

Competition in the chemostat with an external inhibitor

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ICBS2018 : International Conference on Biomathematics in Senegal

Ecole Polytechnique de Thiès, 2018, June 29-July 01



Summary

① Competition of species in the chemostat

- The chemostat

- Maintenance

- Operating diagram

- Competitive exclusion Principle

② Competition in the chemostat with an inhibitor

- External inhibitor

- Operating diagram

- External lethal inhibitor

- Operating diagram

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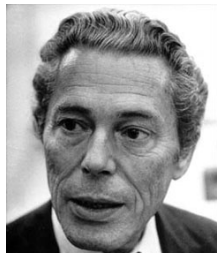
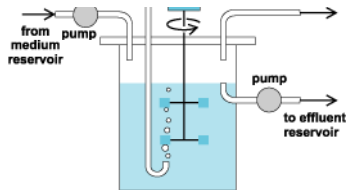
Operating diagram



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

$$\begin{cases} \dot{S} = D(S^{in} - S) - \frac{1}{Y}\mu(S)X \\ \dot{X} = -DX + \mu(S)X \end{cases}$$

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



Steady states

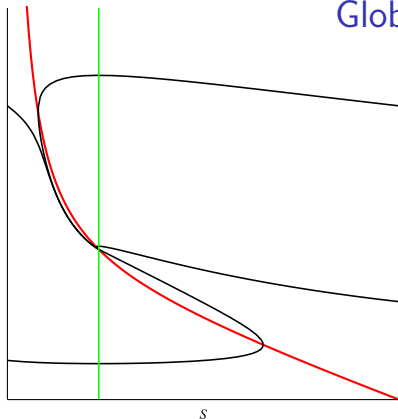
$$\begin{cases} \dot{S} = D(S_{in} - S) - \frac{1}{Y}\mu(S)X \\ \dot{X} = (\mu(S) - D)X \end{cases}$$

- $\mu(S)$ is increasing. Example: Monod function $\mu(S) = \frac{\mu_{max}S}{K+S}$
- $E_0 = (S_{in}, 0)$ (washout) always exists
- $E_1 = (S^*, X^*)$ with $\mu(S^*) = D$ and $X^* = Y(S_{in} - S^*)$ which exists if and only if $S_{in} > S^* \iff \mu(S_{in}) > D$

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

The stability is global (in the positive cone)

Global Stability



Isoclines

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

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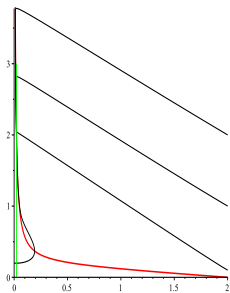
Operating diagram

Maintenance

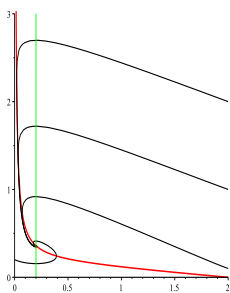
$$\begin{cases} \dot{S} = D(S_{in} - S) - \mu(S)\frac{x}{Y} \\ \dot{x} = (\mu(S) - m - D)x \end{cases}$$

- $\mu(S)$ is increasing
- $\mu(S) = D + m \implies S = S^*$
- $x = x^* = \frac{YD}{D+m}(S_{in} - S^*)$
- The steady state $E^* = (S^*, x^*)$ is stable (GAS) as long as it exists
- Oscillations may occur

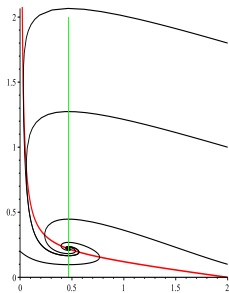
Stables oscillations



$m = 0$



$m = 0.4$



$m = 0.6$

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

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

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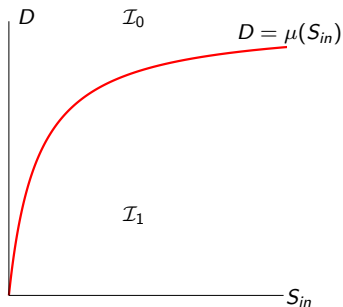
$$\begin{cases} \dot{S} = D(S_{in} - S) - k\mu(S)X \\ \dot{X} = -DX + \mu(S)X \end{cases}$$

