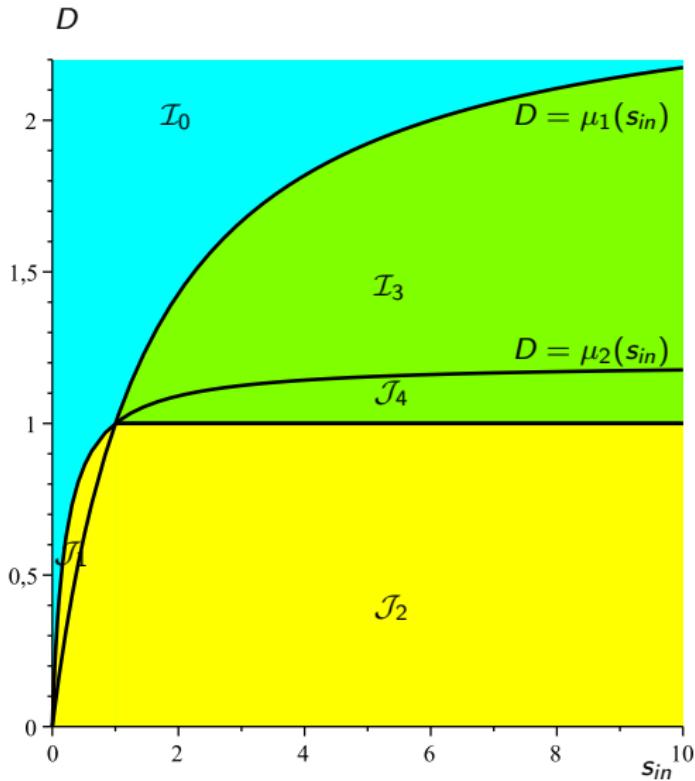
Steady-state	Existence condition	Stability condition
E_0	Always exists	$\mu(s_{in}) < D$
E_1	$\mu(s_{in}) > D$	Stable if it exists

Competition of two species

$$\begin{cases} S' = D(S_{in} - S) - \mu_1(S)x_1 - \mu_2(S)x_2 \\ x'_1 = (\mu_1(S) - D)x_1 \\ x'_2 = (\mu_2(S) - D)x_2 \end{cases}$$

- Break-even concentrations : $\lambda_i = \mu_i^{-1}(D)$
- $E_0 = (S = S_{in}, x_1 = 0, x_2 = 0)$
- $E_1 = (S = \lambda_1, x_1 = S_{in} - \lambda_1, x_2 = 0)$
- $E_2 = (S = \lambda_2, x_1 = 0, x_2 = S_{in} - \lambda_2)$
- If $\lambda_1 < \lambda_2$ then E_1 is GAS.
- Only one species can survive:
Competitive Exclusion Principle (CEP)

Operating diagram



region	E_0	E_1	E_2
$(s_{in}, D) \in \mathcal{J}_0$	S		
$(s_{in}, D) \in \mathcal{J}_1$	U		S
$(s_{in}, D) \in \mathcal{J}_2$	U	U	S
$(s_{in}, D) \in \mathcal{J}_3$	U	S	
$(s_{in}, D) \in \mathcal{J}_4$	U	S	U

Conjecture: CEP holds for $D_i \neq D$

$$\begin{cases} S' = D(S_{in} - S) - \mu_1(S)x_1 - \mu_2(S)x_2 \\ x'_1 = (\mu_1(S) - D_1)x_1 \\ x'_2 = (\mu_2(S) - D_2)x_2 \end{cases}$$

- Break-even concentrations : $\lambda_i = \mu_i^{-1}(D_i)$
- The steady states are the washout $E_0 = (S_{in}, 0, \dots, 0)$ and the steady states

$$E_1 = (\lambda_1, x_1^*, 0), \quad E_2 = (\lambda_2, 0, x_2^*)$$

where $x_i^* = \frac{D}{D_i} (S^{in} - \lambda_i)$

- If $\lambda_1 < \lambda_2$ then E_1 is Locally stable
- Conjecture : If $\lambda_1 < \lambda_2$ then E_1 is GAS: it attracts all solutions such that $x_1(0) > 0$

CEP holds for Monod growth functions

$$\begin{cases} S' &= D(S_{in} - S) - \sum_{i=1}^n \frac{a_i S}{b_i + S} \frac{x_i}{Y_i} \\ x'_i &= \left(\frac{a_i S}{b_i + S} - D_i \right) x_i, \quad i = 1 \dots n \end{cases}$$

- $\lambda_i = \frac{m_i D_i}{a_i - D_i}$.
- Assume that $\lambda_1 < \lambda_2 \leq \dots \leq \lambda_n$. Hsu proved the global asymptotic stability of E_1 using a Lyapunov function

$$V = \int_{\lambda_1}^S \frac{\sigma - \lambda_1}{\sigma} d\sigma + c_1 \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi} d\xi + \sum_{i=2}^n c_i x_i,$$

$$c_i = \frac{1}{Y_i} \frac{a_i}{a_i - D_i}, \quad x_1^* = Y_1 \frac{D}{D_1} (S_{in} - \lambda_1)$$

S.B. Hsu, *Limiting behavior for competing species*. SIAM Journal on Applied Mathematics 34 (1978), 760-763.

Variable yield

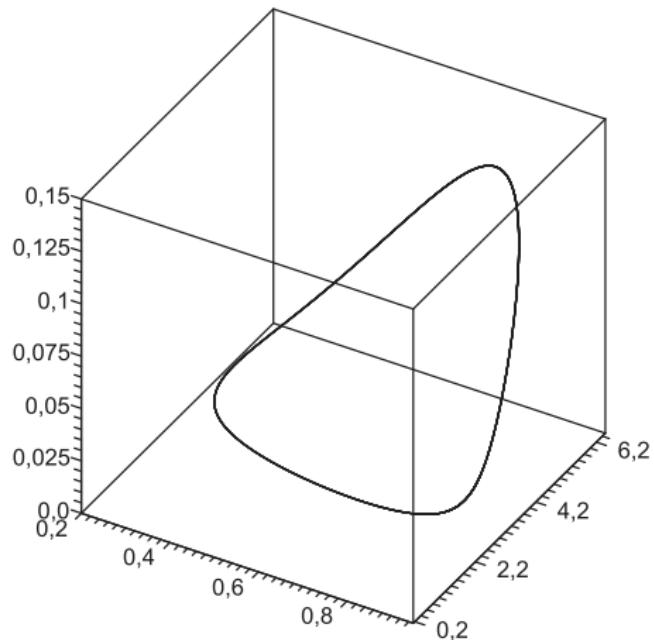
$$S' = 1 - S - \frac{2S}{0.7+S} \frac{x_1}{1+cS^3} - \frac{m_2 S}{6.5+S} \frac{x_2}{120}$$

$$x'_1 = [\frac{2S}{0.7+S} - 1]x_1$$

$$x'_2 = [\frac{m_2 S}{6.5+S} - 1]x_2.$$

Let $c = 50$ and consider m_2 as a bifurcation parameter.
For $m_2 \geq 9.85$ the system exhibits sustained oscillations.
Here we fix $m_2 = 10$.

S.S. Pilyugin, P. Waltman,
Multiple limit cycles in the chemostat with variable yields,
Math. Biosciences, 182, 151–166 (2003).



Variable yields

$$\begin{aligned} S' &= D[S_{in} - S] - \sum_{j=1}^n p_j(S)x_j, \\ x'_i &= [q_i(S) - D_i]x_i, \quad i = 1 \dots n, \end{aligned}$$

- $S(t)$: concentration of nutrient. $x_i(t)$: concentration of the competing species.
- S_{in} : input concentration. D and D_i : removal rates
- $p_i(S)$: uptake rates. $q_i(S)$: growth rates
- $y_i(S) = \frac{q_i(S)}{p_i(S)}$: growth yields
- Extension of classical model $p_i(S) = \frac{q_i(S)}{Y_i}$, for which the yields $y_i(S) = Y_i$ are constant.

J. Arino, S.S. Pilyugin, G.S.K. Wolkowicz, *Considerations on yield, nutrient uptake, cellular growth, and competition in chemostat models*. Canadian Applied Mathematics Quarterly, 11, 107–142 (2003)

Competitive exclusion

Assume that there exist $\alpha_i > 0$ such that for all $0 < S < S_{in}$,

$$f_1(S)p_i(S) > \alpha_i f_i(S)(S_{in} - S).$$

where $f_i(S) = q_i(S) - D_i$, then the equilibrium E_1^* is GAS with respect to the interior of the positive cone.

Proof: Use the Lyapunov function

$$V(S, x_1, \dots, x_n) = \int_{\lambda_1}^S \frac{f_1(\sigma)}{S_{in} - \sigma} d\sigma + \frac{1}{x_1^*} \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi} d\xi + \sum_{i=2}^n \alpha_i x_i,$$

T. Sari, *Competitive Exclusion for Chemostat Equations with Variable Yields*, Acta Appl. Math., 123 (1), 2013, 201–219

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Flocculation

$$\begin{cases} \dot{S} = D(S_{in} - S) - f(S)u - g(S)v \\ \dot{u} = (f(S) - D_0)u - \alpha(\cdot)u + \beta(\cdot)v \\ \dot{v} = (g(S) - D_1)v + \alpha(\cdot)u - \beta(\cdot)v \end{cases}$$

- $u(t)$: concentration of isolated bacteria of the first species.
 $f(\cdot)$: per-capita growth rate of isolated bacteria.
- $v(t)$: concentrations of attached bacteria of the first species.
 $g(\cdot)$: per-capita growth rate of attached bacteria.
- $\alpha(\cdot)u$ and $\beta(\cdot)v$: flocculation and deflocculation rates.
- D_0, D_1 : removal rates of isolated and attached bacteria of the first species.

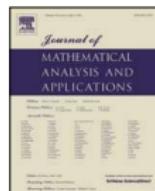


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Extensions of the chemostat model with flocculation

R. Fekih-Salem^{a,b}, J. Harmand^{b,c}, C. Lobry^b, A. Rapaport^{a,b,*}, T. Sari^{b,d}

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PhD of R. Fekih Salem co advised with A. Rapaport and N. Abdellatif



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Emergence of coexistence and limit cycles in the chemostat model with flocculation for a general class of functional responses



R. Fekih-Salem^{a,d,*}, A. Rapaport^{b,e}, T. Sari^{c,f}

Recent works

SIAM J. APPLIED DYNAMICAL SYSTEMS
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Properties of the Chemostat Model with Aggregated Biomass and Distinct Removal Rates*

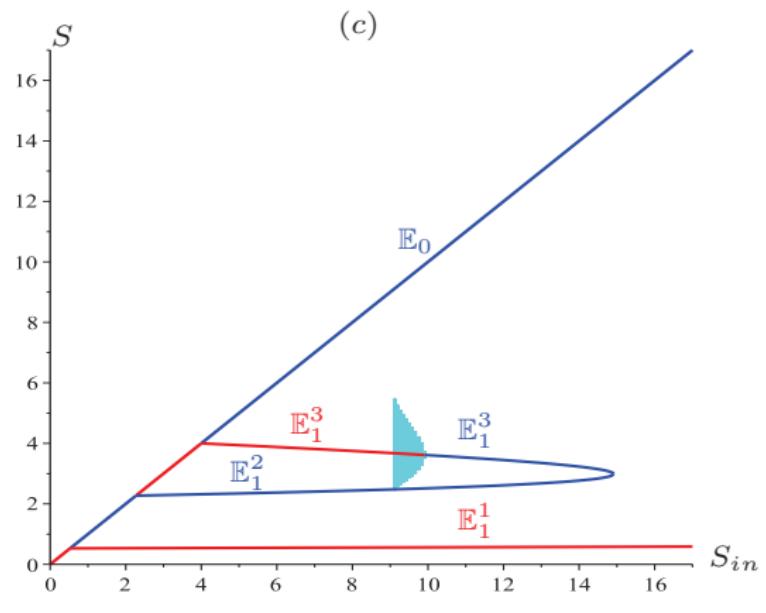
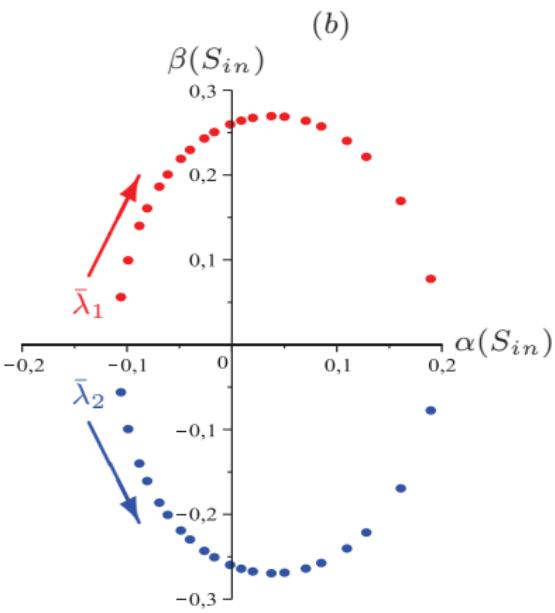
Radhouane Fekih-Salem[†] and Tewfik Sari[‡]

Flocculation: one species

$$\begin{cases} \dot{S} = D(S_{in} - S) - f(S)u - g(S)v \\ \dot{u} = (f(S) - D)u - au^2 + bv \\ \dot{v} = (g(S) - D)v + au^2 - bv \end{cases}$$

