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Abstract. A mechanistic model describing the anaerobic mineralization of chlorophenol in a three-step food-web is investigated. 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. The case of a large class of growth kinetics is considered, instead of specific kinetics. We show that the system can have up to eight types of steady states and we analytically determine the necessary and sufficient conditions for their existence according to the operating parameters. In the particular case without maintenance, the local stability conditions of all steady states are determined. The bifurcation diagram shows the behavior of the process by varying the concentration of influent chlorophenol as the bifurcating parameter. It shows that the system exhibits a bi-stability where the positive steady state can lose stability undergoing a supercritical Hopf bifurcation with the emergence of a stable limit cycle.

1. **Introduction.** The chemostat model is widely used in microbiology and ecology as a mathematical representation of the continuous culture of micro-organisms, that is, the growth of micro-organisms in ecosystems that are continuously fed with nutrients [19, 21, 30]. Several textbooks on the mathematical analysis of this model with one and more species are available [17, 28]. The chemostat model predicts that coexistence of two or more microbial populations competing for a single non-reproducing nutrient is not possible. Only the species with the lowest 'break-even' concentration survives. This result, known as the Competitive Exclusion Principle (CEP), has a long history in the literature of bio-mathematics and the reader may consult [23] and the references therein.

Although the theoretical prediction of the CEP has been corroborated by the experiences of Hansen and Hubell [16], the biodiversity found in nature as well as in biological reactors seems to contradict the CEP. This has led to a great deal of

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mathematical research aimed at extending the chemostat model to better match theory and observations. Among the mechanisms that promote the coexistence of species, we can cite : the crowding effects (see [1, 8] and the references therein), the role of density-dependent growth functions (see [15] and the references therein), more complex food webs (see [2, 20, 33] and the reference therein), the presence of inhibitors that affects the strongest competitor (see [3, 9, 10, 32], and the references therein), the commensalistic relationship where a second species (the commensal) needs the first one (the host) to grow while the host species is not affected by the growth of the commensal one (see [5, 6, 11, 18, 27] and the references therein), the syntrophic relationship where two microbial species depend on each other for survival (see [7, 12, 14, 24, 25, 34] and the reference therein).

Some of these models were constructed to have a better understanding of anaerobic digestion (AD), which is an important process used in the treatment of wastewater and waste, including a large number of species that coexist in a very complex relationship. The full anaerobic digestion model (ADM1) developed in [4] includes 32 state variables and a large number of parameters. Therefore, the qualitative analysis and the control of this model are very difficult because of its complexity and its dependence on many operational variables. The so-called AM2 model developed in [6] represents a two-tiered food-web and provides satisfactory prediction of the AD process by using the parameter identification theory and experimental data. In [14], a three-tiered food-web model including enzymatic degradation of a substrate and commensalistic relationship is considered. In [31], the authors consider a three-tiered food-web with three microbial species (chlorophenol and phenol degraders and hydrogenotrophic methanogen) that encapsulates the essence of the AD process. The corresponding model represents an extension of the model describing the interactions between propionate degraders and hydrogenotrophic methanogens in a two-tiered feeding chain [34].

The aim of our paper is to consider the three-tiered microbial 'food-web', developed in [31] which is written as follows:

$$\begin{cases} \dot{X}_{\mathrm{ch}} &= (Y_{\mathrm{ch}} f_0\left(S_{\mathrm{ch}}, S_{\mathrm{H_2}}\right) - D - k_{\mathrm{dec,ch}}) X_{\mathrm{ch}} \\ \dot{X}_{\mathrm{ph}} &= (Y_{\mathrm{ph}} f_1\left(S_{\mathrm{ph}}, S_{\mathrm{H_2}}\right) - D - k_{\mathrm{dec,ph}}) X_{\mathrm{ph}} \\ \dot{X}_{\mathrm{H_2}} &= (Y_{\mathrm{H_2}} f_2\left(S_{\mathrm{H_2}}\right) - D - k_{\mathrm{dec,H_2}}) X_{\mathrm{H_2}} \\ \dot{S}_{\mathrm{ch}} &= D\left(S_{\mathrm{ch}}^{\mathrm{in}} - S_{\mathrm{ch}}\right) - f_0\left(S_{\mathrm{ch}}, S_{\mathrm{H_2}}\right) X_{\mathrm{ch}} \\ \dot{S}_{\mathrm{ph}} &= D\left(S_{\mathrm{ph}}^{\mathrm{in}} - S_{\mathrm{ph}}\right) + \frac{224}{208}\left(1 - Y_{\mathrm{ch}}\right) f_0\left(S_{\mathrm{ch}}, S_{\mathrm{H_2}}\right) X_{\mathrm{ch}} - f_1\left(S_{\mathrm{ph}}, S_{\mathrm{H_2}}\right) X_{\mathrm{ph}} \\ \dot{S}_{\mathrm{H_2}} &= D\left(S_{\mathrm{H_2}}^{\mathrm{in}} - S_{\mathrm{H_2}}\right) - \frac{16}{208} f_0\left(S_{\mathrm{ch}}, S_{\mathrm{H_2}}\right) X_{\mathrm{ch}} + \frac{32}{224}(1 - Y_{\mathrm{ph}}) f_1\left(S_{\mathrm{ph}}, S_{\mathrm{H_2}}\right) X_{\mathrm{ph}} \\ & \quad - f_2(S_{\mathrm{H_2}}) X_{\mathrm{H_2}}, \end{cases} \tag{1}$$

where X_{ch}, X_{ph} and $X_{\mathrm{H_2}}$ denote, respectively, the chlorophenol, phenol and hydrogen degrader concentrations; f_0, f_1 and f_2 are the corresponding growth rates; S_{ch}, S_{ph} and $S_{\mathrm{H_2}}$ are the chlorophenol, phenol and hydrogen substrates concentrations; $S_{\mathrm{ch}}^{\mathrm{in}}$, $S_{\mathrm{ph}}^{\mathrm{in}}$ and $S_{\mathrm{H_2}}^{\mathrm{in}}$ are the substrate concentrations in the feed bottle; $k_{\mathrm{dec,ch}}, k_{\mathrm{dec,ph}}$ and $k_{\mathrm{dec,H_2}}$ represent the decay rates; D is the dilution rate of the chemostat; Y_{ch}, Y_{ph} and $Y_{\mathrm{H_2}}$ are the yield coefficients.

The choice of the application of chlorophenol-mineralising food-web in [31] is due to the availability of experimental data but the study of model (1) applies to any other similar microbial food chain. Indeed, the parameter values related to hydrogen are deduced from that of ADM1 [4]. For chlorophenol and phenol, they were chosen based on a combination of literature data (see [31] and the references therein). Recently, a rigorous mathematical analysis of this model (1) was done in

[26] with general growth rates but only the chlorophenol inflowing concentration has been taken into account. Using the linear change of variables given by (7) and (8), model (1) can be written as follows:

$$\begin{cases} \dot{x}_0 &= (\mu_0(s_0,s_2)-D-a_0)x_0 \\ \dot{x}_1 &= (\mu_1(s_1,s_2)-D-a_1)x_1 \\ \dot{x}_2 &= (\mu_2(s_2)-D-a_2)x_2 \\ \dot{s}_0 &= D\left(s_0^{\text{in}}-s_0\right)-\mu_0(s_0,s_2)x_0 \\ \dot{s}_1 &= D\left(s_1^{\text{in}}-s_1\right)+\mu_0(s_0,s_2)x_0-\mu_1(s_1,s_2)x_1 \\ \dot{s}_2 &= D\left(s_2^{\text{in}}-s_2\right)-\omega\mu_0(s_0,s_2)x_0+\mu_1(s_1,s_2)x_1-\mu_2(s_2)x_2 \end{cases} \tag{2}$$

where s_i, $i=0,1,2$ are the three substrates; x_i are the three microbial species; μ_i are the specific growth rates given by (9); a_i are the mortality rates; s_i^{in} are the concentrations of the three substrates in the feed device. All the yield coefficients in (1) are normalized to one except of ω.

In [26], system (2) can have at most three types of steady states when $s_0^{\text{in}}>0$ and $s_1^{\text{in}}=s_2^{\text{in}}=0$: the washout steady state, a coexistence steady state of three species and a steady steady state where only the hydrogen degrader is extinct. The local stability analysis is achieved when the maintenance is excluded from system (2) where this six-dimensional model is reduced to a three-dimensional one. A numerical evidence shows that, when maintenance is included, the positive steady state can destabilize through a supercritical Hopf bifurcation with the appearance of a stable periodic orbit [26]. In [29], when maintenance is excluded, the emergence of a supercritical Hopf bifurcation was analytically determined. In [13], the three-tiered model of [31] was studied by neglecting the part of hydrogen produced by the phenol degrader and the mortality rates.

When in addition to $s_0^{\text{in}}>0$, the phenol and hydrogen inflowing concentrations are taken into account ($s_1^{\text{in}}>0$ and $s_2^{\text{in}}>0$), it was proven in [31] that system (1) can have up to eight steady states, a fact that was confirmed in [13] and [29] when a larger class of growth functions is considered, but the maintenance terms are neglected. In [31] most of the results on the existence and stability of steady states of model (1) were obtained only numerically.

In this paper, we generalize [31] by allowing a larger class of growth functions and by giving rigorous proofs for the results on the existence of steady states obtained in [31] for system (1). For this class of growth function, we generalize [13, 29] by allowing maintenance terms and we generalize [26] by allowing phenol and hydrogen inflowing concentrations. More precisely, our main objective is to determine the existence of steady states of model (2) in the general case including maintenance and the inflow of the three substrates. Moreover, we analyze the asymptotic behavior of the system without maintenance and we apply our theoretical results to the three-tiered microbial model (1). Actually, the results on the stability of steady state in [31] were obtained when maintenance terms are included. In a forthcoming publication [22], we study theoretically this case, where system (2) cannot be reduced to a three-dimensional one.

The paper is organized as follows. The next section presents general assumptions for the growth rates and the mathematical analysis of the existence of steady states of model (2) with respect to the operating parameters. In Section 3, the asymptotic behavior analysis of (2) was done in the particular case without maintenance. Considering specific growth rates, numerical simulations are presented in Section 4 as an application of our theoretical results to model (1). Finally, conclusions are

drawn in Section 5. The proofs of all the propositions and theorems are reported in Appendix A. The parameter values and some auxiliary functions are presented in Tables in Appendix B.

2. **Assumptions and steady states.** Considering model (2), we make the following general assumptions on the growth functions which are continuously differentiable ($\mathcal{C}^1$).

(H1) For all $s_0 > 0$ and $s_2 > 0$, $0 < \mu_0(s_0, s_2) < +\infty$, $\mu_0(0, s_2) = 0$, $\mu_0(s_0, 0) = 0$.
No growth can occur for species x_0 without substrates s_0 and s_2.

(H2) For all $s_1 > 0$ and $s_2 \geqslant 0$, $0 < \mu_1(s_1, s_2) < +\infty$, $\mu_1(0, s_2) = 0$.
No growth can occur for species x_1 without substrate s_1.

(H3) For all $s_2 > 0$, $0 < \mu_2(s_2) < +\infty$, $\mu_2(0) = 0$.
No growth can occur for species x_2 without substrate s_2.

(H4) For all $s_0 > 0$ and $s_2 > 0$, $\frac{\partial \mu_0}{\partial s_0}(s_0, s_2) > 0$, $\frac{\partial \mu_0}{\partial s_2}(s_0, s_2) > 0$.
The growth rate of species x_0 increases with substrates s_0 and s_2.

(H5) For all $s_1 > 0$ and $s_2 > 0$, $\frac{\partial \mu_1}{\partial s_1}(s_1, s_2) > 0$, $\frac{\partial \mu_1}{\partial s_2}(s_1, s_2) < 0$.
The growth rate of species x_1 increases with the substrate s_1 but is inhibited by the production of s_2.

(H6) For all $s_2 > 0$, $\mu_2'(s_2) > 0$.
The growth rate of species x_2 increases with substrate s_2.

(H7) 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.
The maximum growth rate of the species x_0 and x_1 increases and decreases, respectively, with the concentration of substrate s_2.

First, we show that the solutions of model (2) are nonnegative and bounded, which is a prerequisite for any reasonable model of the chemostat.

Proposition 1. *For any nonnegative initial conditions, all solutions of system (2) remain nonnegative and are bounded for all $t \geqslant 0$. Moreover, the set*

$$\Omega = \left\{(x_0, x_1, x_2, s_0, s_1, s_2) \in \mathbb{R}^6_+ : \omega x_0 + x_1 + x_2 + 2s_0 + 2s_1 + s_2 \leqslant 2s_0^{\text{in}} + 2s_1^{\text{in}} + s_2^{\text{in}}\right\}$$

is positively invariant and a global attractor for (2).

