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# MATHEMATICAL ANALYSIS OF A THREE-TIERED MODEL OF ANAEROBIC DIGESTION \*

SARRA NOUAOURA<sup>†</sup>, NAHLA ABDELLATIF<sup>†‡</sup>, RADHOUANE FEKIH-SALEM<sup>†§</sup>, AND TEWFIK SARI<sup>¶</sup>

**Abstract.** In this paper, we are interested in a mechanistic model describing the anaerobic mineralization of chlorophenol in a three-step food-web. The model is a six-dimensional system of ordinary differential equations. In our study, the phenol and the hydrogen inflowing concentrations are taken into account as well as the maintenance terms. In previous studies in the existing literature, the stability of the steady states was considered only in the particular case without maintenance, where the model can be reduced to a three-dimensional system. Moreover, we consider the case of a large class of growth kinetics, instead of Monod kinetics. According to the four operating parameters of the process, represented by the dilution rate and input concentrations of the chlorophenol, the phenol and the hydrogen, we show that the system can have up to eight steady states and we analytically determine the necessary and sufficient conditions for their existence and their local stability. In previous studies of the case including maintenance, the stability analysis was performed only numerically. We show that the positive steady state can be unstable and we give numerical evidence for a supercritical Hopf bifurcation with the appearance of a stable periodic orbit. Finally, we give a bifurcation diagram with the concentration of influent chlorophenol as the bifurcating parameter, clarifying the findings of a recent study in literature.

**Key words.** Anaerobic digestion, Bistability, Chemostat, Chlorophenol mineralisation, Hopf bifurcation, Limit cycle.

**AMS subject classifications.** 34A34, 34D20, 37N25, 92B05

**1. Introduction.** The anaerobic digestion is a natural process in which organic material is converted into biogas in an environment without oxygen by the action of a microbial ecosystem. It is used for the treatment of wastewater and has the advantage of producing methane and hydrogen under appropriate conditions. The full Anaerobic Digestion Model No.1.(ADM1) [9] is highly parametrized with a large number of state variables. Whilst suitable for dynamic simulation, analytical results on the model are impossible and only numerical investigations are available [3]. Due to the analytical intractability of the full ADM1, simpler mechanistic models of microbial interaction has been proposed in view of a better understanding of the anaerobic digestion process.

The two-tiered models, which take the form of four-dimensional mathematical models with a cascade of two biological reactions, where one substrate is consumed by one microorganism to produce a product that serves as the main limiting substrate for a second microorganism, are the simplest models which encapsulate the essence of the anaerobic digestion process. Two-tiered models with commensalistic relationship including or not substrate inhibition of the second population are widely considered [1, 2, 11, 15] where the second population (the commensal population) benefits for its growth from the first population (the host population) while the host population

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is not affected by the growth of the commensal population. On the contrary, when the growth of the first population is affected by the growth of the second population, which is the case, for instance, if the first population is itself inhibited by the product (the substrate produced by the first biological reaction that serves as the substrate for the second population), the system describes a syntrophic relationship [4, 5, 7, 12, 13, 18, 22]. Syntrophic models are more realistic simple models of anaerobic digestion than commensalistic models. For more details and informations on commensalism and syntrophy, the reader is referred to [13] and the references therein. An important and interesting extension of the two-tiered models are the eight-dimensional mathematical models, which include syntrophy and inhibition [20, 21].

In this paper, we consider another extension of two-tiered models which consists in a six-dimensional mathematical model obtained by introducing an additional micro-organism and substrate into a two-tiered syntrophic model [6, 14, 17, 19]. The organisms involved in the resulting three-tiered model are the chlorophenol and the phenol degraders and the hydrogenotrophic methanogen. The chlorophenol degrader grows on both chlorophenol and hydrogen and produces phenol. The phenol degrader consumes the phenol to form hydrogen, which inhibits its growth. The hydrogenotrophic methanogen grows on the produced hydrogen. The model includes maintenance, that is, microbial decay terms.

In [19], the existence and stability of the steady states were determined only numerically, using specific growth rates described by double Monod, Monod with product inhibition, and Monod kinetics, respectively, (see formulas (5.1)). It has been shown that the model can have eight steady states. Several operating diagrams, which are the bifurcation diagrams with respect to the four operating parameters (i.e. the dilution rate, the influent chlorophenol, the influent phenol and the influent hydrogen) have been numerically constructed showing the role, and the importance of each operating parameter, in particular for the coexistence of all three species.

An analytical approach, using a general representation of the specific growth rates, is given in [14], in the particular case with only influent chlorophenol in the model. When there is no influent phenol and influent hydrogen the system has only three steady states. The existence of the steady states with and without inclusion of a microbial decay term is given in [14]. With no decay, the six-dimensional mathematical model is reduced to a three-dimensional one and local stability is analytically characterized. The operating diagrams with respect to the dilution rate and the influent chlorophenol, which were obtained numerically in [19] are analytically constructed in [14], showing the possibility of an instability region for the positive steady state. This instability was not depicted in [19]. Numerical simulations were performed, confirming that the region of the instability of the positive steady state actually exists when maintenance is included. Numerical analysis has suggested the presence of a Hopf bifurcation emerging through the positive steady state, with the concentration of influent chlorophenol as the bifurcating parameter.

In [6], the three-tiered model of [14, 19] was simplified by neglecting the part of hydrogen produced by the phenol degrader. Without maintenance, the existence and stability of the eight steady states were analytically characterized. Recently in [17], the original three-tiered model of [14, 19] without neglecting the part of hydrogen produced by the phenol degrader is considered in the case without maintenance. The existence and stability of the eight steady states are analytically characterized and the Hopf bifurcation of the positive steady state, which was numerically observed in [14], is proved.

Here, we focus on the mathematical analysis of the model, extending the works

previously cited [6, 14, 17, 19]. We have generalized the approach presented in [14] by including multiple substrate inflow into the model and characterizing the stability of steady state in the case including maintenance. We have extended [19] by giving analytic results on the existence and stability of the eight steady states and with general growth functions. We have extended [6, 17] by including maintenance. The stability analysis is much more delicate since the model cannot be reduced to a three-dimensional differential system as in the case without maintenance.

This paper is organized as follows: in [section 2](#), we start by presenting the mathematical model with three-tiered microbial species, which takes into account the phenol and the hydrogen inflowing concentrations. We give the general assumptions on the microbial growth functions and some preliminary results on positivity and boundedness of solutions. Next, in [section 3](#), we describe the steady states of the model. In [section 4](#), the necessary and sufficient conditions of existence and stability of the steady states are determined according to the operating parameters. Then, in [section 5](#), we give an application of our theoretical results to the three-tiered model considered in [19]. Then, we conclude by discussing our results in [section 6](#). The definitions and properties of the functions that are reported in the existence and stability conditions of the steady states are given in [Appendix A](#). The proofs of the propositions are reported in [Appendices B to E](#) and [H](#). We present the Liénard-Chipart stability criteria that are used to show the stability of the steady states in [Appendix F](#). Details and complements on the three-tiered model considered in [19] are given in [Appendix G](#). In [Appendix I](#), the numerical simulations confirm our mathematical results. Finally, all the tables of the Appendices are given in [Appendix J](#).

**2. The model.** We consider the system studied in [14], which represents a three-tiered microbial food-web model:

$$(2.1) \quad \begin{cases} \dot{x}_0 &= (\mu_0(s_0, s_2) - D - a_0)x_0 \\ \dot{x}_1 &= (\mu_1(s_1, s_2) - D - a_1)x_1 \\ \dot{x}_2 &= (\mu_2(s_2) - D - a_2)x_2 \\ \dot{s}_0 &= D(s_0^{\text{in}} - s_0) - \mu_0(s_0, s_2)x_0 \\ \dot{s}_1 &= D(s_1^{\text{in}} - s_1) + \mu_0(s_0, s_2)x_0 - \mu_1(s_1, s_2)x_1 \\ \dot{s}_2 &= D(s_2^{\text{in}} - s_2) - \omega\mu_0(s_0, s_2)x_0 + \mu_1(s_1, s_2)x_1 - \mu_2(s_2)x_2 \end{cases}$$

where  $s_0$  is the first substrate (chlorophenol in the application, see [section 5](#)) concentration and  $x_0$  its degrader concentration;  $s_1$  and  $x_1$  for the second substrate (phenol);  $s_2$  and  $x_2$  for the third substrate (hydrogen);  $D$  is the dilution rate;  $\mu_i$  is the specific growth rate;  $s_i^{\text{in}}$  is the inflowing substrate concentration;  $a_i$  is the maintenance (or decay) rate for  $i = 0, 1, 2$  and corresponding to chlorophenol, phenol and hydrogen, respectively. The model considered in [14] incorporates six yield coefficient. However, without loss of generality, they can be normalized to one, except for one of them,  $\omega$ , which is assumed to be a positive constant, see [14]. The model in [14] considers only the input concentration  $s_0^{\text{in}}$ . Here, following [19], we add the inputs  $s_1^{\text{in}}$  and  $s_2^{\text{in}}$ . We assume that the growth functions satisfy the following conditions:

*Hypothesis 2.1.* For all  $s_0 > 0$  and  $s_2 > 0$ ,  $0 < \mu_0(s_0, s_2) < +\infty$ ,  $\mu_0(0, s_2) = 0$ ,  $\mu_0(s_0, 0) = 0$ .

*Hypothesis 2.2.* For all  $s_1 > 0$  and  $s_2 \geq 0$ ,  $0 < \mu_1(s_1, s_2) < +\infty$ ,  $\mu_1(0, s_2) = 0$ .

*Hypothesis 2.3.* For all  $s_2 > 0$ ,  $0 < \mu_2(s_2) < +\infty$ ,  $\mu_2(0) = 0$ .

*Hypothesis 2.4.* For all  $s_0 > 0$  and  $s_2 > 0$ ,  $\frac{\partial \mu_0}{\partial s_0}(s_0, s_2) > 0$ ,  $\frac{\partial \mu_0}{\partial s_2}(s_0, s_2) > 0$ .

*Hypothesis 2.5.* For all  $s_1 > 0$  and  $s_2 > 0$ ,  $\frac{\partial \mu_1}{\partial s_1}(s_1, s_2) > 0$ ,  $\frac{\partial \mu_1}{\partial s_2}(s_1, s_2) < 0$ .

*Hypothesis 2.6.* For all  $s_2 > 0$ ,  $\frac{d\mu_2}{ds_2}(s_2) > 0$ .

*Hypothesis 2.7.* The function  $s_2 \mapsto \mu_0(+\infty, s_2)$  is monotonically increasing and the function  $s_2 \mapsto \mu_1(+\infty, s_2)$  is monotonically decreasing, with  $\mu_1(+\infty, +\infty) = 0$ .

**Hypothesis 2.1** means that no growth can occur for species  $x_0$  without substrates  $s_0$  and  $s_2$ . **Hypothesis 2.2** means that no growth can occur for species  $x_1$  without substrate  $s_1$ . **Hypothesis 2.3** means that the production of  $s_2$  is necessary for the growth of the species  $x_2$ . **Hypothesis 2.4** means that the growth rate of species  $x_0$  increases with substrates  $s_0$  and  $s_2$ . **Hypothesis 2.5** means that the growth rate of the species  $x_1$  increases with the substrate  $s_1$  but is inhibited by the production of  $s_2$ . **Hypothesis 2.6** means that the growth rate of species  $x_2$  increases with substrate  $s_2$ . **Hypothesis 2.7** means that the maximum growth rate of the species  $x_0$  and  $x_1$  increases and decreases, respectively, with the concentration of substrate  $s_2$ .

We have the following result whose proof is standard and is left to the reader:

*Proposition 2.8.* For any non-negative initial conditions, all solutions of system (2.1) are bounded and remain non-negative for all  $t > 0$ .

**3. Steady states.** A steady state exists (or is said to be ‘meaningful’) if and only if all its components are non-negative. This predicts eight possible steady states, labeled below as in [19]:

- SS1, where  $x_0 = 0$ ,  $x_1 = 0$  and  $x_2 = 0$ : the washout steady state where all populations are extinct.
- SS2, where  $x_0 = 0$ ,  $x_1 = 0$  and  $x_2 > 0$ : only the the hydrogenotrophic methanogen population is maintained.
- SS3, where  $x_0 > 0$ ,  $x_1 = 0$  and  $x_2 = 0$ : only the chlorophenol degraders are maintained.
- SS4, where  $x_0 > 0$ ,  $x_1 > 0$  and  $x_2 = 0$ : only the hydrogenotrophic methanogens are washed out.
- SS5, where  $x_0 > 0$ ,  $x_1 = 0$  and  $x_2 > 0$ : only the phenol degraders are washed out.
- SS6, where  $x_0 > 0$ ,  $x_1 > 0$  and  $x_2 > 0$ : all three populations are present.
- SS7, where  $x_0 = 0$ ,  $x_1 > 0$  and  $x_2 = 0$ : only the phenol degraders are present.
- SS8, where  $x_0 = 0$ ,  $x_1 > 0$  and  $x_2 > 0$ : only the chlorophenol degraders are washed out.

*Proposition 3.1.* Assume that **Hypotheses 2.1 to 2.6** hold. The steady states SS1, SS2, ..., SS8, are given in **Table 1**.

*Proof.* The proof is given in **Appendix B**. □

For the description of the steady states given in **Table 1**, together with the statement of their conditions of existence and stability, we need to define some auxiliary functions that are listed in **Table 2**. The existence and properties of these functions are given in **Appendix A**.

**4. Existence and stability of steady states.** We state now the necessary and sufficient conditions of existence and stability of the steady states given in **Table 1**. Any reference to steady state stability should be considered as local exponential stability, that is to say, the real parts of the eigenvalues are negative. In **Table 1**, it is claimed that

TABLE 1

The steady states of (2.1). The functions  $M_0$ ,  $M_1$ ,  $M_2$ ,  $\Psi$ ,  $\psi_0$  and  $\psi_1$  are defined in Table 2.

	$s_0, s_1, s_2$	$x_0, x_1, x_2$
SS1	$s_0 = s_0^{\text{in}}, s_1 = s_1^{\text{in}}, s_2 = s_2^{\text{in}}$	$x_0 = 0, x_1 = 0, x_2 = 0$
SS2	$s_0 = s_0^{\text{in}}, s_1 = s_1^{\text{in}}$ $s_2 = M_2(D + a_2)$	$x_0 = 0, x_1 = 0$ $x_2 = \frac{D}{D+a_2} (s_2^{\text{in}} - M_2(D + a_2))$
SS3	$s_0 = s_0(D, s_0^{\text{in}}, s_2^{\text{in}})$ is a solution of $\psi_0(s_0) = D + a_0$ $s_1 = s_1^{\text{in}} + s_0^{\text{in}} - s_0$ $s_2 = s_2^{\text{in}} - \omega(s_0^{\text{in}} - s_0)$	$x_0 = \frac{D}{D+a_0} (s_0^{\text{in}} - s_0)$ $x_1 = 0$ $x_2 = 0$
SS4	$s_2 = s_2(D, s_0^{\text{in}}, s_1^{\text{in}}, s_2^{\text{in}})$ is a solution of $\Psi(s_2, D) = (1 - \omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}}$ $s_0 = M_0(D + a_0, s_2)$ $s_1 = M_1(D + a_1, s_2)$	$x_0 = \frac{D}{D+a_0} (s_0^{\text{in}} - s_0)$ $x_1 = \frac{D}{D+a_1} (s_0^{\text{in}} - s_0 + s_1^{\text{in}} - s_1)$ $x_2 = 0$
SS5	$s_0 = M_0(D + a_0, M_2(D + a_2))$ $s_1 = s_0^{\text{in}} + s_1^{\text{in}} - s_0$ $s_2 = M_2(D + a_2)$	$x_0 = \frac{D}{D+a_0} (s_0^{\text{in}} - s_0)$ $x_1 = 0$ $x_2 = \frac{D}{D+a_2} (s_2^{\text{in}} - s_2 - \omega(s_0^{\text{in}} - s_0))$
SS6	$s_0 = M_0(D + a_0, M_2(D + a_2))$ $s_1 = M_1(D + a_1, M_2(D + a_2))$ $s_2 = M_2(D + a_2)$	$x_0 = \frac{D}{D+a_0} (s_0^{\text{in}} - s_0)$ $x_1 = \frac{D}{D+a_1} (s_0^{\text{in}} + s_1^{\text{in}} - s_1 - s_0)$ $x_2 = \frac{D}{D+a_2} ((1 - \omega)(s_0^{\text{in}} - s_0) + s_1^{\text{in}} - s_1 + s_2^{\text{in}} - s_2)$
SS7	$s_0 = s_0^{\text{in}}$ $s_1 = s_1(D, s_1^{\text{in}}, s_2^{\text{in}})$ is a solution of $\psi_1(s_1) = D + a_1$ $s_2 = s_1^{\text{in}} - s_1 + s_2^{\text{in}}$	$x_0 = 0,$ $x_1 = \frac{D}{D+a_1} (s_1^{\text{in}} - s_1)$ $x_2 = 0$
SS8	$s_0 = s_0^{\text{in}}$ $s_1 = M_1(D + a_1, M_2(D + a_2))$ $s_2 = M_2(D + a_2)$	$x_0 = 0,$ $x_1 = \frac{D}{D+a_1} (s_1^{\text{in}} - s_1)$ $x_2 = \frac{D}{D+a_2} (s_1^{\text{in}} - s_1 + s_2^{\text{in}} - s_2)$

- The  $s_0$ -component of SS3 is a solution of equation

$$(4.1) \quad \psi_0(s_0) = D + a_0.$$

- The  $s_1$ -component of SS7 is a solution of equation

$$(4.2) \quad \psi_1(s_1) = D + a_1.$$

- The  $s_2$ -component of SS4 is a solution of equation

$$(4.3) \quad \Psi(s_2, D) = (1 - \omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}}.$$

Following [14], we add a hypothesis which then assures that there are at most two steady states of the form SS4.

*Hypothesis 4.1.* In the case  $\omega < 1$ , the function  $\Psi$  has a unique minimum  $\bar{s}_2(D)$  on the interval  $(s_2^0(D), s_2^1(D))$ , such that  $\frac{\partial \Psi}{\partial s_2}(s_2, D) < 0$  on  $(s_2^0(D), \bar{s}_2(D))$  and  $\frac{\partial \Psi}{\partial s_2}(s_2, D) > 0$  on  $(\bar{s}_2(D), s_2^1(D))$ .

The following result determines the conditions under which each of the three equations (4.1)–(4.3) has a solution and gives the number of solutions.

TABLE 2  
Notations, intervals and auxiliary functions.

