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Analysis of the Droop Model with Wall Growth in a Chemostat

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Abstract. In this paper, we construct a simple chemostat-based variable yield model of competition between two bacterial strains, one of which is capable of wall growth [14]. In this model we prove the boundedness of solutions, analyze the local stability of equilibria and establish the global stability for the locally stable extinction equilibrium. Furthermore, when the extinction equilibrium becomes unstable, we prove the existence and uniqueness of the positive equilibrium and the uniform persistence of the system.

1. Introduction and mathematical models

In the mathematical modeling of predator-prey system, we usually assume that the predator's consumption rate C on prey is directly proportional to the growth rate G of predator. We call the ratio of these two rates, G/C, the yield constant γ. In phytoplankton ecology, it has been known that the yield varies depending on the growth rate. Droop [2] is probably the first one to present a variable yield model, or so called "internal" storage model. He proposed the idea that organism consumes nutrient and converts it into internal storage Q (cell quota). When the internal storage Q is below the minimum cell quota $Q_{\min}$, the organism stops growing. When the cell quota is above the minimum cell quota, its growth rate $\mu(Q)$ increases with the cell quota. Furthermore, the nutrient uptake rate $f(S,Q)$ increases with nutrient concentration S and decreases with cell quota Q. In the past fifty years, the variable yield models are well supported by experimental data [7].

In [17], the authors consider simple chemostat equations for two competing microorganisms. The equations take the form

$$\begin{cases} S' = (S^{(0)} - S)D - \frac{f_1(S)}{\gamma_1}x_1 - \frac{f_2(S)}{\gamma_2}x_2, \\ x_1' = (f_1(S) - D)x_1, \\ x_2' = (f_2(S) - D)x_2, \\ S(0) \geq 0,\ x_1(0) \geq 0,\ x_2(0) \geq 0, \end{cases}$$

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where $S^{(0)}$ denotes the input concentration of nutrient and D denotes the dilution rate $(\frac{\text{flow rate}}{\text{volume}})$, $S(t)$ is the concentration of nutrient at time t, $x_i(t)$ is the concentration of i-th micro-organism at time t; γ_i and $f_i(S) = \frac{m_i S}{a_i+S}$ are the yield constant and the growth rate for i-th species respectively.

In [14], the authors studied the wall-effect on micro-organisms in a simple chemostat. Let u be the density of planktonic cells in the channel and w be the density of adherent cells on the wall. The equations for the simple chemostat model with wall effect take the form

$$\begin{cases} S' = (S^{(0)} - S)D - \frac{f_u(S)}{\gamma}u - \frac{f_w(S)}{\gamma}\delta w, \\ u' = (f_u(S) - D)u - \alpha u + \beta\delta w, \\ w' = f_w(S)w - \beta w + \frac{\alpha}{\delta}u, \\ S(0) \geq 0,\ u(0) \geq 0,\ w(0) \geq 0, \end{cases}$$

where α is the rate of adhesion, β is the sloughing rate of adherent bacteria, γ is the yield constant, $f_u(S) := \frac{m_u S}{a_u+S}$ is the specific growth rate of planktonic bacteria, $f_w(S) := \frac{m_w S}{a_w+S}$ is the specific growth rate of adherent bacteria, $\delta = \frac{A}{V}$, which is area-volume ratio, where A and V are the surface area and volume of the growth chamber, respectively [10]. We note that in [14] by scaling the authors assume $\delta = 1$.

Next we construct the following variable-yield model in a simple chemostat with wall growth

$$\begin{cases} S' = (S^{(0)} - S)D - f(S,Q)(u + \delta w), \\ Q' = f(S,Q) - (\mu_1(Q) + \mu_2(Q))Q, \\ u' = (\mu_1(Q) - D)u - \alpha u + \beta\delta w, \\ w' = \mu_2(Q)w - \beta w + \frac{\alpha}{\delta}u, \end{cases} \tag{1.1}$$

$$S(0) \geq 0, \quad Q(0) \geq Q_{\min}, \quad u(0) \geq 0, \quad w(0) \geq 0,$$

where Q is the cell quota and $f(S,Q)$ is the uptake rate for the bacteria both in the channel and on the wall. $\mu_1(Q)$ and $\mu_2(Q)$ are the growth rates of u and w respectively. We assume both of planktonic and adherent bacteria share the same cell quota Q and their growth rates share the same $Q_{\min}$, and

$$\begin{gathered} f(0,Q) = 0, \quad \frac{\partial f}{\partial S} > 0, \quad \frac{\partial f}{\partial Q} < 0, \\ \mu_1(Q) \text{ and } \mu_2(Q) \text{ are continuous and strictly increasing with } Q \geq Q_{\min}. \end{gathered} \tag{1.2}$$

If $Q \leq Q_{\min}$, then $\mu_i(Q) = 0$.

