



**INRA**  
SCIENCE & IMPACT

# Growth rate of microorganisms within an aerobic ecosystem : towards new evidence of density-dependent growth rate

E. Krichen, J. Hamelin, J. J. Godon, N. Bernet, R. Arditi, J. Harmand,  
*SAMI research team, LBE-INRA & INRA-INRIA MODEMIC research  
team*

# Who am I?



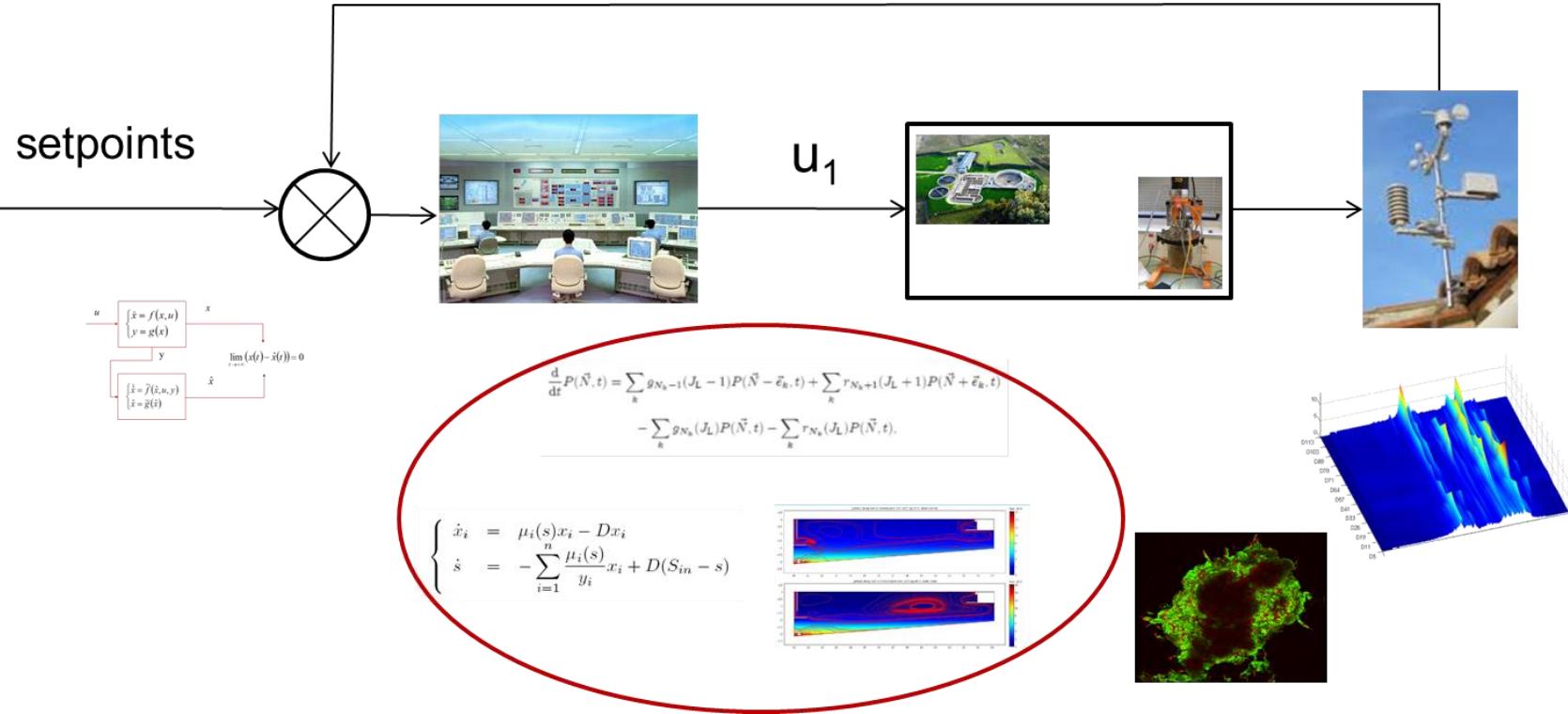
Neither a mathematician, nor a biologist,

I am...

...an engineer in automatic control!

*Modemic*

# Who am I?



# Who am I?



Treating and valorizing waste and biomass using the biological pathway within a framework of bio-refinery.

- Senior Researcher at the LBE-INRA (Environmental Biotechnology Laboratory) of the French National Institute in Agronomic Research in Narbonne.
- About 40 permanent people from INRA, 80 FTE people in total



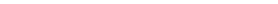


# CONTEXT

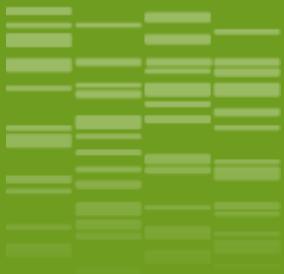
- ❖ A great interest in microbial ecosystem modelling to better understand them
- ❖ A historical controversy about microbial kinetics models
- ❖ Important practical consequences on overall ecosystem performances and on species coexistence



# CONTENT



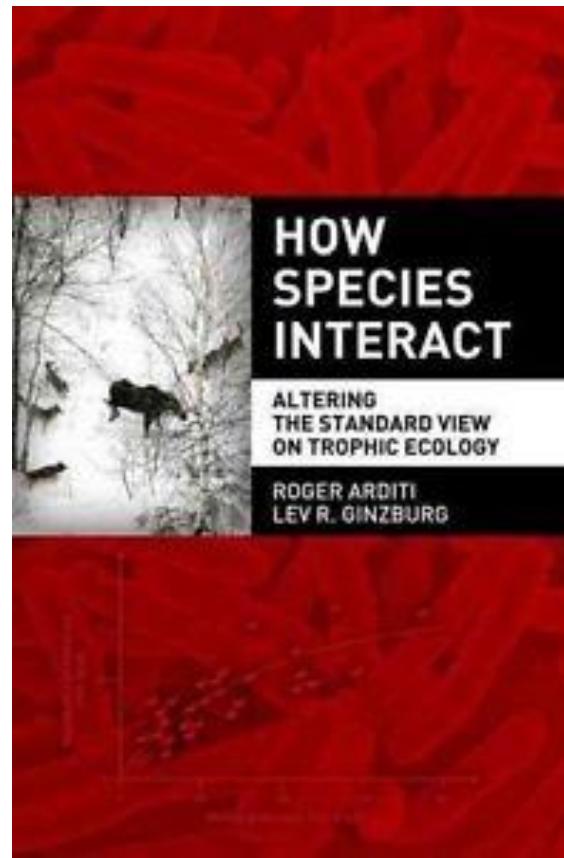
- ❖ Substrat vs density-dependent kinetics : use of retention biomass systems
- ❖ Substrate vs density-dependent kinetics : use of the chemostat
- ❖ Results
- ❖ Conclusions and perspectives



\_01

## **Substrate- vs density-dependent kinetics : use of biomass retention systems**

# SD vs DD : use of biomass retention systems



# SD vs DD : use of biomass retention systems

## □ Substrate-dependent growth rate → $\mu(S)$

- The most common in biotechnology: the Monod function
- No species coexistence in the chemostat (CEP)
- Equivalent to the prey-dependence functional response in ecology

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

## □ Density-dependence growth rate → $\mu(S,X)$

$$\mu\left(\frac{S}{X}\right) = \mu_{\max} \frac{S}{S + K_s X} = \mu_{\max} \frac{S / X}{S / X + K_s}$$

- A particular case: the Contois function – « a ratio-dependent » growth rate
- Known to usually allow a better model-data matching, notably for complex ecosystems
- Equivalent to ratio-dependence functional response in ecology
- Allows coexistence

# SD vs DD : use of biomass retention systems



Available online at [www.sciencedirect.com](http://www.sciencedirect.com)



C. R. Biologies 329 (2006) 40–46



<http://france.elsevier.com/direct/CRASS3/>

Biological modelling / Biomodélisation

A new hypothesis to explain the coexistence of  $n$  species  
in the presence of a single resource

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Presented by Michel Thellier

# SD vs DD : use of biomass retention systems

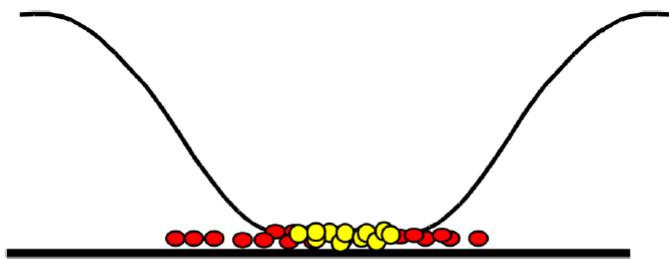


Fig. 5. Growth of a species in a 1D scheme.

Consider the scheme in Fig. 5. We have represented a one-dimensional profile of biomass (in red or dark grey) and substrate in black. Since the biomass is absorbing the substrate, if the diffusion is low compared to the rate of absorption a gradient of concentration is established. The concentration is low at the centre of the biomass since the incoming substrate is absorbed by the biomass that is at the boundary. In a stationary mode we see, on this one-dimensional scheme, that the growth of the population is not proportional to the total population but just on those that are at the two boundaries. The thickness of the layer where the concentration of substrate is positive does not depend on the size of the colony (if it is large enough), but only on the diffusion coefficient of the substrate. This means that, after some transient, the growth of the colony, instead of being exponential, is linear.

# SD vs DD : use of biomass retention systems

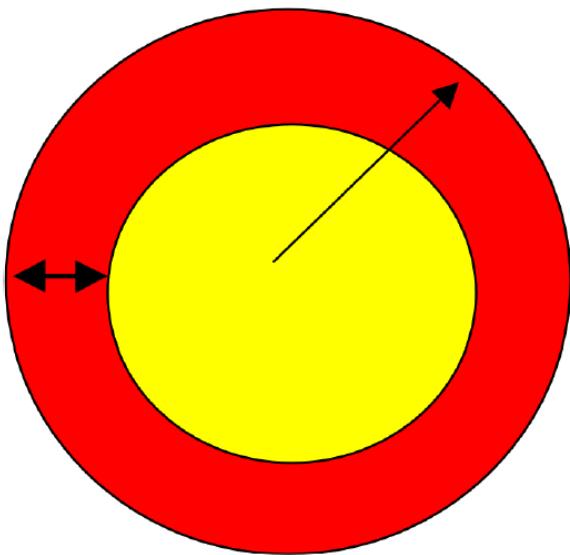


Fig. 6. Growth of a species in a 2D scheme.

For a two-dimensional scheme (Fig. 6) the total population (red or dark grey + yellow or light grey) is proportional to the radius of the ‘colony’, while the active population (the one that has access to the substrate) in red (or dark grey) is contained in the corona, whose thickness only depends on the parameter of diffusion of the substrate, but not on the size of the population. Since the surface of the circle is proportional to the square of the radius and the surface of the corona is proportional to the radius, it turns out that the growth equation is given by:

$$\frac{dX(t)}{dt} = k \sqrt[2]{X(t)} \quad (13)$$

In the case of a three-dimensional scheme (Fig. 7), using the same argumentation, we obtain a growth equation like  $\frac{dX(t)}{dt} = k(\sqrt[3]{X(t)})^2$ , which can be rewritten as  $\frac{dX(t)}{dt} = k \frac{1}{\sqrt[3]{X(t)}} X(t) = g(X(t))X(t)$  with a function  $g$  that is decreasing with  $X$ . This explains our choice for

# SD vs DD : use of biomass retention systems

P. De Leenheer, D. Angeli, E.D. Sontag, A feedback perspective for chemostat models with crowding effects, in: Lecture Notes in Control and Information Sciences, vol. 294, Springer, 2003, pp. 167–174.

The fact that biomass organizes into flocs  
and/or biofilms makes it exhibiting a density-dependent  
growth rate, **a consequence of which coexistence is possible...**

# SD vs DD : use of biomass retention systems



A1

## Modeling Bacteria Flocculation as Density-Dependent Growth

<sup>a</sup> Projet IN

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ssible...

