Mathematical models in biology: The Consumer–Resource relationship

Dynamique collective, systèmes couplés, et applications en biologie/écologie - 10-15/07/2021 - Alger (Algérie)

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July 14, 2021

Summary

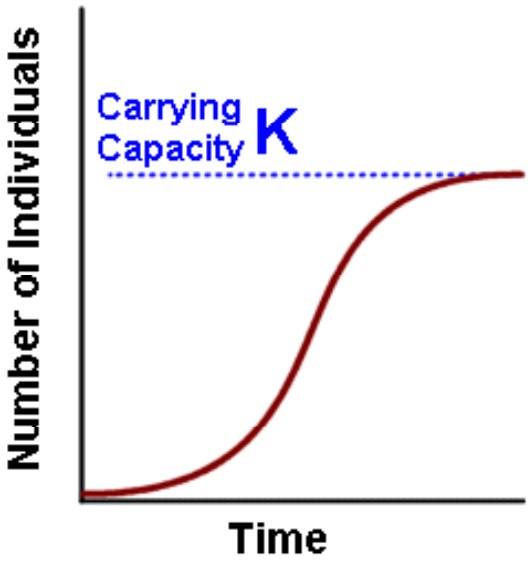
Summary

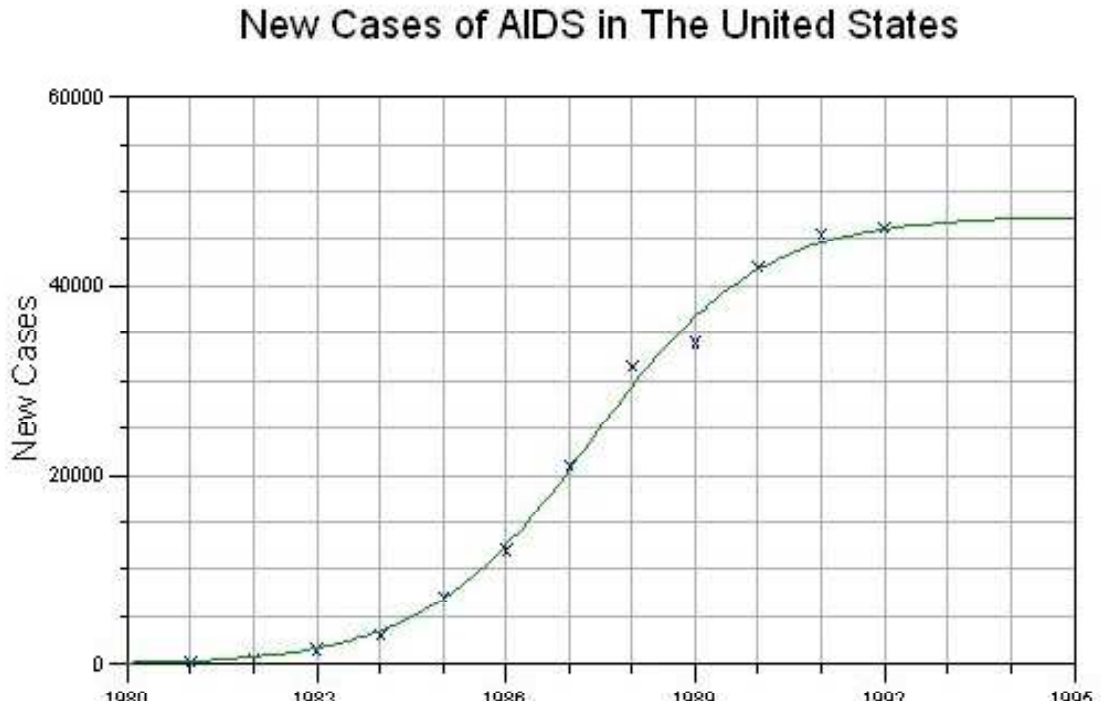
- Croissance exponentielle (Robert Malthus, 1798) :

$$x' = rx$$

- Croissance logistique (François Verhulst, 1832):

$$x' = rx - \alpha x^2 = rx(1 - x/K), \qquad K = r/\alpha$$





- Croissance sur un substrat :

$$x' = kSx, \qquad S' = -\alpha kSx$$

- $S' + \alpha x' = 0 \Longrightarrow S + \alpha x = L = C^{te}$
- On remplace S par $S = L - \alpha x$ dans $x' = kSx$. On obtient

$$x' = k(L - \alpha x)x$$

- On retrouve l'équation logistique

$$x' = kLx - k\alpha x^2 = rx(1 - x/K)$$

avec $r = kL$ et $K = L/\alpha$

AN

ESSAY

ON THE

PRINCIPLE OF POPULATION,

AS IT AFFECTS

THE FUTURE IMPROVEMENT OF SOCIETY.

WITH REMARKS

ON THE SPECULATIONS OF MR. GODWIN,

M. CONDORCET,

AND OTHER WRITERS.

LONDON:

PRINTED FOR J. JOHNSON, IN ST. PAUL'S CHURCH-YARD.

1798.

Thomas Robert Malthus (1766 - 1834)

Malthus, Thomas R.

Modèle de Malthus: $x' = rx$

- $r > 0 : x(t) = x(0)\mathrm{e}^{rt}$ croissance illimitée
- $r < 0 : x(t) = x(0)\mathrm{e}^{rt}$ décroissance vers 0

Thomas Robert Malthus
An Essay on the Principle of Population,
as it Affects the Future Improvement of Society
with Remarks on the Speculations of Mr. Godwin,
M. Condorcet, and Other Writers.
LONDON, PRINTED FOR J. JOHNSON, IN ST. PAUL'S CHURCH-YARD, 1798.
http://www.econlib.org/library/Malthus/malPop1.html

Pierre François Verhulst (1804-1849)

Pierre-François Verhulst, *Notice sur la loi que la population poursuit dans son accroissement*, Correspondance mathématique et physique, no 10, 1838, p. 113-121

Pierre-François Verhulst, *Recherches mathématiques sur la loi d'accroissement de la population*, Nouveaux Mémoires de l'Académie Royale des Sciences et Belles-Lettres de Bruxelles, no 18, 1845, p. 1-42

Pierre-François Verhulst, *Deuxième mémoire sur la loi d'accroissement de la population*, Mémoires de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique, no 20, 1847, p. 1-32

On sait que le célèbre Malthus a établi comme principe que la population humaine tend à croître en progression géométrique, de manière à se doubler après une certaine période, par exemple , tous les vingt-cinq ans. Cette proposition est incontestable, si l'on fait abstraction de la difficulté toujours croissante de se procurer des subsistances lorsque la population a acquis un certain degré d'agglomération. [...] L'accroissement de la population a nécessairement une limite, ne fût-ce que dans l'étendue du sol indispensable pour le logement de cette population.
Soit p la population : représentons par dp l'accroissement infiniment petit qu'elle reçoit pendant un temps infiniment court dt.

Si la population croissait en progression géométrique, nous aurions l'équation

$$dp/dt = mp.$$

Mais comme la vitesse d'accroissement de la population est retardée par l'augmentation même du nombre des habitants, nous devrons retrancher de mp une fonction inconnue de p de manière que la formule à intégrer deviendra

$$\frac{dp}{dt} = mp - \varphi(p)$$

L'hypothèse la plus simple que l'on puisse faire sur la forme de la fonction φ, est de supposer $\varphi(p) = np^2$.
On obtient

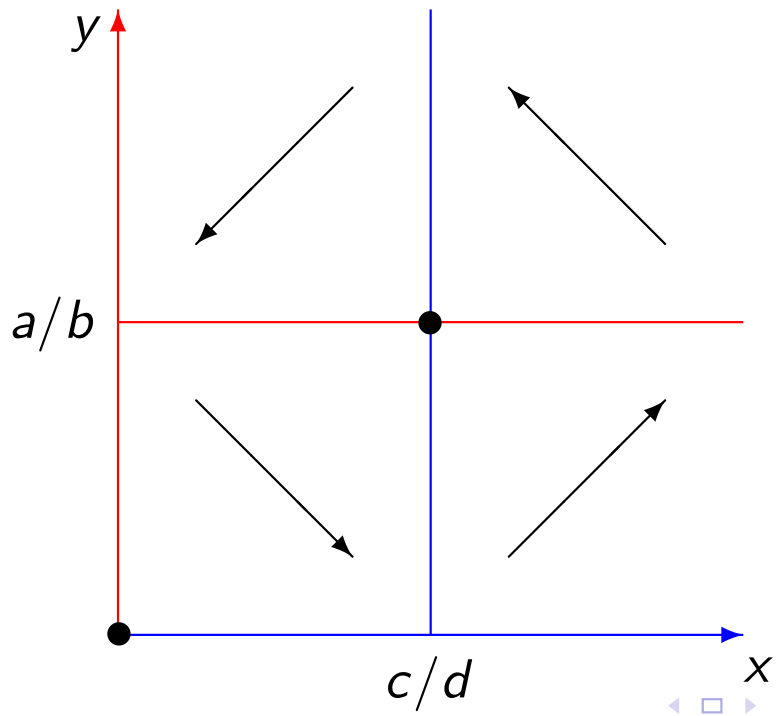
$$\frac{dp}{dt} = mp - np^2$$

Summary

- Modèle de Lotka-Volterra (1925):

$$x' = x(a - by), \qquad y' = y(-c + dx)$$

- Isoclines
  $x' = 0 \iff x = 0$ ou $y = b/a$
  $y' = 0 \iff y = 0$ ou $x = c/d$
- Points d'équilibre



- Première loi de Volterra:

$$x' = x(a - by)$$

$$y' = y(-c + dx)$$

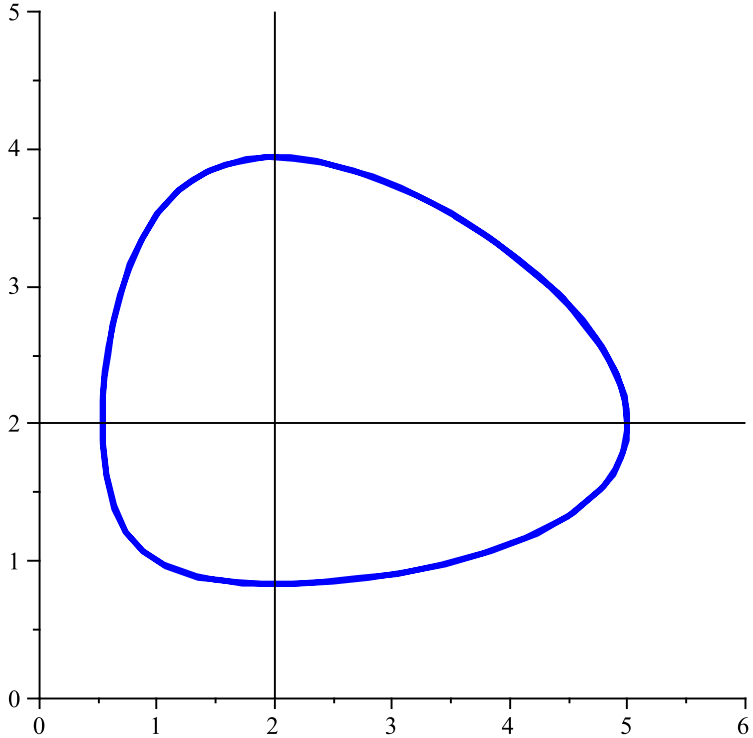
- On a

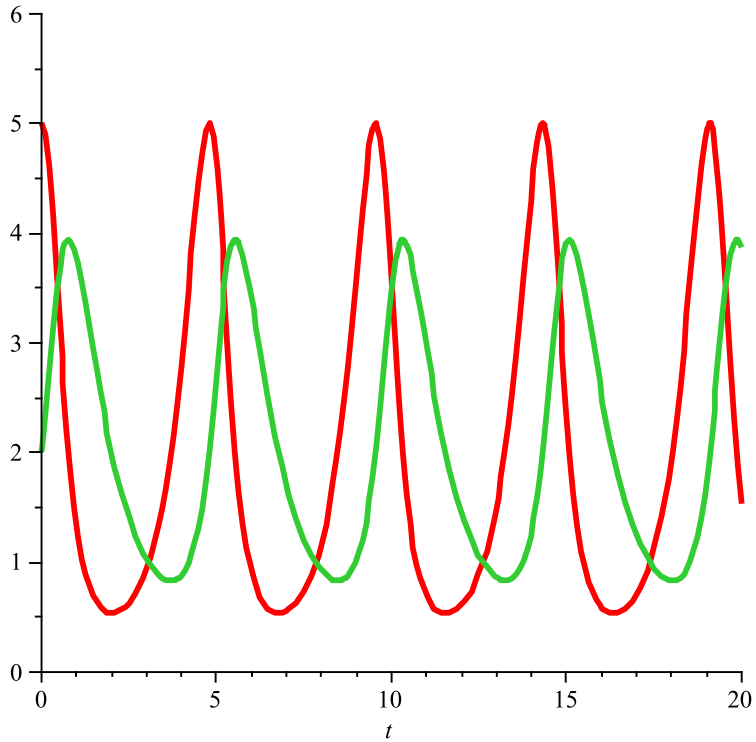
$$\frac{x'(-c + dx)}{x} = \frac{y'(a - by)}{y}$$

- Les solutions sont périodiques

$$c \ln(x) - dx + a \ln(y) - by = C^{te}$$

Première loi de Volterra





- Deuxième loi de Volterra: Soit T la période d'une orbite

$$\frac{x'}{x} = a - by \Longrightarrow [\ln(x(t))]_{t=0}^{T} = aT - b\int_0^T y(t)dt$$

- Comme $[\ln(x(t))]_{t=0}^{T} = 0$, on en déduit $b\int_0^T y(t)dt = aT$
- De même on voit que $d\int_0^T x(t)dt = cT$
- Donc

$$\frac{1}{T}\int_0^T y(t) = \frac{a}{b}, \qquad \frac{1}{T}\int_0^T x(t) = \frac{c}{d}$$

- La valeur moyenne de $x(t)$ est égale à c/d
  La valeur moyenne de $y(t)$ est égale à a/b.

Alfred James Lotka (1880-1949)
Vito Volterra (1860-1940)

A.J. Lotka (1925), *Elements of Physical Biology*

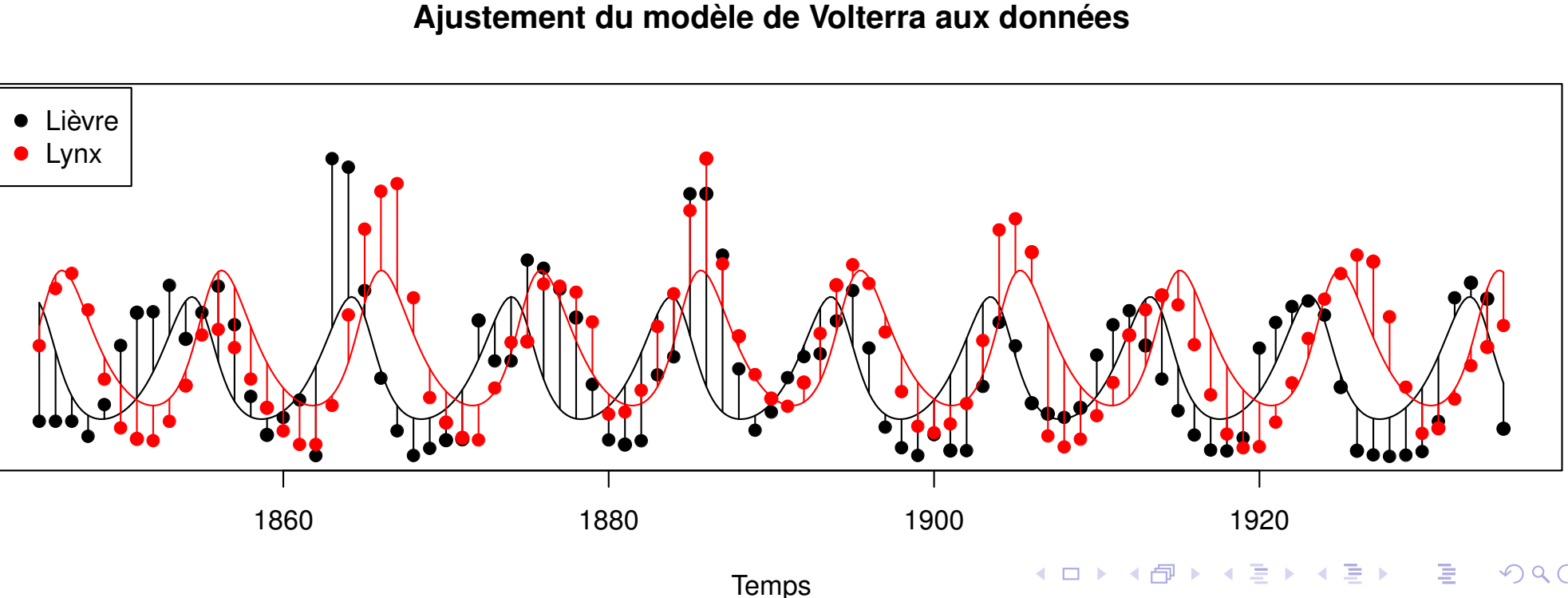
V. Volterra (1926), *Variazioni e fluttuazioni del numero d'individui in specie animai conviventi* Memoria della R. Accademia dei Lincei, 2, 31-113.
Fluctuations in the Abundance of a Species Considered Mathematically, Nature, 118, 558-560.

$x' = x(a - by), \qquad y' = y(-c + dx)$

- x nombre de proies
- y nombre de prédateurs

Confrontations aux données

http://pbil.univ-lyon1.fr/R/enseignement.html
J.R. Lobry, Ajustement du modèle de croissance logistique aux donnees de Verhulst.
J.R. Lobry, Ajustement au modèle de Lotka-Volterra.



Summary

Umberto D'Ancona (1896-1964)

Pendant les dernières années de la Première Guerre Mondiale et les deux ou trois années suivantes, il y avait eu un accroissement important du pourcentage des grands poissons prédateurs pêchés dans les ports de Venise, Trieste et Rijeka

Troisième loi de Volterra

- Les deux populations sont soumises à de la pêche:

$$\begin{array}{l} x' = x(a - by) - kx \\ y' = y(-c + dx) - my \end{array} \Longrightarrow \begin{array}{l} x' = x(a - k - by) \\ y' = y(-c - m + dx) \end{array}$$

- Avant la pêche

$$\frac{1}{T}\int_0^T y(t) = \frac{a}{b}, \qquad \frac{1}{T}\int_0^T x(t) = \frac{c}{d}$$

- Après la pêche

$$\frac{1}{T}\int_0^T y(t) = \frac{a-k}{b} < \frac{a}{b}, \quad \frac{1}{T}\int_0^T x(t) = \frac{c+m}{d} > \frac{c}{d}$$

- Donc la pêche favorise la proie et défavorise le prédateur.

Gestion des bio-agresseurs

En 1886, un parasite du coton, Icerya purchasi, fut introduit par mégarde aux USA. Il ravagea les plantations d'agrumes. On introduisit alors son prédateur naturel australien, la coccinelle Novius cardinalis pour le maintenir à un niveau faible. Plus tard l'utilisation du DDT eut l'effet inverse à celui escompté : le nombre d'Icerya purchasi augmenta. L'explication est simple dans le cadre du modèle de Volterra: l'utilisation du DDT peut être considérée comme une pêche qui conduit à une augmentation du nombre de proies (Icerya purchasi) et une diminution de nombres de prédateurs (Novius cardinalis).

Icerya purchasi et Novius cardinalis

http://www.inra.fr/opie-insectes/illustr/i116couv.htm

Critiques du modèle

Giorgio Israel, La mathématisation du réel, Ed. Seuil, 1996.

Gause (1910-1989), Pearson (1857-1936), Bobenheimer (1897-1959) ont critiqué les statistiques de D'Ancona, qui se range de leur avis et écrit à son beau-père:
[...] je serai bien heureux si l'on pouvait donner des démonstrations expérimentales précises de vos théories mathématiques. [...] Sans doute mes observations sur la pêche dans l'Adriatique du nord devraient donner un soutien plus sûr à vos théories parce qu'elles devraient en démontrer un point essentiel, la troisième loi.

Lettre de U. D'Ancona à V. Volterra

Malheureusement, mes observations statistiques peuvent être aussi interprétées dans un autre sens et Pearson, Bodenheimer et Gause sont de cet avis. Voilà pourquoi moi aussi je dois admettre que ces critiques ont un fondement sérieux. Mes observations peuvent être interpretées dans le sens de votre théorie, mais cela n'est pas un fait absolument indiscutable, il s'agit seulement d'une interprétation. [...] Votre théorie n'est pas le moins du monde touchée par toute cette question.

Lettre de U. D'Ancona à V. Volterra

Il s'agit d'une théorie fondée d'une façon cohérente et vraisemblable et s'accordant avec beaucoup de faits connus et vraisemblables. Elle reste donc une hypothèse de travail qui peut être la source de nouvelles recherches et qui subsiste même si elle n'est pas appuyée sur des preuves empiriques. Il est hors de doute qu'elle peut recevoir une autorité accrue de ces preuves, mais il faut s'assurer quand on les accepte qu'elles soient certaines et démonstratives, sinon il vaut mieux pour vous ne pas lier votre théorie à une base expérimentale qui est sans doute moins solide que la théorie elle-même.

