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► **To cite this version:**

Tahani Mtar, Radhouane Fekih-Salem, Tewfik Sari. Mortality can produce limit cycles in density-dependent models with a predator-prey relationship. 2021. hal-03283371v1

**HAL Id: hal-03283371**

**<https://hal.science/hal-03283371v1>**

Preprint submitted on 10 Jul 2021 (v1), last revised 18 Mar 2022 (v3)

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# MORTALITY CAN PRODUCE LIMIT CYCLES IN DENSITY-DEPENDENT MODELS WITH A PREDATOR-PREY RELATIONSHIP

TAHANI MTAR<sup>a</sup> AND RADHOUANE FEKIH-SALEM<sup>a,c,\*</sup> AND TEWFIK SARI<sup>b</sup>

<sup>a</sup>University of Tunis El Manar, National Engineering School of Tunis, LAMSIN, 1002, Tunis, Tunisia

<sup>b</sup>ITAP, Univ Montpellier, INRAE, Institut Agro, Montpellier, France

<sup>c</sup>University of Monastir, Higher Institute of Computer Science of Mahdia, 5111, Mahdia, Tunisia

ABSTRACT. In this paper, we study an interspecific density-dependent model of two species competing on a single nutrient in a chemostat, taking into account the predator-prey relationship. Without mortality of species, we have proved previously that the system may have a multiplicity of positive steady states that can only appear or disappear through saddle-node or transcritical bifurcations. Including the mortality, we give a complete analysis for the existence and local stability of all steady states of the three-dimensional system which cannot be reduced to a two-dimensional one. We highlight the effect of mortality to destabilize the positive steady state with the emergence of stable limit cycles through supercritical Hopf bifurcations. To describe how the process behaves according to control parameters represented by the dilution rate and the input concentration of the substrate, we determine theoretically the operating diagram by plotting the various conditions of existence and stability and numerically by using MATCONT. The bifurcation diagram according to the input concentration shows the various types of bifurcations of steady states and the coexistence either around a positive steady state or sustained oscillations.

1 **1. Introduction.** The chemostat is an important laboratory apparatus used for  
2 continuous cultures of microorganisms in microbiology and ecology. The mathe-  
3 matical analysis of the classical chemostat model of two or more microbial species  
4 competing for a single limiting nutrient shows that only the species with the lowest  
5 ‘break-even’ concentration survives while all other species are extinct (see, for in-  
6 stance, [21, 40]). This result, known as the Competitive Exclusion Principle (CEP),  
7 has a long history in the literature of bio-mathematics and recently in [35] a new  
8 proof of this principle is given using elementary analysis and comparisons of solu-  
9 tions of ordinary differential equations.

10 Despite the CEP has been confirmed by the experiences of Hansen and Hubbell  
11 [20], this principle contradicts the great biodiversity found in nature as well as

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2010 *Mathematics Subject Classification.* Primary: 34A34, 34D20; Secondary: 92B05, 92D25.

*Key words and phrases.* Density-dependence; Hopf Bifurcation; limit cycle; mortality; operat-  
ing diagram; predator-prey relationship.

The first author thanks the Tunisian Ministry of Higher Education, Scientific Research and  
Technology for financial support and INRAE for hosting her in Montpellier during the preparation  
of this work. This work was supported by the Euro-Mediterranean research network TREASURE  
(<https://www6.inrae.fr/treasure/>).

\* Corresponding author: RADHOUANE FEKIH-SALEM.

12 bioprocesses. To better reconcile theory and observations, several recent extensions  
 13 of this classic chemostat model have been triggered promoting the coexistence of  
 14 microbial species. The reader can find in the existing literature the following  
 15 various coexistence mechanisms: the intra and inter specific competition [1, 9], the  
 16 flocculation [14, 16, 17, 18, 19], the density-dependence of the growth functions  
 17 [7, 15, 22, 27, 28, 29, 30, 33], the predator-prey interactions [6, 26], the complex  
 18 food webs [2, 23, 45], the presence of inhibitors that affects the strongest competitor  
 19 [3, 10, 11], the commensalistic relationship [4, 5, 37], and the syntrophic relationship  
 20 [8, 13, 36, 46].

21 An extension of the classical chemostat model was considered in a series of papers  
 22 by Lobry et al. [22, 27, 28, 29, 30], taking into account general intra and interspe-  
 23 cific density-dependent growth rates with distinct removal rates for each species.  
 24 Considering particular density-dependent growth functions with intraspecific in-  
 25 terference, the numerical simulations in [27] show the coexistence between several  
 26 species for small enough inter specific interference and the exclusion of one species,  
 27 at least, for large enough inter specific interference. In [15], a mathematical analysis  
 28 confirms these numerical results where this system presents the global stability of  
 29 the coexistence steady state for small enough interspecific interference terms while  
 30 this system exhibits bi-stability for large enough interspecific interference. With  
 31 the same removal rates and only interspecific interferences, the coexistence of two  
 32 species is impossible which confirms the CEP [12].

33 The present paper considers a model of two competitors for a single resource  
 34 in a chemostat, with interspecific density-dependent growth functions. The species  
 35 have a predator-prey relationship, that is, the first species (the prey) promotes the  
 36 growth of the second species (the predator) which in turn inhibits the growth of  
 37 the first species. In our study, the mortality (or decay) of two species is taken into  
 38 account and not neglected as in previous studies [12, 33]. The model can be written  
 39 as follows:

$$40 \quad \begin{cases} \dot{S} &= D(S_{in} - S) - f_1(S, x_2)x_1 - f_2(S, x_1)x_2, \\ \dot{x}_1 &= (f_1(S, x_2) - D_1)x_1, \\ \dot{x}_2 &= (f_2(S, x_1) - D_2)x_2, \end{cases} \quad (1)$$

41 where  $S$  is the substrate concentration;  $x_1(t)$  and  $x_2(t)$  are, respectively, the concen-  
 42 trations of prey and predator species;  $D$  and  $S_{in}$  are, respectively, the dilution rate  
 43 and the input substrate concentration in the chemostat;  $f_1$  is the density-dependent  
 44 growth rate of the prey species  $x_1$  that is assumed to be increasing in the variable  $S$   
 45 and decreasing in the predator species  $x_2$ ;  $f_2$  is the density-dependent growth rate  
 46 of the predator species  $x_2$  that is assumed to be increasing in the variable  $S$  and  
 47 increasing in the prey species  $x_1$ ;  $D_i$ ,  $i = 1, 2$  is the removal rate of species  $x_i$  and  
 48 can be modeled as in [17, 39] by

$$49 \quad D_i = \alpha_i D + a_i, \quad i = 1, \dots, n \quad (2)$$

50 where the coefficient  $\alpha_i$  belongs to  $[0, 1]$  and represents the fraction of the prey and  
 51 predator species leaving the reactor as proposed by [5] to model a biomass reactor  
 52 attached to the support or to decouple the residence time of solids and the hydraulic  
 53 residence time ( $1/D$ );  $a_i$  is the nonnegative mortality (or decay) rate of the species  
 54  $x_i$ .

55 In [12, 33], the mathematical analysis of model (1) shows that the system may  
 56 exhibit the coexistence or the bi-stability with a multiplicity of positive steady  
 57 states, in the particular case  $\alpha_i = 1$  and  $a_i = 0$ . Moreover, in [33], the operating

58 diagram shows that all steady states can appear or disappear only through saddle-  
 59 node or transcritical bifurcations according to the control parameters represented by  
 60 the dilution rate and the input concentration of the substrate. Indeed, the operating  
 61 diagram is a very useful tool to determine how a process behaves when all biological  
 62 parameters are fixed and the control parameters are varied, as they are the most  
 63 easily parameters to manipulate in a chemostat. It is studied either numerically as  
 64 in [24, 37, 43, 44, 46] or theoretically as in [1, 3, 8, 11, 10, 15, 18, 21, 33, 36]. In [34],  
 65 we have studied the existence and the local stability of model (1) in the particular  
 66 cas where  $\alpha_i = 1$ .

67 The aim of this paper is to understand the joined effect of mortality and predator-  
 68 prey relationship on the behavior of the density-dependent model considered in  
 69 [12, 33]. In this work, our study provides an extension of the results in [12, 33] by  
 70 considering distinct removal rates where the system cannot be reduced to a two-  
 71 dimensional one. Using the Routh–Hurwitz criterion, we determine the existence  
 72 conditions of all steady states and their local stability according to operating pa-  
 73 rameters. In contrast to the case without mortality where the coexistence may  
 74 occur only around a positive steady state [12, 33], our results show that the mor-  
 75 tality can destabilize the positive steady state through Hopf bifurcation where the  
 76 coexistence can be around a stable limit cycle. It is known that introducing decay  
 77 for the species in the classical predator-prey models in the chemostat results in  
 78 instability and chaos [25]. For more details on food-chains in the chemostat, the  
 79 reader may consult [6, 41, 42]. In our model, the same intrinsic effect of mortality  
 80 on the stability of the positive steady state is observed. Indeed, when mortality is  
 81 included in the density-dependent model with predator-prey relationship, the posi-  
 82 tive steady state is not necessarily stable, when it exists. On the other hand, our  
 83 study provides an important tool for the experimentation which is the operating  
 84 diagram where we succeed to determine the region of the emergence of stable limit  
 85 cycles theoretically from Routh–Hurwitz conditions and numerically by using the  
 86 software MATCONT [32]. Finally, a one-parameter bifurcation diagram determines  
 87 all types of bifurcations.