Some examples of $f(S,Q)$ and $\mu_i(Q)$ are given in [7, 13, 17]:

$$f(S,Q) = \rho(Q)\frac{S}{a+S}, \tag{1.3}$$

$$\rho(Q) = \rho_{\max} - (\rho_{\max} - \rho_{\min})\left(\frac{Q - Q_{\min}}{Q_{\max} - Q_{\min}}\right), \tag{1.4}$$

$$\mu_i(Q) = \mu_{i,\infty}\left(1 - \frac{Q_{\min}}{Q}\right) \quad \text{or} \quad \mu_i(Q) = \mu_{i,\max}\left(\frac{(Q - Q_{\min})_+}{K + (Q - Q_{\min})_+}\right). \tag{1.5}$$

The importance of wall growth was first cited from the work of microbiologists Rolf Freter and his colleagues [3–6]. Their mathematical models of the phenomenon of colonization resistance in the mammalian gut show that the bacteria wall attachment could play a crucial role in the observed stability of the natural microflora of the gut to invasion by non-indigenous micro-organisms [3]. Freter's model is a crude model of biofilm. A biofilm is simply a layer of material coating a surface. It is a comfortable refuge. Examples of a biofilm include the scum that grows on a rock in a stream, dental plague on teeth, the surface slime that forms on the inside surface of water pipes and a similar coating of surface of the large intestine of mammals. These bacterial layers can have serious negative consequences in many man-made environments. They contaminate medical devices such as contact lenses, implants, catheters and stints, they can contaminate food and medical production facilities, air-conditioning and water circulation systems. Biofilms are notoriously difficult to eradicate once established. For more biological references of biofilms, we refer to [1]. The organization of this paper is as follows. In Section 2, we prove the boundedness of the solutions for the system (1.1). In Section 3, we find the equilibria of the system (1.1) and do their stability analysis, prove the uniform persistence for the system (1.1). Section 4 is the discussion section.

2. Boundedness of the solutions of (1.1)

In this section we state and prove the boundedness of the solutions for the variable-yield model of simple chemostat with wall growth (1.1). We note that in (1.1) we assume there is no washout for the adherent cells on the wall. Then it is more technical to prove the boundedness of the solutions of (1.1). Before we do it, we need the following lemmas.

Lemma 2.1. [9] *Let* $x\colon \mathbb{R}_+ \to [a,+\infty)$, $y\colon \mathbb{R}_+ \to [b,+\infty)$ *and* $F\colon [a,+\infty)\times[b,+\infty) \to \mathbb{R}$ *be countinuously differentiable and satisfy*

$$x'(t) \le F(x(t),y(t)), \quad t \ge 0.$$

Suppose

$$\frac{\partial F}{\partial x}(x,y) < 0, \quad \frac{\partial F}{\partial y}(x,y) > 0$$

and suppose that for each $y \in [b, +\infty)$ *there exists a unique solution* $x^* = x^*(y) \in [a, +\infty)$ *of* $F(x, y) = 0$. *If* $\limsup_{t\to\infty} y(t) \le \alpha$, *then*

$$\limsup_{t\to\infty} x(t) \le x^*(\alpha).$$

Lemma 2.1 is a lemma about the internal storage. The following Remark 2.2 follows from Lemma 2.1.

Remark 2.2. From (1.1), $Q' = f(S, Q) - (\mu_1(Q) + \mu_2(Q))Q := F(S, Q)$. From (1.2), $F(S, Q)$ is strictly increasing in S and strictly decreasing in Q. From first equation of (1.1), $\limsup_{t\to\infty} S(t) \le S^{(0)}$. From (1.2), there exists a unique Q^0 such that $f(S^{(0)}, Q^0) - (\mu_1(Q^0) + \mu_2(Q^0))Q^0 = 0$. If $Q_{\min} \le Q(0) \le Q^0$ then by Lemma 2.1, there exists $T > 0$ such that $Q(t) \le Q^0$ for all $t \ge T$. Furthermore, $\liminf_{t\to\infty} S(t) \ge 0$, because from (1.2) $S'(t)\big|_{S=0} = S^{(0)}D > 0$, and $\liminf_{t\to\infty} Q(t) \ge Q_{\min}$, because $Q(0) \ge Q_{\min}$ and $Q'(t)\big|_{Q=Q_{\min}} = f(S, Q_{\min}) \ge 0$.

Hence the internal storage Q is bounded for all $t > 0$.

Lemma 2.3. *For the system* (1.1)*, there exist* $\eta_1, \eta_2 > 0$ *with* $\eta_2 < \eta_1$ *such that*

$$\eta_2 \le \frac{u(t)}{u(t) + \delta w(t)} \le \eta_1$$

for $t \ge T$*, for some* $T > 0$.