Lettre de U. D'Ancona à V. Volterra

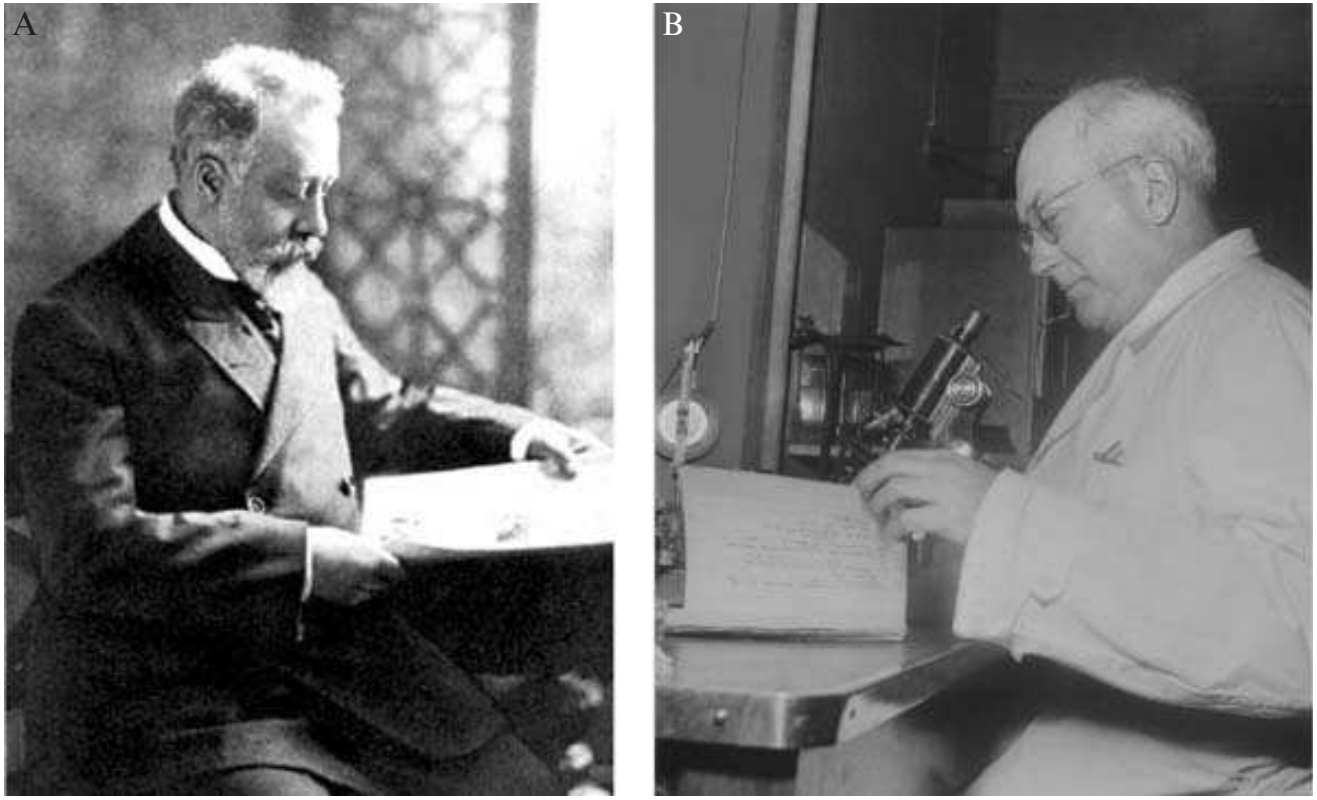
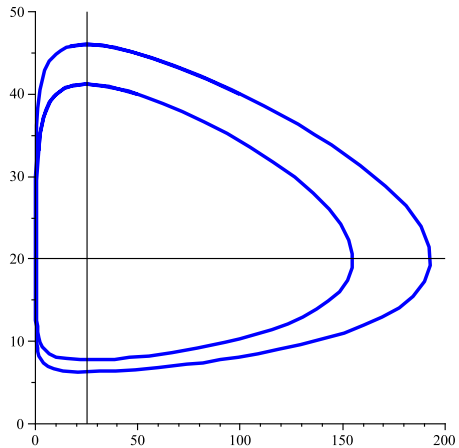
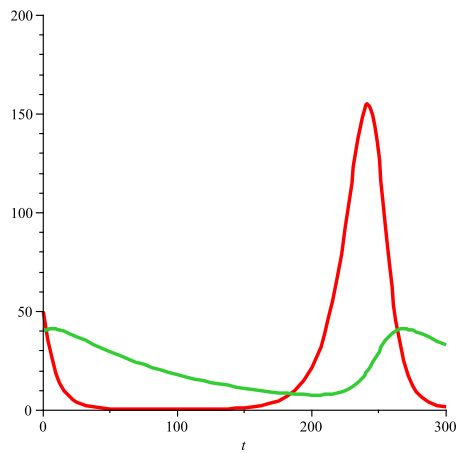


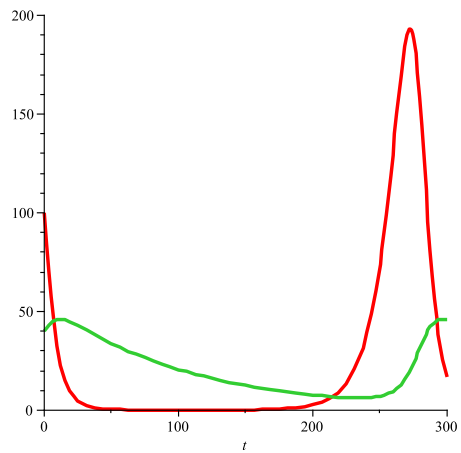
Figure 1. Vito Volterra and Umberto D'Ancona (courtesy of D'Ancona's daughter Claudia).

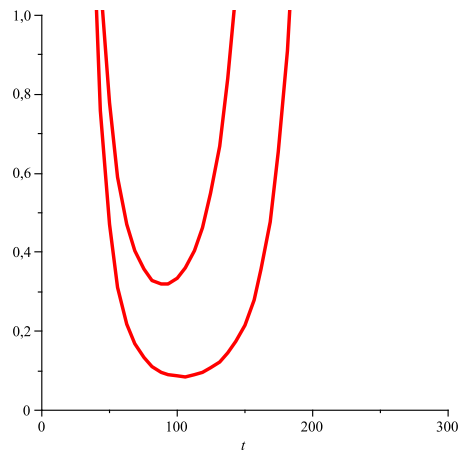
Une autre critique du modèle

$$x' = x(0.1 - 0.005y), \qquad x(0) = 50 \text{ ou } 100$$
$$y' = y(-0.01 + 0.0004y), \qquad y(0) = 40$$

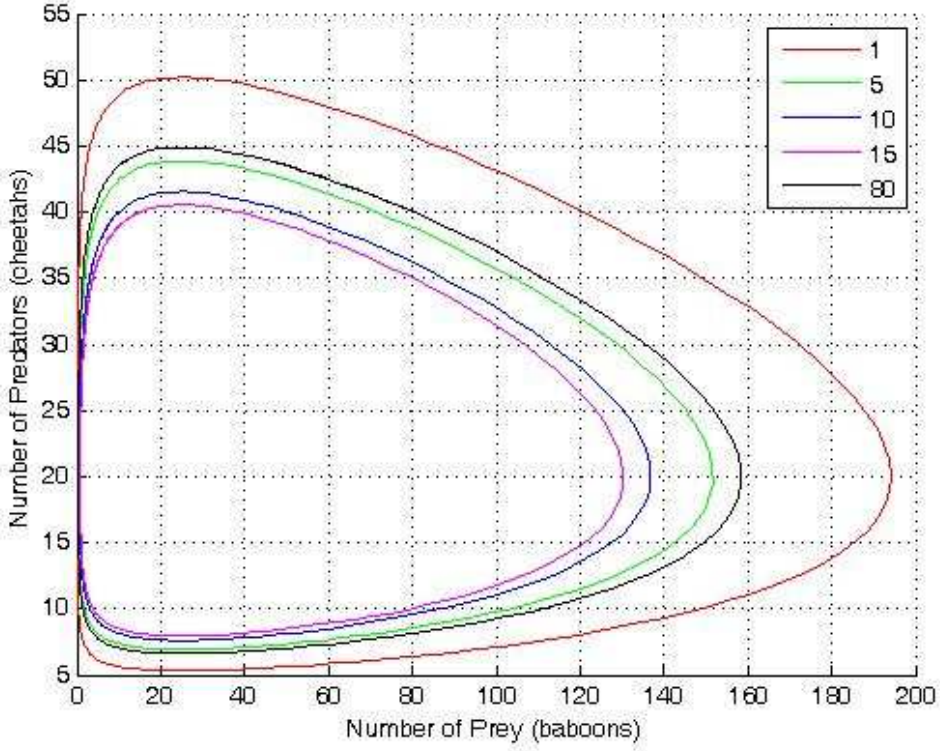


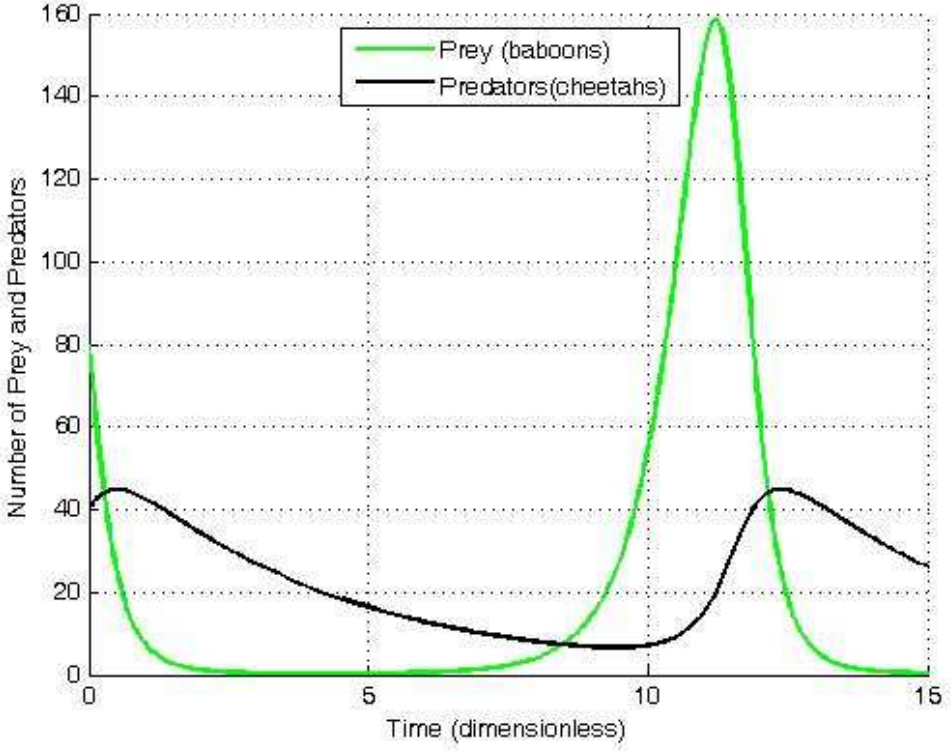






Cheetahs and Baboons





The Atto-fox problem

value zero. Thus the density of infected at the place of origin of the epidemic never becomes zero, it only declines to a minimum of around one atto-fox (10^{-18} of a fox, Hughes 1960) per square kilometre. The model then allows this atto-fox to start the second wave as soon as the susceptible population has regrown sufficiently.

- Lobry, Claude; Sari, Tewfik (2015). "Migrations in the Rosenzweig-MacArthur model and the "atto-fox" problem". Arima. 20: 95–125.
- Mollison, D. (1991). "Dependence of epidemic and population velocities on basic parameters". Math. Biosci. 107 (2): 255–287

The Atto-fox problem

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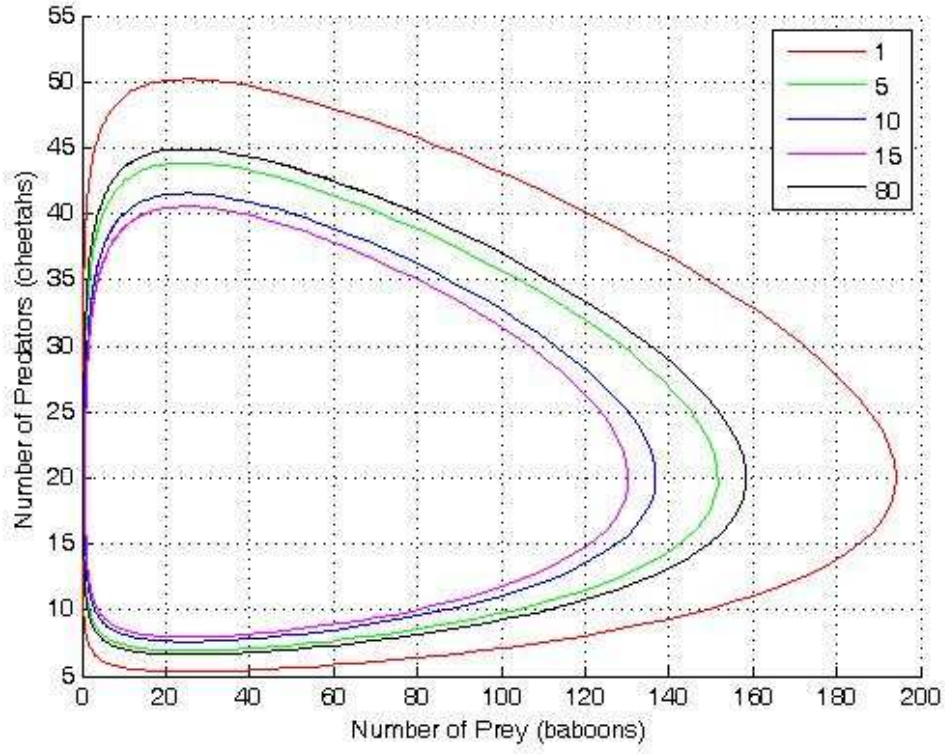

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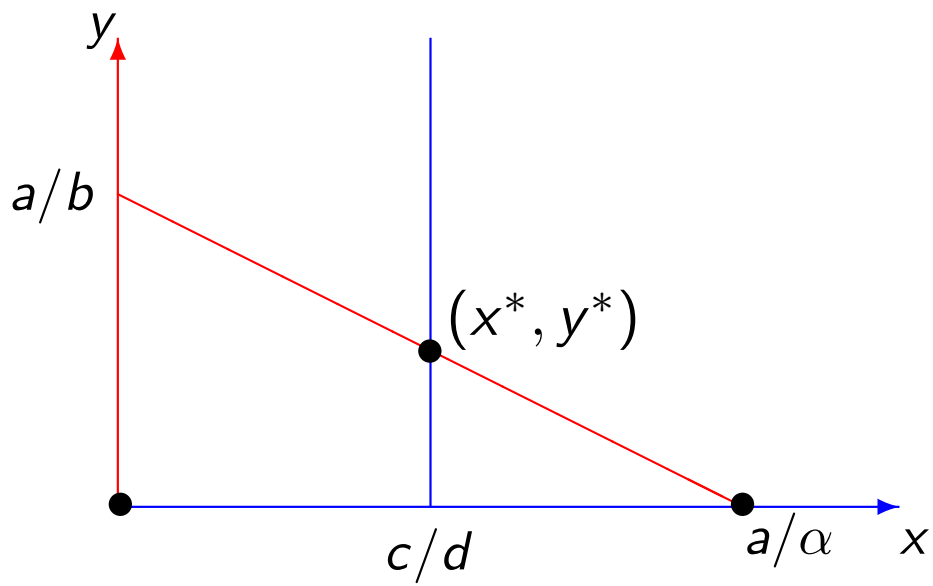
Lotka-Volterra et Atto-fox

- Lotka-Volterra: $x' = ax - bxy, \quad y' = -cy + dxy$
- Points d'équilibre $(0,0)$ and $(c/d, a/b)$
- Linéarisation $A = \begin{pmatrix} a - by & -bx \\ dy & -c + dx \end{pmatrix}$
- En $(0,0)$: $A = \begin{pmatrix} a & 0 \\ 0 & -c \end{pmatrix}$. Les VP sont a et $-c$. L'origine est un point selle.
- En $(c/d, a/b)$: $A = \begin{pmatrix} 0 & -a \\ c & 0 \end{pmatrix}$. Les VP sont imaginaires. On ne peut rien dire sur la nature de l'équilibre.
- L'intégral première $c\ln(x) - dx + a\ln(y) - by = C^{te}$ montre que l'équilibre est un centre.
- Phénomène atto-fox: les solutions s'approchent arbitrairement des axes $x = 0$ et $y = 0$, pour lesquels le modèle n'a pas de sens biologique.

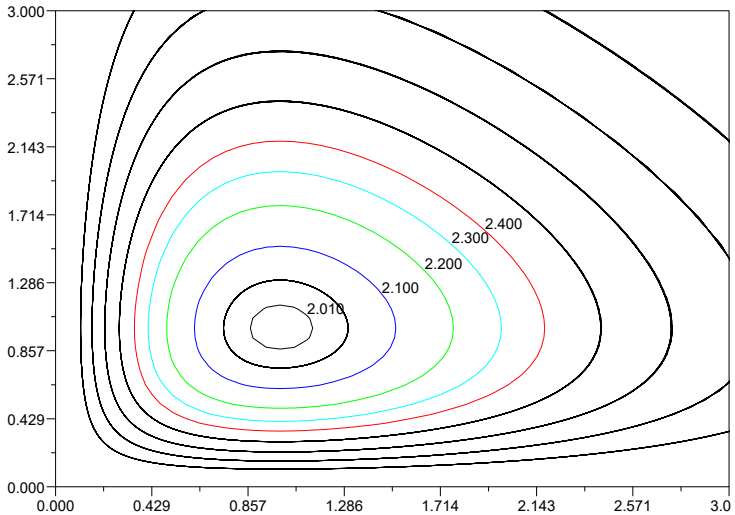
Lotka-Volterra sans Atto-fox

- Lotka-Volterra étendu:
  $x' = ax - \alpha x^2 - bxy, \quad y' = -cy + dxy$
- Isoclines :
  $x' = 0 \Longleftrightarrow x = 0$ ou $a - \alpha x - by = 0$
  $y' = 0 \Longleftrightarrow y = 0$ ou $x = c/d$
- Points d'équilibres: $(0, 0)$, $(a/\alpha, 0)$ et (x^*, y^*)

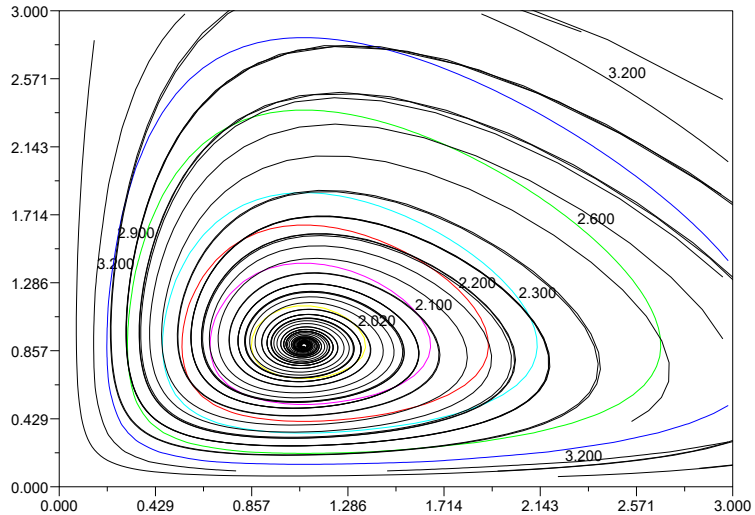


Lotka-Volterra

$\alpha = 0$



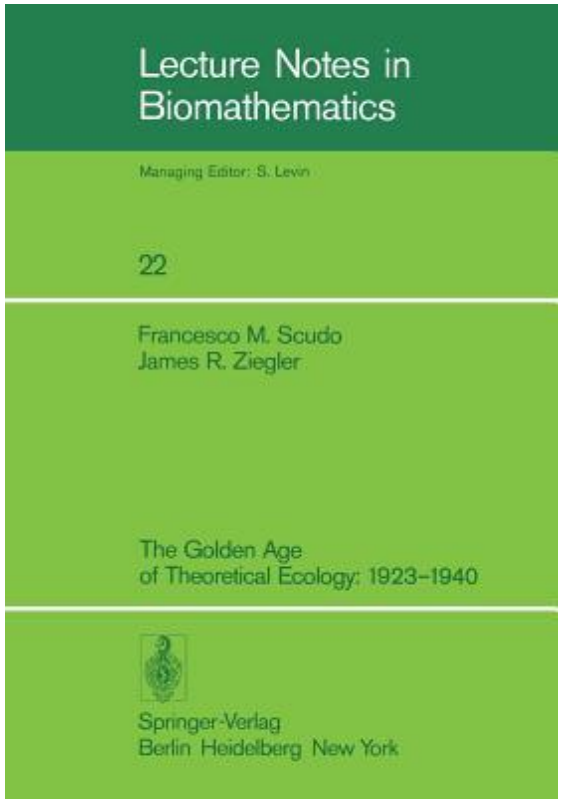
$\alpha > 0$



Summary

The Golden Age of Theoretical Ecology

- Francesco M. Scudo. The "Golden Age" of Theoretical Ecology; A Conceptual Appraisal. Revue européenne des sciences sociales. T. 22, No. 67 (1984), pp. 11-64.
- F.M. Scudo, J.R. Ziegler. The Golden Age of Theoretical Ecology: 1923-1940. Lecture Notes in Biomathematics, Volume 22, Springer-Verlag (1978)



Summary

The Gause model

- Dans le modèle de Lotka-Volterra,

$$x' = ax - bxy, \quad y' = -cy + dxy$$

le terme de prélèvement $-bxy$ est linéaire en la ressource x. Ceci veut dire que si la quantité de ressource double, il en est de même du prélèvement, si elle est multipliée par dix le prélèvement aussi, ce qui n'est pas réaliste. Il y a forcément une limite à la capacité de prélever du consommateur.