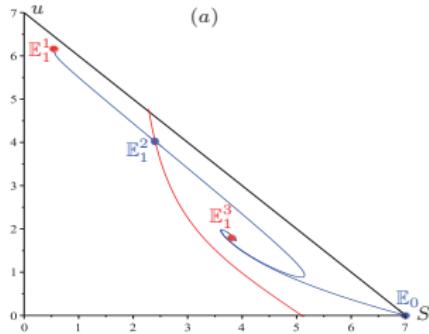
- $E_0 = (S_{in}, 0, 0)$ washout
- $E_1 = (S_1, u_1, v_1)$ with $S_1 > 0, u_1 > 0, v_1 > 0$
- possibility of multiple positive steady states: bistability
- emergence of cycles

One species: Oscillations

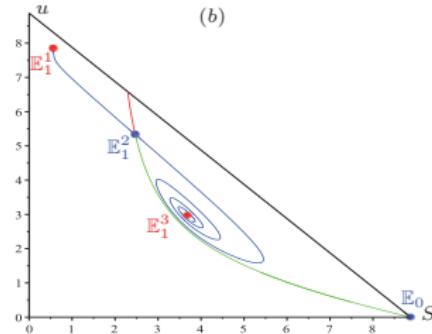


One species: Oscillations

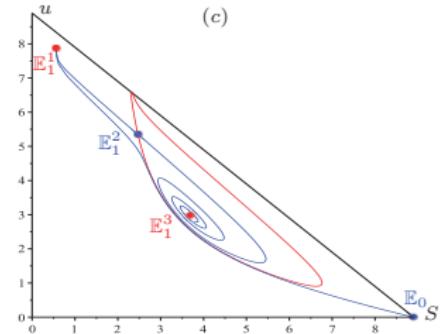
(a)



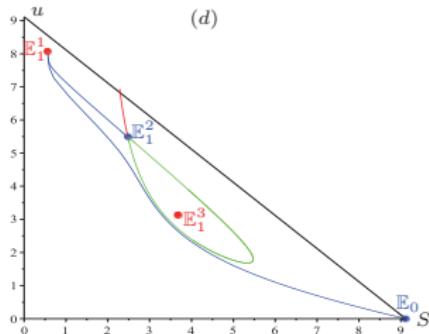
(b)



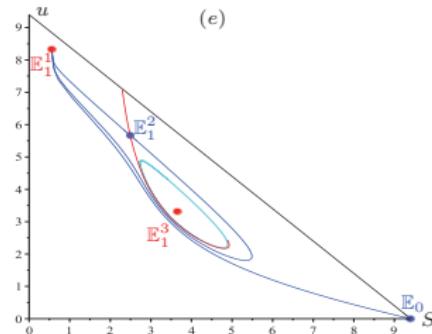
(c)



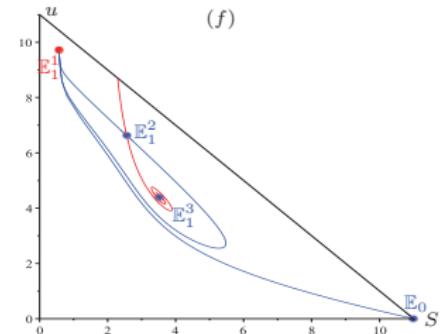
(d)



(e)



(f)

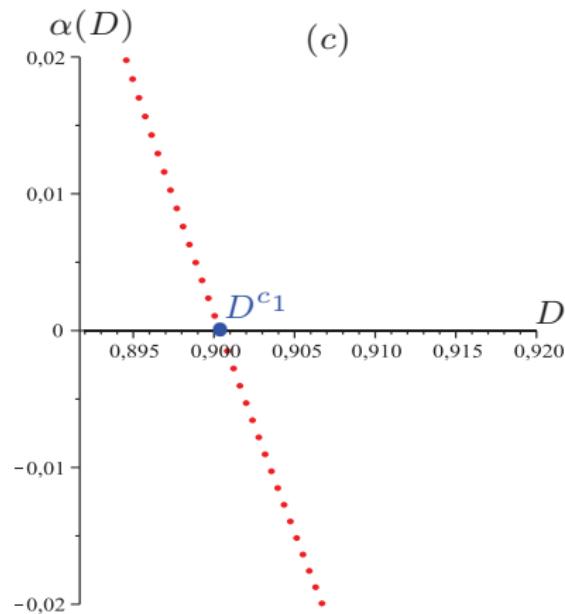
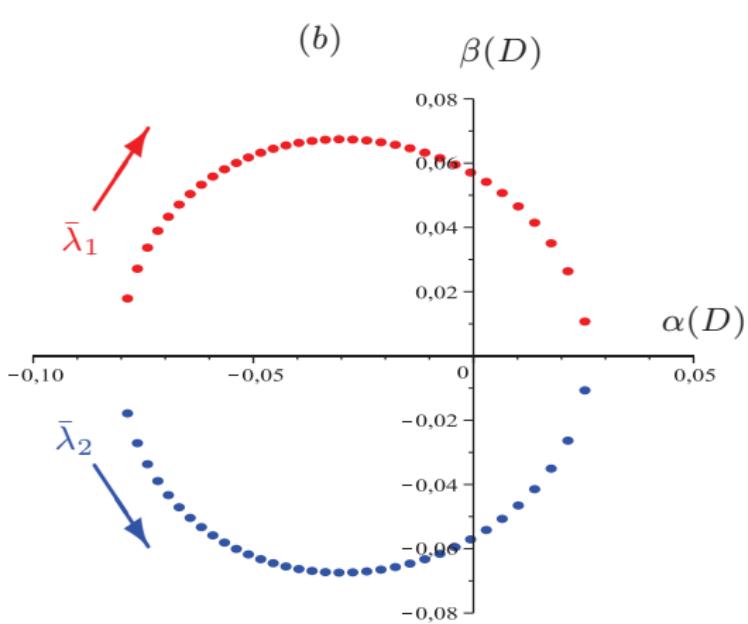


Flocculation: two species

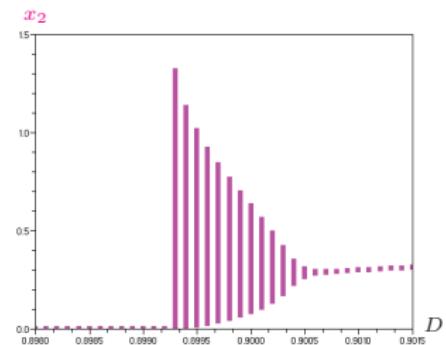
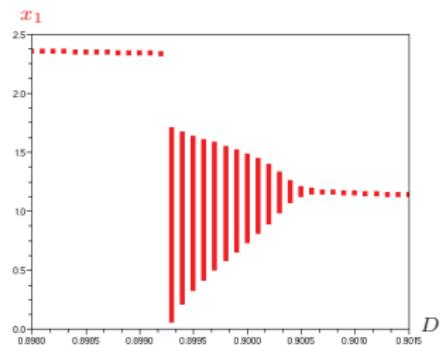
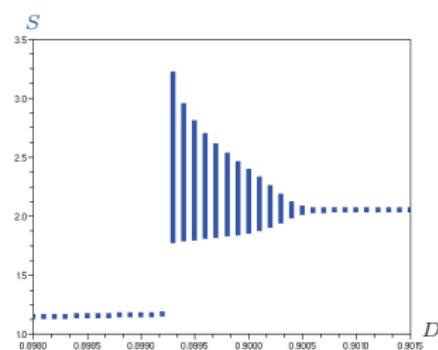
$$\begin{cases} \dot{S} = D(S_{in} - S) - f(S)u - g(S)v - f_2(S)x_2 \\ \dot{u} = (f(S) - D)u - au^2 + bv \\ \dot{v} = (g(S) - D)v + au^2 - bv \\ \dot{x}_2 = (f_2(S) - D)x_2 \end{cases}$$

- $E_0 = (S_{in}, 0, 0, 0)$ washout
- $E_1 = (S_1, u_1, v_1, 0)$ with $S_1 > 0, u_1 > 0, v_1 > 0$
- $E_2 = (\lambda_2, 0, 0, S_{in} - \lambda_2)$
- $E^* = (\lambda_2, u^*, v^*, x_2^*)$
- possibility of multiple positive steady states: bistability
- emergence of cycles

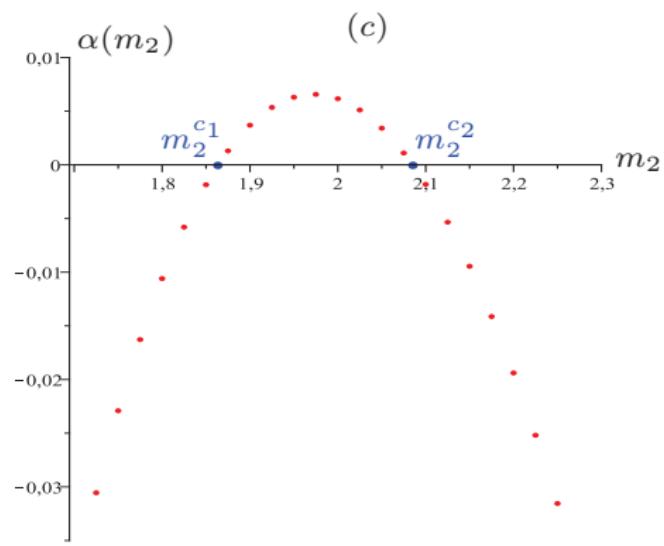
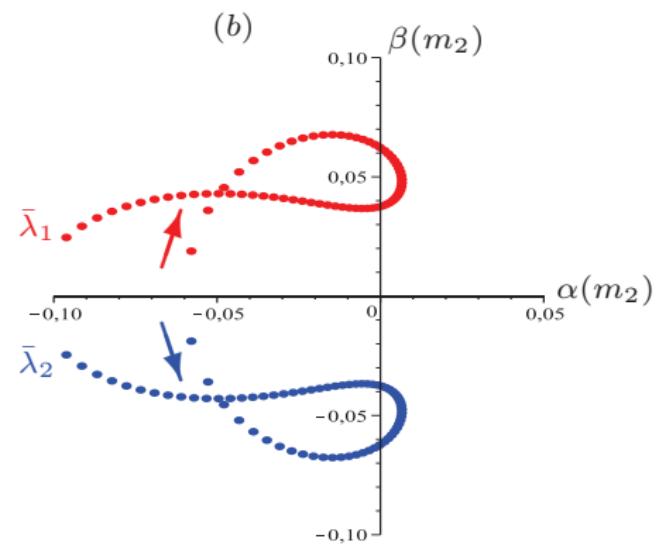
Two species: Oscillations



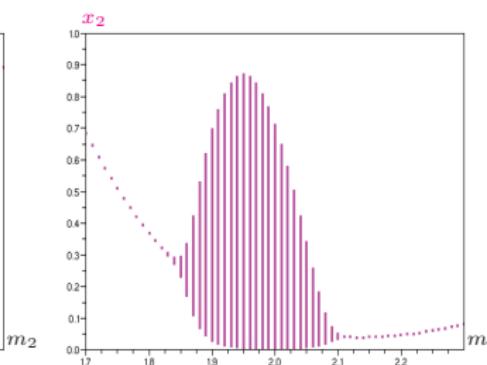
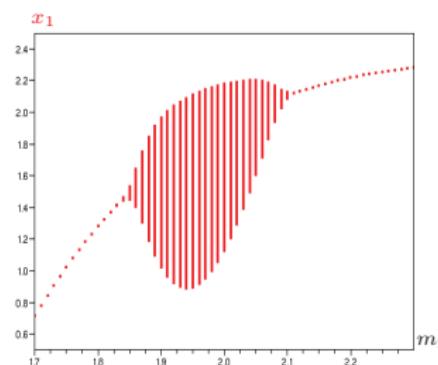
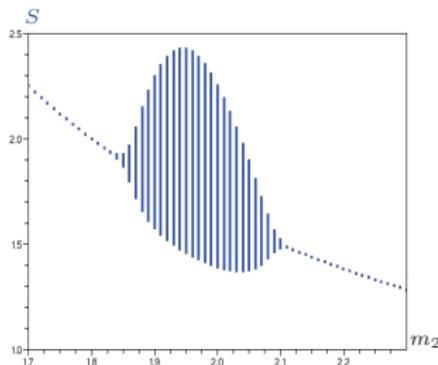
Two species: Oscillations



Two species: Oscillations



Two species: Oscillations



Fast attachment and detachment

- Literature reports flocculation time scales of the order of 1 to 10 min to be compared with bacterial growth times of 1 h to 1 day, and with retention times of a few hours to a few days.
- Considering that attachment and detachment processes may be fast compared to biological time, it is shown in Haegeman and Rapaport (2008) that the reduced dynamics of such systems amounts to have a single biomass compartment for each strain but with a density dependent growth rate.
- It was shown in Fekih-Salem et al (2013) that when attachment and detachment rates are fast one can build a reduced model without distinction between isolated and attached bacteria, but the resulting growth rate is density-dependent as well as the dilution rate, due to the fact that attached and isolated bacteria have different removal rates.