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: $\mu(S)$ increasing

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

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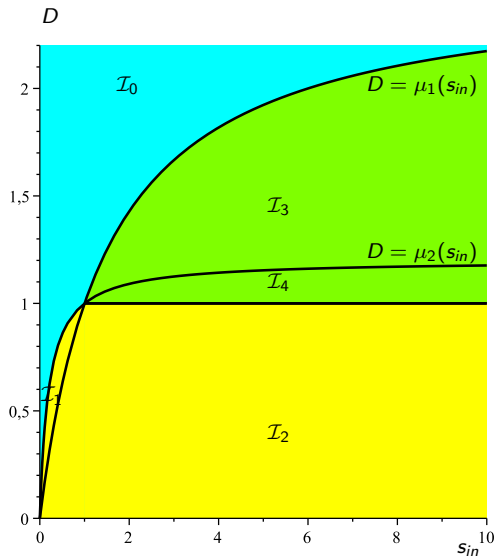
Operating diagram

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 stable (GAS).
- At equilibrium, only one species can survive (Competitive Exclusion Principle)
- The result is true for $n > 2$ competing species

Operating diagram



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

Different removal rates

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

$$D_i = \alpha_i D + m_i, \quad i = 1, 2, \quad (0 \leq \alpha_i \leq 1, \quad m_i \geq 0)$$

- Break-even concentrations : $\lambda_i = \mu_i^{-1}(D_i)$
- $E_0 = (S = S_{in}, x_1 = 0, x_2 = 0)$
- $E_1 = (S = \lambda_1, x_1 = \frac{D}{D_1}(S_{in} - \lambda_1), x_2 = 0)$
- $E_2 = (S = \lambda_2, x_1 = 0, x_2 = \frac{D}{D_2}(S_{in} - \lambda_2))$
- If $\lambda_1 < \lambda_2$ then E_1 is stable and E_2 is unstable.
- **Open problem : LAS \Rightarrow GAS ?**
- If $\mu_i(S) = \frac{m_i}{K_i + S}$ are Monod then E_1 is GAS (Hsu 1978)

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. A 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 Abbes 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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Série Chémostat et bioprocédés

J. Harmand, C. Lobry
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Volume 1

Le chémostat

*théorie mathématique de
la culture continue de micro-organismes*

**Jérôme Harmand, Claude Lobry
Alain Rapaport et Tewfik Sari**

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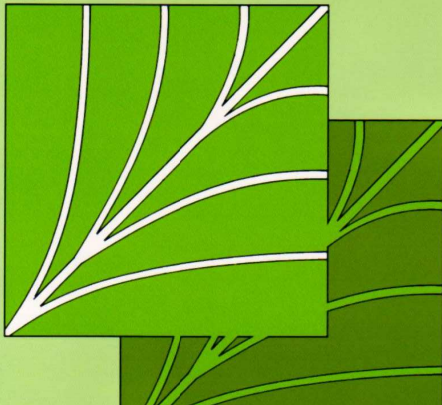
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Hal L. Smith and Paul Waltman

Cambridge Studies in Mathematical Biology

The Theory of the Chemostat

Dynamics of Microbial Competition



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External lethal inhibitor

Operating diagram

Joint work with Dellal and Lakrib

PhD of Mohammed Dellal coadvised with Mustapha Lakrib
(December 2018, Sidi Bel Abbes, Algeria)