- Gause a proposé de remplacer ce terme linéaire par $\mu(x)y$ avec

$$\mu(x) = \begin{cases} \frac{bx}{c+x} & \text{si} \quad x > \alpha \\ 0 & \text{si} \quad x \leq \alpha \end{cases}$$

- On obtient le modèle

$$x' = ax - \mu(x)y, \quad y' = -cy + d\mu(x)y$$

The Gause model

$x' = ax - \mu(x)y$

$y' = -cy + d\mu(x)y$

Système discontinu sur $x = \alpha$

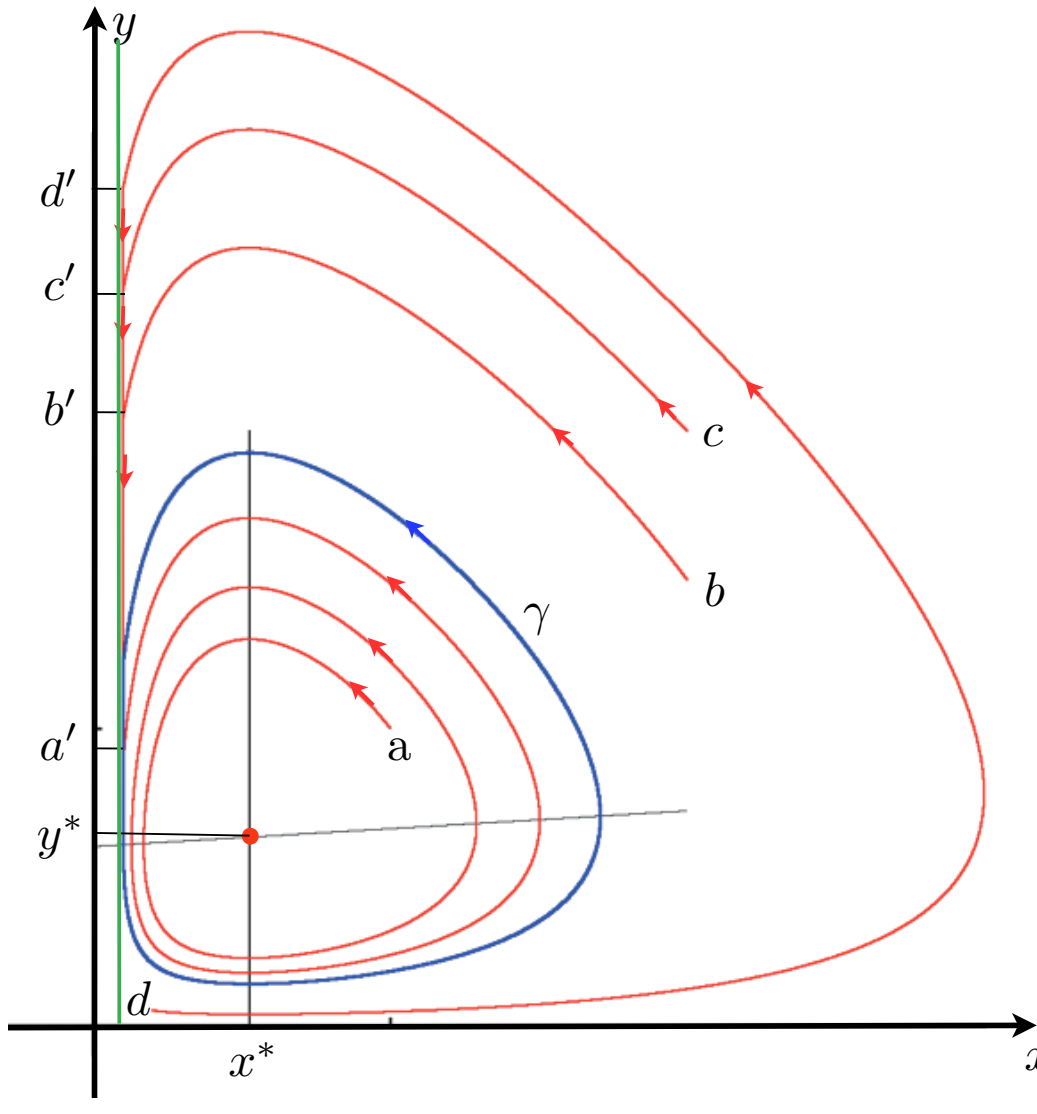
(Théorie de Filippov)

$$x' = 0 \Leftrightarrow \begin{cases} x = 0 \\ \text{ou} \\ y = a(c+x)/b \end{cases}$$

$$y' = 0 \Leftrightarrow \begin{cases} y = 0 \\ \text{ou} \\ bx/(c+x) = c/d \end{cases}$$

Deux points d'équilibre:

$(0,0)$ et (x^*, y^*)



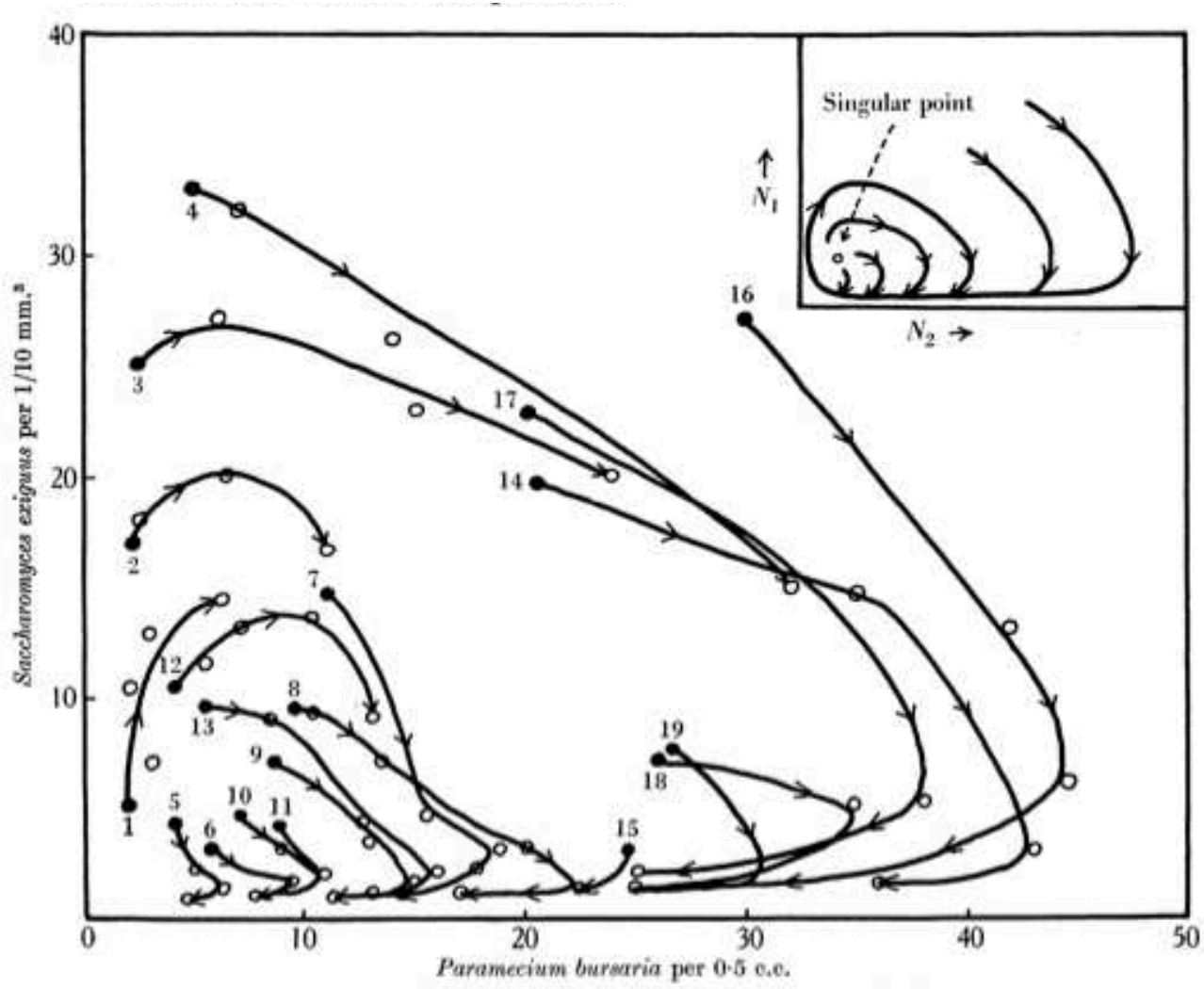


Fig. 4. Interaction between predators (*Paramecium bursaria*) and prey (*Saccharomyces exiguus*).

Gause, G. F., Smaragdova, N. P., Witt, A. A.: Further studies of interaction between predator and prey. J. Anim. Ecol. 5, 1–18 (1936)

Summary

The Rosenzweig-MacArthur model

- On part du modèle de Lotka-Volterra,

$$x' = rx(1 - x/K) - axy, \quad y' = -dy + cxy$$

et on remplcae le terme de prélèvement $-axy$ par un terme de la forme $\mu(x)y$ avec

$$\mu(x) = \frac{ax}{b + x}$$

- Par conséquent le terme de croissance du prédateur cxy doit être remplacé par $(c/a)\mu(x)y$
- On obtient le modèle

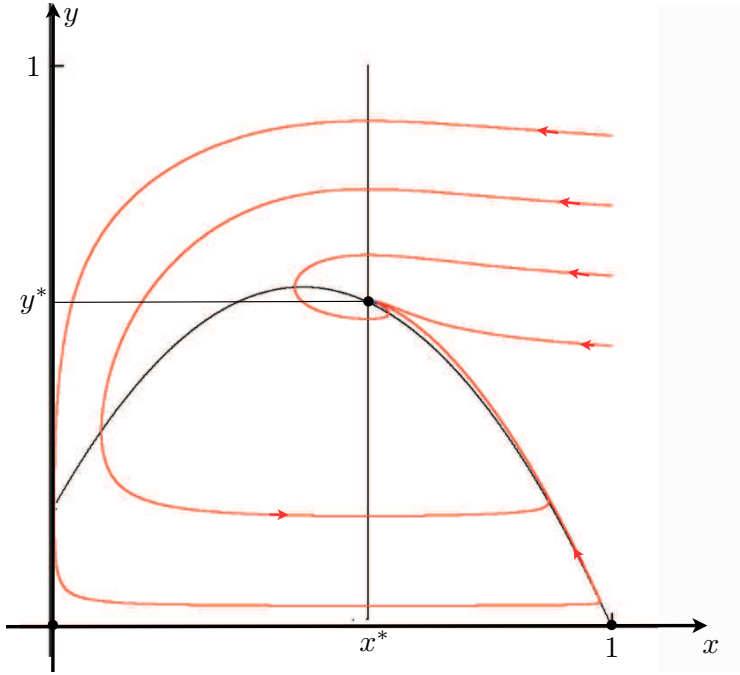
$$x' = rx(1 - x/K) - \frac{ax}{b + x}y, \quad y' = -dy + \frac{cx}{b + x}y$$

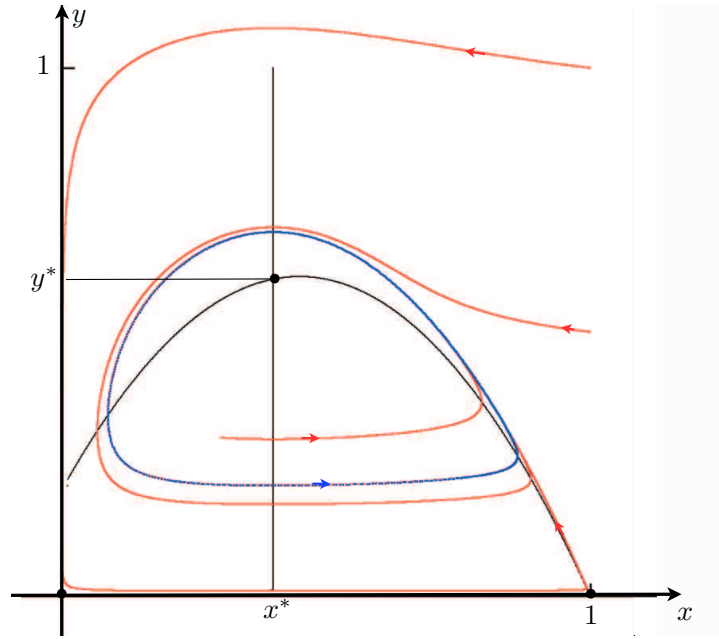
The Rosenzweig-MacArthur model

$$x' = rx(1 - x/K) - \frac{ax}{b+x}y, \quad y' = -dy + \frac{cx}{b+x}y$$

- Isoclines :
  $x' = 0 \Longleftrightarrow x = 0$ ou $y = (r/a)(1 - x/K)(b + x)$
  $y' = 0 \Longleftrightarrow y = 0$ ou $cx/(b + x) = d$
- Points d'équilibres: $(0, 0)$, $(K, 0)$ et (x^*, y^*)

The Rosenzweig-MacArthur model





- $(0,0)$ et $(K,0)$ sont des points selle
- (x^*, y^*) est foyer stable s'il se trouve sur la branche descendante de la parabole.
- (x^*, y^*) est foyer in stable s'il se trouve sur la branche ascendante de la parabole.
- Bifurcation de Poincaré-Andronof-Hopf sur-critique lorsque x^* traverse le sommet de la parabole.

The Rosenzweig-MacArthur model

- On montre que (x^*, y^*) est GAS dès qu'il est sur la branche descendante de la parabole (et donc localement stable)
  - Fonctions de Lyapunov
- On montre qu'il existe un unique cycle limite stable qui entoure l'équilibre (x^*, y^*) est GAS dès qu'il est sur la branche ascendante de la parabole (et donc localement instable)
  - Théorie de Poincaré Bendixon
  - Theorème de Butler-Mc Gehee
  - Indice de stabilité de Poincaré d'un cycle

Rosenzweig MacArthur lent-rapide

$$\begin{aligned} x' &= U(x) - yV(x) \\ y' &= \varepsilon(cV(x) - m)y \end{aligned}$$

$$U(x) = rx\left(1 - \frac{x}{K}\right), \qquad V(x) = \frac{ax}{b+x}$$

- Equation rapide $x' = U(x) - yV(x)$.
- Variété lente
  $x = 0$ ou $y = \varphi(x) = \frac{U(x)}{V(x)} = \frac{r}{a}(b+x)(1-x/K)$.
  $x = 0$ est attractive si $y > \varphi(0)$ et repulsive si $0 < y < \varphi(0)$
- Le modèle réduit sur $x = 0$ est $\dot{y} = -my$

Article de Muratory et Rinaldi

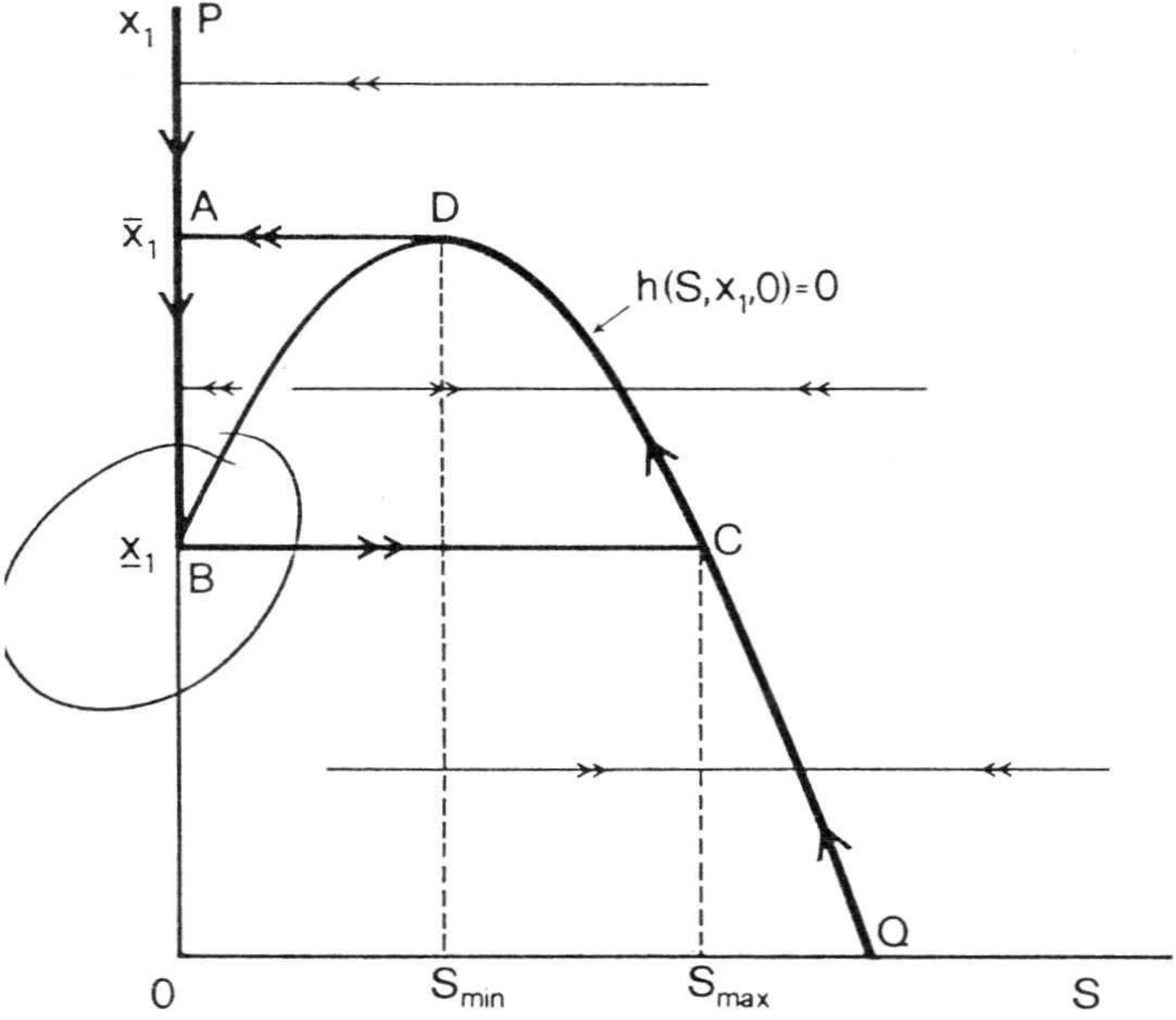
SIAM J. APPL. MATH.
Vol. 49, No. 5, pp. 1462-1472, October 1989

011

REMARKS ON COMPETITIVE COEXISTENCE*

SIMONA MURATORI† AND SERGIO RINALDI†

Abstract. The asymptotic behavior of two predators competing exploitatively for the same prey in a constant environment is analyzed in this paper. Assuming that the prey have fast dynamics, it is proved, through a singular perturbation argument, that the two predators can coexist if the prey and predators' parameters lie within specified ranges. It is also shown that coexistence occurs through a simple periodic behavior: a poor season, characterized by an almost endemic presence of the prey, alternates with a rich season, during which prey are abundant and predators regenerate. This property follows from the geometric nature of the equilibrium manifold and is therefore generic. The results are in agreement with some conjectures supported by computer simulation and with the most recent theoretical findings on competitive coexistence.


x_1
P
A
D
$\bar{x}_1$
$h(S,x_1,0)=0$
$\underline{x}_1$
B
C
Q
0
S_{min}
S_{max}
S

Article de Rinaldi et Muratory

Ecological Modelling, 61 (1992) 287–308
Elsevier Science Publishers B.V., Amsterdam

Slow–fast limit cycles in predator–prey models *

S. Rinaldi [a] and S. Muratori [b]

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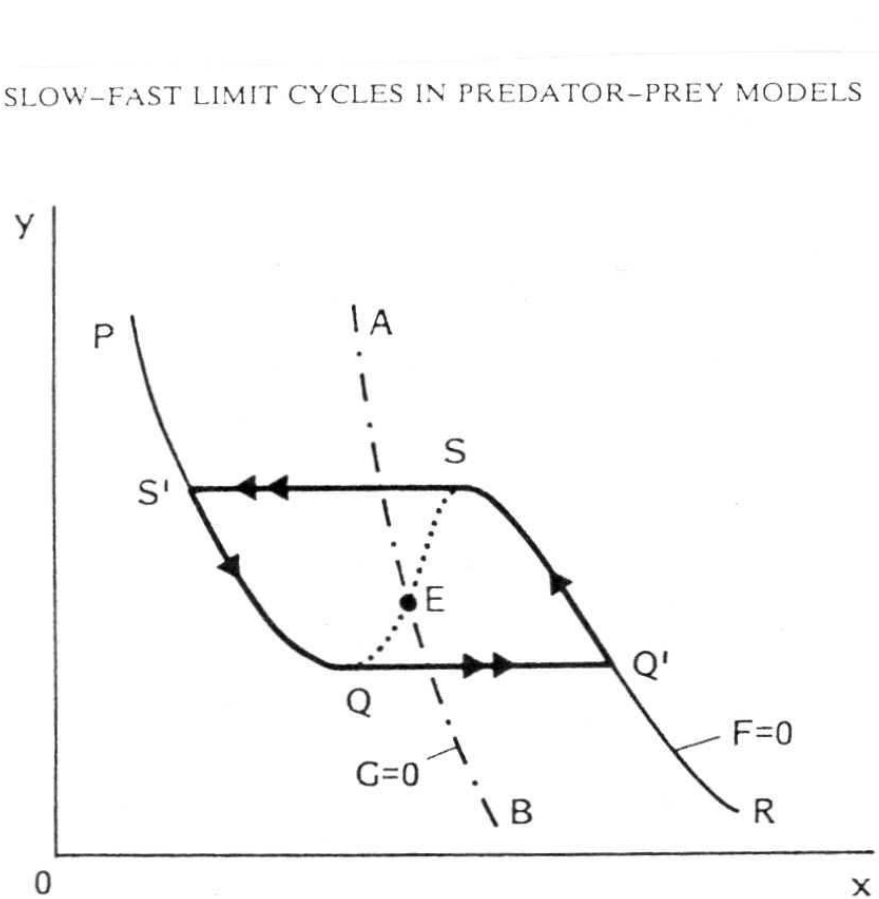
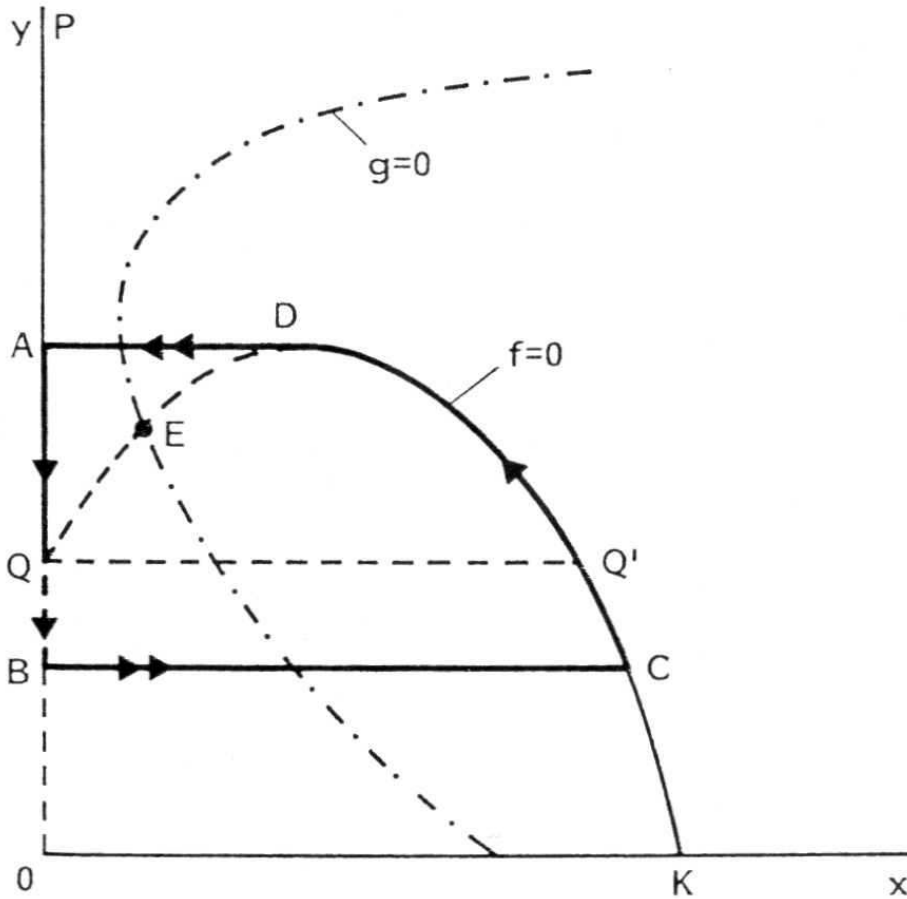
[b] *Centro Teoria dei Sistemi, CNR, Politecnico di Milano, Milano, Italy*

(Accepted 12 November 1991)