Proof. Since $\frac{u}{u+\delta w} \le \frac{u}{\delta w}$, we can consider the upper bound of $\frac{u}{\delta w}$:

$$\left(\frac{u}{\delta w}\right)' = \frac{u'\delta w - u(\delta w)'}{(\delta w)^2} = -\alpha \left(\frac{u}{\delta w}\right)^2 + (\mu_1(Q) - \mu_2(Q) - D - \alpha + \beta)\frac{u}{\delta w} + \beta.$$

From (1.2), the function $\mu_1(Q) - \mu_2(Q) - D - \alpha + \beta$ is the continuous and bounded on $[Q_{\min}, Q^0]$. Let M and m be the maximum and minimum of this function, respectively. Then we obtain

$$\left(\frac{u}{\delta w}\right)' \le -\alpha \left(\frac{u}{\delta w}\right)^2 + M\frac{u}{\delta w} + \beta. \tag{2.1}$$

Since $\alpha > 0$, $\beta > 0$, the right-hand side of (2.1) have two roots p_1 and p_2 with different signs.

Assume $p_1 < 0 < p_2$, then (2.1) can be expressed as

$$\left(\frac{u}{\delta w}\right)' \le -\alpha \left(\frac{u}{\delta w} - p_1\right)\left(\frac{u}{\delta w} - p_2\right), \tag{2.2}$$

where

$$p_1 = \frac{M - \sqrt{M^2 + 4\alpha\beta}}{2\alpha} \quad \text{and} \quad p_2 = \frac{M + \sqrt{M^2 + 4\alpha\beta}}{2\alpha}.$$

Therefore, from (2.2), it follows that

$$\frac{u(t)}{\delta w(t)} \le p_2 + \epsilon \quad \text{for } t \ge T_\epsilon, \text{ for some } T_\epsilon > 0,\ \epsilon > 0 \text{ small.}$$

Similarly, we can get

$$\begin{aligned}\left(\frac{\delta w}{u}\right)' &= \frac{(\delta w)'u - u'\delta w}{u^2} = -\beta\left(\frac{\delta w}{u}\right)^2 + (\mu_2(Q) - \mu_1(Q) + D + \alpha - \beta)\frac{\delta w}{u} + \alpha \\ &\le -\beta\left(\frac{\delta w}{u}\right)^2 - m\frac{\delta w}{u} + \alpha = -\beta\left(\frac{u}{\delta w} - q_1\right)\left(\frac{u}{\delta w} - q_2\right),\end{aligned}$$

where

$$\frac{-m - \sqrt{m^2 + 4\alpha\beta}}{2\beta} = q_1 < 0 < q_2 = \frac{-m + \sqrt{m^2 + 4\alpha\beta}}{2\beta}.$$

Therefore

$$\frac{\delta w(t)}{u(t)} \le q_2 + \epsilon \quad \text{for } t \ge T_\epsilon, \text{ for some } T_\epsilon > 0,\ \epsilon > 0 \text{ small.}$$

Because u and δw are nonnegative, and

$$\frac{1}{1 + q_2 + \epsilon} \le \frac{1}{1 + \frac{\delta w}{u}} = \frac{u}{u + \delta w} \le \frac{u}{\delta w} \le p_2 + \epsilon.$$

Let $\eta_1 = p_2 + \epsilon$, $\eta_2 = \frac{1}{1+q_2+\epsilon}$, then we finish the proof of the lemma. □

Next, we introduce three notations to prove the boundedness of $u(t)$ and $\delta w(t)$ for $t \ge 0$. Let $U = Qu$, $W = Qw$ and $g(S,Q) = \frac{f(S,Q)}{Q}$. Then the system (1.1) is converted into

$$\text{(2.3)} \qquad \begin{cases} S' = (S^{(0)} - S)D - g(S,Q)(U + \delta W), \\ Q' = (g(S,Q) - \mu_1(Q) - \mu_2(Q))Q, \\ U' = (g(S,Q) - \mu_2(Q) - D)U - \alpha U + \beta\delta W, \\ W' = (g(S,Q) - \mu_1(Q))W - \beta W + \frac{\alpha}{\delta}U. \end{cases}$$

Theorem 2.4. *For the system* (2.3)*, the solutions U and W are bounded.*

Proof. By Lemma 2.3, there exist $\eta_1, \eta_2 > 0$ with $\eta_2 \le \frac{U}{U+\delta W} \le \eta_1$ for $t \ge T_\epsilon$, $0 < \eta_2 < 1$.

Consider the variable $Z = S + U + \delta W$, Z satisfies

$$\begin{aligned}Z' &= (S^{(0)} - S)D + (-\mu_2(Q) - D)U + (-\mu_1(Q))\delta W \le (S^{(0)} - S)D - DU \\ &\le (S^{(0)} - S)D - D\eta_2(U + \delta W) \le (S^{(0)} - \eta_2 S)D - D\eta_2(U + \delta W) = (S^{(0)} - \eta_2 Z)D.\end{aligned}$$

Therefore, by the above differential inequalities,

$$S + U + \delta W \le \frac{S^{(0)}}{\eta_2} + \epsilon \quad \text{for } t \ge T_\epsilon,\ T_\epsilon \text{ large.}$$

This implies that $U + \delta W \le \frac{S^{(0)}}{\eta_2} + \epsilon$, since U and W are nonnegative, then $U(t)$ and $W(t)$ are bounded for $t \ge 0$. □

Now, we have shown that $U(t)$ and $W(t)$ are bounded for $t \geq 0$. By Remark 2.2, $0 < Q_{\min} \leq Q(t) \leq Q^0$ for all $t \geq 0$, then we obtain the bounedess of solutions $u(t)$ and $w(t)$ of the system (1.1).