DOI 10.1002/aic.11077

Published online January 2, 2007 in Wiley InterScience ([www.interscience.wiley.com](http://www.interscience.wiley.com)).

Keywords: flocculation, bacterial growth, density-dependence, population balance  
model, activated sludge process

# SD vs DD : use of biomass retention systems



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C. R. Biologies 329 (2006) 63–70



<http://france.elsevier.com/direct/CRASS3/>

Biomodélisation / Biological modelling

## Sur un modèle densité-dépendant de compétition pour une ressource

Claude Lobry, Alain Rapaport\*, Frédéric Mazenc

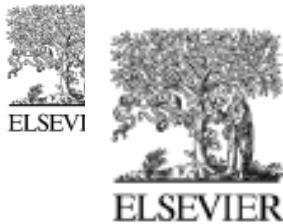
Projet MERE, INRA-INRIA, LASB ENSAM, 2, place Viala, 34060 Montpellier, France

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Présenté par Pierre Auger

# SD vs DD : use of biomass retention systems



Available online at [www.sciencedirect.com](http://www.sciencedirect.com)



C. R. Acad. Sci. Paris, Ser. I 340 (2005) 199–204



<http://france.elsevier.com/direct/CRASS1/>

Ordinary Differential Equations/Automation (theoretical)

\*<sup>a</sup>

## Persistence in ecological models of competition for a single resource

Claude Lobry, Frédéric Mazenc, Alain Rapaport

Projet INRA-INRIA 'MERE', UMR analyse des systèmes et biométrie, 2, place Viala, 34060 Montpellier, France

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Presented by Pierre-Louis Lions

Claude Lobry, Alain Rapaport\*, Frédéric Mazenc

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Présenté par Pierre Auger



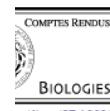
Claude Lobry, Alain Rapaport\*, Frédéric Mazenc

Projet MERE, INRA-INRIA, LASB ENSAM, 2, place Viala, 34060 Montpellier, France

Reçu le 10 juin 2005 ; accepté après révision le 15 novembre 2005

Disponible sur Internet le 20 décembre 2005

Présenté par Pierre Auger



# SD vs DD : use of biomass retention systems



*Journal of Biological Dynamics*  
Vol. 2, No. 1, January 2008, 1–13



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ce

[www.wiley.com](http://www.wiley.com)).  
population balance

A new

## How flocculation can explain coexistence in the chemostat

B. Haegeman<sup>a</sup> and A. Rapaport<sup>b\*</sup>

<sup>a</sup> Projet INRIA M.  
<sup>b</sup> Lal

<sup>a</sup> Laboratoire de Biotechnologie de l'Environnement, INRA, Avenue des Etangs, 11100 Narbonne, France;

<sup>b</sup> UMR Analyse des Systèmes et Biométrie 2 place Pierre Viala, 34060 Montpellier, France



(Received 21 September 2006; final version received 18 June 2007)

We study a chemostat model in which two microbial species grow on a single resource. We show that species coexistence is possible when the species which would normally win the exclusive competition aggregates in flocs. Our mathematical analysis exploits the fact that flocculation is fast compared to biological growth, a common hypothesis in floc models. A numerical study shows the validity of this approach in a large parameter range. We indicate how our model yields a mechanistic justification for the so-called density-dependent growth.

**Keywords:** chemostat; flocculation; competition; persistence; density-dependence

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Received 18 November 2004; accepted 17 December 2004

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Presented by Pierre-Louis Lions

Internet le 20 décembre 2005

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# SD vs DD : use of biomass retention systems



**Empirical Evidence of the Role of Heterogeneity in Ratio-Dependent Consumption**



Roger Arditi; Henni Saiah

*Ecology*, Vol. 73, No. 5 (Oct., 1992), 1544-1551.

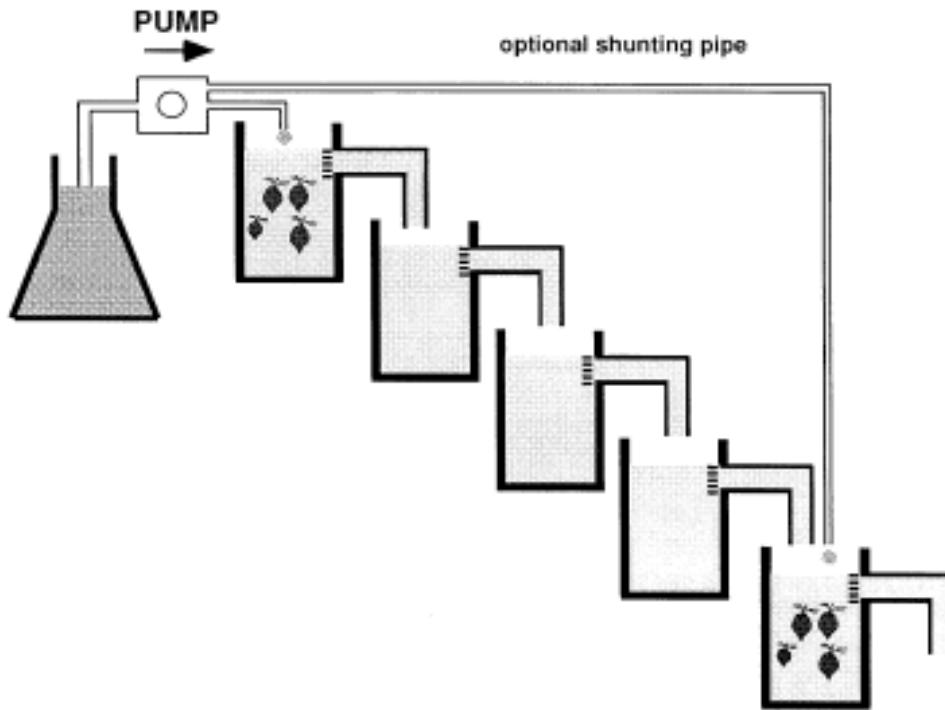
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<http://links.jstor.org/sici?&sici=0012-9658%28199210%2973%3A5%3C1544%3AEBOTRO%3E2.0.CO%3B2-8>

*Ecology* is currently published by The Ecological Society of America.

# SD vs DD : use of biomass retention systems

Experimental evidence of density-dependent growth rate : Experience #1



- If no profile in concentrations along the vessels  $\rightarrow \mu(S)$
- If profile along the different vessels  $\rightarrow \mu(S/X)$

# SD vs DD : use of biomass retention systems

$$\begin{cases} \dot{X}_i = (\mu(\cdot) - m)X_i \\ \dot{S}_i = (S_{i-1} - S_i)D - \mu(\cdot)X_i \\ S_0 = S_{in} \end{cases}$$

- If substrate-dependence growth rate : no profile

$$\begin{cases} \dot{X}_i = (\mu(S_i) - m)X_i = 0 \\ \dot{S}_i = (S_{i-1} - S_i)D - \mu(S_i)X_i = 0 \\ S_0 = S_{in} \end{cases} \quad \xrightarrow{\qquad\qquad\qquad} \quad \begin{aligned} \mu(\bar{S}_i) &= m \Big|_{\forall i} \\ &\quad \& \\ X_i &\Big|_{i>1} = 0 \end{aligned}$$

# SD vs DD : use of biomass retention systems

$$\begin{cases} \dot{X}_i = (\mu(\cdot) - m)X_i \\ \dot{S}_i = (S_{i-1} - S_i)D - \mu(\cdot)X_i \\ S_0 = S_{in} \end{cases}$$

□ If density-dependence growth rate : profile

$$\begin{cases} \dot{X}_i = (\mu(S_i, X_i) - m)X_i = 0 \\ \dot{S}_i = (S_{i-1} - S_i)D - \mu(S_i, X_i)X_i = 0 \\ S_0 = S_{in} \end{cases} \xrightarrow{\hspace{1cm}} \begin{cases} \mu(\bar{S}_i, \bar{X}_i) = m \\ (S_{i-1} - S_i)D = mX_i \end{cases}_{\forall i}$$

# SD vs DD : use of biomass retention systems

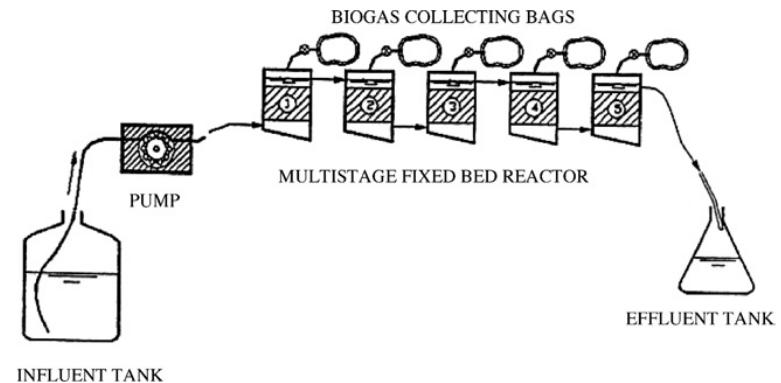
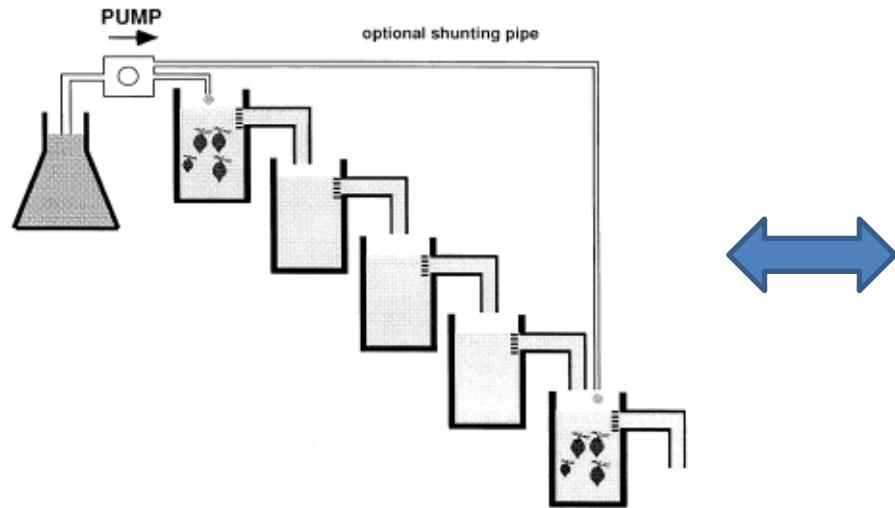
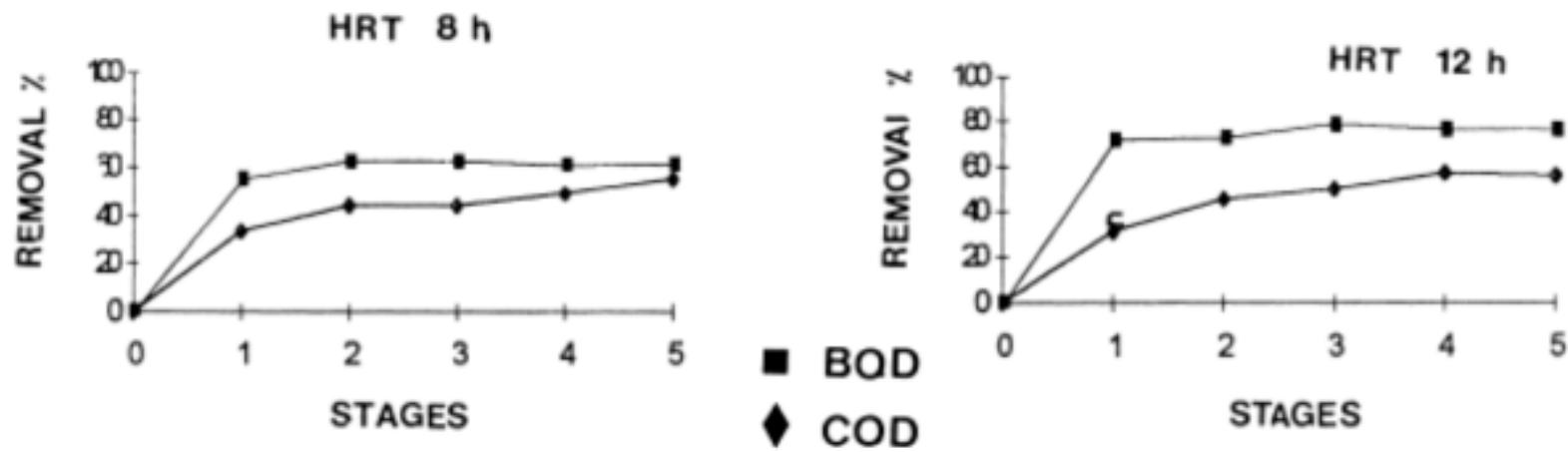


Fig. 2 – Experimental process configuration used by Reyes et al. (1999)\*.

