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About the modelling of Flocculation in the Chemostat *

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Abstract

In this work, we study a model of the chemostat where the species are present in two forms, isolated bacteria, and flocks of bacteria. We show that our model contains a lot of models which was considered in the literature. We assume that the dynamics of flocculation and deflocculation are fast with respect to the growth of the species and we construct a reduced model for which the growth functions depend on the density of the species.

Keywords. Chemostat, density dependent growth functions, flocculation.

1 Introduction

In culture of micro-organisms, the attachment of microbial individuals occurs frequently. The attachment can be either a “wall attachment” such as in the growth of biofilms [5, 7], or simply an aggregation such as in the formation of flocks [44]. Flock formation is often observed in microbial engineering systems such as biological wastewater processing [29, 25, 6] and yeast fermentation [12]. It has a direct impact on growth dynamics, as access to the substrate is limited for micro-organisms inside the flocks. The mechanisms of attachment and detachment result from the coupling of hydrodynamics conditions and biological properties, but are not yet completely understood at the level of microbial individuals. Several attempts of computer models, using individual based representations, have been proposed and are under investigation for the simulation of these phenomena [21, 4, 37, 35, 16, 33, 32, 22, 36, 17, 34, 38]. At a macroscopic level, substrate limitation can be measured experimentally in biofilms or flocks [45, 25, 6]. A rough representation, suited to the macroscopic level, consists in splitting the overall biomass into two parts: a “planctonic biomass”,

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composed of free individuals and a “attached biomass” composed of individuals that are stick together [23]. This consideration leads to a significant change on the performances of bioprocesses, compared to purely planctonic cultures. In a chemostat-like device, planctonic cells are expected to consume easily the substrates necessary for their growth, but are more keen to be carried off by the flow. On the contrary, cells among aggregates or biofilms have a more difficult access to the resources of the bulk fluid, but are more resistant to detachment induced by flow. Therefore, mathematical models are expected to understand and predict the issues of these trade-off. Several extensions of the well-known chemostat model [41], considering two compartments of free and attached biomass for each species have been proposed and studied in the literature. In models with wall attachment [3, 30, 2, 43, 42, 1, 19], attached biomass is assumed to be fixed, and detached individuals return directly to the planctonic compartment. In models with aggregation, aggregates are carried away by the flow but bacteria inside flocks are assumed to have no or reduced access to bulk resources [13, 14]. Considering that attachment and detachment processes are usually fast compared to biological time, it is shown in [14] that the reduced dynamics of such systems amounts to have a single biomass compartment for each strain but with a density dependant growth rate. This justifies the consideration of density dependant growth functions of the chemostat model, as already introduced in the literature. In [27, 28, 26, 24], it has been shown that this could lead to the coexistence of several species in competition on a same limiting resource, invalidating the Competitive Exclusion Principle [15].

In [14], the aggregates are assumed to have no biological growth (i.e. the attachment process is the only source of increase of the attached biomass). Aggregates are also assumed to be washed-out with the same dilution rate than planctonic cells. On the opposite, in wall attachment models, the attached biomass is not washed out at all. We believe that these two opposite cases (same dilution rate than planctonic biomass or no dilution rate) are too extreme to be fully realistic. We propose in this paper to revisit the chemostat model with two compartments, planctonic and aggregated biomass, but assuming that each biomass has its own growth rate and apparent dilution rate. This generalizes the two kind of models that we mention previously.

2 Flocks of bacteria

Consider the following model of the chemostat in which a population of microorganisms compete for a single growth-limiting substrate [31, 41]:

$$\begin{cases} S' &= D[S_{in} - S] - k\mu(S)X \\ X' &= [\mu(S) - D_1]X \end{cases}$$

In these equations, $S(t)$ denotes the concentration of the substrate at time t ; $X(t)$ denotes the concentration of the population of microorganisms at time t ; $\mu(S)$ represents the per-capita growth rate of the population and so $Y = 1/k$ is the growth yield; S_{in} and D denote, respectively, the concentration of substrate

in the feed bottle and the flow rate of the chemostat; each D_1 represents the removal rate of the population.

