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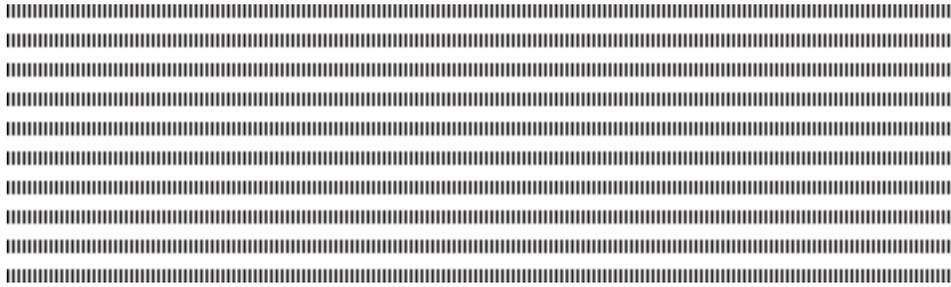
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How intra- and interspecific competitions affect the coexistence in the chemostat

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ABSTRACT. This paper deals with a two-microbial species model in competition for a single-resource in the chemostat including general intra- and interspecific density-dependent growth rates with distinct removal rates for each species. In order to understand the effects of intra- and interspecific interference, this general model is studied by determining the conditions of existence and local stability of steady states. The operating diagrams show how the model behaves by varying the operating parameters and illustrate the effect of the intra- and interspecific interference on the disappearance of coexistence region and the occurrence of bi-stability region.

RÉSUMÉ. Dans ce travail, on étudie un modèle général densité-dépendant intra et inter-spécifique où deux espèces microbiennes sont en compétition pour une seule ressource dans le chémostat avec des taux de prélèvement distincts pour chaque espèce. Afin de comprendre les effets d'interférence intra et inter-spécifique, ce modèle général est analysé en déterminant les conditions d'existence et de stabilité locale des points d'équilibre. Les diagrammes opératoires montrent comment le modèle se comporte en faisant varier les paramètres opératoires et illustrent l'effet d'interférence intra-et inter-spécifique sur la disparition de la région de coexistence et l'émergence d'une région de bistabilité.

KEYWORDS : Bifurcation, Chemostat, Coexistence, Density-dependence

MOTS-CLÉS : Bifurcation, Chémostat, Coexistence, Densité-dépendance



1. Introduction

In the classical chemostat model with several species in competition for a single resource, the well-known Competitive Exclusion Principle (CEP) states that generically at most one species can survive to the competition [5, 8]. Although the theoretical prediction of this model has been corroborated by the experiences of Hansen and Hubbell [5], the biodiversity found in nature as well as in waste-water treatment processes and biological reactors seems to contradict the CEP. In order to construct more coherent models with observations of the real world, different mechanisms of coexistence were proposed in the literature such that the intra- and interspecific interference [1], the flocculation [2, 4] and the density-dependence [6, 7]. The present paper studies how the intra- and interspecific interferences are mechanisms of coexistence for competing species in the chemostat. In this context, we will consider the following two species model with general density-dependent growth functions:

$$\begin{cases} \dot{S} &= D(S_{in} - S) - \mu_1(S, x_1, x_2)x_1 - \mu_2(S, x_2, x_1)x_2 \\ \dot{x}_1 &= [\mu_1(S, x_1, x_2) - D_1]x_1 \\ \dot{x}_2 &= [\mu_2(S, x_2, x_1) - D_2]x_2. \end{cases} \quad (1)$$

where x_i , $i = 1, 2$, denotes the concentration of species i and S is the nutrient concentration; S_{in} and D denote, respectively, the concentration of substrate in the feed bottle and the dilution rate of the chemostat. The D_i are not necessarily equal to D and can be interpreted as the sum of the dilution rate D and the natural death rate of the species: $D_i = D + a_i$, where $a_i \geq 0$. For $i = 1, 2$, $j = 1, 2$, $i \neq j$, $\mu_i(S, x_i, x_j)$ denotes the growth rate of species i . This model was considered in a series of paper by Lobry et al. [6, 7]. Our study provides theoretical explanations for the phenomenon, which was numerically observed in [6], where the coexistence holds when only intraspecific interference occurs, whereas it can disappear when the strength of interspecific interference is large enough. On the other hand, our study describes the operating diagram which shows the stability regions, in dependence of the operating parameters D and S_{in} , when all biological parameters are fixed.