	Definition
$s_0 = M_0(y, s_2)$	For $s_2 \geq 0$ fixed, $s_0 = M_0(y, s_2)$ is the unique solution of equation $\mu_0(s_0, s_2) = y$ . It is defined for $0 \leq y < \mu_0(+\infty, s_2)$ .
$s_1 = M_1(y, s_2)$	For $s_2 \geq 0$ fixed, $s_1 = M_1(y, s_2)$ is the unique solution of equation $\mu_1(s_1, s_2) = y$ . It is defined for $0 \leq y < \mu_1(+\infty, s_2)$ .
$s_2 = M_2(y)$	$s_2 = M_2(y)$ is the unique solution of equation $\mu_2(s_2) = y$ . It is defined for $0 \leq y < \mu_2(+\infty)$ .
$s_2 = M_3(s_0, z)$	For $s_0 \geq 0$ fixed, $s_2 = M_3(s_0, z)$ is the unique solution of equation $\mu_0(s_0, s_2) = z$ . It is defined for $0 \leq z < \mu_0(s_0, +\infty)$ .
$s_2^0 = s_2^0(D)$ and $s_2^1 = s_2^1(D)$	For $D \geq 0$ satisfying the conditions $D + a_0 < \mu_0(+\infty, +\infty)$ and $D + a_1 < \mu_1(+\infty, 0)$ , there exist unique values $s_2^0 = s_2^0(D)$ and $s_2^1 = s_2^1(D)$ , such that $\mu_0(+\infty, s_2^0(D)) = D + a_0$ and $\mu_1(+\infty, s_2^1(D)) = D + a_1$ .
$I_1$ $I_2$	$I_1 = \{D \geq 0 : s_2^0(D) < s_2^1(D)\}$ , $I_2 = \{D \in I_1 : s_2^0(D) < M_2(D + a_2) < s_2^1(D)\}$ .
$\Psi(s_2, D)$	$\Psi(s_2, D) = (1 - \omega)M_0(D + a_0, s_2) + M_1(D + a_1, s_2) + s_2$ . It is defined for $D \in I_1$ and $s_2^0(D) < s_2 < s_2^1(D)$ .
$\phi_1(D)$	$\phi_1(D) = \inf_{s_2^0(D) < s_2 < s_2^1(D)} \Psi(s_2, D) = \Psi(\bar{s}_2(D), D)$ . It is defined for $D \in I_1$ .
$\phi_2(D)$	$\phi_2(D) = \Psi(M_2(D + a_2), D)$ . It is defined for $D \in I_2$ .
$\phi_3(D)$	$\phi_3(D) = \frac{\partial \Psi}{\partial s_2}(M_2(D + a_2), D)$ . It is defined for $D \in I_2$ .
$J_0$ $J_1$	$J_0 = (\max(0, s_0^{\text{in}} - s_2^{\text{in}}/\omega), s_0^{\text{in}})$ $J_1 = (0, s_1^{\text{in}})$
$\psi_0(s_0)$	$\psi_0(s_0) = \mu_0(s_0, s_2^{\text{in}} - \omega(s_0^{\text{in}} - s_0))$ . It is defined for $s_0 \in [\max(0, s_0^{\text{in}} - s_2^{\text{in}}/\omega), +\infty)$ .
$\psi_1(s_1)$	$\psi_1(s_1) = \mu_1(s_1, s_1^{\text{in}} + s_2^{\text{in}} - s_1)$ . It is defined for $s_1 \in [0, s_1^{\text{in}} + s_2^{\text{in}}]$ .
$\varphi_0(D)$	$\varphi_0(D) = M_0(D + a_0, M_2(D + a_2))$ . It is defined for $D \in \{D \geq 0 : s_2^0(D) < M_2(D + a_2)\}$ .
$\varphi_1(D)$	$\varphi_1(D) = M_1(D + a_1, M_2(D + a_2))$ . It is defined for $D \in \{D \geq 0 : M_2(D + a_2) < s_2^1(D)\}$ .

*Lemma 4.2.* The equation  $\psi_0(s_0) = y$  has a solution in the interval  $J_0$  defined in [Table 2](#) if and only if  $\mu_0(s_0^{\text{in}}, s_2^{\text{in}}) > y$ . The mapping  $\psi_0$  is monotonically increasing and thus, if it exists, this solution is unique.

The equation  $\psi_1(s_1) = y$  has a solution in the interval  $J_1$  defined in [Table 2](#) if and only if  $\mu_1(s_1^{\text{in}}, s_2^{\text{in}}) > y$ . The mapping  $\psi_1$  is monotonically increasing and thus, if it exists, this solution is unique.

The equation  $\Psi(s_2, D) = s^{\text{in}}$  has a solution if and only if  $s^{\text{in}} \geq \phi_1(D)$ .

- When  $\omega \geq 1$  then, the mapping  $s_2 \mapsto \Psi(s_2, D)$  is monotonically increasing, and thus, if it exists, this solution is unique. Moreover, if  $\omega > 1$ ,  $\phi_1(D) = -\infty$  and if  $\omega = 1$ ,  $\phi_1(D) = \Psi(s_2^0(D), D) > 0$ .
- When  $\omega < 1$  then, there exist two solutions which are equal when  $s^{\text{in}} = \phi_1(D)$ . Moreover,  $\phi_1(D) > 0$ .

*Proof.* The proof is given in [Appendix C.1](#)  $\square$

The study of stability of SS4 and SS6 is treated separately in [Proposition 4.3](#) and [Proposition 4.4](#). It requires new definitions and notations that are not listed in [Table 2](#). We need the following notations:

$$(4.4) \quad E = \frac{\partial \mu_0}{\partial s_0}(s_0, s_2), \quad F = \frac{\partial \mu_0}{\partial s_2}(s_0, s_2), \quad G = \frac{\partial \mu_1}{\partial s_1}(s_1, s_2), \quad H = -\frac{\partial \mu_1}{\partial s_2}(s_1, s_2),$$

$$(4.5) \quad I = \frac{d\mu_2}{ds_2}(s_2), \quad J = \mu_0(s_0, s_2), \quad K = \mu_1(s_1, s_2), \quad L = \mu_2(s_2).$$

*Proposition 4.3.* When it exists, SS4 is stable if and only if

$$(4.6) \quad \begin{aligned} \frac{\partial \Psi}{\partial s_2}(s_2, D) &> 0, \quad (1 - \omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}} < \phi_2(D), \\ \phi_3(D) &> 0 \quad \text{and} \quad \phi_4(D, s_0^{\text{in}}, s_1^{\text{in}}, s_2^{\text{in}}) > 0, \end{aligned}$$

where  $s_2$  is a solution of [\(4.3\)](#), the functions  $\phi_2$  and  $\phi_3$  are defined in [Table 2](#) and the function  $\phi_4$  is defined by:

$$(4.7) \quad \phi_4(D, s_0^{\text{in}}, s_1^{\text{in}}, s_2^{\text{in}}) = c_1 c_2 c_3 - c_1^2 c_4 - c_3^2,$$

where the coefficients  $c_i$ ,  $i = 1, \dots, 4$  are given by:

$$c_1 = 2D + (E + \omega F)x_0 + (G + H)x_1,$$

$$c_2 = D^2 + (E + \omega F)(D + J)x_0 + (G + H)(D + K)x_1 + (E(G + H) - (1 - \omega)FG)x_0 x_1,$$

$$c_3 = D(E + \omega F)Jx_0 + D(G + H)Kx_1 + (E(G + H) - (1 - \omega)FG)(J + K)x_0 x_1,$$

$$c_4 = (E(G + H) - (1 - \omega)FG)JKx_0 x_1,$$

and the functions  $E, F, G, H, I, J, K$  and  $L$ , defined by [\(4.4\)](#) and [\(4.5\)](#), are evaluated at the components of SS4 given in [Table 1](#).

*Proof.* The proof is given in [Appendix C.3.1](#).  $\square$

*Proposition 4.4.* If it exists, SS6 is stable if and only if  $c_3 > 0$ ,  $c_5 > 0$ ,  $r_4 > 0$  and  $r_5 > 0$ , where these coefficients are defined in [Table 3](#).

*Proof.* The proof is given in [Appendix C.3.2](#).  $\square$

Now, we can state our main result.

*Theorem 4.5.* Assume that [Hypotheses 2.1 to 2.7](#) and [4.1](#) hold. The necessary and sufficient conditions of existence and stability of the steady states are given in [Table 4](#).

*Proof.* The proof of existence conditions is given in [Appendix C.2](#). The stability of SS4 and SS6 follows from [Proposition 4.3](#) and [Proposition 4.4](#), respectively. The proof of stability of all other steady states is given in [Appendix C.3.3](#).  $\square$



TABLE 3

The Liénard-Chipart coefficients for SS6. The functions  $E, F, G, H, I, J, K$  and  $L$ , defined by (4.4) and (4.5), are evaluated at the components of SS6 given in Table 1.

$$\begin{aligned}
c_1 &= 3D + (E + Fw)x_0 + (G + H)x_1 + Ix_2 \\
c_2 &= 3D^2 + (2D + J)(E + \omega F)x_0 + (2D + K)(G + H)x_1 + EIx_0x_2 + GIx_1x_2 \\
&\quad + (2D + L)Ix_2 + (E(G + H) - (1 - \omega)FG)x_0x_1 \\
c_3 &= D^3 + D(D + 2J)(E + \omega F)x_0 + D(D + 2K)(G + H)x_1 + D(D + 2L)Ix_2 \\
&\quad + EI(D + J + L)x_0x_2 + GI(D + K + L)x_1x_2 + EGIx_0x_1x_2 + (E(G + H) \\
&\quad - (1 - \omega)FG)(D + J + K)x_0x_1 \\
c_4 &= D^2(E + \omega F)Jx_0 + D^2(G + H)Kx_1 + D^2ILx_2 + EI(DJ + DL + JL)x_0x_2 \\
&\quad + GI(DK + DL + KL)x_1x_2 + EGI(J + K + L)x_0x_1x_2 + (E(G + H) \\
&\quad - (1 - \omega)FG)(DJ + DK + JK)x_0x_1 \\
c_5 &= DEIJLx_0x_2 + DGIKLx_1x_2 + D(E(G + H) - (1 - \omega)FG)JKx_0x_1 \\
&\quad + EGI(JK + JL + KL)x_0x_1x_2 \\
c_6 &= EGIJKLx_0x_1x_2 \\
\hline
r_0 &= c_1c_2 - c_3, \quad r_1 = c_1c_4 - c_5, \quad r_2 = c_3r_0 - c_1r_1, \quad r_3 = c_5r_0 - c_1^2c_6 \\
r_4 &= r_1r_2 - r_0r_3, \quad r_5 = r_3r_4 - c_1c_6r_2^2
\end{aligned}$$

TABLE 4

The necessary and sufficient conditions of existence and local stability of steady states of (2.1).  $M_0, M_1, M_2, M_3, \Psi, \phi_1, \phi_2, \phi_3, \psi_0, \varphi_0$  and  $\varphi_1$  are given in Table 2,  $\phi_4$  is given in (4.7),  $c_3, c_5, r_4$  and  $r_5$  are defined in Table 3.

	Existence conditions	Stability conditions
SS1	Always exists	$\mu_0(s_0^{\text{in}}, s_2^{\text{in}}) < D + a_0, \mu_1(s_1^{\text{in}}, s_2^{\text{in}}) < D + a_1,$ $\mu_2(s_2^{\text{in}}) < D + a_2$
SS2	$\mu_2(s_2^{\text{in}}) > D + a_2$	$s_0^{\text{in}} < \varphi_0(D), s_1^{\text{in}} < \varphi_1(D)$
SS3	$\mu_0(s_0^{\text{in}}, s_2^{\text{in}}) > D + a_0$	$\mu_1(s_0^{\text{in}} + s_1^{\text{in}} - s_0, s_2^{\text{in}} - \omega(s_0^{\text{in}} - s_0)) < D + a_1,$ $s_2^{\text{in}} - \omega s_0^{\text{in}} < M_2(D + a_2) - \omega\varphi_0(D)$ with $s_0$ solution of equation $\psi_0(s_0) = D + a_0$
SS4	$(1 - \omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}} \geq \phi_1(D),$ $s_0^{\text{in}} > M_0(D + a_0, s_2),$ $s_0^{\text{in}} + s_1^{\text{in}} > M_0(D + a_0, s_2)$ $+ M_1(D + a_1, s_2)$ with $s_2$ solution of equation $\Psi(s_2) = (1 - \omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}}$	$(1 - \omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}} < \phi_2(D),$ $\frac{\partial \Psi}{\partial s_2}(s_2, D) > 0,$ $\phi_3(D) > 0, \phi_4(D, s_0^{\text{in}}, s_1^{\text{in}}, s_2^{\text{in}}) > 0$
SS5	$s_0^{\text{in}} > \varphi_0(D),$ $s_2^{\text{in}} - \omega s_0^{\text{in}} > M_2(D + a_2) - \omega\varphi_0$	$s_0^{\text{in}} + s_1^{\text{in}} < \varphi_0(D) + \varphi_1(D)$
SS6	$(1 - \omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}} > \phi_2(D),$ $s_0^{\text{in}} > \varphi_0, s_0^{\text{in}} + s_1^{\text{in}} > \varphi_0 + \varphi_1$	$c_3 > 0, c_5 > 0, r_4 > 0, r_5 > 0$
SS7	$\mu_1(s_1^{\text{in}}, s_2^{\text{in}}) > D + a_1$	$s_1^{\text{in}} + s_2^{\text{in}} < M_3(s_0^{\text{in}}, D + a_0)$ $+ M_1(D + a_1, M_3(s_0^{\text{in}}, D + a_0)),$ $s_1^{\text{in}} + s_2^{\text{in}} < M_2(D + a_2) + \varphi_1(D)$
SS8	$s_1^{\text{in}} > \varphi_1(D),$ $s_1^{\text{in}} + s_2^{\text{in}} > \varphi_1(D) + M_2(D + a_2)$	$s_0^{\text{in}} < \varphi_0(D)$

*Remark 4.6.* Using Lemma 4.2, we have the following results:

- When it exists, SS2 is unique.
- When it exists, SS7 is unique.
- If  $\omega \geq 1$ , when it exists, SS4 is unique. Its stability condition  $\frac{\partial \Psi}{\partial s_2}(s_2, D) > 0$  is always satisfied. If  $\omega > 1$ ,  $\phi_1(D) = -\infty$ , so that its existence condition

- $(1 - \omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}} \geq \phi_1(D)$  is always satisfied.
- If  $\omega < 1$ , using [Hypothesis 4.1](#), there exist at most two steady states of the form SS4. If  $(1 - \omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}} > \phi_1(D)$ , equation (4.3) has two solutions  $s_2^{*1} < s_2^{*2}$ , such that  $\frac{\partial \Psi}{\partial s_2}(s_2^{*1}, D) < 0$  and  $\frac{\partial \Psi}{\partial s_2}(s_2^{*2}, D) > 0$ . We denote by  $\text{SS4}^1$  the steady state of type SS4 corresponding to  $s_2^{*1}$  while  $\text{SS4}^2$  corresponds to  $s_2^{*2}$ . When it exists,  $\text{SS4}^1$  is unstable. When  $\text{SS4}^2$  exists, its stability condition  $\frac{\partial \Psi}{\partial s_2}(s_2, D) > 0$  is always satisfied.

In the particular cases, where  $s_1^{\text{in}} = 0$  or  $s_2^{\text{in}} = 0$ , some of the steady states described in [Theorem 4.5](#) do not exist and the existence conditions of the existing steady state can be simplified. More precisely, we have the following result.

- Proposition 4.7.*
- If  $s_1^{\text{in}} = 0$  then, SS7 and SS8 do not exist. If  $s_2^{\text{in}} = 0$ , SS2, SS3 and SS5 do not exist. Therefore, in the case where  $s_1^{\text{in}} = s_2^{\text{in}} = 0$ , the steady states SS2, SS3, SS5, SS7 and SS8 do not exist.
  - If  $s_1^{\text{in}} = s_2^{\text{in}} = 0$  then, if  $\omega \geq 1$ , SS4 does not exist and if  $\omega < 1$ , SS4 exists if and only if  $(1 - \omega)s_0^{\text{in}} \geq \phi_1(D)$ .
  - If  $s_1^{\text{in}} = s_2^{\text{in}} = 0$  then, if  $\omega \geq 1$ , SS6 does not exist and if  $\omega < 1$ , SS6 exists if and only if  $(1 - \omega)s_0^{\text{in}} > \phi_2(D)$ .

*Proof.* The proof is given in [Appendix D](#). □

*Remark 4.8.* Assume that  $s_1^{\text{in}} = s_2^{\text{in}} = 0$ . Then, only the steady states SS1, SS4 and SS6 exist. The conditions  $(1 - \omega)s_0^{\text{in}} \geq \phi_1(D)$  and  $(1 - \omega)s_0^{\text{in}} > \phi_2(D)$  of existence of SS4 and SS6, respectively, given in [Proposition 4.7](#) are equivalent to the conditions  $s_0^{\text{in}} \geq F_1(D)$  and  $s_0^{\text{in}} > F_2(D)$ , respectively, given in Lemmas 3 and 4 of [\[14\]](#). Indeed, we have  $F_1(D) = \frac{\phi_1(D)}{1 - \omega}$  and  $F_2(D) = \frac{\phi_2(D)}{1 - \omega}$ . Therefore, we recover the results of [\[14\]](#), where the study is restricted to the case  $s_1^{\text{in}} = s_2^{\text{in}} = 0$ . Notice that, the steady states SS1, SS4 and SS6 were labeled SS1, SS2 and SS3 in [\[14\]](#), respectively.

From [Table 4](#), we can deduce the following result.

*Proposition 4.9.*

- If SS2 or SS3 or SS7 exists then, SS1 is unstable.
- If SS6 exists then, SS2, SS4, SS5 and SS8 are unstable.
- If SS5 exists then, SS2, SS3 and SS8 are unstable.
- If SS8 exists then, SS7 is unstable.

*Proof.* The proof is given in [Appendix E](#). □

Without maintenance, the necessary and sufficient conditions of existence and stability are summarized in [Table 5](#) where the function  $\phi_5$  is defined by

$$(4.8) \quad \phi_5(D, s_0^{\text{in}}, s_1^{\text{in}}, s_2^{\text{in}}) = (EIx_0x_2 + EG\phi_3(D)x_0x_1)(Ix_2 + (G + H)x_1 + (E + \omega F)x_0) + (Ix_2 + (G + H)x_1 + \omega Fx_0)GIx_1x_2,$$

and the functions  $E$ ,  $F$ ,  $G$ ,  $H$  and  $I$ , defined by (4.4) and (4.5), are evaluated at the components of SS6 given in [Table 1](#) and the function  $\phi_3(D)$  is defined in [Table 2](#) with  $a_i = 0$ ,  $i = 0, 1, 2$ . The steady states are deduced from [Table 1](#) by putting  $a_i = 0$ . Except for the stability condition of SS6, all other conditions in [Table 5](#) can be deduced easily from [Table 4](#). In fact, the proofs for SS4 and SS6, which are similar to the one given in [\[14\]](#), make use of the fact that system (2.1) can be reduced to a cascade system (see [Appendix C.3](#) in [\[14\]](#)).

**5. Applications to a chlorophenol-mineralising three-tiered microbial 'food web'.** The aim of this section is to illustrate the theoretical results of this

TABLE 5

The maintenance free case: the necessary and sufficient conditions of existence and local stability of steady states of (2.1).  $M_0, M_1, M_2, M_3, \Psi, \phi_1, \phi_2, \phi_3, \psi_0, \varphi_0$  and  $\varphi_1$  are given in Table 2 with  $a_i = 0, i = 0, 1, 2$ , and  $\phi_5$  is given in (4.8).