Assume that the species is present in two forms: isolated bacteria, of density X_L , and flocks of bacteria, of density X_A . Isolated bacteria and flocks can stick together to form new flocks, with rate $\alpha(\cdot)X_L$, and flocks can split and liberate isolated bacteria, with rate $\beta(\cdot)X_A$:



One obtains the following equations [39]:

$$\begin{cases} \dot{S} &= D(S_{in} - S) - \mu_L(S)X_L - \mu_A(S)X_A \\ \dot{X}_L &= (\mu_L(S) - D_L)X_L - \alpha(\cdot)X_L + \beta(\cdot)X_A \\ \dot{X}_A &= (\mu_A(S) - D_A)X_A + \alpha(\cdot)X_L - \beta(\cdot)X_A \end{cases} \quad (1)$$

3 Examples

Some of the models considered in the existing litterature are examples of (1)

3.1 Adaptative nutrient uptake

Here X_L denotes the low growing cells and X_A denotes the fast growing cells. Let $\alpha(\cdot) = \alpha(S)$, and $\beta(\cdot) = \beta(S)$ then (1) becomes the model considered in [40]:

$$\begin{cases} \dot{S} &= D(S_{in} - S) - \mu_L(S)X_L - \mu_A(S)X_A \\ \dot{X}_L &= (\mu_L(S) - D_L)X_L - \alpha(S)X_L + \beta(S)X_A \\ \dot{X}_A &= (\mu_A(S) - D_A)X_A + \alpha(S)X_L - \beta(S)X_A \end{cases}$$

3.2 Wall growth

Here X_L denotes the density of isolated bacteria, and X_A denotes the density of attached bacteria. Let $\alpha(\cdot) = a$, and $\beta(\cdot) = b$, then (1) becomes the model considered By Pilyugin and Waltman [30]:

$$\begin{cases} \dot{S} &= D(S_{in} - S) - \mu_L(S)X_L - \mu_A(S)X_A \\ \dot{X}_L &= (\mu_L(S) - D_L)X_L - aX_L + bX_A \\ \dot{X}_A &= (\mu_A(S) - D_A)X_A + aX_L - bX_A \end{cases}$$

3.3 Freter model

The previous model is a particular case of the model of Freter [10, 11, 19] for which

$$\alpha(\cdot) = a[1 - W], \quad \beta(\cdot) = b + \mu_A(S)[1 - G(W)]$$

where $W = X_A/X_{A\max}$ and $G(W)$ is decreasing

$$\begin{cases} \dot{S} &= D(S_{in} - S) - \mu_L(S)X_L - \mu_A(S)X_A \\ \dot{X}_L &= (\mu_L(S) - D_L)X_L - a(1 - W)X_L \\ &\quad + bX_A + \mu_A(S)[1 - G(W)]X_A \\ \dot{X}_A &= (\mu_A(S)G(W) - D_A - b)X_A + a[1 - W]X_L \end{cases}$$

In the case where $X_{A\max} = \infty$ one obtains $W = 0$ and if $G(0) = 1$ then $\alpha(\cdot) = a$ and $\beta(\cdot) = b$.

3.4 Flocs of two bacteria

If one takes $\alpha(\cdot) = aX_L$ and $\beta(\cdot) = b$, then (1) becomes

$$\begin{cases} \dot{S} &= D(S_{in} - S) - \mu_L(S)X_L - \mu_A(S)X_A \\ \dot{X}_L &= (\mu_L(S) - D_L)X_L - aX_L^2 + bX_A \\ \dot{X}_A &= (\mu_A(S) - D_A)X_A + aX_L^2 - bX_A \end{cases} \quad (2)$$

This model considered by Hagueman and Rapaport [14, 9] in the case $\mu_A(S) = 0$ where the bacteria in flocks does not consume the substrate and by Fekih-Salem and ali [9] in the more general case $0 \leq \mu_A(S) \leq \mu_L(S)$ where the bacteria in flocs consume less of the substrate than the isolated bacteria. This model was extended also to case of flocs with an arbitrary numbers of bacterias [13]

3.5 Biomass in flocs

If one takes $\alpha(\cdot) = a(X_L + X_A)$ and $\beta(\cdot) = b$ one obtains the following model

$$\begin{cases} \dot{S} &= D(S_{in} - S) - \mu_L(S)X_L - \mu_A(S)X_A \\ \dot{X}_L &= (\mu_L(S) - D_L)X_L - a(X_L + X_A)X_L + bX_A \\ \dot{X}_A &= (\mu_A(S) - D_A)X_A + a(X_L + X_A)X_L - bX_A \end{cases} \quad (3)$$

In this model [39] we do not take in consideration the sizes of the flocks. The biomass of isolated bacteria is denoted by X_L and the biomass in flocks is denoted by X_A . Hence isolated bacteria and isolated bacteria or flocks can stick together to form new flocks, with rate $a(X_L + X_A)X_L$ proportional to both the density of isolated bacteria, that is X_L , and the total biomass density, that is $X_L + X_A$, and flocks can split and liberate isolated bacteria, with rate bX_A proportional the their density X_A .