# SD vs DD : use of biomass retention systems



# SD vs DD : use of biomass retention systems

Testing the « robustness » of the approach with respect to the retention of the biomass

$$\begin{cases} \dot{X}_i = D(\alpha_{i-1}X_{i-1} - \alpha_i DX_i) + (\mu(\cdot) - m)X_i = 0 \\ \dot{S}_i = (S_{i-1} - S_i)D - \mu(S_i, X_i)X_i = 0 \\ S_0 = S_{in} \end{cases}$$

# SD vs DD : use of biomass retention systems

ECOLOGICAL MODELLING 200 (2007) 393–402

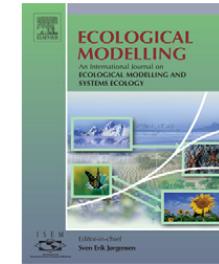


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journal homepage: [www.elsevier.com/locate/ecolmodel](http://www.elsevier.com/locate/ecolmodel)



## Density-dependent kinetics models for a simple description of complex phenomena in macroscopic mass-balance modeling of bioreactors

J. Harmand\*, J.J. Godon

Laboratoire de Biotechnologie de l'Environnement, INRA-LBE, Avenue des étangs, 11100 Narbonne, France

With realistic model parameters, we have shown that the qualitative profile behavior was quite robust with respect to alpha, HG (2007) Ecological Modelling.

# SD vs DD : use of biomass retention systems

Experimental evidence of density-dependent growth rate : Experience #2 - Proposal by RA from experiences reported (and realized!) by Margalef.

RAMÓN MARGALEF

## Perspectives in Ecological Theory

*Standard Book Number: 226-50505-7*

*Library of Congress Catalog Card Number: 68-27291*

THE UNIVERSITY OF CHICAGO PRESS, CHICAGO 60637

The University of Chicago Press, Ltd., London

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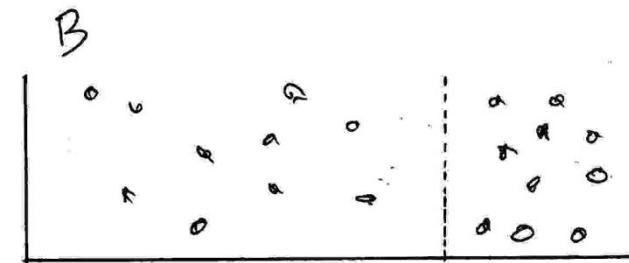
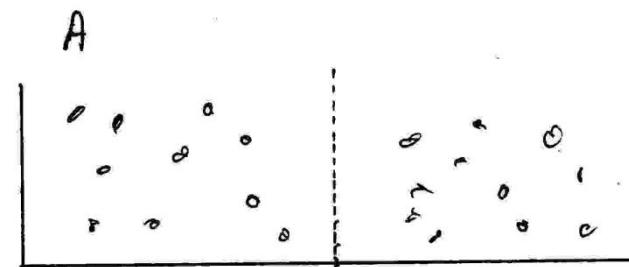
*Published 1968*

*Third Impression 1970*

*Printed in the United States of America*

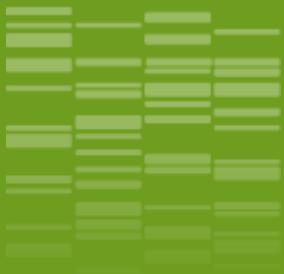
# SD vs DD : use of biomass retention systems

Suppose we have a uniform suspension of several organisms, and a number of them move across a division line from one half of the space to the other half. The population experiences dilution in one part and an increase in concentration in the other. This experiment can be easily done in a U-shaped culture vessel in which the branches are separated by a fritted glass filter that allows passage of the fluid but not the cells. If, after a reasonable time-allowance for development of the mixed population, pressure is used to pump some water across the filter, increasing the volume of one side at the expense of the volume of the other, we have achieved an expansion and a contraction of equivalent systems. I have often done this experiment in practical work with students, and the more dilute subsystem always reacts rapidly and shows characteristics of diminished maturity (lower diversity and a higher ratio of primary production of biomass). Simultaneously, the maturity of other population increases. It is easy to understand that the rate of division is reduced among the more crowded cells and that the more dispersed cells are free to multiply faster; in doing so, the latter show an increase limited, at least in the beginning, to one or a few dominant species. The experiment is, of course, trivial, but it suggests further work in the study of the relations between organization, space, and movements.



# SD vs DD : use of biomass retention systems

- It is very difficult to observe continuously biomass growth rate
- It is difficult to completely isolate a microbial ecosystem while allowing the circulation of substrate
- We could first test alternative experiments...



\_02

## **Substrate- vs density-dependent kinetics : use of the chemostat**

# SD vs DD : Contois's approach

... where (see HARMAND et al. 1990), where

$$R_c = \frac{R_m S_0}{A + S_0}. \quad (6)$$

Estimates of  $R_c$  can be obtained for each culture from the intersection on the  $y$ -axis of the curve giving  $R$  as a function of  $P_e$  (Fig. 2). Of particular interest is the fact that the estimates of  $R_c$  are the same for each culture with the same nitrogen and carbon sources, irrespective of the kind or concentration of the limiting nutrient. Thus, from equation (6), the ratio of the values of  $A$  for each of two such cultures is equal to the ratio of their values of  $S_0$ , or

$$\frac{A'}{A''} = \frac{S'_0}{S''_0}.$$

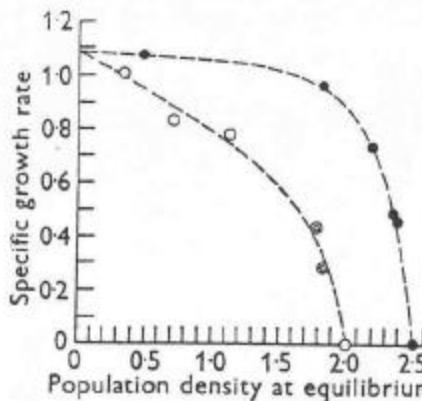


Fig. 2a

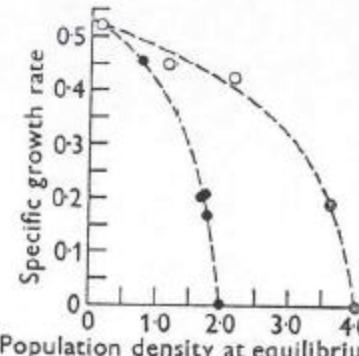


Fig. 2b

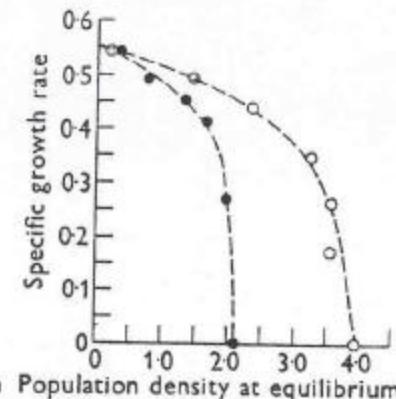


Fig. 2c

# SD vs DD : Contois's approach

$$\frac{1}{R} = \frac{1}{R_m} + \left( \frac{A}{R_m} \right) \left( \frac{1}{S_e} \right). \quad (7)$$

If  $A$  is a function of  $S_0$ ,  $1/R$  should be a linear function of  $1/S_e$  for each culture, but with slope dependent upon  $S_0$ . Figure 4 shows regressions of  $1/S_e$  upon  $1/R$  for the data of Tables 2 and 3 fitted by the method of least squares. The slopes of the regression lines are, respectively, 3.66 and 5.90 for cultures 2A and 2B;