Existence conditions	Stability conditions
SS1 Always exists	$\mu_0(s_0^{\text{in}}, s_2^{\text{in}}) < D, \mu_1(s_1^{\text{in}}, s_2^{\text{in}}) < D, \mu_2(s_2^{\text{in}}) < D$
SS2 $\mu_2(s_2^{\text{in}}) > D$	$s_0^{\text{in}} < \varphi_0(D), s_1^{\text{in}} < \varphi_1(D)$
SS3 $\mu_0(s_0^{\text{in}}, s_2^{\text{in}}) > D$	$\mu_1(s_0^{\text{in}} + s_1^{\text{in}} - s_0, s_2^{\text{in}} - \omega(s_0^{\text{in}} - s_0)) < D,$ $s_2^{\text{in}} - \omega s_0^{\text{in}} < M_2(D) - \omega \varphi_0(D)$ with $s_0$ solution of equation $\psi_0(s_0) = D$
SS4 $s_0^{\text{in}} + s_1^{\text{in}} > M_0(D, s_2) + M_1(D, s_2)$ with $s_2$ solution of equation $\Psi(s_2, D) = (1 - \omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}}$	$(1 - \omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}} < \phi_2(D),$ $\frac{\partial \Psi}{\partial s_2}(s_2, D) > 0, \phi_3(D) > 0$
SS5 $s_0^{\text{in}} > \varphi_0(D),$ $s_2^{\text{in}} - \omega s_0^{\text{in}} > M_2(D) - \omega \varphi_0(D)$	$s_0^{\text{in}} + s_1^{\text{in}} < \varphi_0(D) + \varphi_1(D)$
SS6 $(1 - \omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}} > \phi_2(D),$ $s_0^{\text{in}} > \varphi_0(D), s_0^{\text{in}} + s_1^{\text{in}} > \varphi_0 + \varphi_1$	$\phi_3(D) > 0,$ or $\phi_3(D) < 0$ and $\phi_5(D, s_0^{\text{in}}, s_1^{\text{in}}, s_2^{\text{in}}) > 0$
SS7 $\mu_1(s_1^{\text{in}}, s_2^{\text{in}}) > D$	$s_1^{\text{in}} + s_2^{\text{in}} < M_3(s_0^{\text{in}}, D) + M_1(D, M_3(s_0^{\text{in}}, D)),$ $s_1^{\text{in}} + s_2^{\text{in}} < M_2(D) + \varphi_1(D)$
SS8 $s_1^{\text{in}} > \varphi_1, s_1^{\text{in}} + s_2^{\text{in}} > \varphi_1 + M_2(D)$	$s_0^{\text{in}} < \varphi_0(D)$

paper in the case of the chlorophenol-mineralising three-tiered microbial ‘food web’ considered in [19]. The specific growth rates take the form:

$$(5.1) \quad \begin{aligned} f_0(S_{\text{ch}}, S_{\text{H}_2}) &= \frac{k_{m,\text{ch}} S_{\text{ch}}}{K_{S,\text{ch}} + S_{\text{ch}}} \frac{S_{\text{H}_2}}{K_{S,\text{H}_2,c} + S_{\text{H}_2}}, \\ f_1(S_{\text{ph}}, S_{\text{H}_2}) &= \frac{k_{m,\text{ph}} S_{\text{ph}}}{K_{S,\text{ph}} + S_{\text{ph}}} \frac{1}{1 + S_{\text{H}_2}/K_{I,\text{H}_2}}, \quad f_2(S_{\text{H}_2}) = \frac{k_{m,\text{H}_2} S_{\text{H}_2}}{K_{S,\text{H}_2} + S_{\text{H}_2}}, \end{aligned}$$

where  $S_{\text{ch}}, S_{\text{ph}}$  and  $S_{\text{H}_2}$  are the chlorophenol, phenol and hydrogen substrates concentrations respectively. Let us denote by  $X_{\text{ch}}, X_{\text{ph}}$  and  $X_{\text{H}_2}$  the chlorophenol, phenol and hydrogen degrader concentrations,  $S_{\text{ch},\text{in}}, S_{\text{ph},\text{in}}$  and  $S_{\text{H}_2,\text{in}}$  the inflowing concentrations,  $k_{\text{dec},\text{ch}}, k_{\text{dec},\text{ph}}$  and  $k_{\text{dec},\text{H}_2}$  the decay rates, and by  $Y_{\text{ch}}, Y_{\text{ph}}$  and  $Y_{\text{H}_2}$  the yield coefficients. The equation of the model take the form:

$$(5.2) \quad \begin{cases} \dot{X}_{\text{ch}} = (Y_{\text{ch}} f_0(S_{\text{ch}}, S_{\text{H}_2}) - D - k_{\text{dec},\text{ch}}) X_{\text{ch}} \\ \dot{X}_{\text{ph}} = (Y_{\text{ph}} f_1(S_{\text{ph}}, S_{\text{H}_2}) - D - k_{\text{dec},\text{ph}}) X_{\text{ph}} \\ \dot{X}_{\text{H}_2} = (Y_{\text{H}_2} f_2(S_{\text{H}_2}) - D - k_{\text{dec},\text{H}_2}) X_{\text{H}_2} \\ \dot{S}_{\text{ch}} = D(S_{\text{ch},\text{in}} - S_{\text{ch}}) - f_0(S_{\text{ch}}, S_{\text{H}_2}) X_{\text{ch}} \\ \dot{S}_{\text{ph}} = D(S_{\text{ph},\text{in}} - S_{\text{ph}}) + \frac{224}{208}(1 - Y_{\text{ch}}) f_0(S_{\text{ch}}, S_{\text{H}_2}) X_{\text{ch}} - f_1(S_{\text{ph}}, S_{\text{H}_2}) X_{\text{ph}} \\ \dot{S}_{\text{H}_2} = D(S_{\text{H}_2,\text{in}} - S_{\text{H}_2}) - \frac{16}{208} f_0(S_{\text{ch}}, S_{\text{H}_2}) X_{\text{ch}} - f_2(S_{\text{H}_2}) X_{\text{H}_2} \\ \quad + \frac{32}{224}(1 - Y_{\text{ph}}) f_1(S_{\text{ph}}, S_{\text{H}_2}) X_{\text{ph}} \end{cases}$$

where  $224/208(1 - Y_{\text{ch}})$  represents the fraction of chlorophenol converted to phenol,  $32/224(1 - Y_{\text{ph}})$  represents the fraction of phenol that is transformed to hydrogen and  $16/208$  represents the fraction of hydrogen consumed by the chlorophenol degrader  $X_{\text{ch}}$ . The biological parameter values are provided in Table 10. They were previously used in [9, 14, 19].

Following [14], by using the linear change of variable given by (G.1) and (G.2), the yield coefficients in (5.2) can be normalized to one except of one of them, which is equal to  $\omega \simeq 0.53$ , when the yield coefficients are those given in Table 10. Therefore, (5.2) is of the form (2.1), with  $\omega < 1$ . The specific growth functions (5.1) become the functions defined in (G.3), keep their form by this linear change of variables and satisfy Hypotheses 2.1 to 2.7 and 4.1. Therefore, the results of our paper apply to (5.2). The details are given in Appendix G. For the growth functions (G.3), the various functions defined in Table 2 are listed in Table 13.

In [19], most of the results on the existence and stability of steady states of model (5.2) were obtained numerically. Our analytical study of (2.1) permit to give rigorous proofs for (5.2). From Remark 4.6, as  $\omega < 1$ , the system can have two steady states  $SS4^1$  and  $SS4^2$  of the form  $SS4$ .

In what follows, we consider the input concentrations  $S_{ph,in} = 0$  and  $S_{H_2,in} = 2.67 \times 10^{-5}$ , corresponding to Fig. 3(a) in [19]. We fix  $D = 0.01$ . As a consequence of Theorem 4.5, we obtain the following result which determine the existence and the stability of the steady states of (5.2) with respect to the input concentration  $S_{ch,in}$ .

*Proposition 5.1.* Assume that the biological parameters in (5.2) are given as in Table 10. Assume that  $S_{ph,in} = 0$ ,  $S_{H_2,in} = 2.67 \times 10^{-5}$  and  $D = 0.01$ . Let  $\sigma_i$ ,  $i = 1, \dots, 6$  be the bifurcation values defined in Table 6. The existence and stability of steady states of (5.2), with respect to the input concentration  $S_{ch,in}$  is given in Table 7. The nature of the bifurcations when  $S_{ch,in}$  cross the values  $\sigma_i$ ,  $i = 1, \dots, 6$  is given in Table 8.

*Proof.* The proof is supported by numerical experimentation and is given in Appendix H. □

TABLE 6  
Definitions of the critical values of  $\sigma_i$ ,  $i = 1, \dots, 6$

Definition	Value
$\sigma_1 = M_0(D + a_0, S_{H_2,in}) / (Y_3 Y_4)$	0.003173
$\sigma_2 = \varphi_0(D) / (Y_3 Y_4)$	0.013643
$\sigma_3 = (S_{H_2,in} - M_2(D + a_2) + \omega \varphi_0(D)) / (\omega Y_3 Y_4)$	0.013985
$\sigma_4 = (\phi_1(D) - S_{H_2,in}) / ((1 - \omega) Y_3 Y_4)$	0.029402
$\sigma_5 = (\phi_2(D) - S_{H_2,in}) / ((1 - \omega) Y_3 Y_4)$	0.033292
$\sigma_6$ is the largest root of equation $r_5 = 0$	0.1025

TABLE 7

Existence and stability of steady states, with respect to  $S_{ch,in}$ . The bifurcation values  $\sigma_i$ ,  $i = 1, \dots, 6$  are given in Table 6. The letter *S* (resp. *U*) means that the corresponding steady state is stable (resp. unstable). No letter means that the steady state does not exist.

Interval	SS1	SS2	SS3	SS4 <sup>1</sup>	SS4 <sup>2</sup>	SS5	SS6
$0 < S_{ch,in} < \sigma_1$	U	S					
$\sigma_1 < S_{ch,in} < \sigma_2$	U	S	U				
$\sigma_2 < S_{ch,in} < \sigma_3$	U	U	U			S	
$\sigma_3 < S_{ch,in} < \sigma_4$	U	U	S				
$\sigma_4 < S_{ch,in} < \sigma_5$	U	U	S	U	U		
$\sigma_5 < S_{ch,in} < \sigma_6$	U	U	S	U	U		U
$\sigma_6 < S_{ch,in}$	U	U	S	U	U		S

*Remark 5.2.* Not all of the behaviors described in Table 7 were reported in [19]. For  $D = 0.01$ , the operating diagram of Fig. 3(a) of [19] predicts only three possible behaviors: the stability of SS2, the stability of SS3 and the bistability between SS3 and SS6. Note that the destabilization of SS6 via a Hopf bifurcation with emergence

TABLE 8

The nature of the bifurcations corresponding to the critical values of  $\sigma_i$ ,  $i = 1, \dots, 6$ , defined in Table 6. There exists also a critical value  $\sigma^* \simeq 0.099295$  corresponding to the value of  $S_{\text{ch},\text{in}}$  where the stable limit cycle disappears when  $S_{\text{ch},\text{in}}$  is decreasing.

	Type of the bifurcation
$\sigma_1$	Transcritical bifurcation of SS1 and SS3
$\sigma_2$	Transcritical bifurcation of SS2 and SS5
$\sigma_3$	Transcritical bifurcation of SS3 and SS5
$\sigma_4$	Saddle-node bifurcation of SS4 <sup>1</sup> and SS4 <sup>2</sup>
$\sigma_5$	Transcritical bifurcation of SS4 <sup>1</sup> and SS6
$\sigma^*$	Disappearance of the stable limit cycle
$\sigma_6$	Supercritical Hopf bifurcation

of a stable limit cycle has not been observed in [19]. Even, the possibility of stability of SS5 has not been reported in the operating diagram. Indeed, Fig. 3(a) of [19] does not correctly describe the transition from the region labeled SS2 (and corresponding to the stability of SS2) to the SS3 region. Our results show that this transition is via a SS5 region. The existence of the SS5 region was depicted in Fig. 3(b) of [19] in the case where  $S_{\text{H}_2,\text{in}} = 2.67 \times 10^{-2}$ . However, this region also exists when  $S_{\text{H}_2,\text{in}} = 2.67 \times 10^{-5}$ , but it is very thin, since for  $D = 0.01$  it corresponds to  $\sigma_2 < S_{\text{ch},\text{in}} < \sigma_3$ , where  $\sigma_2 \simeq 0.013643$  and  $\sigma_3 \simeq 0.013985$ .

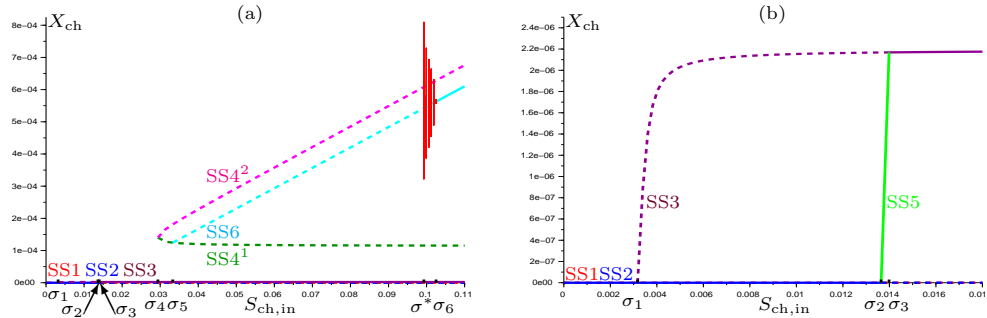


FIG. 5.1. (a) Projections of the  $\omega$ -limit set in variable  $X_{\text{ch}}$  as a function of  $S_{\text{ch},\text{in}} \in [0, 0.11]$ , reveal the occurrence and disappearance of stable limit cycles. (b) A magnification of the transcritical bifurcations when  $S_{\text{ch},\text{in}} \in [0, 0.018]$ .

Figures 5.1 and 5.2 depict the bifurcation diagram of system (5.2) where  $X_{\text{ch}}$  and  $X_{\text{H}_2}$  are represented, respectively, as a function of the bifurcation parameter  $S_{\text{ch},\text{in}}$ . Figure 5.1(b), Figure 5.2(b) and Figure 5.3 depict magnifications of the bifurcation diagram showing the transcritical bifurcations occurring at  $\sigma_1$ ,  $\sigma_2$ ,  $\sigma_3$  and  $\sigma_5$ , the saddle-node bifurcation occurring at  $\sigma_4$ , the Hopf bifurcation occurring at  $\sigma_6$  and the disappearance of the cycle occurring at  $\sigma^*$ . In Figure 5.1(b), the steady states SS1 and SS2 cannot be distinguished since they have both a zero  $X_{\text{ch}}$ -component. Since for  $S_{\text{ch},\text{in}} < \sigma_2$ , SS2 is stable and SS1 is unstable, the  $X_{\text{ch}} = 0$  axis is plotted in blue, which is the color for SS2 in Table 9. In Figure 5.2(b), the steady states SS1 and SS2 are distinguished while SS1 and SS3 cannot be distinguished, since they have both a zero  $X_{\text{H}_2}$ -component. Since for  $S_{\text{ch},\text{in}} > \sigma_3$ , SS3 is stable and SS1 is unstable, the  $X_{\text{H}_2} = 0$  axis is plotted in purple, which is the color for SS3 in Table 9.

Numerical simulations have shown that there exists a critical value  $\sigma^* \in (\sigma_5, \sigma_6)$ , which corresponds to the value of  $S_{\text{ch},\text{in}}$ , where the stable limit cycle that appears

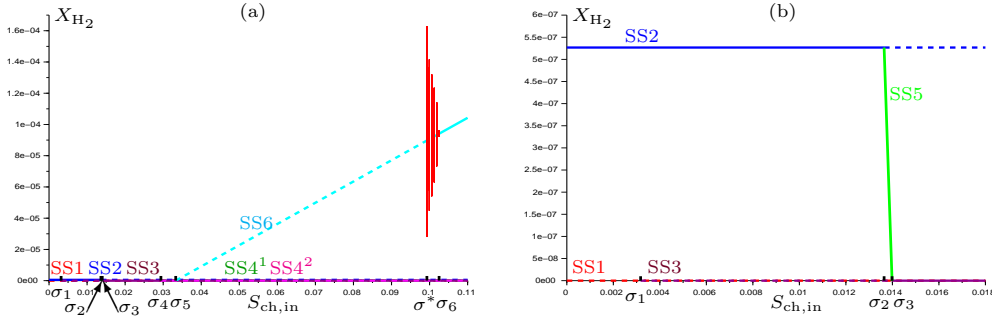


FIG. 5.2. (a) Projections of the  $\omega$ -limit set in variable  $X_{H_2}$  as a function of  $S_{ch,in} \in [0, 0.11]$ , reveal the occurrence and disappearance of stable limit cycles. (b) A magnification of the transcritical bifurcations when  $S_{ch,in} \in [0, 0.018]$ .

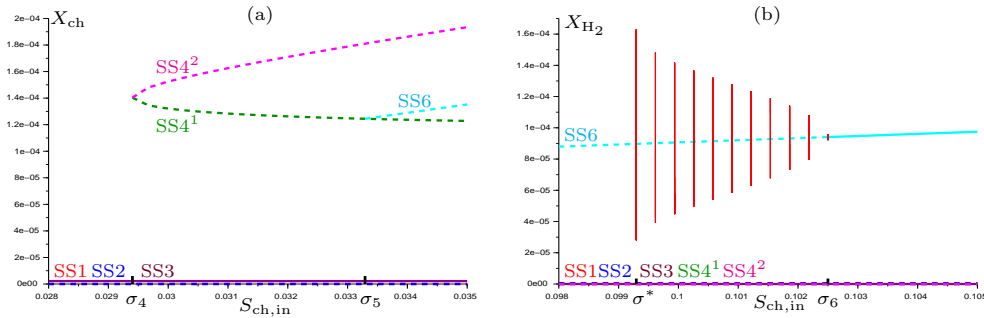


FIG. 5.3. (a) A magnification of saddle-node bifurcation at  $S_{ch,in} = \sigma_4$  and the transcritical bifurcation at  $S_{ch,in} = \sigma_5$  when  $S_{ch,in} \in [0.028, 0.035]$ . (b) A magnification of the appearance and disappearance of stable limit cycles when  $S_{ch,in} \in [0.098, 0.105]$ .

TABLE 9

The colors that are used in Figures 5.1 to 5.3, the solid (resp. dashed) lines are used for stable (resp. unstable) steady states.

SS1	SS2	SS3	SS4 <sup>1</sup>	SS4 <sup>2</sup>	SS5	SS6
Red	Blue	Purple	Dark Green	Magenta	Green	Cyan

for  $S_{ch,in} = \sigma_6$  through a supercritical Hopf bifurcation, disappears when  $S_{ch,in}$  is decreasing. In [17], a numerical study of the bifurcation diagram with respect to the parameter  $D$  is given in the case without maintenance and  $s_1^{in} = s_2^{in} = 0$ . Figure 6 in [17] shows that the disappearance of the limit cycle occurs through a saddle-node bifurcation of limit cycles which gives birth to stable and unstable periodic orbits. We conjecture that in our case also the stable limit cycle disappears by a confluence with an unstable limit cycle. Numerical simulations are shown in Appendix I illustrating the main results of this section namely the bistability with convergence either to SS3 or to a stable limit cycle according to the initial conditions, when  $\sigma^* < S_{ch,in} < \sigma_6$ , and bistability with convergence toward SS3 or SS6, when  $S_{ch,in} > \sigma_6$ .

**6. Discussion.** In this work, we have extended model (5.2) of a chlorophenol-mineralising three-tiered microbial ‘food web’ presented in [19], by considering the model (2.1) with general growth functions. Our study considers the effects of the phenol and hydrogen input concentrations, which were neglected in the analytical analysis given in [14], together with the effects of maintenance terms, which were neglected in the analytical analysis given in [6, 17] and in [14] for the stability analysis.

Our first aim was the theoretical analysis of the three-tiered model by providing

a complete study for the existence and local stability of all steady states. Our mathematical analysis of the model has revealed several possible asymptotic behaviors: [Theorem 4.5](#) provides a complete theoretical description of the existence and stability of the steady states according to the operating parameters  $D$ ,  $s_0^{\text{in}}$ ,  $s_1^{\text{in}}$  and  $s_2^{\text{in}}$ . System (2.1) can have up to eight steady states: the washout steady state which always exists, a positive steady state where all degrader populations are maintained and six other steady states corresponding to the extinction of one or two degrader populations. In [\[19\]](#), the results on the existence and stability of steady states of model (5.2) were obtained only numerically. Our analytical results on the existence and stability of the steady states of (2.1), give rigorous proofs for (5.2).

Our results extend the results on existence and stability of steady states given in [\[6, 14, 17\]](#) obtained in some particular cases of (2.1). In the particular case  $s_0^{\text{in}} > 0$ ,  $s_1^{\text{in}} = s_2^{\text{in}} = 0$ , without phenol and hydrogen input concentrations, considered in [\[14\]](#), system (2.1) can have only up to three steady states: the washout steady state, a positive steady state, where all degrader populations are maintained, and one steady state where only the hydrogen degrader is extinct. In the particular case without maintenance, considered in [\[6, 17\]](#), system (2.1) can have also up to eight steady states, but their stability is much more simpler to study, since the six-dimensional system (2.1) can be reduced to a three-dimensional one.

Our second achievement was to show that the positive steady state of coexistence of all species can be unstable, a fact that has been already depicted in [\[14\]](#), in the particular case  $s_0^{\text{in}} > 0$ ,  $s_1^{\text{in}} = s_2^{\text{in}} = 0$ . In [\[14\]](#), a numerical evidence for the possibility of a Hopf bifurcation is given, with the appearance of a stable limit cycle. In this paper, we give also numerical evidence for a Hopf bifurcation, in the case  $s_0^{\text{in}} > 0$ ,  $s_1^{\text{in}} = 0$  and  $s_2^{\text{in}} > 0$ . It should be noticed that the possibility of the Hopf bifurcation of the positive steady state, is analytically proved in [\[17\]](#), in the case without maintenance which can be reduced to a three-dimensional system. The destabilization of the positive steady state was not detected by the numerical analysis in [\[19\]](#).