4 Two time scales

The general model for the flocculation is

$$\begin{cases} \dot{S} &= D(S_{in} - S) - \mu_L(S)X_L - \mu_A(S)X_A \\ \dot{X}_L &= (\mu_L(S) - D_L)X_L \\ &\quad - \alpha(S, X_A, X_L)X_L + \beta(S, X_A, X_L)X_A \\ \dot{X}_A &= (\mu_A(S) - D_A)X_A \\ &\quad + \alpha(S, X_A, X_L)X_L - \beta(S, X_A, X_L)X_A \end{cases}$$

We assume that the dynamics of flocculation and deflocculation is faster than the growth of the species.

$$\begin{cases} \dot{S} &= D(S_{in} - S) - \mu_L(S)X_L - \mu_A(S)X_A \\ \dot{X}_L &= (\mu_L(S) - D_L)X_L - \frac{\alpha(\cdot)}{\varepsilon}X_L + \frac{\beta(\cdot)}{\varepsilon}X_A \\ \dot{X}_A &= (\mu_A(S) - D_A)X_A + \frac{\alpha(\cdot)}{\varepsilon}X_L - \frac{\beta(\cdot)}{\varepsilon}X_A \end{cases} \quad (4)$$

Notice that

$$\dot{X} = (\mu_L(S) - D_L)X_L + (\mu_A(S) - D_A)X_A$$

where $X = X_L + X_A$ is the total biomass. Thus

- X_L and X_A : are fast variables,
- S and $X = X_L + X_A$: are slow variables.

On the slow manifold $\dot{X}_L = 0$ (or $\dot{X}_A = 0$) one has $\alpha(\cdot)X_L = \beta(\cdot)X_A$. Thus, the slow manifold is obtained by solving the system

$$\alpha(S, X_L, X_A)X_L = \beta(S, X_L, X_A)X_A,$$

$$X_L + X_A = X$$

Hence one has

$$X_L = p(S, X)X, \quad X_A = (1 - p(S, X))X.$$

The reduced model is obtained by replacing the fast variables X_L and X_A in the equation of S and X :

$$\begin{cases} \dot{S} = D(S_{in} - S) - \mu(S, X)X \\ \dot{X} = [\mu(S, X) - D(S, X)]X \end{cases} \quad (5)$$

where

$$\mu(S, X) = p(S, X)\mu_L(S) + (1 - p(S, X))\mu_A(S),$$

$$D(S, X) = p(S, X)D_L + (1 - p(S, X))D_A.$$

Notice that $p(S, X)$ depends on functions $\alpha(\cdot)$ and $\beta(\cdot)$. This is a density dependent growth function model [27, 28, 26].

Examples For system (2) one has

$$\frac{\alpha(\cdot)}{\varepsilon} = \frac{a}{\varepsilon}X_L, \quad \frac{\beta(\cdot)}{\varepsilon} = \frac{b}{\varepsilon}, \quad p(X) = \frac{2}{1 + \sqrt{1 + 4a/bX}}.$$

For system (3) one has

$$\frac{\alpha(\cdot)}{\varepsilon} = \frac{a}{\varepsilon}X, \quad \frac{\beta(\cdot)}{\varepsilon} = \frac{b}{\varepsilon}, \quad p(X) = \frac{b}{b + aX}.$$

Theorem 4.1 *Let $(S(t), X_L(t), X_A(t))$ be the solution of (4) with initial condition*

$$S(0) \geq 0, \quad X_L(0) > 0, X_A(0) \geq 0$$

Let $(\bar{S}(t), \bar{X}(t))$ be the solution of the reduced problem (5) with initial conditions

$$\bar{S}(0) = S(0), \quad \bar{X}(t) = X_L(0) + X_A(0)$$

Then we have

$$S(t) \approx \bar{S}(t), \quad X(t) \approx \bar{X}(t)$$

uniformly for $t \in [0, +\infty[$, and

$$X_L(t) \approx p(\bar{S}(t), \bar{x}(t))\bar{X}(t), \quad X_A(t) \approx (1 - p(\bar{S}(t), \bar{x}(t)))\bar{x}(t)$$