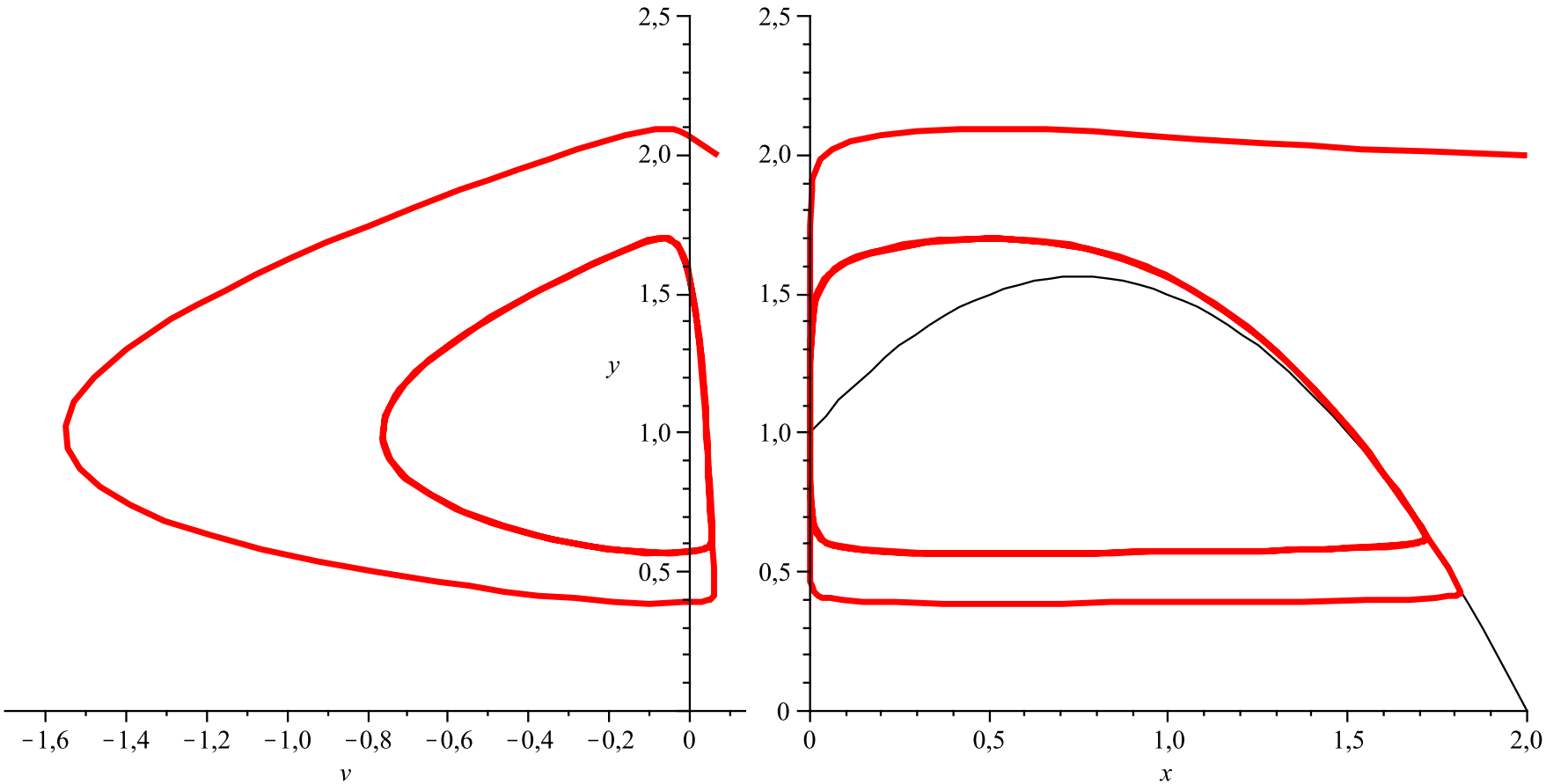
Finally, we briefly discuss the consequences of our results on the geometry of the limit cycles that can be present in food chain systems and forest ecosystems and we revise our theory of competitive coexistence (Muratori and Rinaldi, 1989a), where the problem of slow–fast cycles of predator–prey systems was not yet fully understood.

Rinaldi and Muratory paper

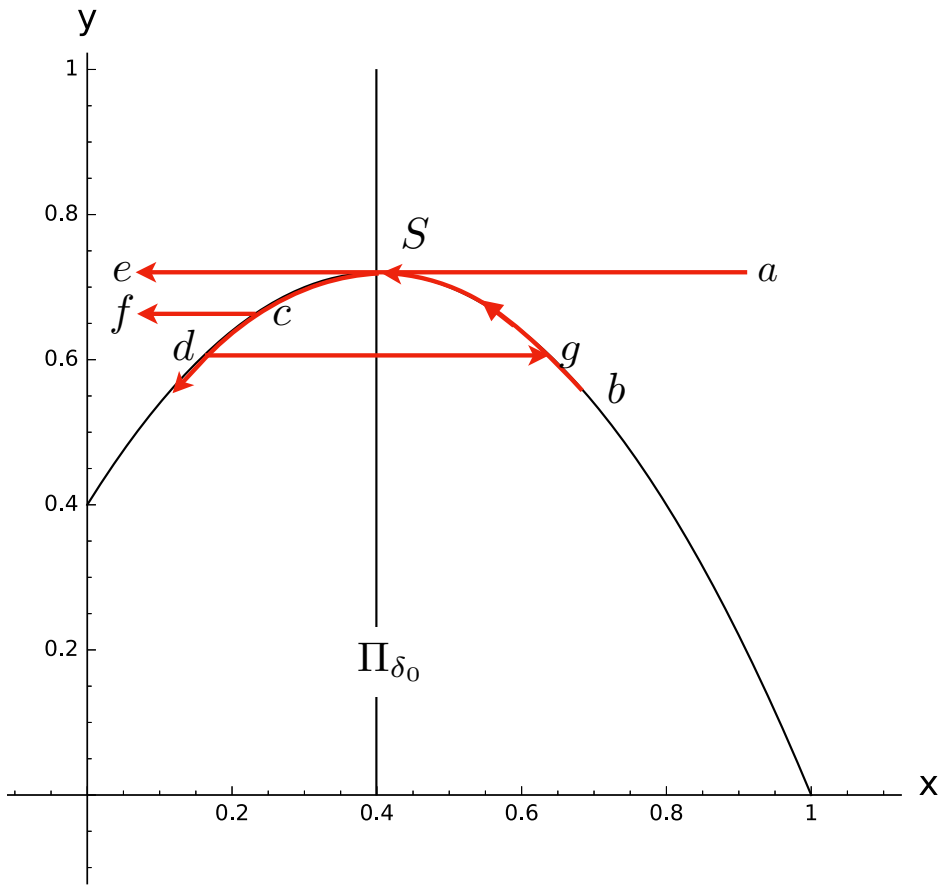




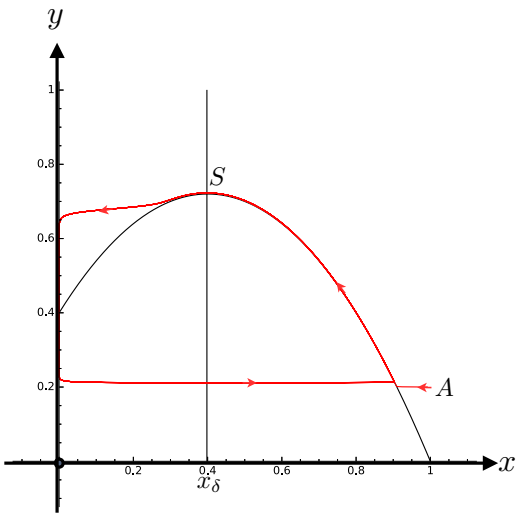
Numerical solution : $\varepsilon = 0.1$



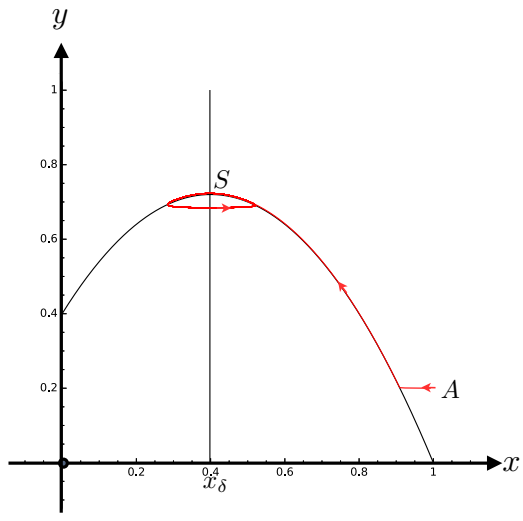
Canards



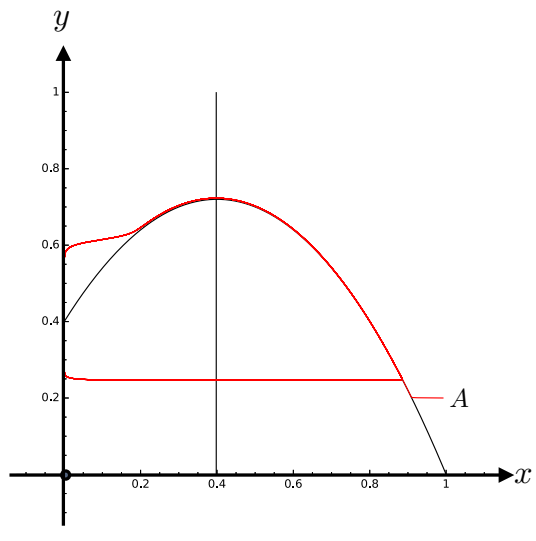
Canards



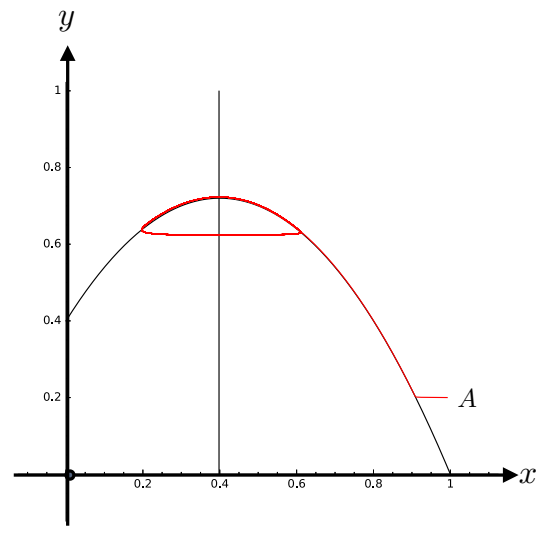
$\delta = 0.66561 \quad x_{min} = 1.49\ 10^{-12}$



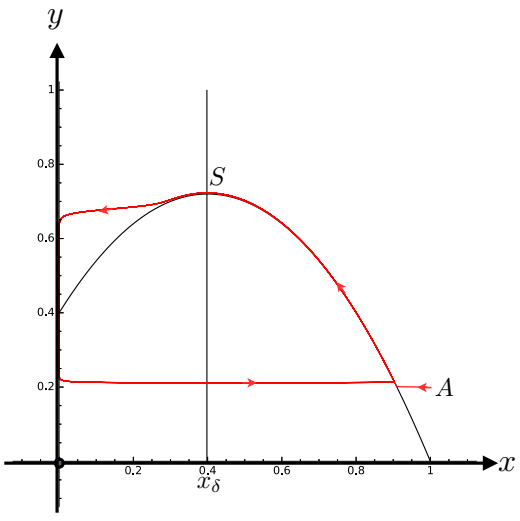
$\delta = 0.66562$



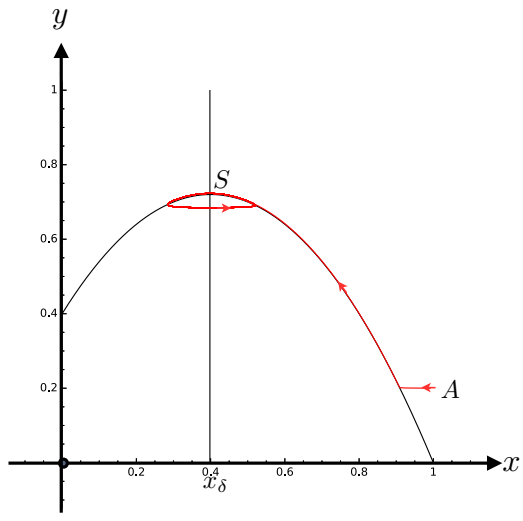
$\delta = 0.6656168070 \quad x_{min} = 1.75\ 10^{-8}$



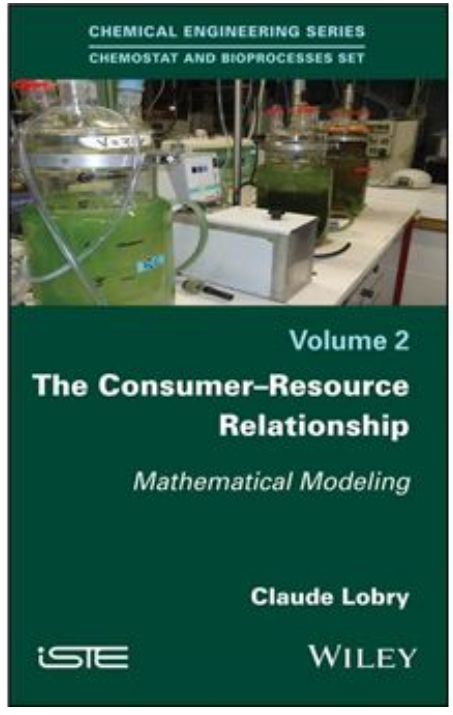
$\delta = 0.6656168071$

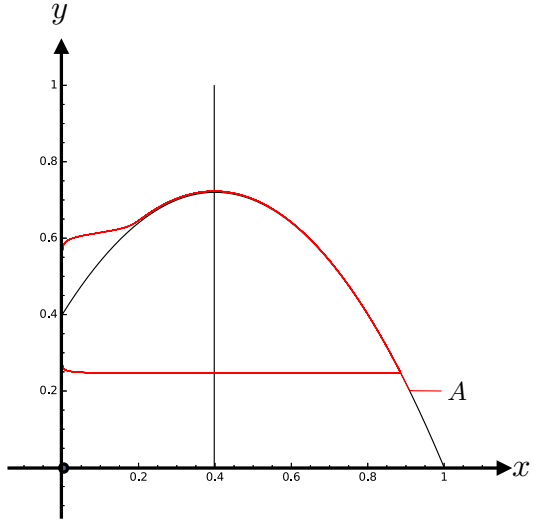


$\delta = 0.66561 \quad x_{min} = 1.49\ 10^{-12}$

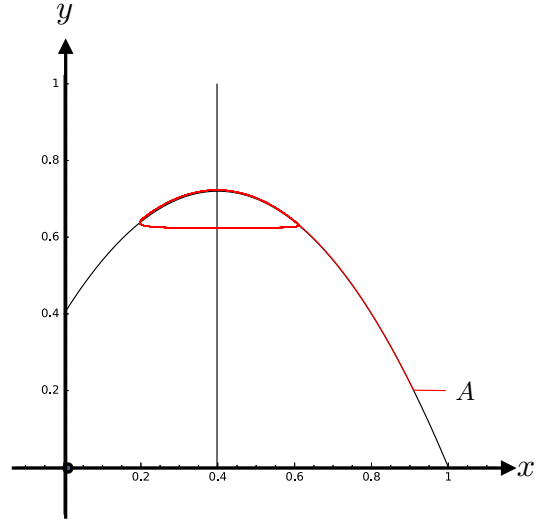


$\delta = 0.66562$





$\delta = 0.6656168070 \quad x_{min} = 1.75\ 10^{-8}$



$\delta = 0.6656168071$

Summary

The Chemostat: Continuous culture

Microbiology (2005), **151**, 3153–3159 DOI 10.1099/mic.0.27924-0

Review

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Continuous culture – making a comeback?

Paul A. Hoskisson[1] and Glyn Hobbs[2]

[1]Department of Molecular and Cell Biology, University of Aberdeen, Institute of Medical Science, Foresterhill, Aberdeen AB25 2ZD, UK

[2]School of Biomolecular Sciences, Liverpool John Moores University, Byrom Street, Liverpool L3 3AF, UK

The system and term chemostat were invented by Novick & Szilard (1950), although simultaneously and independently the 'bactogène', a virtually identical device, was developed by Monod (1950). The basis of both is that the specific growth rate of an organism, relative to its theoretical maximum, is governed by the external substrate concentration of a limiting nutrient.

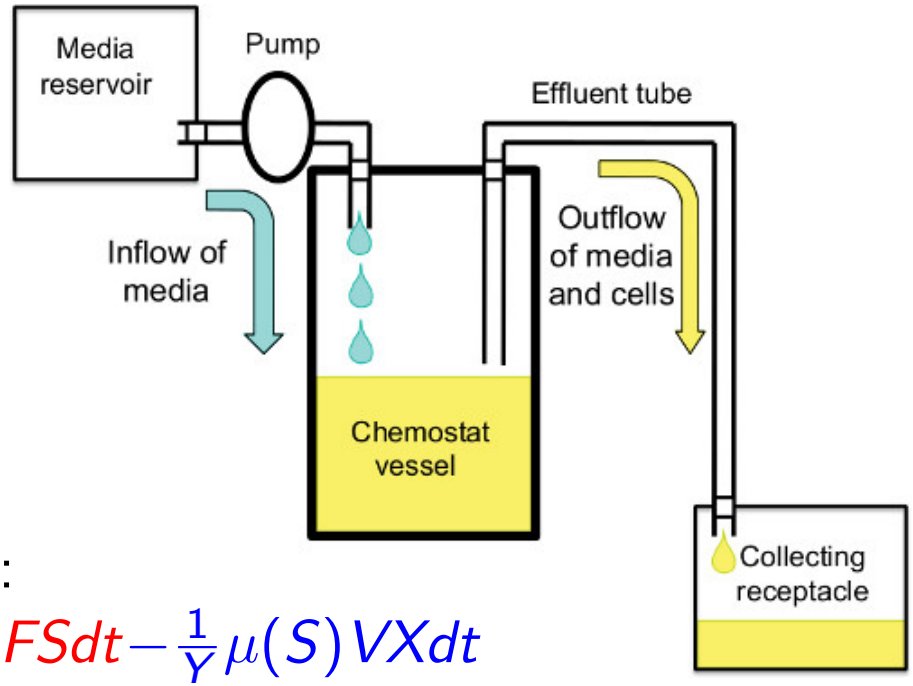
The bactogène-chemostat

$$\begin{array}{rcrcl} \frac{dS}{dt} & = & DS_{in} - DS & - & \frac{1}{Y}\mu(S)X \\ \frac{dX}{dt} & = & -DX & + & \mu(S)X - kX \end{array}$$

- X: density of the species
- S: density of the substrate
- S_{in}: inflow substrate
- $\mu(S)$: growth function
- $D = F/V$: Dilution rate
- Y: Yield coefficient
- k: decay rate of the species
- Law of conservation of mass:

  $VS\,|_{t+dt} - VS\,|_t = FS_{in}dt - FSdt - \frac{1}{Y}\mu(S)VXdt$

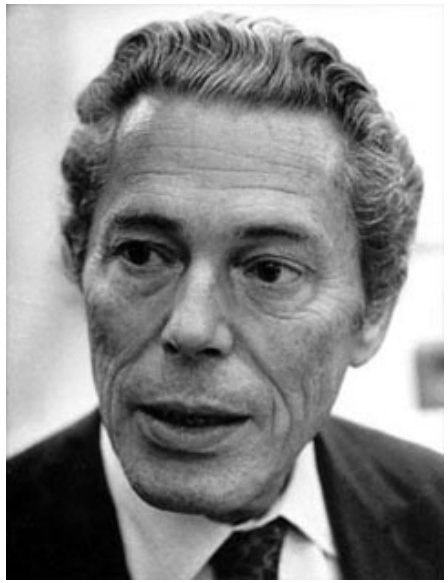
  $VX\,|_{t+dt} - Vx\,|_t = -FXdt + \mu(S)VXdt - kVXdt$
- Divide by Vdt



$$\begin{array}{rcrcl} \frac{S|_{t+dt} - S|_t}{dt} & = & \frac{F}{V}S_{in} - \frac{F}{V}S & - & \frac{1}{Y}\mu(S)X \\ \frac{X|_{t+dt} - X|_t}{dt} & = & -\frac{F}{V}X & + & \mu(S)X - kX \end{array}$$

The inventors of the chemostat

- Jacques Monod
  (Nobel Prize 1965)
  J. Monod (1950), *La technique de culture continue: théorie et applications*. Ann. Inst. Past., 79, 390-410.
- Aaron Novick and Leo Szilard
  (Manhattan Project)
  A. Novick and L. Szilard (1950), *Description of the chemostat*. Science, 112, 715-716



Gujer (or Petersen) Matrix

- The mathematical equations of the model

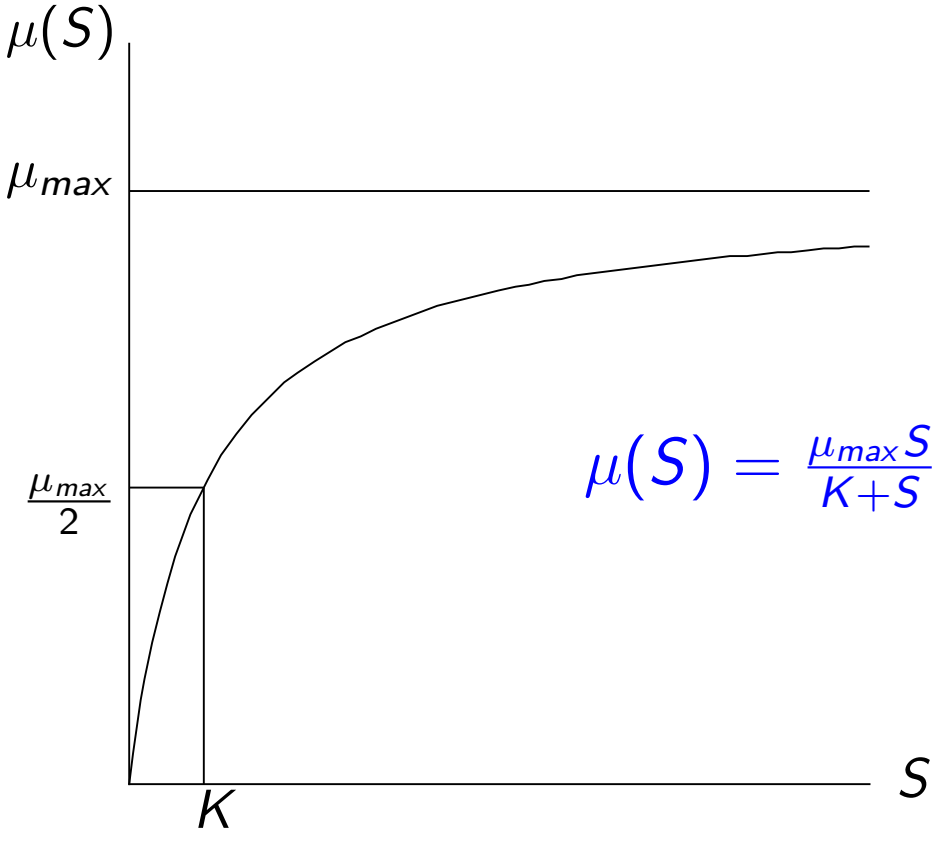
$$\begin{array}{rcll} \frac{dS}{dt} & = & \boxed{DS_{in} - DS} & \boxed{- \frac{1}{Y}\mu(S)X} \\ \frac{dX}{dt} & = & \boxed{-DX} & \boxed{+ \mu(S)X - kX} \end{array}$$