In order that the results can be useful in practice, one should have a description of the operating diagrams which describe the existence and stability of steady states with respect to the operating parameters. In [\[19\]](#), the operating diagrams were obtained numerically. The region of instability of the coexistence steady state was not depicted. The more precise operating diagram showing the region of instability of the positive steady state was given in [\[14\]](#) in the case without phenol and hydrogen input concentrations. In [\[14\]](#), the operating diagrams were obtained analytically only in the case without maintenance. It is a challenge for future work to use our characterizations of existence and stability conditions of steady states to obtain analytically the operating diagram. As it was stated in [Remark 5.2](#), the bifurcation diagram with the chlorophenol input concentration as the bifurcating parameter shown in [Figures 5.1 and 5.2](#) proves that some of the operating diagrams obtained in [\[19\]](#) have omitted important transition phenomena between steady states.

**Appendix A. Definitions and notations.** In this section, we prove that the functions listed in [Table 2](#) are well defined, and we give their properties.

Let  $s_2 \geq 0$  be fixed. Using [Hypotheses 2.1 and 2.4](#), there exists a unique function

$$y \in [0, \mu_0(+\infty, s_2)) \mapsto M_0(y, s_2) \in [0, +\infty),$$

such that for  $s_0 \geq 0$ ,  $s_2 \geq 0$  and  $y \in [0, \mu_0(+\infty, s_2))$ , we have:

$$(A.1) \quad s_0 = M_0(y, s_2) \iff y = \mu_0(s_0, s_2).$$

Let  $s_2 \geq 0$  be fixed. Using [Hypotheses 2.2](#) and [2.5](#), there exists a unique function

$$y \in [0, \mu_1(+\infty, s_2)) \mapsto M_1(y, s_2) \in [0, +\infty),$$

such that for  $s_1 \geq 0$ ,  $s_2 \geq 0$  and  $y \in [0, \mu_1(+\infty, s_2))$ , we have:

$$(A.2) \quad s_1 = M_1(y, s_2) \iff y = \mu_1(s_1, s_2).$$

Using [Hypotheses 2.3](#) and [2.6](#), there exists a unique function

$$y \in [0, \mu_2(+\infty)) \mapsto M_2(y) \in [0, +\infty),$$

such that for  $s_2 \geq 0$  and  $y \in [0, \mu_2(+\infty))$ , we have:

$$(A.3) \quad s_2 = M_2(y) \iff y = \mu_2(s_2).$$

Let  $s_0 \geq 0$  be fixed. Using [Hypotheses 2.1](#) and [2.4](#), there exists a unique function

$$z \in [0, \mu_0(s_0, +\infty)) \mapsto M_3(s_0, z) \in [0, +\infty),$$

such that for  $s_0 \geq 0$ ,  $s_2 \geq 0$  and  $z \in [0, \mu_0(s_0, +\infty))$ , we have:

$$(A.4) \quad s_2 = M_3(s_0, z) \iff z = \mu_0(s_0, s_2).$$

Note that, from [Hypotheses 2.4](#) and [2.5](#), we have

$$(A.5) \quad \begin{aligned} \frac{\partial M_0}{\partial y}(y, s_2) &= \left[ \frac{\partial \mu_0}{\partial s_0}(s_0, s_2) \right]^{-1} > 0, & \frac{\partial M_1}{\partial y}(y, s_2) &= \left[ \frac{\partial \mu_1}{\partial s_1}(s_1, s_2) \right]^{-1} > 0, \\ \frac{\partial M_3}{\partial z}(s_0, z) &= \left[ \frac{\partial \mu_0}{\partial s_2}(s_0, s_2) \right]^{-1} > 0, \end{aligned}$$

$$(A.6) \quad \begin{aligned} \frac{\partial M_0}{\partial s_2}(y, s_2) &= -\frac{\partial \mu_0}{\partial s_2}(s_0, s_2) \left[ \frac{\partial \mu_0}{\partial s_0}(s_0, s_2) \right]^{-1} < 0, \\ \frac{\partial M_1}{\partial s_2}(y, s_2) &= -\frac{\partial \mu_1}{\partial s_2}(s_1, s_2) \left[ \frac{\partial \mu_1}{\partial s_1}(s_1, s_2) \right]^{-1} > 0. \end{aligned}$$

For  $D \geq 0$  satisfying the conditions  $D + a_0 < \mu_0(+\infty, +\infty)$  and  $D + a_1 < \mu_1(+\infty, 0)$ , there exist unique values  $s_2^0 = s_2^0(D)$  and  $s_2^1 = s_2^1(D)$ , such that  $\mu_0(+\infty, s_2^0(D)) = D + a_0$  and  $\mu_1(+\infty, s_2^1(D)) = D + a_1$  (see Fig. 2(a) of [\[14\]](#)). The definition domains of all the other functions in [Table 2](#) are deduced from those of the functions  $M_0$ ,  $M_1$  and  $M_2$ .

**Appendix B. Proof of [Proposition 3.1](#).** A steady state of [\(2.1\)](#) is obtained by setting the right-hand sides equal to zero:

$$(B.1) \quad [\mu_0(s_0, s_2) - D - a_0] x_0 = 0$$

$$(B.2) \quad [\mu_1(s_1, s_2) - D - a_1] x_1 = 0$$

$$(B.3) \quad [\mu_2(s_2) - D - a_2] x_2 = 0$$

$$(B.4) \quad D(s_0^{\text{in}} - s_0) - \mu_0(s_0, s_2) x_0 = 0$$

$$(B.5) \quad D(s_1^{\text{in}} - s_1) + \mu_0(s_0, s_2) x_0 - \mu_1(s_1, s_2) x_1 = 0$$

$$(B.6) \quad D(s_2^{\text{in}} - s_2) + \mu_1(s_1, s_2) x_1 - \omega \mu_0(s_0, s_2) x_0 - \mu_2(s_2) x_2 = 0.$$



Using (B.1)+(B.4), (B.2)-(B.1)+(B.5) and (B.3)+ $\omega$ (B.1)  
-(B.2)+(B.6), one obtains the set of equations

$$(B.7) \quad \begin{cases} D(s_0^{\text{in}} - s_0) - (D + a_0)x_0 = 0 \\ D(s_1^{\text{in}} - s_1) + (D + a_0)x_0 - (D + a_1)x_1 = 0 \\ D(s_2^{\text{in}} - s_2) - \omega(D + a_0)x_0 + (D + a_1)x_1 - (D + a_2)x_2 = 0. \end{cases}$$

We can solve (B.7) and obtain  $x_0$ ,  $x_1$  and  $x_2$  with respect to  $s_0$ ,  $s_1$  and  $s_2$ :

$$(B.8) \quad x_0 = \frac{D}{D + a_0} (s_0^{\text{in}} - s_0),$$

$$(B.9) \quad x_1 = \frac{D}{D + a_1} (s_0^{\text{in}} - s_0 + s_1^{\text{in}} - s_1),$$

$$(B.10) \quad x_2 = \frac{D}{D + a_2} ((1 - \omega)(s_0^{\text{in}} - s_0) + s_1^{\text{in}} - s_1 + s_2^{\text{in}} - s_2).$$

We can also solve (B.7) and obtain  $s_0$ ,  $s_1$  and  $s_2$  with respect to  $x_0$ ,  $x_1$  and  $x_2$ :

$$(B.11) \quad s_0 = s_0^{\text{in}} - \frac{D + a_0}{D} x_0,$$

$$(B.12) \quad s_1 = s_1^{\text{in}} + \frac{D + a_0}{D} x_0 - \frac{D + a_1}{D} x_1,$$

$$(B.13) \quad s_2 = s_2^{\text{in}} - \omega \frac{D + a_0}{D} x_0 + \frac{D + a_1}{D} x_1 - \frac{D + a_2}{D} x_2.$$

For the steady state SS1,  $x_0 = x_1 = x_2 = 0$ . Hence, (B.11)–(B.13) result in  $s_0 = s_0^{\text{in}}$ ,  $s_1 = s_1^{\text{in}}$  and  $s_2 = s_2^{\text{in}}$ .

For the steady state SS2,  $x_0 = x_1 = 0$  and  $x_2 > 0$ . Hence, (B.11) and (B.12) result in  $s_0 = s_0^{\text{in}}$  and  $s_1 = s_1^{\text{in}}$ . Therefore, (B.10) results in

$$x_2 = \frac{D}{D + a_2} (s_2^{\text{in}} - s_2).$$

Since  $x_2 > 0$ , (B.3) results in  $\mu_2(s_2) = D + a_2$ . Using definition (A.3) of  $M_2$ , we have

$$s_2 = M_2(D + a_2).$$

For the steady state SS3,  $x_1 = x_2 = 0$  and  $x_0 > 0$ . Hence, (B.8) results in

$$x_0 = \frac{D}{D + a_0} (s_0^{\text{in}} - s_0).$$

Using this expression together with  $x_1 = x_2 = 0$  in (B.12) and (B.13) result in

$$(B.14) \quad s_1 = s_1^{\text{in}} + s_0^{\text{in}} - s_0 \quad \text{and} \quad s_2 = s_2^{\text{in}} - \omega(s_0^{\text{in}} - s_0).$$

Since  $x_0 > 0$ , (B.1) results in

$$(B.15) \quad \mu_0(s_0, s_2) = D + a_0.$$

Replacing  $s_2$  by its expression (B.14) with respect to  $s_0$  in (B.15) results in

$$\psi_0(s_0) = D + a_0,$$

where  $\psi_0$  is the function defined in Table 2 by:

$$\psi_0(s_0) = \mu_0(s_0, s_2^{\text{in}} - \omega(s_0^{\text{in}} - s_0)).$$

For the steady state SS4,  $x_0 > 0$ ,  $x_1 > 0$  and  $x_2 = 0$ . Hence, (B.8) and (B.9) result in

$$(B.16) \quad x_0 = \frac{D}{D + a_0} (s_0^{\text{in}} - s_0) \quad \text{and} \quad x_1 = \frac{D}{D + a_1} (s_0^{\text{in}} - s_0 + s_1^{\text{in}} - s_1).$$

Since  $x_0 > 0$  and  $x_1 > 0$ , (B.1) and (B.2) result in  $\mu_0(s_0, s_2) = D + a_0$  and  $\mu_1(s_1, s_2) = D + a_1$ . Therefore, using definitions (A.1) and (A.2) of  $M_0$  and  $M_1$ , we have

$$(B.17) \quad s_0 = M_0(D + a_0, s_2) \quad \text{and} \quad s_1 = M_1(D + a_1, s_2).$$

Using (B.16) together with  $x_2 = 0$  in (B.13), we have

$$(B.18) \quad s_2 = s_2^{\text{in}} - \omega(s_0^{\text{in}} - s_0) + s_0^{\text{in}} - s_0 + s_1^{\text{in}} - s_1.$$

Replacing  $s_0$  and  $s_1$  by their expressions (B.17) with respect to  $s_2$  in (B.18), it follows that,  $s_2$  is a solution of equation

$$\Psi(s_2, D) = (1 - \omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}},$$

where  $\Psi$  is the function defined in Table 2 by:

$$\Psi(s_2, D) = (1 - \omega)M_0(D + a_0, s_2) + M_1(D + a_1, s_2) + s_2.$$

For the steady state SS5,  $x_0 > 0$ ,  $x_2 > 0$  and  $x_1 = 0$ . Using (B.8) together with  $x_1 = 0$  in (B.12) results in

$$s_1 = s_1^{\text{in}} - s_0 + s_0^{\text{in}}.$$

Using this expression in (B.10) results in

$$x_2 = \frac{D}{D + a_2} (s_2^{\text{in}} - s_2 - \omega(s_0^{\text{in}} - s_0)).$$

Since  $x_0 > 0$  and  $x_2 > 0$ , (B.1) and (B.3) result in  $\mu_0(s_0, s_2) = D + a_0$  and  $\mu_2(s_2) = D + a_2$ . Therefore, using definitions (A.1) and (A.3) of  $M_0$  and  $M_2$ , we have

$$s_2 = M_2(D + a_2) \quad \text{and} \quad s_0 = M_0(D + a_0, M_2(D + a_2)).$$

For the steady state SS6,  $x_0 > 0$ ,  $x_1 > 0$  and  $x_2 > 0$ . Then, as a consequence of (B.1)–(B.3), we obtain:

$$\mu_0(s_0, s_2) = D + a_0, \quad \mu_1(s_1, s_2) = D + a_1, \quad \mu_2(s_2) = D + a_2.$$

Using definitions (A.1)–(A.3) of the functions  $M_0$ ,  $M_1$  and  $M_2$ , it follows that  $s_2$ ,  $s_0$  and  $s_1$  are given by:

$$s_2 = M_2(D + a_2), \quad s_0 = M_0(D + a_0, s_2), \quad s_1 = M_1(D + a_1, s_2),$$

which prove the  $s$ -components of SS6 in Table 1. (B.8)–(B.10) give the  $x$ -components of SS6 in Table 1.

For the steady state SS7,  $x_0 = x_2 = 0$  and  $x_1 > 0$ . Hence, (B.11) results in  $s_0 = s_0^{\text{in}}$ . From (B.9), we have

$$x_1 = \frac{D}{D + a_1} (s_1^{\text{in}} - s_1).$$

Using this expression together with  $x_0 = x_2 = 0$  in (B.13) results in

$$(B.19) \quad s_2 = s_1^{\text{in}} - s_1 + s_2^{\text{in}}.$$

Since  $x_1 > 0$ , then, as a consequence of (B.2), we obtain:

$$\mu_1(s_1, s_2) = D + a_1.$$

Replacing  $s_2$  by its expression (B.19) with respect to  $s_1$  results in

$$\psi_1(s_1) = D + a_1,$$

where  $\psi_1$  is the function defined in Table 2 by:

$$\psi_1(s_1) = \mu_1(s_1, s_1^{\text{in}} - s_1 + s_2^{\text{in}}).$$

For the steady state SS8,  $x_0 = 0$ ,  $x_1 > 0$  and  $x_2 > 0$ . Hence, (B.11) results in  $s_0 = s_0^{\text{in}}$ . Using this expression in (B.9) and (B.10) results in

$$x_1 = \frac{D}{D + a_1} (s_1^{\text{in}} - s_1), \quad x_2 = \frac{D}{D + a_2} (s_1^{\text{in}} - s_1 + s_2^{\text{in}} - s_2).$$

Since  $x_1 > 0$  and  $x_2 > 0$ , as a consequence of (B.2) and (B.3), we have  $\mu_1(s_1, s_2) = D + a_1$  and  $\mu_2(s_2) = D + a_2$ . Therefore, using definitions (A.2) and (A.3) of the functions  $M_1$  and  $M_2$ , it follows that  $s_2$  and  $s_1$  are given by:

$$s_2 = M_2(D + a_2), \quad s_1 = M_1(D + a_1, M_2(D + a_2)).$$

**Appendix C. Proof of Theorem 4.5.** We first give the proof of Lemma 4.2 which determines the conditions under which each of the three equations (4.1)–(4.3) has a solution and the number of solutions, that is to say the existence conditions of the steady states SS3, SS7 and SS4, respectively.

**C.1. Proof of Lemma 4.2.** Recall that  $J_0 = (\max(0, s_0^{\text{in}} - s_2^{\text{in}}/\omega), s_0^{\text{in}})$ . If  $s_2^{\text{in}} - \omega s_0^{\text{in}} > 0$ , one has  $\psi_0(0) = \mu_0(0, s_2^{\text{in}} - \omega s_0^{\text{in}}) = 0$  and if  $s_2^{\text{in}} - \omega s_0^{\text{in}} \leq 0$ , one has  $s_0^{\text{in}} - s_2^{\text{in}}/\omega \geq 0$ , so that  $\psi_0(s_0^{\text{in}} - s_2^{\text{in}}/\omega) = \mu_0(s_0^{\text{in}} - s_2^{\text{in}}/\omega, 0) = 0$ . Thus,  $\psi_0(\max(0, s_0^{\text{in}} - s_2^{\text{in}}/\omega)) = 0$ . On the other hand,  $\psi_0(s_0^{\text{in}}) = \mu_0(s_0^{\text{in}}, s_2^{\text{in}})$ . Therefore, there exists a solution  $s_0 \in J_0$  satisfying  $\psi_0(s_0) = y$  if and only if  $\mu_0(s_0^{\text{in}}, s_2^{\text{in}}) > y$ . Since  $\psi_0$  is monotonically increasing, if it exists, this solution is unique. Indeed, we have

$$\frac{d\psi_0}{ds_0}(s_0) = \frac{\partial \mu_0}{\partial s_0}(s_0, s_2^{\text{in}} - \omega(s_0^{\text{in}} - s_0)) + \omega \frac{\partial \mu_0}{\partial s_2}(s_0, s_2^{\text{in}} - \omega(s_0^{\text{in}} - s_0)),$$

which is positive thanks to Hypothesis 2.4. Recall that  $J_1 = (0, s_1^{\text{in}})$ . We have  $\psi_1(0) = \mu_1(0, s_1^{\text{in}} + s_2^{\text{in}}) = 0$  and  $\psi_1(s_1^{\text{in}}) = \mu_1(s_1^{\text{in}}, s_2^{\text{in}})$ . Therefore, there exists a

solution  $s_1 \in J_1$  satisfying  $\psi_1(s_1) = y$  if and only if  $\mu_1(s_1^{\text{in}}, s_2^{\text{in}}) > y$ . Since  $\psi_1$  is monotonically increasing, if it exists, this solution is unique. Indeed, we have

$$\frac{d\psi_1}{ds_1}(s_1) = \frac{\partial\mu_1}{\partial s_1}(s_1, s_1^{\text{in}} + s_2^{\text{in}} - s_1) - \frac{\partial\mu_1}{\partial s_2}(s_1, s_1^{\text{in}} + s_2^{\text{in}} - s_1),$$

which is positive thanks to [Hypothesis 2.5](#). Let us consider now the existence of solution of equation  $\Psi(s_2, D) = s^{\text{in}}$ . From the definitions of  $s_2^0(D)$  and  $s_2^1(D)$  given in [Table 2](#), we have  $M_0(D + a_0, s_2^0(D)) = +\infty$  and  $M_1(D + a_1, s_2^1(D)) = +\infty$ . From the definition of  $\Psi(s_2, D)$  given in [Table 2](#), it follows that,

- for all  $\omega > 0$ , we have  $\lim_{s_2 \rightarrow s_2^1(D)} \Psi(s_2, D) = +\infty$ ,
- for all  $\omega > 1$ , we have  $\lim_{s_2 \rightarrow s_2^0(D)} \Psi(s_2, D) = -\infty$ ,
- for all  $\omega < 1$ , we have  $\lim_{s_2 \rightarrow s_2^0(D)} \Psi(s_2, D) = +\infty$ ,
- for all  $\omega = 1$ , we have  $\Psi(s_2^0(D), D) = \phi_1(D)$ .

Moreover, we have

$$(C.1) \quad \frac{\partial\Psi}{\partial s_2}(s_2, D) = (1 - \omega) \frac{\partial M_0}{\partial s_2}(D + a_0, s_2) + \frac{\partial M_1}{\partial s_2}(D + a_1, s_2) + 1.$$

Under [Hypotheses 2.4](#) and [2.5](#), for all  $y \in (0, \mu_0(+\infty, s_2))$  and  $s_2 > 0$ , we have  $\frac{\partial M_0}{\partial s_2}(y, s_2) < 0$  and for all  $y \in (0, \mu_1(+\infty, s_2))$  and  $s_2 > 0$ , we have  $\frac{\partial M_1}{\partial s_2}(y, s_2) > 0$  (see formulas in [\(A.6\)](#)). Therefore, for  $\omega \geq 1$ , the function  $s_2 \mapsto \Psi(s_2, D)$  is monotonically increasing. If  $\omega = 1$  then,  $\Psi(s_2^0(D), D) > 0$ . From [Hypothesis 4.1](#), if  $\omega < 1$ , the equation  $\Psi(s_2, D) = s^{\text{in}}$  has two solutions if and only if  $s^{\text{in}} \geq \phi_1(D)$ . This completes the proof.

**C.2. Existence of the steady states.** The steady state SS1 always exists.

The steady state SS2 exists if and only if  $x_2 > 0$ , that is to say  $s_2^{\text{in}} > M_2(D + a_2)$ , which is equivalent to  $\mu_2(s_2^{\text{in}}) > D + a_2$ , thanks to [Hypothesis 2.6](#).