uniformly for $t \in [t_0, +\infty[$, where $t_0 > 0$ is arbitrarily small,

5 Density dependent growth function

These examples have motivated the study of the reduced model

$$\begin{cases} \dot{S} = D(S_{in} - S) - \mu(S, X)X \\ \dot{X} = [\mu(S, X) - D(X)]X \end{cases}$$

where

$$\mu(S, X) = p(X)\mu_L(S) + (1 - p(X))\mu_A(S), \quad D(X) = p(X)D_L + (1 - p(X))D_A.$$

We assume that $\mu_L(S)$ and $\mu_A(S)$ are increasing and $\mu_L(S) \geq \mu_A(S)$, $D_L \geq D_A$. and $0 \leq p(X) \leq 1$, $p(0) = 1$, $p(\infty) = 0$, $p'(X) < 0$. The equilibria of the system are given by

$$\begin{cases} D(S_{in} - S) - \mu(S, X)X = 0 \\ [\mu(S, X) - D(X)]X = 0 \end{cases}$$

If $X = 0$ then $S = S_{in}$ so that one has the washout equilibrium: $E_0 = (S_{in}, 0)$.

If $\mu(S, X) = D(X)$, then $D(S_{in} - S) = XD(X)$. Hence

$$S = G(X) := S_{in} - \frac{XD(X)}{D}.$$

The mapping $S \mapsto G(X)$ is decreasing. Notice

$$\lambda_L = \mu_L^{-1}(D_L), \quad \lambda_A = \mu_A^{-1}(D_A).$$

Then equation $\mu(S, X) = D(X)$ defines a function $S = F(X)$ such that $F(0) = \lambda_L$ and $F(\infty) = \lambda_A$. The positive equilibria of the system are given by the intersections of the graphs of $S = F(X)$ and $S = G(X)$, see Figure 1. If $\lambda_L < \lambda_A$ the function $S \mapsto F(S)$ is increasing and we have the following result

Proposition 5.1 *If $\lambda_L < S_{in}$, there is a unique positive equilibrium. It is stable. If $\lambda_L > S_{in}$, there is no positive equilibrium.*

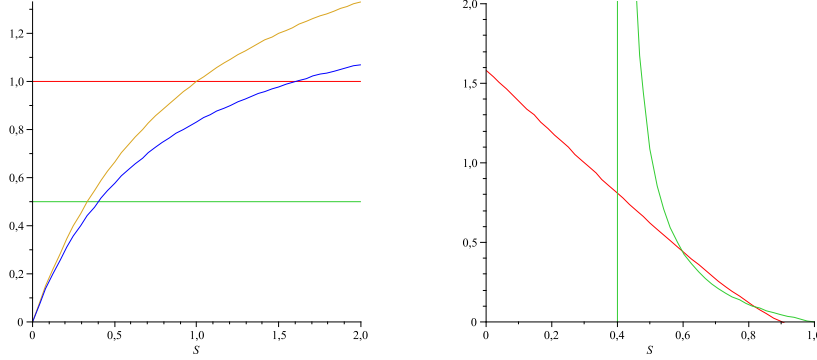


Figure 1: On the left the growth functions μ_L and μ_A . On the right, the mappings $S \mapsto F(S)$ and $S \mapsto G(S)$ showing the existence of two positive equilibria in the case when $\lambda_L > S_{in}$.

If $\lambda_L > \lambda_A$ the function $S \mapsto F(S)$ is decreasing, see Figure 1, and we have the following result

Proposition 5.2 *If $\lambda_L < S_{in}$, then there exists at least one positive equilibrium. One can have an odd number of equilibria which are alternatively stable and unstable. If $\lambda_L > S_{in}$, then one can have 0 or an even number of equilibria which are alternatively stable and unstable.*

Hence in the case when $\lambda_L > \lambda_A$, the system can exhibit bistability, see Figure 2: The washout equilibrium is stable together with the positive equilibrium corresponding to the lowest value of S . The domains of attraction of the stable equilibria are separated by the stable separatrix of the positive saddle node. The simulations shown in Figures 1 and 2 were obtained for the following Monod functions

$$\mu_L(S) = \frac{2S}{1+S}, \quad \mu_A(S) = \frac{1.5S}{0.8+S}$$

and the following values of the parameters

$$D_L = D = 1, \quad D_A = 0.5, \quad a = 4, \quad b = 1, \quad S_{in} = 0.9.$$

6 N -species

We consider here the case of N -species competing for a substrate. We assume that each species is present in two forms: isolated bacteria of density u_i , and bacteria in flocks, of density v_i , $1 \leq i \leq n$. We assume that isolated bacteria can