A steady state exists (or is said to be 'meaningful') if and only if all its components are nonnegative. This predicts eight possible steady states, labeled below as in [31]:

- SS1 ($x_0 = 0$, $x_1 = 0$, $x_2 = 0$): the washout of all three microbial populations.
- SS2 ($x_0 = 0$, $x_1 = 0$, $x_2 > 0$): only the hydrogen degraders are maintained.
- SS3 ($x_0 > 0$, $x_1 = 0$, $x_2 = 0$): only the chlorophenol degraders are maintained.
- SS4 ($x_0 > 0$, $x_1 > 0$, $x_2 = 0$): only the hydrogen degraders are washed out.
- SS5 ($x_0 > 0$, $x_1 = 0$, $x_2 > 0$): only the phenol degraders are washed out.
- SS6 ($x_0 > 0$, $x_1 > 0$, $x_2 > 0$): all three microbial populations are present.
- SS7 ($x_0 = 0$, $x_1 > 0$, $x_2 = 0$): only the phenol degraders are present.
- SS8 ($x_0 = 0$, $x_1 > 0$, $x_2 > 0$): only the chlorophenol degraders are washed out.

To determine these steady states, we need to define some auxiliary functions that are listed in Table 1. The existence and definition domains of these functions are all relatively straightforward and can be found as in [26]. Following [26], we add a hypothesis on the function Ψ which then assures that there are at most two steady states of the form SS4.

(H8) When $\omega < 1$, the function Ψ has a unique minimum $\overline{s}_2 = \overline{s}_2(D)$ on the interval $\left(s_2^0, s_2^1\right)$, such that $\frac{\partial \Psi}{\partial s_2}(s_2, D) < 0$ on $\left(s_2^0, \overline{s}_2\right)$ and $\frac{\partial \Psi}{\partial s_2}(s_2, D) > 0$ on $\left(\overline{s}_2, s_2^1\right)$.

As we will show in Section 4, this hypothesis (H8) is fulfilled with the specific growth rates (9). Now, we can state our main result.

TABLE 1. Notations, intervals and auxiliary functions.

	Definition
$s_i = M_i(y, s_2)$ $i = 0, 1$	Let $s_2 \geqslant 0$. $s_i = M_i(y, s_2)$ is the unique solution of $\mu_i(s_i, s_2) = y$, for all $0 \leqslant y < \mu_i(+\infty, s_2)$
$s_2 = M_2(y)$	$s_2 = M_2(y)$ is the unique solution of $\mu_2(s_2) = y$, for all $0 \leqslant y < \mu_2(+\infty)$
$s_2 = M_3(s_0, z)$	Let $s_0 \geqslant 0$. $s_2 = M_3(s_0, z)$ is the unique solution of $\mu_0(s_0, s_2) = z$, for all $0 \leqslant z < \mu_0(s_0, +\infty)$
$s_2^i = s_2^i(D)$ $i = 0, 1$	$s_2^i = s_2^i(D)$ is the unique solution of $\mu_i\left(+\infty, s_2\right) = D + a_i$, for all $D + a_0 < \mu_0(+\infty, +\infty)$, $\mu_1(+\infty, +\infty) < D + a_1 < \mu_1(+\infty, 0)$, resp.
$I_1, \quad I_2$	$I_1 = \left\{D \geqslant 0 : s_2^0 < s_2^1\right\}$, $I_2 = \left\{D \in I_1 : s_2^0 < M_2(D + a_2) < s_2^1\right\}$
$\Psi(s_2, D)$	$\Psi\left(s_2, D\right) = (1-\omega) M_0(D + a_0, s_2) + M_1(D + a_1, s_2) + s_2$, for all $D \in I_1$ and $s_2^0 < s_2 < s_2^1$
$\phi_1(D)$	$\phi_1(D) = \inf_{s_2^0 < s_2 < s_2^1} \Psi(s_2, D)$, for all $D \in I_1$
$\phi_2(D)$	$\phi_2(D) = \Psi\left(M_2(D + a_2), D\right)$, for all $D \in I_2$
$\phi_3(D)$	$\phi_3(D) = \frac{\partial \Psi}{\partial s_2}\left(M_2(D + a_2), D\right)$, for all $D \in I_2$
$J_0, \quad J_1$	$J_0 = \left(\max\left(0, s_0^{\text{in}} - s_2^{\text{in}}/\omega\right), s_0^{\text{in}}\right)$, $J_1 = \left(0, s_1^{\text{in}}\right)$
$\psi_0(s_0)$	$\psi_0(s_0) = \mu_0\left(s_0, s_2^{\text{in}} - \omega\left(s_0^{\text{in}} - s_0\right)\right)$, for all $s_0 \geqslant \max\left(0, s_0^{\text{in}} - s_2^{\text{in}}/\omega\right)$
$\psi_1(s_1)$	$\psi_1(s_1) = \mu_1\left(s_1, s_2^{\text{in}} + s_1^{\text{in}} - s_1\right)$, for all $s_1 \in \left[0, s_1^{\text{in}} + s_2^{\text{in}}\right]$
$\varphi_i(D)$ $i = 0, 1$	$\varphi_i(D) = M_i\left(D + a_i, M_2(D + a_2)\right)$, resp., for all, $D \in \left\{D \geqslant 0 : s_2^0 < M_2(D + a_2)\right\}$, $D \in \left\{D \geqslant 0 : M_2(D + a_2) < s_2^1\right\}$

Theorem 1. *Assume that Hypotheses (H1) to (H6) hold. The steady states SS1, SS2,..., SS8, of (2) are given in Table 2. Assume also that Hypothesis (H7) holds. The necessary and sufficient conditions of existence of the steady states are given in Table 3. When they exist, all steady states (except SS4) are unique.*

- *If $\omega \geqslant 1$, when it exists, SS4 is unique.*
- *If $\omega < 1$, assuming also that (H8) holds, the system has generically two steady states of the form SS4.*

Remark 1. If $\omega < 1$, equation $\Psi(s_2, D) = (1-\omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}}$ has two solutions s_2^{*1} and s_2^{*2} if and only if $(1-\omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}} > \phi_1(D)$, so that $\frac{\partial \Psi}{\partial s_2}\left(s_2^{*1}, D\right) < 0$ and $\frac{\partial \Psi}{\partial s_2}\left(s_2^{*2}, D\right) > 0$ (see Fig. 1). We denote by SS4^1 and SS4^2 the steady states of type SS4 corresponding to s_2^{*1} and s_2^{*2}, respectively. These steady states coalesce when $(1-\omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}} = \phi_1(D)$.

In the particular cases, where $s_1^{\text{in}} = 0$ or $s_2^{\text{in}} = 0$, some of the steady states described in Theorem 1 do not exist and the existence conditions of the existing steady states can be simplified. More precisely, we have the following result.

Proposition 2. *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. If $s_1^{\text{in}} = s_2^{\text{in}} = 0$, we have:*

TABLE 2. Steady states of (2). All functions are defined in Table 1.

	s_0, s_1, s_2 and x_0, x_1, x_2 components
SS1	$s_0 = s_0^{\text{in}}$, $s_1 = s_1^{\text{in}}$, $s_2 = s_2^{\text{in}}$ and $x_0 = 0$, $x_1 = 0$, $x_2 = 0$
SS2	$s_0 = s_0^{\text{in}}$, $s_1 = s_1^{\text{in}}$, $s_2 = M_2(D + a_2)$ and $x_0 = 0$, $x_1 = 0$, $x_2 = \frac{D}{D+a_2}\left(s_2^{\text{in}} - s_2\right)$
SS3	$s_1 = s_1^{\text{in}} + s_0^{\text{in}} - s_0$ and $s_2 = s_2^{\text{in}} - \omega\left(s_0^{\text{in}} - s_0\right)$, where s_0 is a solution of $\psi_0(s_0) = D + a_0$ and $x_0 = \frac{D}{D+a_0}\left(s_0^{\text{in}} - s_0\right)$, $x_1 = 0$, $x_2 = 0$
SS4	$s_0 = M_0(D + a_0, s_2)$ and $s_1 = M_1(D + a_1, s_2)$, where s_2 is a solution of $\Psi(s_2, D) = (1-\omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}}$ and $x_0 = \frac{D}{D+a_0}\left(s_0^{\text{in}} - s_0\right)$, $x_1 = \frac{D}{D+a_1}\left(s_0^{\text{in}} - s_0 + s_1^{\text{in}} - s_1\right)$, $x_2 = 0$
SS5	$s_0 = \varphi_0(D)$, $s_1 = s_1^{\text{in}} + s_0^{\text{in}} - s_0$, $s_2 = M_2(D + a_2)$ and $x_0 = \frac{D}{D+a_0}\left(s_0^{\text{in}} - s_0\right)$, $x_1 = 0$, $x_2 = \frac{D}{D+a_2}\left(s_2^{\text{in}} - s_2 - \omega\left(s_0^{\text{in}} - s_0\right)\right)$
SS6	$s_0 = \varphi_0(D)$, $s_1 = \varphi_1(D)$, $s_2 = M_2(D + a_2)$ and $x_0 = \frac{D}{D+a_0}\left(s_0^{\text{in}} - s_0\right)$, $x_1 = \frac{D}{D+a_1}\left(s_0^{\text{in}} - s_0 + s_1^{\text{in}} - s_1\right)$, $x_2 = \frac{D}{D+a_2}\left((1-\omega)(s_0^{\text{in}} - s_0) + s_1^{\text{in}} - s_1 + s_2^{\text{in}} - s_2\right)$
SS7	$s_0 = s_0^{\text{in}}$ and $s_2 = s_2^{\text{in}} + s_1^{\text{in}} - s_1$, where s_1 is a solution of $\psi_1(s_1) = D + a_1$ and $x_0 = 0$, $x_1 = \frac{D}{D+a_1}\left(s_1^{\text{in}} - s_1\right)$, $x_2 = 0$
SS8	$s_0 = s_0^{\text{in}}$, $s_1 = \varphi_1(D)$, $s_2 = M_2(D + a_2)$ and $x_0 = 0$, $x_1 = \frac{D}{D+a_1}\left(s_1^{\text{in}} - s_1\right)$, $x_2 = \frac{D}{D+a_2}\left(s_1^{\text{in}} - s_1 + s_2^{\text{in}} - s_2\right)$

TABLE 3. Existence conditions of steady states of (2). All functions are given in Table 1.

	Existence conditions
SS1	Always exists
SS2	$\mu_2\left(s_2^{\text{in}}\right) > D + a_2$
SS3	$\mu_0\left(s_0^{\text{in}}, s_2^{\text{in}}\right) > D + a_0$
SS4	$(1-\omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}} \geqslant \phi_1(D)$, $s_0^{\text{in}} > M_0(D + a_0, s_2)$, $s_0^{\text{in}} + s_1^{\text{in}} > M_0(D + a_0, s_2) + M_1(D + a_1, s_2)$ with s_2 solution of equation $\Psi(s_2, D) = (1-\omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}}$
SS5	$s_0^{\text{in}} > \varphi_0(D)$, $s_2^{\text{in}} - \omega s_0^{\text{in}} > M_2(D + a_2) - \omega\varphi_0(D)$
SS6	$(1-\omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}} > \phi_2(D)$, $s_0^{\text{in}} > \varphi_0(D)$, $s_0^{\text{in}} + s_1^{\text{in}} > \varphi_0(D) + \varphi_1(D)$
SS7	$\mu_1\left(s_1^{\text{in}}, s_2^{\text{in}}\right) > D + a_1$
SS8	$s_1^{\text{in}} > \varphi_1(D)$, $s_1^{\text{in}} + s_2^{\text{in}} > \varphi_1(D) + M_2(D + a_2)$

- *The steady states SS2, SS3, SS5, SS7 and SS8 do not exist.*
- *If $\omega \geqslant 1$, SS4 and SS6 do not exist. If $\omega < 1$, SS4 and SS6 exist, respectively, if and only if*

$$(1-\omega)s_0^{\text{in}} \geqslant \phi_1(D) \quad \textit{and} \quad (1-\omega)s_0^{\text{in}} > \phi_2(D). \tag{3}$$

Remark 2. Assume that $s_1^{\text{in}} = s_2^{\text{in}} = 0$. Then, only the steady states SS1, SS4 and SS6 can exist. The existence conditions (3) of SS4 and SS6, respectively, are equivalent to the following conditions given in Lemmas 3 and 4 of [26]:

$$s_0^{\text{in}} \geqslant F_1(D) := \tfrac{\phi_1(D)}{1-\omega} \quad \text{and} \quad s_0^{\text{in}} > F_2(D) := \tfrac{\phi_2(D)}{1-\omega}.$$

Hence, we recover the results of [26] where the study is restricted to the case $s_1^{\text{in}} = s_2^{\text{in}} = 0$. Notice that, in [26], the steady states SS1, SS4 and SS6 were labeled SS1, SS2 and SS3, respectively.