For convenience, we use the abbreviations LES for Locally Exponentially Stable steady states in all that follows. The proof of all results may be found in [3]. For $i = 1, 2$, $j = 1, 2$, $i \neq j$, we make the following assumptions.

(H1) $\mu_i(0, x_i, x_j) = 0$ and $\mu_i(S, x_i, x_j) > 0$ for all $S > 0$, $x_1 \geq 0$ and $x_2 \geq 0$.

(H2) $\frac{\partial \mu_i}{\partial S}(S, x_i, x_j) > 0$, $\frac{\partial \mu_i}{\partial x_i}(S, x_i, x_j) \leq 0$ and $\frac{\partial \mu_i}{\partial x_j}(S, x_i, x_j) \leq 0$ for all $S > 0$, $x_1 \geq 0$ and $x_2 \geq 0$.

Condition (H1) means that the growth can take place if and only if the substrate is present. Condition (H2) means that the growth rate of each species increases with the concentration of substrate and is inhibited by intra- and interspecific interference.

2. Study of the model

In the following, we study the existence conditions and local stability of all corresponding steady states of (1) that has the following types of steady states:

– $\mathcal{E}_0 = (S_{in}, 0, 0)$, called the washout, where both populations are extinct: $x_1 = x_2 = 0$. This steady state always exists.

– $\mathcal{E}_1 = (\tilde{S}_1, \tilde{x}_1, 0)$, where second population is extinct: $x_2 = 0$ and $\tilde{x}_1 > 0$.

– $\mathcal{E}_2 = (\tilde{S}_2, 0, \tilde{x}_2)$, where first population is extinct: $x_1 = 0$ and $\tilde{x}_2 > 0$.

– $\mathcal{E}^* = (S^*, x_1^*, x_2^*)$, where both populations survive: $x_1^* > 0, x_2^* > 0$.

The components $S = \tilde{S}_i$ and $x = \tilde{x}_i$ of a boundary steady state \mathcal{E}_i are the solutions of equations

$$D(S_{in} - \tilde{S}_i) = D_i \tilde{x}_i, \quad \mu_i(\tilde{S}_i, \tilde{x}_i, 0) = D_i.$$

Straightforward calculations show that we have the following result which gives the condition of existence of a boundary steady state \mathcal{E}_i .

Proposition 2.1. *Let \mathcal{E}_i be a steady state of (1) with $\tilde{x}_i > 0$ and $x_j = 0, j \neq i$. Then \tilde{S}_i is given by $\tilde{S}_i = S_{in} - \frac{D_i}{D} \tilde{x}_i$ where $x_i = \tilde{x}_i$ is the solution of*

$$\mu_i\left(S_{in} - \frac{D_i}{D} x_i, x_i, 0\right) = D_i. \quad (2)$$

This steady state exists if and only if

$$\mu_i(S_{in}, 0, 0) > D_i \quad (3)$$

holds. If it exists then it is unique.

The component $S = S^*$ of a coexistence steady state \mathcal{E}^* is given by $S^* = S_{in} - \frac{D_1}{D} x_1^* - \frac{D_2}{D} x_2^*$ and the components $(x_1 = x_1^*, x_2 = x_2^*)$ must be a solution of

$$\begin{cases} f_1(x_1, x_2) = 0 \\ f_2(x_1, x_2) = 0, \end{cases} \quad (4)$$

$$f_i(x_1, x_2) := \mu_i\left(S_{in} - \frac{D_1}{D} x_1 - \frac{D_2}{D} x_2, x_i, x_j\right) - D_i, \text{ for } i = 1, 2, j = 1, 2, i \neq j. \quad (5)$$