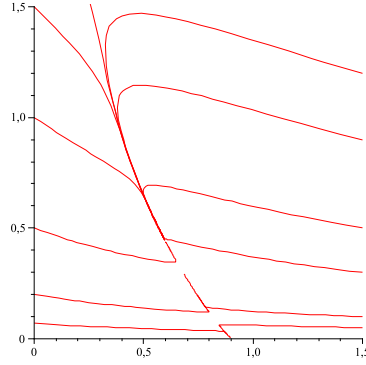


Figure 2: The system exhibits bistability.

stick with isolated bacteria or flocks to form new flocks with rate $\alpha_i(\cdot)u_i$ and we assume that flocks can liberate isolated bacteria with rate $\beta_i(\cdot)v_i$. The model equation are:

$$\begin{cases} \dot{S} = D(S_{in} - S) - \sum_{i=1}^n [\mu_{i1}(S)u_i + \mu_{i2}(S)v_i] \\ \dot{u}_i = (\mu_{i1}(S) - D)u_i - \alpha_i(\cdot)u_i + \beta_i(\cdot)v_i, & \text{for } 1 \leq i \leq n \\ \dot{v}_i = (\mu_{i2}(S) - D)v_i + \alpha_i(\cdot)u_i - \beta_i(\cdot)v_i, & \text{for } 1 \leq i \leq n \end{cases} \quad (6)$$

We consider here the case [39] where

$$\alpha_i(\cdot) = \sum_{j=1}^n A_{ij}x_j, \quad \beta_i(\cdot) = B_i$$

where A_{ij} and B_i are nonnegative constants. Moreover, we assume that the dynamics of flocculation and deflocculation are fast compared with the dynamics of the growth of bacteria, that is que l'on a

$$A_{ij} = \frac{a_{ij}}{\varepsilon}, \quad B_i = \frac{b_i}{\varepsilon},$$

The quasi steady state reduction of this model is the following reduced model

$$\begin{cases} \dot{S} = D(S_{in} - S) - \sum_{i=1}^n \mu_i(S, x_1, \dots, x_n)x_i \\ \dot{x}_i = [\nu_i(S, x_1, \dots, x_n) - D_i(x_1, \dots, x_n)]x_i, & \text{où } 1 \leq i \leq n \end{cases} \quad (7)$$

where

$$\mu_i(S, x_1, \dots, x_n) = \frac{b_i\mu_{i1}(S) + \sum_{j=1}^n a_{ij}x_j\mu_{i2}(S)}{b_i + \sum_{j=1}^n a_{ij}x_j},$$

$$D_i(x_1, \dots, x_n) = \frac{Db_i + D_i \sum_{j=1}^n a_{ij}x_j}{b_i + \sum_{j=1}^n a_{ij}x_j}.$$

This approach give a motivation to density dependent growth function models [27, 28, 26].

7 Conclusion

In this work, we have analysed a general model of the chemostat with planctonic and attached biomass, under the assumption that attachment and detachment processes are fast compared to the biological scale. Each compartment of the biomass is characterized by its specific growth rate and apparent dilution rate, generalizing previous models of biofilms (with no dilution rate for the attached bacteria) or models of perfect flocks (with no growth rate for inside individuals). Our study reveals that the reduced dynamics may exhibit a bi-stable behavior even though each growth function is monotonic. This phenomenon is new and is usually met in chemostat but when the growth function is non-monotonic (such as the Haldane law). Here, it can be explained by the conjunction of different growth rate and dilution rate that leads to a density dependency of both apparent growth rate and dilution rate in the reduced dynamics.