3. Stability analysis of the system (1.1)

There are at most two equilibria of the system (1.1), namely, the extinction equilibrium E_0 and possibly the coexistence equilibrium E_1, where $E_0 = (S^{(0)}, Q^0, 0, 0)$ which always exists and Q^0 satisfies $f(S^{(0)}, Q^0) - (\mu_1(Q^0) + \mu_2(Q^0))Q^0 = 0$.

In our stability analysis, we discuss the following:

(1) The stability of E_0.

(2) The existence and uniqueness of E_1. (We will give the formula of E_1 in (3.8).)

(3) Uniform persistence of the system (1.1).

Since the uniform persistence of the system (1.1) is related to the boundary dynamics of (1.1). Therefore, we first need to study the stability of E_0.

3.1. The local stability analysis of extinction equilibrium

First, we do the local stability analysis for E_0. Let $J(E_0)$ be the Jacobian matrix evaluated at E_0:

$$J(E_0) = \begin{pmatrix} -D & 0 & -f(S^{(0)}, Q^0) & -\delta f(S^{(0)}, Q^0) \\ a_{11} & a_{22} & 0 & 0 \\ 0 & 0 & \mu_1(Q^0) - D - \alpha & \beta\delta \\ 0 & 0 & \frac{\alpha}{\delta} & \mu_2(Q^0) - \beta \end{pmatrix}, \tag{3.1}$$

where

$$a_{11} = \frac{\partial f}{\partial S}\Big|_{(S,Q)=(S^{(0)},Q^0)},$$
$$a_{22} = \frac{\partial f}{\partial Q}\Big|_{(S,Q)=(S^{(0)},Q^0)} - (\mu_1'(Q^0) + \mu_2'(Q^0))Q^0 - (\mu_1(Q^0) + \mu_2(Q^0)).$$

Let the eigenvalues of $J(E_0)$ be λ_1, λ_2, λ_3, λ_4, where

$$\lambda_1 = -D < 0, \quad \lambda_2 = a_{22} < 0.$$

Our basic hypothesis is

(H) $\qquad E_0$ is a hyperbolic equilibrium, i.e., $\lambda_i \neq 0$ for all $i = 1, 2, 3, 4$.

Claim: E_0 is either a locally asymptotically stable equilibrium or a saddle point.

Compute the eigenvalues λ_3 and λ_4: From (3.1), λ_3 and λ_4 satisfy

$$\begin{aligned} \lambda_3 + \lambda_4 &= \mu_1(Q^0) - D - \alpha + \mu_2(Q^0) - \beta, \\ \lambda_3\lambda_4 &= (\mu_1(Q^0) - D - \alpha)(\mu_2(Q^0) - \beta) - \alpha\beta. \end{aligned} \tag{3.2}$$

Denote $A(Q^0) = \mu_1(Q^0) - D - \alpha$ and $B(Q^0) = \mu_2(Q^0) - \beta$, then we have

$$\lambda_3 = \frac{(A(Q^0) + B(Q^0)) + \sqrt{(A(Q^0) - B(Q^0))^2 + 4\alpha\beta}}{2},$$
$$\lambda_4 = \frac{(A(Q^0) + B(Q^0)) - \sqrt{(A(Q^0) - B(Q^0))^2 + 4\alpha\beta}}{2} < \lambda_3.$$

If $\lambda_3 < 0$, i.e., $(A(Q^0) + B(Q^0)) + \sqrt{(A(Q^0) - B(Q^0))^2 + 4\alpha\beta} < 0$, then E_0 is locally asymptotically stable (LAS).

Otherwise under (H), $(A(Q^0) + B(Q^0)) + \sqrt{(A(Q^0) - B(Q^0))^2 + 4\alpha\beta} > 0$, then E_0 is a saddle point.

3.2. The global stability analysis of extinction equilibrium

In order to establish the global stability, we introduce a set $I = \{(S, Q, u, w) \in \mathbb{R}^4; S \in [0, S^{(0)}], Q \in [Q_{\min}, Q^0], u > 0, w > 0\}$. It is easy to verify that I is a positively invariant set for the system (1.1) by Remark 2.2. We will prove the global stability in I by Kamke theorem [8, 15].