Fast attachment and detachment

$$\begin{cases} \dot{S} = D(S_{in} - S) - f(S)u - g(S)v \\ \dot{u} = (f(S) - D_0)u - A(S, v, u)u + B(S, u, v)v \\ \dot{v} = (g(S) - D_1)v + A(S, v, u)u - B(S, u, v)v \end{cases}$$

The dynamics of attachment and detachment is much faster than the growth of the species

$$A(S, u, v) = \frac{\alpha(S, u, v)}{\varepsilon}, \quad B(S, u, v) = \frac{\beta(S, u, v)}{\varepsilon}$$

$$\begin{cases} \dot{S} = D(S_{in} - S) - f(S)u - g(S)v \\ \dot{u} = (f(S) - D_0)u - \frac{\alpha(S, u, v)}{\varepsilon}u + \frac{\beta(S, u, v)}{\varepsilon}v \\ \dot{v} = (g(S) - D_1)v + \frac{\alpha(S, u, v)}{\varepsilon}u - \frac{\beta(S, u, v)}{\varepsilon}v \end{cases}$$

Fast and slow dynamics

$$\begin{cases} \dot{S} = D(S_{in} - S) - f(S)u - g(S)v \\ \dot{u} = (f(S) - D_0)u - \frac{\alpha(S,u,v)}{\varepsilon}u + \frac{\beta(S,u,v)}{\varepsilon}v \\ \dot{v} = (g(S) - D_1)v + \frac{\alpha(S,u,v)}{\varepsilon}u - \frac{\beta(S,u,v)}{\varepsilon}v \end{cases}$$

The dynamics of the total biomass $x = u + v$ is given by

$$\dot{x} = (f(S) - D_0)u + (g(S) - D_1)v.$$

Thus, u and v are fast variables, while S and x are slow ones. In the variables (S, x, p) , where $p = u/x$ is the proportion of u in x

$$\begin{cases} \dot{S} = D(S_{in} - S) - f(S)px - g(S)(1-p)x \\ \dot{x} = (f(S) - D_0)px + (g(S) - D_1)(1-p)x \\ \dot{p} = p(1-p)[(f(S) - D_0) - (g(S) - D_1)] - \frac{\alpha(\cdot)}{\varepsilon}p + \frac{\beta(\cdot)}{\varepsilon}(1-p) \end{cases}$$

Réduction des systèmes lents-rapides

$$\begin{cases} \varepsilon \dot{x} = f(x, y, \varepsilon) \\ \dot{y} = g(x, y, \varepsilon) \end{cases}$$

- ε est petit
- Le système est approximé par la solution du problème réduit

$$\dot{y} = g(h(y), y, 0)$$

- Ici $x = h(y)$ est une solution de l'équation $f(x, y, 0) = 0$.
- Cette méthode est appelée l'approximation quasi stationnaire.

Champs lents-rapides: $x \in \mathbb{R}^n$, $y \in \mathbb{R}^m$

$$(1_\varepsilon) \begin{cases} \varepsilon \frac{dx}{dt} = f(x, y, \varepsilon) \\ \frac{dy}{dt} = g(x, y, \varepsilon) \end{cases} \xrightleftharpoons{t=\varepsilon\tau} (2_\varepsilon) \begin{cases} \frac{dx}{d\tau} = f(x, y, \varepsilon) \\ \frac{dy}{d\tau} = \varepsilon g(x, y, \varepsilon) \end{cases}$$

$$\frac{dx}{d\tau} = \frac{dx}{dt} \frac{dt}{d\tau} = \varepsilon \frac{dx}{dt} \quad \frac{dy}{d\tau} = \frac{dy}{dt} \frac{dt}{d\tau} = \varepsilon \frac{dy}{dt}$$

$$(1_0) \begin{cases} 0 = f(x, y, 0) \\ \frac{dy}{dt} = g(x, y, 0) \end{cases} \quad (2_0) \begin{cases} \frac{dx}{d\tau} = f(x, y, 0) \\ \frac{dy}{d\tau} = 0 \end{cases}$$

Convention

$$\dot{x} = \frac{dx}{dt} \quad \dot{y} = \frac{dy}{dt} \quad x' = \frac{dx}{d\tau} \quad y' = \frac{dy}{d\tau}$$

Fast and slow dynamics

$$\begin{cases} S' = \varepsilon (D(S_{in} - S) - f(S)px - g(S)(1-p)x) \\ x' = \varepsilon ((f(S) - D_0)px + (g(S) - D_1)(1-p)x)) \\ p' = \varepsilon p(1-p) [(f(S) - D_0) - (g(S) - D_1)] - \alpha(\cdot)p + \beta(\cdot)(1-p) \end{cases}$$

The equation can be written $p' = F(S, x, p)$ where

$$F(S, x, p) = \beta(S, px, (1-p)x) - (\alpha(S, px, (1-p)x) + \beta(S, px, (1-p)x))p$$

The slow manifold is given by equation

$$F(S, x, p) = 0 \iff p = p(S, x)$$

Reduced model

The reduced system is obtained by replacing $p = p(S, x)$ in the slow equations

$$\begin{cases} \dot{S} = D(S_{in} - S) - f(S)p_x - g(S)(1-p)x \\ \dot{x} = (f(S) - D_0)p_x + (g(S) - D_1)(1-p)x \end{cases}$$

We obtain

$$\begin{cases} \dot{S} = D(S_{in} - S) - \mu(S, x)x \\ \dot{x} = (\mu(S, x) - d(S, x))x \end{cases}$$

where

$$\mu(S, x) = p(S, x)f(S) + (1 - p(S, x))g(S),$$

$$d(S, x) = p(S, x)D_0 + (1 - p(S, x))D_1.$$

Flocculation with several species

- the n species are competing on a same limiting resource, and that each species is present in two forms: isolated bacteria, of density u_i , and bacteria in flocks, of density v_i
- isolated bacteria can stick with isolated bacteria with flocks to form new flocks, with rate $\alpha_i(\cdot)u_i$.
- flocks can split and liberate isolated bacteria with rate $\beta_i(\cdot)v_i$.

$$u_i \xrightarrow{\alpha_i(\cdot)u_i} v_i, \quad u_i \xleftarrow{\beta_i(\cdot)v_i} v_i.$$

Then the equations are

$$\begin{cases} \dot{S} = D(S_{in} - S) - \sum_{i=1}^n (f_i(S)u_i + g_i(S)v_i) \\ \dot{u}_i = (f_i(S) - D_{0i})u_i - \alpha_i(\cdot)u_i + \beta_i(\cdot)v_i, \\ \dot{v}_i = (g_i(S) - D_{1i})v_i + \alpha_i(\cdot)u_i - \beta_i(\cdot)v_i \end{cases}$$

Fast attachment and detachment

$$\begin{cases} \dot{S} = D(S_{in} - S) - \sum_{i=1}^n (f_i(S)u_i + g_i(S)v_i) \\ \dot{u}_i = (f_i(S) - D_{0i})u_i - \frac{1}{\varepsilon} \sum_{j=1}^n a_{ij}x_j u_i + \frac{1}{\varepsilon} b_i v_i, \\ \dot{v}_i = (g_i(S) - D_{1i})v_i + \frac{1}{\varepsilon} \sum_{j=1}^n a_{ij}x_j u_i - \frac{1}{\varepsilon} b_i v_i \end{cases}$$

In the variables S, x_i, u_i , the system is written

$$\begin{cases} \dot{S} = D(S_{in} - S) - \sum_{i=1}^n [f_i(S)u_i + g_i(S)(x_i - u_i)] \\ \dot{x}_i = f_i(S)u_i + g_i(S)(x_i - u_i) - D_{0i}u_i - D_{1i}(x_i - u_i), \\ \dot{u}_i = (f_i(S) - D_{0i})u_i - \frac{1}{\varepsilon} \sum_{j=1}^n a_{ij}x_j u_i + \frac{b_i}{\varepsilon}(x_i - u_i) \end{cases}$$

Reduced model

This is a slow/fast system with the variables S, x_i are slow and the variables u_i fast. The fast equations are

$$u'_i = - \sum_{j=1}^n a_{ij} x_j u_i + b_i(x_i - u_i),$$

The slow manifold (or quasi steady-state) is given by

$$u_i = p_i(x)x_i, \quad p_i(x) = \frac{b_i}{b_i + \sum_{j=1}^n a_{ij}x_j},$$

The reduced model is

$$\begin{cases} \dot{S} = D(S_{in} - S) - \sum_{i=1}^n \mu_i(S, x)x_i \\ \dot{x}_i = (\mu_i(S, x) - d_i(x))x_i, \quad i = 1 \dots n \end{cases}$$

$$\mu_i(S, x) = f_i(S)p_i(x) + g_i(S)(1-p_i(x)), \quad d_i(x) = D_{0i}p_i(x) + D_{1i}(1-p_i(x)), \quad i = 1 \dots n$$

Summary

- ① Competition of species in the chemostat
- ② Flocculation (PhD of R. Fekih-Salem)
- ③ Density dependent growth functions (PhD of R. Fekih-Salem)
- ④ Inhibitors (PhDs of M. Dellal and B. Bar)
- ⑤ Commensalism (PhD of B. Benyahia)
- ⑥ Mutualism, Syntrophy (PhDs of M. El Hajji and Y. Daoud)
- ⑦ Other mechanisms of coexistence

Density dependent growth functions

- The classical chemostat

$$\begin{cases} \dot{S} = D(S_{in} - S) - \sum_{i=1}^n \mu_i(S)x_i \\ \dot{x}_i = (\mu_i(S) - D_i)x_i, \quad i = 1 \dots n \end{cases}$$

cannot have a steady state where all x_i are positive. Indeed

$$\mu_i(S) = D_i, \quad i = 1 \dots n$$

cannot have a solution in general.

- The density dependent chemostat

$$\begin{cases} \dot{S} = D(S_{in} - S) - \sum_{i=1}^n \mu_i(S, x)x_i \\ \dot{x}_i = (\mu_i(S, x) - d_i(x))x_i, \quad i = 1 \dots n \end{cases}$$

can have. Indeed, if all x_i are positive, we must solve a set of n equations with n unknown variables $\mathbf{x} = (x_1, \dots, x_n)$

$$\begin{cases} \mu_1(S, x) = d_1(x) \\ \dots \\ \mu_n(S, x) = d_n(x) \end{cases} \implies \begin{cases} x_1 = X_1(S) \\ \dots \\ x_n = X_n(S) \end{cases}$$

Intraspecific competition

$$\begin{cases} \dot{S} = D(S_{in} - S) - \sum_{i=1}^n \mu_i(S, x_i) x_i \\ \dot{x}_i = (\mu_i(S, x_i) - d_i(x_i)) x_i, \quad i = 1 \cdots n \end{cases}$$

- At steady state, $x_i = 0$ or x_i is a solution of

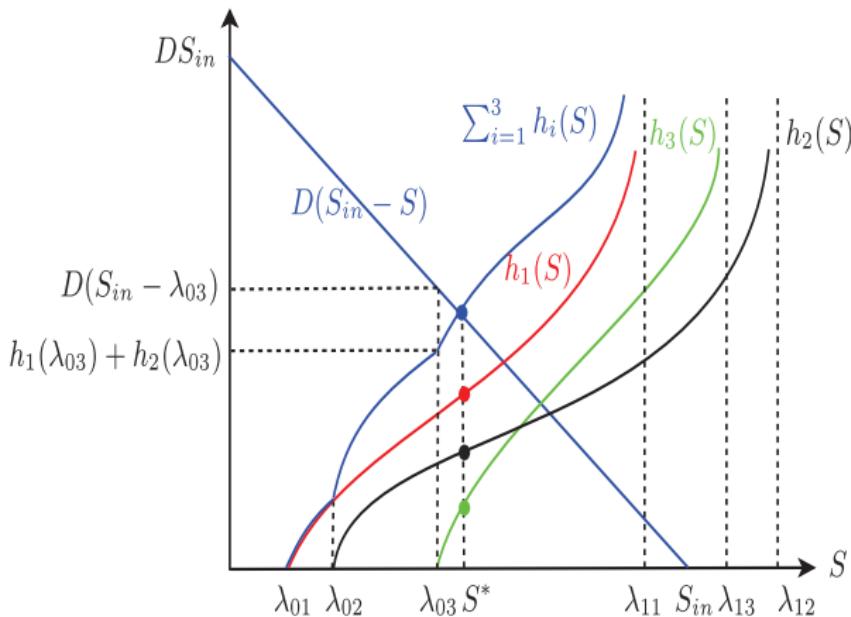
$$\mu_i(S, x_i) = d_i(x_i) \implies x_i = X_i(S), \quad i = 1, \dots, n$$

- $\frac{\partial \mu_i}{\partial S} > 0$, $\frac{\partial \mu_i}{\partial x_i} < 0$, $d_i''(x_i) \leq 0$ and $[x_i d_i(x_i)]' > 0$
- Replacing $x_i = X_i(S)$ and $\mu_i(S, x) = d_i(X_i(S))$ in the first equation gives an equation in the single variable S

$$D(S_{in} - S) = \sum_{i=1}^n h_i(S), \quad h_i(S) = d_i(X_i(S))X_i(S).$$

- Solving this equation gives S and then, the possibility of a positive steady state.

The steady state characteristic



R. Fekih-Salem, J. Harmand, C. Lobry, A. Rapaport and T. Sari. *Extensions of the chemostat model with flocculation*. J. Math. Anal. Appl., 397 (2013), 292–306.