R. E. Lenski and S. Hattingh (1986)

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

H. L. Smith and P. Waltman (1995)

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

M. Dellal, M. Lakrib and T. S. (2018)



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

Mohamed Dellal^{a,b}, Mustapha Lakrib^b, Tewfik Sari^c

^a Université des Etudiants, Tlemcen 14000, Algérie

^b Laboratoire de Mathématiques, Université Djillali Liabli, Sidi Bel Abbes 22000, Algérie

^c IRAM, Inrae, Montpellier SupAgro, University of Montpellier, Montpellier, France

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	$\lambda^- < \lambda_2 < \min(\lambda^+, S^0)$	$(A+B)(A+B+C)C > BEF$

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

$$A = f(p_c)f_1'(\lambda_2)x_c, \quad B = f_2'(\lambda_2)y_c, \quad C = 1 + g'(p_c)y_c$$

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

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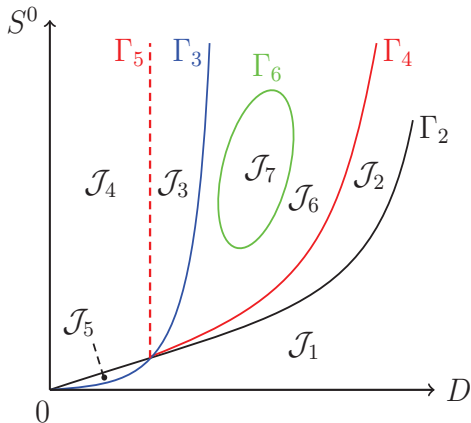
External inhibitor

Operating diagram

External lethal inhibitor

Operating diagram

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

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

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

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

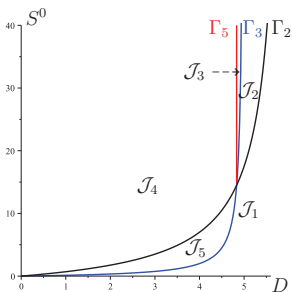
S. B. Hsu and P. Waltman (1991, 2004).

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.

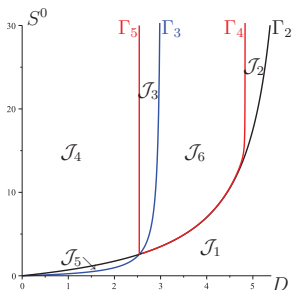
Operating diagram: $p^0 = 0$



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.

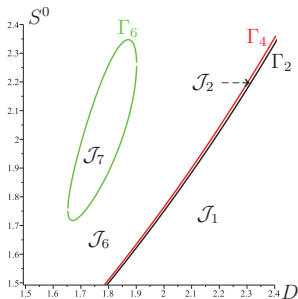
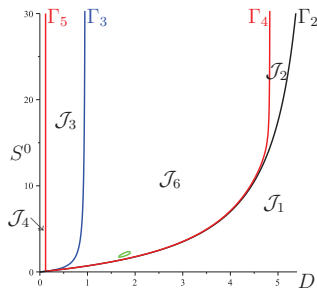
Operating diagram: $p^0 = 0.1$



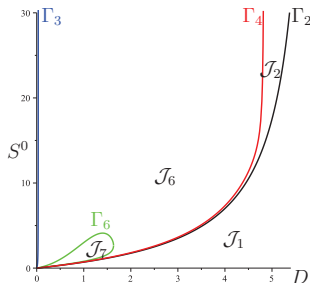
Regions	E_0	E_1	E_2	E_c
\mathcal{J}_1	S			
\mathcal{J}_2	U		S	
\mathcal{J}_3	U	U	U	S
\mathcal{J}_4	U	S	U	
\mathcal{J}_5	U	S		
\mathcal{J}_6	U		U	S