Hydrodynamics | Biology

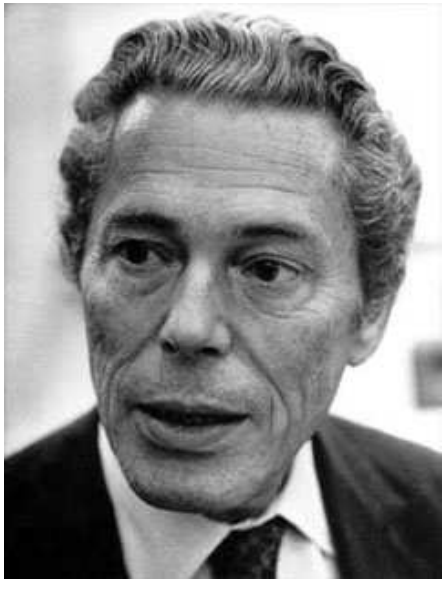
- The Monod growth function: $\mu(S) = \frac{\mu_{max} S}{K+S}$
- 2 state variables (S and X), 2 processes (growth of X and decay of X), 4 parameters (m, K, Y and k)
- The Gujer representation

Component $i \rightarrow$	1	2	Rate
$\downarrow$ Process j	S	X	
1. Growth of X	$-\frac{1}{Y}$	1	$\frac{\mu_{max} S}{K+S} X$
2. Decay of X		-1	kX

The growth function of Jacques Monod (1910-1976)



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



μ_{max}: maximum growth rate

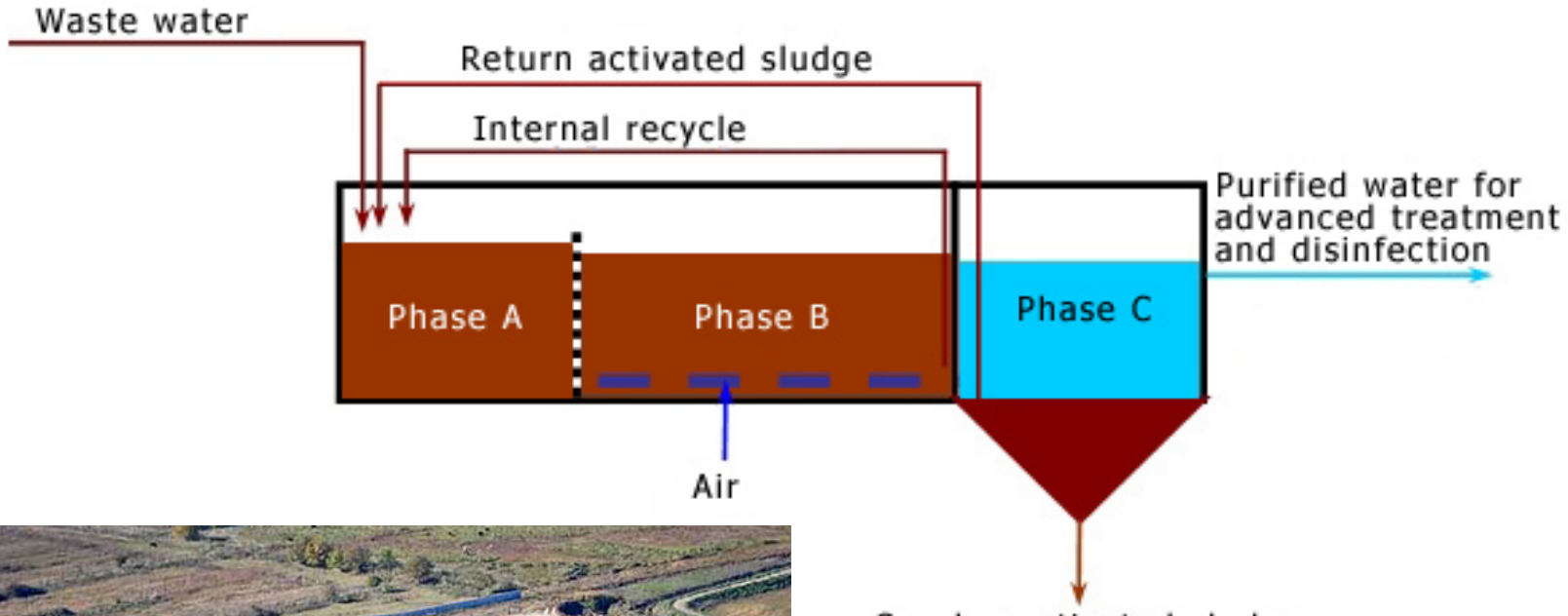
K: half saturation constant

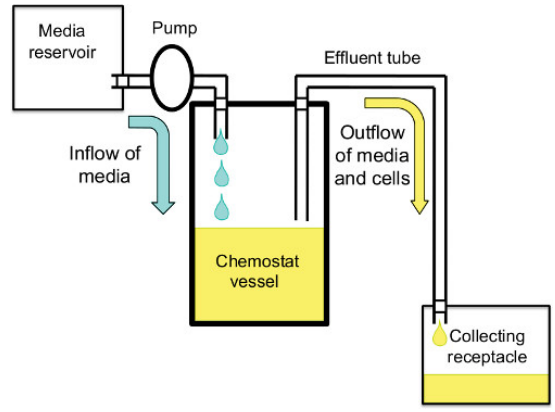
Break-even concentration: $\mu(S) = D \Longleftrightarrow S = \lambda(D)$

J. Monod (1942). Recherches sur la Croissance des Cultures Bactériennes. Paris: Hermann & Co.

J. Monod (1949). The growth of bacterial cultures. Annu Rev Microbiol 3, 371–394.

Biological Waste Water Treatment





http://tradearabia.com/news/cons_349461.html

Modelling activated sludge process: ASM's family

In 1987, the International Association on Water Quality formed a task group to promote the development and facilitate the application of practical model for design and operation of biological wastewater systems.

ASM1: Organic and Nitrogen removal

- 13 State Variables
- 8 Processes
- 19 Parameters

ASM2: Organic, Nitrogen and Phosphorus removal

- 19 State Variables
- 19 Processes
- 64 Parameters

Modelling activated sludge process: ASM's family

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ASM1: Organic and Nitrogen removal

- 13 State Variables
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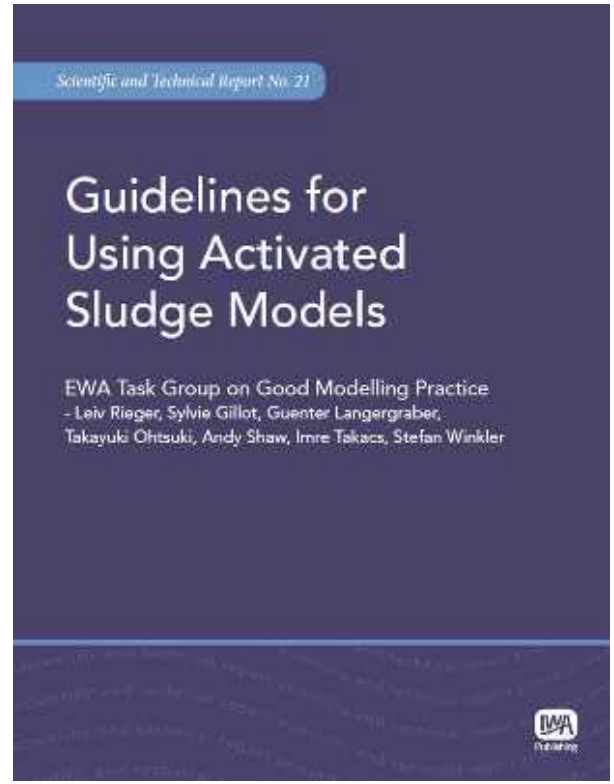
- 19 State Variables
- 19 Processes
- 64 Parameters

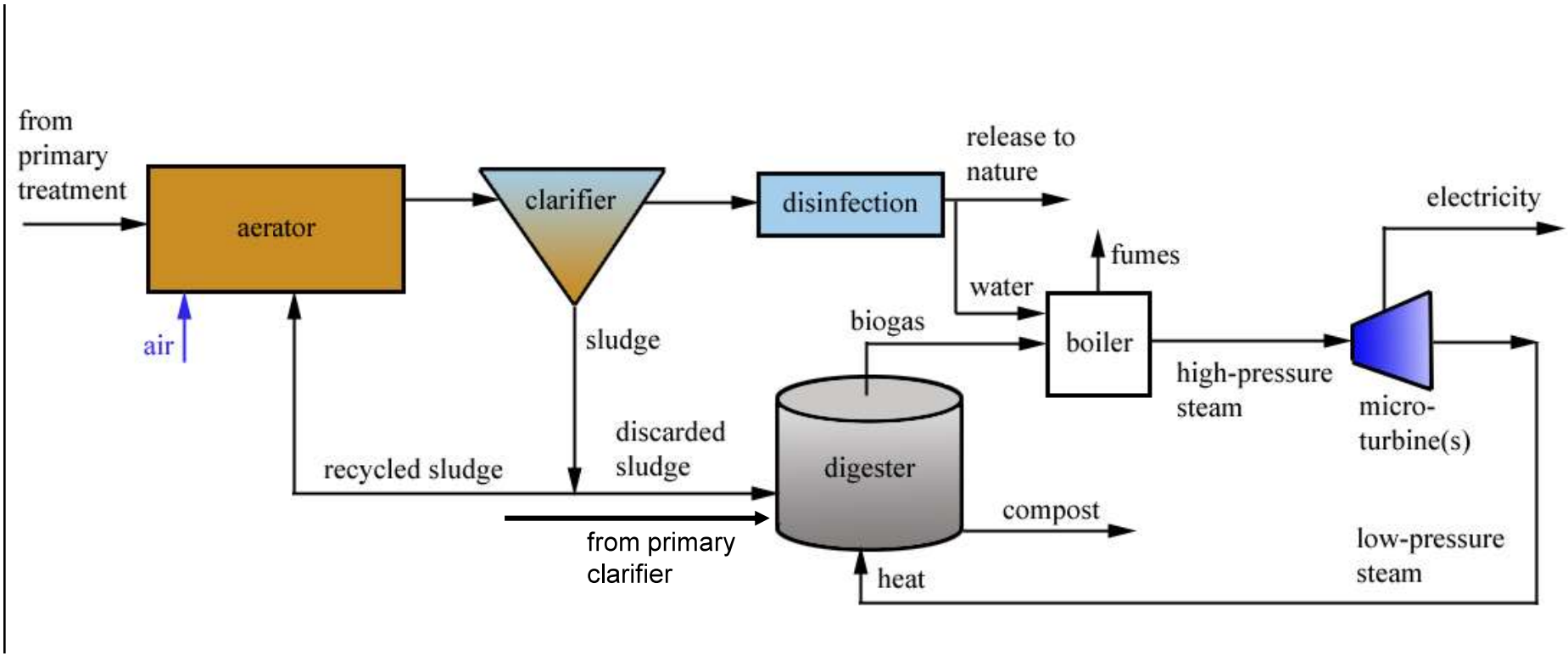
ASM1: the Gujer Matrix

Component → i	1	2	3	4	5	6	7	8	9
j Process ↓	S_I	S_S	X_I	X_S	$X_{B,H}$	$X_{B,A}$	X_P	S_O	S_{NO}
1 Aerobic growth of heterotrophs		$-\frac{1}{Y_H}$			1			$-\frac{1-Y_H}{Y_H}$	
2 Anoxic growth of heterotrophs		$-\frac{1}{Y_H}$			1				$\frac{1-Y_H}{2.86Y_H}$
3 Aerobic growth of autotrophs						1		$-\frac{4.57}{Y_A}+1$	$\frac{1}{Y_A}$
4 'Decay' of heterotrophs				$1-f_P$	−1		f_P		
5 'Decay' of autotrophs				$1-f_P$		−1	f_P		
6 Ammonification of soluble organic nitrogen									
7 'Hydrolysis' of entrapped organics		1		−1					
8 'Hydrolysis' of entrapped organic nitrogen									
Observed Conversion Rates [ML^{-3}T^{-1}]	$r_i = \sum_j \nu_{ij}\rho_j$								
Stoichiometric Parameters: Heterotrophic yield: Y_H Autotrophic yield: Y_A Fraction of biomass yielding particulate products: f_P Mass N/Mass COD in biomass: i_{XB} Mass N/Mass COD in products from biomass: i_{XP}	Soluble inert organic matter [M(COD)L^{-3}]	Readily biodegradable substrate [M(COD)L^{-3}]	Particulate inert organic matter [M(COD)L^{-3}]	Slowly biodegradable substrate [M(COD)L^{-3}]	Active heterotrophic biomass [M(COD)L^{-3}]	Active autotrophic biomass [M(COD)L^{-3}]	Particulate products arising from biomass decay [M(COD)L^{-3}]	Oxygen (negative COD) [M(−COD)L^{-3}]	Nitrate and nitrite nitrogen [M(N)L^{-3}]

10 S_{NH}	11 S_{ND}	12 X_{ND}	13 S_{ALK}	Process Rate, ρ_j [ML^{-3}T^{-1}]
$-i_{XB}$			$-\frac{i_{XB}}{14}$	$\hat{\mu}_H\left(\frac{S_S}{K_S+S_S}\right)\left(\frac{S_O}{K_{O,H}+S_O}\right)X_{B,H}$
$-i_{XB}$			$\frac{1-Y_H}{14\cdot 2.86Y_H}-\frac{i_{XB}}{14}$	$\hat{\mu}_H\left(\frac{S_S}{K_S+S_S}\right)\left(\frac{K_{O,H}}{K_{O,H}+S_O}\right)\left(\frac{S_{NO}}{K_{NO}+S_{NO}}\right)\eta_g X_{B,H}$
$-i_{XB}-\frac{1}{Y_A}$			$-\frac{i_{XB}}{14}-\frac{1}{7Y_A}$	$\hat{\mu}_A\left(\frac{S_{NH}}{K_{NH}+S_{NH}}\right)\left(\frac{S_O}{K_{O,A}+S_O}\right)X_{B,A}$
		$i_{XB}-f_P i_{XP}$		$b_H X_{B,H}$
		$i_{XB}-f_P i_{XP}$		$b_A X_{B,A}$
1	−1		$\frac{1}{14}$	$k_a S_{ND} X_{B,H}$
				$k_h\frac{X_S/X_{B,H}}{K_X+(X_S/X_{B,H})}\left[\left(\frac{S_O}{K_{O,H}+S_O}\right)+\eta_h\left(\frac{K_{O,H}}{K_{O,H}+S_O}\right)\left(\frac{S_{NO}}{K_{NO}+S_{NO}}\right)\right]X_{B,H}$
	1	−1		$\rho_7(X_{ND}/X_S)$
$r_i = \sum_j \nu_{ij}\rho_j$				
NH_4+NH_3 nitrogen [M(N)L^{-3}]	Soluble biodegradable organic nitrogen [M(N)L^{-3}]	Particulate biodegradable organic nitrogen [M(N)L^{-3}]	Alkalinity – Molar units	Kinetic Parameters: Heterotrophic growth and decay: $\hat{\mu}_H$, K_S, $K_{O,H}$, K_{NO}, b_H Autotrophic growth and decay: $\hat{\mu}_A$, K_{NH}, $K_{O,A}$, b_A Correction factor for anoxic growth of heterotrophs: η_g Ammonification: k_a Hydrolysis: k_h, K_X Correction factor for anoxic hydrolysis: η_h



Anaerobic Digestion



Anaerobic Digestion process: ADM's family

ADM1:

- 24 State Variables
- 19 Processes
- 108 Parameters

- D.J. Batstone, J. Keller, I. Angelidaki, S.V. Kalyuzhnyi, S.G. Pavlostathis, A. Rozzi, W.T.M. Sanders, H. Siegrist, V.A. Vavilin; The IWA Anaerobic Digestion Model No 1 (ADM1). Water Sci Technol 1 May 2002; 45 (10): 65–73. doi:10.2166/wst.2002.0292
- M. C. Tomei, C. M. Braguglia, G. Cento & G. Mininni (2009) Modeling of Anaerobic Digestion of Sludge, Critical Reviews in Environmental Science and Technology, 39:12, 1003-1051, DOI: 10.1080/10643380801977818

ADM1: the Gujer Matrix

TABLE 20a. Stoichimetric coefficients and process rates for biochemical reactions assumed in the ADM1 model for soluble compounds (Batstone et al., 2002)

Component i→	1	2	3	4	5	6	7	8	9	10	11	12	Rate ρ_j
Processj ↓	S_{su}	S_{aa}	S_{fa}	S_{va}	S_{bu}	S_{pro}	S_{ac}	S_{h2}	S_{ch4}	S_{IC}	S_{IN}	S_i	(kg COD m^{-3} d^{-1})
1. Disintegration												$f_{sI,xc}$	$k_{dis}X_c$
2. Carbohydrate hydrolysis	1												$k_{hyd,ch}X_{ch}$
3. Protein hydrolysis		1											$k_{hyd,pr}X_{pro}$
4. Lipid hydrolysis	$1-f_{fa,li}$		$f_{fa,li}$										$k_{hyd,li}X_{li}$
5. Sugar consumption	−1				$(1-Y_{su})f_{bu,su}$	$(1-Y_{su})f_{pro,su}$	$(1-Y_{su})f_{ac,su}$	$(1-Y_{su})f_{h2,su}$		$-\sum_{i=1-9,11-24} C_i\nu_{i,5}$	$-Y_{su}N_{bac}$		$k_{m,su}\frac{S_{su}}{K_S+S_{su}}X_{su}I_{pH}I_{IN,lim}$
6. Amino acid consumption		−1		$(1-Y_{aa})f_{va,aa}$	$(1-Y_{aa})f_{bu,aa}$	$(1-Y_{aa})f_{pro,aa}$	$(1-Y_{aa})f_{ac,aa}$	$(1-Y_{aa})f_{h2,aa}$		$-\sum_{i=1-9,11-24} C_i\nu_{i,6}$	N_{aa}-$Y_{aa}N_{bac}$		$k_{m,aa}\frac{S_{aa}}{K_S+S_{aa}}X_{aa}I_{pH}I_{IN,lim}$
7. LCFA consumption			−1				$(1-Y_{fa})0.7$	$(1-Y_{fa})0.3$			$-Y_{fa}N_{bac}$		$k_{m,fa}\frac{S_{fa}}{K_S+S_{fa}}X_{fa}I_{pH}I_{IN,lim}I_{h2}$
8. Valerate consumption				−1		$(1-Y_{c4})0.54$	$(1-Y_{c4})0.31$	$(1-Y_{c4})0.15$			$-Y_{c4}N_{bac}$		$k_{m,c4}\frac{S_{va}}{K_S+S_{va}}X_{c4}\frac{1}{1+S_{bu}/S_{va}}I_{pH}I_{IN,lim}I_{h2}$
9. Butyrate consumption					−1		$(1-Y_{c4})0.8$	$(1-Y_{c4})0.2$			$-Y_{c4}N_{bac}$		$k_{m,c4}\frac{S_{bu}}{K_S+S_{bu}}X_{c4}\frac{1}{1+S_{va}/S_{bu}}I_{pH}I_{IN,lim}I_{h2}$
10. Propionate consumption						−1	$(1-Y_{pro})0.57$	$(1-Y_{pro})0.43$		$-\sum_{i=1-9,11-24} C_i\nu_{i,10}$	$-Y_{pro}N_{bac}$		$k_{m,pr}\frac{S_{pro}}{K_S+S_{pro}}X_{pro}I_{pH}I_{IN,lim}I_{h2}$
11. Acetate consumption							−1		$(1-Y_{ac})$	$-\sum_{i=1-9,11-24} C_i\nu_{i,11}$	$-Y_{ac}N_{bac}$		$k_{m,ac}\frac{S_{ac}}{K_S+S_{ac}}X_{ac}I_{pH}I_{IN,lim}I_{NH3,Xac}$
12. Hydrogen consumption								−1	$(1-Y_{h2})$	$-\sum_{i=1-9,11-24} C_i\nu_{i,12}$	-$Y_{h2}N_{bac}$		$k_{m,h2}\frac{S_{h2}}{K_S+S_{h2}}X_{h2}I_{pH}I_{IN,lim}$
13. X_{su} biomass decay													$k_{dec,Xsu}X_{su}$
14. X_{aa} biomass decay													$k_{dec,Xaa}X_{aa}$
15. X_{fa} biomass decay													$k_{dec,Xfa}X_{fa}$
16. X_{c4}biomass decay													$k_{dec,Xc4}X_{c4}$
17. X_{pro} biomass decay													$k_{dec,Xpro}X_{pro}$
18. X_{ac} biomass decay													$k_{dec,Xac}X_{ac}$
19. X_{h2} biomass decay													$k_{dec,Xh2}X_{h2}$

ADM1: the Gujer Matrix (continued)

TABLE 20b. Stoichimetric coefficients and process rates for biochemical reactions assumed in the ADM1 model for particulate compounds (Batstone et al., 2002)

Component i→	13	14	15	16	17	18	19	20	21	22	23	24	Rate ρ_i
Processj ↓	X_c	X_{ch}	X_{pr}	X_{li}	X_{su}	X_{aa}	X_{fa}	X_{c4}	X_{pro}	X_{ac}	X_{h2}	X_i	(kg COD m^{-3} d^{-1})
1. Disintegration	−1	f_{chXc}	f_{prXc}	$f_{li,Xc}$								$f_{XI,Xc}$	$k_{dis}X_c$
2. Carbohydrate hydrolysis		−1											$k_{hyd,ch}X_{ch}$
3. Protein hydrolysis			−1										$k_{hyd,pr}X_{pro}$
4. Lipid hydrolysis				−1									$k_{hyd,li}X_{li}$
5. Sugar consumption					Y_{su}								$k_{m,su}\frac{S_{su}}{K_S+S_{su}}X_{su}I_{pH}I_{IN,lim}$
6. Amino acid consumption						Y_{aa}							$k_{m,aa}\frac{S_{aa}}{K_S+S_{aa}}X_{aa}I_{pH}I_{IN,lim}$
7. LCFA consumption							Y_{fa}						$k_{m,fa}\frac{S_{fa}}{K_S+S_{fa}}X_{fa}I_{pH}I_{IN,lim}I_{h2}$
8. Valerate consumption								Y_{c4}					$k_{m,c4}\frac{S_{va}}{K_S+S_{va}}X_{c4}\frac{1}{1+S_{bu}/S_{va}}I_{pH}I_{IN,lim}I_{h2}$
9. Butyrate consumption								Y_{c4}					$k_{m,c4}\frac{S_{bu}}{K_S+S_{bu}}X_{c4}\frac{1}{1+S_{va}/S_{bu}}I_{pH}I_{IN,lim}I_{h2}$
10. Propionate consumption									Y_{pro}				$k_{m,pr}\frac{S_{pro}}{K_S+S_{pro}}X_{pro}I_{pH}I_{IN,lim}I_{h2}$
11. Acetate consumption										Y_{ac}			$k_{m,ac}\frac{S_{ac}}{K_S+S_{ac}}X_{ac}I_{pH}I_{IN,lim}I_{NH3,Xac}$
12. Hydrogen consumption											Y_{h2}		$k_{m,h2}\frac{S_{h2}}{K_S+S_{h2}}X_{h2}I_{pH}I_{IN,lim}$
13. X_{su} biomass decay	1				−1								$k_{dec,Xsu}X_{su}$
14. X_{aa} biomass decay	1					−1							$k_{dec,Xaa}X_{aa}$
15. X_{fa} biomass decay	1						−1						$k_{dec,Xfa}X_{fa}$
16. X_{c4}biomass decay	1							−1					$k_{dec,Xc4}X_{c4}$
17. X_{pro} biomass decay	1								−1				$k_{dec,Xpro}X_{pro}$
18. X_{ac} biomass decay	1									−1			$k_{dec,Xac}X_{ac}$
19. X_{h2}biomass decay	1										−1		$k_{dec,Xh2}X_{h2}$