Crowding effect

$$\begin{cases} \dot{S} = D(S_{in} - S) - \sum_{i=1}^n \mu_i(S)x_i \\ \dot{x}_i = (\mu_i(S) - a_i x_i - D_i)x_i, \quad i = 1 \dots n \end{cases}$$

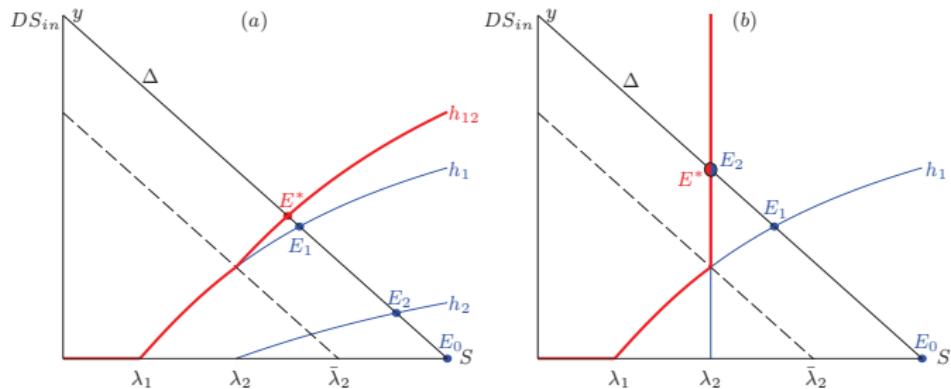
- At steady state, $x_i = 0$ or x_i is a solution of

$$\mu_i(S) = D_i - a_i x_i \implies x_i = X_i(S) := \frac{\mu_i(S) - D_i}{a_i}, \quad S \geq \lambda_i$$

- Replacing $x_i = X_i(S)$ in the first equation gives an equation in the single variable S

$$D(S_{in} - S) = \sum_{i=1}^n h_i(S), \quad h_i(S) = \mu_i(S)X_i(S).$$

The steady state characteristic ($n = 2$)

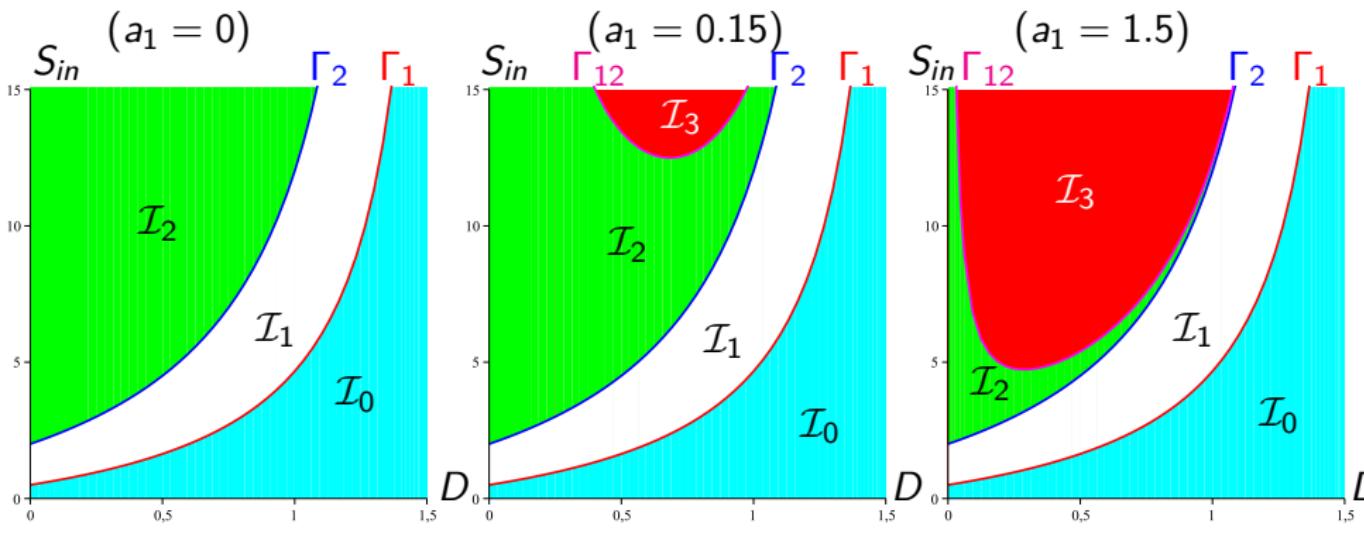


- $a_1 > 0$. (a): $a_2 > 0$. (a): $a_2 = 0$.
- interspecific competition of x_1 (the winning species) is sufficient to obtain coexistence

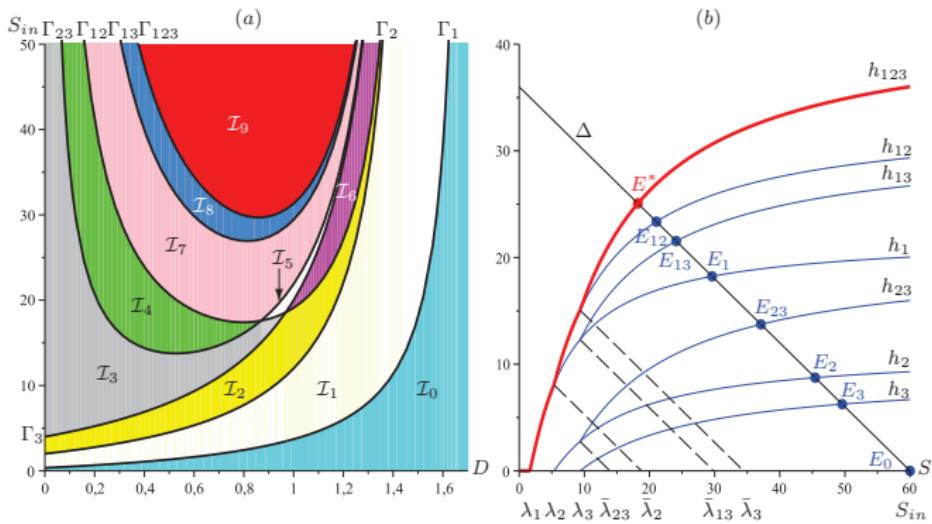
N. Abdellatif, R. Fekih-Salem and T. Sari, *Competition for a single resource and coexistence of several species in the chemostat*, Math. Biosci. Eng., **13** (2016), 631–652.

Operating diagram ($n = 2$)

Region	E_0	E_1	E_2	E^*
$(D, S_{in}) \in \mathcal{I}_0$	S			
$(D, S_{in}) \in \mathcal{I}_1$	U	S		
$(D, S_{in}) \in \mathcal{I}_2$	U	S	U	
$(D, S_{in}) \in \mathcal{I}_3$	U	U	U	S



The case $n > 2$



N. Abdellatif, R. Fekih-Salem and T. Sari, *Competition for a single resource and coexistence of several species in the chemostat*, Math. Biosci. Eng., **13** (2016), 631–652.

COMPETITION FOR A SINGLE RESOURCE AND COEXISTENCE OF SEVERAL SPECIES IN THE CHEMOSTAT

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(Communicated by Patrick De Leenheer)

Intra and interspecific competition

- We have not at our disposal a mathematical study of the density dependent chemostat

$$\begin{cases} \dot{S} = D(S_{in} - S) - \sum_{i=1}^n \mu_i(S, x) x_i \\ \dot{x}_i = (\mu_i(S, x) - D_i) x_i, \quad i = 1 \dots n \end{cases}$$

- The particular case $\mu_i(S, x_1, \dots, x_n) = \nu_i(S, x_i + \alpha \sum_{j \neq i} x_j)$ where α denotes the interspecific competition was considered numerically.
- The coexistence which was predicted when $\alpha = 0$ (only intraspecific competition is present), is still a property of the model when α is small enough but it is no longer the case when α is sufficiently large.

C. Lobry and J. Harmand, A new hypothesis to explain the coexistence of n species in the presence of a single resource, *C. R. Biol.*, 329 (2006), 40–46.

Two species

$$\begin{cases} \dot{S} = D(S_{in} - S) - \mu_1(S, x_1, x_2)x_1 - \mu_2(S, x_2, x_1)x_2 \\ \dot{x}_1 = [\mu_1(S, x_1, x_2) - D_1]x_1 \\ \dot{x}_2 = [\mu_2(S, x_2, x_1) - D_2]x_2. \end{cases}$$

- $D_i = D + a_i$, where $a_i \geq 0$.
- This condition means that the dilution rate of the species is the sum of the dilution rate of the chemostat and a specific mortality rate of the species (it is used only in the stability analysis of positive steady states)
- $\frac{\partial \mu_i}{\partial S}(S, x_i, x_j) > 0$, $\frac{\partial \mu_i}{\partial x_i}(S, x_i, x_j) \leq 0$ and $\frac{\partial \mu_i}{\partial x_j}(S, x_i, x_j) \leq 0$
- This condition means that the growth rate of each species increases with the concentration of substrate and is inhibited by intra- and interspecific competition.

Steady states

$$\begin{cases} \dot{S} = D(S_{in} - S) - \mu_1(S, x_1, x_2)x_1 - \mu_2(S, x_2, x_1)x_2 \\ \dot{x}_1 = [\mu_1(S, x_1, x_2) - D_1]x_1 \\ \dot{x}_2 = [\mu_2(S, x_2, x_1) - D_2]x_2. \end{cases}$$

- $\mathcal{E}_0 = (S_{in}, 0, 0)$: both populations are extinct (washout).
- $\mathcal{E}_1 = (\tilde{S}_1, \tilde{x}_1, 0)$: the second population is extinct.
- $\mathcal{E}_2 = (\tilde{S}_2, 0, \tilde{x}_2)$: the first population is extinct.
- $\mathcal{E}^* = (S^*, x_1^*, x_2^*)$: both populations survive.

Positive steady states

- $S^* = S_{in} - \frac{D_1}{D}x_1^* - \frac{D_2}{D}x_2^*$ where $(x_1 = x_1^*, x_2 = x_2^*)$ must be a solution of

$$\begin{cases} f_1(x_1, x_2) := \mu_1 \left(S_{in} - \frac{D_1}{D}x_1 - \frac{D_2}{D}x_2, x_1, x_2 \right) - D_1 = 0 \\ f_2(x_1, x_2) := \mu_2 \left(S_{in} - \frac{D_1}{D}x_1 - \frac{D_2}{D}x_2, x_2, x_1 \right) - D_2 = 0 \end{cases}$$

- Equations $f_1 = 0$ and $f_2 = 0$ defines curves γ_1 and γ_2 which are the graphs of decreasing functions
- Let \tilde{x}_1 , \tilde{x}_2 , \bar{x}_1 and \bar{x}_2 be defined by

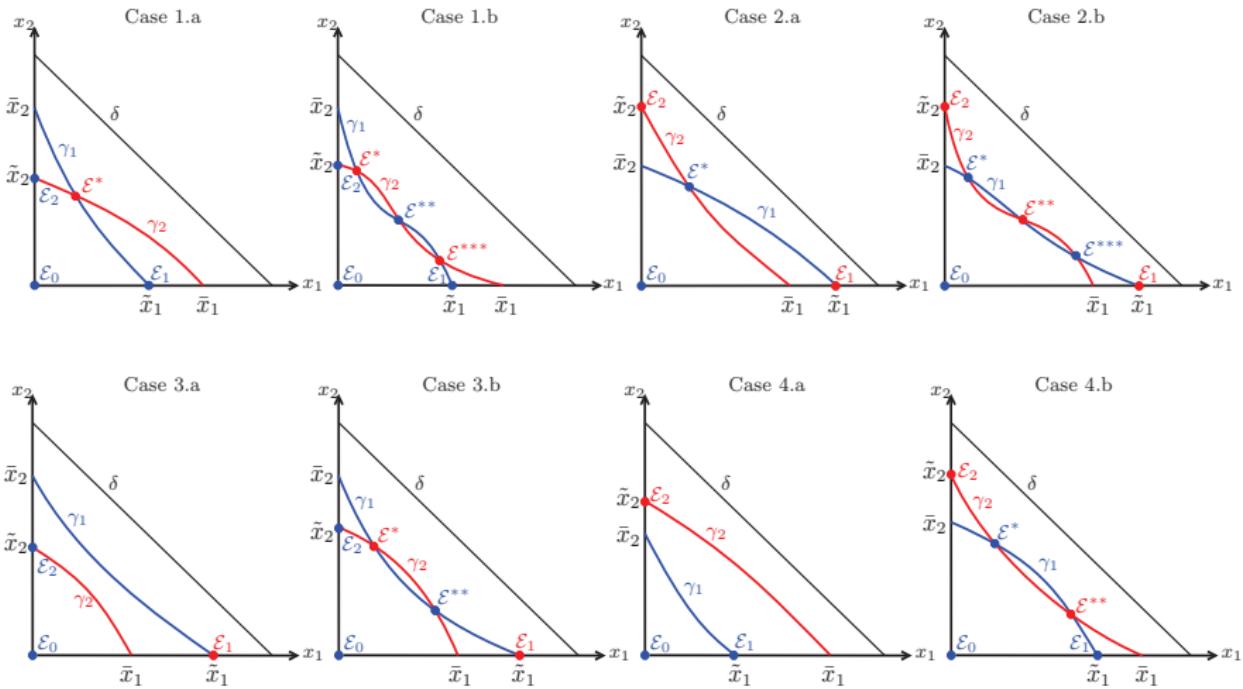
$$f_1(\tilde{x}_1, 0) = 0, \quad f_2(0, \tilde{x}_2) = 0, \quad f_1(0, \bar{x}_2) = 0, \quad f_2(\bar{x}_1, 0) = 0.$$