88 The paper is structured as follows. We first introduce in Section 2 assumptions  
 89 on the growth functions and preliminary results. Then, we determine the necessary  
 90 and sufficient conditions of existence and stability of the steady states using the null-  
 91 cline method. In Section 3, we determine theoretically the operating diagrams and  
 92 then numerically by using MATCONT. In Section 4, we study the one-parameter  
 93 bifurcation diagram with respect to the input concentration  $S_{in}$ . The numerical  
 94 simulations validate the theoretical analysis of the operating diagram. Some con-  
 95 clusions are drawn in Section 5. All the proofs are reported in A. In Appendix B,  
 96 we construct the operating diagram. In Appendix C, a numerical study of the Hopf  
 97 bifurcation is provided with respect to  $S_{in}$ . Finally, all the parameter values used  
 98 in simulations are provided in Appendix D.

99 **2. Assumptions and mathematical analysis.** In this paper, we assume that  
 100 the growth function  $f_i(S, x_j)$ ,  $i = 1, 2$ ,  $j = 1, 2$ ,  $i \neq j$  is continuously differentiable  
 101 ( $\mathcal{C}^1$ ) and satisfies the following hypotheses.

102 (H1) For all  $x_j \geq 0$  and  $S > 0$ ,  $f_i(0, x_j) = 0$  and  $f_2(S, 0) = 0$ .

103 (H2) For all  $S > 0$ ,  $x_1 > 0$  and  $x_2 \geq 0$ ,  $\frac{\partial f_i}{\partial S}(S, x_j) > 0$ ,  $\frac{\partial f_1}{\partial x_2}(S, x_2) < 0$  and  
 104  $\frac{\partial f_2}{\partial x_1}(S, x_1) > 0$ .

105 Assumption (H1) means that the substrate is necessary for the growth of each  
 106 species and the prey species  $x_1$  is necessary for the growth of the predator species  
 107  $x_2$ . Assumption (H2) means that the growth rate of the prey species  $x_1$  increases  
 108 with the concentration of the substrate  $S$  and is inhibited by the second species  $x_2$ .  
 109 While the growth of the predator species  $x_2$  is increasing with the concentration of  
 110 the substrate  $S$  and the prey species  $x_1$ . We now prove the following result.

**Proposition 1.** *Assume that assumptions (H1)-(H2) hold. For any nonnegative initial condition, the solution of system (1) exists for all  $t \geq 0$ , remains nonnegative and is bounded. In addition, the set*

$$\Omega = \{(S, x_1, x_2) \in \mathbb{R}_+^3 : S + x_1 + x_2 \leq DS_{in}/D_{\min}\}$$

111 *is positively invariant and is a global attractor for the dynamics (1), where  $D_{\min} =$*   
 112  *$\min(D, D_1, D_2)$ .*

113 Now, we shall discuss the existence of steady states of system (1) and then their  
 114 asymptotic stability. A steady state of (1) exists or is said to be ‘meaningful’ if  
 115 and only if all its components are nonnegative. The steady states are given by the  
 116 solutions of the following system:

$$117 \quad \begin{cases} 0 &= D(S_{in} - S) - f_1(S, x_2)x_1 - f_2(S, x_1)x_2, \\ 0 &= (f_1(S, x_2) - D_1)x_1, \\ 0 &= (f_2(S, x_1) - D_2)x_2. \end{cases} \quad (3)$$

118 If  $x_1 = 0$  and  $x_2 > 0$ , we obtain  $D_2 = 0$  from assumption (H1), which is impossible.  
 119 Thus, system (1) can have at most three types of steady states labeled as follows:

- 120 •  $\mathcal{E}_0$  ( $x_1 = x_2 = 0$ ): the washout of two species which always exists.
- 121 •  $\mathcal{E}_1$  ( $x_1 > 0, x_2 = 0$ ): only prey species is present.
- 122 •  $\mathcal{E}^*$  ( $x_1 > 0, x_2 > 0$ ): the coexistence of two species.

123 From (H2), the function  $S \mapsto f_1(S, 0)$  is increasing. Hence, if  $D < (f_1(+\infty, 0) -$   
 124  $a_1)/\alpha_1$ , then there exists a unique solution  $S = \lambda_1(D)$  (called the *break-even con-*  
 125 *centration*) of equation

$$126 \quad f_1(S, 0) = \alpha_1 D + a_1. \quad (4)$$

127 If  $D \geq (f_1(+\infty, 0) - a_1)/\alpha_1$ , we let  $\lambda_1(D) = +\infty$ . The following result determines  
 128 the existence condition of the steady state  $\mathcal{E}_1$  according to operating parameters.

129 **Proposition 2.** *Assume that (H1) and (H2) hold. The boundary steady state*  
 130  *$\mathcal{E}_1 = (\tilde{S}, \tilde{x}_1, 0)$  of system (1) is defined by*

$$131 \quad \tilde{S} = \lambda_1(D) \quad \text{and} \quad \tilde{x}_1 = \frac{D}{D_1}(S_{in} - \lambda_1(D)). \quad (5)$$

132 *It exists if and only if*

$$133 \quad S_{in} > \lambda_1(D). \quad (6)$$

134 *When it exists,  $\mathcal{E}_1$  is unique.*

135 In what follows, we determine the existence condition of the positive steady state  
 136  $\mathcal{E}^* = (S^*, x_1^*, x_2^*)$  where the components  $S = S^*$ ,  $x_1 = x_1^*$  and  $x_2 = x_2^*$  must be the  
 137 solutions of (3) with  $x_1 > 0$  and  $x_2 > 0$ . That is,  $S^*$ ,  $x_1^*$  and  $x_2^*$  are the solutions of  
 138 the set of equations

$$139 \quad D(S_{in} - S) = D_1 x_1 + D_2 x_2 \quad (7)$$

$$140 \quad f_1(S, x_2) = D_1 \quad (8)$$

$$141 \quad f_2(S, x_1) = D_2. \quad (9)$$

142 From (7), the solution  $S^*$  is given by

$$143 \quad S^* = S_{in} - D_1 x_1^*/D - D_2 x_2^*/D. \quad (10)$$

144 Replacing  $S^*$  by this expression in (8,9), we see that  $(x_1 = x_1^*, x_2 = x_2^*)$  must be a  
145 solution of

$$146 \quad \begin{cases} \tilde{f}_1(x_1, x_2) := f_1(S_{in} - D_1 x_1/D - D_2 x_2/D, x_2) - D_1 = 0 \\ \tilde{f}_2(x_1, x_2) := f_2(S_{in} - D_1 x_1/D - D_2 x_2/D, x_1) - D_2 = 0. \end{cases} \quad (11)$$

Note that the functions  $\tilde{f}_i$ ,  $i = 1, 2$ ,  $j = 1, 2$ ,  $i \neq j$  are defined on the set

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

147 In addition,  $S^*$  is positive if and only if  $D_1 x_1^*/D + D_2 x_2^*/D < S_{in}$ , that is, (11) has  
148 a positive solution in the interior  $\dot{M}$  of  $M$ . In what follows, we define the line  $\delta$  by  
149  $D_1 x_1/D + D_2 x_2/D = S_{in}$  and we need the next notations:

$$150 \quad E = \frac{\partial f_1}{\partial S}, \quad F = \frac{\partial f_2}{\partial S}, \quad G = -\frac{\partial f_1}{\partial x_2}, \quad H = \frac{\partial f_2}{\partial x_1}. \quad (12)$$

151 We have used the opposite sign of the partial derivative  $G = -\partial f_1/\partial x_2$ , such that  
152 all constants involved in the computation become positive. To solve (11) in  $\dot{M}$ , we  
153 need the following Lemmas 1, 2 and 3 where the proofs are similar to those in [34].

**Lemma 1.** *Assume that assumptions (H1)-(H2) and condition (6) hold. The equation  $\tilde{f}_1(x_1, x_2) = 0$  defines a smooth decreasing function*

$$F_1 : [0, \tilde{x}_1] \longrightarrow [0, \tilde{x}_2] \\ x_1 \longmapsto F_1(x_1) = x_2,$$

154 such that  $F_1(\tilde{x}_1) = 0$ ,  $F_1(0) = \tilde{x}_2$  and

$$155 \quad -\frac{D_1}{D_2} < F_1'(x_1) = -\frac{D_1 E}{D_2 E + G} < 0, \quad \text{for all } x_1 \in [0, \tilde{x}_1], \quad (13)$$

156 where  $\tilde{x}_2$  is the unique solution of the equation  $\tilde{f}_1(0, x_2) = 0$ . In addition, the graph  
157  $\gamma_1$  of  $F_1$  lies in  $\dot{M}$ , that is,  $(x_1, F_1(x_1)) \in \dot{M}$  for all  $x_1 \in (0, \tilde{x}_1)$  (see Fig. 1).

