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Some non-intuitive properties of simple extensions of the chemostat model

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We show how the consideration of two compartments in the well known chemostat model could lead to non-intuitive messages in terms of performances and stability. These compartments and their interconnections represent spatial patterns and interplay with species biodiversity. The case of an inhibited resource is also considered, for which we also study the effect of a bio-augmentation.

1. Introduction

The chemostat model appears in the fifteens as the mathematical representation of the microbial growth in the chemostat experimental device, invented simultaneously by Monod (1950) and Novick and Szilard (1950). If s and x denote respectively the substrate and biomass concentrations in a culture vessel of volume V, their time evolution are modeled by the following system of ordinary differential equations

$$\begin{aligned}\dot{s} &= -\frac{1}{Y}\mu(s)x + -\frac{Q}{V}(S_{in}-s)\\ \dot{x} &= \mu(s)x - \frac{Q}{V}x\end{aligned} \tag{1}$$

where Y[1] is the yield conversion of substrate into biomass, $\mu(\cdot)$ the specific growth rate of the micro-organisms (which is non-negative function, null only at $s=0$), Q the input flow and S_{in} the input concentration of substrate. Later, this model has been used to represent many other ecosystems in natural environments (Hasler and Johnson, 1954; Veldcamp, 1977; Higashi et al., 1998), which have in common a continuous culture of micro-organisms. This model (or close versions of it) is often found in bio-mathematics, theoretical ecology or bio-processes literature (see for instance Pirt, 1975; Panikov, 1995; Koch et al., 1998; Bastin and Dochain, 1990). More generally, it is a popular model of resource-consumer in living sciences (although the word "chemostat" is not always used).

The model (1) is based on several essential assumptions: (1) The micro-organisms introduced in the vessel are of a single species; (2) The substrate (of concentration s) is the single limiting resource for growth; (3) The vessel is perfectly mixed; (4) Its volume is constant (i.e. the input and output flows are both equal to Q. Many extensions of this model have been studied to better suit real ecosystems, introducing considerations such as species competition, multiple limiting resources, non-perfectly mixed medium, etc. Most of the studies in bio-mathematics and theoretical ecology have been conducted with the objective to characterize the composition and the spatial distribution of the asymptotic solutions (see for instance Hsu et al., 1977; Hofbauer and So, 1994; Smith and Waltman, 1995; Amarasekare and Nisbet, 2001; Gravel et al., 2010). The performances of the related ecosystems are usually not addressed in those theoretical studies. This is different in bio-processes literature. Optimizing the performances is of primer interest, but mixed cultures are rarely considered.

The objective of the present paper is to review studies of extensions of the model (1) that have revealed "non-intuitive" messages (in the sense that the conclusions cannot be deduced straightforwardly from the equations) related to the performances.

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[1] Without any loss of generality one can assume $Y=1$ in Eq. (1) by simply denoting the quantity X/Y by X.

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We do not pretend here to be exhaustive but we focus on situations for which a certain kind of complexity could emerge from quite simple ecosystems. More precisely, we consider structures of the model (1) in a few compartments that can change radically the behavior of the solutions and its performances. The consideration of spatial compartments in the chemostat model (also named *gradostat* which refers to the experimental device proposed by Lovitt and Wimpenny (1981)) is not new (Stephanopoulos and Fredrickson, 2006; Tang, 1986, 1994; Jaeger et al., 1987; Smith and Tang, 1989; Smith et al., 1991; Smith and Waltman, 1991; Hofbauer and So, 1994; Lenas et al., 1998; Amarasekare and Nisbet, 2001; Nakaoka and Takeuchi, 2006; Gaki et al., 2009; Gravel et al., 2010), but we focus here on the output performances of the systems. From another view point, interconnected chemostats are often considered in biotechnology for optimizing the productivity (Luyben and Tramper, 1982; Hill and Robinson, 1989; Harmand et al., 1999; de Gooijer et al., 1996; Dramé et al., 2006; Nelson and Sidhu, 2006) but most of the time the configurations are in series with pure culture. In the present work, we consider more general interconnection structures and the possibilities of having several species in different niches. The paper is organized as follows. In Section 2, we analyze the effect of a spatialisation described in terms of interconnected compartments, and show how interconnection patterns could impact the performances. In Section 3 we study the interest for having a diversity in the compartments. In Section 4, we consider inhibitory resources and demonstrate the role of patterns on the ecosystem stability and its performances. Finally, in Section 5, the bio-augmentation is analyzed in terms of another mean that could impact the stability of the ecosystem.