We recall that a system $\dot{x} = f(x)$, $f\colon D \subseteq \mathbb{R}^n \to \mathbb{R}^n$ is cooperative [15], where D is an open set in $\mathbb{R}^n$, if

$$\frac{\partial f_i}{\partial x_j} \ge 0 \quad \text{for } x \in D,\ i, j = 1, 2, \ldots, n \text{ and } i \neq j.$$

Theorem 3.1. *Under hypothesis* (H), *if the extinction equilibrium of the system* (1.1) E_0 *is locally asymptotically stable, then* E_0 *is globally asymptotically stable in* I.

Proof. First, we consider the subsystem in the invariant set I as

$$\begin{pmatrix} u \\ \delta w \end{pmatrix}' = \begin{pmatrix} \mu_1(Q) - D - \alpha & \beta \\ \alpha & \mu_2(Q) - \beta \end{pmatrix} \begin{pmatrix} u \\ \delta w \end{pmatrix}. \tag{3.3}$$

Obviously, we obtain the following in I that

$$\begin{pmatrix} u \\ \delta w \end{pmatrix}' \le \begin{pmatrix} \mu_1(Q^0) - D - \alpha & \beta \\ \alpha & \mu_2(Q^0) - \beta \end{pmatrix} \begin{pmatrix} u \\ \delta w \end{pmatrix}.$$

Let

$$u' = (\mu_1(Q^0) - D - \alpha)u + \beta\delta w \quad \text{and} \quad (\delta w)' = (\mu_2(Q^0) - \beta)\delta w + \alpha u. \tag{3.4}$$

We note that the system (3.4) is a cooperative system.

Consider the linear and cooperative system

$$\begin{pmatrix} x \\ y \end{pmatrix}' = \begin{pmatrix} \mu_1(Q^0) - D - \alpha & \beta \\ \alpha & \mu_2((Q^0)) - \beta \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}. \tag{3.5}$$

The initial value of u and δw of the system (3.5) are same as the system (3.3). The eigenvalues of (3.5) are λ_3 and λ_4.

Under hypothesis (H) if the extinction equilibrium of the system (1.1) E_0 is locally asymptotically stable, then λ_3 and λ_4 are negative. So $(x(t), y(t)) \to (0,0)$ as $t \to \infty$.

By Kamke's theorem [8, 15], differential inequalities for cooperative system (3.4), we have

$$(0,0) \le (u(t), \delta w(t)) \le (x(t), y(t)). \tag{3.6}$$

Taking limit as $t \to \infty$ for the inequality (3.6), then

$$(0,0) \le \lim_{t\to\infty} (u(t), \delta w(t)) \le \lim_{t\to\infty} (x(t), y(t)) = (0,0).$$

This completes the proof of Theorem 3.1. □

3.3. Uniform persistence of the system (1.1)

In this section, we concern about the uniform persistence of the system (1.1) in the interior and apply the theory of uniform persistence [16, 17] by investigating boundary dynamical behavior. We shall obtain the uniform persistence by analyzing the stability property of extinction equilibrium. The following Lemma 3.2 gives a necessary and sufficient condition for the uniform persistence of the system (1.1).

Let

$$X = \left\{(S, Q, u, w) \mid 0 \le S \le S^{(0)}, Q_{\min} \le Q \le Q^0, u \ge 0, w \ge 0\right\}$$

and $\mathring{X}$ be the interior of X.

Let $X_0 = \left\{(S, Q, u, w) \mid 0 \le S \le S^{(0)}, Q_{\min} \le Q \le Q^0, u = 0, w = 0\right\}$ and define the persistent function $\rho\colon X \to \mathbb{R}_+$, $\rho(S, Q, u, w) = uw$. Let $M^+(E_0)$ be the stable manifold of the equilibrium E_0. By Theorems 4.5 and 8.17 in [16], we have

Lemma 3.2. *Let* (H) *hold. If* (i) X_0 *is positively invariant,* (ii) $M^+(E_0) \cap \rho^{-1}(0, \infty) = \emptyset$, *and* (iii) *there is no homoclinic orbit joining* E_0 *to itself, then the system* (1.1) *is uniformly* ρ*-persistent in* $\mathring{X}$*, i.e., there exists* $\alpha > 0$ *such that*

$$\liminf_{t \to \infty} \rho(S(t), Q(t), u(t), w(t)) \geq \alpha$$

for all $(S(0), Q(0), u(0), w(0)) \in \mathring{X}$.

Theorem 3.3. *Let* (H) *hold and* E_0 *be a saddle point. Then the system* (1.1) *is uniformly persistent.*

Proof. First, we consider the subsystem of (1.1):

$$\begin{cases} u' = (\mu_1(Q) - D)u - \alpha u + \beta\delta w, \\ \delta w' = \mu_2(Q)\delta w - \beta\delta w + \alpha u. \end{cases}$$

If $u(0) = 0$ and $w(0) = 0$ then from the uniqueness of solutions of ODE, it follows that $u(t) \equiv 0$ and $w(t) \equiv 0$ for all $t \geq 0$. Hence X_0 is positively invariant.