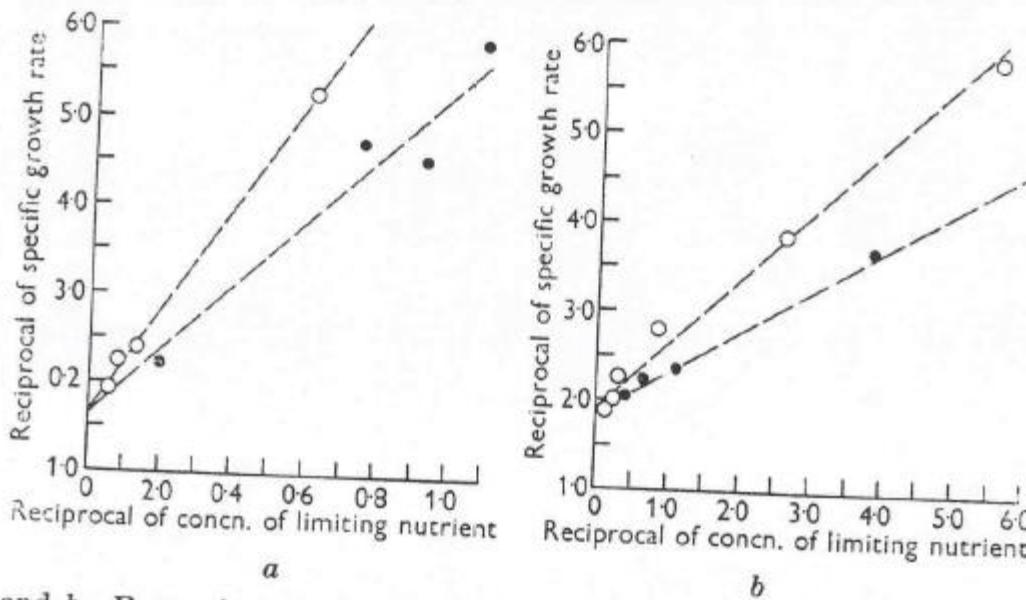


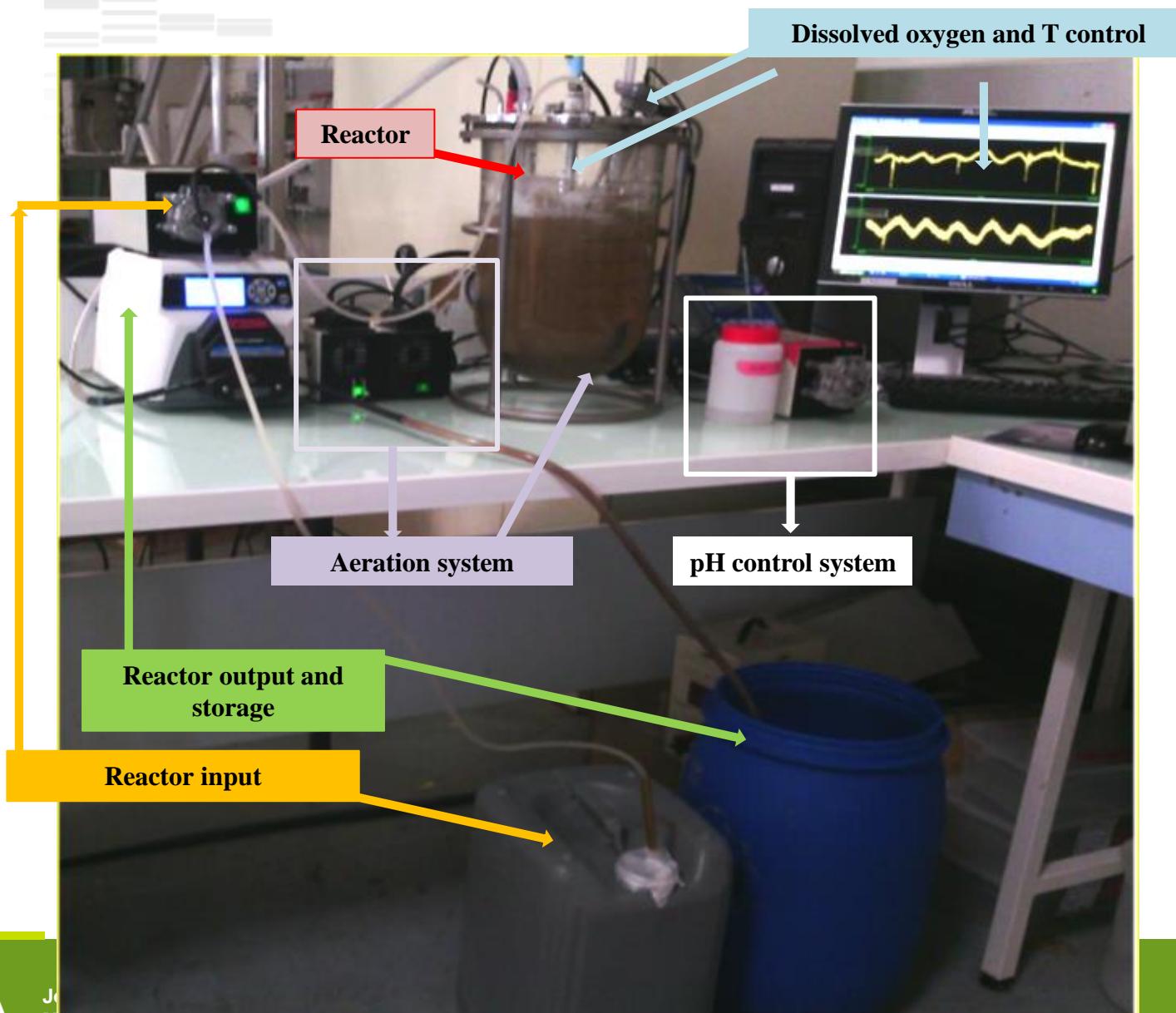
Fig. 4a and b. Regression of reciprocals of the concentration of limiting nutrient upon reciprocals of specific growth rate in continuous cultures of *Aerobacter aerogenes*.  
(a) Data of Table 2; ● = culture 2A, ○ = culture 2B. (b) Data of Table 3; ● = culture 3A, ○ = culture 3B.

# SD vs DD : use of the chemostat

$$\begin{cases} \dot{X} = (\mu(\cdot) - m)X \\ \dot{S} = (S_{in} - S)D - \mu(\cdot)X \end{cases}$$

- If  $\mu(\cdot) = \mu(S)$  then the steady state  $S$  **does not** depend on  $S_{in}$
- If  $\mu(\cdot) = \mu(S, X)$  then the steady state  $S$  **does** depend on  $S_{in}$

# SD vs DD : use of the chemostat



# SD vs DD : use of the chemostat

- Inoculum: aerobic biomass from the WWTP of Narbonne
- Limiting substrate : ethanol from (bad!) wine from the Narbonne area (about 80% of the total COD)
- Complemented with P ( $\text{NH}_4\text{H}_2\text{PO}_4$ ) and N ( $\text{NH}_4\text{Cl}$ ) with a C/N/P ratio of 100/5/1

# SD vs DD : use of the chemostat

SE1:

Increasing input concentrations Sin.  
Low towards high biomass  
concentrations

1g/l

2g/l

4g/l

SE2:

Decreasing input concentrations  
Sin. High towards low biomass  
concentrations

8g/l

6g/l

4g/l

2g/l

1g/l



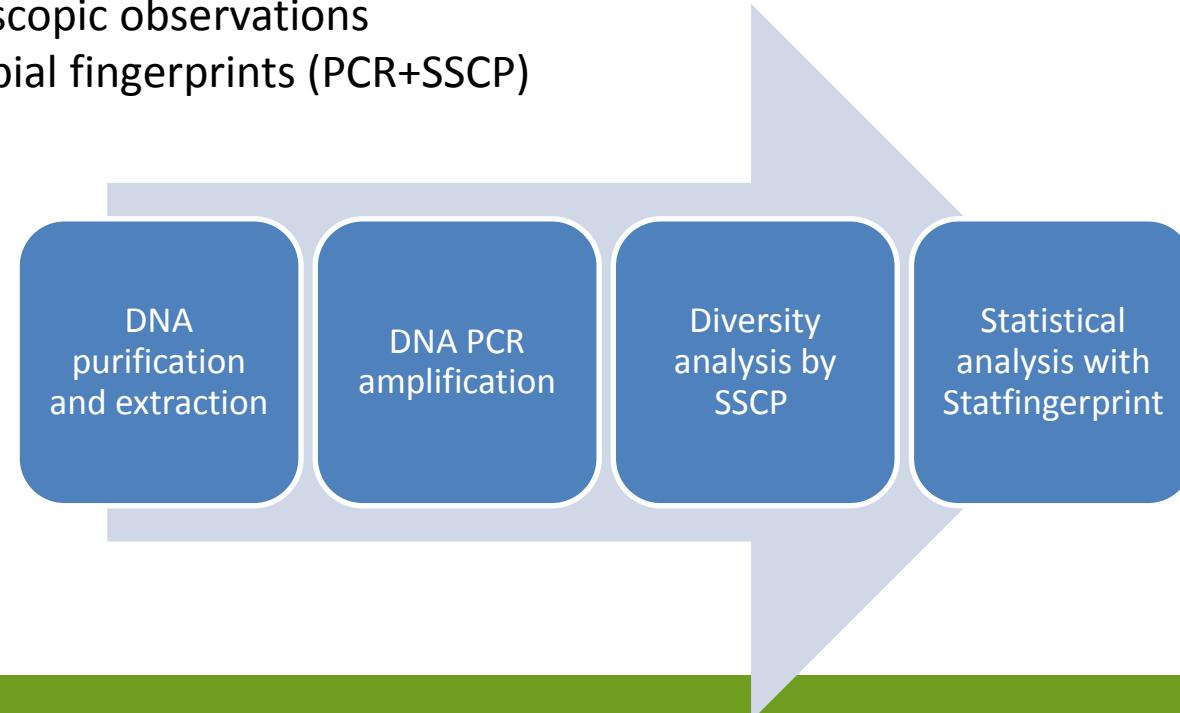
# SD vs DD : use of the chemostat

## □ Classical monitoring:

- SS: Suspended Solids (the active biomass)
- sCOD: soluble Chemical Oxygen Demand
- Sin: Total COD in the input

## □ Other measurements

- Granulometry
- Microscopic observations
- Microbial fingerprints (PCR+SSCP)



# SD vs DD : use of the chemostat

One general model

$$\mu(S, X) = \mu_{\max} \frac{S}{X^\alpha + aS + b}$$

Model #1

$$\mu(S, X) = \mu_{\max} \frac{S}{X^\alpha}$$

Model #3 (Contois)

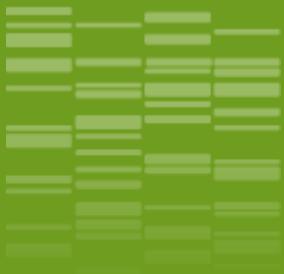
$$\mu\left(\frac{S}{X}\right) = \mu_{\max} \frac{\frac{S}{X}}{a + \frac{S}{X}} = \mu_{\max} \frac{S}{aX + S}$$

Model #2

$$\mu(S, X) = \mu_{\max} \frac{S}{X^\alpha + a}$$

Model #4 (Monod)

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

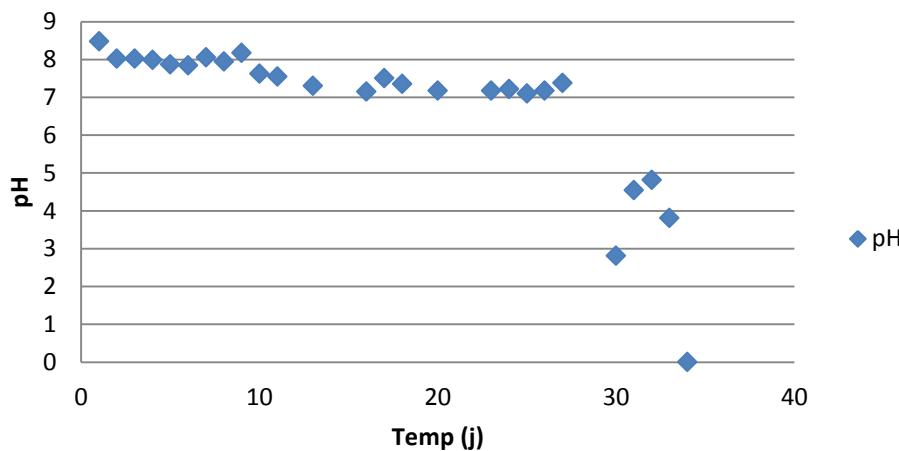


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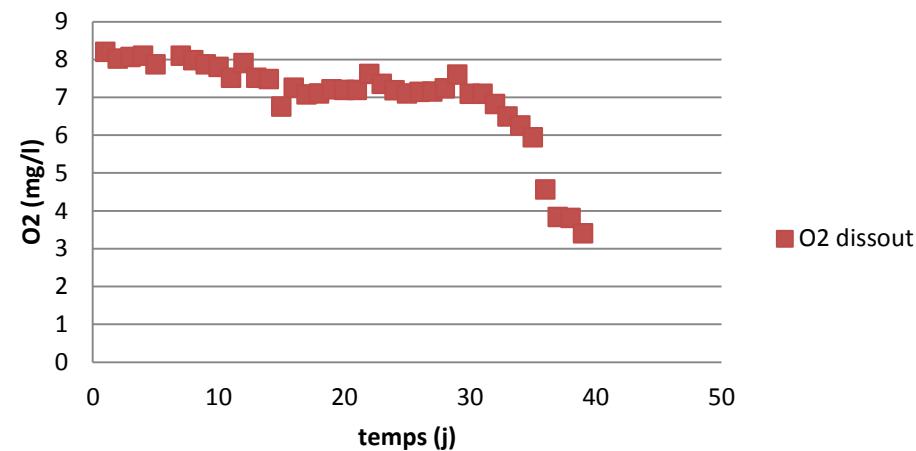
## Results