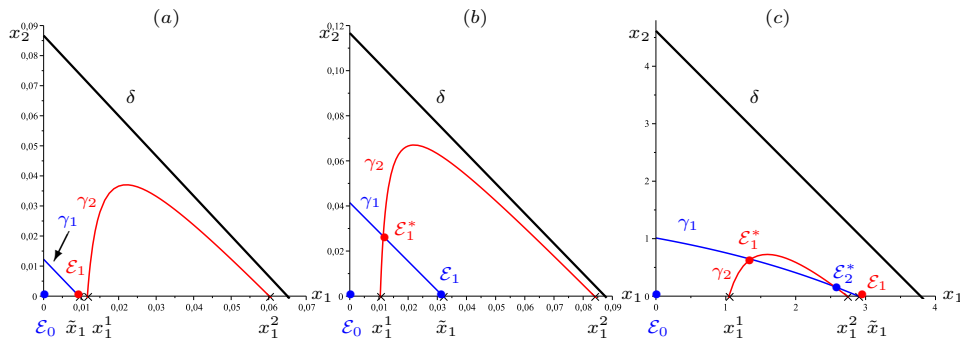


FIGURE 1. Number of positive steady states: (a) Case 1: no positive steady state when  $(S_{in}, D) = (0.26, 0.1)$ , (b) Case 2: an odd number when  $(S_{in}, D) = (0.35, 0.1)$ , (c) Case 3: an even number when  $(S_{in}, D) = (4.5, 0.8)$ .

158 To define the function  $x_2 = F_2(x_1)$  of equation  $\tilde{f}_2(x_1, x_2) = 0$ , we will need of  
159 the following Lemma to determine the necessary and sufficient condition for the  
160 existence of solutions of the equation  $\tilde{f}_2(x_1, 0) = 0$ .

161 **Lemma 2.** Under assumptions (H1)-(H2), the equation  $\tilde{f}_2(x_1, 0) = 0$  has a solution  
 162 in  $[0, DS_{in}/D_1]$  if and only if,

$$163 \quad \max_{x_1 \in [0, DS_{in}/D_1]} f_2(S_{in} - D_1 x_1/D, x_1) \geq D_2. \quad (14)$$

164 Generically, we have an even number of solutions in  $[0, DS_{in}/D_1]$ .

165 For simplicity, we add the following assumption which is satisfied by the specific  
 166 growth rates (22).

167 (H3) Equation  $\tilde{f}_2(x_1, 0) = 0$  has at most two solutions  $x_1^1$  and  $x_1^2$  in  $[0, DS_{in}/D_1]$ .

168 The proof of the maximum number of solutions of the equation  $\tilde{f}_2(x_1, 0) = 0$  for  
 169 the specific growth rates (22) is similar to that in Appendix B of [34]. When the  
 170 function  $x_1 \mapsto \tilde{f}_2(x_1, 0)$  is multimodal, the study of this general case can be treated  
 171 similarly, without added difficulty. In this particular case, we obtain the next result.

**Lemma 3.** Assume that assumptions (H1) to (H3) and condition (14) hold, the  
 equation  $\tilde{f}_2(x_1, x_2) = 0$  defines a smooth function

$$\begin{aligned} F_2 : [x_1^1, x_1^2] &\longrightarrow [0, DS_{in}/D_2[ \\ x_1 &\longmapsto F_2(x_1) = x_2, \end{aligned}$$

172 such that  $F_2(x_1^1) = F_2(x_1^2) = 0$  and

$$173 \quad -\frac{D_1}{D_2} < F_2'(x_1) = -\frac{D_1}{D_2} + \frac{D}{D_2} \frac{H}{F}, \quad \text{for all } x_1 \in [x_1^1, x_1^2], \quad (15)$$

174 where  $x_1^1$  and  $x_1^2$  are the solutions of the equation  $\tilde{f}_2(x_1, 0) = 0$ . In addition, the  
 175 graph  $\gamma_2$  of  $F_2$  lies in  $\mathring{M}$  where  $(x_1, F_2(x_1)) \in \mathring{M}$  for all  $x_1 \in (x_1^1, x_1^2)$  (see Fig. 1).

176 Applying the previous lemmas, we establish in the following proposition the  
 177 necessary and sufficient condition of the existence of the coexistence steady state  
 178  $\mathcal{E}^*$ .

179 **Proposition 3.** Assume that assumptions (H1) to (H3) and conditions (6) and  
 180 (14) hold. A positive steady state  $\mathcal{E}^* = (S^*, x_1^*, x_2^*)$  of (1) exists if and only if the  
 181 curves  $\gamma_1$  and  $\gamma_2$  have a positive intersection, where  $S^*$  is given by (10) and  $(x_1^*, x_2^*)$   
 182 is a positive solution of equations

$$183 \quad x_2 = F_1(x_1) \quad \text{and} \quad x_2 = F_2(x_1). \quad (16)$$

184 According to the position of  $\tilde{x}_1$  between  $x_1^1$  and  $x_1^2$ , there exist three cases that  
 185 must be distinguished:

$$186 \quad \text{Case 1 : } \tilde{x}_1 < x_1^1 < x_1^2, \quad \text{Case 2 : } x_1^1 < \tilde{x}_1 < x_1^2, \quad \text{Case 3 : } x_1^1 < x_1^2 < \tilde{x}_1. \quad (17)$$

When hypotheses (H1)-(H3) and condition (14) hold, one has

$$f_2 \left( \lambda_1(D), \frac{D}{D_1} (S_{in} - \lambda_1(D)) \right) < D_2 \Leftrightarrow \text{Case 1 or Case 3} \quad (18)$$

$$f_2 \left( \lambda_1(D), \frac{D}{D_1} (S_{in} - \lambda_1(D)) \right) > D_2 \Leftrightarrow \text{Case 2.} \quad (19)$$

187 **Remark 1.** 1. Let  $S \geq 0$ .  $x_1 = \lambda_2(S, y)$  is the unique solution of equation  $y =$   
 188  $f_2(S, x_1)$ . Since the function  $x_1 \mapsto f_2(S, x_1)$  is increasing, then the function  
 189  $y \mapsto \lambda_2(S, y)$  is well defined and strictly increasing for  $y \in [0, \sup_{x_1 \geq 0} f_2(S, x_1)]$ .

190 2. Condition (18) is equivalent to

$$191 \quad S_{in} < \lambda_1(D) + \frac{D_1}{D} \lambda_2(\lambda_1(D), D_2) := \varphi(D). \quad (20)$$

192 Inversely, condition (19) is equivalent to  $S_{in} > \varphi(D)$ .

193 As a consequence of the previous results, we obtain the following proposition  
 194 which determines the multiplicity of positive steady states of (1) according to the  
 195 three cases of (17) or (equivalently) the two conditions in (18, 19) which depend on  
 196 the operating parameters (see Fig. 1).

197 **Proposition 4.** *Assume that hypotheses (H1) to (H3) and conditions (6) and (14)*  
 198 *hold.*

- 199 1. *In Case 1, there is no positive steady state.*
- 200 2. *In Case 2, there exists at least one positive steady state. Generically, the*  
 201 *system has an odd number of positive steady states.*
- 202 3. *In Case 3, generically system (1) has no positive steady state or an even*  
 203 *number of positive steady states.*

204 Now, we determine the local stability of all steady states of (1) by using the  
 205 abbreviation LES for Locally Exponentially Stable steady states.

206 **Proposition 5.** *Assume that assumptions (H1)-(H3) hold.*

- 207 1.  $\mathcal{E}_0$  *is LES if and only if*  $S_{in} < \lambda_1(D)$ .
- 208 2.  $\mathcal{E}_1$  *is LES if and only if*  $S_{in} < \varphi(D)$ .
- 209 3.  $\mathcal{E}^* = (S^*, x_1^*, x_2^*)$  *is LES if and only if*  $F'_1(x_1^*) < F'_2(x_1^*)$  *and*

$$210 \quad c_4(D, S_{in}) := D_1 E^2 x_1^2 + D_2 F^2 x_2^2 + DD_1 E x_1 + DD_2 F x_2 \\ + (D_1 E F + (D_1 - D) F G + D_2 E F + (D - D_2) E H) x_1 x_2 \\ + (E H - F G + G H) (E x_1^2 x_2 + F x_1 x_2^2) > 0. \quad (21)$$

211 *where the functions E, F, G and H are defined by (12), and are evaluated at  $\mathcal{E}^*$ .*

**Remark 2.** In the particular case without mortality of species ( $D_i = D$ ), the Routh–Hurwitz coefficient given by (21) becomes

$$c_4(D, S_{in}) = D(E^2 x_1^2 + F^2 x_2^2 + D(E x_1 + F x_2)) + 2DEF x_1 x_2 + \frac{c_3}{D}(E x_1 + F x_2),$$

212 where the expression of  $c_3$  is given by (25). Using the second expression of  $c_3$  given  
 213 by (27), we find the result of [33] in this particular case  $D_i = D$  such that the  
 214 stability of the coexistence steady state  $\mathcal{E}^*$  depends on the sign of  $F'_2(x_1^*) - F'_1(x_1^*)$   
 215 or equivalently the relative positions of the two curves  $\gamma_1$  and  $\gamma_2$ .