The steady state SS3 exists if and only if equation [\(4.1\)](#) has a positive solution and the  $s_1$ ,  $s_2$  and  $x_0$ -components of SS3 defined in [Table 1](#) are positive. This condition is equivalent to say that  $0 < s_0 < s_0^{\text{in}}$  and  $s_0 > s_0^{\text{in}} - s_2^{\text{in}}/\omega$ . Therefore, [\(4.1\)](#) must have a solution in the interval  $J_0$ . Using [Lemma 4.2](#), [\(4.1\)](#) has a solution in the interval  $J_0$  if and only if  $\mu_0(s_0^{\text{in}}, s_2^{\text{in}}) > D + a_0$ . If it exists, this solution is unique.

The steady state SS4 exists if and only if equation [\(4.3\)](#) has a solution which is, according to [Lemma 4.2](#), equivalent to the condition  $(1 - \omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}} \geq \phi_1(D)$ , and the solution  $s_2^*$  of [\(4.3\)](#) is such that the  $x_0$  and  $x_1$ -components defined in [Table 1](#) are positive which is equivalent to  $s_0^{\text{in}} > M_0(D + a_0, s_2)$  and  $s_0^{\text{in}} + s_1^{\text{in}} > M_0(D + a_0, s_2) + M_1(D + a_1, s_2)$ .

The steady state SS5 exists if and only if its components  $x_0$ ,  $x_2$  and  $s_1$  defined in [Table 1](#) are positive. This condition is equivalent to  $s_0^{\text{in}} > s_0$  and  $s_2^{\text{in}} - \omega s_0^{\text{in}} > s_2 - \omega s_0$ . Using the  $s_0$  and  $s_2$ -components of SS5 in [Table 1](#), it follows that, the existence conditions of SS5 in [Table 4](#) must be satisfied.

The steady state SS6 exists if and only if its  $x$ -components defined in [Table 1](#) are positive which is equivalent to the conditions  $s_0^{\text{in}} > s_0$ ,  $s_1^{\text{in}} + s_0^{\text{in}} > s_0 + s_1$  and  $(1 - \omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}} > (1 - \omega)s_0 + s_1 + s_2$  are satisfied. Using the  $s$ -components of SS6 in [Table 1](#), these conditions are the same as the existence conditions of SS6 in [Table 4](#).

The steady state SS7 exists if and only if [\(4.2\)](#) has a positive solution and the  $s_2$  and  $x_1$ -components of SS7 defined in [Table 1](#) are positive. This last condition is

equivalent to  $0 < s_1 < s_1^{\text{in}}$ . Consequently, (4.2) must have a solution in the interval  $J_1$ . Using Lemma 4.2, there exists a solution  $s_1 \in J_1$ , satisfying (4.2), if and only if  $\mu_1(s_1^{\text{in}}, s_2^{\text{in}}) > D + a_1$ . If it exists, this solution is unique.

The steady state SS8 exists if and only if its components  $x_1$  and  $x_2$  are positive. This is equivalent to  $s_1^{\text{in}} > s_1$  and  $s_1^{\text{in}} + s_2^{\text{in}} > s_1 + s_2$ . Using the  $s$ -components of SS8 defined in Table 1, these conditions are the same as those for the existence of SS8 in Table 4.

**C.3. Stability of the steady states.** The local stability of the steady states is determined by the eigenvalues of the Jacobian matrix of system (2.1) evaluated at the steady state. The Jacobian matrix of (2.1) corresponds to the  $6 \times 6$  matrix:

$$\mathcal{J} = \begin{bmatrix} J-D-a_0 & 0 & 0 & Ex_0 & 0 & Fx_0 \\ 0 & K-D-a_1 & 0 & 0 & Gx_1 & -Hx_1 \\ 0 & 0 & L-D-a_2 & 0 & 0 & Ix_2 \\ -J & 0 & 0 & -D-Ex_0 & 0 & -Fx_0 \\ J & -K & 0 & Ex_0 & -D-Gx_1 & Fx_0+Hx_1 \\ -\omega J & K & -L & -\omega Ex_0 & Gx_1 & -D-\omega Fx_0-Hx_1-Ix_2 \end{bmatrix},$$

where the functions  $E, F, G, H, I, J, K$  and  $L$  are defined by (4.4) and (4.5), and are evaluated at the steady state. We have used the opposite sign of the partial derivative  $H = -\partial\mu_1/\partial s_2$ , such that all constants involved in the computation become positive. The stability of the steady state is investigated by analyzing the real parts of the eigenvalues of  $\mathcal{J}$ , which are the roots of the characteristic polynomial.

**C.3.1. Proof of Proposition 4.3.** For SS4, the characteristic polynomial is

$$P_4(\lambda) = (\lambda - \lambda_1)(\lambda + D) (\lambda^4 + c_1\lambda^3 + c_2\lambda^2 + c_3\lambda + c_4),$$

where  $\lambda_1 = \mu_2(s_2) - D - a_2$  with  $s_2$  is defined by (4.3) and the coefficients  $c_i$  for  $i = 1, \dots, 4$  are defined in Proposition 4.3. From Lemma F.1, all of the roots of the fourth order polynomial have negative real parts if and only if  $c_i > 0$ , for  $i = 1, 3, 4$  and  $r_1 = c_1c_2c_3 - c_1^2c_4 - c_3^2 > 0$ . From the expression of  $c_1$  given in Proposition 4.3, we always have  $c_1 > 0$ . Moreover,  $c_3 > 0$  and  $c_4 > 0$  if and only if

$$(C.2) \quad E(G + H) - (1 - \omega)FG > 0.$$

Using (4.4) and (A.6), we have

$$\frac{\partial M_0}{\partial s_2}(D + a_0, s_2) = -\frac{F}{E} \quad \text{and} \quad \frac{\partial M_1}{\partial s_2}(D + a_1, s_2) = \frac{H}{G}.$$

Using (C.1), it follows that

$$\frac{\partial \Psi}{\partial s_2}(s_2, D) = -\frac{F}{E}(1 - \omega) + \frac{H}{G} + 1 = \frac{E(G + H) - (1 - \omega)FG}{EG}.$$

Since  $E$  and  $G$  are positive, condition (C.2) is equivalent to  $\frac{\partial \Psi}{\partial s_2}(s_2, D) > 0$ .

From definition (4.7) of  $\phi_4$  and since  $\mu_2$  is increasing, it follows that, SS4 is stable if and only if

$$(C.3) \quad s_2 < M_2(D + a_2), \quad \frac{\partial \Psi}{\partial s_2}(s_2, D) > 0 \quad \text{and} \quad \phi_4(D, s_0^{\text{in}}, s_1^{\text{in}}, s_2^{\text{in}}) > 0.$$

When  $s_2^1 \leq M_2(D + a_2)$ , the  $s_2$ -component of SS4 satisfies  $s_2 < s_2^1 \leq M_2(D + a_2)$ . Thus, SS4 is stable if and only if the second and the third conditions of (C.3) hold. When  $M_2(D + a_2) < s_2^1$ , we will prove that (C.3) is equivalent to (4.6). To this end, assume first that  $\omega \geq 1$ . If  $s_2 < M_2(D + a_2)$ , then  $s_2^0 \leq s_2 < M_2(D + a_2) < s_2^1$ . From Lemma 4.2, the mapping  $s_2 \mapsto \Psi(s_2, D)$  is increasing for all  $s_2 \in (s_2^0, s_2^1)$ . Hence, the condition  $s_2 < M_2(D + a_2)$  is equivalent to

$$(C.4) \quad (1 - \omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}} = \Psi(s_2, D) < \Psi(M_2(D + a_2), D) = \phi_2(D).$$

In addition, we have  $\phi_3(D) > 0$  for all  $D \in I_2$ . Now, when  $\omega < 1$ , from Lemma 4.2 and using Hypothesis 4.1, equation (4.3) has at most two solutions  $s_2^{*1} < s_2^{*2}$ , such that  $\frac{\partial \Psi}{\partial s_2}(s_2^{*1}, D) < 0$  and  $\frac{\partial \Psi}{\partial s_2}(s_2^{*2}, D) > 0$  (see Figure G.1). Thus, the steady state SS4<sup>1</sup> corresponding to  $s_2^{*1}$  is unstable. For the steady state SS4<sup>2</sup> corresponding to  $s_2^{*2}$ , the condition  $s_2^{*2} < M_2(D + a_2)$  implies the first and the second condition of (4.6) since the mapping  $s_2 \mapsto \Psi(s_2, D)$  is increasing on  $(\bar{s}_2, s_2^1)$ . On the other hand, if the first condition of (4.6) or equivalently (C.4) holds, then

$$s_2^{*2} < M_2(D + a_2) \quad \text{or} \quad s_2^0 < M_2(D + a_2) < s_2^{*1}.$$

This last condition is in contradiction with the second condition of (4.6). This completes the proof of the proposition.

**C.3.2. Proof of Proposition 4.4.** For the positive steady state SS6, the characteristic polynomial is given by:

$$P_6(\lambda) = \lambda^6 + c_1\lambda^5 + c_2\lambda^4 + c_3\lambda^3 + c_4\lambda^2 + c_5\lambda + c_6,$$

where  $c_i$ ,  $i = 1, \dots, 6$  are defined in Table 3. From Lemma F.2, all of the roots of the sixth order polynomial have negative real parts if and only if  $c_i > 0$ ,  $i = 1, 3, 5, 6$  and  $r_j > 0$ ,  $j = 4, 5$ , where  $c_i$  and  $r_j$  are listed in Table 3. Since  $c_1$  and  $c_6$  are positive, the proof is complete.

**C.3.3. Stability of all other steady states.** For SS1, the characteristic polynomial is

$$P_1(\lambda) = (\lambda - \lambda_1)(\lambda - \lambda_2)(\lambda - \lambda_3)(\lambda + D)^3,$$

where  $\lambda_1 = \mu_0(s_0^{\text{in}}, s_2^{\text{in}}) - D - a_0$ ,  $\lambda_2 = \mu_1(s_1^{\text{in}}, s_2^{\text{in}}) - D - a_1$  and  $\lambda_3 = \mu_2(s_2^{\text{in}}) - D - a_2$ . Therefore, SS1 is stable if and only if  $\lambda_1 < 0$ ,  $\lambda_2 < 0$  and  $\lambda_3 < 0$ , that is, the stability conditions of SS1 in Table 4 hold.

For SS2, the characteristic polynomial is

$$P_2(\lambda) = (\lambda - \lambda_1)(\lambda - \lambda_2)(\lambda + D)^2(\lambda^2 + c_1\lambda + c_2),$$

where  $\lambda_1 = \mu_0(s_0^{\text{in}}, M_2(D + a_2)) - D - a_0$ ,  $\lambda_2 = \mu_1(s_1^{\text{in}}, M_2(D + a_2)) - D - a_1$ ,  $c_1 = D + Ix_2$  and  $c_2 = LIx_2$ . Since  $c_1 > 0$  and  $c_2 > 0$ , the real parts of the roots of the quadratic factor are negative. Therefore, SS2 is stable if and only if  $\lambda_1 < 0$  and  $\lambda_2 < 0$ . Since  $M_0$  and  $M_1$  are increasing (see formulas in (A.5)), these conditions are equivalent to the stability conditions of SS2 in Table 4.

For SS3, the characteristic polynomial is

$$P_3(\lambda) = (\lambda - \lambda_1)(\lambda - \lambda_2)(\lambda + D)^2(\lambda^2 + c_1\lambda + c_2),$$

where  $\lambda_1 = \mu_1(s_0^{\text{in}} - s_0 + s_1^{\text{in}}, s_2^{\text{in}} - \omega(s_0^{\text{in}} - s_0)) - D - a_1$ ,  $\lambda_2 = \mu_2(s_2^{\text{in}} - \omega(s_0^{\text{in}} - s_0)) - D - a_2$ ,  $c_1 = D + (E + \omega F)x_0$  and  $c_2 = J(E + \omega F)x_0$ , where  $s_0$  is the solution in

the interval  $J_0$  of equation  $\psi_0(s_0) = D + a_0$ . Since  $c_1 > 0$  and  $c_2 > 0$ , the real parts of the roots of the quadratic factor are negative. Therefore, SS3 is stable if and only if  $\lambda_1 < 0$  and  $\lambda_2 < 0$ . The condition  $\lambda_1 < 0$  is the first stability condition of SS3 in Table 4. Since  $M_2$  is increasing from (A.5), the condition  $\lambda_2 < 0$  is equivalent to

$$(C.5) \quad s_2^{\text{in}} - \omega(s_0^{\text{in}} - s_0) < M_2(D + a_2) \iff s_0 < (M_2(D + a_2) - s_2^{\text{in}}) / \omega + s_0^{\text{in}}.$$

As the function  $\psi_0$  is increasing, (C.5) is equivalent to

$$(C.6) \quad \psi_0(s_0) < \psi_0\left(\frac{M_2(D + a_2) - s_2^{\text{in}}}{\omega} + s_0^{\text{in}}\right).$$

From the definition of the function  $\psi_0$  together with the condition  $\psi_0(s_0) = D + a_0$  defining  $s_0$ , we deduce that (C.6) is equivalent to

$$D + a_0 < \mu_0\left(\frac{M_2(D + a_2) - s_2^{\text{in}}}{\omega} + s_0^{\text{in}}, M_2(D + a_2)\right).$$

Since  $M_0$  is increasing, this condition is equivalent to the second stability condition of SS3 in Table 4.

For SS5, the characteristic polynomial is

$$P_5(\lambda) = (\lambda - \lambda_1)(\lambda + D)(\lambda^4 + c_1\lambda^3 + c_2\lambda^2 + c_3\lambda + c_4),$$

where  $\lambda_1 = \mu_1(s_0^{\text{in}} + s_1^{\text{in}} - M_0(D + a_0, M_2(D + a_2)), M_2(D + a_2)) - D - a_1$  and the coefficients  $c_i$  are given by:

$$\begin{aligned} c_1 &= 2D + (E + \omega F)x_0 + Ix_2, \\ c_2 &= D^2 + (E + \omega F)(D + J)x_0 + I(D + L)x_2 + EIx_0x_2, \\ c_3 &= D(E + \omega F)Jx_0 + DILx_2 + EI(J + L)x_0x_2 \quad \text{and} \quad c_4 = EIJLx_0x_2. \end{aligned}$$

From Lemma F.1, the roots of the fourth order polynomial are of negative real parts if and only if

$$(C.7) \quad c_i > 0, \quad \text{for } i = 1, 3, 4 \quad \text{and} \quad r_1 = c_1c_2c_3 - c_1^2c_4 - c_3^2 > 0.$$

We always have  $c_i > 0$  for  $i = 1, 3, 4$ . We can write  $r_1$  as follows:

$$\begin{aligned} r_1 &= DJ[(D + J)(E + \omega F)^3 - E^3J]x_0^3 + D^2I^3Lx_2^3 + E^2I^2(E + \omega F)(J + L)x_0^3x_2^2 + DEI^3(J + 2L)x_0x_2^3 \\ &\quad + E^2I^3(J + L)x_0^2x_2^3 + EI[D(2J + L)(E + \omega F)^2 + \omega FJ^2(2E + \omega F)]x_0^3x_2 + 3D^3I^2Lx_2^2 \\ &\quad + D^2J[3D(E + \omega F)^2 + F\omega J(2E + \omega F)]x_0^2 + EI^2[D(J + L)(5E + 3\omega F) + F\omega(J^2 + L^2)]x_0^2x_2^2 \\ &\quad + DI[F\omega(DF\omega(2J + L) + F\omega J(J + 2L) + DE(9J + 5L) + 2EJ^2) + DE^2(7J + 4L)]x_0^2x_2 \\ &\quad + DI^2[DE(4J + 7L) + F\omega L(2J + L) + DF\omega(J + 2L)]x_0x_2^2 + 2D^4J(E + \omega F)x_0 + 2D^4ILx_2 \\ &\quad + D^2I[D(J + L)(5E + 3\omega F) + 2F\omega JL]x_0x_2 + (D^2 + DEx_0 + DIx_2 + EIx_0x_2)(EJx_0 - ILx_2)^2. \end{aligned}$$

Thus,  $r_1 > 0$ . Consequently, the conditions (C.7) are satisfied. Therefore, SS5 is stable if and only if  $\lambda_1 < 0$ . Since  $M_1$  is increasing, this condition is equivalent to the stability condition of SS5 in Table 4.

For SS7, the characteristic polynomial is

$$P_7(\lambda) = (\lambda - \lambda_1)(\lambda - \lambda_2)(\lambda + D)^2(\lambda^2 + c_1\lambda + c_2),$$

where  $\lambda_1 = \mu_0(s_0^{\text{in}}, s_1^{\text{in}} - s_1 + s_2^{\text{in}}) - D - a_0$ ,  $\lambda_2 = \mu_2(s_1^{\text{in}} - s_1 + s_2^{\text{in}}) - D - a_2$ ,  $c_1 = D + (G + H)x_1$  and  $c_2 = K(G + H)x_1$  where  $s_1$  is the solution in the interval  $J_1$  of

equation  $\psi_1(s_1) = D + a_1$ . Since  $c_1 > 0$  and  $c_2 > 0$ , the real parts of the roots of the quadratic factor are negative. Therefore, SS7 is stable if and only if  $\lambda_1 < 0$  and  $\lambda_2 < 0$ . Since the functions  $M_2$  and  $M_3$  are increasing from (A.5), the conditions  $\lambda_1 < 0$  and  $\lambda_2 < 0$  are equivalent to

$$(C.8) \quad s_1 > s_1^{\text{in}} + s_2^{\text{in}} - M_3(s_0^{\text{in}}, D + a_0) \quad \text{and} \quad s_1 > s_1^{\text{in}} + s_2^{\text{in}} - M_2(D + a_2).$$

Since the function  $\psi_1$  is increasing, (C.8) is equivalent to

$$\psi_1(s_1) > \psi_1(s_1^{\text{in}} + s_2^{\text{in}} - M_3(s_0^{\text{in}}, D + a_0)), \quad \psi_1(s_1) > \psi_1(s_1^{\text{in}} + s_2^{\text{in}} - M_2(D + a_2)).$$

From the definition of the function  $\psi_1$  together with the condition  $\psi_1(s_1) = D + a_1$  which defines  $s_1$ , the preceding conditions are equivalent to

$$\begin{aligned} \mu_1(s_1^{\text{in}} + s_2^{\text{in}} - M_3(s_0^{\text{in}}, D + a_0), M_3(s_0^{\text{in}}, D + a_0)) &< D + a_1, \\ \mu_1(s_1^{\text{in}} + s_2^{\text{in}} - M_2(D + a_2), M_2(D + a_2)) &< D + a_1. \end{aligned}$$

Since  $M_1$  is increasing, these conditions are equivalent to the stability conditions of SS7 in Table 4.

For SS8, the characteristic polynomial is

$$P_8(\lambda) = (\lambda - \lambda_1)(\lambda + D)(\lambda^4 + c_1\lambda^3 + c_2\lambda^2 + c_3\lambda + c_4),$$

where  $\lambda_1 = \mu_0(s_0^{\text{in}}, M_2(D + a_2)) - D - a_0$  and the coefficients  $c_i$  are given by:

$$\begin{aligned} c_1 &= 2D + (G + H)x_1 + Ix_2, \\ c_2 &= D^2 + (G + H)(D + K)x_1 + I(D + L)x_2 + GIx_1x_2, \\ c_3 &= D(G + H)Kx_1 + DILx_2 + GI(K + L)x_1x_2 \quad \text{and} \quad c_4 = GIKLx_1x_2. \end{aligned}$$

From Lemma F.1, the roots of the fourth order polynomial are of negative real parts if and only if

$$(C.9) \quad c_i > 0, \quad \text{for} \quad i = 1, 3, 4 \quad \text{and} \quad r_1 = c_1c_2c_3 - c_1^2c_4 - c_3^2 > 0.$$

We always have  $c_i > 0$ , for  $i = 1, 3, 4$ . We can write  $r_1$  as follows:

$$\begin{aligned} r_1 = &DK [(D + K)(G + H)^3 - G^3K] x_1^3 + D^2I^3Lx_2^3 + G^2I^2(G + H)(K + L)x_1^3x_2^2 + G^2I^3(K + L)x_1^2x_2^3 \\ &+ GI [D(2K + L)(G + H)^2 + HK^2(2G + H)] x_1^3x_2 + DGI^3(K + 2L)x_1x_2^3 + 3D^3I^2Lx_2^2 \\ &+ D^2K [3D(G + H)^2 + HK(2G + H)] x_1^2 + GI^2 [D(K + L)(5G + 3H) + H(K^2 + L^2)] x_1^2x_2^2 \\ &+ DI [H(DH(2K + L) + HK(K + 2L) + DG(9K + 5L) + 2GK^2) + DG^2(7K + 4L)] x_1^2x_2 \\ &+ DI^2 [DG(4K + 7L) + HL(2K + L) + DH(K + 2L)] x_1x_2^2 + 2D^4K(G + H)x_1 + 2D^4ILx_2 \\ &+ D^2I [D(K + L)(5G + 3H) + 2HKL] x_1x_2 + (D^2 + DGx_1 + DIx_2 + GIx_1x_2)(GKx_1 - ILx_2)^2. \end{aligned}$$

Thus,  $r_1 > 0$ . Consequently, the conditions (C.9) are satisfied. Finally, SS8 is stable if and only if  $\lambda_1 < 0$ , that is to say  $\mu_0(s_0^{\text{in}}, M_2(D + a_2)) < D + a_0$ . Since  $M_0$  is increasing, this condition is equivalent to the stability condition of SS8 in Table 4.