# Evidence of problems with data from SE1 (for $\text{SiN} = 2$ and $4\text{g/L}$ )

pH dynamic during SE1

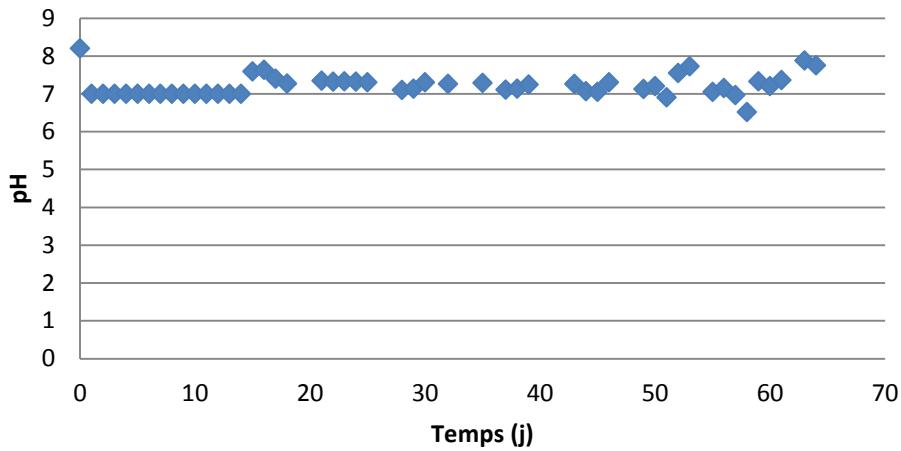


DO dynamic during SE1

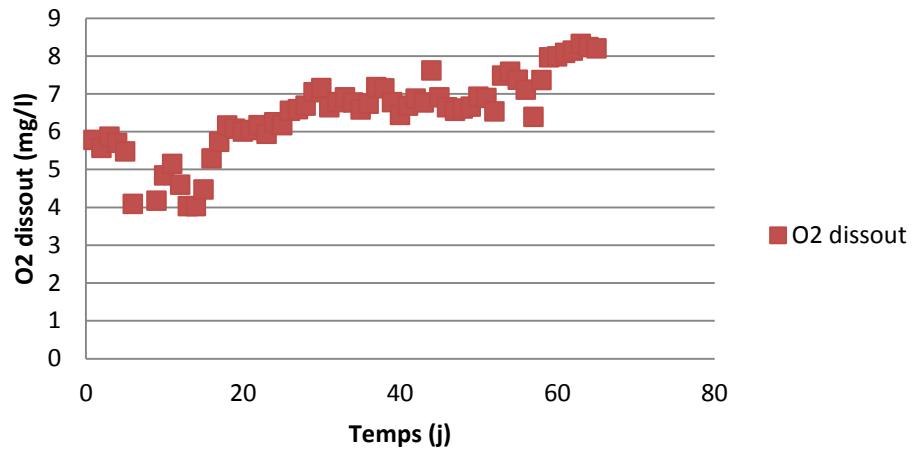


# Regulation of pH and DO for SE2

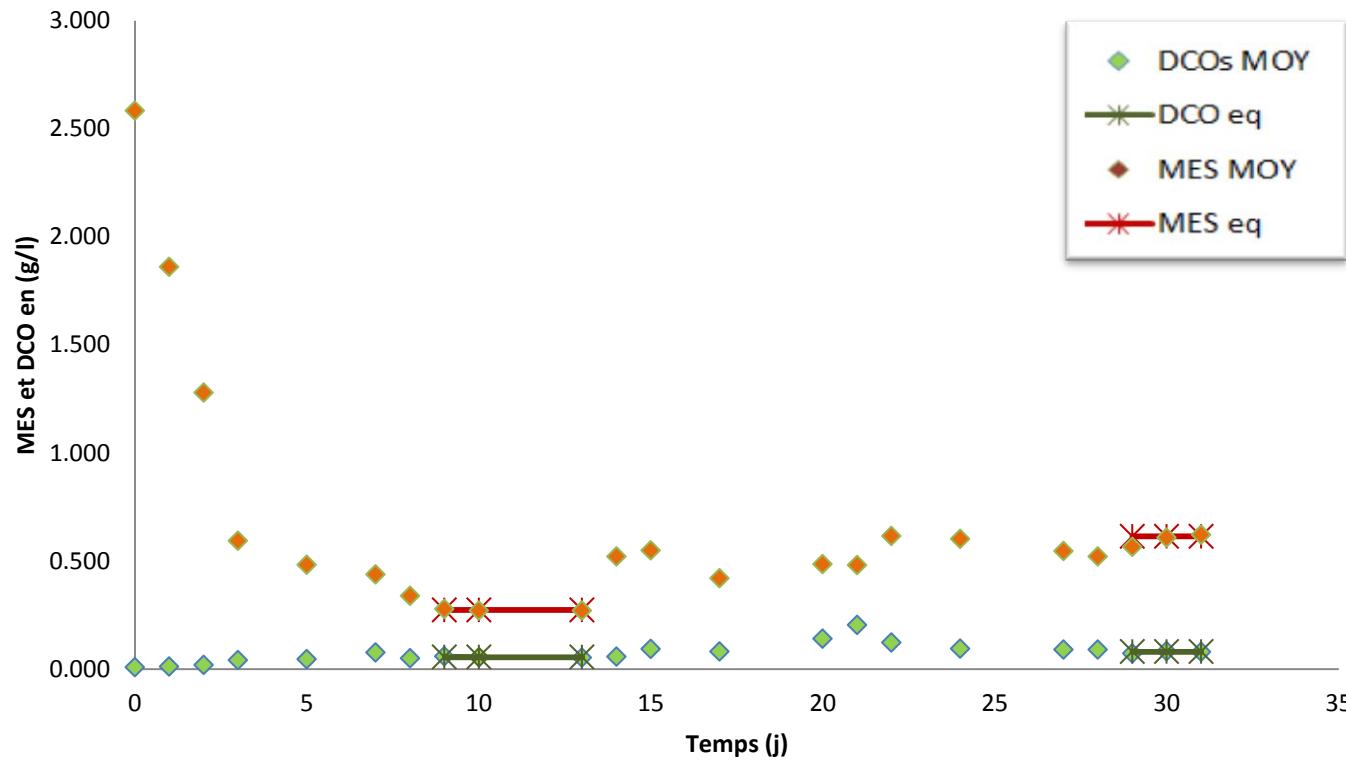
Variation du pH pour SE2



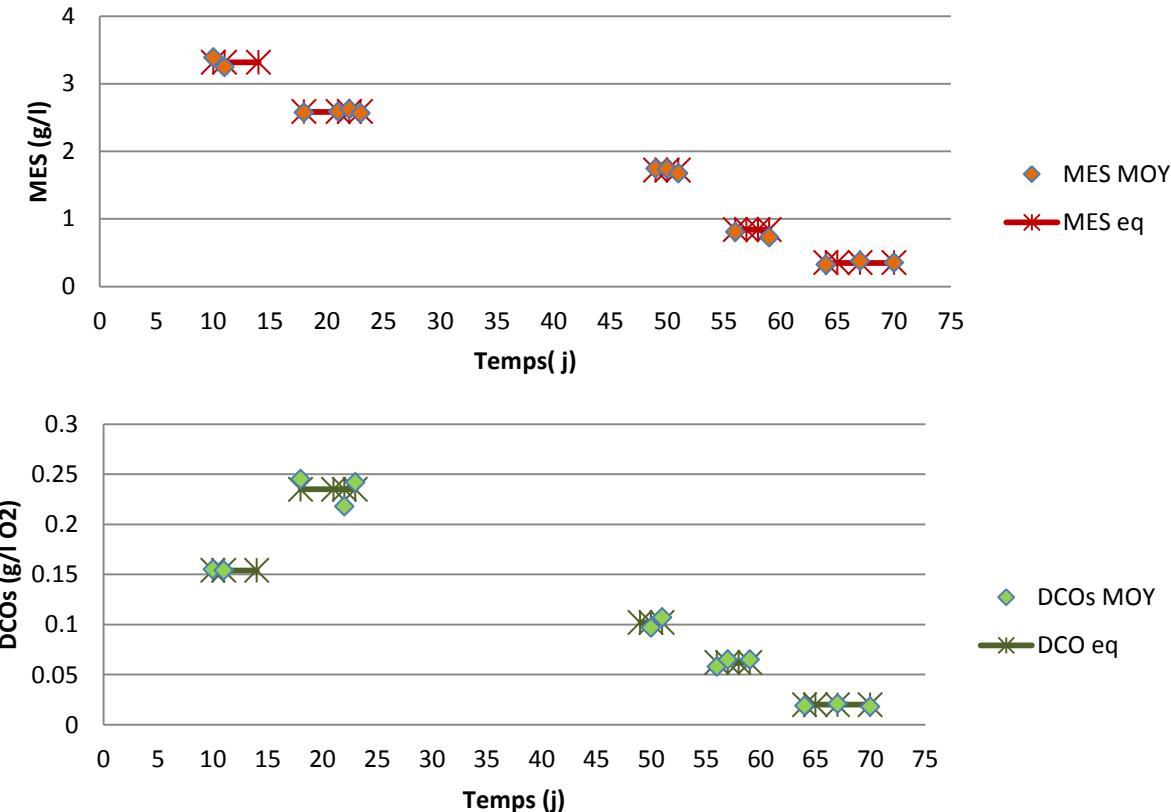
Variation de l'O2 dissout



# SS and COD

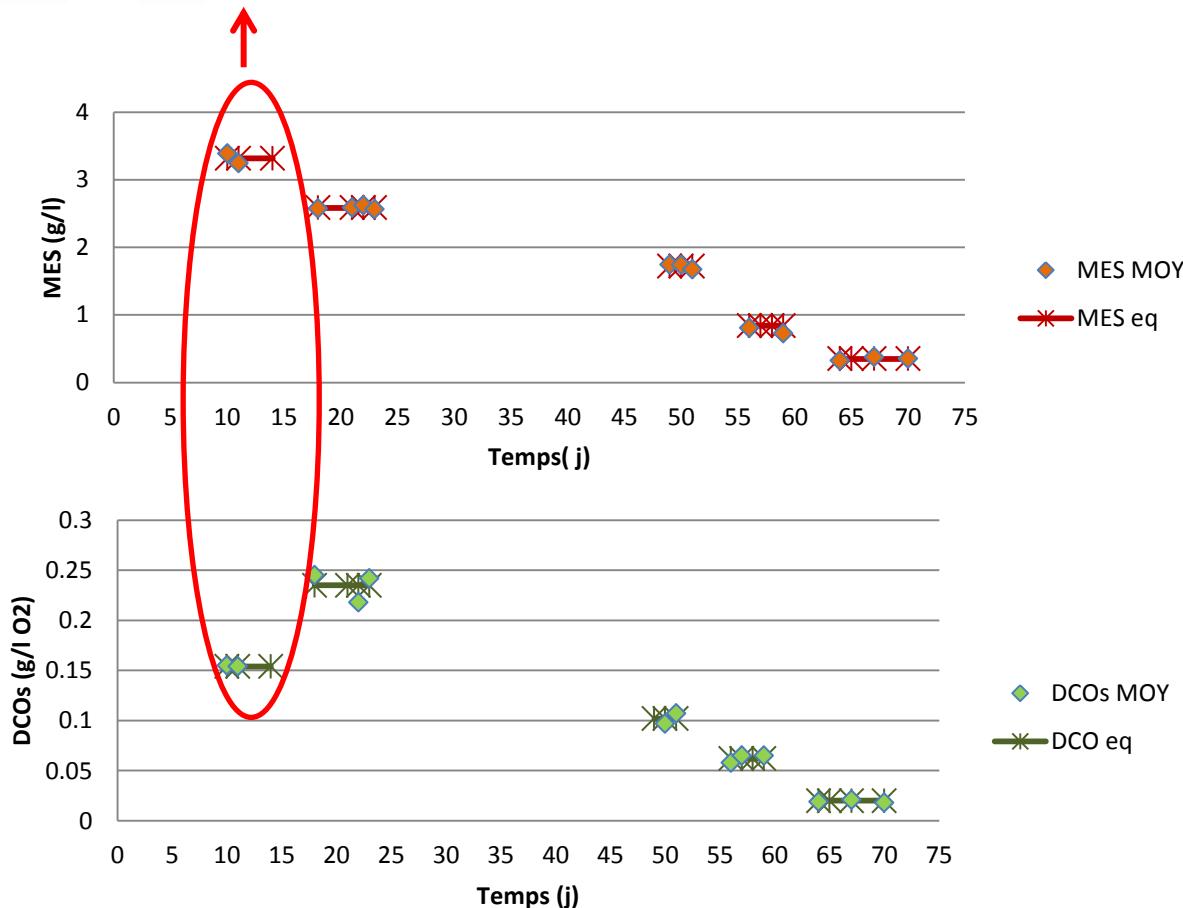


# Steady states



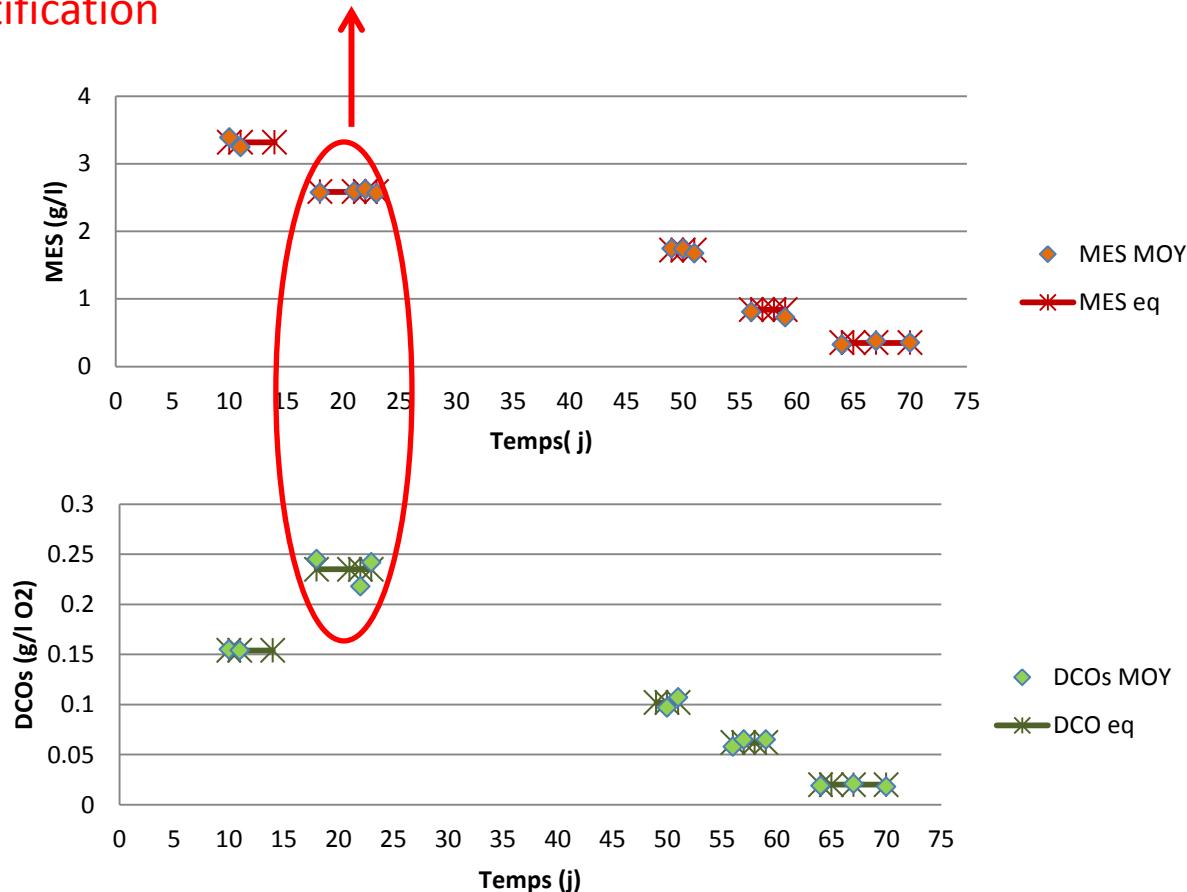
# Steady states

Pb: pump and measurement problems – Exclusion of data for identification



# Steady states

Pb: when the wine changed (at  $S_{in}=5\text{g/L}$ ), X decreased while  $S_{in}$  increased (we expect this is due to oxygen depletion after the overload) – Exclusion of data for identification