2. Spatial patterns in the chemostat

In this section, we assume that the growth function $\mu(\cdot)$ is monotonically increasing. A usual function is given by the Monod's expression (see Fig. 11 in Appendix A):

$$\mu(s) = \mu_{\max} \frac{s}{K_s + s}. \qquad (2)$$

For convenience we denote the dilution rate $D = \frac{Q}{V}$, and define, as it is often made in the literature, the *break-even concentration* associated to the growth function as

$$\lambda(D) = \left\| \begin{array}{lll} s \text{ s.t.} \mu(s) = D & \text{when} \quad \max & {}_s \mu(s) > D, \\ +\infty & \text{otherwise.} & \end{array} \right)$$

Let us first recall the classical results about the asymptotic behavior of the solutions of the model (1) (see for instance Smith and Waltman (1995); HLRR17). The equilibria are the wash-out $E_0 = (S_{in}, 0)$ and a positive steady state $E_1 = (\lambda(D), S_{in} - \lambda(D))$ which exists when $\lambda(D) < S_{in}$. Under this last condition, E_0 is unstable and any solution with $x(0) > 0$ converges asymptotically to E_1. On the contrary, when $\lambda(D) \geq S_{in}$, any solution converges asymptotically to E_0. Therefore, a property of the model (1) is that for a given dilution rate D, the output substrate concentration at steady state is equal to $\lambda(D)$ independently of the input concentration S_{in}, provided S_{in} to be larger to $\lambda(D)$. It is well known that this property is no longer satisfied when there is spatial heterogeneity (see for instance Lovitt and Wimpenny, 1981; Hill and Robinson, 1989 where expressions of the output concentrations at steady state depend on the input concentration). Performances of an ecosystem can be measured by different indexes. We consider here an index that measures the ability of an ecosystem to convert a resource. More precisely, for a given value S_{in} of the resource density at the inlet, we define its output density at steady state, denoted $s^{\star}_{out}$, as the performance index. To grasp the effect of spatial structures on this performance index, we consider three patterns depicted in Fig. 1 for a given total volume V and input flow rate Q.

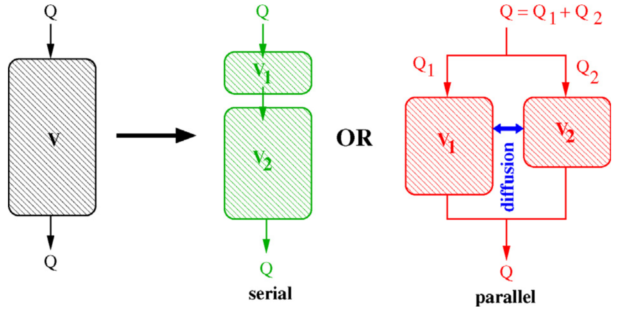

Fig. 1. Consideration of three spatial patterns with same total volume V.

We compare the smallest value $s^{\star}_{out}$ for each configuration. For the single tank configuration, $s^{\star}_{out}$ is simply given by $\lambda(Q/V)$. For the serial configuration, $s^{\star}_{out}$ is function of the volume ratio $r = V_1/V$. For the parallel configuration, $s^{\star}_{out}$ is function of r, the ratio of flow distribution $\alpha = Q_1/Q$ and the diffusion parameter d between the two volumes. The systems of Eqs. (13) and (14) for the serial in parallel configurations are given in Appendix A. One has the following result.

Proposition 1. *For a given input flow rate Q and volume V, there exists a threshold* $\bar{S}_{in} > 0$ *such that the smallest output concentration* $s^{\star}_{out}$ *is reached for a serial configuration when* $S_{in} > \bar{S}_{in}$, *and for a parallel configuration when* $S_{in} < \bar{S}_{in}$. *Moreover, in this last case, the map* $d \mapsto s^{\star}_{out}(d)$ *admits an unique minimum for a* $d^{\star} < +\infty$ *Furthermore, there exists another threshold* $\underline{S}_{in} < \bar{S}_{in}$ *such that* $d^{\star} = 0$ *for* $S_{in} < \underline{S}_{in}$ *and* $d^{\star} > 0$ *for* $S_{in} \in (\underline{S}_{in}, \bar{S}_{in})$.

These results have been proved in Haidar et al. (2011) for linear growth functions and later extended to Monod functions in Haidar (2011). We illustrate these results for a linear growth function with total volume V and input flow rate Q such that $\lambda(Q/V) = 1$. For the single tank configuration, the output concentration at steady state is thus equal to 1. The threshold $\bar{S}_{in}$ can be computed to be equal to 2.

In Fig. 2, the output concentration at steady state $s^{\star}_{out}$ has been plotted for various values of S_{in} as function of the parameters of the serial or parallel configurations. On can first see that for any value of S_{in}, there always exists a serial or parallel configuration such that $s^{\star}_{out} < 1$ (that is consequently better than having a single tank). When S_{in} is above the threshold $\bar{S}_{in} = 2$, the parallel configurations have always $s^{\star}_{out}$ above 1 and there exist values of r such that the serial configuration has $s^{\star}_{out}$ under 1. For S_{in} below the threshold, conclusions are reversed: the serial configuration has $s^{\star}_{out}$ always larger than 1, while there exist parameter values of d such that the parallel configuration has $s^{\star}_{out}$ lower than 1. Moreover, one can see that for values of S_{in} under the threshold but no too low, the smallest value of $s^{\star}_{out}$ is obtained for a positive value of the diffusion parameter d.

3. Biodiversity and spatial patterns

Now we consider the case of two species (or two consumers) of concentrations x_1, x_2 in competition for the single limiting resource in the chemostat. A straightforward extension of the mono-specific model (1) is given by the system (where the yield parameter Y has

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