**Appendix D. Proof of Proposition 4.7.** If  $s_1^{\text{in}} = 0$  then,  $\mu_1(s_1^{\text{in}}, s_2^{\text{in}}) = 0$ , so that the conditions  $\mu_1(s_1^{\text{in}}, s_2^{\text{in}}) > D + a_1$  and  $s_1^{\text{in}} > \varphi_1(D)$  of existence of SS7 and SS8, respectively, cannot be satisfied. Therefore, SS7 and SS8 do not exist. If  $s_2^{\text{in}} = 0$  then,  $\mu_2(s_2^{\text{in}}) = 0$  and  $\mu_0(s_0^{\text{in}}, s_2^{\text{in}}) = 0$ , so that the existence conditions  $\mu_2(s_2^{\text{in}}) > D + a_2$ ,



$\mu_0(s_0^{\text{in}}, s_2^{\text{in}}) > D + a_0$  of SS2 and SS3 cannot be satisfied, respectively. Moreover, the second existence condition of SS5 implies that

$$s_0^{\text{in}} < \varphi_0(D) - \frac{M_2(D + a_2)}{\omega} < \varphi_0(D),$$

which is in contradiction with the first existence condition of SS5. Therefore, SS2, SS3 and SS5 do not exist.

Assume that  $s_1^{\text{in}} = s_2^{\text{in}} = 0$ . If  $\omega = 1$ , the first existence condition of SS4 in Table 4 is written  $0 \geq \phi_1(D)$ . This condition cannot be satisfied, since  $\phi_1(D) = \Psi(s_2^0(D), D) > 0$  from Lemma 4.2. Thus, the steady state SS4 does not exist if  $\omega = 1$ .

When  $\omega > 1$ ,  $s_2$  is solution of equation

$$(1 - \omega)s_0^{\text{in}} = (1 - \omega)s_0 + s_1 + s_2.$$

Hence,

$$(1 - \omega)(s_0^{\text{in}} - s_0) = s_1 + s_2.$$

Since  $s_1 > 0$  and  $s_2 > 0$ , then, we have necessarily

$$(1 - \omega)(s_0^{\text{in}} - s_0) > 0,$$

so that  $s_0^{\text{in}} - s_0 < 0$ . From the  $x_0$ -component of SS4 in Table 1, we deduce that  $x_0 < 0$ . Thus, SS4 does not exist if  $\omega > 1$ .

When  $s_1^{\text{in}} = s_2^{\text{in}} = 0$ , the  $s_2$ -component of SS4 becomes the solution of equation

$$(1 - \omega)s_0^{\text{in}} = \Psi(s_2, D).$$

From the definition of  $\Psi$  in Table 2, it follows that,

$$s_0^{\text{in}} = M_0(D + a_0, s_2) + \frac{M_1(D + a_1, s_2) + s_2}{(1 - \omega)}.$$

If  $0 < \omega < 1$ , then

$$s_0^{\text{in}} > M_0(D + a_0, s_2) + M_1(D + a_1, s_2) > M_0(D + a_0, s_2),$$

thus, the second and the third existence conditions of SS4 in Table 4 are satisfied when  $\omega < 1$ . Therefore, SS4 exists if and only if the first existence condition of SS4 in Table 4 is satisfied. This condition becomes in the particular case  $s_1^{\text{in}} = s_2^{\text{in}} = 0$ ,  $(1 - \omega)s_0^{\text{in}} \geq \phi_1(D)$ .

Regarding the steady state SS6 in the particular case  $s_1^{\text{in}} = s_2^{\text{in}} = 0$ , the first existence condition in Table 4 becomes

$$(D.1) \quad (1 - \omega)s_0^{\text{in}} > \phi_2(D),$$

which is equivalent to

$$(1 - \omega)(s_0^{\text{in}} - \varphi_0(D)) > \varphi_1(D) + M_2(D + a_2).$$

When  $\omega \geq 1$ , this last inequality cannot hold, since  $s_0^{\text{in}} > \varphi_0(D)$ , so that the steady state SS6 does not exist.

If  $\omega < 1$ , condition (D.1) implies that

$$(1 - \omega)s_0^{\text{in}} > (1 - \omega)\varphi_0(D) + (1 - \omega)\varphi_1(D),$$

that is,

$$s_0^{\text{in}} > \varphi_0(D) + \varphi_1(D) > \varphi_0(D),$$

which are the second and the third existence conditions of SS6 in Table 4. Thus, the existence condition of SS6 is only condition (D.1).

**Appendix E. Proof of Proposition 4.9.** If SS2 exists then, its condition of existence  $\mu_2(s_2^{\text{in}}) > D + a_2$  holds. Therefore, the condition  $\mu_2(s_2^{\text{in}}) < D + a_2$  of stability of SS1 is not satisfied.

If SS3 exists then, its condition of existence  $\mu_0(s_0^{\text{in}}, s_2^{\text{in}}) > D + a_0$  holds. Therefore, the condition  $\mu_0(s_0^{\text{in}}, s_2^{\text{in}}) < D + a_0$  of stability of SS1 is not satisfied.

If SS7 exists then, its condition of existence  $\mu_1(s_1^{\text{in}}, s_2^{\text{in}}) > D + a_1$  holds. Therefore, the condition  $\mu_1(s_1^{\text{in}}, s_2^{\text{in}}) < D + a_1$  of stability of SS1 is not satisfied.

If SS6 exists then, the conditions

$$(1 - \omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}} > \phi_2(D), \quad s_0^{\text{in}} > \varphi_0(D), \quad s_0^{\text{in}} + s_1^{\text{in}} > \varphi_0(D) + \varphi_1(D)$$

hold. Therefore, the condition  $s_0^{\text{in}} < \varphi_0(D)$  of stability of SS2 or SS8 is not satisfied, the condition  $(1 - \omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}} < \phi_2(D)$  of stability of SS4 is not satisfied, and the condition  $s_0^{\text{in}} + s_1^{\text{in}} < \varphi_0(D) + \varphi_1(D)$  of stability of SS5 is not satisfied.

If SS5 exists then, its conditions of existence

$$s_0^{\text{in}} > \varphi_0(D) \quad \text{and} \quad s_2^{\text{in}} - \omega s_0^{\text{in}} > M_2(D + a_2) - \omega \varphi_0(D)$$

hold. Therefore, the condition  $s_0^{\text{in}} < \varphi_0(D)$  of stability of SS2 or SS8 is not satisfied and the condition  $s_2^{\text{in}} - \omega s_0^{\text{in}} < M_2(D + a_2) - \omega \varphi_0(D)$  of stability of SS3 is not satisfied.

If SS8 exists then, its conditions of existence  $s_1^{\text{in}} + s_2^{\text{in}} > \varphi_1(D) + M_2(D + a_2)$  holds. Therefore, the condition  $s_1^{\text{in}} + s_2^{\text{in}} < \varphi_1(D) + M_2(D + a_2)$  of stability of SS7 is not satisfied.

### Appendix F. Liénard-Chipart stability criteria.

*Lemma F.1.* Consider the fourth order polynomial  $\tilde{P}_4(\lambda)$  with real coefficients given by:

$$\tilde{P}_4(\lambda) = c_0\lambda^4 + c_1\lambda^3 + c_2\lambda^2 + c_3\lambda + c_4.$$

All of the roots of the polynomial  $\tilde{P}_4(\lambda)$  have negative real part if and only if

$$(F.1) \quad c_i > 0, \quad \text{for } i = 1, 3, 4, \quad \text{and} \quad r_1 = c_3r_0 - c_1^2c_4 > 0,$$

where  $r_0 = c_1c_2 - c_0c_3$ .

*Proof.* From the Liénard-Chipart stability criteria (see Gantmacher [8], Theorem 11), all of the roots of the polynomial  $\tilde{P}_4$  have negative real part if and only if

$$(F.2) \quad c_i > 0, \quad i = 1, 3, 4, \quad \det(\Delta_2) > 0 \quad \text{and} \quad \det(\Delta_4) > 0,$$

where  $\Delta_2$  and  $\Delta_4$  are the Hurwitz matrices defined by:

$$\Delta_2 = \begin{bmatrix} c_1 & c_3 \\ c_0 & c_2 \end{bmatrix} \quad \text{and} \quad \Delta_4 = \begin{bmatrix} c_1 & c_3 & 0 & 0 \\ c_0 & c_2 & c_4 & 0 \\ 0 & c_1 & c_3 & 0 \\ 0 & c_0 & c_2 & c_4 \end{bmatrix}.$$

Conditions (F.2) are equivalent to

$$(F.3) \quad c_i > 0, \quad i = 1, 3, 4, \quad r_0 = c_1c_2 - c_0c_3 > 0 \quad \text{and} \quad r_1 = c_3r_0 - c_1^2c_4 > 0.$$

When all conditions (F.3) hold, the condition  $r_1 > 0$  implies that  $r_0 > 0$ . Thus, conditions (F.3) are equivalent to (F.1).  $\square$

*Lemma F.2.* Consider the six order polynomial  $\tilde{P}_6(\lambda)$  with real coefficients given by:

$$\tilde{P}_6(\lambda) = c_0\lambda^6 + c_1\lambda^5 + c_2\lambda^4 + c_3\lambda^3 + c_4\lambda^2 + c_5\lambda + c_6.$$

All of the roots of the polynomial  $\tilde{P}_6(\lambda)$  have negative real part if and only if

$$(F.4) \quad c_i > 0, \quad i = 1, 3, 5, 6, \quad r_4 > 0 \quad \text{and} \quad r_5 > 0,$$

where  $r_4 = r_1r_2 - r_0r_3$  and  $r_5 = r_3r_4 - c_1c_6r_2^2$ , with

$$r_0 = c_1c_2 - c_0c_3, \quad r_1 = c_1c_4 - c_0c_5, \quad r_2 = c_3r_0 - c_1r_1 \quad \text{and} \quad r_3 = c_5r_0 - c_1^2c_6.$$

*Proof.* From the Liénard-Chipart stability criteria (see Gantmacher [8], Theorem 11), all of the roots of the polynomial  $\tilde{P}_6$  have negative real part if and only if

$$(F.5) \quad c_i > 0, \quad i = 1, 3, 5, 6, \quad \det(\Delta_2) > 0, \quad \det(\Delta_4) > 0 \quad \text{and} \quad \det(\Delta_6) > 0,$$

where  $\Delta_2$ ,  $\Delta_4$  and  $\Delta_6$  are the Hurwitz matrices defined by:

$$\Delta_2 = \begin{bmatrix} c_1 & c_3 \\ c_0 & c_2 \end{bmatrix}, \quad \Delta_4 = \begin{bmatrix} c_1 & c_3 & c_5 & 0 \\ c_0 & c_2 & c_4 & c_6 \\ 0 & c_1 & c_3 & c_5 \\ 0 & c_0 & c_2 & c_4 \end{bmatrix}, \quad \Delta_6 = \begin{bmatrix} c_1 & c_3 & c_5 & 0 & 0 & 0 \\ c_0 & c_2 & c_4 & c_6 & 0 & 0 \\ 0 & c_1 & c_3 & c_5 & 0 & 0 \\ 0 & c_0 & c_2 & c_4 & c_6 & 0 \\ 0 & 0 & c_1 & c_3 & c_5 & 0 \\ 0 & 0 & c_0 & c_2 & c_4 & c_6 \end{bmatrix}.$$

Conditions (F.5) are equivalent to

$$(F.6) \quad c_i > 0, \quad i = 1, 3, 5, 6, \quad r_0 > 0, \quad r_4 = r_1r_2 - r_0r_3 > 0, \quad r_5 = r_3r_4 - c_1c_6r_2^2 > 0.$$

When all conditions (F.6) hold, the condition  $r_5 > 0$  implies that  $r_3 > 0$ , that is,  $c_5r_0 > c_6c_1^2$  which implies that  $r_0 > 0$ . Hence, conditions (F.6) are equivalent to (F.4).  $\square$

**Appendix G. A chlorophenol-mineralising three-tiered microbial ‘food web’.** Following [14], model (5.2) considered in [19] can be rescaled to obtain model (2.1) using the following change of variables:

$$(G.1) \quad \begin{aligned} x_0 &= \frac{Y_3Y_4}{Y_0}X_{\text{ch}}, & x_1 &= \frac{Y_4}{Y_1}X_{\text{ph}}, & x_2 &= \frac{1}{Y_2}X_{\text{H}_2}, \\ s_0 &= Y_3Y_4S_{\text{ch}}, & s_1 &= Y_4S_{\text{ph}}, & s_2 &= S_{\text{H}_2}. \end{aligned}$$

The inflowing concentrations are given by:

$$(G.2) \quad s_0^{\text{in}} = Y_3Y_4S_{\text{ch,in}}, \quad s_1^{\text{in}} = Y_4S_{\text{ph,in}}, \quad s_2^{\text{in}} = S_{\text{H}_2,\text{in}},$$

the death rates are  $a_0 = k_{\text{dec,ch}}$ ,  $a_1 = k_{\text{dec,ph}}$ ,  $a_2 = k_{\text{dec,H}_2}$ , and the yield coefficients are

$$Y_0 = Y_{\text{ch}}, \quad Y_1 = Y_{\text{ph}}, \quad Y_2 = Y_{\text{H}_2}, \quad Y_3 = 224/208(1 - Y_0), \quad Y_4 = 32/224(1 - Y_1)$$

with  $\omega = \frac{16}{208Y_3Y_4} = \frac{1}{2(1-Y_{\text{ch}})(1-Y_{\text{ph}})}$ . When the yield coefficients are those given in Table 10, we have  $\omega \simeq 0.53$ . The growth functions take the form:

$$(G.3) \quad \begin{aligned} \mu_0(s_0, s_2) &= \frac{m_0 s_0}{K_0 + s_0} \frac{s_2}{L_0 + s_2}, \\ \mu_1(s_1, s_2) &= \frac{m_1 s_1}{K_1 + s_1} \frac{1}{1 + s_2/K_I}, \quad \mu_2(s_2) = \frac{m_2 s_2}{K_2 + s_2}, \end{aligned}$$

where

$$\begin{aligned} m_0 &= Y_0 k_{m,\text{ch}}, & K_0 &= Y_3 Y_4 K_{S,\text{ch}}, & L_0 &= K_{S,\text{H}_2,\text{c}}, & m_1 &= Y_1 k_{m,\text{ph}}, \\ K_1 &= Y_4 K_{S,\text{ph}}, & K_I &= K_{I,\text{H}_2}, & m_2 &= Y_2 k_{m,\text{H}_2}, & K_2 &= K_{S,\text{H}_2}. \end{aligned}$$

The growth functions (G.3) satisfy Hypotheses 2.1 to 2.7 and 4.1. For these growth functions, the various functions defined in Table 2 are listed in Table 13.

From the expression of  $\Psi$  given in Table 13, straightforward calculations shows that, for all  $s_2 \in (s_2^0(D), s_2^1(D))$ ,

$$\frac{\partial^2 \psi}{\partial s_2^2}(s_2, D) = \frac{(1-\omega)2K_0(D+a_0)}{m_0 - D - a_0} \frac{L_0 + s_2^0(D)}{(s_2 - s_2^0(D))^3} + \frac{2K_1(K_I + s_2^1(D))}{(s_2^1(D) - s_2)^3},$$

which is positive since  $\omega < 1$  and  $m_0 > D + a_0$ . Thus, the function  $s_2 \mapsto \Psi(s_2, D)$  is convex and fulfills Hypothesis 4.1. Hence, model (5.2) has two steady states  $\text{SS4}^1$  and  $\text{SS4}^2$  of the form  $\text{SS4}$  (see Figure G.1).

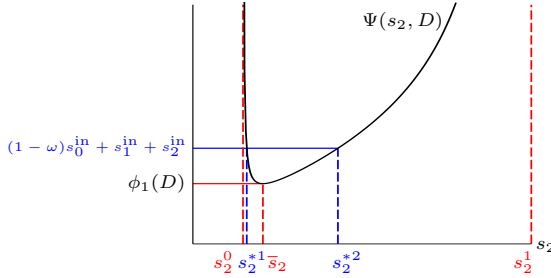


FIG. G.1. The curve of the function  $\Psi(\cdot, D)$ , where  $s_2^{*1}$  and  $s_2^{*2}$  are the solutions of the equation  $\Psi(s_2, D) = (1-\omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}}$ .

**Appendix H. Proof of Proposition 5.1.** We assume that the biological parameter values in model (5.2) are provided in Table 10. We assume that  $S_{\text{ph},\text{in}} = 0$ ,  $S_{\text{H}_2,\text{in}} = 2.67 \times 10^{-5}$  as in Fig. 3(a) from [19]. We assume that  $D = 0.01$ . As said in section 5 and Appendix G, Theorem 4.5 applies to model (5.2). Using the change of variables (G.2), the necessary and sufficient existence and stability conditions of steady states of (5.2), as stated in Table 4, are summarized in Table 14. Since  $s_1^{\text{in}} = 0$ ,  $\text{SS7}$  and  $\text{SS8}$  do not exist, as shown in Proposition 4.7. Using Table 14, we see that:

- $\text{SS1}$  always exists and is unstable, since the second stability condition in Table 14 does not hold, as

$$(H.1) \quad \mu_2(S_{\text{H}_2,\text{in}}) \simeq 1.0845 > D + a_2 = 0.03.$$

- $\text{SS2}$  exists, since the existence condition in Table 14 holds from (H.1). It is stable if and only if

$$S_{\text{ch},\text{in}} < \frac{\varphi_0(D)}{Y_3 Y_4} =: \sigma_2.$$

- SS3 exists if and only if  $\mu_0(S_{\text{ch,in}}Y_3Y_4, S_{\text{H}_2,\text{in}}) > D + a_0$ , which is equivalent to

$$S_{\text{ch,in}} > \frac{M_0(D + a_0, S_{\text{H}_2,\text{in}})}{Y_3Y_4} =: \sigma_1.$$

For  $S_{\text{ch,in}} = \sigma_1$ , there is a transcritical bifurcation of SS3 and SS1. Consider the function  $y = F(S_{\text{ch,in}})$  defined by:

$$(H.2) \quad F(S_{\text{ch,in}}) = \mu_1(S_{\text{ch,in}}Y_3Y_4 - s_0, S_{\text{H}_2,\text{in}} + \omega(S_{\text{ch,in}}Y_3Y_4 - s_0)),$$

where  $s_0$  depends also on  $S_{\text{ch,in}}$ . Recall that  $s_0$  is the unique solution of equation  $\psi_0(s_0) = D + a_0$  and  $\psi_0$  is defined in Table 13. The first stability condition of SS3 in Table 14 is written  $F(S_{\text{ch,in}}) < D + a_1$ . Figure H.1 shows that this condition holds for all  $S_{\text{ch,in}} > \sigma_1$ , since the maximum of the function  $F$  is smaller than 0.0013 and  $D + a_1 = 0.03$ . From the second stability condition in Table 14, SS3 is stable if and only if

$$S_{\text{ch,in}} > \frac{S_{\text{H}_2,\text{in}} - M_2(D + a_2) + \omega\varphi_0(D)}{\omega Y_3Y_4} =: \sigma_3.$$

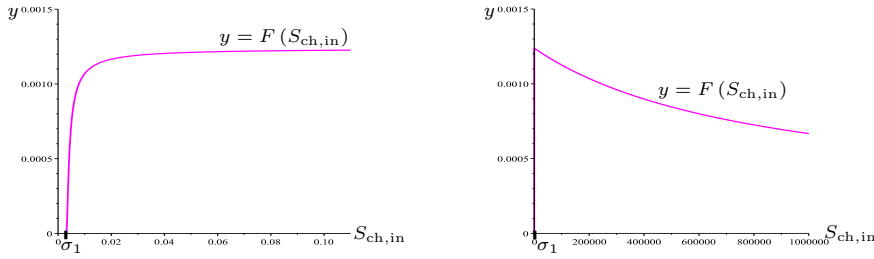


FIG. H.1. The curve of the function  $y = F(S_{\text{ch,in}})$  where function  $F$  is defined by (H.2), showing that  $F(S_{\text{ch,in}}) < 0.0013$ , for all  $S_{\text{ch,in}} > \sigma_1$ .