- Four cases must be distinguished

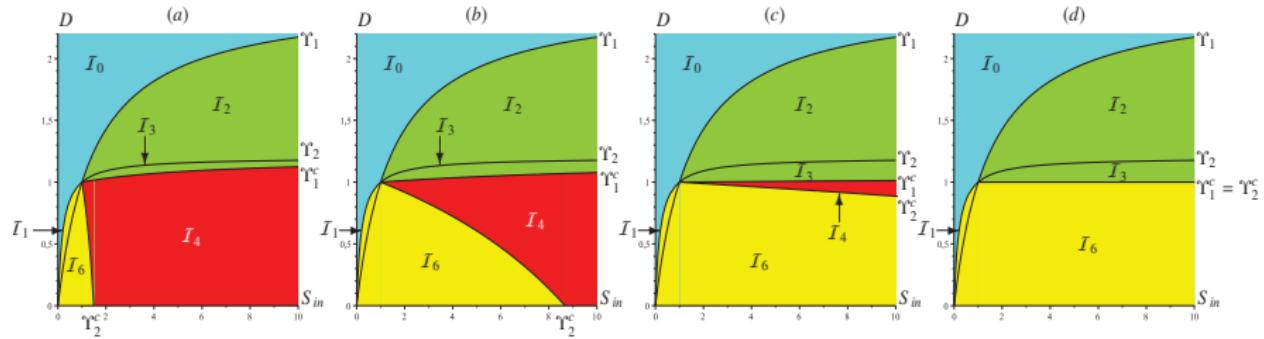
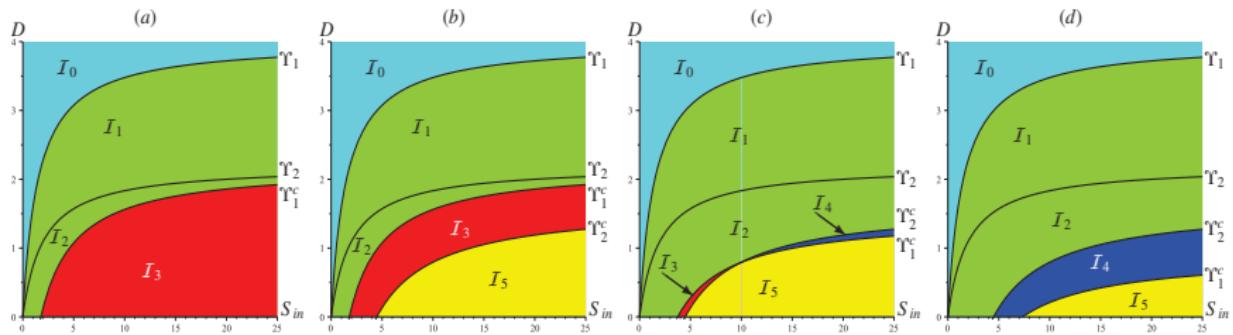
$$(\text{Case 1}) : \bar{x}_1 > \tilde{x}_1 \& \bar{x}_2 > \tilde{x}_2, \quad (\text{Case 2}) : \bar{x}_1 < \tilde{x}_1 \& \bar{x}_2 < \tilde{x}_2$$

$$(\text{Case 3}) : \bar{x}_1 < \tilde{x}_1 \& \bar{x}_2 > \tilde{x}_2, \quad (\text{Case 4}) : \bar{x}_1 > \tilde{x}_1 \& \bar{x}_2 < \tilde{x}_2$$

The four cases



Operating diagram

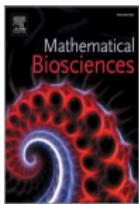




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A density-dependent model of competition for one resource in the chemostat



Radhouane Fekih-Salem^{a,d,*}, Claude Lobry^b, Tewfik Sari^{c,e}

Summary

- ① Competition of species in the chemostat
- ② Flocculation (PhD of R. Fekih-Salem)
- ③ Density dependent growth functions (PhD of R. Fekih-Salem)
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- ⑦ Other mechanisms of coexistence

External inhibitor

PhD of Mohammed Dellal coadvised with Mustapha Lakrib
(February, 28, 2019, Sidi Bel Abbes, Algeria)

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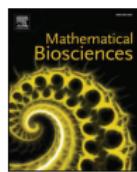
Mathematical Biosciences xxx (xxxx) xxx-xxx



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The operating diagram of a model of two competitors in a chemostat with an external inhibitor

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External inhibition

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

- One species is sensitive and the other is resistant.
- 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 resistant species is able to remove the inhibitor from the environment

The inhibitor is not removed: $g(p) = 0$

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

$p(t)$ tends to p^0 and the system is reduced to

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

- $E_0 = (S^0, 0, 0, p^0)$
- $E_1 = (\lambda^+, S^0 - \lambda^+, 0, p^0)$ where $f_1(\lambda^+) = \frac{D}{f(p^0)}$
- $E_2 = (\lambda_2, 0, S^0 - \lambda_2, p^0)$ where $f_2(\lambda_2) = D$

if $\lambda^+ < \lambda_2$, E_1 is Stable and E_2 is unstable
if $\lambda^+ > \lambda_2$, E_2 is Stable and E_1 is unstable

The inhibitor is removed

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

- $E_0 = (S^0, 0, 0, p^0)$.
- $E_1 = (\lambda^+, S^0 - \lambda^+, 0, p^0)$
- $E_2 = (\lambda_2, 0, S^0 - \lambda_2, p^*)$
- $E_c = (\lambda_2, x_c, y_c, p_c)$

$$f_1(\lambda^+) = \frac{D}{f(p^0)}, \quad f_2(\lambda_2) = D, \quad W(p^*) = S^0 - \lambda_2$$

$$f(p_c) = \frac{D}{f_1(\lambda_2)}, \quad y_c = W(p_c), \quad x_c(D) = S^0 - \lambda_2 - y_c$$

with

$$W(p) = \frac{D(p^0 - p)}{g(p)}$$

Existence and stability

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

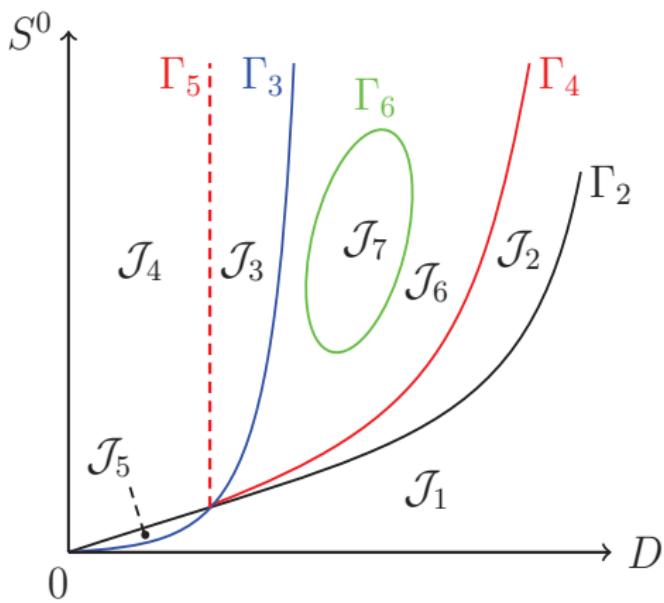
	Existence	Stability
E_0	Always	$\min(\lambda^+, \lambda_2) > S^0$
E_1	$\lambda^+ < S^0$	$\lambda^+ < \lambda_2$
E_2	$\lambda_2 < S^0$	$\lambda_2 < \lambda^-$
E_c	$\lambda^- < \lambda_2 < \min(\lambda^+, S^0)$	$(A + B)(A + B + C)C > BEF$

$$f_1(\lambda^-) = \frac{D}{f(p^*)}, \quad f_1(\lambda^+) = \frac{D}{f(p^0)}, \quad f_2(\lambda_2) = D$$

$$A = f(p_c)f'_1(\lambda_2)x_c, \quad B = f'_2(\lambda_2)y_c, \quad C = 1 + g'(p_c)y_c$$

$$E = g(p_c), \quad F = -f'(p_c)f_1(\lambda_2)x_c,$$

Operating diagram



Regions	E_0	E_1	E_2	E_c
\mathcal{J}_1	S			
\mathcal{J}_2	U		S	
\mathcal{J}_3	U	U	U	S
\mathcal{J}_4	U	S	U	
\mathcal{J}_5	U	S		
\mathcal{J}_6		U	U	S
\mathcal{J}_7	U	U	U	

Application

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

$$f(p) = e^{-\mu p}, \quad f_1(S) = \frac{m_1 S}{a_1 + S}, \quad f_2(S) = \frac{m_2 S}{a_2 + S}, \quad g(p) = \frac{\delta p}{K + p}$$

$$\mu = 5 \quad m_1 = 5 \quad a_1 = 0.5 \quad m_2 = 6 \quad a_2 = 3.5 \quad \delta = 50 \quad K = 0.1$$

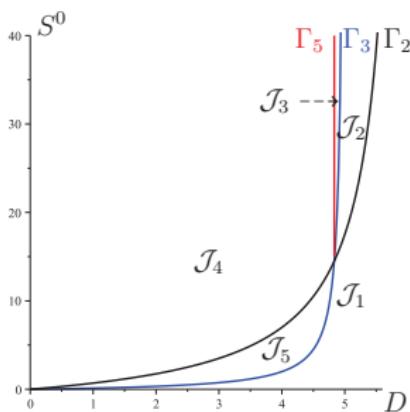
S. B. Hsu and P. Waltman (1991, 2004).

Studied the stability of steady states,

Noticed that the positive steady state E_c can be unstable

Showed that for $S^0 = 1$, $p^0 = 1$ and $D = 1$, it is unstable.

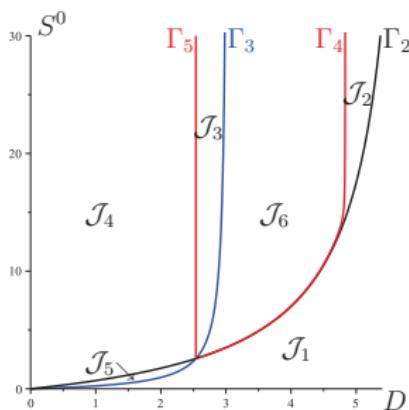
Operating diagram: $p^0 = 0$



Regions	E_0	E_1	E_2
\mathcal{J}_1	S		
\mathcal{J}_2	U		S
\mathcal{J}_3	U	U	S
\mathcal{J}_4	U	S	U
\mathcal{J}_5	U	S	

TABLE 5. Existence and stability of equilibria in the regions of the operating diagram of Figure 6.

Operating diagram: $p^0 = 0.1$



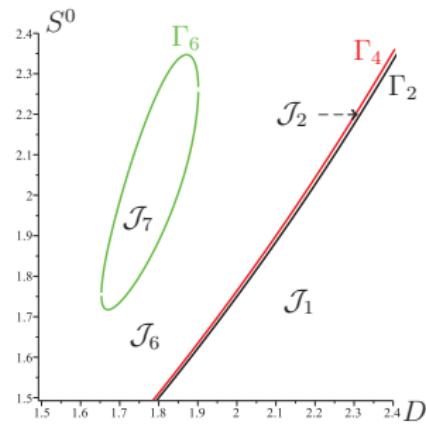
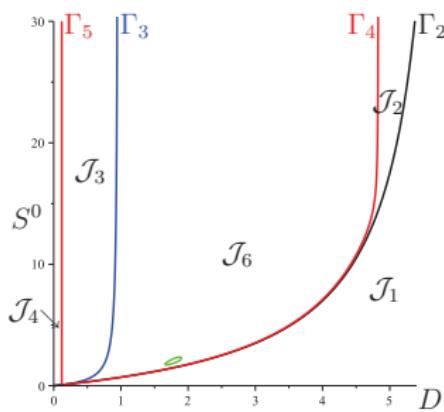
Regions	E_0	E_1	E_2	E_c
\mathcal{J}_1	S			
\mathcal{J}_2	U		S	
\mathcal{J}_3	U	U	U	S
\mathcal{J}_4	U	S	U	
\mathcal{J}_5	U	S		
\mathcal{J}_6	U		U	S

TABLE 6. Existence and stability of equilibria in the regions of the operating diagram of Figure 7.

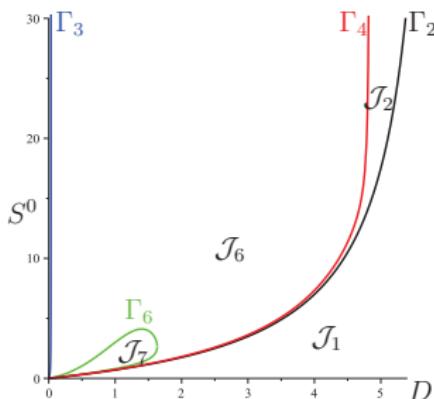
Regions	E_0	E_1	E_2	E_c
\mathcal{J}_1	S			
\mathcal{J}_2	U		S	
\mathcal{J}_3	U	U	U	S
\mathcal{J}_4	U	S	U	U
\mathcal{J}_6	U		U	S
\mathcal{J}_7	U		U	U

Operating diagram: $p^0 = 0.33$

TABLE 7. Existence and stability of equilibria in the regions of the operating diagram of Figure 8.