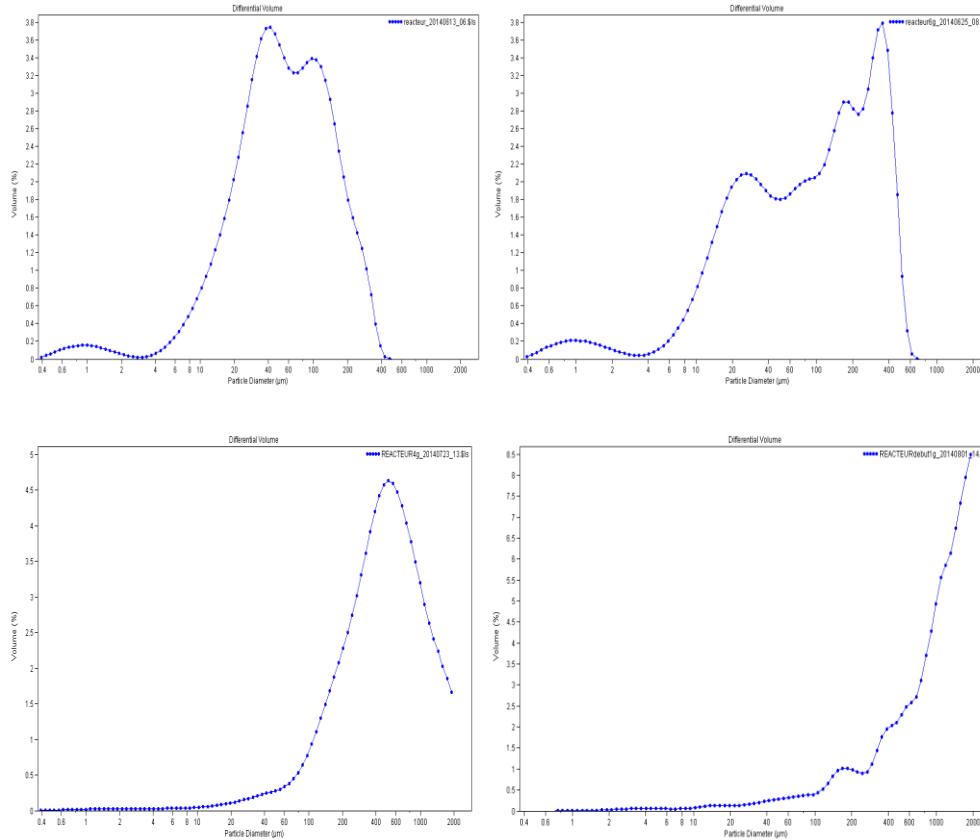
# Steady states

	Série 1 (SE1)		Série 2 (SE2)		
Sin	Sin=0,916	Sin=1,950	Sin=3,930	Sin=2,002	Sin=0,947
X (g/l)	0,273	0,614	1,705	0,838	0,349
S (g/l O <sub>2</sub> )	0,055	0,08	0,102	0,062	0,02
ΔS	0,025		0,04	0,042	
S/X	0,202	0,13	0,06	0,074	0,056
Δ(S/X)	0,072		0,014	0,018	

Conclusion from the analysis of « raw data »:  
Neither « pure » Monod nor Contois...

# Granumoletry (only for SE2)

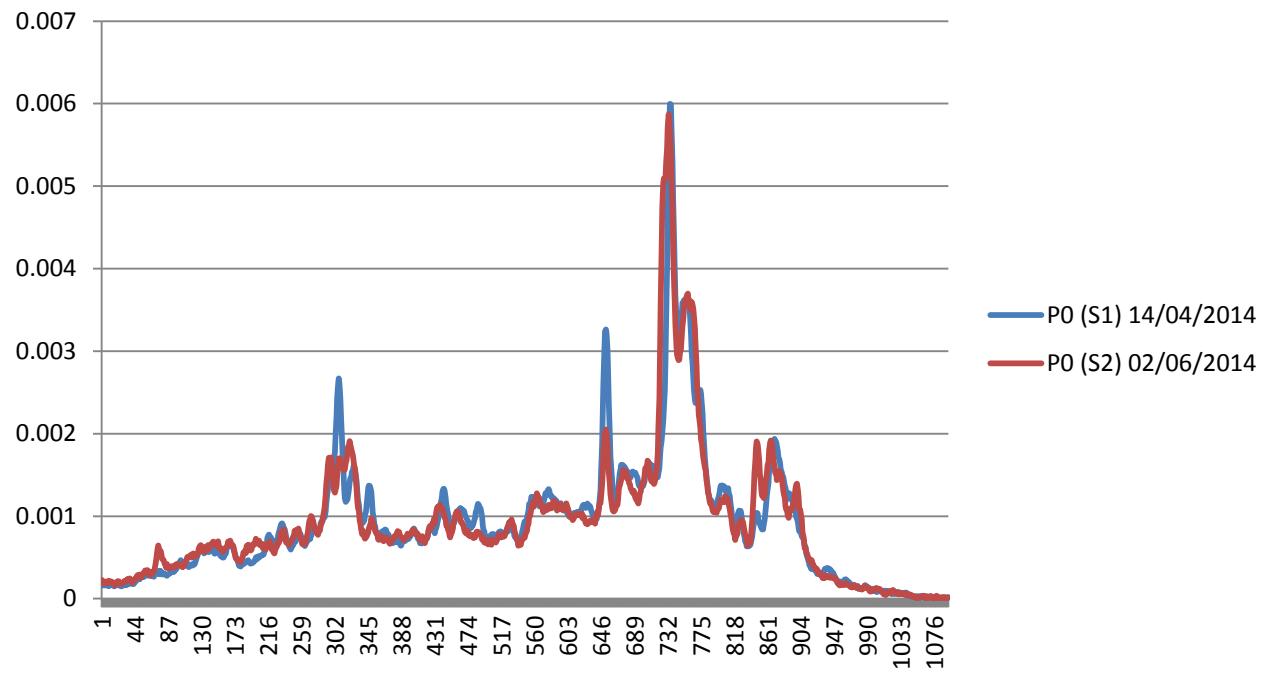
Smaller the Sin, larger the flocs!



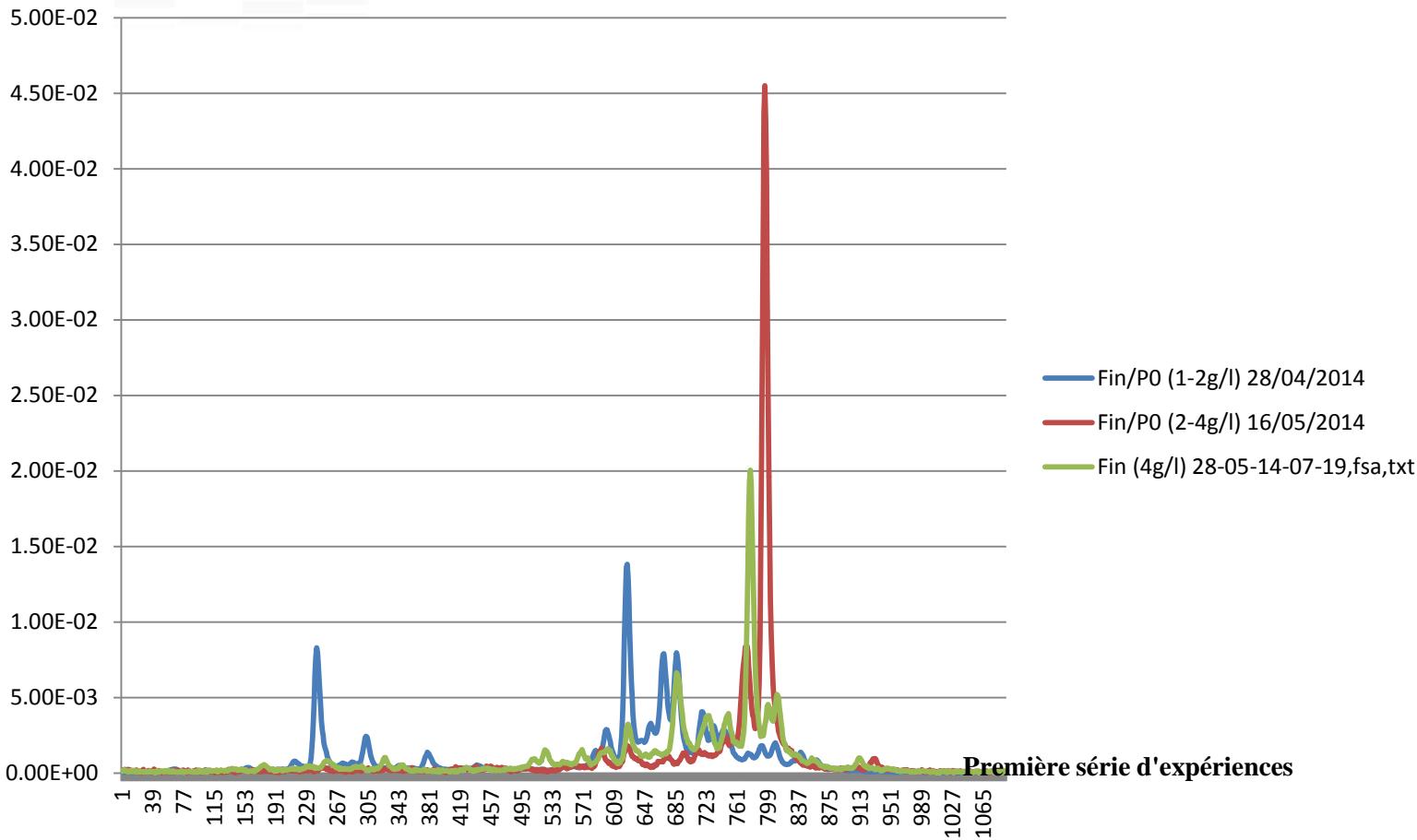
Sin decreasing  $\Leftrightarrow$  structuration of the bacteria in flocs