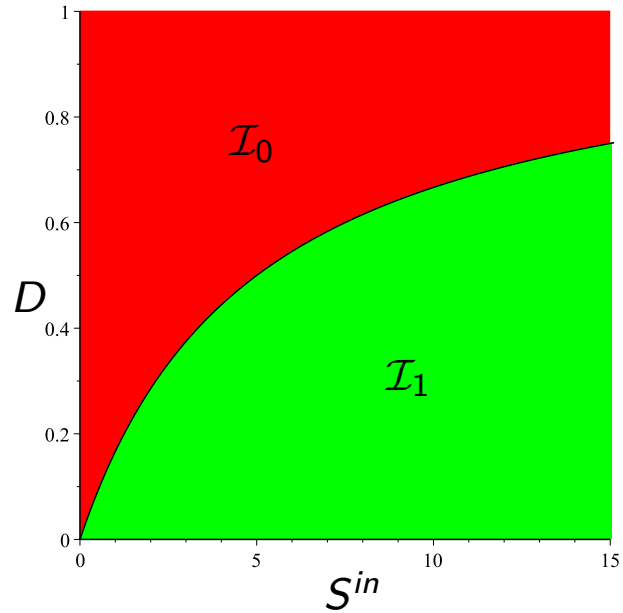
The operating diagram

$$\begin{array}{rcl} dS/dt & = & D(S^{in} - S) - \frac{1}{Y}\mu(S)X \\ dX/dt & = & (\mu(S) - D - k)\,X \end{array}$$

with $\mu(S)$ Monod

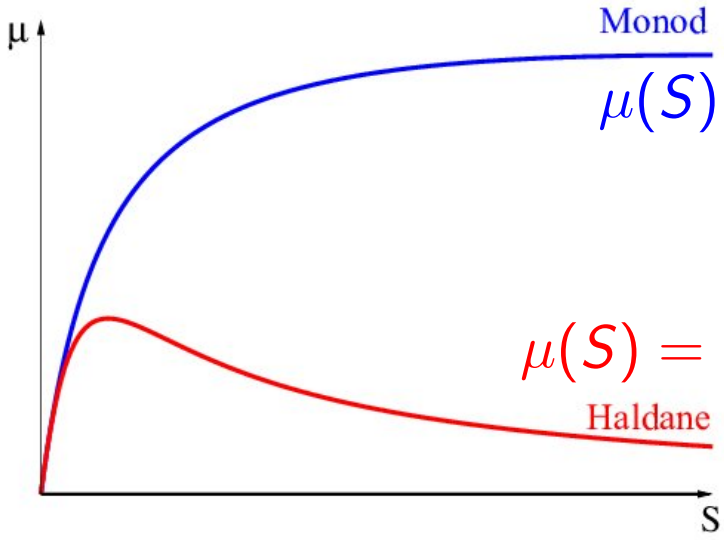
- Operating parameters: S^{in} and $D = F/V$
- Washout $E_0 = (S^{in}, 0)$
- Positive steady state $E_1 = (S^*, X^*)$, where $S^* = \lambda(D + k)$ and $X^* = \frac{YD}{D+k}(S^{in} - S^*)$
- Existence and stability of steady states

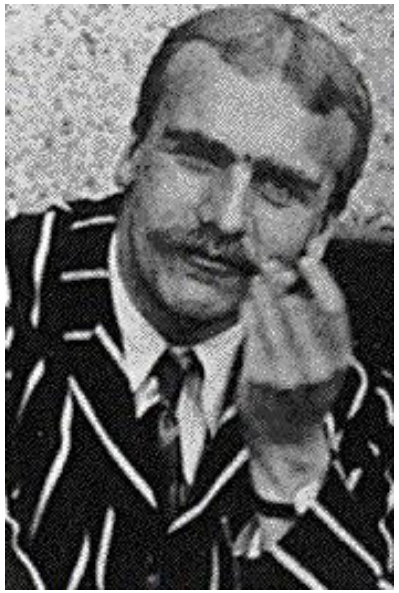
region	E_0	E_1
$(S^{in}, D) \in \mathcal{I}_0$	GAS	
$(S^{in}, D) \in \mathcal{I}_1$	U	GAS



- The green region $\mathcal{I}_1$ is the "target" operating region, as it corresponds to the global stability of the positive steady state
- The red region $\mathcal{I}_0$ should be avoided, as it corresponds to washout.

Substrate inhibition: The growth function of John Burdon Sanderson Haldane (1892-1964)





- The maximum growth rate is $\mu(S_{max}) = \frac{\mu_{max}}{1+2\sqrt{K/K_i}}$ where $S_{max} = \sqrt{KK_i}$
- When $K_i \to \infty$, $\frac{\mu_{max} S}{K+S+S^2/K_i} \to \frac{\mu_{max} S}{K+S}$ (Monod function)
- Break-even concentrations: $\mu(S) = D \Leftrightarrow S = \lambda_i(D), i = 1, 2$

J.B.S. Haldane (1930) Enzymes. London, New York, Longmans (MIT Press, 1965).
J.F. Andrews (1968). A mathematical model for the continuous culture of microorganisms utilizing inhibitory substance. Biotech. Bioeng., 10 (6), 707-723

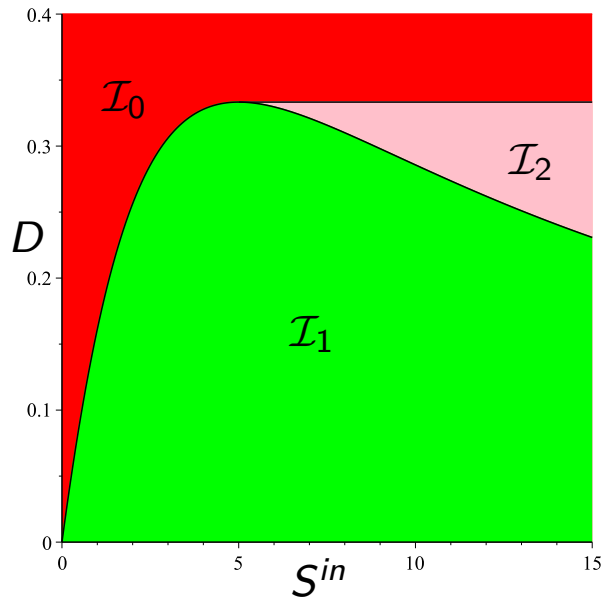
Operating diagram

$$\begin{array}{rcl} dS/dt & = & D(S^{in} - S) - \frac{1}{Y}\mu(S)X \\ dX/dt & = & (\mu(S) - D - k)\,X \end{array}$$

with $\mu(S)$ Haldane

- Washout: $E_0 = (S^{in}, 0)$
- Two positive steady state $E_i = (S_i^*, X_i^*)$, where $S_i^* = \lambda_i(D + k)$ and $X_i^* = \frac{YD}{D+k}(S^{in} - S_i^*), i = 1, 2$
- Existence and stability of steady states

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



- The green region $\mathcal{I}_1$ is the "target" operating region, as it corresponds to the global stability of the positive steady state
- In the pink bistability region $\mathcal{I}_2$ the asymptotic behavior depends on the intitial condition

Rendement ou Yield

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

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

- $\mu(S)$ croissance
- $\nu(S) = \frac{1}{Y}\mu(S)$ consommation
- D fixe $\mu(S^*)$ et donc S^*
- S_{in} fixe alors $x^* = Y(S_{in} - S^*)$
- Les solutions tendent vers (S^*, x^*)

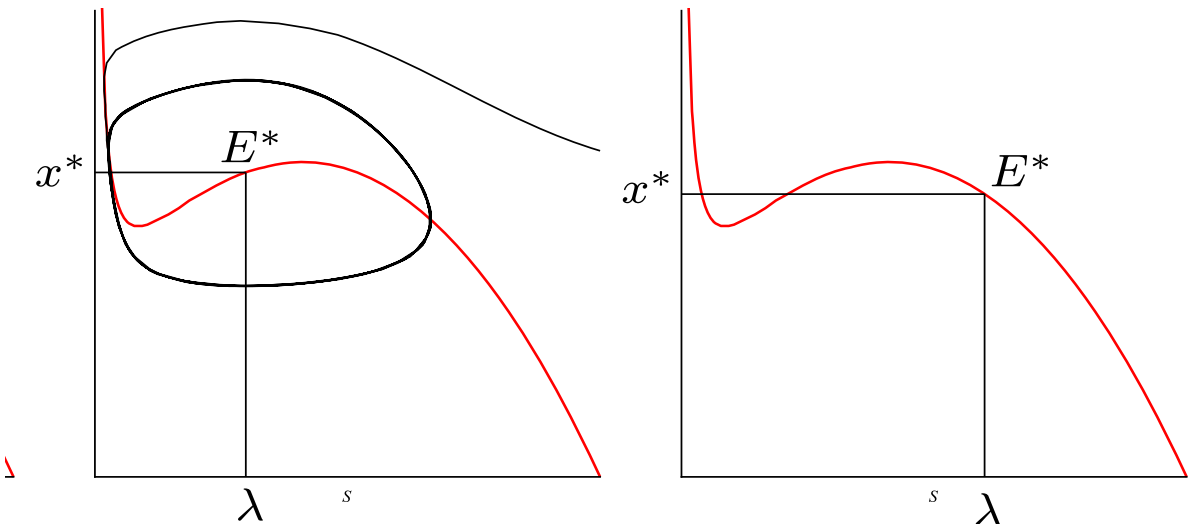
Yield variable

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

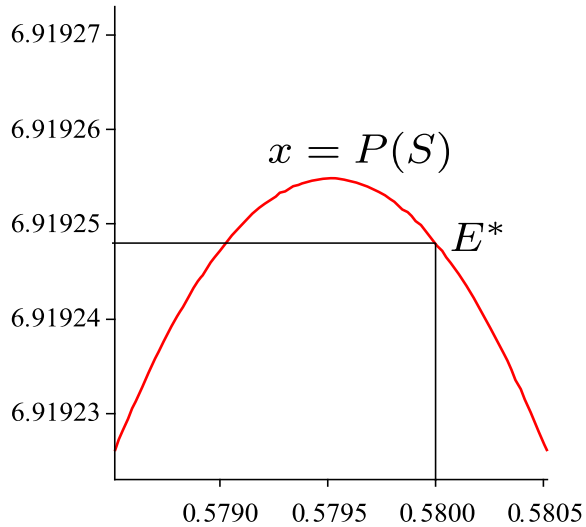
$$\begin{cases} \dot{S} = D(S_{in} - S) - \nu(S)x \\ \dot{x} = (Y(S)\nu(S) - D)x \end{cases}$$

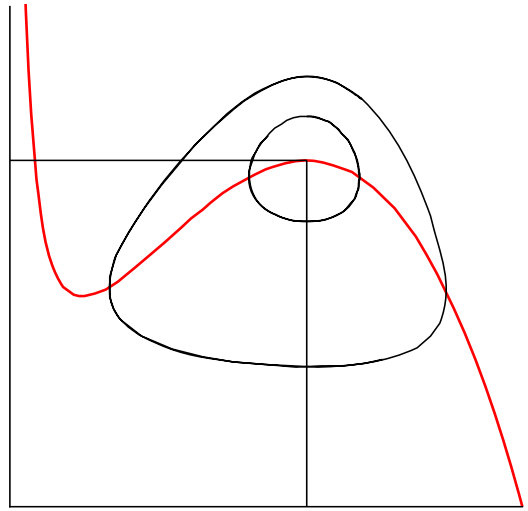
- $\mu(S)$ croissance
- $\nu(S) = \frac{1}{Y(S)}\mu(S)$ consommation
- D fixe $\mu(S^*)$ et donc S^*
- S_{in} fixe alors $x^* = Y(S^*)(S_{in} - S^*)$
- Il peut y avoir des cycles autour de (S^*, x^*)

Cycle



Cycles



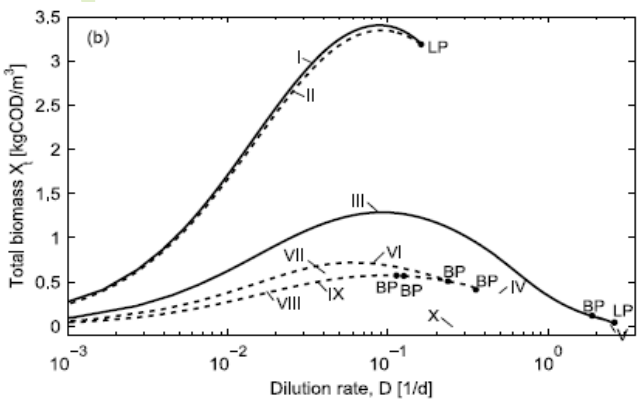


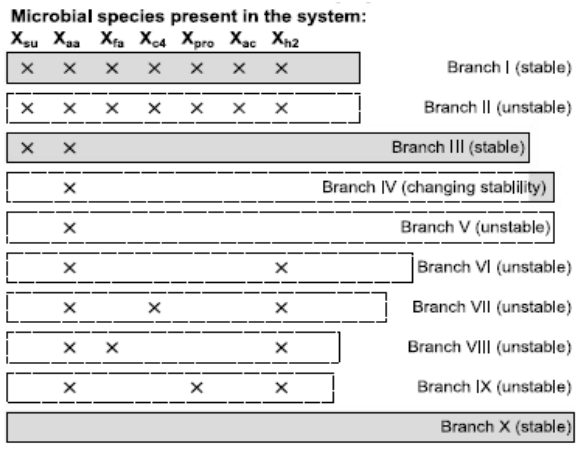
Bifurcation de Hopf sous critique avec apparition de deux cycle, le plus grand stable et le plus petit, instable entourant un point d'équilibre stable

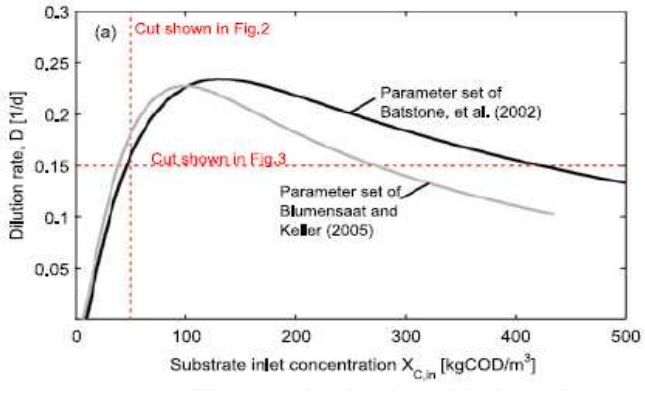
$$\begin{cases} \dot{S} = 1 - S - \frac{2S}{0.58+S} \frac{x}{1+46S^2} \\ \dot{x} = \left(\frac{2S}{0.58+S} - 1 \right) x \end{cases}$$

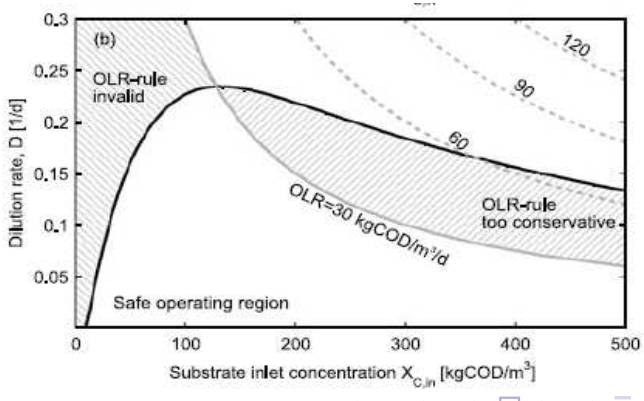
Operating diagram of the ADM1 model

A. Bornhöft, R. Hanke-Rauschenbach, K. Sundmacher (2013). Steady-state analysis of the Anaerobic Digestion Model No. 1 (ADM1). Nonlinear Dynamics, 73, 535-549









Summary

Volterra model of competition

$$\begin{cases} N_1' &= r_1 N_1 (b_1 - a_{11} N_1 - a_{12} N_2) \\ N_2' &= r_2 N_2 (b_2 - a_{21} N_1 - a_{22} N_2) \end{cases}$$

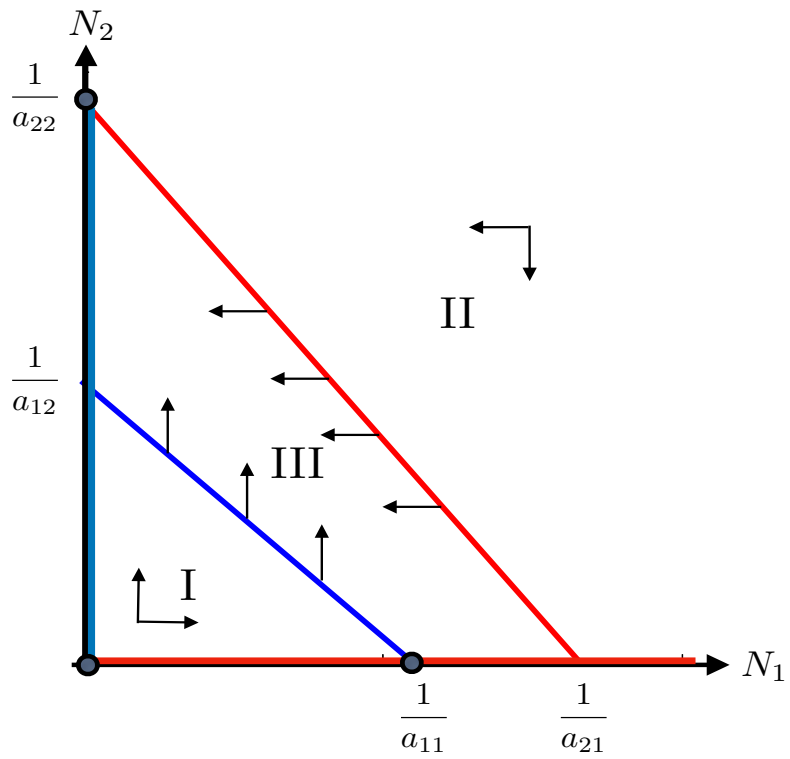
- Isoclines:

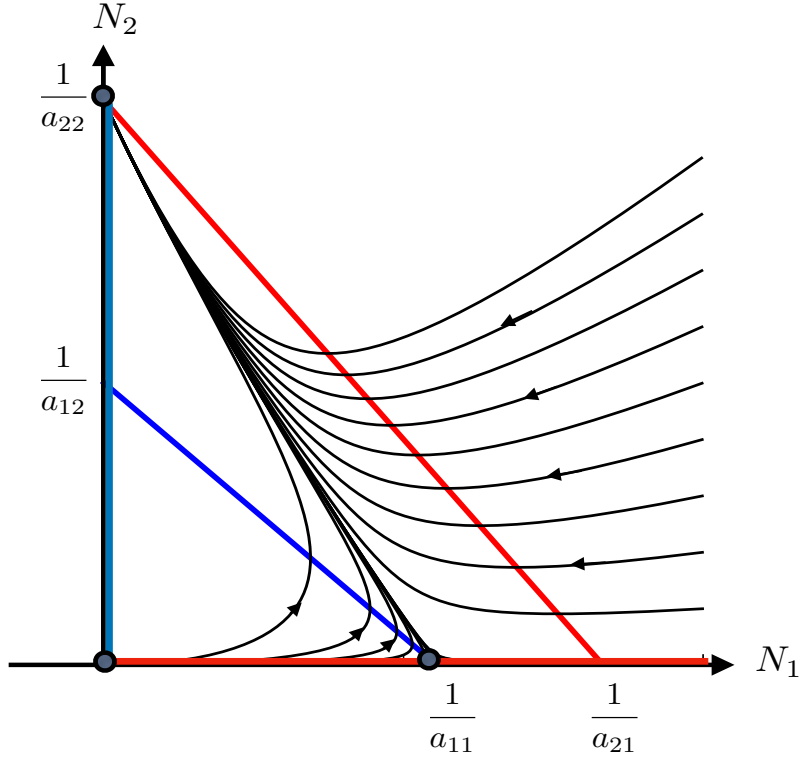
$$N_1' = 0 \Longleftrightarrow N_1 = 0 \text{ ou } b_1 - a_{11} N_1 - a_{12} N_2 = 0$$

$$N_2' = 0 \Longleftrightarrow N_2 = 0 \text{ ou } b_2 - a_{21} N_1 - a_{22} N_2 = 0$$

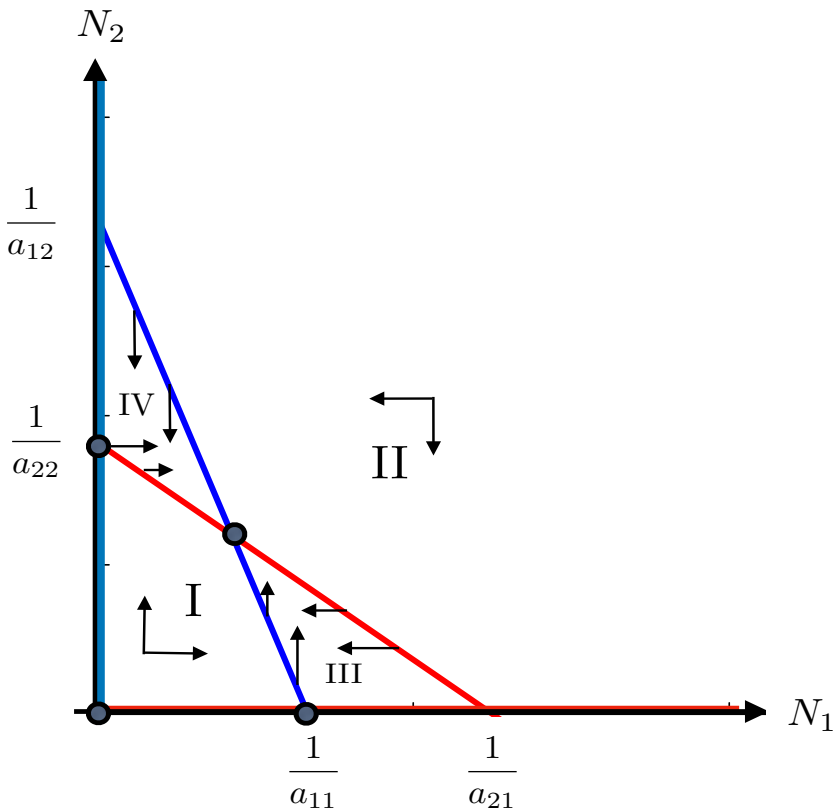
- Points d'équilibres: $(0, 0)$, $(0, b_2/a_{22})$, $(b_1/a_{11}, 0)$ et (x^*, y^*) (éventuellement)
- Exercice: Linéariser autour des équilibres et déterminer la nature de ces points