The functions (5) are defined on the set

$$M = \left\{ (x_1, x_2) \in \mathbb{R}_+^2 : \frac{D_1}{D} x_1 + \frac{D_2}{D} x_2 \leq S_{in} \right\}. \quad (6)$$

S^* is positive if and only if (4) has a solution in the interior M° of M , defined by (6). To solve (4) in this open M° , we need the following result:

Lemme 2.1. *Assume that (3) holds for $i = 1, 2$ and let \tilde{x}_i be a solution of (2). The equation $f_i(x_1, x_2) = 0$ defines a smooth decreasing function*

$$F_i : [0, \tilde{x}_i] \rightarrow \mathbb{R}, \quad x_i \mapsto F_i(x_i)$$

such that $F_i(\tilde{x}_i) = 0$ and the graph γ_i of F_i lies in M° (see Figure 1). More precisely, $(x_1, F_1(x_1)) \in M^\circ$ [resp. $(F_2(x_2), x_2) \in M^\circ$] for all $x_i \in (0, \tilde{x}_i)$.

Notice that $F_i : [0, \tilde{x}_i] \rightarrow [0, \bar{x}_j], x_i \mapsto F_i(x_i)$, where $\bar{x}_j = F_i(0)$ is the unique solution of

$$\mu_i\left(S_{in} - \frac{D_j}{D} x_j, 0, x_j\right) = D_i. \quad (7)$$

The following four cases must be distinguished (see Fig. 1):

$$\text{Case 1: } \bar{x}_1 > \tilde{x}_1 \quad \text{and} \quad \bar{x}_2 > \tilde{x}_2, \quad \text{Case 2: } \bar{x}_1 < \tilde{x}_1 \quad \text{and} \quad \bar{x}_2 < \tilde{x}_2, \quad (8)$$

$$\text{Case 3: } \bar{x}_1 < \tilde{x}_1 \quad \text{and} \quad \bar{x}_2 > \tilde{x}_2, \quad \text{Case 4: } \bar{x}_1 > \tilde{x}_1 \quad \text{and} \quad \bar{x}_2 < \tilde{x}_2. \quad (9)$$

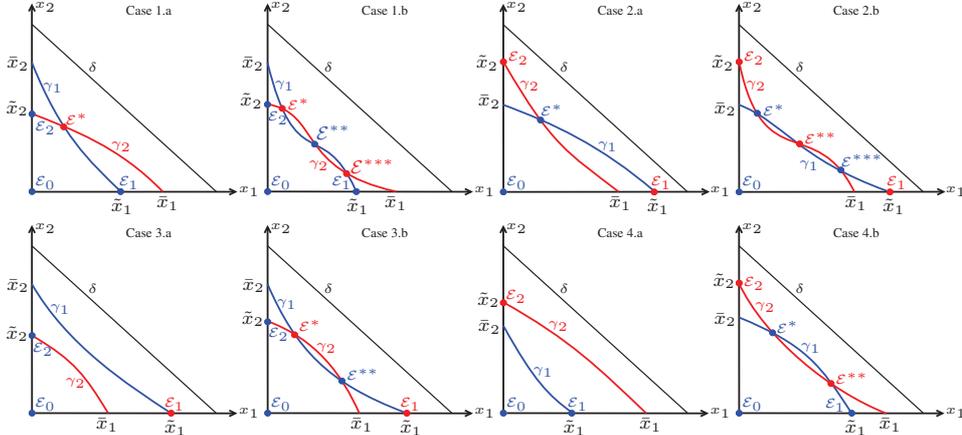


Figure 1: Case 1: (a) unique intersection, (b) an odd number of intersections. Case 2: (a) unique intersection, (b) an odd number of intersections. Case 3: (a) no intersection, (b) an even number of intersections. Case 4: (a) no intersection, (b) an even number of intersections.