3. **Study of the model without maintenance.** In this section, we determine the existence and stability conditions of steady states of model (2) in the particular

case without maintenance. To this end, we define the function ϕ_4 by

$$\begin{aligned}\phi_4\left(D, s_0^{\text{in}}, s_1^{\text{in}}, s_2^{\text{in}}\right) &= (EIx_0x_2 + EG\phi_3(D)x_0x_1)(Ix_2 + (G+H)x_1 \\ &\quad +(E+\omega F)x_0) + (Ix_2 + (G+H)x_1 + \omega F x_0)GIx_1x_2,\end{aligned} \tag{4}$$

where

$$E = \frac{\partial \mu_0}{\partial s_0}(s_0, s_2), F = \frac{\partial \mu_0}{\partial s_2}(s_0, s_2), G = \frac{\partial \mu_1}{\partial s_1}(s_1, s_2), H = -\frac{\partial \mu_1}{\partial s_2}(s_1, s_2), I = \mu_2'(s_2) \tag{5}$$

and the functions E, F, G, H and I, are evaluated at the components of SS6 given in Table 2 with $a_0 = a_1 = a_2 = 0$.

Theorem 2. *Assume that Hypotheses (H1) to (H8) hold. Without maintenance, the steady states and their existence conditions of (2) are given in Tables 2 and 3 by putting $a_0 = a_1 = a_2 = 0$. In addition, the necessary and sufficient conditions of local stability of the steady states are given in Table 4.*

TABLE 4. Maintenance free case: the stability conditions of steady states of (2). All functions are given in Table 1 with $a_0 = a_1 = a_2 = 0$, while ϕ_4 is defined by (4).

	Stability conditions
SS1	$\mu_0\left(s_0^{\text{in}}, s_2^{\text{in}}\right) < D, \quad \mu_1\left(s_1^{\text{in}}, s_2^{\text{in}}\right) < D, \quad \mu_2\left(s_2^{\text{in}}\right) < D$
SS2	$s_0^{\text{in}} < \varphi_0(D), \quad s_1^{\text{in}} < \varphi_1(D)$
SS3	$\mu_1\left(s_1^{\text{in}} + s_0^{\text{in}} - s_0, s_2^{\text{in}} - \omega\left(s_0^{\text{in}} - s_0\right)\right) < D, \quad s_2^{\text{in}} - \omega s_0^{\text{in}} < M_2(D) - \omega\varphi_0(D)$, with s_0 solution of equation $\psi_0(s_0) = D$
SS4	$(1-\omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}} < \phi_2(D), \quad \frac{\partial \Psi}{\partial s_2}(s_2, D) > 0, \quad \phi_3(D) > 0$, with s_2 solution of equation $\Psi(s_2, D) = (1-\omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}}$
SS5	$s_0^{\text{in}} + s_1^{\text{in}} < \varphi_0(D) + \varphi_1(D)$
SS6	$\phi_3(D) \geqslant 0, \quad \text{or} \quad \phi_3(D) < 0 \quad \text{and} \quad \phi_4\left(D, s_0^{\text{in}}, s_1^{\text{in}}, s_2^{\text{in}}\right) > 0$
SS7	$s_1^{\text{in}} + s_2^{\text{in}} < M_3\left(s_0^{\text{in}}, D\right) + M_1\left(D, M_3\left(s_0^{\text{in}}, D\right)\right), \quad s_1^{\text{in}} + s_2^{\text{in}} < M_2(D) + \varphi_1(D)$
SS8	$s_0^{\text{in}} < \varphi_0(D)$

Remark 3. If $\omega \geqslant 1$, when SS4 exists, its stability condition $\frac{\partial \Psi}{\partial s_2}(s_2, D) > 0$ is always satisfied (see Lemma 3). If $\omega < 1$, when SS4[1] exists, it is unstable (see Remark 1). When SS4[2] exists, its stability condition $\frac{\partial \Psi}{\partial s_2}(s_2, D) > 0$ is always satisfied.

4. **Application to a chlorophenol-mineralising three-tiered microbial 'food web'.** The aim of this section is to illustrate the theoretical results of this paper in the case of the chlorophenol-mineralising three-tiered microbial model (1) considered in [31] where the specific growth rates take the form:

$$\begin{aligned} f_0\left(S_{\text{ch}}, S_{\text{H}_2}\right) &= \frac{k_{m,\text{ch}} S_{\text{ch}}}{K_{S,ch} + S_{\text{ch}}} \frac{S_{H_2}}{K_{S,\text{H}_2,c} + S_{\text{H}_2}}, \\ f_1\left(S_{\text{ph}}, S_{\text{H}_2}\right) &= \frac{k_{m,\text{ph}} S_{\text{ph}}}{K_{S,\text{ph}} + S_{\text{ph}}} \frac{1}{1 + S_{\text{H}_2}/K_{I,\text{H}_2}}, \quad f_2\left(S_{\text{H}_2}\right) = \frac{k_{m,\text{H}_2} S_{\text{H}_2}}{K_{S,\text{H}_2} + S_{\text{H}_2}}. \end{aligned} \tag{6}$$

The biological parameter values are provided in Table 10. They were previously used in [26, 31]. Following [26], model (1) can be rescaled to obtain model (2) using the following change of variables:

$$x_0 = \frac{Y}{Y_0} X_{\text{ch}}, \; x_1 = \frac{Y_4}{Y_1} X_{\text{ph}}, \; x_2 = \frac{1}{Y_2} X_{\text{H}_2}, \; s_0 = Y S_{\text{ch}}, \; s_1 = Y_4 S_{\text{ph}}, \; s_2 = S_{\text{H}_2}, \tag{7}$$

where $Y = Y_3 Y_4$. The inflowing concentrations are given by:

$$s_0^{\text{in}} = Y S_{\text{ch}}^{\text{in}}, \quad s_1^{\text{in}} = Y_4 S_{\text{ph}}^{\text{in}}, \quad s_2^{\text{in}} = S_{\text{H}_2}^{\text{in}}, \tag{8}$$

the decay rates are $a_0 = k_{\mathrm{dec,ch}}$, $a_1 = k_{\mathrm{dec,ph}}$, $a_2 = k_{\mathrm{dec,H_2}}$ (with units d^{-1}), the yield coefficients are

$$Y_0 = Y_{\mathrm{ch}},\ Y_1 = Y_{\mathrm{ph}},\ Y_2 = Y_{\mathrm{H_2}},\ Y_3 = \tfrac{224}{208}(1-Y_0),\ Y_4 = \tfrac{32}{224}(1-Y_1),$$

with $\omega = \frac{16}{208Y}$. When the yield coefficients are those given in Table 10, we have $\omega \simeq 0.53$. The growth functions take the form:

$$\mu_0(s_0,s_2) = \tfrac{m_0 s_0}{K_0+s_0}\tfrac{s_2}{L_0+s_2},\quad \mu_1(s_1,s_2) = \tfrac{m_1 s_1}{K_1+s_1}\tfrac{1}{1+s_2/K_I},\quad \mu_2(s_2) = \tfrac{m_2 s_2}{K_2+s_2}, \tag{9}$$

where

$$m_0 = Y_0 k_{m,\mathrm{ch}},\quad K_0 = Y K_{S,\mathrm{ch}},\quad L_0 = K_{S,\mathrm{H_2,c}},\quad m_1 = Y_1 k_{m,\mathrm{ph}},$$
$$K_1 = Y_4 K_{S,\mathrm{ph}},\quad K_I = K_{I,\mathrm{H_2}},\quad m_2 = Y_2 k_{m,\mathrm{H_2}},\quad K_2 = K_{S,\mathrm{H_2}}.$$

For the specific growth functions (9), various functions defined in Table 1 are listed in Table 11. From the expression of Ψ in Table 11, a straightforward calculation shows that, for all $s_2 \in \left(s_2^0, s_2^1\right)$,

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

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 (H8) (see Figure 1). Furthermore, model (1) is of the form (2) where the growth functions (9) satisfy Hypotheses (H1) to (H8). Consequently, the results of our paper apply to model (1).

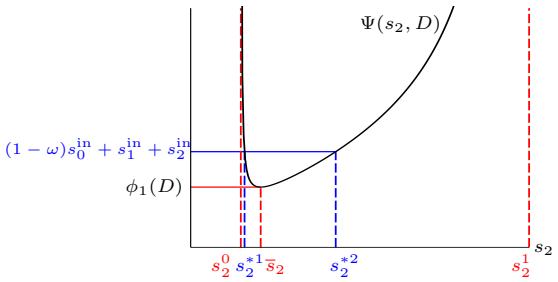

FIGURE 1. Curve of the function $\Psi(., D)$, where s_2^{*1} and s_2^{*2} are the solutions of equation $\Psi(s_2, D) = (1-\omega)s_0^{\mathrm{in}} + s_1^{\mathrm{in}} + s_2^{\mathrm{in}}$.

Using the steady states in Table 2 and the auxiliary functions given in Table 11 in the case of specific growth functions (9), a straightforward computation shows that all components of the steady states of model (2) are the same as those in [31] where another rescaling model and change of variables are used. However, the existence conditions in Table 3 of SS3, SS4 and SS7 were not established in [31] (see Appendix C.3, C.4 and C.7) where they were checked only numerically, by considering the roots of polynomials of degree 2 or 3 (see formulas (C.3), (C.11) and (C.49)), respectively. All other existence conditions were established in [31]. Hence, our analytical study of model (2) permits to give rigorous proofs for (1).

In what follows, we consider the input concentrations $S_{\mathrm{ph}}^{\mathrm{in}} = 0$ and $S_{\mathrm{H_2}}^{\mathrm{in}} = 2.67 \times 10^{-5}$, corresponding to Fig. 3(a) in [31] when $D = 0.01$ and $k_{\mathrm{dec,ch}} = k_{\mathrm{dec,ph}} = k_{\mathrm{dec,H_2}} = 0$. As a consequence of Theorem 2, we obtain the following result which determines the existence and the stability of the steady states of (1) with respect to the input concentration $S_{\mathrm{ch}}^{\mathrm{in}}$.

Proposition 3. *Assume that the biological parameters in (1) are given as in Table 10. Assume that* $S_{\rm ph}^{\rm in} = 0$, $S_{\rm H_2}^{\rm in} = 2.67\times10^{-5}$, $D = 0.01$ *and* $k_{\rm dec,ch} = k_{\rm dec,ph} = k_{\rm dec,H_2} = 0$. *Let* σ_i, $i = 1,\dots,6$ *be the bifurcation values defined in Table 5. The existence and stability of steady states of (1), with respect to the input concentration* $S_{\rm ch}^{\rm in}$ *is given in Table 6. The nature of the bifurcations when* $S_{\rm ch}^{\rm in}$ *crosses the values* σ_i, $i = 1,\dots,6$ *is given in Table 7.*

TABLE 5. Definitions of the critical values of σ_i, $i = 1,\dots,6$.

Definition	Value
$\sigma_1 = M_0\left(D, S_{\rm H_2}^{\rm in}\right)/Y$	0.001017
$\sigma_2 = (\phi_1(D) - S_{\rm H_2}^{\rm in})/((1-\omega)Y)$	0.009159
$\sigma_3 = \varphi_0(D)/Y$	0.010846
$\sigma_4 = (S_{\rm H_2}^{\rm in} - M_2(D) + \omega\varphi_0(D))/(\omega Y)$	0.011191
$\sigma_5 = (\phi_2(D) - S_{\rm H_2}^{\rm in})/((1-\omega)Y)$	0.016575
σ_6 is the solution of equation $\phi_4(S_{\rm ch}^{\rm in}) = 0$	0.029877

TABLE 6. Existence and stability of steady states, with respect to $S_{\rm ch}^{\rm in}$. 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 of $S_{\rm ch}^{\rm in}$	SS1	SS2	SS3	SS4^1	SS4^2	SS5	SS6
$(0,\sigma_1)$	U	S					
(σ_1,σ_2)	U	S	U				
(σ_2,σ_3)	U	S	U	U	U		
(σ_3,σ_4)	U	U	U	U	U	S	
(σ_4,σ_5)	U	U	S	U	U		
(σ_5,σ_6)	U	U	S	U	U		U
$(\sigma_6,+\infty)$	U	U	S	U	U		S

TABLE 7. Nature of the bifurcations corresponding to the critical values of σ_i, $i = 1,\dots,6$, defined in Table 5. There exists also a critical value $\sigma^* \simeq 0.029638$ corresponding to the value of $S_{\rm ch}^{\rm in}$ where the stable limit cycle disappears when $S_{\rm ch}^{\rm in}$ is decreasing.