# Molecular biology

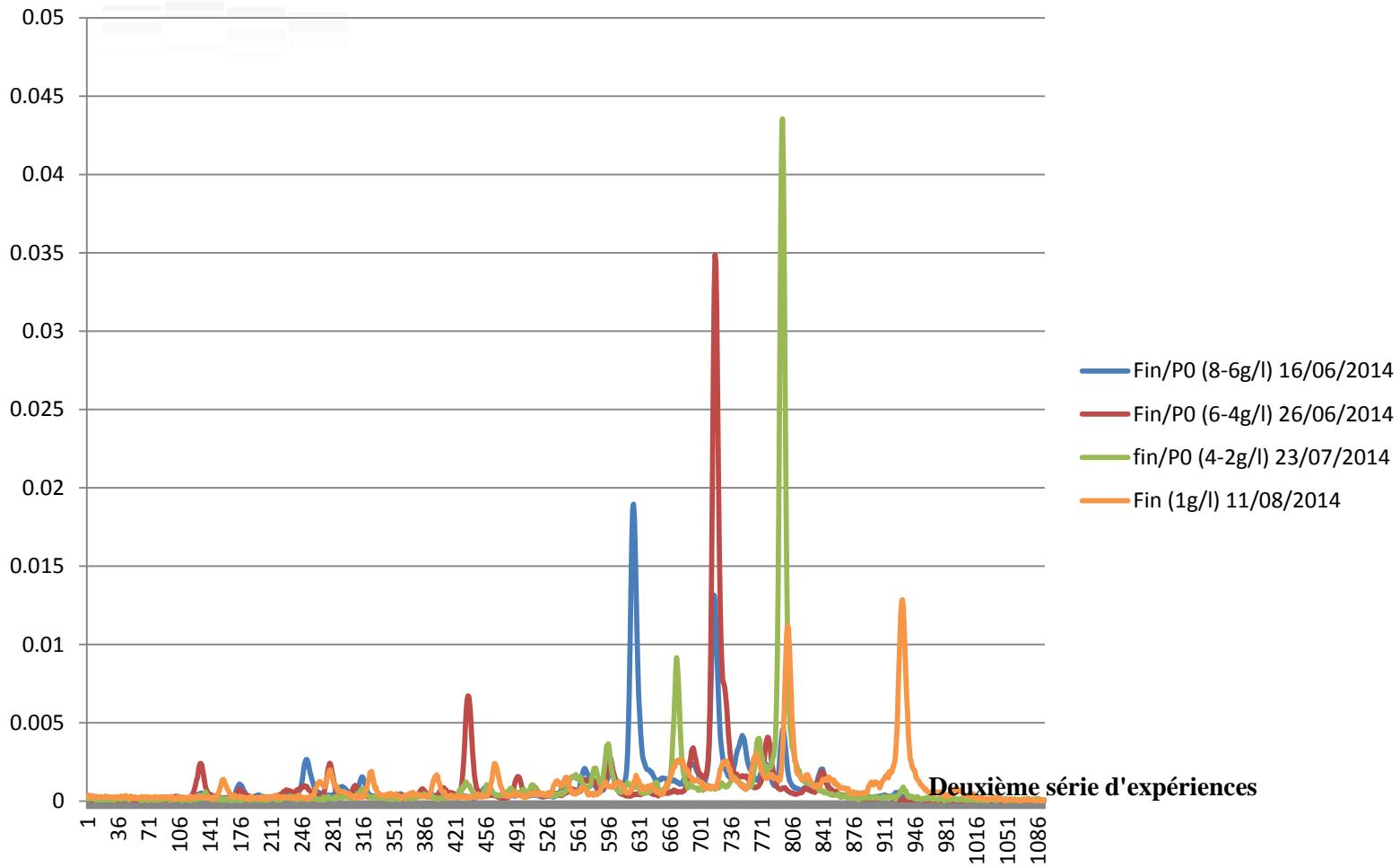
Complex inocula from Narbonne's WWTP (aerobic system)



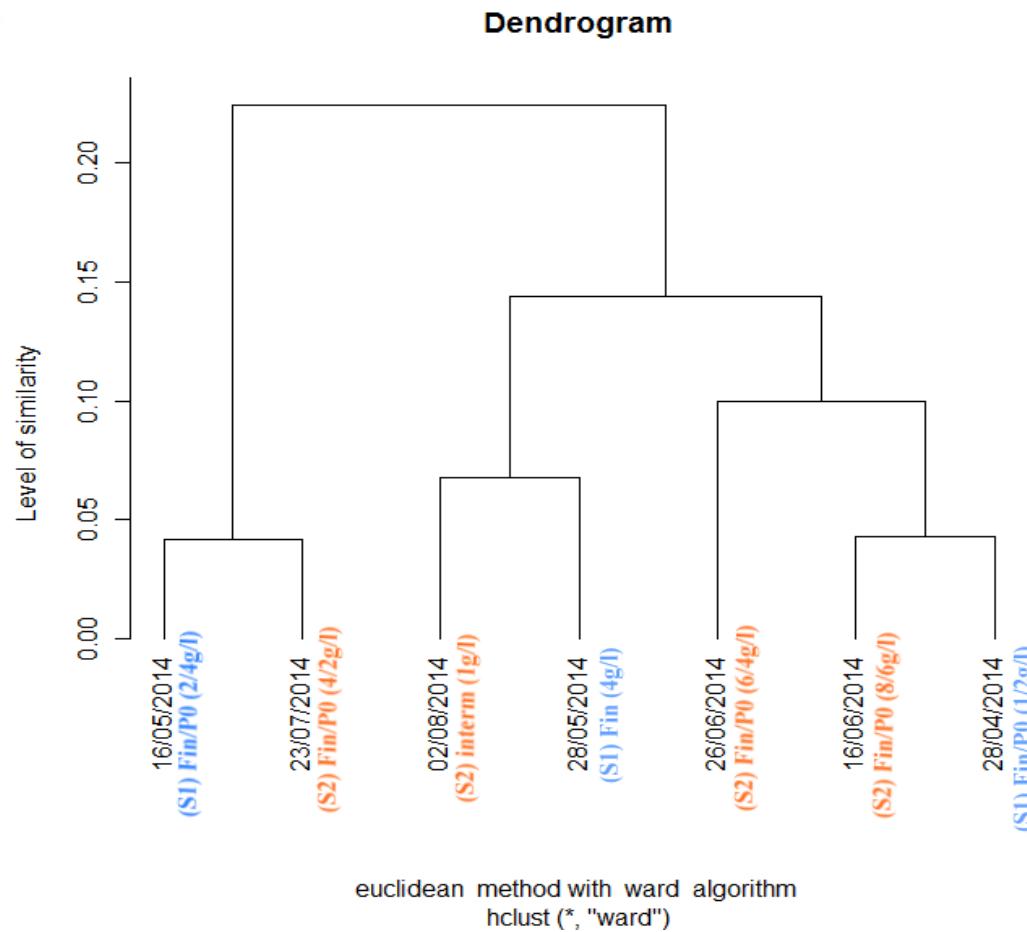
# Molecular biology



# Molecular biology



# Molecular biology



# Molecular biology

Sin	Position	Sample	Number_of_Peaks	minus_log_Simpson	1_minus_Simpson
1g/l	P0 <sub>1</sub>	14-04-14	32	5,03181585	0,99347305
	inter	20-04-14	11	2,74102012	0,93549549
2g/l	fin / P0	28-04-14	19	3,39710054	0,96652983
	inter	06-05-14	28	4,47599853	0,98862115
4g/l	fin/P0	16-05-14	9	1,96756095	0,86020259
	inter	22-05-14	17	3,60197554	0,9727302
	fin/P0	28-05-14	20	3,43884443	0,96789824

# Molecular biology

8g/l	P0 <sub>2</sub>	02-06-14	38	6,03617806	0,99760932
	inter	06-06-14	16	3,35000663	0,96491588
	fin/P0	16-06-14	16	3,15513331	0,95736728
6g/l	inter	20-06-14	10	2,34228466	0,90389219
	fin	26-06-14	17	2,23618943	0,89313505
	P0	27-06-14	16	2,33088957	0,90279077
4g/l	inter	30-06-14	21	3,18047805	0,95843422
	inter	04-07-14	20	2,97036081	0,9487152
	inter	11-07-14	21	2,00671292	0,86557017
	inter	17-07-14	7	1,91613	0,85282457
	fin/P0	23-07-14	16	2,0964877	0,87711271
	inter	28-07-14	16	2,97766021	0,94908818
2g/l	fin/P0	31-07-14	23	3,32422731	0,96399967
	inter	02-08-14	18	2,03074237	0,86876194
	inter	06-08-14	34	3,84963304	0,97871245
	inter	11-08-14	25	3,64312032	0,97382944
	fin	13-08-14	38	4,03030716	0,98223113

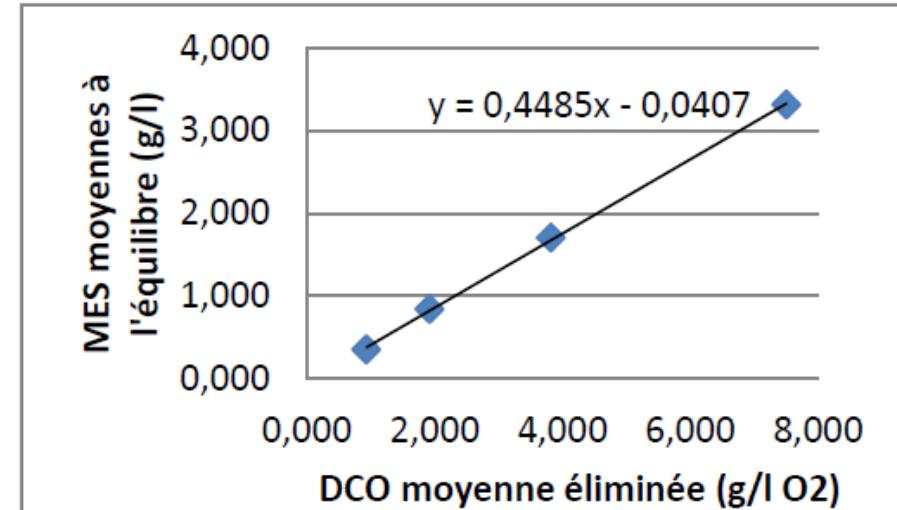
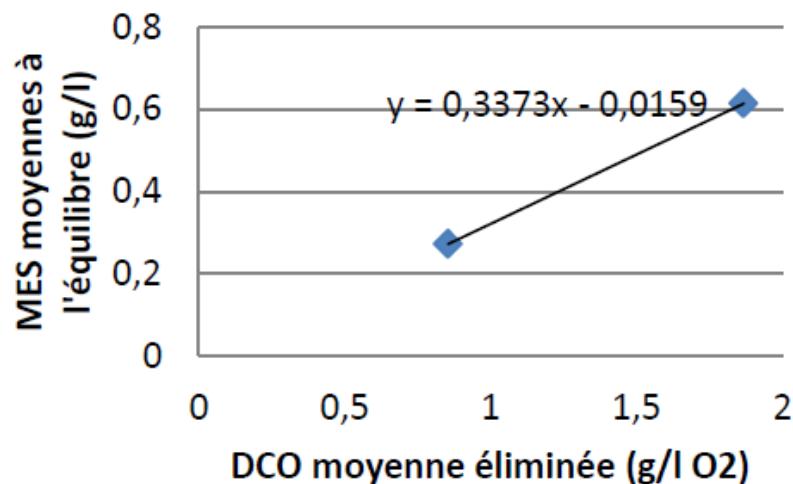


# Molecular biology

- The ecosystem modifies at each load change
- With respect to the inoculum, it simplifies all over the experiment
- There is no resilience ( $X \text{ g/L}$  in SE1 differs from the microbial structure of  $X \text{ g/L}$  in SE2)
- Consequence : use of a specific model for each data set...