- Recall that  $\omega \simeq 0.53 < 1$  for the set of parameters given in Table 10. Therefore, equation

$$\Psi(s_2, D) = (1 - \omega)Y_3Y_4S_{\text{ch,in}} + S_{\text{H}_2,\text{in}}$$

admits two solutions  $s_2^{*1}$  and  $s_2^{*2}$  which correspond to two steady states  $\text{SS4}^1$  and  $\text{SS4}^2$ , respectively. When it exists,  $\text{SS4}^1$  is unstable, as stated in Remark 4.6. From Table 14, the first existence condition of these steady states holds if and only if

$$S_{\text{ch,in}} \geq \frac{\phi_1(D) - S_{\text{H}_2,\text{in}}}{(1 - \omega)Y_3Y_4} =: \sigma_4.$$

Figure H.2 shows that the second existence condition of  $\text{SS4}^1$  and  $\text{SS4}^2$  in Table 14 holds, for all  $S_{\text{ch,in}} \in [\sigma_4, 0.11]$ , since the straight line of equation  $y = S_{\text{ch,in}}Y_3Y_4$  is above the curves of the functions  $y = M_0(D + a_0, s_2^{*i}) + M_1(D + a_1, s_2^{*i})$ , for  $i = 1, 2$ , respectively.  $\text{SS4}^2$  is unstable, since the third stability condition does not hold as  $\phi_3(D) \simeq -1996.917 < 0$ . Therefore,  $\text{SS4}^1$  and  $\text{SS4}^2$  exist and are unstable for all  $S_{\text{ch,in}} \geq \sigma_4$ . They disappear for  $S_{\text{ch,in}} < \sigma_4$ . For  $S_{\text{ch,in}} = \sigma_4$  there is a saddle-node bifurcation. For  $S_{\text{ch,in}} = \sigma_5$  there is a transcritical bifurcation of  $\text{SS4}^1$  and SS6.

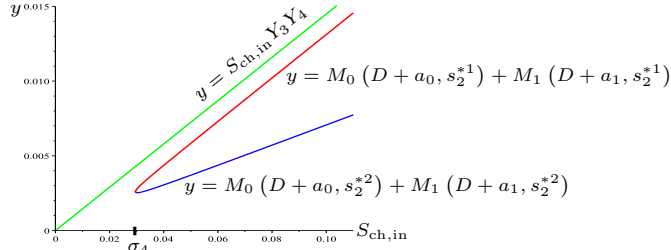


FIG. H.2. The green line of equation  $y = Y_3 Y_4 S_{\text{ch,in}}$  is above the red and blue curves of the functions  $M_0(D + a_0, s_2^{*i}) + M_1(D + a_1, s_2^{*i})$ , for  $i = 1, 2$ , which correspond to the steady states  $\text{SS4}^1$  and  $\text{SS4}^2$ , respectively.

- From Table 14,  $\text{SS5}$  exists if and only if

$$\sigma_2 := \frac{\varphi_0(D)}{Y_3 Y_4} < S_{\text{ch,in}} < \frac{S_{\text{H}_2,\text{in}} - M_2(D + a_2) + \omega \varphi_0(D)}{\omega Y_3 Y_4} =: \sigma_3.$$

For  $S_{\text{ch,in}} = \sigma_2$  there is a transcritical bifurcation of  $\text{SS5}$  and  $\text{SS2}$ . For  $S_{\text{ch,in}} = \sigma_3$  there is a transcritical bifurcation of  $\text{SS5}$  and  $\text{SS3}$ . When it exists,  $\text{SS5}$  is stable since

$$S_{\text{ch,in}} < \sigma_3 \simeq 0.013985 < \frac{\varphi_0(D) + \varphi_1(D)}{Y_3 Y_4} \simeq 0.02304.$$

- From Table 14,  $\text{SS6}$  exists if and only if

$$S_{\text{ch,in}} > \frac{\phi_2(D) - S_{\text{H}_2,\text{in}}}{(1 - \omega) Y_3 Y_4} =: \sigma_5 \simeq 0.033292, S_{\text{ch,in}} > \frac{\varphi_0(D) + \varphi_1(D)}{Y_3 Y_4} \simeq 0.02304.$$

Then,  $\text{SS6}$  exists if and only if  $S_{\text{ch,in}} > \sigma_5$ . For the stability of  $\text{SS6}$ , we plot the functions  $c_3$ ,  $c_5$ ,  $r_4$  and  $r_5$  with respect to  $S_{\text{ch,in}} > \sigma_5$ . Figure H.3 shows that  $c_3(S_{\text{ch,in}})$ ,  $c_5(S_{\text{ch,in}})$ ,  $r_4(S_{\text{ch,in}})$  and  $r_5(S_{\text{ch,in}})$  are all positive if and only if  $S_{\text{ch,in}} > \sigma_6$  where  $\sigma_6 \simeq 0.1025$  is the largest root of equation  $r_5(S_{\text{ch,in}}) = 0$ . We give now numerical evidence for a Hopf bifurcation for  $S_{\text{ch,in}} = \sigma_6$ . To show that the positive steady state  $\text{SS6}$  is destabilized due to Hopf bifurcation, we determine numerically the eigenvalues of the Jacobian matrix of system (5.2) at this steady state and we plot them with respect to  $S_{\text{ch,in}}$ , see Figure H.4. The Jacobian matrix evaluated at  $\text{SS6}$  has two negative eigenvalues and two pairs of complex conjugate eigenvalues. Figure H.4 shows that eigenvalues 5 and 6 both cross the imaginary axis at the critical value  $S_{\text{ch,in}} = \sigma_6$ , from positive half-plane to negative half-plane, and the real parts of all eigenvalues 1, 2, 3 and 4 remain negative. Therefore, the steady state  $\text{SS6}$  changes its stability through a supercritical Hopf bifurcation with the appearance of a stable limit cycle that we illustrate in the following section.

The plots of Figures G.1 and H.1 to H.4 were performed with Maple [10], which is used in particular for the computations of coefficients  $c_3$ ,  $c_5$ ,  $r_4$  and  $r_5$ , evaluated at  $\text{SS6}$ , and the computations of the eigenvalues of the Jacobian matrix evaluated at  $\text{SS6}$ . The plots of Figures 5.1 to 5.3 were performed with Scilab [16] by using the formulas of the steady state components given in Table 1. The various functions appearing in these formulas are given in Table 13.

**Appendix I. Numerical simulations.** In this section, we present in Figures I.1 to I.7 several numerical simulations which illustrate our findings. The plots

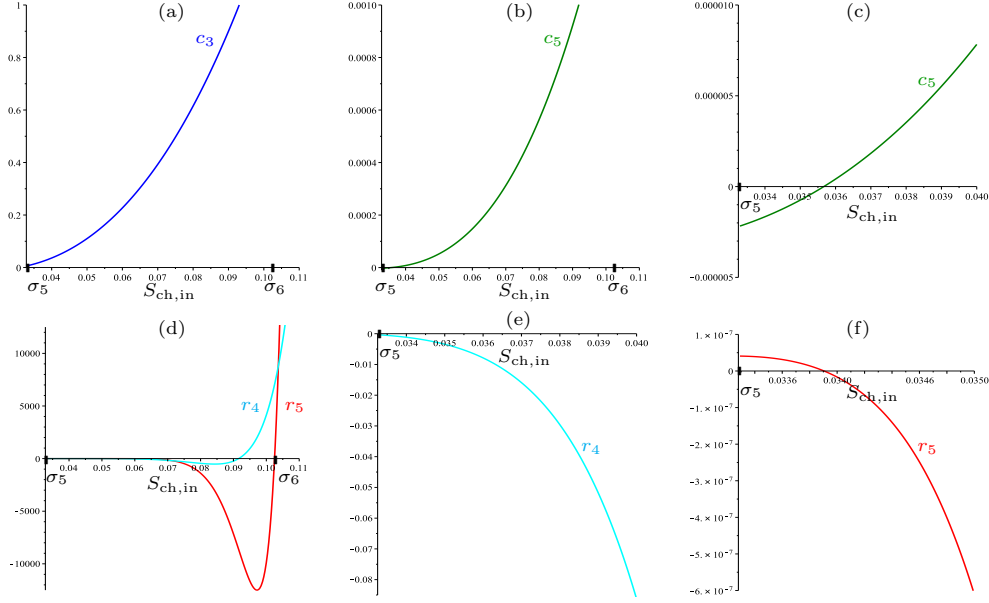


FIG. H.3. The curves of the functions  $c_3(S_{ch,in})$ ,  $c_5(S_{ch,in})$ ,  $r_4(S_{ch,in})$  and  $r_5(S_{ch,in})$  for  $S_{ch,in} > \sigma_5$  show that all these functions are positive if and only if  $S_{ch,in} > \sigma_6$ , the largest root of equation  $r_5 = 0$ . (a) The curve of  $c_3$ . (b) The curve of  $c_5$ . (c) A magnification of the curve of  $c_5$ . (d) the curves of  $r_4$  and  $r_5$ . (e) A magnification of the curve of  $r_4$ . (f) A magnification of the curve of  $r_5$ .

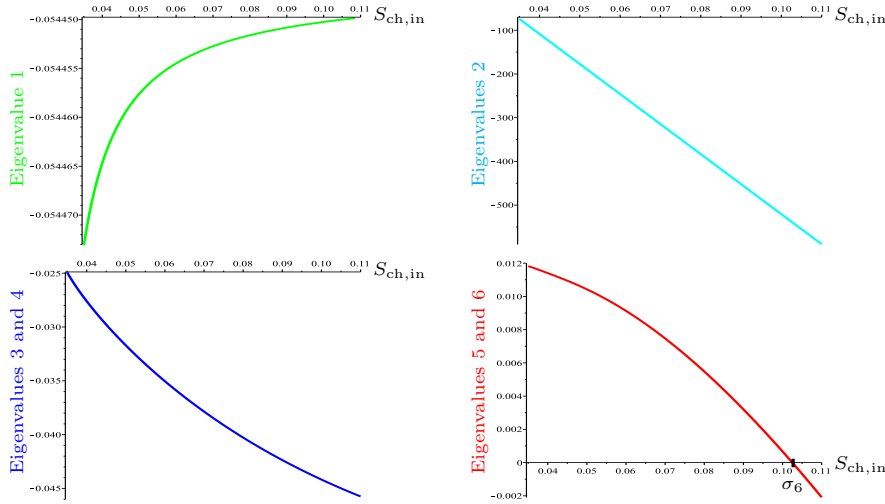


FIG. H.4. Real parts of the eigenvalues as a function of  $S_{ch,in} \in [0.035, 0.11]$ , when  $D = 0.01$ ,  $S_{ph,in} = 0$  and  $S_{H_2,in} = 2.67 \times 10^{-5}$ . On this picture, green and cyan colors for two negative eigenvalues, blue and red colors for two pairs of complex conjugate eigenvalues.

of Figures I.1 to I.7 were performed with Scilab [16]. The numerical simulations presented in Figure H.4 in previous section and Figures I.1 to I.7 were performed on the dimensionless form of (5.2) used in [19]. Indeed, in the original form (5.2), numerical instabilities arise in numerical schemes. To reduce the number of parameters describing the dynamics and facilitate numerical simulations, the following rescaling of the

variables was used in [19]:

$$(I.1) \quad \begin{aligned} X_0 &= \frac{X_{\text{ch}}}{K_{\text{S,ch}}Y_{\text{ch}}}, & X_1 &= \frac{X_{\text{ph}}}{K_{\text{S,ph}}Y_{\text{ph}}}, & X_2 &= \frac{X_{\text{H}_2}}{K_{\text{S,H}_2}Y_{\text{H}_2}}, \\ S_0 &= \frac{S_{\text{ch}}}{K_{\text{S,ch}}}, & S_1 &= \frac{S_{\text{ph}}}{K_{\text{S,ph}}}, & S_2 &= \frac{S_{\text{H}_2}}{K_{\text{S,H}_2}}, & \tau &= k_{\text{m,ch}}Y_{\text{ch}}t. \end{aligned}$$

Then, with these changes of variables the system given in (5.2) reduced to system

$$(I.2) \quad \begin{cases} \frac{dX_0}{d\tau} = (\nu_0(S_0, S_2) - \alpha - k_0)X_0 \\ \frac{dX_1}{d\tau} = (\nu_1(S_1, S_2) - \alpha - k_1)X_1 \\ \frac{dX_2}{d\tau} = (\nu_2(S_2) - \alpha - k_2)X_2 \\ \frac{dS_0}{d\tau} = \alpha(u_f - S_0) - \nu_0(S_0, S_2)X_0 \\ \frac{dS_1}{d\tau} = \alpha(u_g - S_1) + \omega_0\nu_0(S_0, S_2)X_0 - \nu_1(S_1, S_2)X_1 \\ \frac{dS_2}{d\tau} = \alpha(u_h - S_2) - \omega_2\nu_0(S_0, S_2)X_0 + \omega_1\nu_1(S_1, S_2)X_1 - \nu_2(S_2)X_2. \end{cases}$$

The operating parameters are

$$\alpha = \frac{D}{k_{\text{m,ch}}Y_{\text{ch}}}, \quad u_f = \frac{S_{\text{ch,in}}}{K_{\text{S,ch}}}, \quad u_g = \frac{S_{\text{ph,in}}}{K_{\text{S,ph}}}, \quad u_h = \frac{S_{\text{H}_2,\text{in}}}{K_{\text{S,H}_2}}.$$

The yield coefficients are

$$\omega_0 = \frac{K_{\text{S,ch}}}{K_{\text{S,ph}}} \frac{224}{208} (1 - Y_{\text{ch}}), \quad \omega_1 = \frac{K_{\text{S,ph}}}{K_{\text{S,H}_2}} \frac{32}{224} (1 - Y_{\text{ph}}), \quad \omega_2 = \frac{16}{208} \frac{K_{\text{S,ch}}}{K_{\text{S,H}_2}}.$$

The death rates are

$$k_0 = \frac{k_{\text{dec,ch}}}{k_{\text{m,ch}}Y_{\text{ch}}}, \quad k_1 = \frac{k_{\text{dec,ph}}}{k_{\text{m,ch}}Y_{\text{ch}}}, \quad k_2 = \frac{k_{\text{dec,H}_2}}{k_{\text{m,ch}}Y_{\text{ch}}}.$$

The growth functions are

$$\nu_0(S_0, S_2) = \frac{S_0}{1 + S_0} \frac{S_2}{K_P + S_2}, \quad \nu_1(S_1, S_2) = \frac{\phi_1 S_1}{1 + S_1} \frac{S_2}{1 + K_I S_2}, \quad \nu_2(S_2) = \frac{\phi_2 S_2}{1 + S_2},$$

where the biological parameters are given by

$$\phi_1 = \frac{k_{\text{m,ph}}Y_{\text{ph}}}{k_{\text{m,ch}}Y_{\text{ch}}}, \quad \phi_2 = \frac{k_{\text{m,H}_2}Y_{\text{H}_2}}{k_{\text{m,ch}}Y_{\text{ch}}}, \quad K_P = \frac{K_{\text{S,H}_2,C}}{K_{\text{S,H}_2}}, \quad K_I = \frac{K_{\text{S,H}_2}}{K_{\text{I,H}_2}}.$$

The trajectories in Figures I.1 to I.7 were presented according to the variables of model (5.2) using the change of variables (I.1). In Figures I.1 to I.3, the projections of the orbits of the six-dimensional phase space into the three-dimensional space  $(X_{\text{ch}}, X_{\text{ph}}, X_{\text{H}_2})$  shows the appearance and disappearance of a stable limit cycle for different values of  $S_{\text{ch,in}} > \sigma_5$  where the steady states in blue are unstable and those in red are stable. The plot of the limit cycle was obtained by solving the ordinary differential equations using the default solver “*lsoda*” from the ODEPACK package in Scilab.

Tables 11 and 12 present the components of the stable steady states SS3 and SS6, and all the initial conditions chosen to trace the different trajectories of model (5.2) in Figures I.1 to I.7 in the following three cases where the steady states SS1, SS2, SS4<sup>1</sup> and SS4<sup>2</sup> are unstable :



- For  $S_{\text{ch},\text{in}} \in (\sigma_5, \sigma^*)$ , the numerical simulations done for various positive initial conditions permit to conjecture the global asymptotic stability of SS3 (see Figure I.1).
- For  $S_{\text{ch},\text{in}} \in (\sigma^*, \sigma_6)$ , the system exhibits a bistability with two basins of attraction: one toward the stable limit cycle and the second toward SS3. Figure I.2 illustrates that the trajectories in pink and cyan converge toward the stable limit cycle in red, while the green trajectory converges toward the steady state SS3. For the initial condition in Table 12, the time course in Figure I.4 illustrates the positive, periodic solution representing the coexistence of the three species. The sustained oscillations prove the stability of the limit cycle. However, Figure I.5 shows the time course of the green trajectory in Figure I.2.
- For  $S_{\text{ch},\text{in}} > \sigma_6$ , the system exhibits a bistability between SS6 and SS3. Figure I.3 shows that the cyan trajectory converges to the stable focus SS6, while the green trajectory converges to SS3. Figures I.6 and I.7 illustrate the time courses corresponding to the cyan and the green trajectories in Figure I.3, respectively.

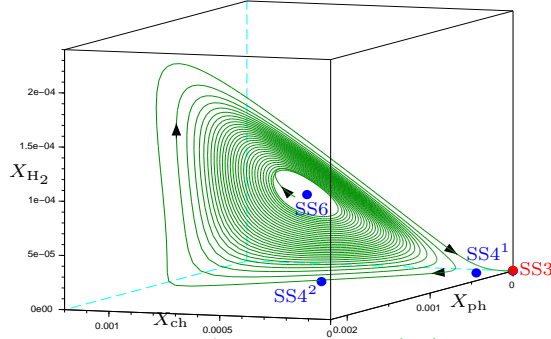


FIG. I.1. Case  $S_{\text{ch},\text{in}} = 0.098 < \sigma^*$ : the solution of (5.2) converges to SS3.

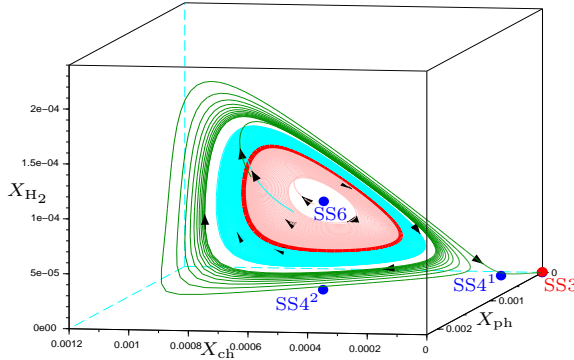


FIG. I.2. Case  $\sigma^* < S_{\text{ch},\text{in}} = 0.0995 < \sigma_6$ : bistability with convergence either to the stable limit cycle (in red) or to SS3.

**Appendix J. Tables.** In this section, we give the tables that are used in the previous sections. In Table 10, we provide the biological parameter values. In Tables 11 and 12, we provide the components of SS3 and SS6, and the initial conditions used in Figures I.1 to I.7, respectively. In Table 13, we present the auxiliary functions in the case of the growth functions given by (G.3). In Table 14, we provide the necessary and sufficient conditions for the existence and the local stability of steady states.