216 The necessary and sufficient conditions of existence and local stability of all  
 steady states of (1) are summarized in Table 1.

TABLE 1. Necessary and sufficient conditions of existence and stability of steady states of system (1) where  $c_4$  is defined by (21).

	Existence	Local stability
$\mathcal{E}_0$	always exists	$S_{in} < \lambda_1(D)$
$\mathcal{E}_1$	$S_{in} > \lambda_1(D)$	$S_{in} < \varphi(D)$
$\mathcal{E}^*$	$S_{in} > \varphi(D)$ or $S_{in} < \varphi(D)$ and (16) has a solution	$F'_2(x_1^*) > F'_1(x_1^*)$ and $c_4(D, S_{in}) > 0$



218 **3. Operating diagram.** The aim of this section is to describe theoretically the  
 219 operating diagram of system (1). We use MAPLE [31] to draw the curves that  
 220 separate the different regions of existence and stability of the steady states of (1).  
 221 Then, we use MATCONT [32] to analyse numerically this operating diagram. This  
 222 diagram allows to understand and classify the qualitative changes of the asymptotic  
 223 behavior of (1) under variation of the concentration of the substrate in the feed  
 224 bottle  $S_{in}$  and the dilution rate  $D$ . Since all other parameters in (1) cannot be  
 225 easily manipulated by the biologist, we fix it as provided in Table 7. To construct  
 226 the operating diagram, we first define in Table 2 the set of curves  $\Upsilon = \{\Upsilon_1, \Upsilon_2, \Upsilon_3\}$   
 227 which are the boundaries of different regions of the  $(S_{in}, D)$ -plane. As stated in the  
 228 following result, the curves in the set  $\Upsilon$  separate the operating plane  $(S_{in}, D)$  into  
 four regions, denoted  $\mathcal{J}_k$ ,  $k = 1, \dots, 4$ , and defined in Table 3.

TABLE 2. The set of curves  $\Upsilon$  and the corresponding colors in Figs. 2 and 3 where  $\varphi(D)$  and  $c_4$  are defined by (20) and (21), resp.

$\Upsilon$	Color
$\Upsilon_1 = \{(S_{in}, D) : S_{in} = \lambda_1(D)\}$	Black
$\Upsilon_2 = \{(S_{in}, D) : S_{in} = \varphi(D)\}$	Blue
$\Upsilon_3 = \{(S_{in}, D) : c_4(S_{in}, D) = 0\}$	Green

229

230 **Proposition 6.** Assume that assumptions (H1)-(H2) hold and the biological pa-  
 231 rameter values are provided as of Figs. 2 and 3 in Table 7. The existence and  
 232 the stability of the steady states of (1) in the four regions  $\mathcal{J}_k$ ,  $k = 1, \dots, 4$  of the  
 233 operating diagram are determined in Table 3.

TABLE 3. Existence and stability of steady states according to regions in the operating diagrams of Figs. 2 and 3. The letter S (resp. U) means stable (resp. unstable) steady state. Absence of letter means that the corresponding steady state does not exist.

Condition	Region	Color	$\mathcal{E}_0$	$\mathcal{E}_1$	$\mathcal{E}^*$
$S_{in} < \lambda_1(D)$	$\mathcal{J}_1$	Cyan	S		
$\lambda_1(D) < S_{in} < \varphi(D)$	$\mathcal{J}_2$	Pink	U	S	
$\varphi(D) < S_{in}$ and $c_4(S_{in}, D) > 0$	$\mathcal{J}_3$	Grey	U	U	S
$\varphi(D) < S_{in}$ and $c_4(S_{in}, D) < 0$	$\mathcal{J}_4$	Yellow	U	U	U

234 To illustrate the operating diagram, we consider the following specific growth  
 235 rates that satisfying the conditions (H1)-(H2):

$$236 \quad f_1(S, x_2) = \frac{m_1 S}{K_1 + S} \frac{1}{1 + x_2/L_1}, \quad f_2(S, x_1) = \frac{m_2 S}{K_2 + S} \frac{x_1}{L_2 + x_1}, \quad (22)$$

237 where  $m_1$ ,  $m_2$  are the maximum growth rates;  $K_1$ ,  $K_2$  and  $L_2$  are the Michaelis-  
 238 Menten constants;  $L_1$  is the inhibition factor due to  $x_2$  for the growth of the species  
 239  $x_1$ .

240 **Remark 3.** To determine the curve  $\Upsilon_3$  in the operating diagram of (1), we have  
 241 used the steady state characteristic method introduced by Lobry et al. [29, 30]  
 242 that we present in Appendix B. This method is often used to provide a geometric  
 243 description of the existence and the asymptotic stability of all steady states, see for  
 244 instance [1, 15, 17].

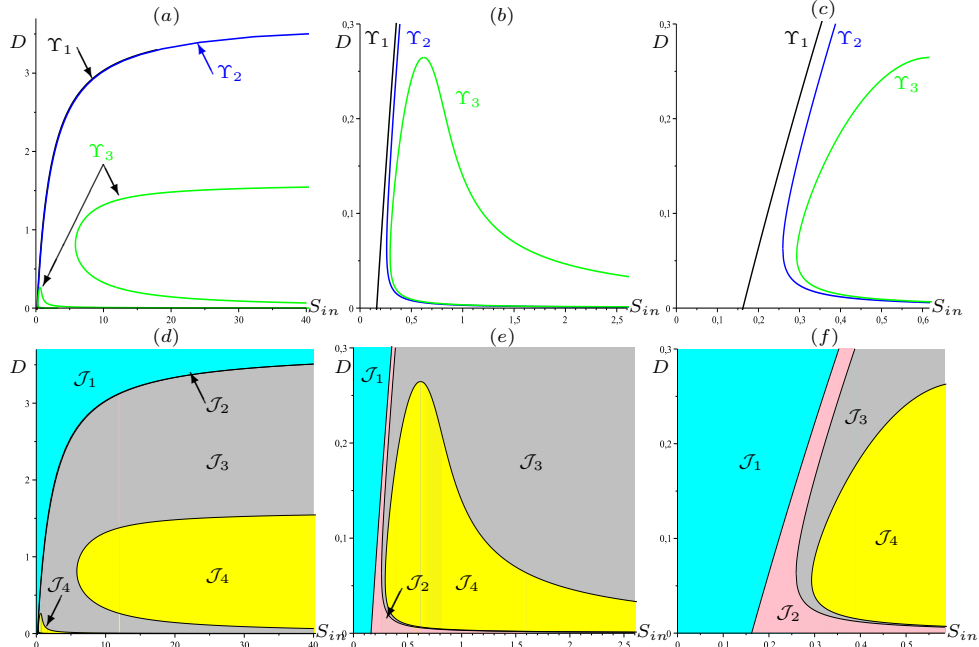


FIGURE 2. Operating diagram of (1) in MAPLE. (b)-(e) Magnification when  $(S_{in}, D) \in [0, 2.6] \times [0, 0.3]$ . (c)-(f) Magnification when  $(S_{in}, D) \in [0, 0.6] \times [0, 0.3]$ .

245 We also used the software MATCONT [32] to determine numerically this oper-  
 246 ating diagram that we present in Fig. 3. Although it is identical to the theoretical  
 247 operating diagram in Fig. 2, it must be stressed that they were obtained by com-  
 248 pletely different methods. The diagram in Fig. 2 is obtained by using our theoretical  
 249 results and drawing the  $\Upsilon_i$  curves, defined in Table 2, that separate the different  
 250 regions of the operating diagram, whereas the diagram in Fig. 3 is obtained numerically using MATCONT.

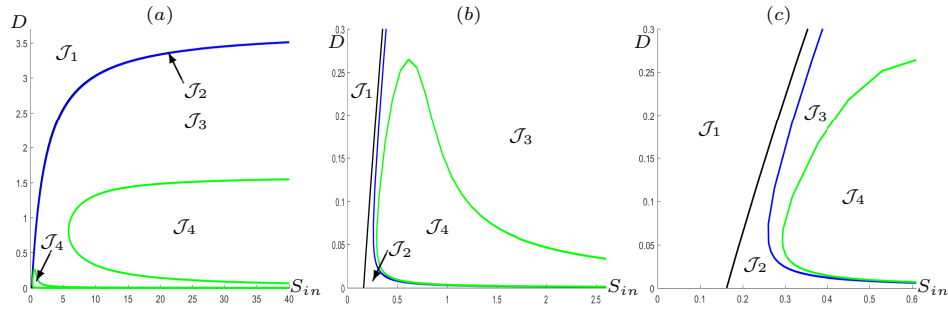


FIGURE 3. Operating diagram of (1) in MATCONT. (b) Magnification when  $(S_{in}, D) \in [0, 2.6] \times [0, 0.3]$ . (c) Magnification when  $(S_{in}, D) \in [0, 0.6] \times [0, 0.3]$ .