# Modeling

Yield coefficient  $Y = \frac{X}{S_{in} - S}$



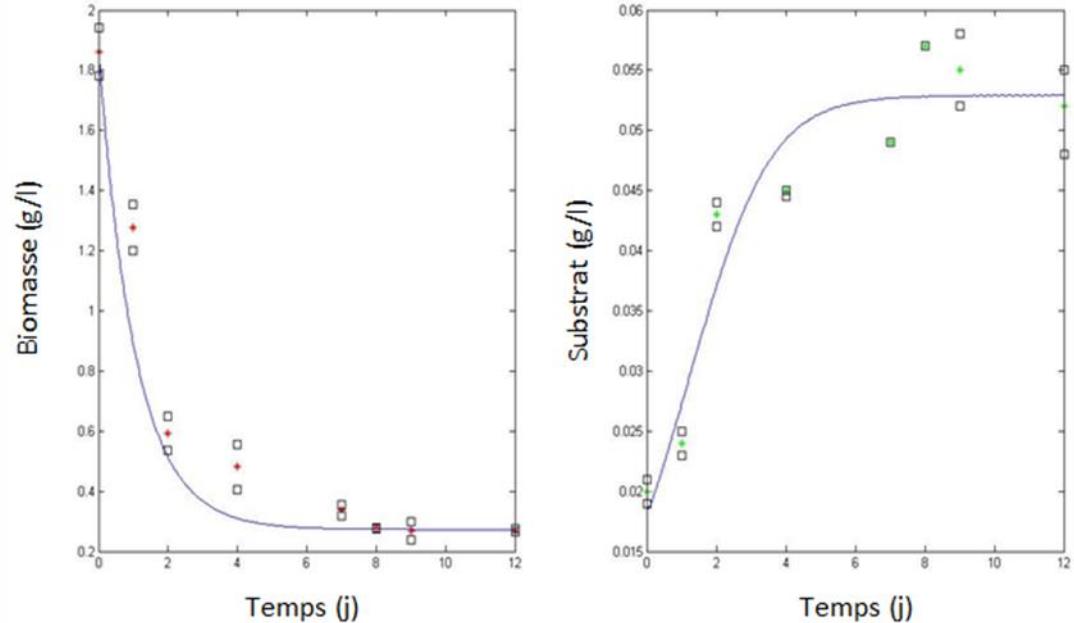
Séries d'expériences	Série 1		Série 2			
$S_{in}$ (g/l)	1	2	8	4	2	1
$Y$ calculé	0,3165	0,3287	0,4477	0,4454	0,4321	0,3762

# Modeling

Kinetics coefficients: SE1, Sin=1g/L

SE1,  
Sin=1g/l

Best match with Density-dependent model #1



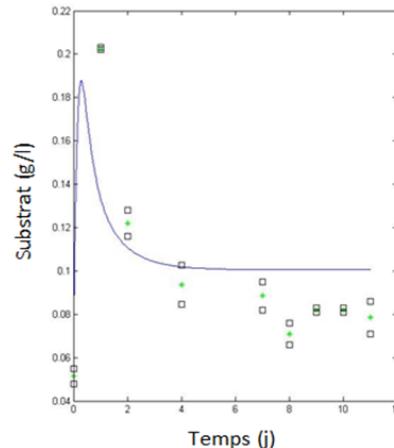
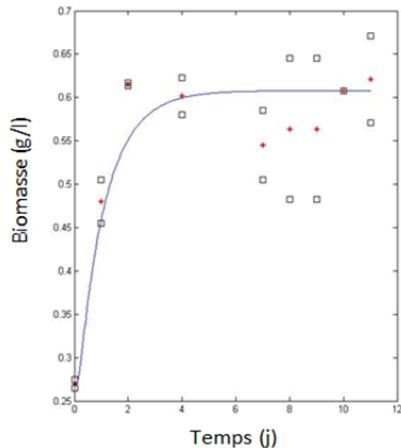
$$\mu(S, X) = \mu_{\max} \frac{S}{X^\alpha}$$

	P	Min	Max	Moy
Sin=	$\mu_{\max}$	10,3812	10,388	10,3846
1g/l	$\alpha$	0,4215	0,4223	0,4219
	Jmin		0,2136	

# Modeling

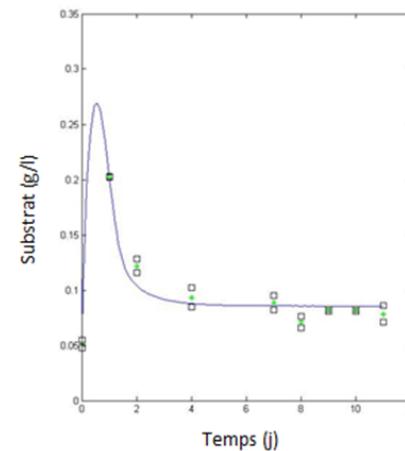
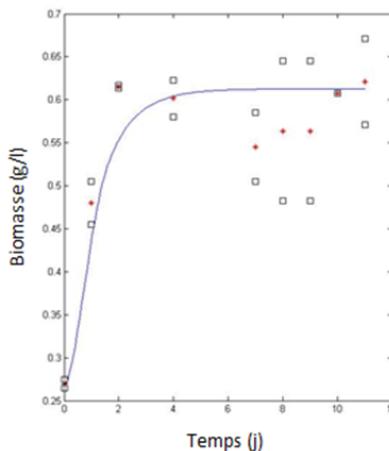
Kinetics coefficients: SE1,  $Sin=2g/L$

SE1,  
 $Sin=2g/l$



	P	Min	Max	Moy
$Sin=$	$\mu_{max}$	9,4516	9,4582	9,4549
$2g/l$	$\alpha$	0	0	0
	$J_{min}$		0,2336	

Monod:  
 $\mu(S)$



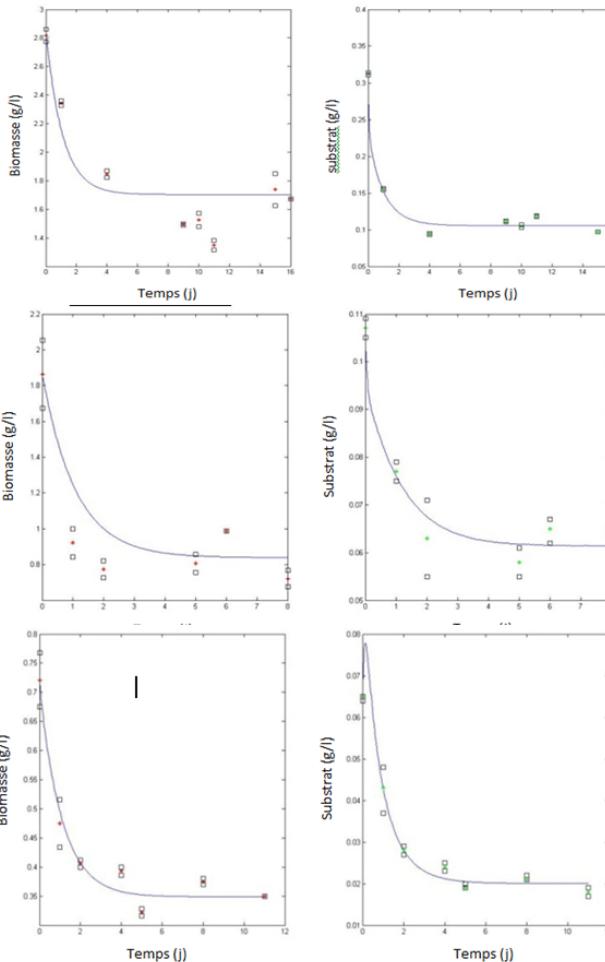
Best match with Monod

	P	Min	Max	Moy
$Sin=$	$\mu_{max}$	2,1655	2,1658	2,16565
$2g/l$	$k_s$	0,1096	0,1096	0,1096
	$J_{min}$		0,0354	

# Modeling

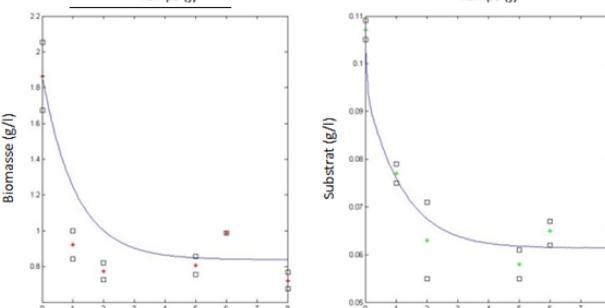
Kinetics coefficients: SE2 - Best match with Density-dependent model #1

$S_{in}=4\text{g/l}$



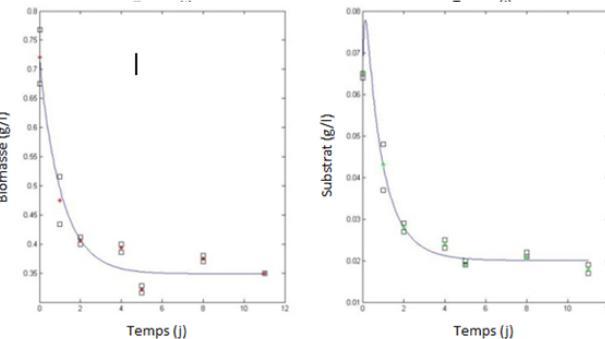
	P	Min	Max	Moy
$S_{in}=4\text{g/l}$	$\mu_{max}$	33,9525	33,9833	33,9679
	$\alpha$	2,5474	2,548	2,5477
	$J_{min}$		0,3382	

$S_{in}=2\text{g/l}$

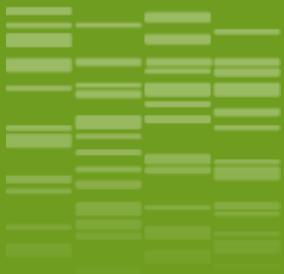


	P	Min	Max	Moy
$S_{in}=2\text{g/l}$	$\mu_{max}$	11,3921	11,4604	11,42625
	$\alpha$	1,5037	1,5437	1,5237
	$J_{min}$		0,2069	

$S_{in}=1\text{g/l}$



	P	Min	Max	Moy
$S_{in}=1\text{g/l}$	$\mu_{max}$	1,6201	1,6349	1,6275
	$\alpha$	3,1678	3,1773	3,17255
	$J_{min}$		0,0061	



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## Conclusions and perspectives

# Conclusions...

- Raw data : neither Monod nor Contois;
- The load, whether it is increasing or decreasing, highly influences the microbial community structure (smaller the  $S_{in}$ , larger the flocs from Exp.2). Thus it was decided to identify one model for each experiment;
- 4 over 5 data sets are better explained by density-dependent growth rates even for low  $S_{in}$ ;
- Hyp: substrate-dependence we could have seen appearing for low  $S_{in}$  was compensated by a high structuration of the biomass in flocs.

## ...and perspectives

- Possible modeling biases due i) to the fact we did not take into account non-biodegradable COD and ii) possible errors in data analysis. Modeling should be revisited soon...
- Could an alternative possible substrate-dependent model better explain data?

$$\begin{cases} \dot{X} = (\mu(S) - m)X \\ \dot{S} = (S_{in} - S)D - \mu(S)X \\ \dot{S}_d = (S_{d,in} - S_d)D \end{cases}$$

$$S_{in, Total} = S_{in} + S_{d,in}$$

$$S_{Measured} = S + S_d$$



# Thank you for your attention!