Next, we prove $M^+(E_0) \cap \rho^{-1}(0, \infty) = \emptyset$. Let η_1, η_2, η_3, η_4 be the the corresponding eigenvectors of $J(E_0)$ to the eigenvalues λ_1, λ_2, λ_3, λ_4. Obviously, if $\eta_1, \eta_2 \in \partial X$ then $\operatorname{span}\langle \eta_1, \eta_2 \rangle \cap \mathring{X} = \emptyset$. There are two cases for the instability of E_0:

Case 1: E_0 is a repeller ($\lambda_3 > \lambda_4 > 0$) in X.

Case 2: E_0 is saddle point ($\lambda_3 > 0 > \lambda_4$). (Our assumption is $\lambda_3 > \lambda_4$ in Section 3.2.)

For Case 1, the stable manifold of E_0 is certainly not include the space spanned by η_3 and η_4 since the $\lambda_3 > \lambda_4 > 0$. This implies that $M^+(E_0) = \operatorname{span}\langle \eta_1, \eta_2 \rangle \subset \partial X$. Obviously, $M^+(E_0) \cap \mathring{X} = \emptyset$.

For Case 2, we check that the direction of η_4 will be neither $(S, Q, +, +)$ nor $(S, Q, -, -)$. Denote η_4 as $(\xi_1, \xi_2, \xi_3, \xi_4)$ satisfying

$$(\lambda_4 I - J(E_0))\eta_4 = 0. \tag{3.7}$$

To investigate the signs of ξ_3 and ξ_4, we need to solve (3.7) and get a relationship between ξ_3 and ξ_4. From (3.7) we have

$$\begin{aligned} (\lambda_4 + D)\xi_1 + f(S^{(0)}, Q^0)\xi_3 + \delta f(S^{(0)}, Q^0)\xi_4 &= 0, \\ (\lambda_4 - (\mu_1(Q^0) - D - \alpha))\xi_3 - \beta\delta\xi_4 &= 0, \\ -\frac{\alpha}{\delta}\xi_3 + (\lambda_4 - \mu_2(Q^0) + \beta)\xi_4 &= 0. \end{aligned}$$

Hence

$$\xi_4 = \frac{\lambda_4 - (\mu_1(Q^0) - D - \alpha)}{\beta\delta}\xi_3.$$

To show $\frac{\lambda_4-(\mu_1(Q^0)-D-\alpha)}{\beta\delta}<0$, i.e., $\lambda_4-A(Q^0)<0$ if and only if

$$\begin{aligned}
&\frac{(A(Q^0)+B(Q^0))-\sqrt{(A(Q^0)-B(Q^0))^2+4\alpha\beta}}{2}-A(Q^0)<0\\
\iff\ &(A(Q^0)+B(Q^0))-\sqrt{(A(Q^0)-B(Q^0))^2+4\alpha\beta}<2A(Q^0)\\
\iff\ &B(Q^0)-A(Q^0)<\sqrt{(A(Q^0)-B(Q^0))^2+4\alpha\beta}.
\end{aligned}\tag{3.8}$$

If $B(Q^0)-A(Q^0)\le 0$, (3.8) holds trivially. If $B(Q^0)-A(Q^0)>0$, then obviously (3.8) hold. So $\eta_4\notin\mathring{X}$ and $M^+(E_0)=\operatorname{span}\langle\eta_1,\eta_2,\eta_4\rangle$. In Case 2, $M^+(E_0)\cap\mathring{X}=\emptyset$. Therefore, we have shown $M^+(E_0)\cap\mathring{\Omega}=\emptyset$ in Cases 1 and 2. This completes the proof of $M^+(E_0)\cap\rho^{-1}(0,\infty)=\emptyset$.

The system (1.1) is reduced to the following system in the set X_0:

$$\begin{gathered}
S'=(S^{(0)}-S)D,\quad Q'=f(S,Q)-(\mu_1(Q)+\mu_2(Q))Q,\\
S(0)\ge 0,\quad Q^0\ge Q(0)\ge Q_{\min}.
\end{gathered}\tag{3.9}$$

We can find that

$$\begin{aligned}
&\frac{\partial S'}{\partial S}=-D<0,\\
&\frac{\partial Q'}{\partial Q}=\frac{\partial f}{\partial Q}-(\mu_1'(Q)+\mu_2'(Q))Q-(\mu_1(Q)+\mu_2(Q))<0.
\end{aligned}$$

By the Negative–Bendixson criterion [8], we can get $\frac{\partial S'}{\partial S}+\frac{\partial Q'}{\partial Q}<0$, and $\lim_{t\to\infty}S(t)=S^{(0)}$, $\lim_{t\to\infty}Q(t)=Q^0$, $\lim_{t\to-\infty}S(t)=0$.