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

Operating diagram: $p^0 = 0.33$



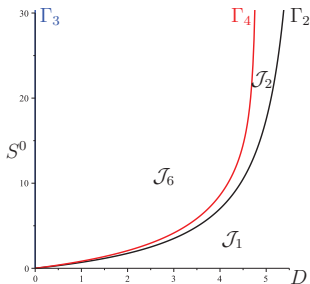
Operating diagram: $p^0 = 1$



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}_6	U		U	S
\mathcal{J}_7	U		U	U

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

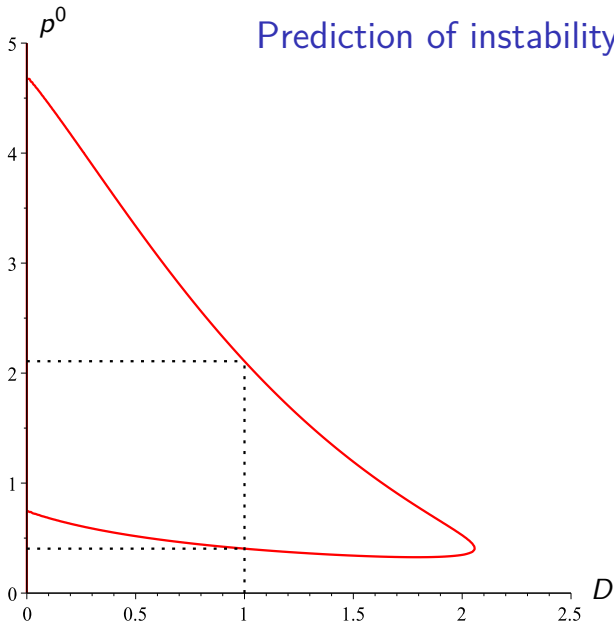
Operating diagram: $p^0 = 4.72$



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		S	

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

Prediction of instability of E_c



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Joint work with Bar and Lakrib

PhD of Bachir Bar coadvised with Mustapha Lakrib
(December 2018, Tlemcen, Algeria)

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

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

B. Bar and T. S. (submitted)

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	$\lambda^- < \lambda_2 < \min(\lambda^+, S^0)$	$A_3(A_1A_2 - A_3) > A_1^2A_4$

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

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

Summary

① Competition of species in the chemostat

The chemostat

Maintenance

Operating diagram

Competitive exclusion Principle

② Competition in the chemostat with an inhibitor

External inhibitor

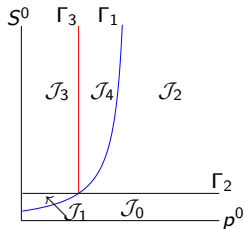
Operating diagram

External lethal inhibitor

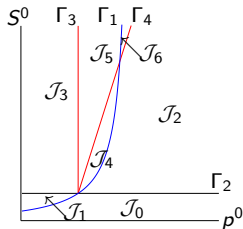
Operating diagram

Operating diagram

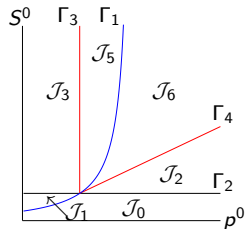
Regions	\mathcal{J}_0	\mathcal{J}_1	\mathcal{J}_2	\mathcal{J}_3	\mathcal{J}_4	\mathcal{J}_5^S	\mathcal{J}_5^U	\mathcal{J}_6^S	\mathcal{J}_6^U
E_0	S	U	U	U	U	U	U	U	U
E_1		S		S	U	U	U		
E_2			S	U	S	U	U	U	U
E_c						S	U	S	U



$(g = 0)$



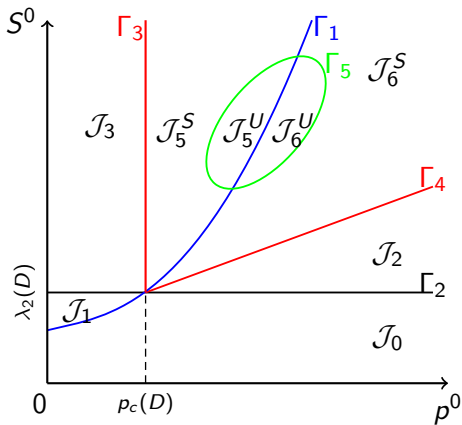
$(g > 0)$



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

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		
E_2			S	U	S	U	U	U	U
E_c						S	U	S	U