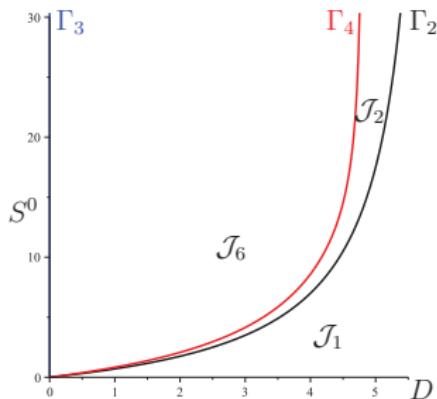
Operating diagram: $p^0 = 1$



Regions	E_0	E_1	E_2	E_c
J_1	S			
J_2	U		S	
J_3	U	U	U	S
J_6	U		U	S
J_7	U	U	U	U

TABLE 8. Existence and stability of equilibria in the regions of the operating diagram of Figure 9.

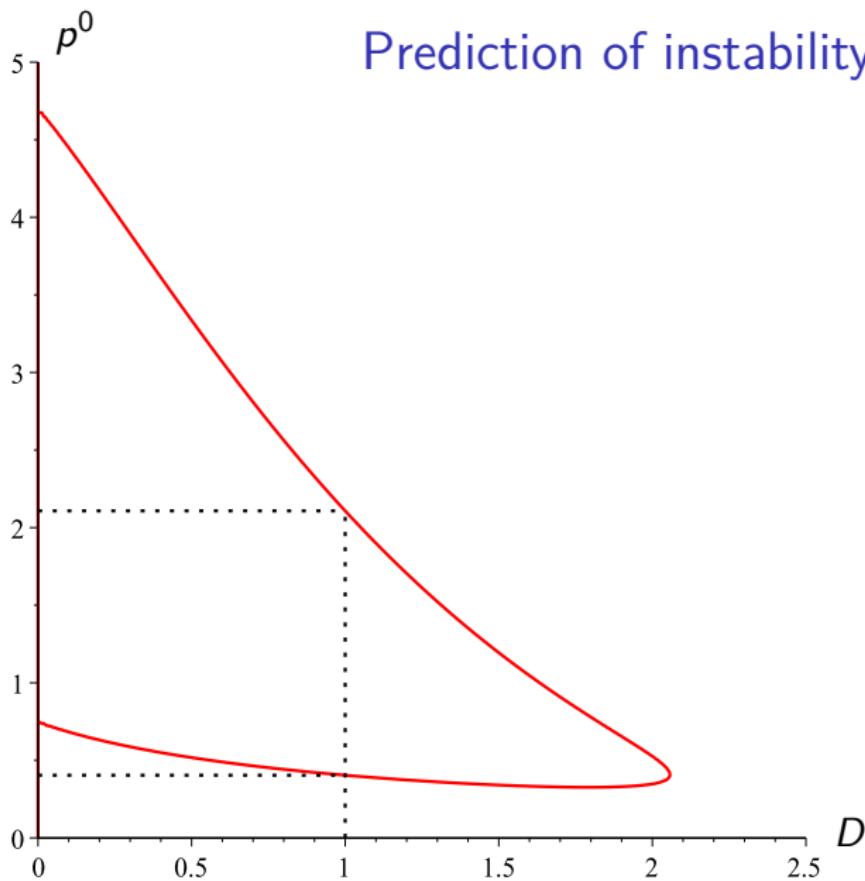
Operating diagram: $p^0 = 4.72$



Regions	E_0	E_1	E_2	E_c
\mathcal{J}_1	S			
\mathcal{J}_2	U		S	
\mathcal{J}_3	U	U	U	S
\mathcal{J}_6	U	U	U	S

TABLE 9. Existence and stability of equilibria in the regions of the operating diagram of Figure 10.

Prediction of instability of E_c



External lethal inhibitor

PhD of Bachir Bar coadvised with Mustapha Lakrib
(February, 27, 2019, Tlemcen, Algeria)

DISCRETE AND CONTINUOUS
DYNAMICAL SYSTEMS SERIES B

doi:10.3934/dcdsb.2019203

THE OPERATING DIAGRAM FOR A MODEL OF COMPETITION IN A CHEMOSTAT WITH AN EXTERNAL LETHAL INHIBITOR

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(Communicated by Pierre Magal)

External lethal inhibition

$$\begin{cases} S' = (S^0 - S)D - f_1(S)x - f_2(S)y \\ x' = [f_1(S) - D - \gamma p]x \\ y' = [f_2(S) - D]y \\ p' = (p^0 - p)D - g(p)y \end{cases}$$

- One species is sensitive and the other is resistant.
- 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 resistant species is able to remove the inhibitor from the environment

The inhibitor is not removed: $g(p) = 0$

$$\begin{cases} S' &= (S^0 - S)D - f_1(S)x - f_2(S)y \\ x' &= [f_1(S) - D - \gamma p]x \\ y' &= [f_2(S) - D]y \\ p' &= (p^0 - p)D \end{cases}$$

$p(t)$ tends to p^0 and the system is reduced to

$$\begin{cases} S' &= (S^0 - S)D - f_1(S)x - f_2(S)y \\ x' &= [f_1(S) - D - \gamma p^0]x \\ y' &= [f_2(S) - D]y \end{cases}$$

- $E_0 = (S^0, 0, 0, p^0)$
- $E_1 = \left(\lambda^+, \frac{D}{D + \gamma p^0} (S^0 - \lambda^+), 0, p^0\right)$ where $f_1(\lambda^+) = D + \gamma p^0$
- $E_2 = (\lambda_2, 0, S^0 - \lambda_2, p^0)$ where $f_2(\lambda_2) = D$

if $\lambda^+ < \lambda_2$, E_1 is Stable and E_2 is unstable
if $\lambda^+ > \lambda_2$, E_2 is Stable and E_1 is unstable

The inhibitor is removed

$$\begin{cases} S' = (S^0 - S)D - f_1(S)x - f_2(S)y \\ x' = [f_1(S) - D - \gamma p]x \\ y' = [f_2(S) - D]y \\ p' = (p^0 - p)D - g(p)y \end{cases}$$

- $E_0 = (S^0, 0, 0, p^0)$.
- $E_1 = \left(\lambda^+, \frac{D}{D+\gamma p^0} (S^0 - \lambda^+), 0, p^0\right)$
- $E_2 = (\lambda_2, 0, S^0 - \lambda_2, p^*)$
- $E_c = (\lambda_2, x_c, y_c, p_c)$

$$f_1(\lambda^+) = D + \gamma p^0, \quad f_2(\lambda_2) = D, \quad W(p^*) = S^0 - \lambda_2$$

$$p_c = \frac{f_1(\lambda_2) - D}{\gamma}, \quad y_c = W(p_c), \quad x_c(D) = \frac{D}{D + \gamma p_c} (S^0 - \lambda_2 - y_c)$$

with

$$W(p) = \frac{D(p^0 - p)}{g(p)}$$

Existence and stability

$$\begin{cases} S' = (S^0 - S)D - f_1(S)x - f_2(S)y \\ x' = [f_1(S) - D - \gamma p]x \\ y' = [f_2(S) - D]y \\ p' = (p^0 - p)D - g(p)y \end{cases}$$

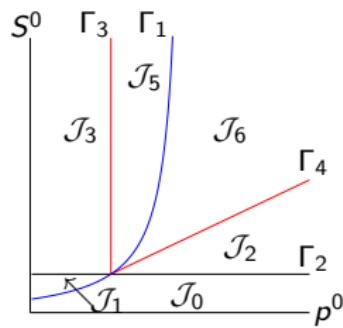
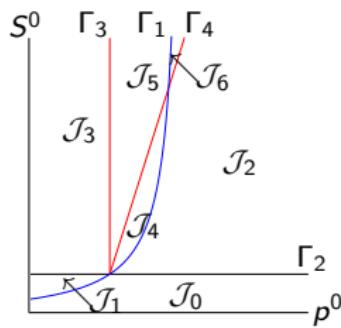
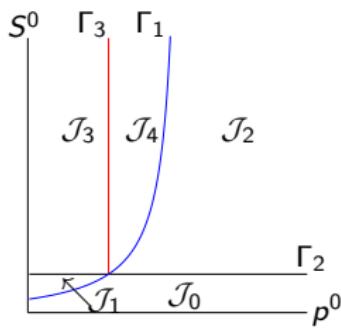
	Existence	Stability
E_0	Always	$\min(\lambda^+, \lambda_2) > S^0$
E_1	$\lambda^+ < S^0$	$\lambda^+ < \lambda_2$
E_2	$\lambda_2 < S^0$	$\lambda_2 < \lambda^-$
E_c	$\lambda^- < \lambda_2 < \min(\lambda^+, S^0)$	$A_3(A_1A_2 - A_3) > A_1^2A_4$

$$f_1(\lambda^-) = D + \gamma p^*, \quad f_1(\lambda^+) = D + \gamma p^0, \quad f_2(\lambda_2) = D$$

$$A_i = \dots, \quad i = 1 \dots 4$$

Operating diagram

Regions	\mathcal{J}_0	\mathcal{J}_1	\mathcal{J}_2	\mathcal{J}_3	\mathcal{J}_4	\mathcal{J}_5^S	\mathcal{J}_5^U	\mathcal{J}_6^S	\mathcal{J}_6^U
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	U	S	U



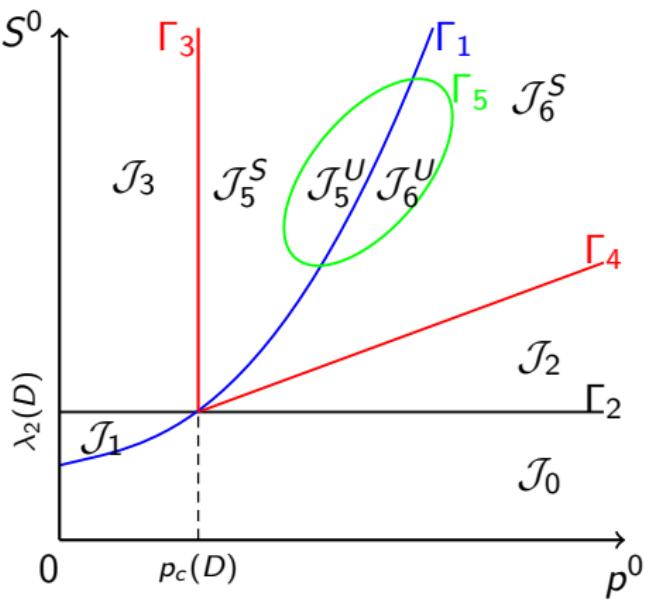
$(g = 0)$

$(g > 0)$

$(g > 0, \mathcal{J}_4 = \emptyset)$

Operating diagram

Regions	\mathcal{J}_0	\mathcal{J}_1	\mathcal{J}_2	\mathcal{J}_3	\mathcal{J}_4	\mathcal{J}_5^S	\mathcal{J}_5^U	\mathcal{J}_6^S	\mathcal{J}_6^U
E_0	S	U	U	U	U	U	U	U	U
E_1		S		S	U	U	U	U	
E_2			S	U	S	U	U	U	U
E_c						S	U	S	U



Application

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

$$f_1(S) = \frac{m_1 S}{a_1 + S}, \quad f_2(S) = \frac{m_2 S}{a_2 + S}, \quad g(p) = \frac{\delta p}{K + p}$$

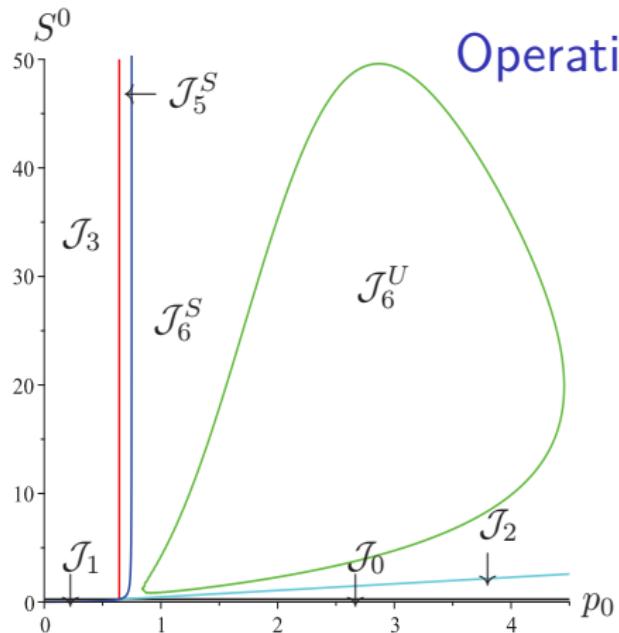
$$m_1 = 4 \quad a_1 = 0.03 \quad m_2 = 5 \quad a_2 = 1 \quad \delta = 5 \quad K = 1.3 \quad \gamma = 4$$