Définition 2.1. A positive steady state $\mathcal{E}^* = (S^*, x_1^*, x_2^*)$ of (1) is said to be blue [resp. red] if and only if, on the right of (x_1^*, x_2^*) , the tangent of γ_1 at point (x_1^*, x_2^*) is above [resp. under] the tangent of γ_2 at point (x_1^*, x_2^*) .

Théorème 2.1. Assume that (H1), (H2) and (3), for $i = 1, 2$ hold.

1) Blue positive steady states are unstable. If for all S, x_1, x_2 ,

$$\frac{\partial \mu_1}{\partial x_1} < \frac{\partial \mu_1}{\partial x_2} \quad \text{and} \quad \frac{\partial \mu_2}{\partial x_2} < \frac{\partial \mu_2}{\partial x_1} \quad (10)$$

hold, or $D_1 = D_2 = D$, then red positive steady states are LES, that is to say, positive steady states are alternatively unstable and LES.

2) If Case 1 holds, the system can have generically an odd number of positive steady states, while \mathcal{E}_1 and \mathcal{E}_2 are unstable. The positive steady states at the left-hand end and right-hand end are red (see Fig. 1, Case 1). If, in addition, for all S, x_1, x_2 ,

$$\frac{\partial \mu_1}{\partial x_1} < \frac{D_1}{D_2} \frac{\partial \mu_1}{\partial x_2} \quad \text{and} \quad \frac{\partial \mu_2}{\partial x_2} < \frac{D_2}{D_1} \frac{\partial \mu_2}{\partial x_1} \quad (11)$$

hold, then the positive steady state is unique (see Fig. 1, Case 1.a).

3) If Case 2 holds, the system can have generically an odd number of positive steady states, while \mathcal{E}_1 and \mathcal{E}_2 are LES. The positive steady states at the left-hand end and right-hand end are blue (see Fig. 1, Case 2). If, in addition, for all S, x_1, x_2 ,

$$\frac{\partial \mu_1}{\partial x_1} > \frac{D_1}{D_2} \frac{\partial \mu_1}{\partial x_2} \quad \text{and} \quad \frac{\partial \mu_2}{\partial x_2} > \frac{D_2}{D_1} \frac{\partial \mu_2}{\partial x_1} \quad (12)$$

hold, then \mathcal{E}^* is unique and unstable (see Fig. 1, Case 2.a).

4) If Case 3 [resp. Case 4] holds, then generically the system has no positive steady state or an even number of positive steady states where \mathcal{E}_1 is LES [resp. unstable] and \mathcal{E}_2 is unstable [resp. LES]. The positive steady state at the right-hand [resp. left-hand] end, if it exists, is blue (see Fig. 1). If, in addition, (11) or (12) hold, then the system has no positive steady state (see Fig. 1, Case 3.a [resp. Case 4.a]).

3. Operating diagram

The operating diagram shows how the system behaves when we vary the two control parameters S_{in} and D in (1). We restrict our attention to the case where $D_1 = D_2 = D$ and the growth function μ_i is the modified Monod function

$$\mu_i(S, x_i, x_j) = \frac{m_i S}{k_i + S + \beta_i(x_i + \alpha_i x_j)}, \quad i = 1, 2, \quad (13)$$

where m_i denotes the maximum growth rate, k_i the half-saturation constant; β_i the inhibition factor for the growth of the species i due to intra- and interspecific interference; α_i is a nonnegative parameter which denotes the strength of the interspecific interference. Let Υ_i be the curve of equation $D = \mu_i(S_{in}, 0, 0)$, $i = 1, 2$,

$$\Upsilon_i = \{(S_{in}, D) : D = \mu_i(S_{in}, 0, 0)\}.$$

Recall that \tilde{x}_i and \bar{x}_i are defined as the solutions of (2) and (7), respectively. These equations become now

$$\mu_i(S_{in} - \tilde{x}_i, \tilde{x}_i, 0) = D, \quad \mu_j(S_{in} - \bar{x}_i, 0, \bar{x}_i) = D, \quad i = 1, 2, j = 1, 2, \quad i \neq j.$$