Application

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

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

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

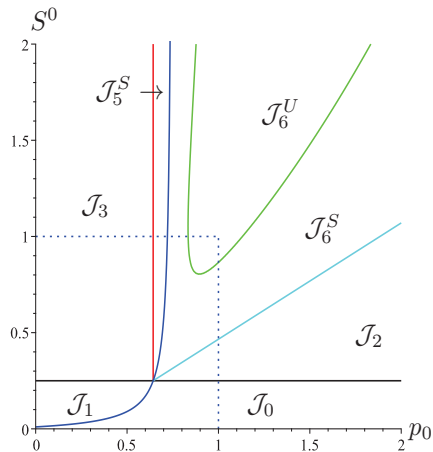
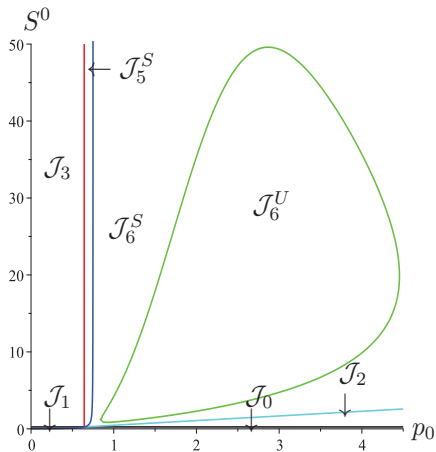
S. B. Hsu, Y.S. Li and P. Waltman (2000)

Studied the stability of steady states,

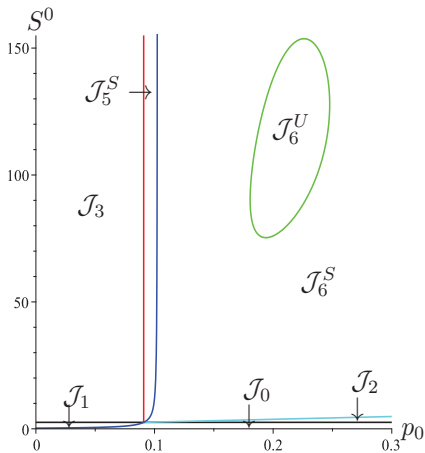
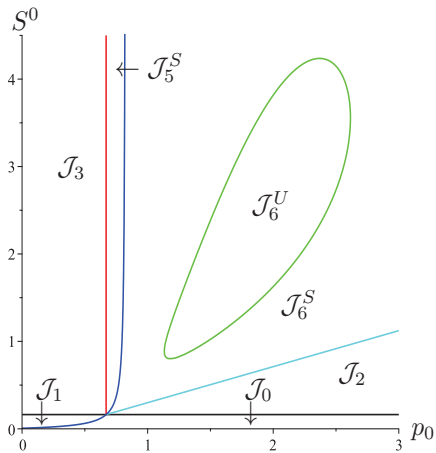
Noticed that the positive steady state E_c can be unstable