S. B. Hsu, Y.S. Li and P. Waltman (2000)

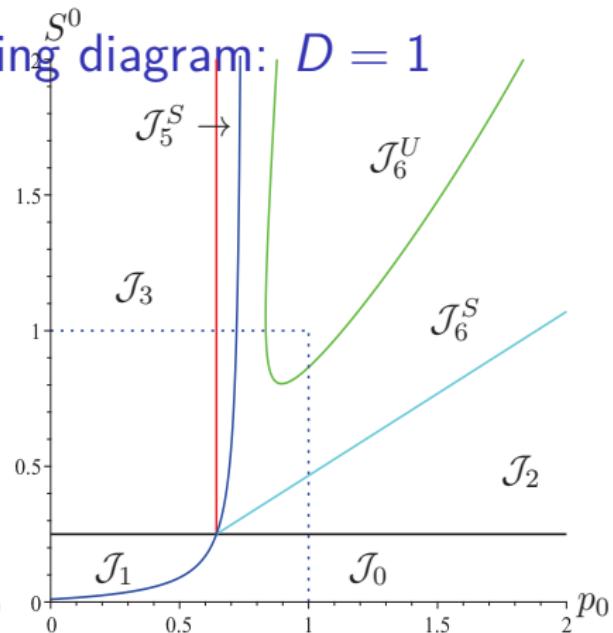
Studied the stability of steady states,

Noticed that the positive steady state E_c can be unstable

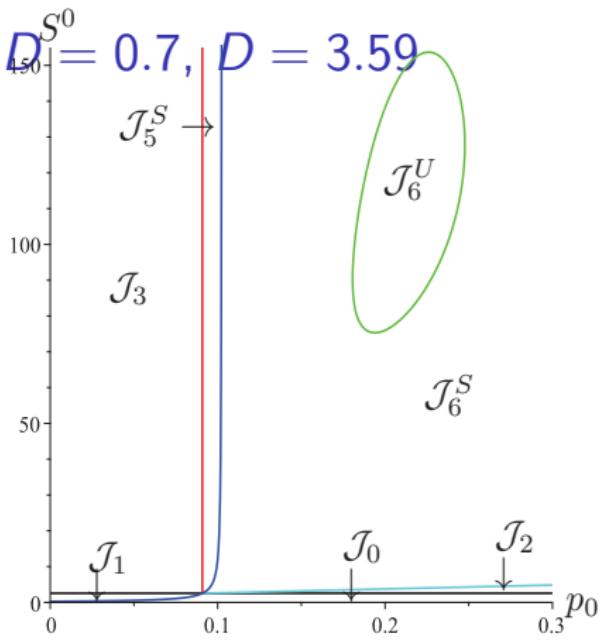
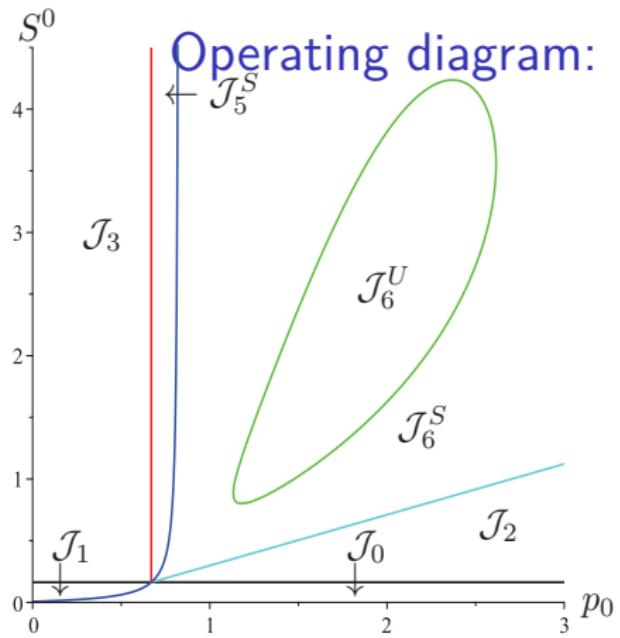
Showed that for $S^0 = 1$, $p^0 = 1$ and $D = 1$, it is unstable.



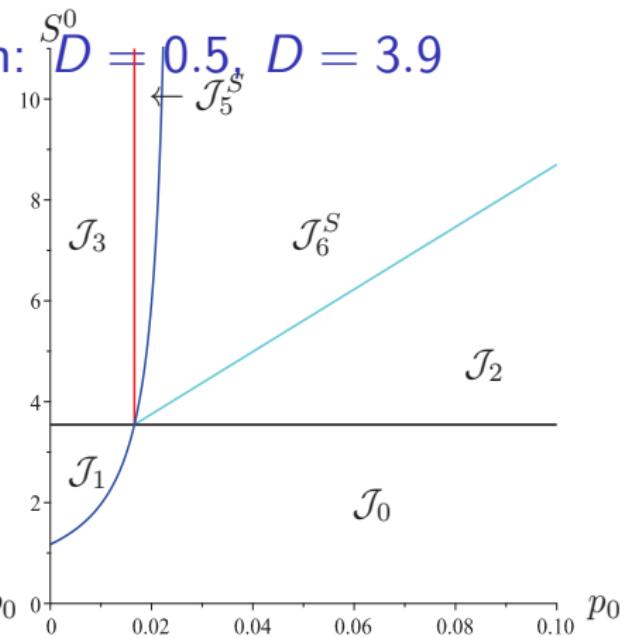
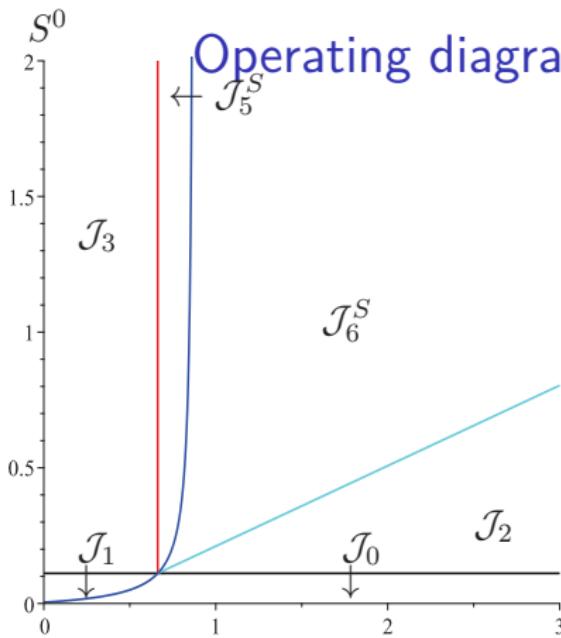
Operating diagram: $D = 1$



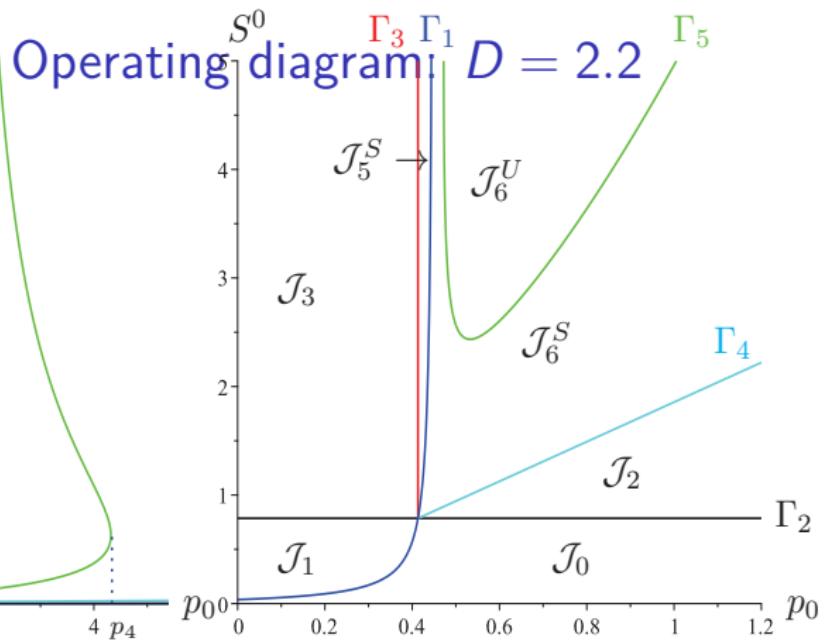
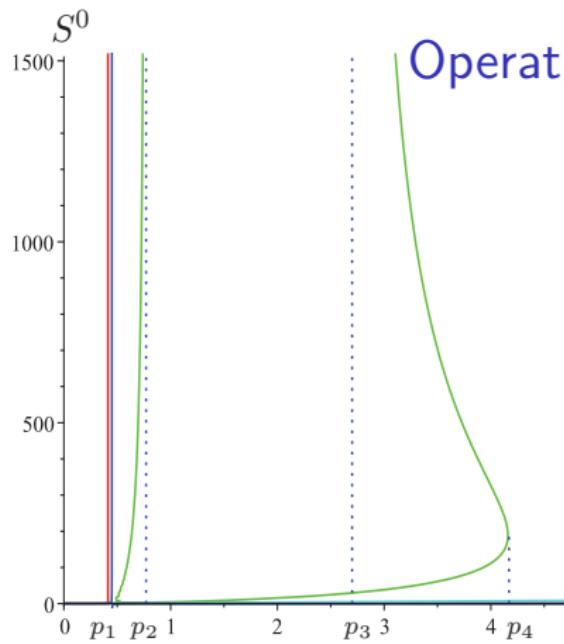
Regions	\mathcal{J}_0	\mathcal{J}_1	\mathcal{J}_2	\mathcal{J}_3	\mathcal{J}_4	\mathcal{J}_5^S	\mathcal{J}_5^U	\mathcal{J}_6^S	\mathcal{J}_6^U
E_0	S	U	U	U	U	U	U	U	U
E_1		S		S	U	U	U		
E_2			S	U	S	U	U	U	U
E_c						S	U	S	U



Regions	\mathcal{J}_0	\mathcal{J}_1	\mathcal{J}_2	\mathcal{J}_3	\mathcal{J}_4	\mathcal{J}_5^S	\mathcal{J}_5^U	\mathcal{J}_6^S	\mathcal{J}_6^U
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	U	S	U	

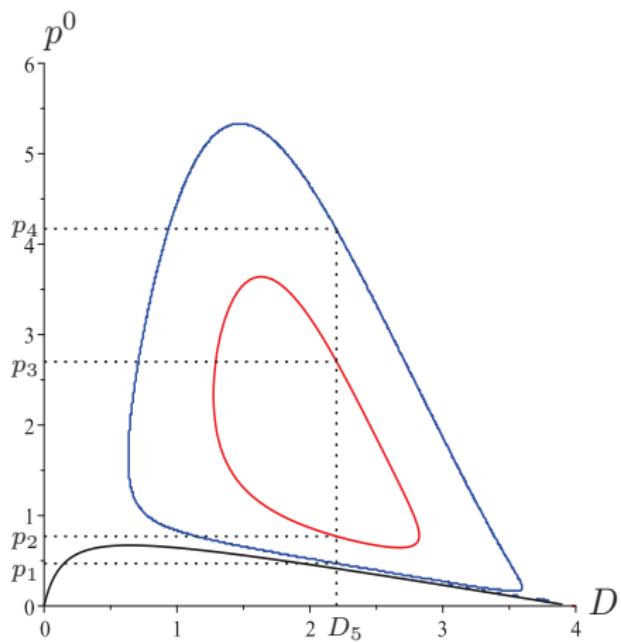


Regions	\mathcal{J}_0	\mathcal{J}_1	\mathcal{J}_2	\mathcal{J}_3	\mathcal{J}_4	\mathcal{J}_5^S	\mathcal{J}_5^U	\mathcal{J}_6^S	\mathcal{J}_6^U
E_0	S	U	U	U	U	U	U	U	U
E_1		S		S	U	U	U		
E_2			S	U	S	U	U	U	U
E_c						S	U	S	U



Regions	\mathcal{J}_0	\mathcal{J}_1	\mathcal{J}_2	\mathcal{J}_3	\mathcal{J}_4	\mathcal{J}_5^S	\mathcal{J}_5^U	\mathcal{J}_6^S	\mathcal{J}_6^U
E_0	S	U	U	U	U	U	U	U	U
E_1	S		S	U	U	U	U		
E_2		S	U	S	U	U	U	U	U
E_c					S	U	S	S	U

Prediction of instability of E_c



Summary

- ① Competition of species in the chemostat
- ② Flocculation (PhD of R. Fekih-Salem)
- ③ Density dependent growth functions (PhD of R. Fekih-Salem)
- ④ Inhibitors (PhDs of M. Dellal and B. Bar)
- ⑤ Commensalism (PhD of B. Benyahia)
- ⑥ Mutualism, Syntrophy (PhDs of M. El Hajji and Y. Daoud)
- ⑦ Other mechanisms of coexistence

Mixed culture:

$$S_1 \xrightarrow{\mu_1(\cdot)} X_1 + S_2, \quad S_2 \xrightarrow{\mu_2(\cdot)} X_2$$

$$\begin{cases} \dot{S}_1 = D(S_1^{in} - S_1) - k_1\mu_1(\cdot)X_1 \\ \dot{X}_1 = -DX_1 + \mu_1(\cdot)X_1 \\ \dot{S}_2 = -DS_2 + k_3\mu_1(\cdot)X_1 - k_2\mu_2(\cdot)X_2 \\ \dot{X}_2 = -DX_2 + \mu_2(\cdot)X_2 \end{cases}$$