Therefore, \tilde{x}_i and \bar{x}_i depend on the operating parameters S_{in} and D . We denote them by $\tilde{x}_i(S_{in}, D)$ and $\bar{x}_i(S_{in}, D)$. Define the sets

$$\Upsilon_i^c = \{(S_{in}, D) : \tilde{x}_i(S_{in}, D) = \bar{x}_i(S_{in}, D)\},$$

which are curves in the generic case. In Fig. 2, the curves Υ_i and Υ_i^c , $i = 1, 2$ separate the operating plane (S_{in}, D) in at most six regions, labeled as \mathcal{I}_k , $k = 0, \dots, 5$. The regions \mathcal{I}_4 and \mathcal{I}_5 are empty in case (a) and the regions \mathcal{I}_4 and \mathcal{I}_3 are empty in case (b) and (d), respectively. Table 1 shows the existence and stability of steady states in the regions \mathcal{I}_k , of the operating diagram, in Fig. 2.

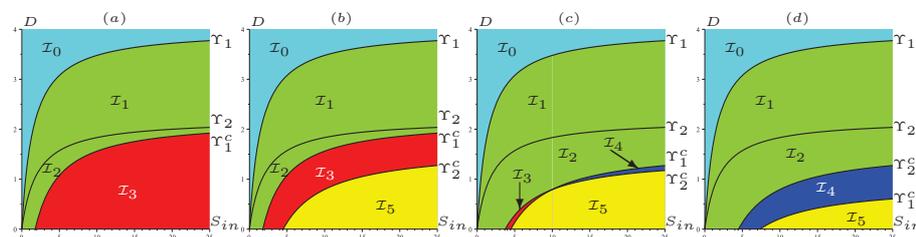


Figure 2: Operating diagrams of (1). Cyan color represents the region of washout (\mathcal{E}_0 is LES), red color represents the region of coexistence (\mathcal{E}^* is LES), blue color represents the region of bi-stability (\mathcal{E}_1 and \mathcal{E}_2 are LES), green [resp. yellow] color represents a region of competitive exclusion (\mathcal{E}_1 [resp. \mathcal{E}_2] is LES).

Fig. 2 shows how this region of coexistence changes and even disappears when interspecific interference is added in the model. For instance, if the first species interspecific coefficient is fixed, then varying the second species interspecific coefficient leads to a reduction of the coexistence region \mathcal{I}_3 until the occurrence of bi-stability region \mathcal{I}_4 , followed by the disappearance of the coexistence region \mathcal{I}_3 (see Fig. 2(a-b-c-d)).

Region	\mathcal{E}_0	\mathcal{E}_1	\mathcal{E}_2	\mathcal{E}^*
$(S_{in}, D) \in \mathcal{I}_0$	S			
$(S_{in}, D) \in \mathcal{I}_1$	U	S		
$(S_{in}, D) \in \mathcal{I}_2$	U	S	U	
$(S_{in}, D) \in \mathcal{I}_3$	U	U	U	S
$(S_{in}, D) \in \mathcal{I}_4$	U	S	S	U
$(S_{in}, D) \in \mathcal{I}_5$	U	U	S	

Table 1: Existence and local stability of steady states.

4. Conclusion

In this work, we analyzed the effect of the intra- and interspecific interference on the coexistence of microbial species in a chemostat, by allowing a large classe of response functions with differential removal rates. For this class of response functions, we distinguished four cases, (8) and (9), which are qualitatively similar to the cases encountered in the classical Lotka-Volterra competition model. When the intraspecific interference is dominant with respect to interspecific interference there exists at most one positive steady state, that is LES if it exists. Inversely, when the intraspecific interference is dominated by interspecific interference, there exists at most one positive steady state, that is unstable if it exists. The operating diagrams show how regions of coexistence and bi-stability of steady states vary with intra- and interspecific interference. More precisely, increasing the values of interspecific interference terms reduces the region of coexistence and increases the regions of competitive exclusion with the occurrence of a bi-stability region.

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