	Type of the bifurcation
σ_1	Transcritical bifurcation of SS1 and SS3
σ_2	Saddle-node bifurcation of SS4^1 and SS4^2
σ_3	Transcritical bifurcation of SS2 and SS5
σ_4	Transcritical bifurcation of SS3 and SS5
σ_5	Transcritical bifurcation of SS4^1 and SS6
σ^*	Disappearance of the stable limit cycle
σ_6	Supercritical Hopf bifurcation

Figs. 2 and 3 depict the bifurcation diagram of system (1) where $X_{\rm ch}$ is represented as a function of the bifurcation parameter $S_{\rm ch}^{\rm in}$. Figs. 2(b) and 3 show magnifications of the bifurcation diagram showing the transcritical bifurcations occurring at σ_1, σ_3, σ_4 and σ_5, the saddle-node bifurcation occurring at σ_2, the Hopf bifurcation occurring at σ_6, and the disappearance of the cycle occurring at σ^*. In Fig. 2(b), the steady states SS1 and SS2 cannot be distinguished since they have

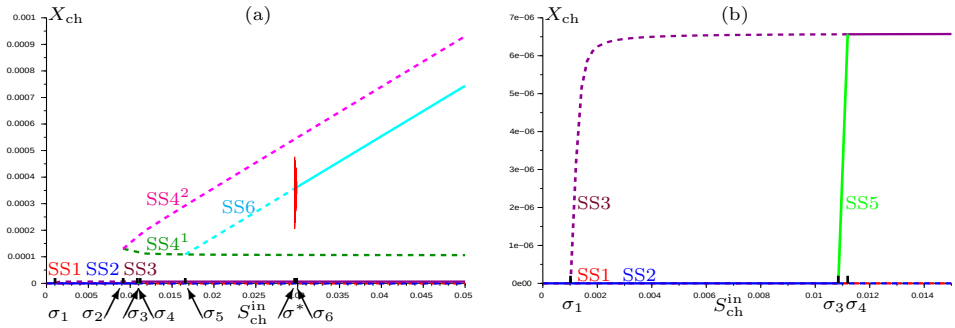

FIGURE 2. (a) Projection of the ω-limit set in variable X_{ch} as a function of $S_{ch}^{in} \in [0, 0.05]$ (b) A magnification of the transcritical bifurcations occurring at σ_1, σ_3 and σ_4 when $S_{ch}^{in} \in [0, 0.015]$.

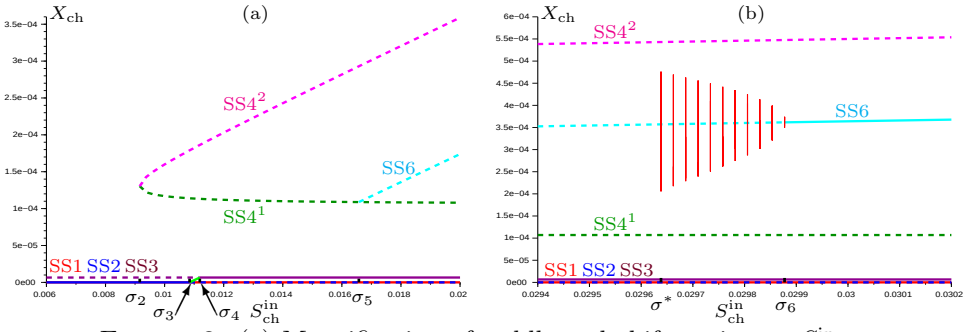

FIGURE 3. (a) Magnification of saddle-node bifurcation at $S_{ch}^{in} = \sigma_2$ and the transcritical bifurcation at $S_{ch}^{in} = \sigma_5$ when $S_{ch}^{in} \in [0.006, 0.02]$. (b) Magnification of the appearance and disappearance of stable limit cycles when $S_{ch}^{in} \in [0.0294, 0.0302]$.

TABLE 8. Colors used in Figs. 2 and 3. The solid (resp. dashed) lines are used for stable (resp. unstable) steady states.

SS1	SS2	SS3	SS4^1	SS4^2	SS5	SS6
Red	Blue	Purple	Dark Green	Magenta	Green	Cyan

both a zero X_{ch}-component. Since for $S_{ch}^{in} < \sigma_3$, SS2 is stable and SS1 is unstable, the $X_{ch} = 0$ axis is plotted in blue, which is the color for SS2 in Table 8.

Numerical simulations have shown that there exists a critical value $\sigma^* \in (\sigma_5, \sigma_6)$, which corresponds to the value of S_{ch}^{in}, where the stable limit cycle that appears for $S_{ch}^{in} = \sigma_6$ through a supercritical Hopf bifurcation, disappears when S_{ch}^{in} is decreasing. In [29], a numerical study of the bifurcation diagram with respect to the parameter D is given in the case without maintenance and $s_1^{in} = s_2^{in} = 0$. Fig. 6 in [29] shows that the disappearance of the stable limit cycle occurs through a saddle-node bifurcation with another unstable limit cycle. We conjecture that in our case also the stable limit cycle disappears by a confluence with an unstable limit cycle at $S_{ch}^{in} = \sigma^*$.

When $S_{ch}^{in} \in (\sigma^*, \sigma_6)$, the system exhibits a bi-stability with convergence either to SS3 or to a stable limit cycle according to the initial condition. Fig. 4 illustrates the three-dimensional space where the trajectories in yellow and blue converge toward

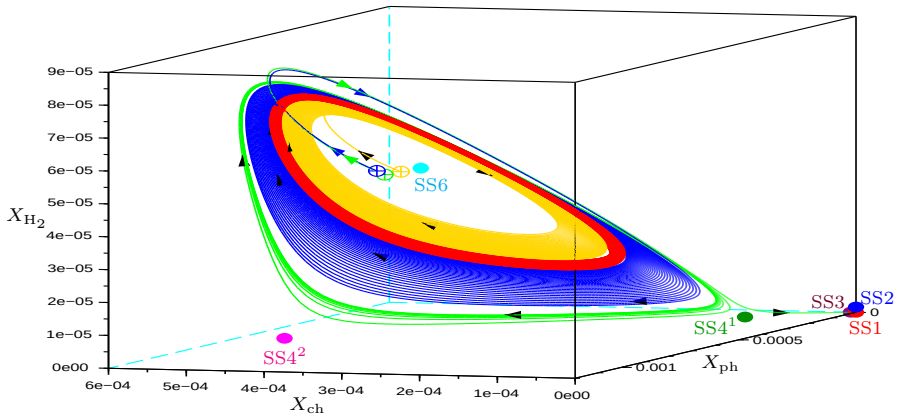

FIGURE 4. Case $S_{ch}^{in} = 0.029639 \in (\sigma^*, \sigma_6)$: bi-stability of the limit cycle (in red) and SS3.

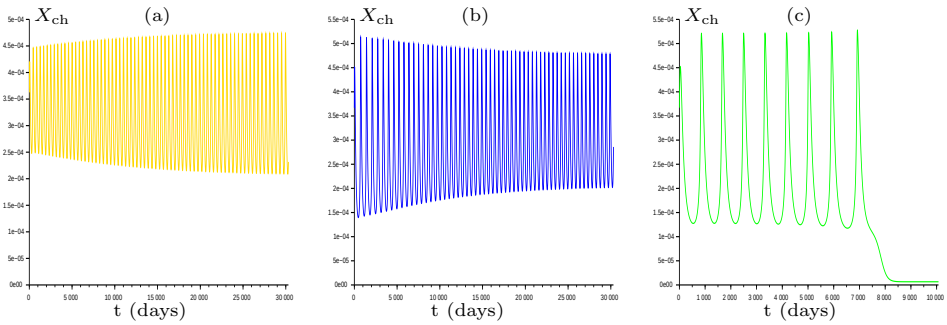

FIGURE 5. Case $S_{ch}^{in} = 0.029639 \in (\sigma^*, \sigma_6)$: trajectories of X_{ch} corresponding to those in Fig. 4 showing the sustained oscillations in yellow (a) and blue (b) or the convergence to SS3 in green (c).

the stable limit cycle in red, while the green trajectory converges toward the steady state SS3. Fig. 5 illustrates the time courses of the yellow and blue trajectories in Fig. 4 proving that the oscillations are maintained with a positive periodic solution. Concerning the green trajectory, the period and the amplitude of oscillations are slightly increased until their destruction over time so that the solution converges to SS3. Finally, when $S_{ch}^{in} > \sigma_6$, the system exhibits also a bi-stability which becomes between SS3 and SS6.

5. **Conclusion.** In this work, we have extended model (1) of a chlorophenol-mineralising three-tiered microbial 'food web' presented in [31], by considering the model (2) with general growth functions. Our first aim was the theoretical analysis of (2) by providing the existence conditions of all steady states with respect to the operating parameters. Our study considers the effects of the phenol and hydrogen input concentrations, which were neglected in the analytical analysis given in [26], together with the effects of maintenance terms, which were neglected in the theoretical analysis given in [13, 29]. System (2) can have up to eight types of steady states: the washout steady state which always exists, a coexistence steady state of

all degrader populations and six other steady states corresponding to the extinction of one or two degrader populations. Each type of steady state is unique except that of the exclusion only of the hydrogen degraders (SS4) where there are at most two steady states of this type.

In [31], results on the existence of some steady states of model (1) were obtained only numerically without knowing their exact number. Our analytical results on the existence of the steady states of (2) give rigorous proofs for (1).

Our second achievement was to determine theoretically the asymptotic behavior of system (2) in the particular case without maintenance and to analyze numerically the bifurcation diagram by varying the chlorophenol input concentration when $s_1^{\text{in}} = 0$. It shows that the system exhibits a bi-stability where the coexistence steady state can destabilize undergoing a supercritical Hopf bifurcation with the occurrence of a stable periodic solution. These interest phenomena have been already depicted in [26], in the particular case $s_0^{\text{in}} > 0$, $s_1^{\text{in}} = s_2^{\text{in}} = 0$. The possibility of the Hopf bifurcation of the positive steady state is analytically proved in [29], in the case without maintenance. The destabilization of the positive steady state was not detected by the numerical analysis of the operating diagram in [31].

Our works under investigation will focus on the analysis of the stability of steady states of (2) including maintenance and on the operating diagrams which were obtained numerically in [31]. In fact, the operating diagram is very useful for the biologist as discussed in [3, 9, 10] because it allows to predict qualitatively the different asymptotic behaviors of the process according to their control parameters.

Appendix A. Proofs.

Proof of Proposition 1. Since the vector field defined by (2) is $\mathcal{C}^1$, the uniqueness of solution to initial value problems holds. From (2), for $i = 0, 1, 2$,

$$x_i(\tau) = 0, \text{ for any } \tau \geqslant 0 \quad \Rightarrow \quad \dot{x}_i(\tau) = 0.$$

If $x_i(0) = 0$, then $x_i(t) = 0$ for all t since the boundary face where $x_i \equiv 0$ is invariant in the vector field C^1 by system (2). If $x_i(0) > 0$, then $x_i(t) > 0$ for all t since $x_i \equiv 0$ cannot be reached in finite time by trajectories such that $x_i(0) > 0$ by the uniqueness of solutions. On the other hand, one has

$$\begin{aligned}
&s_0(\tau) = 0, \text{ for any } \tau \geqslant 0 \quad \Rightarrow \quad \dot{s}_0(\tau) = Ds_0^{\text{in}} \\
&s_1(\tau) = 0, \text{ for any } \tau \geqslant 0 \quad \Rightarrow \quad \dot{s}_1(\tau) = Ds_1^{\text{in}} + \mu_0(s_0(\tau), s_2(\tau))x_0(\tau) \\
&s_2(\tau) = 0, \text{ for any } \tau \geqslant 0 \quad \Rightarrow \quad \dot{s}_2(\tau) = Ds_2^{\text{in}} + \mu_1(s_1(\tau), 0)x_1(\tau).
\end{aligned}$$

Similarly to case x_i, if $\dot{s}_i(\tau) = 0$, then $s_i(t) \geqslant 0$ for all t. In addition, if $\dot{s}_i(\tau) > 0$, then $s_i(t) \geqslant 0$ for all t. Indeed, for example, consider the case of s_0 where D and s_0^{in} are positive with $s_0(0) \geqslant 0$. Assume that it exists $\tau > 0$ such that $s_0(\tau) = 0$ and $s_0(t) > 0$ for all $t \in (0, \tau)$. It follows that $\dot{s}_0(\tau) \leqslant 0$, which is the desired contradiction with $\dot{s}_0(\tau) = Ds_0^{\text{in}} > 0$.