251 The following result determines the nature of all types of bifurcations of system  
 252 (1) that might happen by crossing the various regions of the operating diagrams  
 253  $(S_{in}, D)$  through the curves of  $\Upsilon$  where the steady states coalesce and can change  
 254 stability.  
 255

256 **Proposition 7.** *The bifurcation analysis of the steady states of (1) by crossing*  
 257 *the curves of  $\Upsilon$  according to the operating parameters  $S_{in}$  and  $D$  is summarized in*  
 258 *Table 4.*

TABLE 4. Nature of bifurcations of the steady states of (1) by crossing to the surfaces of  $\Upsilon$ . The letter TB (resp. SHB) means a transcritical bifurcation (resp. Supercritical Hopf bifurcation).

Curve	Transition	Bifurcation
$\Upsilon_1$	$\mathcal{J}_1$ to $\mathcal{J}_2$	TB: $\mathcal{E}_0 = \mathcal{E}_1$
$\Upsilon_2$	$\mathcal{J}_2$ to $\mathcal{J}_3$	TB: $\mathcal{E}_1 = \mathcal{E}^*$
$\Upsilon_3$	$\mathcal{J}_3$ to $\mathcal{J}_4$	SHB: $\mathcal{E}^*$

259 Figs. 4(a)-(b) show how the coexistence region around a stable limit cycle  $\mathcal{J}_4$   
 260 is reduced by decreasing the values of  $a_1$  and  $a_2$  to 0. For  $a_1 = a_2 = 0$ , Fig. 4(c)  
 261 shows the disappearance of this region  $\mathcal{J}_4$  which confirms our result in [33] where  
 262 the process cannot admit a limit cycle without mortality, that is, for some removal  
 263 rates of species. Therefore, the destabilization of the positive steady state is due to  
 264 the mortality and is similar to some results obtained in the existing literature on  
 the classical predator-prey model in the chemostat [25].

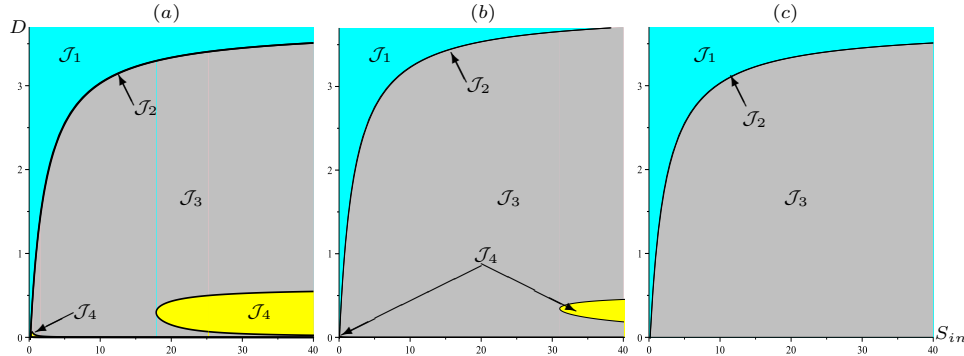


FIGURE 4. Operating diagram of (1) showing the disappearance of the region  $\mathcal{J}_4$  when  $a_1$  and  $a_2$  diminish.

265

266 **4. One-parameter bifurcation diagram and numerical simulations.** This  
 267 section is devoted to study the one-parameter bifurcation diagram of system (1)  
 268 and to validate our mathematical results in the previous sections by some numerical  
 269 simulations. First, we determine the bifurcation diagram showing the behavior of  
 270 the process by varying the input substrate concentration  $S_{in}$  as the bifurcating  
 271 parameter where the dilution rate  $D$  is fixed. However, the results are the same  
 272 regardless of which operating parameter is varied, that is, the end results are similar  
 273 when we vary the dilution rate  $D$ . All other parameters of system (1) are fixed (see  
 274 Table 7). The following result determines the one-parameter bifurcation diagram  
 275 according to  $S_{in}$  from the operating diagram of Fig. 2 (or equivalently of Fig. 3)  
 276 when the dilution rate  $D = 0.25$ .

277 **Proposition 8.** *Assume that the biological parameters in (1) are given as in Table*  
 278 *7 using the specific growth rates (22) with  $D = 0.25$ . The existence and stability*

279 of steady states of (1) according to  $S_{in}$  are given in Table 6 where the bifurcation  
 280 values  $\sigma_i, i = 1, \dots, 5$  and the corresponding nature of the bifurcations are defined  
 281 in Table 5.

TABLE 5. Definitions of the critical values  $\sigma_i, i = 1, \dots, 5$  of  $S_{in}$  and the corresponding nature of bifurcations when  $D = 0.25$ .

Definition	Value	Bifurcation
$\sigma_1 = \lambda_1(D)$	0.31884	TB
$\sigma_2 = \varphi(D)$	0.35394	TB
$\sigma_3$ is the first solution of equation $c_4(S_{in}) = 0$	0.52555	SHB
$\sigma_4$ is the second solution of equation $c_4(S_{in}) = 0$	0.71593	SHB
$\sigma_5$ is the third solution of equation $c_4(S_{in}) = 0$	12.4809	SHB

TABLE 6. Existence and stability of steady states according to  $S_{in}$ .

Interval of $S_{in}$	$\mathcal{E}_0$	$\mathcal{E}_1$	$\mathcal{E}^*$
$(0, \sigma_1)$	S		
$(\sigma_1, \sigma_2)$	U	S	
$(\sigma_2, \sigma_3)$	U	U	S
$(\sigma_3, \sigma_4)$	U	U	U
$(\sigma_4, \sigma_5)$	U	U	S
$(\sigma_5, +\infty)$	U	U	U

282 Fig. 5 represents the one-parameter bifurcation diagram of system (1) where  
 283 the  $\omega$ -limit set is projected in coordinate  $S$  depending on the control parameter  
 284  $S_{in}$ . Indeed, in Fig. 5(a), we observe more clearly the transcritical bifurcations  
 285 occurring at  $\sigma_1$  and  $\sigma_2$ , and the occurrence of a stable limit cycle via a supercritical  
 286 Hopf bifurcation at  $\sigma_3$  and then their disappearance via a second supercritical Hopf  
 287 bifurcation at  $\sigma_4$ . Once again, increasing further  $S_{in}$ , a stable limit cycle emerges  
 288 through a supercritical Hopf bifurcation at  $\sigma_5$  as shown in Fig. 5(b). Then, the  
 oscillations are sustained for all  $S_{in} > \sigma_5$ .

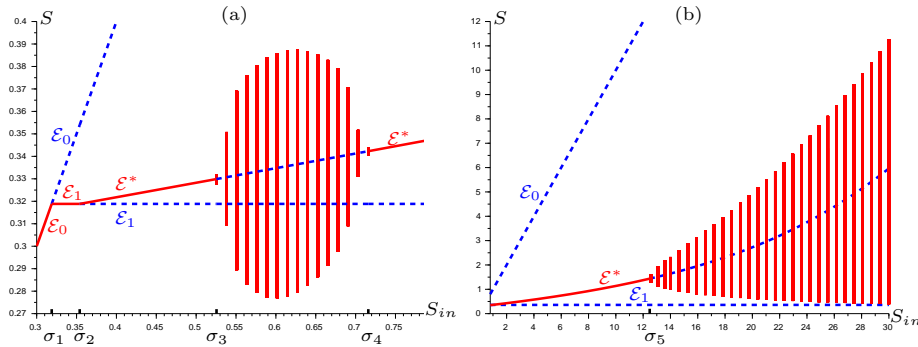


FIGURE 5. Scilab simulation showing projections of the  $\omega$ -limit set in variable  $S$  when  $D = 0.25$ : (a) emergence and the disappearance of limit cycle at  $\sigma_3$  and  $\sigma_4$  for  $S_{in} \in [0.3, 0.8]$ ; (b) emergence of limit cycle at  $\sigma_5$  for  $S_{in} \in [0.8, 30]$ .

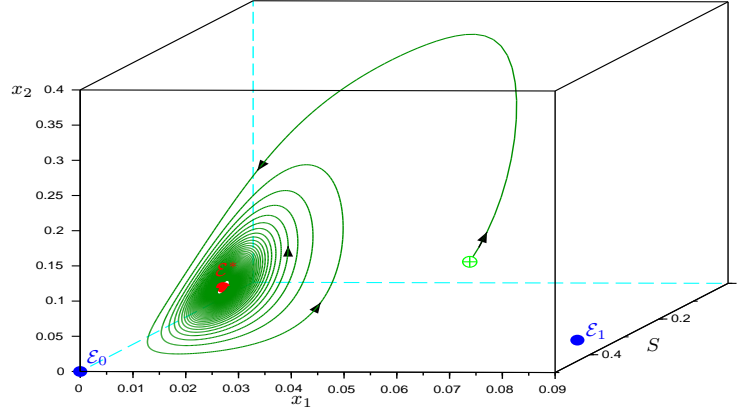


FIGURE 6. Case  $S_{in} = 0.5 \in ]\sigma_2, \sigma_3[$  and  $D = 0.25$ : convergence to  $\mathcal{E}^*$ .