- S_1, S_2 : concentrations of substrate and product
- X_1, X_2 : concentrations of bacteria
- S_1^{in} : input concentration of substrate
- D : Dilution rate
- k_1, k_2, k_3 : stoichiometric coefficients (inverses of yields)
- $\mu_1(\cdot), \mu_2(\cdot)$: specific growth functions

Commensalism

'Two populations of microorganisms which grow in a mixed culture and interact in such a way that one population (the commensal population) depends for its growth on the other population and thus benefits from the interaction while the other population (the host) is not affected by the growth of the commensal population constitutes an example of commensalism.'

$$\mu_1(\cdot) = \mu_1(S_1), \quad \mu_2(\cdot) = \mu_2(S_2)$$

are monotone increasing (Monod) or can exhibit a maximum if the growth is inhibited at high substrate concentrations (Haldane)

$$\left\{ \begin{array}{lcl} \dot{S}_1 & = & D(S_1^{in} - S_1) - k_3 \mu_1(S_1) X_1 \\ \dot{X}_1 & = & -DX_1 + \mu_1(S_1) X_1 \\ \dot{S}_2 & = & -DS_2 + k_1 \mu_1(S_1) X_1 - k_2 \mu_2(S_2) X_2 \\ \dot{X}_2 & = & -DX_2 + \mu_2(S_2) X_2 \end{array} \right.$$

AM2 model

$$\begin{cases} \dot{S}_1 = D(S_1^{in} - S_1) - k_3\mu_1(S_1)X_1 \\ \dot{X}_1 = -\alpha DX_1 + \mu_1(S_1)X_1 \\ \dot{S}_2 = D(S_2^{in} - S_2) + k_1\mu_1(S_1)X_1 - k_2\mu_2(S_2)X_2 \\ \dot{X}_2 = -\alpha DX_2 + \mu_2(S_2)X_2 \end{cases}$$

PHD of Boumédiène Benyahia coadvised by B. Cherki and J. Harmand

AM2 model

- $E_1^0 = (S_{1in}, 0, S_{2in}, 0)$, washout of X_1 and X_2 .
- $E_1^i = (S_{1in}, 0, S_2^{i*}, X_2^i)$, $i = 1, 2$, washout of X_1 but not of X_2 .
- $E_2^0 = (S_1^*, X_1^*, S_{2in}^*, 0)$, washout of X_2 but not of X_1 .
- $E_2^i = (S_1^*, X_1^*, S_2^{i*}, X_2^{i*})$, $i = 1, 2$, coexistence of X_1 and X_2 .

Journal of Process Control 22 (2012) 1008–1019



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Bifurcation and stability analysis of a two step model for monitoring anaerobic digestion processes[☆]

B. Benyahia^{a,b,*}, T. Sari^{b,c}, B. Cherki^a, J. Harmand^{b,d}

AM2: Existence and Stability of steady states

If $S_{1in} < S_1^*$ then we have 3 sub-cases:

Condition	E_1^0	E_1^1	E_1^2
$S_{2in} < S_2^{1*} < S_2^{2*}$	S		
$S_2^{1*} < S_{2in} < S_2^{2*}$	U	S	
$S_2^{1*} < S_2^{2*} < S_{2in}$	S	S	U

If $S_{1in} > S_1^*$ then we have 6 sub-cases:

Condition	E_1^0	E_1^1	E_1^2	E_2^0	E_2^1	E_2^2
$S_{2in} < S_{2in}^* < S_2^{1*} < S_2^{2*}$	U			S		
$S_{2in} < S_2^{1*} < S_{2in}^* < S_2^{2*}$	U			U	S	
$S_{2in} < S_2^{1*} < S_2^{2*} < S_{2in}^*$	U			S	S	U
$S_2^{1*} < S_{2in} < S_{2in}^* < S_2^{2*}$	U	U		U	S	
$S_2^{1*} < S_{2in} < S_2^{2*} < S_{2in}^*$	U	U		S	S	U
$S_2^{1*} < S_2^{2*} < S_{2in} < S_{2in}^*$	U	U	U	S	S	U

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- ⑥ Mutualism, Syntrophy (PhDs of M. El Hajji and Y. Daoud)
- ⑦ Other mechanisms of coexistence

Syntrophy

$$\begin{cases} \dot{S}_1 = D(S_1^{in} - S_1) - k_3\mu_1(S_1, S_2)X_1 \\ \dot{X}_1 = \mu_1(S_1, S_2)X_1 - DX_1 \\ \dot{S}_2 = k_1\mu_1(S_1, S_2)X_1 - DS_2 - k_2\mu_2(S_2)X_2 \\ \dot{X}_2 = \mu_2(S_2)X_2 - DX_2 \end{cases}$$

- The first organism is inhibited by high concentrations of the product S_2
- Therefore, the extent to which the substrate S_1 is degraded by the organism X_1 depends on the efficiency of the removal of the product S_2 by the bacteria X_2

THE MATHEMATICAL ANALYSIS OF A SYNTROPHIC RELATIONSHIP BETWEEN TWO MICROBIAL SPECIES IN A CHEMOSTAT

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(Communicated by Patrick de Leenheer)

Mutualism

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Vol. 3, No. 6, November 2009, 635–647



Association between competition and obligate mutualism in a chemostat

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11100 Narbonne, France

Synthropy

Math. Model. Nat. Phenom. 13 (2018) 31
<https://doi.org/10.1051/mmnp/2018037>

Mathematical Modelling of Natural Phenomena
www.mmnp-journal.org

STEADY STATE ANALYSIS OF A SYNTROPHIC MODEL: THE EFFECT OF A NEW INPUT SUBSTRATE CONCENTRATION

Y. DAOUD^{1,2,*}, N. ABDELLATIF^{1,5}, T. SARI^{3,6} AND J. HARMAND⁴

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Coexistence of species

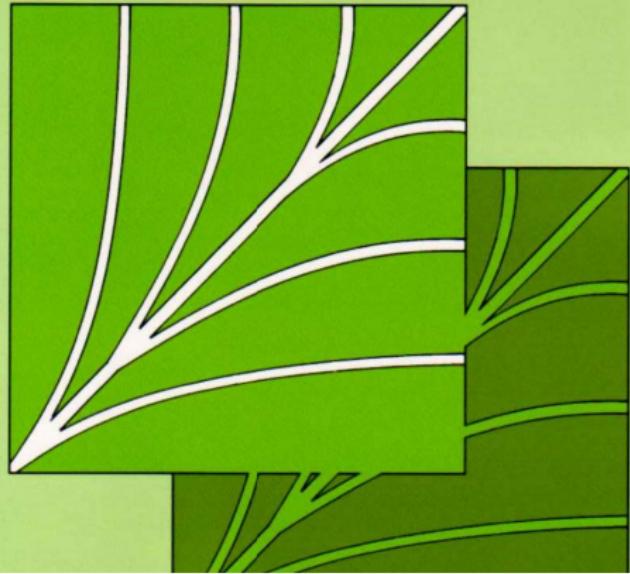
- Periodic inputs
- Prey-predator interactions (PhD of T. Mtar)
- Delays (PhD of H. Berhoune)
- More complex interactions (PhD of S. Nouaoura)

Hal L. Smith and Paul Waltman

Cambridge Studies in Mathematical Biology

The Theory of the Chemostat

Dynamics of Microbial Competition





CHÉMOSTAT ET BIOPROCÉDÉS

Série coordonnée par Claude Lobry

Inventé par J. Monod, et indépendamment par A. Novick et L. Szilard en 1950, le chémostat est à la fois un dispositif de laboratoire de culture en continu de micro-organismes et une abstraction d'écosystème traversé par un flux nutritif.

Cet ouvrage est consacré à l'étude des modèles mathématiques de croissance d'une espèce isolée ainsi que des modèles de compétition de plusieurs espèces. Il intègre des travaux récents d'écologie théorique et de dynamique des populations. À travers une démarche modélisatrice, les hypothèses et les conclusions des principaux résultats mathématiques sont analysées et interprétées sous un angle critique. Une très large place est faite aux simulations numériques dont l'usage raisonné est préconisé.

Le chémostat s'adresse aux personnes possédant des prérequis mathématiques généraux équivalents à ceux d'une première année d'école d'ingénieur ou d'une licence de sciences. Une annexe détaillée sur les équations différentielles présente les notions et résultats spécifiques utilisés dans cet ouvrage.

Les auteurs

Jérôme Harmand est chercheur au Laboratoire de Biotechnologie de l'Environnement de l'Institut National de la Recherche Agronomique à Narbonne. Habilité à diriger des recherches en automatique, il travaille sur la modélisation et le contrôle des écosystèmes microbiens et des bioprocédés, notamment pour le traitement de l'eau et des déchets et pour leur valorisation.

Claude Lobry, a soutenu une thèse à l'Université de Grenoble en « théorie mathématique des systèmes ». Professeur à Bordeaux puis Nice, ses recherches portent sur l'automatique (systèmes non linéaires), les équations différentielles (perturbations singulières) et la dynamique des populations.

Alain Rapaport est chercheur au Département de Mathématiques et Informatique Appliquées de l'Inra, habilité à diriger des recherches en mathématiques appliquées. Il travaille notamment sur la modélisation et l'optimisation des bioprocédés et met au point des lois de commande. Le modèle du chémostat et ses dérivés sont essentiels dans ses recherches.

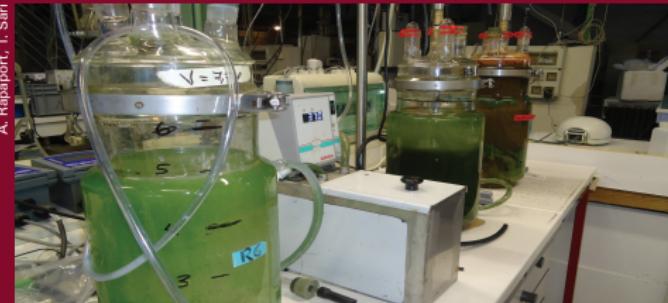
Tewfik Sari est docteur d'Etat en mathématiques. Il a été professeur dans les Universités de Sidi Bel Abbès et de Mulhouse. Il est depuis 2011 directeur de recherche à Irstea. Ses recherches portent sur les systèmes dynamiques et les biomathématiques.

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References

- B. Haegeman, C. Lobry and J. Harmand, Modeling bacteria flocculation as density-dependent growth, *AICHE J.*, **53** (2007), 535–539.
- B. Haegeman and A. Rapaport, How flocculation can explain coexistence in the chemostat, *J. Biol. Dyn.*, **2** (2008), 1–13.
- J. Harmand and J. J. Godon, Density-dependent kinetics models for a simple description of complex phenomena in macroscopic mass-balance modeling of bioreactors. *Ecological Modelling* 200 (2007) 393–402
- J. Harmand, A. Rapaport, D. Dochain and C. Lobry, Microbial ecology and bioprocess control: Opportunities and challenges, *Journal of Process Control*, **18** (2008), 865–875.
- C. Lobry and J. Harmand, A new hypothesis to explain the coexistence of n species in the presence of a single resource, *C. R. Biol.*, **329** (2006), 40–46.
- C. Lobry and F. Mazenc, Effect on persistence of intra-specific competition in competition models, *Electron. J. Diff. Eqns.*, **125** (2007), 1–10.

References

- C. Lobry, F. Mazenc and A. Rapaport, Persistence in ecological models of competition for a single resource, *C. R. Acad. Sci. Paris, Ser. I*, **340** (2005), 199–204.
- C. Lobry, A. Rapaport and F. Mazenc, Sur un modèle densité-dépendant de compétition pour une ressource, *C. R. Biol.*, **329** (2006), 63–70.
- T. Sari, A Lyapunov function for the chemostat with variable yields, *C. R. Math. Acad. Sci. Paris*, **348**, (2010), 747–751 .
- T. Sari, Competitive Exclusion for Chemostat Equations with Variable Yields, *Acta Appl. Math.*, **123** (1), 2013, 201–219.
- T. Sari and F. Mazenc, Global dynamics of the chemostat with different removal rates and variable yields, *Math. Biosci. Eng.*, **8** (2011), 827–840.

References

- M. Dellal, M. Lakrib, T. Sari. The operating diagram of a model of two competitors in a chemostat with an external inhibitor. *Math. Biosci.*, 302 (2018), 27-45.
- B. Bar, T. Sari. The operating diagram for a model of competition in a chemostat with an external lethal inhibitor. *Discrete & Continuous Dynamical Systems - B* (2019), doi: 10.3934/dcdsb.2019203
- R. E. Lenski and S. Hattingh (1986). Coexistence of two competitors on one resource and one inhibitor: a chemostat model based on bacteria and antibiotics, *Journal of Theoretical Biology*, 122, 83-93.
- S. B. Hsu and P. Waltman (1991). Analysis of a model of two competitors in a chemostat with an external inhibitor, *SIAM Journal on Applied Mathematics*, 52, 528-540.
- H. L. Smith and P. Waltman (1995). *The theory of the chemostat: Dynamics of microbial competition*, Cambridge University Press, Cambridge (new edition 2008).
- S. B. Hsu and P. Waltman (2004). A survey of mathematical models of competition with an inhibitor, *Mathematical Biosciences*, 187, 53-91.