Further, by considering $z = \omega x_0 + x_1 + x_2 + 2s_0 + 2s_1 + s_2$, we obtain from (2)

$$\dot{z} = D\left(2s_0^{\text{in}} + 2s_1^{\text{in}} + s_2^{\text{in}} - z\right) - \omega a_0 x_0 - a_1 x_1 - a_2 x_2 \leqslant D\left(2s_0^{\text{in}} + 2s_1^{\text{in}} + s_2^{\text{in}} - z\right).$$

Using Gronwall's lemma, we have

$$z(t) \leqslant 2s_0^{\text{in}} + 2s_1^{\text{in}} + s_2^{\text{in}} + \left(z(0) - \left(2s_0^{\text{in}} + 2s_1^{\text{in}} + s_2^{\text{in}}\right)\right)e^{-Dt}, \quad \text{for all} \quad t \geqslant 0. \tag{10}$$

Consequently,

$$z(t) \leqslant \max\left(z(0), 2s_0^{\text{in}} + 2s_1^{\text{in}} + s_2^{\text{in}}\right), \quad \text{for all} \quad t \geqslant 0. \tag{11}$$

Thus, the solutions of (2) are positively bounded and are defined for all $t \geqslant 0$. From (11), it can be deduced that the set Ω is positively invariant and from (10), it is a global attractor for (2). □

To determine the number of SS3, SS4 and SS7-type steady states and the conditions of their existence, we need the following result.

Lemma 3. *The equation $\psi_i(s_0) = y$, $i = 0, 1$, has a solution in the interval J_i defined in Table 1 if and only if $\mu_i\left(s_i^{\text{in}}, s_2^{\text{in}}\right) > y$. The mapping ψ_i 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 $s^{\text{in}} \geqslant \phi_1(D)$.*

- *When $\omega \geqslant 1$, 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 $\omega = 1$, $\phi_1(D) = \Psi\left(s_2^0(D), D\right) > 0$.*
- *When $\omega < 1$, there exist two solutions which are equal when $s^{\text{in}} = \phi_1(D)$. Moreover, $\phi_1(D) > 0$.*

Proof. Recall that $J_0 = \left(\max\left(0, s_0^{\text{in}} - s_2^{\text{in}}/\omega\right), s_0^{\text{in}}\right)$. If $s_2^{\text{in}} - \omega s_0^{\text{in}} > 0$, one has $\psi_0(0) = \mu_0\left(0, s_2^{\text{in}} - \omega s_0^{\text{in}}\right) = 0$ and if $s_2^{\text{in}} - \omega s_0^{\text{in}} \leqslant 0$, then $\psi_0\left(s_0^{\text{in}} - s_2^{\text{in}}/\omega\right) = \mu_0\left(s_0^{\text{in}} - s_2^{\text{in}}/\omega, 0\right) = 0$. Thus, $\psi_0\left(\max\left(0, s_0^{\text{in}} - s_2^{\text{in}}/\omega\right)\right) = 0$. On the other hand, $\psi_0\left(s_0^{\text{in}}\right) = \mu_0\left(s_0^{\text{in}}, s_2^{\text{in}}\right)$. Therefore, there exists a solution $s_0 \in J_0$ satisfying $\psi_0(s_0) = y$ if and only if $\mu_0\left(s_0^{\text{in}}, s_2^{\text{in}}\right) > y$. Since ψ_0 is monotonically increasing, if it exists, this solution is unique. Indeed, we have

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

which is positive thanks to (H4). Now, recall that $J_1 = \left(0, s_1^{\text{in}}\right)$. We have $\psi_1(0) = \mu_1\left(0, s_1^{\text{in}} + s_2^{\text{in}}\right) = 0$ and $\psi_1\left(s_1^{\text{in}}\right) = \mu_1\left(s_1^{\text{in}}, s_2^{\text{in}}\right)$. Therefore, there exists a solution $s_1 \in J_1$ satisfying $\psi_1(s_1) = y$ if and only if $\mu_1\left(s_1^{\text{in}}, s_2^{\text{in}}\right) > y$. Since ψ_1 is monotonically increasing, if it exists, this solution is unique. Indeed, we have

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

which is positive thanks to (H5). Let us consider now the existence of solution of the equation $\Psi(s_2, D) = s^{\text{in}}$. From the definitions of s_2^0 and s_2^1 given in Table 1, we have $M_0\left(D + a_0, s_2^0\right) = +\infty$ and $M_1\left(D + a_1, s_2^1\right) = +\infty$. From the definition of $\Psi(s_2, D)$ given in Table 1, we have

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

Moreover, we have for all $s_2 \in \left(s_2^0, s_2^1\right)$ and $D \in I_1$,

$$\frac{\partial \Psi}{\partial s_2}(s_2, D) = (1 - \omega)\frac{\partial M_0}{\partial s_2}(D + a_0, s_2) + \frac{\partial M_1}{\partial s_2}(D + a_1, s_2) + 1. \tag{12}$$

Let $s_2 > 0$. Under (H4) and (H5), we have

$$\begin{aligned} \frac{\partial M_0}{\partial s_2}(y, s_2) &= -\frac{\partial \mu_0}{\partial s_2}(s_0, s_2)\left[\frac{\partial \mu_0}{\partial s_0}(s_0, s_2)\right]^{-1} < 0, \text{ for all } y \in (0, \mu_0(+\infty, s_2)), \\ \frac{\partial M_1}{\partial s_2}(y, s_2) &= -\frac{\partial \mu_1}{\partial s_2}(s_1, s_2)\left[\frac{\partial \mu_1}{\partial s_1}(s_1, s_2)\right]^{-1} > 0, \text{ for all } y \in (0, \mu_1(+\infty, s_2)). \end{aligned} \tag{13}$$

For $\omega \geqslant 1$, we deduce that the function $s_2 \mapsto \Psi(s_2, D)$ is monotonically increasing by using (12). If $\omega = 1$, then $\Psi\left(s_2^0, D\right) > 0$. When $\omega < 1$, the remaining assertions follow immediately by using assumption (H8). □

Proof of Theorem 1. The steady states are obtained by setting the right-hand sides of equations in (2) equal to zero:

$$[\mu_0(s_0,s_2) - D - a_0]\, x_0 = 0 \tag{14}$$
$$[\mu_1(s_1,s_2) - D - a_1]\, x_1 = 0 \tag{15}$$
$$[\mu_2(s_2) - D - a_2]\, x_2 = 0 \tag{16}$$
$$D\left(s_0^{\text{in}} - s_0\right) - \mu_0(s_0,s_2)\, x_0 = 0 \tag{17}$$
$$D\left(s_1^{\text{in}} - s_1\right) + \mu_0(s_0,s_2)\, x_0 - \mu_1(s_1,s_2)\, x_1 = 0 \tag{18}$$
$$D\left(s_2^{\text{in}} - s_2\right) + \mu_1(s_1,s_2)\, x_1 - \omega\mu_0(s_0,s_2)\, x_0 - \mu_2(s_2)\, x_2 = 0. \tag{19}$$

Using (17)+(14), (18)-(14)+(15) and (19)+ ω(14)-(15)+(16), one obtains the set of equations

$$\begin{cases} D\left(s_0^{\text{in}} - s_0\right) - (D + a_0)\, x_0 = 0 \\ D\left(s_1^{\text{in}} - s_1\right) + (D + a_0)\, x_0 - (D + a_1)\, x_1 = 0 \\ D\left(s_2^{\text{in}} - s_2\right) - \omega\,(D + a_0)\, x_0 + (D + a_1)\, x_1 - (D + a_2)x_2 = 0. \end{cases} \tag{20}$$

We can solve (20) and obtain x_0, x_1 and x_2 with respect to s_0, s_1 and s_2:

$$x_0 = \tfrac{D}{D+a_0}\left(s_0^{\text{in}} - s_0\right), \tag{21}$$
$$x_1 = \tfrac{D}{D+a_1}\left(s_0^{\text{in}} - s_0 + s_1^{\text{in}} - s_1\right), \tag{22}$$
$$x_2 = \tfrac{D}{D+a_2}\left((1-\omega)\left(s_0^{\text{in}} - s_0\right) + s_1^{\text{in}} - s_1 + s_2^{\text{in}} - s_2\right). \tag{23}$$

We can also solve (20) and obtain s_0, s_1 and s_2 with respect to x_0, x_1 and x_2:

$$s_0 = s_0^{\text{in}} - \tfrac{D+a_0}{D} x_0, \tag{24}$$
$$s_1 = s_1^{\text{in}} + \tfrac{D+a_0}{D} x_0 - \tfrac{D+a_1}{D} x_1, \tag{25}$$
$$s_2 = s_2^{\text{in}} - \omega\tfrac{D+a_0}{D} x_0 + \tfrac{D+a_1}{D} x_1 - \tfrac{D+a_2}{D} x_2. \tag{26}$$

- For the steady state SS1, $x_0 = x_1 = x_2 = 0$. Hence, (24), (25) and (26) result in $s_0 = s_0^{\text{in}}$, $s_1 = s_1^{\text{in}}$ and $s_2 = s_2^{\text{in}}$. Thus, SS1 always exists.
- For SS2, $x_0 = x_1 = 0$ and $x_2 > 0$. Hence, (24) and (25) result in $s_0 = s_0^{\text{in}}$ and $s_1 = s_1^{\text{in}}$. Therefore, (23) results in

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

  Since $x_2 > 0$, (16) results in $\mu_2(s_2) = D + a_2$. Using definition of M_2 in Table 1, we have

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

  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 $\mu_2\left(s_2^{\text{in}}\right) > D + a_2$, thanks to (H6).
- For SS3, $x_1 = x_2 = 0$ and $x_0 > 0$. Hence, (21) results in

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

  Using this expression together with $x_1 = x_2 = 0$ in (25) and (26) result in

  $$s_1 = s_1^{\text{in}} + s_0^{\text{in}} - s_0 \quad \text{and} \quad s_2 = s_2^{\text{in}} - \omega(s_0^{\text{in}} - s_0). \tag{27}$$

  Since $x_0 > 0$, (14) results in

  $$\mu_0(s_0,s_2) = D + a_0. \tag{28}$$

  Replacing s_2 by its expression (27) with respect to s_0 in (28) results in

  $$\psi_0(s_0) = D + a_0, \tag{29}$$

where ψ_0 is the function defined in Table 1. SS3 exists if and only if equation (29) has a positive solution and the s_1, s_2 and x_0-components 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, (29) must have a solution in the interval J_0. Using Lemma 3, (29) has a solution in the interval J_0 if and only if $\mu_0\left(s_0^{\text{in}}, s_2^{\text{in}}\right) > D + a_0$. If it exists, this solution is unique.

- For SS4, $x_0 > 0$, $x_1 > 0$ and $x_2 = 0$. Hence, (21) and (22) result in

$$x_0 = \tfrac{D}{D+a_0}\left(s_0^{\text{in}} - s_0\right) \quad \text{and} \quad x_1 = \tfrac{D}{D+a_1}\left(s_0^{\text{in}} - s_0 + s_1^{\text{in}} - s_1\right). \tag{30}$$

Since $x_0 > 0$ and $x_1 > 0$, (14) and (15) result in $\mu_0(s_0, s_2) = D + a_0$ and $\mu_1(s_1, s_2) = D + a_1$. Using definitions of M_0 and M_1 in Table 1, we obtain

$$s_0 = M_0(D + a_0, s_2) \quad \text{and} \quad s_1 = M_1(D + a_1, s_2). \tag{31}$$

Using (30) together with $x_2 = 0$ in (26), we have

$$s_2 = s_2^{\text{in}} - \omega\left(s_0^{\text{in}} - s_0\right) + s_0^{\text{in}} - s_0 + s_1^{\text{in}} - s_1. \tag{32}$$

Replacing s_0 and s_1 by their expressions (31) with respect to s_2 in (32), it follows that, s_2 is a solution of equation

$$\Psi\left(s_2, D\right) = (1-\omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}}, \tag{33}$$

where Ψ is the function defined in Table 1. According to Lemma 3, SS4 exists if and only if $(1-\omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}} \geqslant \phi_1(D)$, and the solution s_2 of (33) is such that the x_0 and x_1-components are positive which is equivalent to $s_0^{\text{in}} > M_0\left(D + a_0, s_2\right)$ and $s_0^{\text{in}} + s_1^{\text{in}} > M_0\left(D + a_0, s_2\right) + M_1\left(D + a_1, s_2\right)$. The existence of a unique or two steady states of the form SS4 according to ω follows immediately from Lemma 3.