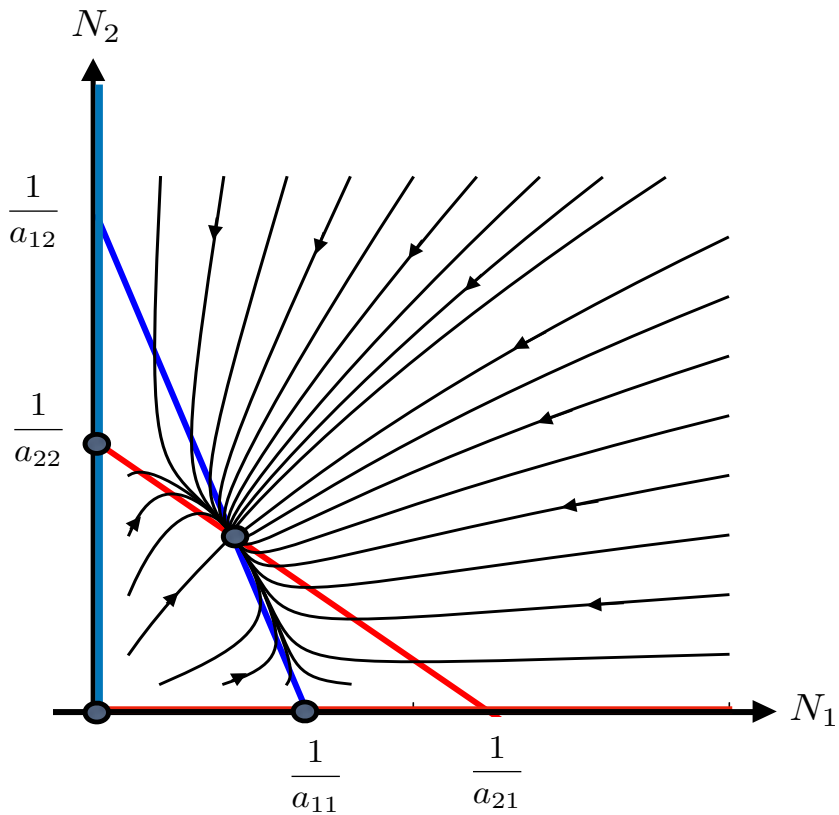
Exclusion compétitive



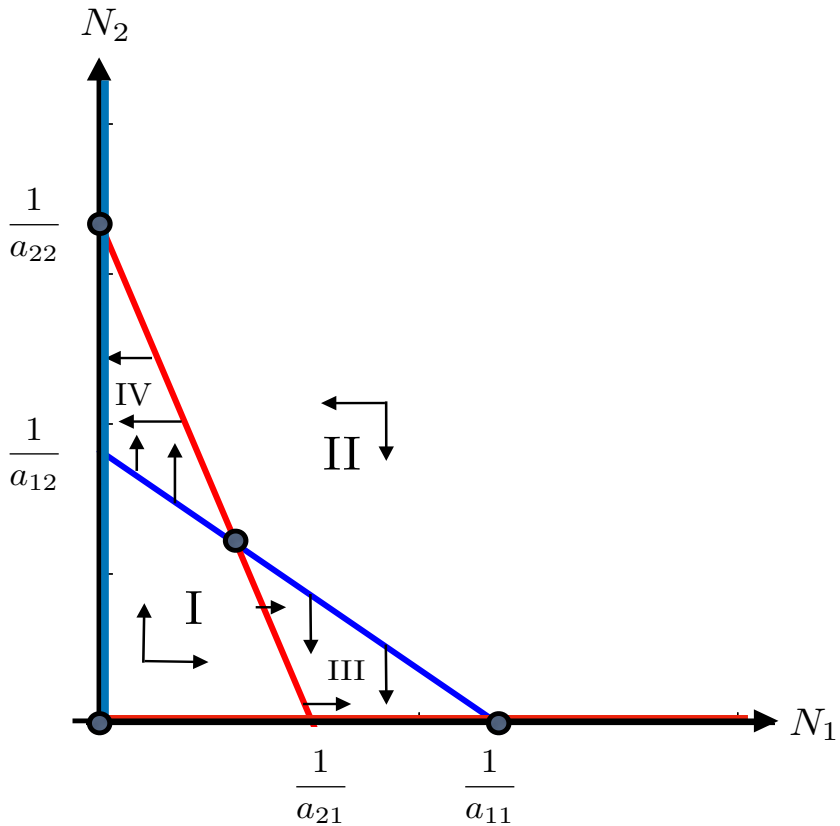


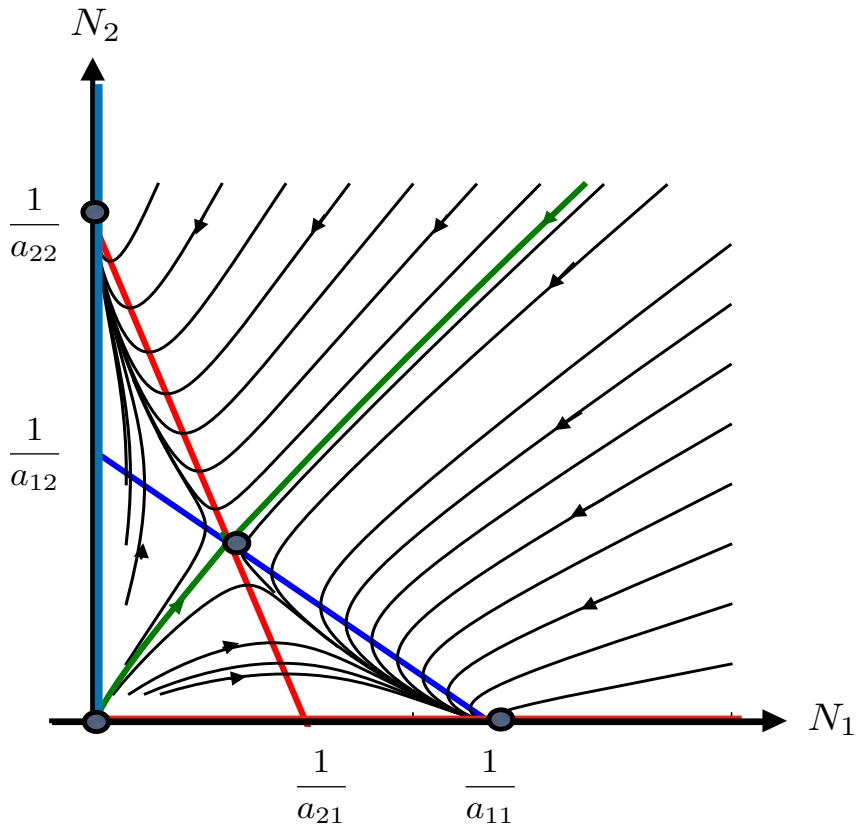
Coexistence





Bistability





Summary

Rosenzweig-MacArthur model of competition

$$\begin{cases} x' &= f(x) - \sum_{i=1}^{2} \mu_i(x) y_i \\ y_i' &= (c_i \mu_i(x) - d_i) y_i, \qquad i = 1, 2 \end{cases}$$

- $f(x) = rx(1 - x/K)$ et $\mu_i(x) = a_i x/(b_i + x)$.
- Isoclines:

$$x' = 0 \Longleftrightarrow f(x) = \sum_{i=1}^{2} \mu_i(x) y_i$$

$$y_i' = 0 \Longleftrightarrow y_i = 0 \text{ ou } \mu_i(x) = d_i/c_i, \qquad i = 1, 2$$

- Equilibres:
  - $(0, 0, 0)$
  - $(K, 0, 0)$
  - $(x_1^*, y_1^*, 0)$, $\quad \mu_1(x_1^*) = \frac{d_1}{c_1}, \quad y_1^* = \frac{c_1}{d_1} f(x_1^*), \quad x_1^* < K$
  - $(x_2^*, 0, y_2^*)$, $\quad \mu_2(x_2^*) = \frac{d_2}{c_2}, \quad y_2^* = \frac{c_2}{d_2} f(x_2^*), \quad x_2^* < K$

Théorème d'exclusion compétitive

On suppose que $x_1^* < x_2^*$ et $x_1^* < K$, de sorte que $E_1 = (x_1^*, y_1^*, 0)$ existe. Alors E_1 est localement asymptotiquement stable, $(0, 0, 0)$ et $(K, 0, 0)$ sont instables et et $E_2 = (x_2^*, 0, y_2^*)$, s'i existe, est instable.

- C'est l'espèce qui a le plus petit x^* qui survit à la compétition, c'est donc celle qui fait la "meilleure utilisation du substrat".
- Il suffit de linéariser le système aux points d'équilibre.
- Le résultat s'étend à n espèces en compétition sur une ressource.
- Le résultat s'étend à une grande classe de modèles avec μ_i croissante et f remplacée par une fonction positive sur $(0, K)$ et négative pour $x > K$.
- La coexistence est possible le long de solutions périodiques

Summary

Coexistence through periodic solutions

- G. HARDIN, The competitive exclusion principle, Science 131 (1960), 1292-1298.
- S. LEVIN, Community equilibria and stability, and an extension of the competitive exclusion principle, Amer. Naturalist 104, No. 939 (1970), 413-423.
- A. REXIGNO AND I. RICHARDSON, On the competitive exclusion principle, Bull. Math. Biophys. 27, special issue (1965), 85-89.
- R. ARMSTRONG AND R. MCGEHEE, Coexistence of species competing for shared resources, Theoret. Population Biology 9 (1976), 317-328.
- R. MCGEHEE AND R. ARMSTRONG, Some Mathematical Problems Concerning the Ecological Principle of Competitive Exclusion, JOURNAL OF DIFFERENTIAL EQUATIONS 23, 30-52 (1977)

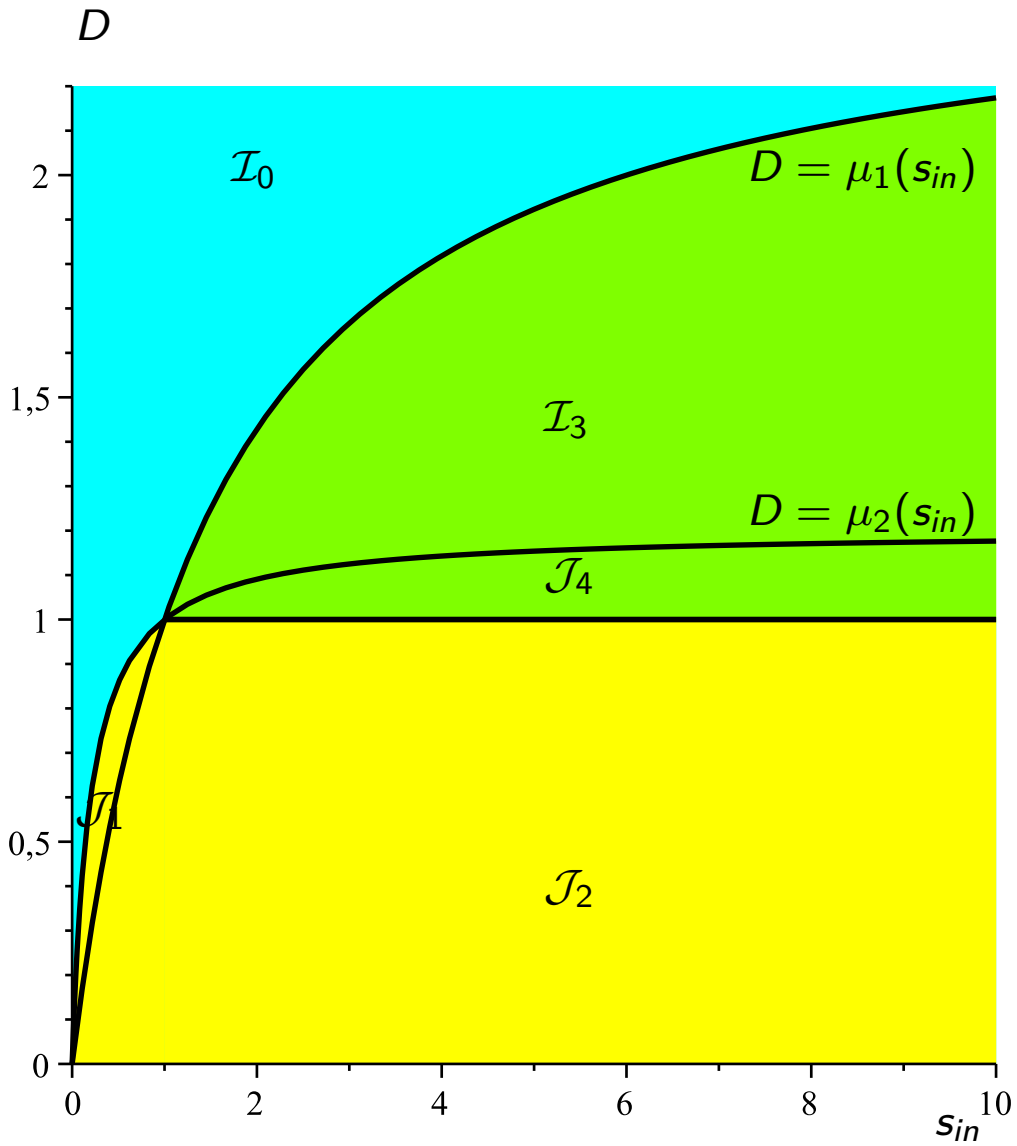
Summary

Competion 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 : $\lambda_i = \mu_i^{-1}(D)$
- $E_0 = (S = S_{in}, x_1 = 0, x_2 = 0)$
- $E_1 = (S = \lambda_1, x_1 = S_{in} - \lambda_1, x_2 = 0)$
- $E_2 = (S = \lambda_2, x_1 = 0, x_2 = S_{in} - \lambda_2)$
- Si $\lambda_1 < \lambda_2$ alors E_1 est stable.
- At equilibrium, only one species can survice (Competitite Exclusion Principle)

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

Competitive exclusion Principle (CEP)

$$\begin{cases} S' &= D(S_{in} - S) - \sum_{i=1}^{n} \mu_i(S) x_i \\ x_i' &= (\mu_i(S) - D)x_i, \qquad i = 1 \cdots n \end{cases}$$

- All μ_i are increasing. $\lambda_i = \mu_i^{-1}(D)$
- Si $\lambda_1 < S^{in}$ et

$$\lambda_1 < \lambda_i \text{ pour tout } i \geq 2$$

alors toutes les solutions $(S(t), x_1(t), \cdots, x_n(t))$ convergent vers

$$S = \lambda_1, \quad x_1 = S_{in} - \lambda_1, \quad x_2 = 0, \cdots, \quad x_n = 0$$

- A l'équilibre, seule l'espèce x_1 survie, et toutes les autres sont exclues par la compétition

Conjecture: CEP hols for $D_i \neq D$

$$\begin{cases} S' &= D(S_{in} - S) - \sum_{i=1}^{n} \mu_i(S) x_i \\ x_i' &= (\mu_i(S) - D_i) x_i, \qquad i = 1 \cdots n \end{cases}$$

- Break-even concentrations : $\lambda_i = \mu_i^{-1}(D_i)$
- The only steady states are

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

and

$$E_i = (\lambda_i, x_1^*, \cdots, x_n^*)$$

where $x_i^* = \frac{D}{D_i}(S^{in} - \lambda_i)$ and $x_j^* = 0$ for $j \neq i$

- Conjecture : If $\lambda_1 < \lambda_i$for $i \geq 2$ then E_1 is globally asymptotically stable: it attracts all solutions such that $x_1(0) > 0$

CEP hols for Monod growth functions

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

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

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

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

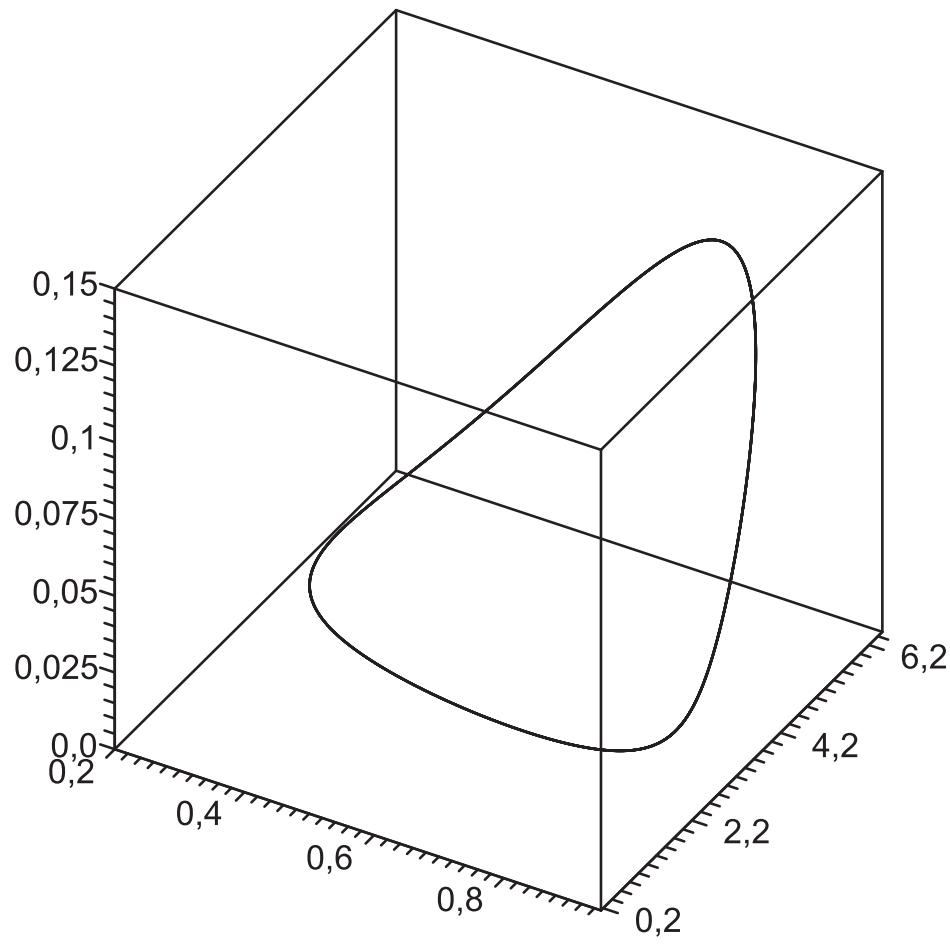
S.B. Hsu, *Limiting behavior for competing species*. SIAM Journal on Applied Mathematics 34 (1978), 760-763.

Variable yield

$$
\begin{aligned}
S' &= 1 - S - \frac{2S}{0.7+S}\frac{x_1}{1+cS^3} - \frac{m_2 S}{6.5+S}\frac{x_2}{120} \\
x_1' &= \left[\frac{2S}{0.7+S} - 1\right]x_1 \\
x_2' &= \left[\frac{m_2 S}{6.5+S} - 1\right]x_2 .
\end{aligned}
$$

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

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

- $S(t)$: 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

$$\begin{aligned} S' &= D(S_{in} - S) - \sum_{j=1}^{n} p_j(S)x_j \\ x_i' &= f_i(S)x_i, \qquad\qquad i = 1 \cdots n, \end{aligned}$$

where $f_i(S) = q_i(S) - D_i$.
The growth rate $f_i(S)$ satisfies

$$f_i(S) < 0 \text{ for } 0 \leq S < \lambda_i \text{ and } f_i(\lambda_i) = 0,$$

where λ_i are the break-even concentrations.
Remark : without loss of generality we can assume that $D = 1$ and $S_{in} = 1$.
Hint: use the change of variables

$$\overline{S} = \frac{S}{S_{in}}, \quad \overline{t} = Dt, \quad \overline{p}_i(\overline{S}) = \frac{p_i(S_{in}\overline{S})}{S_{in}D}, \quad \overline{f}_i(\overline{S}) = \frac{f_i(S_{in}\overline{S})}{D},$$

Competitive exclusion

$$\begin{aligned} S' &= 1 - S - \sum_{j=1}^{n} p_j(S)x_j \\ x_i' &= f_i(S)x_i, \qquad\qquad i = 1 \cdots n, \end{aligned}$$

A necessary condition to avoid washout of the species is that $\lambda_i < 1$ for at least one species. Assume that the species are labeled so that $0 < \lambda_1 < 1$. Then

$$E_1^* = (\lambda_1, x_1^*, 0, \cdots, 0),$$

where $x_1 = x_1^* = P_1(\lambda_1)$ is an equilibrium. Here $P_1(S) = \frac{1-S}{p_1(S)}$. Using linearization about E_1^* one proves that the equilibrium (**??**) is locally exponentially stable if and only if $f_1'(\lambda_1) > 0$ and $P_1'(\lambda_1) < 0$.

We consider the global asymptotic stability of E_1^*.

$$S' = 1 - S - \sum_{j=1}^{n} p_j(S)x_j,$$
$$x_i' = f_i(S)x_i, \quad i = 1 \cdots n,$$

- Assume that $p_i(0) = 0$ and $p_i(S) > 0$ for $S > 0$
- Assume that $f_i(S) < 0$ for $0 \leq S < \lambda_i$ and $f_i(\lambda_i) = 0$
- Assume that $\lambda_1 < 1$ and for all $0 < S < 1$,

$$(S - \lambda_1)f_1(S) > 0, \text{ for } S \neq \lambda_1,$$

$$(S - \lambda_1)(P_1(S) - P_1(\lambda_1)) < 0, \text{ for } S \neq \lambda_1,$$

where $P_1(S) = \frac{1-S}{p_1(S)}$.

- Assume that there exist constants $\alpha_i > 0$ for each $i \geq 2$ satisfying $\lambda_i < 1$, such that for all $0 < S < 1$,

$$f_1(S)p_i(S) > \alpha_i f_i(S)(1 - S).$$

- Then the equilibrium E_1^* is GAS with respect to the interior of the positive cone.