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For the numerical simulations, we have used Maple [31] to plot the Figs. 1, 2, 4, 10, 11 and 12, MATCONT [32] for Fig. 3 and Scilab [38] for Figs. 5, 6, 7 and 8. The limit cycles in Figs. 5, 7 and 8 were plotted by solving the ordinary differential equations using the default solver “*lsoda*” from the ODEPACK package in Scilab. To validate the previous results, we illustrate in the following the three-dimensional phase plot and the trajectories over time in some interesting cases.

- For  $S_{in} \in ]\sigma_2, \sigma_3[$ , the numerical simulations done in the three-dimensional phase space  $(S, x_1, x_2)$  for various positive initial conditions permit to conjecture the global convergence towards  $\mathcal{E}^*$  (see Fig. 6).
- For  $S_{in} \in ]\sigma_3, \sigma_4[$ , the numerical simulations done for various positive initial conditions permit to conjecture the global asymptotic stability of a stable limit cycle (see Fig. 7).
- For  $S_{in} > \sigma_5$ , Fig. 8 shows the trajectory starting from a neighborhood of  $\mathcal{E}^*$  of size order  $\epsilon = 10^{-3}$  is approaching a stable limit cycle as time goes where the system exhibits sustained oscillations.

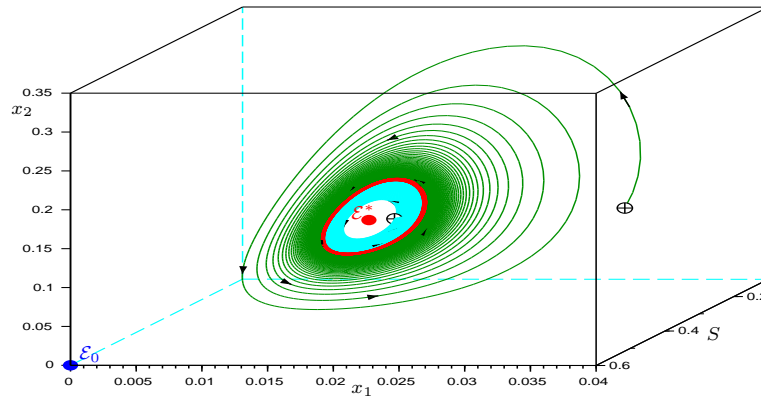


FIGURE 7. Case  $S_{in} = 0.6 \in ]\sigma_3, \sigma_4[$  and  $D = 0.25$ : convergence towards a stable limit cycle (in red).

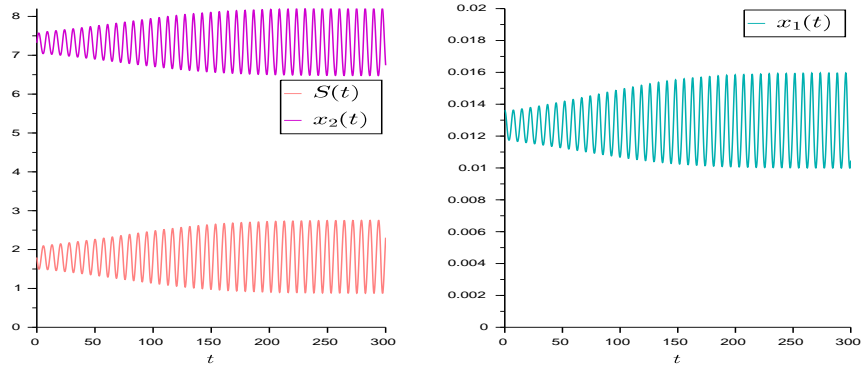


FIGURE 8. Case  $S_{in} = 15 > \sigma_5$  and  $D = 0.25$ : convergence to a stable limit cycle showing the sustained oscillations.

305 **5. Conclusion.** In this paper, we have extended the mathematical analysis of the  
 306 interspecific density-dependent model (1) describing a predator-prey relationship  
 307 between two microbial species in a chemostat, by considering the effect of mortality  
 308 with distinct disappearance rates. Using the nullcline method [15, 33], the necessary  
 309 and sufficient conditions of existence of all steady states of (1) are determined  
 310 according to the parameter control. Indeed, this method provides a geometric  
 311 description of the existence of the boundary steady states which are unique and the  
 312 multiplicity of the positive steady states. For the local stability of the positive steady  
 313 state, we have used the Routh–Hurwitz criterion (26) since we cannot determine  
 314 explicitly the eigenvalues of the Jacobian matrix at this point, in contrast to the  
 315 boundary steady states, the stability conditions are determined explicitly. We show  
 316 that the positive steady state can destabilize with emergence of a stable limit cycle  
 317 via a supercritical Hopf bifurcation.

318 Using the necessary and sufficient conditions of existence and stability of all  
 319 steady states, the operating diagrams are analyzed analytically to determine the  
 320 behavior of the system according to the concentration of substrate in the feed bottle  
 321  $S_{in}$  and the dilution rate  $D$ . These conditions are plotted in MAPLE using specific  
 322 growth functions given by (22). Then, these theoretically results on the operating  
 323 diagram are validated numerically using MATCONT.

324 In fact, the process exhibits an even richer set of possible behaviors illustrated  
 325 in the operating diagram: either the washout ( $\mathcal{J}_1$ ) or the exclusion of the preda-  
 326 tor ( $\mathcal{J}_2$ ) or the coexistence of the predator-prey species around a positive steady  
 327 state ( $\mathcal{J}_3$ ) or a stable limit cycles ( $\mathcal{J}_4$ ). The one-parameter bifurcation diagram is  
 328 determined according to the input substrate concentration  $S_{in}$  as the bifurcating  
 329 parameter. It shows the transcritical bifurcation as well as the three supercritical  
 330 Hopf bifurcations with the appearance and the disappearance of the stable peri-  
 331 odic orbits. The numerical simulations illustrate the three-dimensional phase space  
 332 showing the coexistence around a coexistence steady state or a stable limit cycle,  
 333 while the time course shows the sustained oscillations.

334 The comparison of our results with those in the existing literature [12, 33] proves  
 335 that the addition of mortality terms of the species in the interspecific density-  
 336 dependent model (1) with a predator-prey relationship can destabilize the positive  
 337 steady states but not the global behavior of the process where the mortality of

338 species could lead to the occurrence of stable limit cycles with the coexistence of  
339 species.

### 340 Appendix A. Proofs.

**Proof of Proposition 1.** Since the vector field defined by (1) is  $C^1$ , the uniqueness of a solution to initial value problems holds. From (1), for  $i = 1, 2$ ,

$$x_i(t_0) = 0, \text{ for any } t_0 \geq 0 \implies \dot{x}_i = 0.$$

If  $x_i(0) = 0$ , then  $x_i(t) = 0$  for all  $t$  since the boundary face where  $x_i \equiv 0$  is invariant in the vector field  $C^1$  by system (1). If  $x_i(0) > 0$ , then  $x_i(t) > 0$  for all  $t$  since  $x_i \equiv 0$  cannot be reached in finite time by trajectories such that  $x_i(0) > 0$  by the uniqueness of solutions. On the other hand, one has

$$S(t_0) = 0, \text{ for any } t_0 \geq 0 \implies \dot{S}(t_0) = DS_{in} > 0.$$

Consequently, we have  $S(t) \geq 0$  for all  $t$ . In fact, assume that  $S(0) \geq 0$  and that it exists  $t_0 > 0$ , such that  $S(t_0) = 0$  and  $S(t) > 0$  for  $t \in (0, t_0)$ . Then,  $\dot{S}(t_0) \leq 0$  which contradicts  $\dot{S}(t_0) > 0$ . Therefore, the solutions remain non-negative. Let  $z = S + x_1 + x_2$ . From system (1), we have

$$\dot{z} = D(S_{in} - S) - D_1x_1 - D_2x_2.$$

Consequently,

$$\dot{z} \leq D_{\min}(DS_{in}/D_{\min} - z).$$

341 Using Gronwall's lemma, we obtain

$$342 \quad z(t) \leq DS_{in}/D_{\min} + (z(0) - DS_{in}/D_{\min})e^{-D_{\min}t} \text{ for all } t \geq 0. \quad (23)$$

We deduce that

$$z(t) \leq \max(z(0), DS_{in}/D_{\min}) \text{ for all } t \geq 0.$$

343 Therefore, the solutions of (1) are positively bounded and are defined for all  $t \geq 0$ .  
344 From (23), we deduce that the set  $\Omega$  is positively invariant and is a global attractor  
345 for (1).  $\square$

346 **Proof of Proposition 2.** For  $\mathcal{E}_1$ ,  $x_1 > 0$  and  $x_2 = 0$ . From the second equation of  
347 (3) and the definition (4) of the break-even concentration, it follows that  $S = \lambda_1(D)$ .  
348 From the first equation of (3), we obtain the  $x_1$  component. Thus,  $\mathcal{E}_1$  exists if and  
349 only if  $x_1 > 0$ , that is, condition (6) holds.  $\square$

**Proof of Proposition 5.** Using the notation (12), the Jacobian matrix of (1) at  $(S, x_1, x_2)$  corresponds to the  $3 \times 3$  matrix:

$$J = \begin{bmatrix} -D - Ex_1 - x_2F & -f_1(S, x_2) - Hx_2 & Gx_1 - f_2(S, x_1) \\ Ex_1 & f_1(S, x_2) - D_1 & -Gx_1 \\ Fx_2 & Hx_2 & f_2(S, x_1) - D_2 \end{bmatrix}.$$

For  $\mathcal{E}_0 = (S_{in}, 0, 0)$ , the eigenvalues are the roots of the following characteristic polynomial

$$P(\lambda) = (\lambda + D)(\lambda + D_2)(\tilde{\lambda}_1 - \lambda)$$

350 where  $\tilde{\lambda}_1 = f_1(S_{in}, 0) - D_1$ . Thus,  $\mathcal{E}_0$  is LES if and only if  $f_1(S_{in}, 0) < D_1$ , that is,  
351  $S_{in} < \lambda_1(D)$ .