- For SS5, $x_0 > 0$, $x_2 > 0$ and $x_1 = 0$. Using (21) together with $x_1 = 0$ in (25) results in

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

Using (21) and this expression in (23) results in

$$x_0 = \tfrac{D}{D+a_0}\left(s_0^{\text{in}} - s_0\right) \quad \text{and} \quad x_2 = \tfrac{D}{D+a_2}\left(s_2^{\text{in}} - s_2 - \omega\left(s_0^{\text{in}} - s_0\right)\right).$$

Since $x_0 > 0$ and $x_2 > 0$, (14) and (16) result in $\mu_0(s_0, s_2) = D + a_0$ and $\mu_2(s_2) = D + a_2$. Using definitions of M_0, M_2 and φ_0 in Table 1, it follows that

$$s_2 = M_2(D + a_2) \quad \text{and} \quad s_0 = \varphi_0(D).$$

SS5 exists if and only if its components x_0, x_2 and s_1 are positive. This condition is equivalent to $s_0^{\text{in}} > \varphi_0(D)$ and $s_2^{\text{in}} - \omega s_0^{\text{in}} > M_2(D + a_2) - \omega\varphi_0(D)$.

- For SS6, $x_0 > 0$, $x_1 > 0$ and $x_2 > 0$. Then, as a consequence of (14), (15) and (16), 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 of M_0, M_1, M_2, φ_0 and φ_1 in Table 1, it follows that s_2, s_0 and s_1 are given by:

$$s_2 = M_2(D + a_2), \quad s_0 = \varphi_0(D), \quad s_1 = \varphi_1(D),$$

(21), (22) and (23) give the x-components of SS6 in Table 2. SS6 exists if and only if its x-components are positive, that is, $s_0^{\text{in}} > s_0$, $s_1^{\text{in}} + s_0^{\text{in}} > s_0 + s_1$ and $(1-\omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}} > (1-\omega)s_0 + s_1 + s_2$. Using the s-components of SS6, these conditions are the same as those in Table 3.

- For SS7, $x_0 = x_2 = 0$ and $x_1 > 0$. Hence, (24) results in $s_0 = s_0^{\text{in}}$. From (22), we have
$$x_1 = \frac{D}{D+a_1}\left(s_1^{\text{in}} - s_1\right).$$
Using this expression together with $x_0 = x_2 = 0$ in (26) results in
$$s_2 = s_2^{\text{in}} + s_1^{\text{in}} - s_1. \tag{34}$$
Since $x_1 > 0$, then, as a consequence of (15), we obtain:
$$\mu_1(s_1, s_2) = D + a_1.$$
Replacing s_2 by its expression (34) with respect to s_1 results in
$$\psi_1(s_1) = D + a_1, \tag{35}$$
where ψ_1 is defined in Table 1. SS7 exists if and only if equation (35) has a positive solution and the s_2 and x_1-components of SS7 are positive. This last condition is equivalent to $0 < s_1 < s_1^{\text{in}}$, that is, (35) must have a solution in the interval J_1. Using Lemma 3, there exists a solution $s_1 \in J_1$, satisfying (35), if and only if $\mu_1\left(s_1^{\text{in}}, s_2^{\text{in}}\right) > D + a_1$. If it exists, this solution is unique.
- For SS8, $x_0 = 0$, $x_1 > 0$ and $x_2 > 0$. Hence, (24) results in $s_0 = s_0^{\text{in}}$. Using this expression in (22) and (23) results in
$$x_1 = \frac{D}{D+a_1}\left(s_1^{\text{in}} - s_1\right), \quad x_2 = \frac{D}{D+a_2}\left(s_1^{\text{in}} - s_1 + s_2^{\text{in}} - s_2\right).$$
Since $x_1 > 0$ and $x_2 > 0$, as a consequence of (15) and (16), we have $\mu_1(s_1, s_2) = D + a_1$ and $\mu_2(s_2) = D + a_2$. Using definitions of M_1, M_2 and $\varphi_1(D)$ in Table 1, it follows that s_2 and s_1 are given by:
$$s_2 = M_2(D + a_2), \quad s_1 = \varphi_1(D).$$
SS8 exists if and only if its components x_1 and x_2 are positive, that is, $s_1^{\text{in}} > s_1$ and $s_1^{\text{in}} + s_2^{\text{in}} > s_1 + s_2$. Using the s-components of SS8, these conditions are the same as those in Table 3.

□

Proof of Proposition 2. If $s_1^{\text{in}} = 0$, then $\mu_1\left(s_1^{\text{in}}, s_2^{\text{in}}\right) = 0$, so that the conditions $\mu_1\left(s_1^{\text{in}}, s_2^{\text{in}}\right) > D + a_1$ 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 $\mu_2\left(s_2^{\text{in}}\right) = 0$ and $\mu_0\left(s_0^{\text{in}}, s_2^{\text{in}}\right) = 0$, so that the existence conditions $\mu_2\left(s_2^{\text{in}}\right) > D + a_2$, $\mu_0\left(s_0^{\text{in}}, s_2^{\text{in}}\right) > D + a_0$ 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 3 is written $0 \geqslant \phi_1(D)$. This condition cannot be satisfied, since $\phi_1(D) = \Psi\left(s_2^0, D\right) > 0$ from Lemma 3. Thus, SS4 does not exist if $\omega = 1$. When $\omega > 1$, we have s_2 is solution of equation
$$(1 - \omega)\left(s_0^{\text{in}} - s_0\right) = s_1 + s_2.$$
Since $s_1 > 0$ and $s_2 > 0$, then we have necessarily
$$(1 - \omega)\left(s_0^{\text{in}} - s_0\right) > 0,$$

so that $s_0^{\text{in}} - s_0 < 0$, which contradicts the positivity of the x_0-component of SS4 in Table 2. 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

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

If $0 < \omega < 1$, then

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

thus, the second and the third existence conditions of SS4 in Table 3 are satisfied when $\omega < 1$. Therefore, SS4 exists if and only if $(1-\omega)s_0^{\text{in}} \geqslant \phi_1(D)$.

Regarding the steady state SS6 in the particular case $s_1^{\text{in}} = s_2^{\text{in}} = 0$, the first existence condition in Table 3 becomes

$$(1-\omega)s_0^{\text{in}} > \phi_2(D), \tag{36}$$

which is equivalent to

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

When $\omega \geqslant 1$, this last inequality cannot hold, since $s_0^{\text{in}} > \varphi_0(D)$, so that SS6 does not exist. If $\omega < 1$, condition (36) 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 3. Thus, (36) is the only existence condition of SS6. □

Proof of Theorem 2. In the particular case without maintenance, the steady states and their existence conditions are easily obtained from Tables 2 and 3 by putting $a_i = 0$, $i = 0, 1, 2$. To analyze the local stability, we use the change of variables:

$$z_0 = x_0 + s_0, \quad z_1 = x_1 + s_1 - x_0, \quad z_2 = \omega x_0 - x_1 + x_2 + s_2, \tag{37}$$

such that model (2) takes the form

$$\left\{\begin{array}{rcl} \dot{x}_0 &=& -Dx_0 + \mu_0\left(z_0 - x_0, z_2 - \omega x_0 + x_1 - x_2\right)x_0 \\ \dot{x}_1 &=& -Dx_1 + \mu_1\left(z_1 + x_0 - x_1, z_2 - \omega x_0 + x_1 - x_2\right)x_1 \\ \dot{x}_2 &=& -Dx_2 + \mu_2\left(z_2 - \omega x_0 + x_1 - x_2\right)x_2 \\ \dot{z}_0 &=& D\left(s_0^{\text{in}} - z_0\right) \\ \dot{z}_1 &=& D\left(s_1^{\text{in}} - z_1\right) \\ \dot{z}_2 &=& D\left(s_2^{\text{in}} - z_2\right). \end{array}\right. \tag{38}$$

The steady states SS1, SS2,..., SS8 of (38) now take the form $\left(x_0, x_1, x_2, s_0^{\text{in}}, s_1^{\text{in}}, s_2^{\text{in}}\right)$ where the x_0-components of each steady state are given by those in Table 2 with $a_i = 0$. The Jacobian matrix of (38) has an upper block triangular form:

$$\mathbf{J} = \begin{bmatrix} \mathbf{J_1} & \mathbf{J_2} \\ \mathbf{0} & \mathbf{J_3} \end{bmatrix}, \quad \text{where} \quad \mathbf{J_2} = \begin{bmatrix} Ex_0 & 0 & Fx_0 \\ 0 & Gx_1 & -Hx_1 \\ 0 & 0 & Ix_2 \end{bmatrix},$$

$$\mathbf{J_1} = \begin{bmatrix} \mu_0 - D - (E+\omega F)x_0 & Fx_0 & -Fx_0 \\ (G+\omega H)x_1 & \mu_1 - D - (G+H)x_1 & Hx_1 \\ -\omega I x_2 & Ix_2 & \mu_2 - D - Ix_2 \end{bmatrix}, \tag{39}$$

and $\mathbf{J_3}$ is the 3×3 diagonal matrix whose diagonal elements are all $-D$. Consequently, three eigenvalues of $\mathbf{J}$ are given by $-D$ and the three other eigenvalues are given by those of the 3×3 upper-left matrix $\mathbf{J_1}$. Thus, the stability of the steady state is determined by the sign of the real parts of the eigenvalues of $\mathbf{J_1}$. Note that, the functions E, F, G, H and I defined by (5) 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.

- For SS1, the characteristic polynomial of $\mathbf{J_1}$ is $P_1(\lambda) = (\lambda-\lambda_1)(\lambda-\lambda_2)(\lambda-\lambda_3)$, where
$$\lambda_1 = \mu_0\left(s_0^{\text{in}}, s_2^{\text{in}}\right) - D, \quad \lambda_2 = \mu_1\left(s_1^{\text{in}}, s_2^{\text{in}}\right) - D, \quad \lambda_3 = \mu_2\left(s_2^{\text{in}}\right) - D.$$
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 of $\mathbf{J_1}$ is $P_2(\lambda) = (\lambda-\lambda_1)(\lambda-\lambda_2)(\lambda-\lambda_3)$, where
$$\lambda_1 = \mu_0\left(s_0^{\text{in}}, M_2(D)\right) - D, \quad \lambda_2 = \mu_1\left(s_1^{\text{in}}, M_2(D)\right) - D, \quad \lambda_3 = -Ix_2.$$
As $\lambda_3 < 0$, SS2 is stable if and only if $\lambda_1 < 0$ and $\lambda_2 < 0$. Since M_0 and M_1 are increasing, these conditions are equivalent to the stability conditions of SS2 in Table 4.
- For SS3, the characteristic polynomial of $\mathbf{J_1}$ is $P_3(\lambda) = (\lambda-\lambda_1)(\lambda-\lambda_2)(\lambda-\lambda_3)$, where
$$\lambda_1 = \mu_1\left(s_1^{\text{in}} + s_0^{\text{in}} - s_0, s_2^{\text{in}} - \omega\left(s_0^{\text{in}} - s_0\right)\right) - D, \quad \lambda_2 = \mu_2\left(s_2^{\text{in}} - \omega\left(s_0^{\text{in}} - s_0\right)\right) - D,$$
and $\lambda_3 = -(E+\omega F)x_0$, where s_0 is the solution in the interval J_0 of equation $\psi_0(s_0) = D$. As $\lambda_3 < 0$, 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, the condition $\lambda_2 < 0$ is equivalent to
$$s_2^{\text{in}} - \omega\left(s_0^{\text{in}} - s_0\right) < M_2(D) \quad \Longleftrightarrow \quad s_0 < \left(M_2(D) - s_2^{\text{in}}\right)/\omega + s_0^{\text{in}}. \tag{40}$$
As the function ψ_0 is increasing and $\psi_0(s_0) = D$, (40) is equivalent to
$$D < \mu_0\left(\left(M_2(D) - s_2^{\text{in}}\right)/\omega + s_0^{\text{in}}, M_2(D)\right).$$
Since M_0 is increasing, this condition is equivalent to the second stability condition of SS3 in Table 4.
- For SS4, the characteristic polynomial of $\mathbf{J_1}$ is $P_4(\lambda) = (\lambda-\lambda_1)(\lambda^2 + c_1\lambda + c_2)$, where
$$\lambda_1 = \mu_2(s_2) - D,\ c_1 = (E+\omega F)x_0 + (G+H)x_1,\ c_2 = (E(G+H) + (\omega-1)FG)x_0x_1,$$
and s_2 is defined by (33). We always have $c_1 > 0$. Using (5) and (13), we obtain
$$\frac{\partial M_0}{\partial s_2}(D, s_2) = -\frac{F}{E} \quad \text{and} \quad \frac{\partial M_1}{\partial s_2}(D, s_2) = \frac{H}{G}.$$
Using (12), it follows that
$$\frac{\partial \Psi}{\partial s_2}(s_2, D) = \frac{F}{E}(\omega-1) + \frac{H}{G} + 1 = \frac{E(G+H)+(\omega-1)FG}{EG}. \tag{41}$$
Since E and G are positive, condition $c_2 > 0$ is equivalent to $\frac{\partial \Psi}{\partial s_2}(s_2, D) > 0$. As μ_2 is increasing, SS4 is stable if and only if
$$s_2 < M_2(D) \quad \text{and} \quad \frac{\partial \Psi}{\partial s_2}(s_2, D) > 0,$$
which is equivalent to
$$(1-\omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}} < \phi_2(D), \quad \phi_3(D) > 0 \quad \text{and} \quad \frac{\partial \Psi}{\partial s_2}(s_2, D) > 0. \tag{42}$$