Hence there is no homoclinic orbit in the system (3.9). Therefore, by Lemma 3.2 and Theorem 2.4, the system (1.1) is ρ-uniformly persistent in $\mathring{X}$, i.e., there exists $\alpha>0$ such that $u(t)w(t)\ge\alpha>0$ for $t\ge 0$. From Theorem 2.4, it follows that $u(t)\ge\alpha/w_{\max}$, $w(t)\ge\alpha/u_{\max}$ for all $t\ge T$, where $u_{\max}$ and $w_{\max}$ are upper bounds of $u(t)$ and $w(t)$. □

From [18], uniform persistence of the system (1.1) implies the existence of coexistence equilibrium $E_1=(S^*,Q^1,u^*,w^*)$. From (1.1), Q^1 satisfies

$$\begin{vmatrix}\mu_1(Q^1)-D-\alpha & \beta\delta\\ \frac{\alpha}{\delta} & \mu_2(Q^1)-\beta\end{vmatrix}=0,\tag{3.10}$$

S^* satisfies $f(S^*,Q^1)-(\mu_1(Q^1)+\mu_2(Q^1))Q^1=0$ and

$$\begin{aligned}
(\mu_1(Q^1)-D-\alpha)u^*&=-\beta\delta w^*<0,\\
(\mu_2(Q^1)-\beta)w^*&=-\frac{\alpha}{\delta}u^*<0.
\end{aligned}\tag{3.11}$$

3.4. The existence and uniqueness of coexistence equilibrium

Theorem 3.4. *Let* (H) *hold. If E_0 is unstable then the system* (1.1) *is uniformly persistent. Furthermore, there exists a unique coexistence equilibrium E_1 of the system* (1.1).

Proof. By Theorem 3.3, we know that the uniform persistence of the system (1.1) is equivalent to the instability of E_0. If the system (1.1) is uniformly persistent, then there exists a positive equilibrium of system (1.1) by Theorem 3.3 in [18].

Next, we show that the positive equilibrium is unique. Assume there are two solutions Q^1 and Q^2 to (3.10) with $Q^1 > 0$, $Q^2 > 0$ and $Q^1 \neq Q^2$. Assume $Q^1 > Q^2$. Then, by the Rolle's theorem, there exists $\xi \in (Q^2, Q^1)$ such that

$$\frac{d}{dQ}[(\mu_1(Q) - D - \alpha)(\mu_2(Q) - \beta) - \alpha\beta]\Big|_{Q=\xi} = 0,$$

i.e.,

$$(\mu_1(\xi) - D - \alpha)\mu_2'(\xi) + \mu_1'(\xi)(\mu_2(\xi) - \beta) = 0. \tag{3.12}$$

From (3.11), $\mu_1(Q^1) - D - \alpha$ and $\mu_2(Q^1) - \beta$ are both negative, then by monotonicity of μ_1 and μ_2, then $\mu_1(\xi) - D - \alpha < \mu_1(Q^1) - D - \alpha < 0$ and $\mu_2(\xi) - \beta < \mu_2(Q^1) - \beta < 0$. Since $\mu_1'(\xi)$ and $\mu_2'(\xi)$ are positive, we get a contradiction to (3.12). Therefore, the coexistence equilibrium of the system (1.1) E_1 is unique. □

3.5. The local stability analysis of coexistence equilibrium

We have established the existence and uniqueness of coexistence equilibrium E_1. In this section, we give the condition for the local asymptotic stability of E_1. First, we consider the Jacobian matrix evaluated at E_1:

$$J(E_1) = \begin{pmatrix} b_{11} & b_{12} & -f(S^*, Q^1) & -\delta f(S^*, Q^1) \\ b_{21} & b_{22} & 0 & 0 \\ 0 & u^*\mu_1'(Q^1) & \mu_1(Q^1) - D - \alpha & \beta\delta \\ 0 & w^*\mu_2'(Q^1) & \frac{\alpha}{\delta} & \mu_2(Q^1) - \beta \end{pmatrix},$$

where

$$\begin{aligned} b_{11} &= -D - (u^* + \delta w^*)\frac{\partial f}{\partial S}\Big|_{(S,Q)=(S^*,Q^1)} < 0, \\ b_{12} &= -(u^* + \delta w^*)\frac{\partial f}{\partial Q}\Big|_{(S,Q)=(S^*,Q^1)} \geq 0, \\ b_{21} &= \frac{\partial f}{\partial S}\Big|_{(S,Q)=(S^*,Q^1)} > 0, \\ b_{22} &= \frac{\partial f}{\partial Q}\Big|_{(S,Q)=(S^*,Q^1)} - (\mu_1'(Q^1) + \mu_2'(Q^1))Q^1 - (\mu_1(Q^1) + \mu_2(Q^1)) < 0. \end{aligned} \tag{3.13}$$