For  $\mathcal{E}_1 = (\lambda_1(D), \tilde{x}_1, 0)$ , the characteristic polynomial is

$$P(\lambda) = (\tilde{\lambda}_1 - \lambda)(\lambda^2 + c_1\lambda + c_2)$$

352 where  $\tilde{\lambda}_1 = \tilde{f}_2(\tilde{x}_1, 0)$ ,  $c_1 = D + \tilde{x}_1 E$  and  $c_2 = D_1 \tilde{x}_1 E$ . Since  $c_1 > 0$  and  $c_2 > 0$ , the  
 353 real parts of the roots of the quadratic factor are negative. Therefore,  $\mathcal{E}_1$  is LES if  
 354 and only if  $\tilde{f}_2(\tilde{x}_1, 0) < 0$ , that is, condition (18) holds.

355 For  $\mathcal{E}^* = (S^*, x_1^*, x_2^*)$ , the characteristic polynomial is

$$356 \quad P(\lambda) = \lambda^3 + c_1 \lambda^2 + c_2 \lambda + c_3, \quad (24)$$

where

$$\begin{aligned} c_1 &= D + E x_1^* + F x_2^*, & c_2 &= D_1 E x_1^* + D_2 F x_2^* + (GH + EH - FG) x_1^* x_2^* \\ c_3 &= (DGH + D_2 EH - D_1 FG) x_1^* x_2^*. \end{aligned} \quad (25)$$

357 Since  $c_1 > 0$ , according to the Routh–Hurwitz criterion,  $\mathcal{E}^*$  is LES if and only if

$$358 \quad c_3 > 0 \quad \text{and} \quad c_4(S_{in}, D) = c_1 c_2 - c_3 > 0 \quad (26)$$

where the function  $c_4$  can be written as its expression (21). Using the expressions of  $F'_1$  in (13) and of  $F'_2$  in (15), we obtain

$$F'_1(x_1) - F'_2(x_1) = \frac{D_1 FG - D_2 EH - DGH}{D_2 F(D_2 E/D + G)}.$$

359 Consequently, at  $\mathcal{E}^*$ , we have

$$360 \quad c_3 = (F'_2(x_1^*) - F'_1(x_1^*)) D_2 F [D_2 E/D + G] x_1^* x_2^*. \quad (27)$$

361 Thus,  $\mathcal{E}^*$  is LES if and only if  $F'_2(x_1^*) > F'_1(x_1^*)$  and condition (21) holds.  $\square$

362 **Appendix B. Construction of the operating diagrams in Fig. 2.** In this  
 363 section, we present the method used to construct theoretically the operating di-  
 364 agrams presented in Fig. 2. To this end, we plot the various curves from the  
 365 existence and stability conditions which depend on the operating parameters. In  
 366 addition, we will see in the following that the proof is based on the existence and  
 367 stability conditions in Table 1 and is supported by numerical experimentation when  
 368 the biological parameter values are fixed in Table 7. From Table 1, the steady state  
 369  $\mathcal{E}_0$  always exists and is stable if and only if  $S_{in} < \lambda_1(D)$ , that is, it is stable in  
 370 the region bounded by the curve  $\Upsilon_1$  and located above this curve, see Fig. 2. The  
 371 steady state  $\mathcal{E}_1$  exists in the region bounded by the curve  $\Upsilon_1$  and located below this  
 372 curve and is stable in the region bounded by the curve  $\Upsilon_2$  and located at the left  
 373 of this curve. The steady state  $\mathcal{E}^*$  exists in the region bounded by the curve  $\Upsilon_2$   
 374 and located at the right of this curve. To determine the sign of  $c_3(S_{in}, D)$  in the  
 375 operating diagram and the curve  $\Upsilon_3$  defined by  $c_4(S_{in}, D) = 0$ , we use the concept  
 376 of *steady-state characteristic* which we apply in the following as in [17]. A positive  
 377 steady state  $\mathcal{E}^* = (S^*, x_1^*, x_2^*)$  is a solution of the set of equations

$$378 \quad \begin{cases} D(S_{in} - S) &= D_1 x_1 + D_2 x_2, \\ f_1(S, x_2) &= D_1, \\ f_2(S, x_1) &= D_2. \end{cases} \quad (28)$$

From the second and the third equations of (28), we can define the solutions  $x_2$  and  
 $x_1$ , respectively, as functions of  $S$ , that is, there exist  $S \mapsto X_2(S)$  and  $S \mapsto X_1(S)$   
 such that

$$f_1(S, X_2(S)) = D_1 \quad \text{and} \quad f_2(S, X_1(S)) = D_2.$$

More precisely, let  $S \geq 0$ . From (H2), the function  $x_2 \mapsto f_1(S, x_2)$  is decreasing.  
 Thus, the equation  $f_1(S, x_2) = D_1$  has a unique solution  $x_2 = X_2(S)$  if and only if

$$f_1(S, +\infty) < D_1 \leq f_1(S, 0), \quad \text{that is,} \quad S \in I_1 = [\lambda_1, \lambda'_1),$$



where  $\lambda_1$  is defined by (4) and  $\lambda'_1$  is the unique solution, if it exists, of the equation

$$f_1(S, +\infty) = D_1.$$

If  $D_1 > f_1(S, +\infty)$  for all  $S \geq 0$ , then we put  $\lambda'_1 = +\infty$ . Note that the function  $X_2(\cdot)$  is increasing and satisfies  $X_2(\lambda_1) = 0$  and  $X_2(\lambda'_1) = +\infty$ . From (H1) and (H2), the function  $x_1 \mapsto f_2(S, x_1)$  is increasing and  $f_2(S, 0) = 0$ . Hence, the equation  $f_2(S, x_1) = D_2$  has a unique solution  $x_1 = X_1(S)$  if and only if

$$D_2 < f_2(S, +\infty), \quad \text{that is,} \quad S > \lambda'_2,$$

where  $\lambda'_2$  is the unique solution, if it exists, of the equation

$$f_2(S, +\infty) = D_2.$$

379 If  $D_2 > f_2(S, +\infty)$  for all  $S \geq 0$ , then we put  $\lambda'_2 = +\infty$ . Note that the function  
380  $X_1(\cdot)$  is decreasing and satisfies  $X_1(\lambda'_2) = +\infty$ .

Let  $C_j(S)$ ,  $j = 3, 4$  be the functions defined by the same formulas as (25) and (26), respectively, where the functions  $E, F, G$  are  $H$  in these functions depends only on  $x_1, x_2$  and  $S$ . But, as the  $x_i = X_i(S)$ ,  $i = 1, 2$ , then these functions  $C_j$  depend only on  $S$ . More precisely, we have

$$c_j(S_{in}, D) = C_j(S^*(S_{in}, D)), \quad j = 3, 4.$$

381 where  $S^*(S_{in}, D)$  is the solution of equation

$$382 \quad D(S_{in} - S) = H(S) := D_1 X_1(S) + D_2 X_2(S). \quad (29)$$

383 Fig. 9 illustrates that the function  $C_3(S)$  is positive for various values of  $D$  from  
384 the starting points in red of coordinates  $(\max(\lambda_1(D), \lambda'_2(D)), 0)$ . Note that for the  
385 specific growth rates (22),  $\lambda'_1 = +\infty$  since  $D_1 > f_1(S, +\infty) = 0$  for all  $S \geq 0$ .  
386 According to expression (27), this positivity of  $C_3(S)$  for any value of  $D$  in its  
387 definition domain shows that  $F'_2(x_1^*) > F'_1(x_1^*)$  for this set of parameters in Table 7.  
388 Thus, system (1) cannot exhibit a multiplicity of positive steady states appearing  
through saddle-node bifurcations and other regions in the operating diagram.

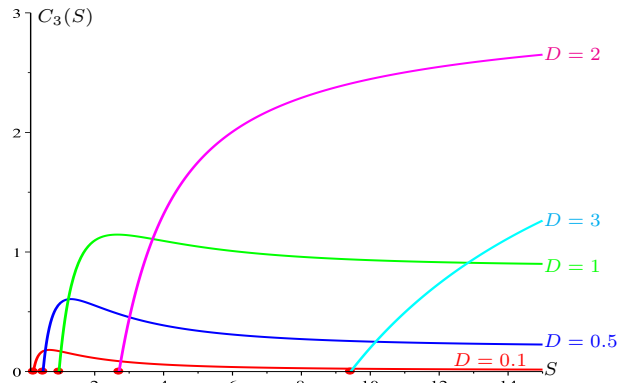


FIGURE 9. Curves of the function  $C_3(S)$  for different values of  $D$  when  $S > \max(\lambda_1(D), \lambda'_2(D))$ .