Indeed, when $\omega \geqslant 1$, the mapping $s_2 \mapsto \Psi(s_2, D)$ is increasing for all $s_2 \in (s_2^0, s_2^1)$ (see Lemma 3). Hence, the condition $s_2 < M_2(D)$ is equivalent to

$$(1-\omega)s_0^{\text{in}} + s_1^{\text{in}} + s_2^{\text{in}} = \Psi(s_2, D) < \Psi(M_2(D), D) = \phi_2(D). \tag{43}$$

In addition, $s_2 < M_2(D)$ implies that $\phi_3(D) > 0$. Now, when $\omega < 1$, from Lemma 3 and using Hypothesis (H8), equation (33) has at most two solutions $s_2^{*1} < s_2^{*2}$, such that $\frac{\partial \Psi}{\partial s_2}\left(s_2^{*1}, D\right) < 0$ and $\frac{\partial \Psi}{\partial s_2}\left(s_2^{*2}, D\right) > 0$ (see Fig. 1). Moreover, the mapping $s_2 \mapsto \Psi(s_2, D)$ is increasing for all $s_2 \in \left(\overline{s}_2, s_2^1\right)$. Thus, the condition $s_2^{*2} < M_2(D)$ implies the first and the second conditions of (42). Inversely, if the first condition of (42) or equivalently (43) holds, then

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

This last condition is in contradiction with the second condition of (42).

- For SS5, the characteristic polynomial of $\mathbf{J_1}$ is $P_5(\lambda) = (\lambda - \lambda_1)(\lambda^2 + c_1\lambda + c_2)$, where

$$\lambda_1 = \mu_1\left(s_0^{\text{in}} + s_1^{\text{in}} - M_0(D, M_2(D)), M_2(D)\right) - D,\ c_1 = (E + \omega F)x_0 + Ix_2,$$

and $c_2 = EIx_0x_2$. As $c_1 > 0$ and $c_2 > 0$, SS5 is stable if and only if $\lambda_1 < 0$. Since M_1 is increasing, this stability condition of SS5 is equivalent to that in Table 4.
- For SS6, the characteristic polynomial of $\mathbf{J_1}$ is $P_6(\lambda) = \lambda^3 + c_1\lambda^2 + c_2\lambda + c_3$, where

$$c_1 = Ix_2 + (G+H)x_1 + (E+\omega F)x_0, \quad c_3 = EGIx_0x_1x_2$$
$$c_2 = (E(G+H) + (\omega - 1)FG)x_0x_1 + EIx_0x_2 + GIx_1x_2.$$

From (41), one has $E(G+H) + (\omega-1)FG = EG\phi_3(D)$. Since c_1 and c_3 are positive, according to the Routh–Hurwitz criterion, SS6 is stable if and only if

$$\phi_4\left(D, s_0^{\text{in}}, s_1^{\text{in}}, s_2^{\text{in}}\right) := c_1c_2 - c_3 > 0, \tag{44}$$

where the function ϕ_4 can be written as its expression (4). If $\phi_3(D) \geqslant 0$, then condition (44) holds so that SS6 is stable.
- For SS7, the characteristic polynomial of $\mathbf{J_1}$ is $P_7(\lambda) = (\lambda - \lambda_1)(\lambda - \lambda_2)(\lambda - \lambda_3)$, where

$$\lambda_1 = \mu_0\left(s_0^{\text{in}}, s_2^{\text{in}} + s_1^{\text{in}} - s_1\right) - D, \lambda_2 = \mu_2\left(s_2^{\text{in}} + s_1^{\text{in}} - s_1\right) - D, \lambda_3 = -(G+H)x_1,$$

where s_1 is the solution in the interval J_1 of equation $\psi_1(s_1) = D$. Since $\lambda_3 < 0$, SS7 is stable if and only if $\lambda_1 < 0$ and $\lambda_2 < 0$. Since the functions M_2 and M_3 are increasing, the conditions $\lambda_1 < 0$ and $\lambda_2 < 0$ are equivalent to

$$s_1 > s_2^{\text{in}} + s_1^{\text{in}} - M_3\left(s_0^{\text{in}}, D\right), \quad s_1 > s_2^{\text{in}} + s_1^{\text{in}} - M_2(D). \tag{45}$$

Since the function ψ_1 is increasing and $\psi_1(s_1) = D$, (45) is equivalent to

$$\mu_1\left(s_2^{\text{in}} + s_1^{\text{in}} - M_3\left(s_0^{\text{in}}, D\right), M_3\left(s_0^{\text{in}}, D\right)\right) < D,\ \mu_1\left(s_2^{\text{in}} + s_1^{\text{in}} - M_2(D), M_2(D)\right) < D.$$

Since M_1 is increasing, these stability conditions of SS7 are equivalent to those in Table 4.
- For SS8, the characteristic polynomial of $\mathbf{J_1}$ is $P_8(\lambda) = (\lambda - \lambda_1)(\lambda^2 + c_1\lambda + c_2)$, where

$$\lambda_1 = \mu_0\left(s_0^{\text{in}}, M_2(D)\right) - D, \quad c_1 = (G+H)x_1 + Ix_2, \quad c_2 = GIx_1x_2.$$

As c_1 and c_2 are positive, SS8 is stable if and only if $\lambda_1 < 0$. Since M_0 is increasing, this stability condition of SS8 is equivalent to that in Table 4.

□

Proof of Proposition 3. Using the change of variables (8) and from Tables 3 and 4, the necessary and sufficient conditions of existence and stability of steady states of (1) are summarized in Table 9 when $S^{\text{in}}_{\text{ph}} = 0$ and $k_{\text{dec,ch}} = k_{\text{dec,ph}} = k_{\text{dec,H}_2} = 0$. Since $s^{\text{in}}_1 = 0$, SS7 and SS8 do not exist, as shown in Proposition 2. Using Table 9, we see that:

TABLE 9. Existence and local stability conditions of steady states of (1), when $S^{\text{in}}_{\text{ph}} = 0$ and $k_{\text{dec,ch}} = k_{\text{dec,ph}} = k_{\text{dec,H}_2} = 0$. All functions are given in Tables 1 and 11, while ϕ_4 and μ_i are given by (4) and (9).

	Existence conditions	Stability conditions
SS1	Always exists	$\mu_0\left(YS^{\text{in}}_{\text{ch}}, S^{\text{in}}_{\text{H}_2}\right) < D$, $\mu_2\left(S^{\text{in}}_{\text{H}_2}\right) < D$
SS2	$\mu_2\left(S^{\text{in}}_{\text{H}_2}\right) > D$	$YS^{\text{in}}_{\text{ch}} < \varphi_0(D)$
SS3	$\mu_0\left(YS^{\text{in}}_{\text{ch}}, S^{\text{in}}_{\text{H}_2}\right) > D$	$\mu_1\left(YS^{\text{in}}_{\text{ch}} - s_0, S^{\text{in}}_{\text{H}_2} + \omega\left(YS^{\text{in}}_{\text{ch}} - s_0\right)\right) < D$ $S^{\text{in}}_{\text{H}_2} - \omega YS^{\text{in}}_{\text{ch}} < M_2(D) - \omega\varphi_0(D)$ with s_0 solution of $\psi_0(s_0) = D$
SS4	$(1-\omega)YS^{\text{in}}_{\text{ch}} + S^{\text{in}}_{\text{H}_2} \geqslant \phi_1(D)$, $YS^{\text{in}}_{\text{ch}} > M_0(D, s_2) + M_1(D, s_2)$ with s_2 solution of $\Psi(s_2, D) = (1-\omega)YS^{\text{in}}_{\text{ch}} + S^{\text{in}}_{\text{H}_2}$	$(1-\omega)YS^{\text{in}}_{\text{ch}} + S^{\text{in}}_{\text{H}_2} < \phi_2(D)$, $\frac{\partial\Psi}{\partial s_2}(s_2, D) > 0, \quad \phi_3(D) > 0$
SS5	$YS^{\text{in}}_{\text{ch}} > \varphi_0(D)$, $S^{\text{in}}_{\text{H}_2} - \omega YS^{\text{in}}_{\text{ch}} > M_2(D) - \omega\varphi_0(D)$	$YS^{\text{in}}_{\text{ch}} < \varphi_0(D) + \varphi_1(D)$
SS6	$(1-\omega)YS^{\text{in}}_{\text{ch}} + S^{\text{in}}_{\text{H}_2} > \phi_2(D)$, $YS^{\text{in}}_{\text{ch}} > \varphi_0(D) + \varphi_1(D)$	$\phi_3(D) \geqslant 0$ or $\phi_3(D) < 0$ and $\phi_4(D, S^{\text{in}}_{\text{ch}}, S^{\text{in}}_{\text{H}_2}) > 0$

- SS1 always exists and is unstable, since the second stability condition in Table 9 does not hold, as
$$\mu_2\left(S^{\text{in}}_{\text{H}_2}\right) \simeq 1.0845 > D = 0.01. \tag{46}$$
- SS2 exists, since the existence condition in Table 9 holds from (46). It is stable if and only if
$$S^{\text{in}}_{\text{ch}} < \varphi_0(D)/Y =: \sigma_3.$$
- SS3 exists if and only if $\mu_0\left(YS^{\text{in}}_{\text{ch}}, S^{\text{in}}_{\text{H}_2}\right) > D$, which is equivalent to
$$S^{\text{in}}_{\text{ch}} > (M_0(D, S^{\text{in}}_{\text{H}_2}))/Y =: \sigma_1.$$
For $S^{\text{in}}_{\text{ch}} = \sigma_1$, there is a transcritical bifurcation of SS3 and SS1, which have the same components at σ_1 (see Table 2). Consider the function $y = F(S^{\text{in}}_{\text{ch}})$ defined by:
$$F(S^{\text{in}}_{\text{ch}}) = \mu_1(YS^{\text{in}}_{\text{ch}} - s_0, S^{\text{in}}_{\text{H}_2} + \omega(YS^{\text{in}}_{\text{ch}} - s_0)), \tag{47}$$
where s_0 depends also on $S^{\text{in}}_{\text{ch}}$. The first stability condition of SS3 in Table 9 is written $F\left(S^{\text{in}}_{\text{ch}}\right) < D$. Fig. 6 shows that this condition holds for all $S^{\text{in}}_{\text{ch}} > \sigma_1$, since the maximum of the function F is smaller than 0.0013 and $D = 0.01$. From the second stability condition, SS3 is stable if and only if
$$S^{\text{in}}_{\text{ch}} > \frac{S^{\text{in}}_{\text{H}_2} - M_2(D) + \omega\varphi_0(D)}{\omega Y} =: \sigma_4.$$

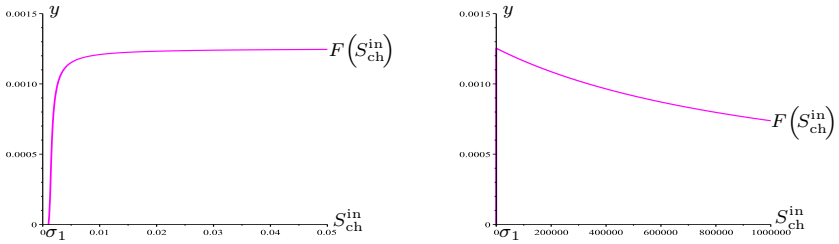

FIGURE 6. Curve of the function $y = F\left(S_{\text{ch}}^{\text{in}}\right)$ showing that $F\left(S_{\text{ch}}^{\text{in}}\right) < 0.0013$, for all $S_{\text{ch}}^{\text{in}} > \sigma_1$.