References

- [1] M. Ballyk, D. Jones and H. Smith Microbial competition in reactors with wall attachment: a comparison of chemostat and plug flow models. *Microbial Ecology* 41 (2001) 210–221.
- [2] M. Ballyk and H. Smith, A model of microbial growth in a plug flow reactor with wall attachment, *Mathematical Biosciences* 158 (1999) 95–126.
- [3] B.C. Baltzis and A.G. Fredrickson, Competition of two microbial populations for a single resource in a chemostat when one of them exhibits wall attachment, *Biotechnol. Bioeng* 25 (1983) 2419–39.
- [4] L. Benefield and F. Molz. Mathematical simulation of a biofilm process. *Biotechnol. Bioeng* 27 (1985) 921–931.
- [5] J.D. Bryers. Biofilm formation and chemostat dynamics: pure and mixed culture considerations. *Biotechnol. Bioeng.* 26 (1984) 948–958.
- [6] Z.C. Chiu, M.Y. Chen, D.J. Lee, C.H. Wang and J.Y. Lai, Oxygen diffusion and consumption in active aerobic granules of heterogeneous structure, *Appl. Microbiol. Biotechnol.* 75 (2007) 685–691.
- [7] J. Costerton, Overview of microbial biofilms. *J. Indust. Microbiol.* 15 (1995) 137–140.

- [8] R. Fekih Salem, T. Sari and N. Abdellatif. Sur un modèle de compétition et de coexistence dans le chemostat. *CARI'10, Proceedings of the 10th African Conference on Research in Computer Science and Applied Mathematics*, E. Badouel, A. Sbihi and I. Lokpo (Editors), INRIA (2010) 437–444.
- [9] R. Fekih-Salem, T. Sari and A. Rapaport. La floculation et la coexistence dans le chemostat, *Proceedings of the 5th conference on Trends in Applied Mathematics in Tunisia, Algeria, Morocco*, Sousse, 23-26 Avril 2011, Tunisia, M. Hassine and M. Moakher (Editors), Centre de Publication Universitaire (2011) 477–483.
- [10] R. Freter. Mechanisms that control the microflora in the large intestine, In: *D. Hentges, (ed) Human Intestinal Microflora in Health and Disease*, Academic Press, NewYork, (1983)
- [11] R. Freter, H. Brickner and S. Temme. An understanding of colonization resistance of the mammalian large intestine requires mathematical analysis. *Microecology and Therapy* 16 (1986) 147–155.
- [12] M. Ginovart, D. López, A. Giró and M. Silbert, Flocculation in brewing yeasts: A computer simulation study, *BioSystems* 83 (2006) 51–55.
- [13] B. Haegeman, C. Lobry and J. Harmand. Modelling Bacteria Flocculation as Density-Dependent Growth, *AIChE* 53(2) (2007) 535–539.
- [14] B. Haegeman and A. Rapaport, How flocculation can explain coexistence in the chemostat. *J. Biol. Dyn.* 2 (1) (2008) 1–13.
- [15] G. Hardin, The competition exclusion principle. *Science* 131 (1960) 1292–1298
- [16] S.W. Hermanowicz. Two-dimensional simulations of biofilm development: effects of external environmental conditions. *Water Sci. Technol.* 39 (1999) 107–114.
- [17] H. Horn, H. Reiff and E. Morgenroth Simulation of Growth and Detachment in Biofilm Systems Under Defined Hydrodynamic Conditions, *Biotechnology and Bioengineering* 81 (5) (2003) 607–617.
- [18] D. Jones and H.L. Smith, Microbial competition for nutrient and wall sites in plug flow. *SIAM J. Applied Math.* 60 (2000) 1576–1600.
- [19] D. Jones, H. Kojouharov, D. Le and H.L. Smith, The Freter model: A simple model of biofilm formation. *J. Math. Biol.* 47 (2003) 137–152.
- [20] D. Jones, H. Kojouharov and H.L. Smith, Bacterial wall attachment in a flow reactor. *SIAM J. Appl. Math.* 62 (2000) 1728–1771.
- [21] J.C. Kissel, P.L. McCarty and R.L. Street. Numerical simulation of mixed culture biofilm. *J. Environ. Eng. ASCE* 110 (1984) 393–411.