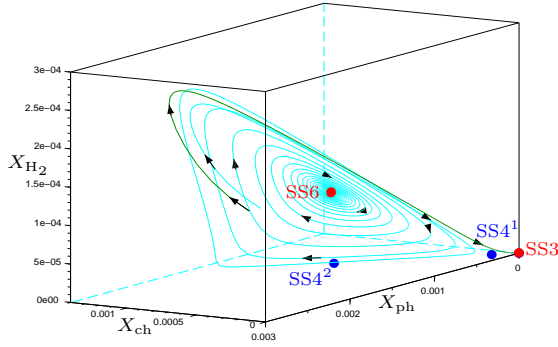


FIG. I.3. The case  $\sigma_6 < S_{ch,in} = 0.11$  : bistability with convergence either to SS6 or to SS3.

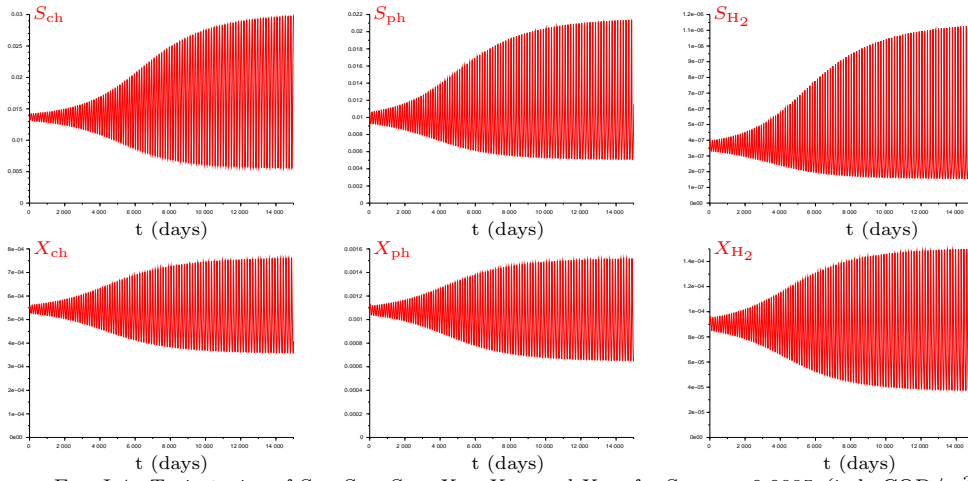


FIG. I.4. Trajectories of  $S_{ch}, S_{ph}, S_{H_2}, X_{ch}, X_{ph}$  and  $X_{H_2}$  for  $S_{ch,in} = 0.0995$  (in  $\text{kgCOD}/\text{m}^3$ ): Convergence to the stable limit cycle.

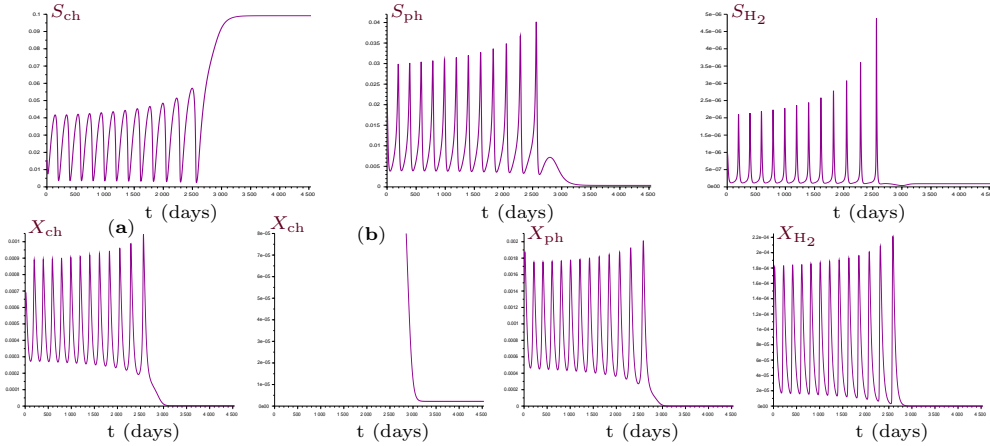


FIG. I.5. Trajectories of  $S_{ch}, S_{ph}, S_{H_2}, X_{ch}, X_{ph}$  and  $X_{H_2}$  for  $S_{ch,in} = 0.0995$  (in  $\text{kgCOD}/\text{m}^3$ ): Convergence to the stable steady state SS3. (b) A magnification of (a) showing that the solution of (5.2) converges to the nonzero  $X_{ch}$ -component of SS3.

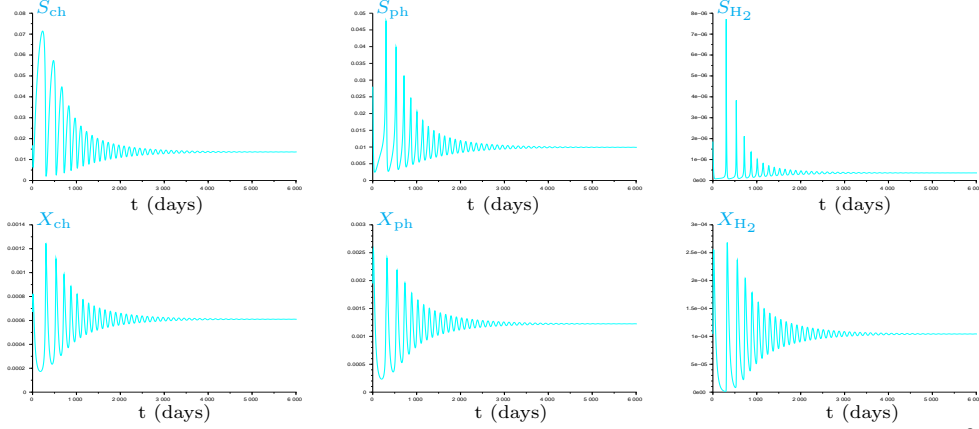


FIG. I.6. Trajectories of  $S_{ch}$ ,  $S_{ph}$ ,  $S_{H_2}$ ,  $X_{ch}$ ,  $X_{ph}$  and  $X_{H_2}$  for  $S_{ch,in} = 0.11$  (in  $\text{kgCOD}/\text{m}^3$ ): Convergence to the positive steady state SS6.

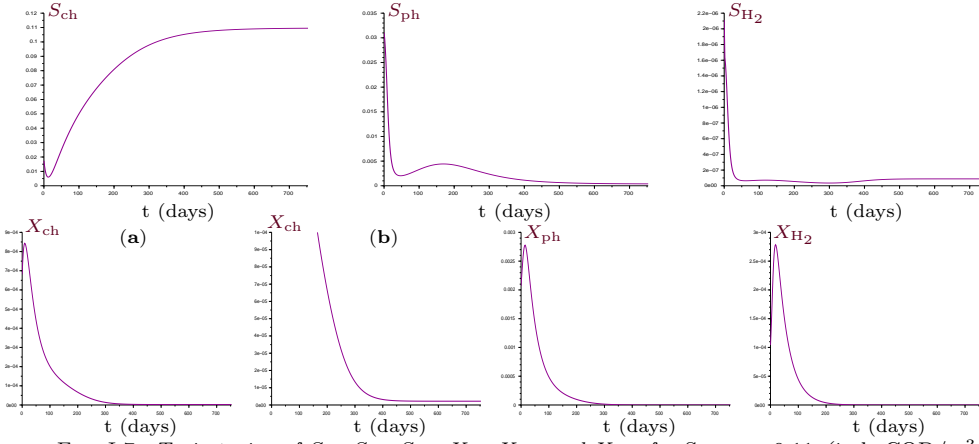


FIG. I.7. Trajectories of  $S_{ch}$ ,  $S_{ph}$ ,  $S_{H_2}$ ,  $X_{ch}$ ,  $X_{ph}$  and  $X_{H_2}$  for  $S_{ch,in} = 0.11$  (in  $\text{kgCOD}/\text{m}^3$ ): Convergence to the stable steady state SS3. (b) A magnification of (a) showing that the solution of (5.2) converges to the nonzero  $X_{ch}$ -component of SS3.

TABLE 10

Nominal parameter values, where  $i = \text{ch}, \text{ph}, \text{H}_2$ . Units are expressed in Chemical Oxygen Demand (COD).

Parameters	Nominal values	Units
$k_{m,ch}$	29	$\text{kgCOD}_S/\text{kgCOD}_X/\text{d}$
$K_{S,ch}$	0.053	$\text{kgCOD}/\text{m}^3$
$Y_{ch}$	0.019	$\text{kgCOD}_X/\text{kgCOD}_S$
$k_{m,ph}$	26	$\text{kgCOD}_S/\text{kgCOD}_X/\text{d}$
$K_{S,ph}$	0.302	$\text{kgCOD}/\text{m}^3$
$Y_{ph}$	0.04	$\text{kgCOD}_X/\text{kgCOD}_S$
$k_{m,H_2}$	35	$\text{kgCOD}_S/\text{kgCOD}_X/\text{d}$
$K_{S,H_2}$	$2.5 \times 10^{-5}$	$\text{kgCOD}/\text{m}^3$
$K_{S,H_2,c}$	$1.0 \times 10^{-6}$	$\text{kgCOD}/\text{m}^3$
$Y_{H_2}$	0.06	$\text{kgCOD}_X/\text{kgCOD}_S$
$k_{dec,i}$	0.02	$\text{d}^{-1}$
$K_{I,H_2}$	$3.5 \times 10^{-6}$	$\text{kgCOD}/\text{m}^3$

TABLE 11

The steady states SS3 and SS6 of model (5.2) corresponding to Figures I.1 to I.7. The biological parameters are provided in Table 10. The operating parameters are  $D = 0.01$ ,  $S_{ph,in} = 0$ ,  $S_{H_2,in} = 2.67 \times 10^{-5}$  and  $S_{ch,in}$  given in the second column.

Figure	$S_{ch,in}$	SS3 = $(X_{ch}, 0, 0, S_{ch}, S_{ph}, S_{H_2})$ SS6 = $(X_{ch}, X_{ph}, X_{H_2}, S_{ch}, S_{ph}, S_{H_2})$
I.1	0.098	$(2.19 \cdot 10^{-6}, 0, 0, 9.77 \cdot 10^{-2}, 3.65 \cdot 10^{-4}, 9.17 \cdot 10^{-8})$ $(5.34 \cdot 10^{-4}, 1.06 \cdot 10^{-3}, 8.80 \cdot 10^{-5}, 1.36 \cdot 10^{-2}, 9.93 \cdot 10^{-3}, 3.62 \cdot 10^{-7})$
I.2	0.0995	$(2.19 \cdot 10^{-6}, 0, 0, 9.92 \cdot 10^{-2}, 3.65 \cdot 10^{-4}, 9.12 \cdot 10^{-8})$
I.4		$(5.44 \cdot 10^{-4}, 1.08 \cdot 10^{-3}, 9.00 \cdot 10^{-5}, 1.36 \cdot 10^{-2}, 9.93 \cdot 10^{-3}, 3.62 \cdot 10^{-7})$
I.5		
I.3	0.11	$(2.19 \cdot 10^{-6}, 0, 0, 1.10 \cdot 10^{-1}, 3.65 \cdot 10^{-4}, 8.79 \cdot 10^{-8})$
I.6		$(6.10 \cdot 10^{-4}, 1.22 \cdot 10^{-3}, 1.04 \cdot 10^{-4}, 1.36 \cdot 10^{-2}, 9.93 \cdot 10^{-3}, 3.62 \cdot 10^{-7})$
I.7		

TABLE 12

The initial conditions of solutions of model (5.2) in Figures I.1 to I.7 are obtained from the initial conditions of the solutions of model (I.2) by using the change of variables (I.1). The initial conditions of (I.2) are given by  $X_i(0) = X_i^* + \varepsilon$  and  $S_i(0) = S_i^* + \varepsilon$ ,  $i = 0, 1, 2$  where  $X_i^*$  and  $S_i^*$  are the components of SS6 and  $\varepsilon$  is given in the second column. When there is more than one trajectory in the figure, its color is indicated in the first column.

Figure Color	$\varepsilon$	$(X_{ch}(0), X_{ph}(0), X_{H_2}(0), S_{ch}(0), S_{ph}(0), S_{H_2}(0))$
I.1	$9.7 \cdot 10^{-3}$	$(5.44 \cdot 10^{-4}, 1.17 \cdot 10^{-3}, 8.80 \cdot 10^{-5}, 1.42 \cdot 10^{-2}, 1.29 \cdot 10^{-2}, 6.05 \cdot 10^{-7})$
I.2	$10^{-2}$	$(5.54 \cdot 10^{-4}, 1.20 \cdot 10^{-3}, 9.00 \cdot 10^{-5}, 1.42 \cdot 10^{-2}, 1.29 \cdot 10^{-2}, 6.12 \cdot 10^{-7})$
Pink		
Cyan		
Green	$3.5 \cdot 10^{-2}$	$(5.79 \cdot 10^{-4}, 1.50 \cdot 10^{-3}, 9.00 \cdot 10^{-5}, 1.55 \cdot 10^{-2}, 2.05 \cdot 10^{-2}, 1.24 \cdot 10^{-6})$
I.3	$6 \cdot 10^{-2}$	$(6.71 \cdot 10^{-4}, 1.95 \cdot 10^{-3}, 1.04 \cdot 10^{-4}, 1.68 \cdot 10^{-2}, 2.80 \cdot 10^{-2}, 1.86 \cdot 10^{-6})$
Cyan		
Green		
I.4	$2 \cdot 10^{-3}$	$(5.46 \cdot 10^{-4}, 1.10 \cdot 10^{-3}, 9.00 \cdot 10^{-5}, 1.37 \cdot 10^{-2}, 1.05 \cdot 10^{-2}, 4.12 \cdot 10^{-7})$
I.5	$3.5 \cdot 10^{-2}$	$(5.79 \cdot 10^{-4}, 1.50 \cdot 10^{-3}, 9.00 \cdot 10^{-5}, 1.55 \cdot 10^{-2}, 2.05 \cdot 10^{-2}, 1.24 \cdot 10^{-6})$
I.6		
I.7		

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TABLE 13

Notations, intervals and auxiliary functions in the case of growth functions given by (G.3).

Interval and auxiliary function	Definition domain
$M_0(y, s_2) = \frac{yK_0(L_0 + s_2)}{m_0s_2 - y(L_0 + s_2)}$	$0 \leq y < \frac{m_0s_2}{L_0 + s_2}$
$M_1(y, s_2) = \frac{yK_1(K_I + s_2)}{m_1K_I - y(K_I + s_2)}$	$0 \leq y < \frac{m_1K_I}{K_I + s_2}$
$M_2(y) = \frac{yK_2}{m_2 - y}$	$0 \leq y < m_2$
$M_3(s_0, z) = \frac{zL_0(K_0 + s_0)}{m_0s_0 - z(K_0 + s_0)}$	$0 \leq z < \frac{m_0s_0}{K_0 + s_0}$
$s_2^0(D) = \frac{L_0(D + a_0)}{m_0 - D - a_0}$	$D + a_0 < m_0$
$s_2^1(D) = \frac{K_I(m_1 - D - a_1)}{D + a_1}$	$D + a_1 < m_1$
$I_1 = \{D \geq 0 : s_2^0(D) < s_2^1(D)\}$	
$I_2 = \{D \in I_1 : s_2^0(D) < M_2(D + a_2) < s_2^1(D)\}$	
$\Psi(s_2, D) = (1 - \omega) \frac{(D + a_0)K_0(L_0 + s_2)}{m_0s_2 - (D + a_0)(L_0 + s_2)} + \frac{(D + a_1)K_1(K_I + s_2)}{m_1K_I - (D + a_1)(K_I + s_2)} + s_2$	$\{D \in I_1 : s_2^0(D) < s_2 < s_2^1(D)\}$
$\phi_1(D) = \inf_{s_2^0(D) < s_2 < s_2^1(D)} \Psi(s_2, D)$	$D \in I_1$
$\phi_2(D) = \Psi(M_2(D + a_2), D)$	$D \in I_2$
$\phi_3(D) = \frac{\partial \Psi}{\partial s_2}(M_2(D + a_2), D)$	$D \in I_2$
$\psi_0(s_0) = \frac{m_0s_0(s_2^{\text{in}} - \omega(s_0^{\text{in}} - s_0))}{(K_0 + s_0)(L_0 + s_2^{\text{in}} - \omega(s_0^{\text{in}} - s_0))}$	$s_0 \in [\max(0, s_0^{\text{in}} - s_2^{\text{in}}/\omega), +\infty)$
$\psi_1(s_1) = \frac{m_1s_1K_I}{(K_1 + s_1)(K_I + s_1^{\text{in}} + s_2^{\text{in}} - s_1)}$	$s_1 \in [0, s_1^{\text{in}} + s_2^{\text{in}}]$
$\varphi_0(D) = M_0(D + a_0, M_2(D + a_2))$	$\{D \geq 0 : s_2^0(D) < M_2(D + a_2)\}$
$\varphi_1(D) = M_1(D + a_1, M_2(D + a_2))$	$\{D \geq 0 : M_2(D + a_2) < s_2^1(D)\}$

pp. 1–22, <https://doi.org/10.1051/mmnp/2018037>.

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TABLE 14

The necessary and sufficient conditions of existence and local stability of steady states of (5.2), when  $S_{\text{ph,in}} = 0$ .  $M_0, M_1, M_2, \Psi, \phi_1, \phi_2, \phi_3, \psi_0, \varphi_0$  and  $\varphi_1$  are given in Table 13,  $\mu_0$  and  $\mu_2$  are given by (G.3),  $\phi_4$  is given in (4.7),  $c_3, c_5, r_4$  and  $r_5$  are defined by Table 3.

	Existence conditions	Stability conditions
SS1	Always exists	$\mu_0 (S_{\text{ch,in}}Y_3Y_4, S_{\text{H}_2,\text{in}}) < D + a_0$ and $\mu_2 (S_{\text{H}_2,\text{in}}) < D + a_2$
SS2	$\mu_2 (S_{\text{H}_2,\text{in}}) > D + a_2$	$S_{\text{ch,in}}Y_3Y_4 < \varphi_0(D)$
SS3	$\mu_0 (S_{\text{ch,in}}Y_3Y_4, S_{\text{H}_2,\text{in}}) > D + a_0$	$s_0$ , solution of equation $\psi_0(s_0) = D + a_0$ satisfies $\mu_1 (S_{\text{ch,in}}Y_3Y_4 - s_0, S_{\text{H}_2,\text{in}} + \omega (S_{\text{ch,in}}Y_3Y_4 - s_0)) < D + a_1$ and $S_{\text{H}_2,\text{in}} - \omega S_{\text{ch,in}}Y_3Y_4 < M_2(D + a_2) - \omega\varphi_0(D)$
SS4	$(1 - \omega)S_{\text{ch,in}}Y_3Y_4 + S_{\text{H}_2,\text{in}} \geq \phi_1(D)$ and $s_2$ , solution of equation $\Psi(s_2) = (1 - \omega)S_{\text{ch,in}}Y_3Y_4 + S_{\text{H}_2,\text{in}}$ satisfies $S_{\text{ch,in}}Y_3Y_4 > M_0(D + a_0, s_2) + M_1(D + a_1, s_2)$	$(1 - \omega)S_{\text{ch,in}}Y_3Y_4 + S_{\text{H}_2,\text{in}} < \phi_2(D)$ , $\frac{\partial \Psi}{\partial s_2}(s_2, D) > 0$ , $\phi_3(D) > 0$ , and $\phi_4(D, S_{\text{ch,in}}, S_{\text{H}_2,\text{in}}) > 0$
SS5	$S_{\text{ch,in}}Y_3Y_4 > \varphi_0(D)$ and $S_{\text{H}_2,\text{in}} - \omega S_{\text{ch,in}}Y_3Y_4 > M_2(D + a_2) - \omega\varphi_0(D)$	$S_{\text{ch,in}}Y_3Y_4 < \varphi_0(D) + \varphi_1(D)$
SS6	$(1 - \omega)S_{\text{ch,in}}Y_3Y_4 + S_{\text{H}_2,\text{in}} > \phi_2(D)$ and $S_{\text{ch,in}}Y_3Y_4 > \varphi_0(D) + \varphi_1(D)$	$c_3 > 0, c_5 > 0, r_4 > 0$ and $r_5 > 0$

<https://doi.org/10.3934/mbe.2012.9.627>.

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