- Recall that $\omega \simeq 0.53 < 1$ for the set of parameters given in Table 10. Therefore, equation $\Psi(s_2, D) = (1-\omega)YS_{\text{ch}}^{\text{in}} + S_{\text{H}_2}^{\text{in}}$ admits two solutions s_2^{*1} and s_2^{*2} which correspond to two steady states SS4^1 and SS4^2, respectively. When it exists, SS4^1 is unstable, as stated in Remark 3. From Table 9, the first existence condition of these steady states holds if and only if

$$S_{\text{ch}}^{\text{in}} \geq \frac{\phi_1(D) - S_{\text{H}_2}^{\text{in}}}{(1-\omega)Y} =: \sigma_2.$$

Fig. 7 shows that the second existence condition of SS4^1 and SS4^2 in Table 9 holds, for all $S_{\text{ch}}^{\text{in}} \in [\sigma_2, 0.05]$, since the straight line of equation $y = YS_{\text{ch}}^{\text{in}}$ is above the curves of the functions $y = M_0\left(D, s_2^{*i}\right) + M_1\left(D, s_2^{*i}\right)$, for $i = 1, 2$, respectively. SS4^2 is unstable, since the third stability condition does not hold as $\phi_3(D) \simeq -6513 < 0$. Therefore, SS4^1 and SS4^2 exist and are unstable for all $S_{\text{ch}}^{\text{in}} \geq \sigma_2$. They disappear for $S_{\text{ch}}^{\text{in}} < \sigma_2$. For $S_{\text{ch}}^{\text{in}} = \sigma_2$ there is a saddle-node bifurcation. For $S_{\text{ch}}^{\text{in}} = \sigma_5$ there is a transcritical bifurcation of SS4^1 and SS6.

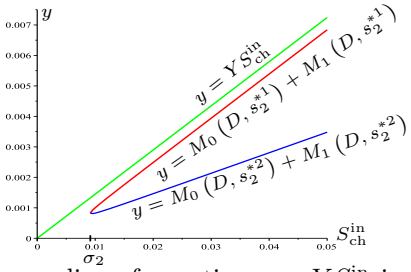

FIGURE 7. The green line of equation $y = YS_{\text{ch}}^{\text{in}}$ is above the red and blue curves of the functions $M_0\left(D, s_2^{*i}\right) + M_1\left(D, s_2^{*i}\right)$, $i = 1, 2$.

- From Table 9, SS5 exists if and only if

$$\sigma_3 := \frac{\varphi_0(D)}{Y} < S_{\text{ch}}^{\text{in}} < \frac{S_{\text{H}_2}^{\text{in}} - M_2(D) + \omega\varphi_0(D)}{\omega Y} =: \sigma_4.$$

For $S_{\text{ch}}^{\text{in}} = \sigma_3$, there is a transcritical bifurcation of SS5 and SS2. For $S_{\text{ch}}^{\text{in}} = \sigma_4$, there is a transcritical bifurcation of SS5 and SS3. When it exists, SS5 is stable since

$$S_{\text{ch}}^{\text{in}} < \sigma_4 \simeq 0.011191 < \frac{\varphi_0(D) + \varphi_1(D)}{Y} \simeq 0.013717.$$

- From Table 9, SS6 exists if and only if

$$S_{\text{ch}}^{\text{in}} > \frac{\phi_2(D) - S_{\text{H}_2}^{\text{in}}}{(1-\omega)Y} =: \sigma_5 \simeq 0.016575, \quad S_{\text{ch}}^{\text{in}} > \frac{\varphi_0(D) + \varphi_1(D)}{Y} \simeq 0.013717.$$

Then, SS6 exists if and only if $S_{\text{ch}}^{\text{in}} > \sigma_5$. For the stability of SS6, we have $\phi_3(D) < 0$ and we plot the functions ϕ_4 with respect to $S_{\text{ch}}^{\text{in}}$. Fig. 8 shows

that the equation $\phi_4(S_{\text{ch}}^{\text{in}}) = 0$ has a unique solution $\sigma_6 \simeq 0.029877$ such that $\phi_4(S_{\text{ch}}^{\text{in}}) < 0$ for all $\sigma_5 < S_{\text{ch}}^{\text{in}} < \sigma_6$ and $\phi_4(S_{\text{ch}}^{\text{in}}) > 0$ for all $S_{\text{ch}}^{\text{in}} > \sigma_6$.

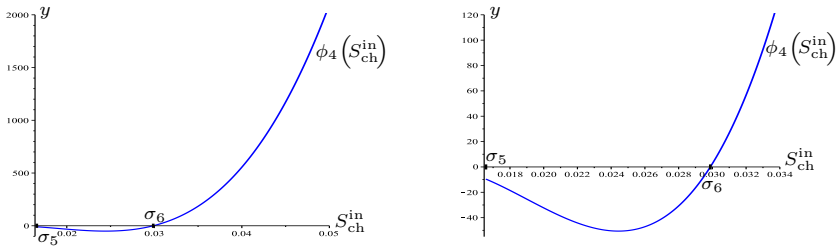

FIGURE 8. Curve of the function $\phi_4\left(S_{\text{ch}}^{\text{in}}\right)$ for $S_{\text{ch}}^{\text{in}} > \sigma_5$ and the solution σ_6 of equation $\phi_4\left(S_{\text{ch}}^{\text{in}}\right) = 0$. (e) A magnification for $S_{\text{ch}}^{\text{in}} \in (\sigma_5, 0.034)$.

To give a numerical evidence of the Hopf bifurcation occurring through the positive steady state SS6 as $S_{\text{ch}}^{\text{in}}$ varies, we determine the eigenvalues of the matrix $\mathbf{J_1}$ defined by (39) and evaluated at this steady state. Fig. 9(a) shows that one eigenvalue $\lambda_1\left(S_{\text{ch}}^{\text{in}}\right)$ remains negative for all $S_{\text{ch}}^{\text{in}} \in (\sigma_5, 0.05]$. Fig. 9(b) shows that the two other eigenvalues are real and distinct for all $S_{\text{ch}}^{\text{in}} \in (\sigma_5, \sigma^\star)$ and we denote them by $\lambda_2\left(S_{\text{ch}}^{\text{in}}\right)$ and $\lambda_3\left(S_{\text{ch}}^{\text{in}}\right)$, then they become a complex-conjugate pair for all $S_{\text{ch}}^{\text{in}} \in (\sigma^\star, 0.05)$ and we denote them by

$$\lambda_{2,3}\left(S_{\text{ch}}^{\text{in}}\right) = \alpha\left(S_{\text{ch}}^{\text{in}}\right) \pm i\beta\left(S_{\text{ch}}^{\text{in}}\right),$$

which becomes purely imaginary for the particular value $S_{\text{ch}}^{\text{in}} = \sigma_6$ such that $\alpha(\sigma_6) = 0$, with $\beta(\sigma_6) \neq 0$. Moreover, one has

$$\frac{d\alpha}{dS_{\text{ch}}^{\text{in}}}(\sigma_6) > 0.$$

Therefore, SS6 changes its stability through a supercritical Hopf bifurcation with the emergence of a stable limit cycle that we illustrate in Fig. 4.

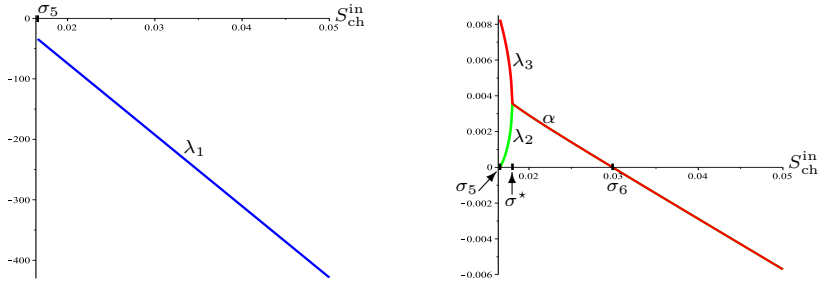

FIGURE 9. Three eigenvalues of the matrix $\mathbf{J_1}$ evaluated at SS6 as a function of $S_{\text{ch}}^{\text{in}}$. Real part of the pair of eigenvalues $\lambda_{2,3}$ for $S_{\text{ch}}^{\text{in}} \in (\sigma^\star, 0.05]$ where $\sigma^\star = 0.018$.

□

Appendix B. **Tables.** In this section, we provide the biological parameter values in Table 10 and we present in Table 11 various auxiliary functions defined in Table 1 in the case of specific growth functions (9).

TABLE 10. Nominal parameter values. Units are expressed in Chemical Oxygen Demand (COD).

Parameter	Wade et al. [31]	Unit
$k_{m,\mathrm{ch}}$	29	
$k_{m,\mathrm{ph}}$	26	$\mathrm{kgCOD_S/kgCOD_X/d}$
$k_{m,\mathrm{H_2}}$	35	
$K_{S,\mathrm{ch}}$	0.053	
$K_{S,\mathrm{H_2,c}}$	10^{-6}	
$K_{S,\mathrm{ph}}$	0.302	$\mathrm{kgCOD/m^3}$
$K_{I,\mathrm{H_2}}$	3.5×10^{-6}	
$K_{S,\mathrm{H_2}}$	2.5×10^{-5}	
Y_{ch}	0.019	
Y_{ph}	0.04	$\mathrm{kgCOD_X/kgCOD_S}$
$Y_{\mathrm{H_2}}$	0.06	

TABLE 11. Auxiliary functions in the case of growth functions given by (9).

Auxiliary function	Definition domain
$M_0(y,s_2)=\frac{yK_0(L_0+s_2)}{m_0s_2-y(L_0+s_2)}$	$0\leqslant y<\frac{m_0s_2}{L_0+s_2}$
$M_1(y,s_2)=\frac{yK_1(K_I+s_2)}{m_1K_I-y(K_I+s_2)}$	$0\leqslant y<\frac{m_1K_I}{K_I+s_2}$
$M_2(y)=\frac{yK_2}{m_2-y}$	$0\leqslant y<m_2$
$M_3(s_0,z)=\frac{zL_0(K_0+s_0)}{m_0s_0-z(K_0+s_0)}$	$0\leqslant z<\frac{m_0s_0}{K_0+s_0}$
$s_2^0(D)=\frac{L_0(D+a_0)}{m_0-D-a_0}$	$D+a_0<m_0$
$s_2^1(D)=\frac{K_I(m_1-D-a_1)}{D+a_1}$	$D+a_1<m_1$
$\Psi(s_2,D)=(1-\omega)\frac{(D+a_0)K_0(L_0+s_2)}{m_0s_2-(D+a_0)(L_0+s_2)}$ $+\frac{(D+a_1)K_1(K_I+s_2)}{m_1K_I-(D+a_1)(K_I+s_2)}+s_2$	$\left\{D\in I_1 : s_2^0<s_2<s_2^1\right\}$
$\psi_0(s_0)=\frac{m_0s_0\left(s_2^{\mathrm{in}}-\omega\left(s_0^{\mathrm{in}}-s_0\right)\right)}{(K_0+s_0)\left(L_0+s_2^{\mathrm{in}}-\omega\left(s_0^{\mathrm{in}}-s_0\right)\right)}$	$s_0\in\left[\max\left(0,s_0^{\mathrm{in}}-s_2^{\mathrm{in}}/\omega\right),+\infty\right)$
$\psi_1(s_1)=\frac{m_1s_1K_I}{(K_1+s_1)\left(K_I+s_2^{\mathrm{in}}+s_1^{\mathrm{in}}-s_1\right)}$	$s_1\in\left[0,s_1^{\mathrm{in}}+s_2^{\mathrm{in}}\right]$

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