- [22] J. Kreft, C. Picioreanu, J. Wimpenny and M. van Loosdrecht. Individual-based modelling of biofilms. *Microbiol Sgm* 147 (2001) 2897–2912.
- [23] R. Kreikenbohm and W. Stephan. Application of a two-compartment model to the wall growth of *Pelobacter acidigallici* under continuous culture conditions. *Biotechnol. Bioeng.* 27 (1985) 296–301.
- [24] P. De Leenheer, D. Angeli and E.D. Sontag. Crowding effects promote coexistence in the chemostat. *Journal of Mathematical Analysis and Applications* 319 (1) (2006) 48–60.
- [25] B. Li and L. Bishop, Micro-profiles of activated sludge floc determined using microelectrodes, *Water Res.* 38 (2004) 1248–1258.
- [26] C. Lobry and J. Harmand. A new hypothesis to explain the coexistence of n species in the presence of a single resource, *Comptes rendus Biologies* 329 (2006) 40–46.
- [27] C. Lobry, F. Mazenc and A. Rapaport. Persistence in ecological models of competition for a single resource, *C.R. Acad. Sci. Paris, Ser I* 340 (2004) 199–240.
- [28] C. Lobry, F. Mazenc, A. Rapaport. Sur un modèle densité-dépendant de compétition pour une ressource, *Comptes rendus Biologies* 329 (2006) 63–70.
- [29] A.P. Martins, C. Picioreanu, J.J. Heijnen and M.C.M. Van Loosdrecht, Three-dimensional dual-morphotype species modeling of activated sludge flocs, *Environ. Sci. Technol.* 38 (2004) 5632–5641.
- [30] S. Pilyugin and P. Waltman. The simple chemostat with wall growth, *SIAM J. Appl. Math.* 59(5) (1999) 1552–1572.
- [31] J. Monod, La technique de culture continue. Théorie et applications. *Ann. Inst. Pasteur* 79 (1950) 390–410
- [32] E. Morgenroth, H. Eberl and M. van Loosdrecht. Evaluating 3-D and 1-D mathematical models for mass transport in heterogeneous biofilms. *Water Sci. Technol.* 41 (2000) 347–356.
- [33] D. Noguera, G. Pizarro, D. Stahl and B. Rittmann. Simulation of multi-species biofilm development in three dimensions. *Water Sci. Technol.* 39 (1999) 123–130.
- [34] C. Picioreanu, J.U. Kreft and M. van Loosdrecht. Particle-Based Multidimensional Multispecies Biofilm Model. *Applied and Environmental Microbiology* 70(5) (2004) 3024–3040.
- [35] C. Picioreanu, M. van Loosdrecht and J. Heijnen. A new combined differential-discrete cellular automaton approach for biofilm modeling: application for growth in gel beads. *Biotechnol. Bioeng.* 57 (1998) 718–731.

- [36] C. Picioreanu, M. van Loosdrecht and J. Heijnen. Two-dimensional model of biofilm detachment caused by internal stress from liquid flow. *Biotechnol. Bioeng.* 72 (2001) 205–218.
- [37] P. Reichert. Concepts underlying a computer program for the identification and simulation of aquatic systems (AQUASIM 1.0). Du bendorf: Schriftenreihe der EAWAG (1994).
- [38] V. Saravanan and T.R. Sreekrishnan. Modelling anaerobic biofilm reactors, a review. *Journal of Environmental Management* 81 (2006) 1–18.
- [39] T. Sari, N. Abdellatif, B. Benyahia, M.L. Diagne, M. El Hajji and R. Fekih-Salem. Modélisation mathématique en biologie : compétition, coexistence et croissance, *Proceedings of the 5th conference on Trends in Applied Mathematics in Tunisia, Algeria, Morocco*, Sousse, 23-26 Avril 2011, Tunisia, M. Hassine and M. Moakher (Editors), Centre de Publication Universitaire (2011) 19–25
- [40] B. Tang, A. Sittomer and T. Jackson, Population dynamics and competition in chemostat models with adaptative nutrient uptake. *J. Math. Biol.* 35 (1997) 453–479.
- [41] H.L. Smith and P. Waltman, The Theory of the Chemostat, Dynamics of Microbial Competition. Cambridge University Press, 1995.
- [42] H.L. Smith and X.-Q. Zhao, Microbial Growth in a Plug Flow Reactor with Wall Adherence and Cell Motility, *Journal of Mathematical Analysis and Applications* 241 (2000) 134–155.
- [43] E. Stemmons and H.L. Smith, Competition in a chemostat with wall attachment. *SIAM J. Appl. Math.* 61 (2000) 567–595.
- [44] D.N. Thomas, S.J. Judd and N. Fawcett, Flocculation modelling: A review, *Water Res.* 33 (1999) 1579–1592.
- [45] H. Topiwala and G. Hamer, Effect of wall growth in steady state continuous culture, *Biotech. Bioeng.* 13 (1971) 919–922.

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