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

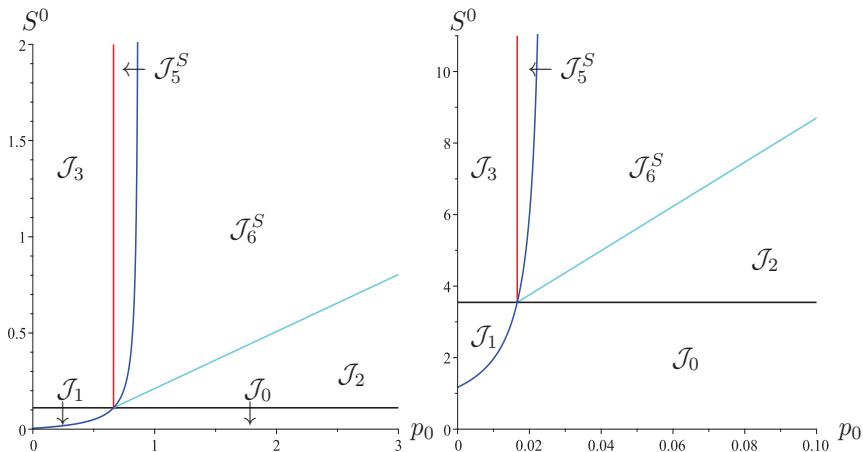
Operating diagram: $D = 1$



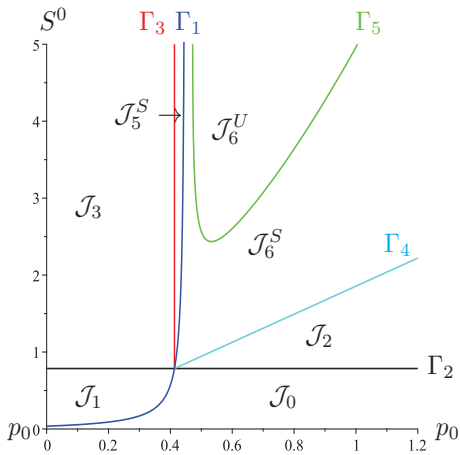
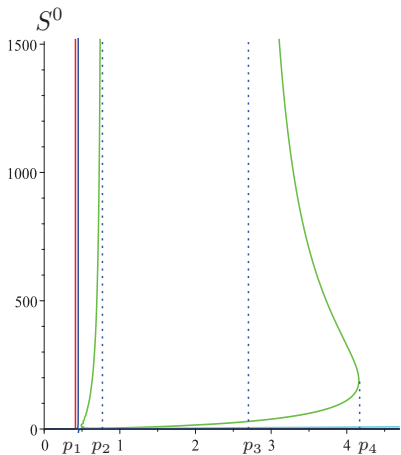
Operating diagram: $D = 0.7, D = 3.59$



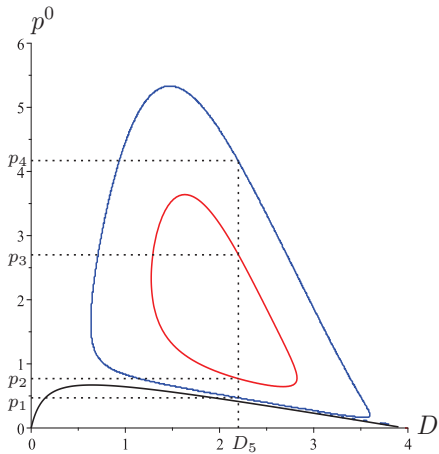
Operating diagram: $D = 0.5, D = 3.9$



Operating diagram: $D = 2.2$



Prediction of instability of E_c



References

- B. Bar, T. Sari (submitted). The operating diagram of a model of competition model in the chemostat with an external lethal inhibitor, submitted.
- M. Dellal, M. Lakrib, T. Sari. The operating diagram of a model of competition model in the chemostat with an external inhibitor. *Mathematical Biosciences*, Available online, 24 May, 2018.
- 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, Y. S. Li, and P. Waltman (2000), Competition in the presence of a lethal external inhibitor, *Mathematical Biosciences*, 167, 177-199.
- 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.
- S. B. Hsu and P. Waltman (2004). A survey of mathematical models of competition with an inhibitor, *Mathematical Biosciences*, 187, 53-91.
- H. L. Smith and P. Waltman (1995, 2008). *The theory of the chemostat: Dynamics of microbial competition*, Cambridge University Press.

Merci pour votre attention

感谢您的关注

Thank you for your attention

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