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

Proof

Use the Lyapunov function

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

$$V' = \frac{f_1(S)}{1-S} S' + \frac{1}{x_1^*} \frac{x_1 - x_1^*}{x_1} x_1' + \sum_{i=2}^{n} \alpha_i x_i'.$$

Therefore $(S' = [1 - S - \sum_{i=1}^{n} p_i(S) x_i],\ x_i' = f_i(S) x_i, \quad i = 1 \cdots n$ and $x_1^* = P_1(\lambda_1))$

$$V' = x_1 f_1(S) \left[\frac{1}{P_1(\lambda_1)} - \frac{1}{P_1(S)} \right] + \sum_{i=2}^{n} x_i \frac{\alpha_i f_i(S)(1-S) - f_1(S) p_i(S)}{1-S}.$$

Hence $V' \leq 0$ and $V' = 0$ if and only if $x_i = 0$ for $i = 1 \cdots n$ or $S = \lambda_1$ and $x_i = 0$ for $i = 2 \cdots n$. Using the Krasovskii-LaSalle extension theorem, the ω-limit set of the trajectory is E_1^*.

Summary

Commensalism

- The mathematical equations of the model

$$\begin{array}{lcll} dS_1/dt & = & D(S_1^{in} - S_1) & -\frac{1}{Y_1}\mu_1(S_1)X_1 \\ dX_1/dt & = & -DX_1 & +\mu_1(S_1)X_1 - k_1X_1 \\ dS_2/dt & = & \frac{1}{Y_3}\mu_1(S_1)X_1 - DS_2 & -\frac{1}{Y_2}\mu_2(S_2)X_2 \\ dX_2/dt & = & -DX_2 & +\mu_2(S_2)X_2 - k_2X_2 \end{array}$$

with Monod growth functions $\mu_i(S_i)$, $i = 1, 2$

- The Gujer matrix

Component $i \rightarrow$ $\downarrow$ Process j	1 S_1	2 S_2	1 X_1	1 X_2	Rate
1. Growth of X_1	$-\frac{1}{Y_1}$	$\frac{1}{Y_3}$	1	0	$\frac{m_1 S_1}{K_1+S_1}X_1$
2. Growth of X_2	0	$-\frac{1}{Y_2}$	0	1	$\frac{m_2 S_2}{K_2+S_2}X_2$
3. Decay of X_1			-1		k_1X_1
3. Decay of X_2				-1	k_2X_2

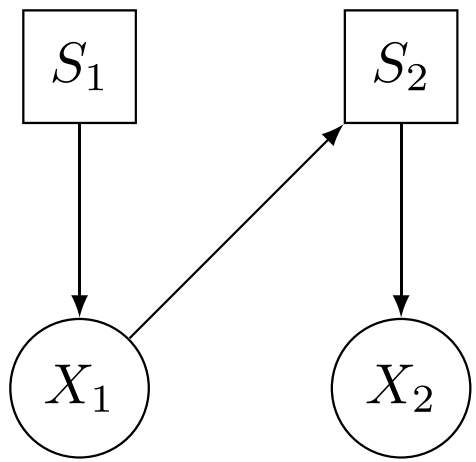
Commensalism

- The mathematical equations of the model

$$
\begin{array}{lcll}
dS_1/dt & = & D(S_1^{in} - S_1) & -\frac{1}{Y_1}\mu_1(S_1)X_1 \\
dX_1/dt & = & -DX_1 & +\mu_1(S_1)X_1 - k_1X_1 \\
dS_2/dt & = & \frac{1}{Y_3}\mu_1(S_1)X_1 - DS_2 & -\frac{1}{Y_2}\mu_2(S_2)X_2 \\
dX_2/dt & = & -DX_2 & +\mu_2(S_2)X_2 - k_2X_2
\end{array}
$$

  with Monod growth functions $\mu_i(S_i)$, $i = 1, 2$

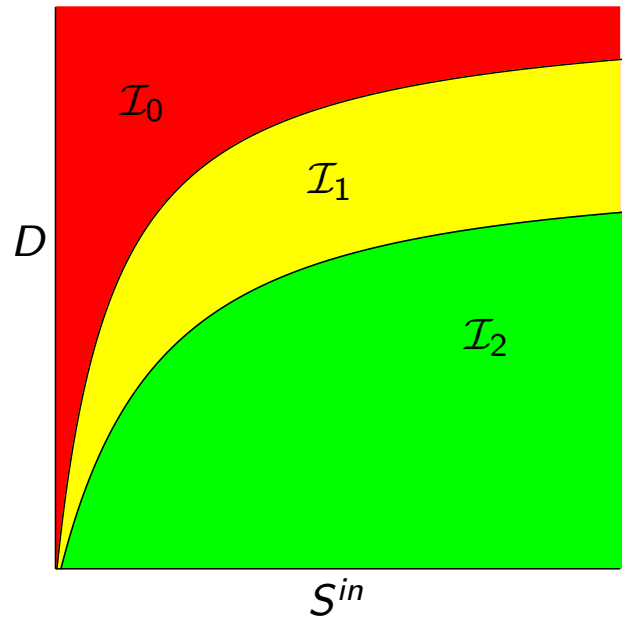
- Two step representation



Commensalism (Operating diagram)

- Washout $E_0 = (S_1^{in}, 0, 0, 0)$
- Washout of X_2 $E_1 = (S_1^*, X_1^*, \bar{S}_2, 0)$
- Coexistence $E_c = (S_1^*, X_1^*, S_2^*, X_2^*)$, where
  $S_i^* = \lambda_i(D + k_i)$, $i = 1, 2$
  $\bar{S}_2 = \frac{Y_1}{Y_3}(S_1^{in} - S_1^*)$
  $X_1^* = \frac{Y_1 D}{D+k_1}(S_1^{in} - S_1^*)$
  $X_2^* = \frac{Y_2 D}{D+k_2}(S_1^{in} - S_1^* - S_2^*)$
- Existence and stability of steady states

region	E_0	E_1	E_c
$(S^{in}, D) \in \mathcal{I}_0$	GAS		
$(S^{in}, D) \in \mathcal{I}_1$	U	GAS	
$(S^{in}, D) \in \mathcal{I}_2$	U	U	GAS



- The green region $\mathcal{I}_2$ is the "target" operating region, as it corresponds to the global stability of the coexistence steady state

Syntrophy

- The mathematical equations of the model

$$
\begin{array}{lcll}
dS_1/dt & = & D(S_1^{in} - S_1) & -\frac{1}{Y_1}\mu_1(S_1, S_2)X_1 \\
dX_1/dt & = & -DX_1 & +\mu_1(S_1, S_2)X_1 - k_1 X_1 \\
dS_2/dt & = & \frac{1}{Y_3}\mu_1(S_1, S_2)X_1 - DS_2 & -\frac{1}{Y_2}\mu_2(S_2)X_2 \\
dX_2/dt & = & -DX_2 & +\mu_2(S_2)X_2 - k_2 X_2
\end{array}
$$

$\mu_1(S_1, S_2) = \text{Monod} \times I_1$, $I_1 = \frac{1}{1+S_2/L_1}$, and $\mu_2(S_2)$ Monod

- The Gujer matrix

Component $i \rightarrow$	1	2	1	1	Rate
$\downarrow$ Process j	S_1	S_2	X_1	X_2	
1. Growth of X_1	$-\frac{1}{Y_1}$	$\frac{1}{Y_3}$	1	0	$\frac{m_1 S_1}{K_1+S_1}\frac{1}{1+S_2/L_1}X_1$
2. Growth of X_2	0	$-\frac{1}{Y_2}$	0	1	$\frac{m_2 S_2}{K_2+S_2}X_2$
3. Decay of X_1			-1		$k_1 X_1$
3. Decay of X_2				-1	$k_2 X_2$

Syntrophy

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\begin{array}{lcll}
dS_1/dt & = & D(S_1^{in} - S_1) & -\frac{1}{Y_1}\mu_1(S_1, S_2)X_1 \\
dX_1/dt & = & -DX_1 & +\mu_1(S_1, S_2)X_1 - k_1X_1 \\
dS_2/dt & = & \frac{1}{Y_3}\mu_1(S_1, S_2)X_1 - DS_2 & -\frac{1}{Y_2}\mu_2(S_2)X_2 \\
dX_2/dt & = & -DX_2 & +\mu_2(S_2)X_2 - k_2X_2
\end{array}
$$

$\mu_1(S_1, S_2) = \text{Monod} \times I_1$, $I_1 = \frac{1}{1+S_2/L_1}$, and $\mu_2(S_2)$ Monod

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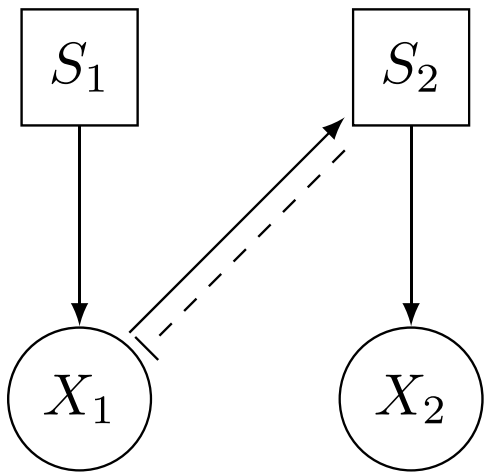

Syntrophy (Operating diagram)

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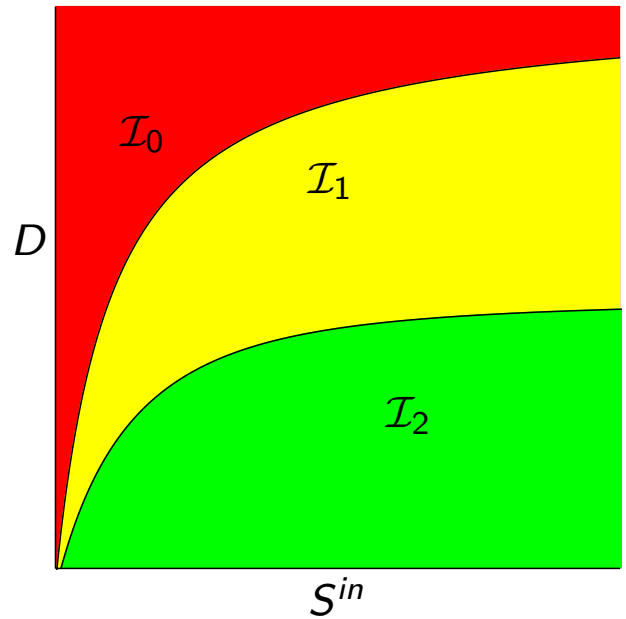
- Washout of X_2 $E_1 = (\bar{S}_1, \bar{X}_1, \bar{S}_2, 0)$, where $\bar{S}_i = ...$, $i = 1, 2$ and $\bar{X}_1 = ...$
- Coexistence $E_c = (S_1^*, X_1^*, S_2^*, X_2^*)$, where $S_i^* = ...$ and $\bar{X}_i^* = ...$, $i = 1, 2$
- Existence and stability of steady states

region	E_0	E_1	E_c
$(S^{in}, D) \in \mathcal{I}_0$	S		
$(S^{in}, D) \in \mathcal{I}_1$	U	S	
$(S^{in}, D) \in \mathcal{I}_2$	U	U	S



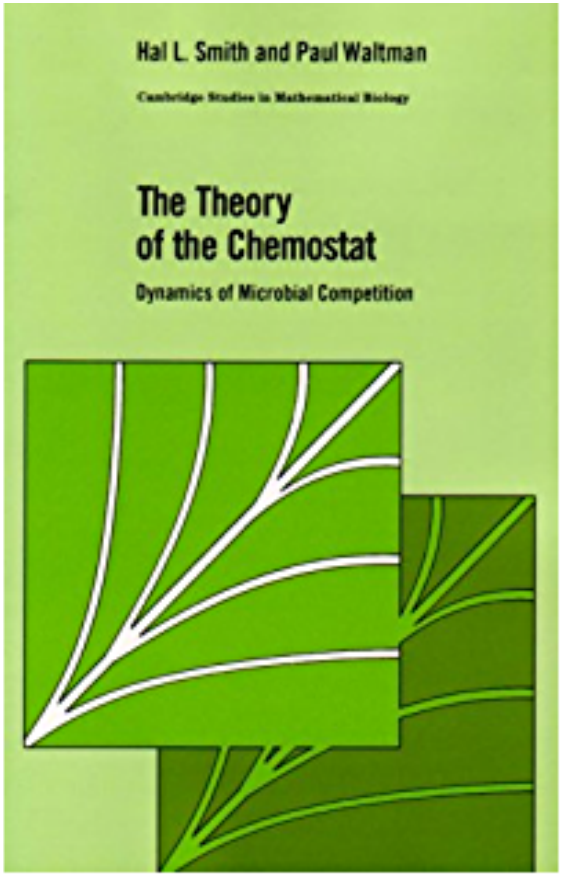
- The green region $\mathcal{I}_2$ is the "target" operating region, as it corresponds to the stability of the coexistence steady state
- The global asymptotic stability is a difficult mathematical question since the system is four dimensional.
- Without decay terms, the system is GAS

Summary

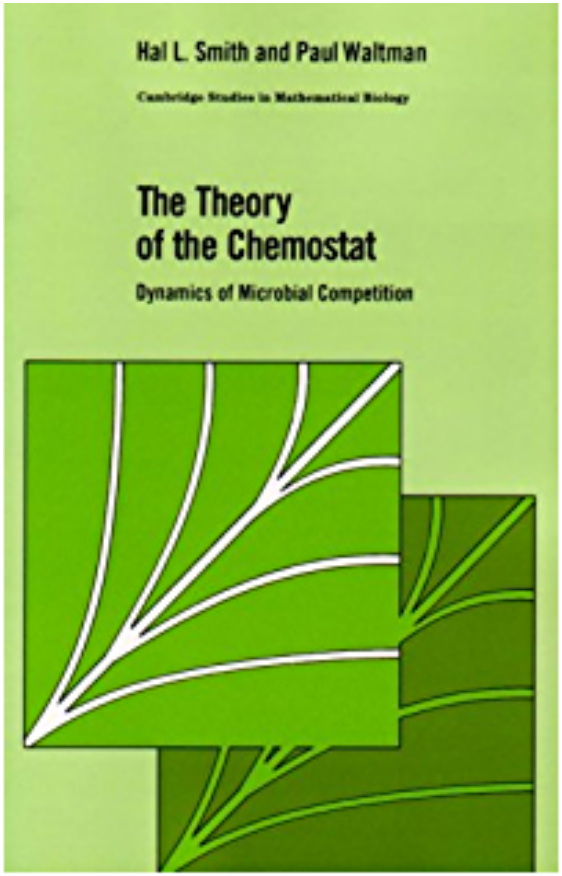
The Treasure network

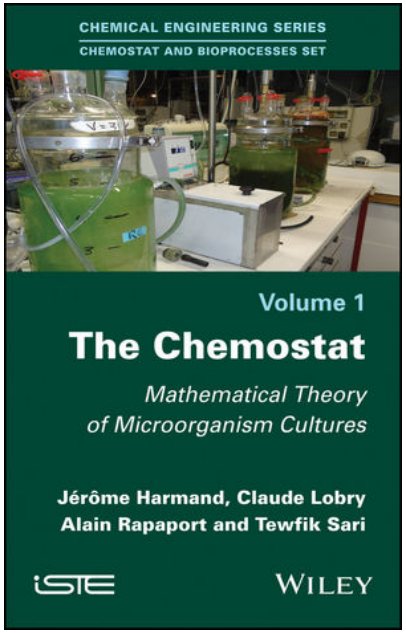
- TREASURE (for **Trea**tment and **Su**stainable **R**euse of **E**ffluents in semiarid climates) is an Euro-Mediterranean research network associating research labs and researchers about biological wastewater treatment plants and microbial ecosystems.
- Created in 2006. 15th anniversary, to be held in Tlemcen (Algeria) in November 2021
- Partners: Researchers and Labs in Algeria, Egypt, France, Greece, Italy, Lebanon, Morocco, Spain and Tunisia
- Coordinator : Jérôme Harmand, INRAE, Narbonne, France
- Seminars, summer schools and workshop (one per year)
- 25 Coadvised PhDs since 2010
- https://www6.inrae.fr/treasure/

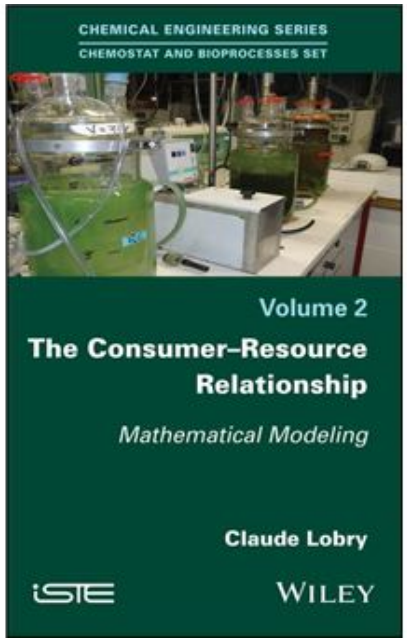
Some books on the chemostat

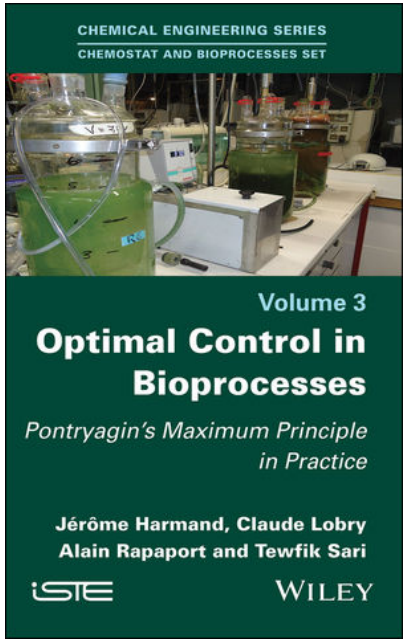


Some books on the chemostat

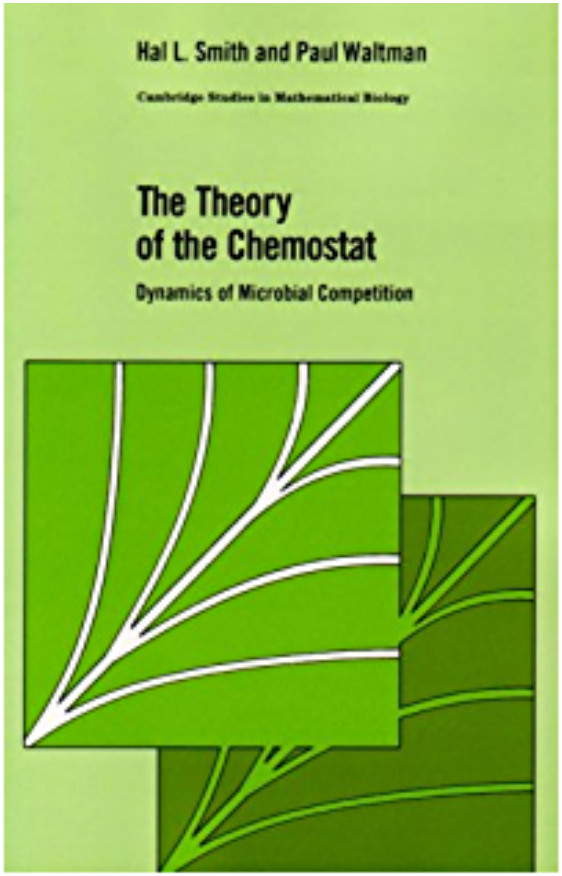


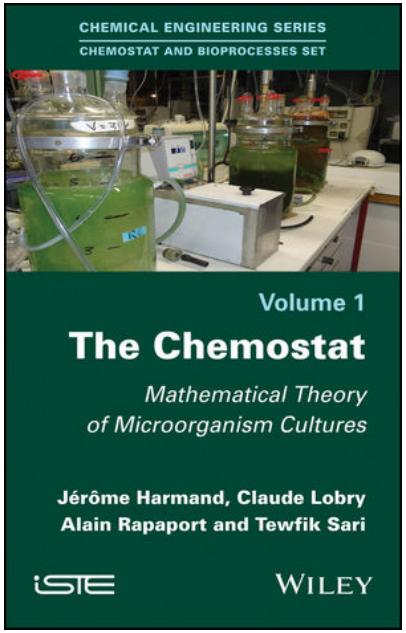


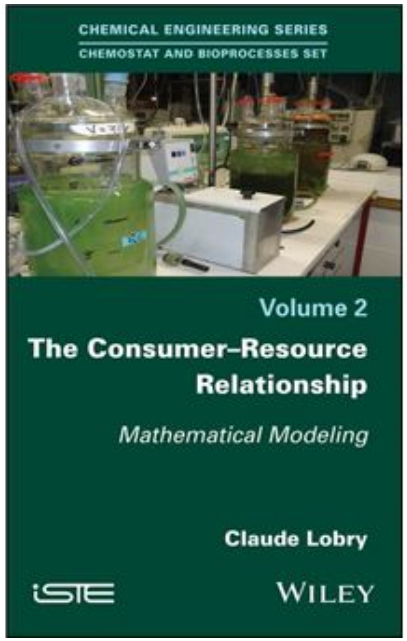


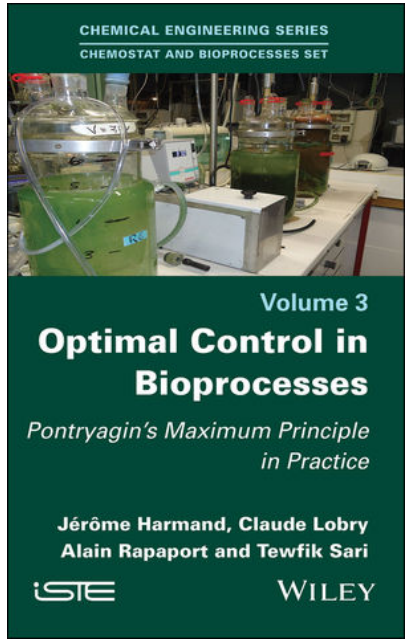


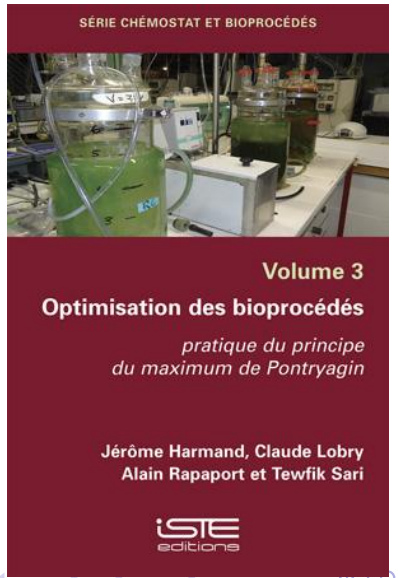
Some books on the chemostat











Thank you for your attention