389

In Fig. 10, the curve of the function  $H(S)$  is colored in blue when  $C_4(S) < 0$ , that is, when the positive steady state is unstable. It is colored in red when  $C_4(S) > 0$ , that is, when the positive steady state is stable. From (29), the critical value of  $S_{in}$

corresponding to Hopf bifurcation when  $C_4(S) = 0$  (or also when the curve of  $H(S)$  changes color) is given by

$$S_{in} = H(S)/D - S.$$

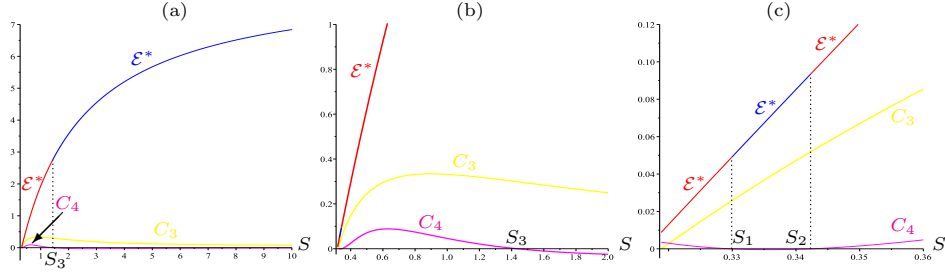


FIGURE 10. (a) Steady-state characteristics describing the local asymptotic behavior of the positive steady state  $\mathcal{E}^*$  when  $D = 0.25$ . Magnification for (b)  $S \leq 2$  and (c)  $0.32 \leq S \leq 0.36$ .

390

391 In particular, if the equation  $C_4(S) = 0$  has  $n$  solutions  $S_i$ , for  $i = 1, \dots, n$ , with  
 392  $n$  is the number of solutions, we have

393

$$\sigma_{i+2} = H(S_i)/D - S_i. \quad (30)$$

394 Finally, using a procedure in  $D$ , we can determine the curve  $\Upsilon_3$  corresponding to  
 395 Hopf bifurcation in the operating diagram of Fig. 2.

396 For the set of parameters in Table 7 corresponding to the operating diagram  
 397 in Fig. 2, the numerical simulations show that the equation  $C_4(S) = 0$  has three  
 398 solutions  $S_i$ ,  $i = 1, 2, 3$  for  $0 < D < D^* \simeq 0.2648$  (see Fig. 11). Using (30), we can  
 399 deduce the corresponding three critical values  $\sigma_i$ ,  $i = 3, 4, 5$ , which are provided in  
 400 Table 5 and shown in Fig. 5. Moreover, these critical values correspond to the curve  
 401  $\Upsilon_3$  in Fig. 2. However, when  $D^* < D < D_{\max} \simeq 1.595$ , the equation  $c_4(S) = 0$  has  
 a unique solution  $S_1$  that corresponds to the unique critical value  $\sigma_3$ .

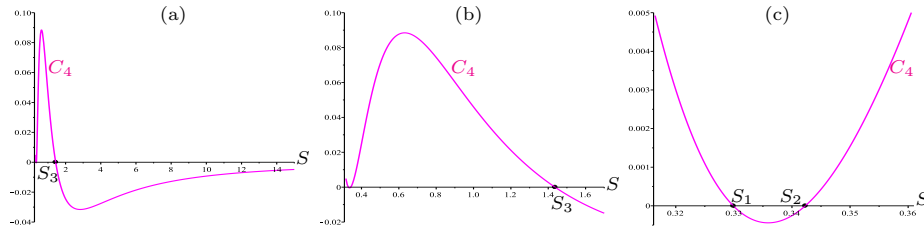


FIGURE 11. Case  $D = 0.25 \leq D^* \simeq 0.2648$ : (a) Change of sign of  $C_4$  when  $S_1 \simeq 0.3299$  (or equivalently  $\sigma_3 \simeq 0.5255$ ),  $S_2 \simeq 0.3423$  (or equivalently  $\sigma_4 \simeq 0.7159$ ) and  $S_3 \simeq 1.4365$  (or equivalently  $\sigma_5 \simeq 12.4809$ ). (b)-(c) Magnifications for  $S \in [0.316, 1.7]$  and  $S \in [0.316, 0.361]$ .

402

403 **Appendix C. Numerical evidence of the Hopf bifurcation.** To understand  
 404 and analyze the change of local stability occurring through the positive steady  
 405 state  $\mathcal{E}^*$  as  $S_{in}$  varies, we determine numerically the eigenvalues of the Jacobian  
 406 matrix  $\mathcal{J}$  at  $\mathcal{E}^*$  by solving the roots of the characteristic polynomial (24). Indeed,

407 this characteristic polynomial has one negative eigenvalue and one pair of complex-  
408 conjugate eigenvalues

$$409 \quad \bar{\lambda}_j = \mu(S_{in}) \pm i\nu(S_{in}), \quad j = 1, 2. \quad (31)$$

410 Increasing the operating parameter  $S_{in}$ , this pair (31) crosses the imaginary axis  
411 first at the critical values  $\sigma_3$  from negative to positive half plane and second it  
412 returns to the negative half plane at  $\sigma_4$  and finally it returns again to the positive  
413 half plane at  $\sigma_5$  (see Fig. 12), that is, it becomes purely imaginary for  $\sigma_i$ ,  $i = 3, 4, 5$   
414 such that  $\mu(\sigma_i) = 0$ , with  $\nu(\sigma_i) \neq 0$ . In addition, numerically, we check the following  
415 inequality

$$416 \quad \frac{d\mu}{dS_{in}}(\sigma_i) \neq 0, \quad i = 3, 4, 5. \quad (32)$$

417 This is consistent with Fig. 5, showing that, as  $S_{in}$  increases and crosses  $\sigma_i$ ,  $i =$   
418  $3, 4, 5$ , the positive steady state  $\mathcal{E}^*$  changes its stability through three supercritical  
419 Hopf bifurcations with the occurrence or disappearance of a stable limit cycle that  
we illustrate in Figs. 7 and 8.

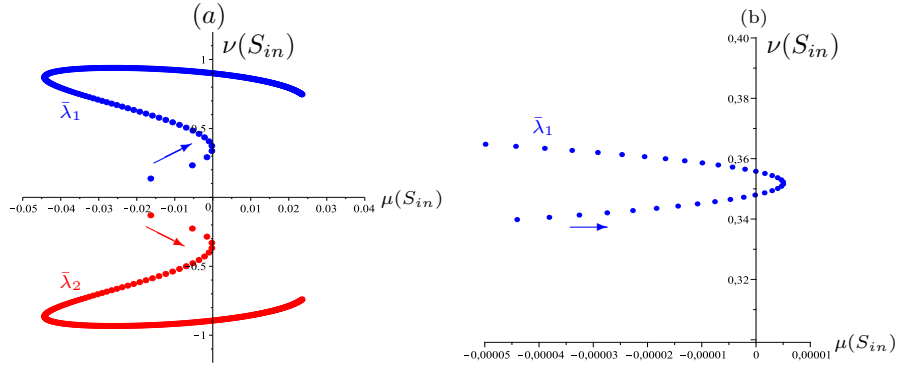


FIGURE 12. (a) Variation of the pair of complex-conjugate eigenvalues (31) as  $S_{in}$  increases from 0 to 40 when  $D = 0.25$ . (b) Magnification on  $\bar{\lambda}_1$  for  $S_{in} \in [0.4, 0.8]$ .

420

421 **Appendix D. Parameter values used for numerical simulations.** All the  
422 values of the parameters used in the numerical simulations are provided in Table 7.

TABLE 7. Parameter values used for model (1) when the growth rates  $f_1$  and  $f_2$  are given by (22).

Parameter	$m_1$	$K_1$	$L_1$	$m_2$	$K_2$	$L_2$	$\alpha_1$	$\alpha_2$	$a_1$	$a_2$
Fig. 1(c)	2.75	2	1.2	2.95	1.8	1.5	$10^{-3}$	0.1	0.95	0.7
Figs. 1(a,b),2,3,5-12									0.3	0.2
Fig. 4(a)				8	0.1	0.2	1	1	0.3	0.05
Fig. 4(b)	4	2	3						0.1	0.05
Fig. 4(c)									0	0

423

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523 *E-mail address:* [tahani.mtar@enit.utm.tn](mailto:tahani.mtar@enit.utm.tn)

524 *E-mail address:* [radhouene.fekihsalem@isima.rnu.tn](mailto:radhouene.fekihsalem@isima.rnu.tn)

525 *E-mail address:* [tewfik.sari@inrae.fr](mailto:tewfik.sari@inrae.fr)