The characteristic polynomial of $J(E_1)$ is $\det(\theta I - J(E_1))$, which is expanded as

$$c_0\theta^4 + c_1\theta^3 + c_2\theta^2 + c_3\theta + c_4 = 0.$$

From (3.10), (3.11) and (3.13), it follows that

$$\begin{aligned}
b_{11} + b_{22} < 0, \quad b_{11}b_{22} - b_{21}b_{12} < 0, \quad c_0 = 1 > 0,\\
c_1 = -(\mu_1(Q^1) + \mu_2(Q^1) - D - \alpha - \beta) - b_{11} - b_{22} > 0,\\
c_2 = b_{11}b_{22} - b_{21}b_{12} + (\mu_1(Q^1) + \mu_2(Q^1) - D - \alpha - \beta)(b_{11} + b_{22}) > 0,\\
c_3 = -(b_{11}b_{22} - b_{21}b_{12})[\mu_1(Q^1) + \mu_2(Q^1) - D - \alpha - \beta]\\
+ b_{21}f(S^*, Q^1)[\mu_1'(Q^1)u^* + \mu_2'(Q^1)\delta w^*] > 0,\\
c_4 = b_{21}f(S^*, Q^1)\begin{vmatrix} u^*\mu_1'(Q^1) & \mu_1(Q^1) - D - \alpha - \beta \\ \delta w^*\mu_2'(Q^1) & -\mu_2(Q^1) + \alpha + \beta \end{vmatrix} > 0.
\end{aligned}$$

Theorem 3.5. (i) *If $c_1c_2c_3 > c_1^2c_4 + c_3^2$, then the coexistence equilibrium E_1 is locally asymptotically stable.*

(ii) *If Hopf bifurcation occurs then $c_1c_2c_3 = c_1^2c_4 + c_3^2$.*

Proof. (i) The Routh–Hurwitz criterion [8, p. 58] for the case $n = 4$ is $c_1 > 0$, $c_2 > 0$, $c_4 > 0$ and $c_3(c_1c_2 - c_3) > c_1^2c_4$. Hence if $c_3(c_1c_2 - c_3) > c_1^2c_4$, then E_1 is locally asymptotically stable.

(ii) If Hopf bifurcation occurs for some bifurcation parameters, then the characteristic polynomial $\det(\theta I - J(E_1))$ takes the form

$$(\theta^2 + a\theta + b)(\theta^2 + \omega^2) \quad \text{where } a > 0,\ b > 0,\ \omega \neq 0$$

or

$$\theta^4 + a\theta^3 + (b + \omega^2)\theta^2 + a\omega^2\theta + b\omega^2.$$

Then $c_1 = a$, $c_2 = b + \omega^2$, $c_3 = a\omega^2$, $c_4 = b\omega^2$. It is easy to verify

$$c_1c_2c_3 = c_1^2c_4 + c_3^2. \qquad \square$$

4. Discussion

We have discussed a Droop model with wall growth in a simple chemostat. We summarize the results as below. Under the assumption (H), the system (1.1) has only two rest points, a washout state E_0 and a coexistence state E_1:

(1) The solutions of the system (1.1) are bounded.

(2) If E_0 is locally asymptotically stable, then E_0 is globally asymptotically stable.

(3) If E_0 is unstable, then the system (1.1) is uniformly persistent and the existence of positive equilibrium E_1 follows (see [18]).

(4) If E_1 exists, then E_1 is unique and we conjecture that E_1 is globally asymptotically stable.

In the following we plot the operation diagram in $D - S^{(0)}$ parameter space with parameters, given by $\alpha = 0.2$, $\beta = 0.4$, $a = 2.5$, $\rho_{\max} = 1$, $\rho_{\min} = 0$, $Q_{\max} = 6$, $Q_{\min} = 2$, $\delta = 0.8$, $K = 2$, $\mu_{\max,1} = 5$, $\mu_{\max,2} = 3$, $\rho_{\max}$, $\rho_{\min}$ in (1.4), (1.5).

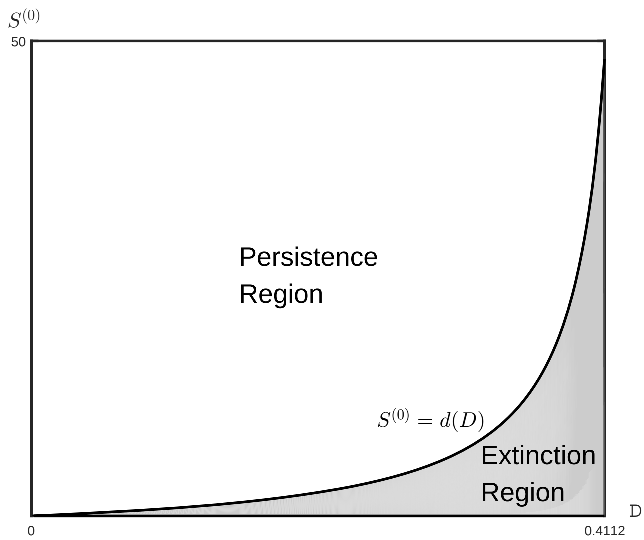

Figure 4.1: Operation diagram.

Remark 4.1. The extinction and persistence regions in this diagram are separated by a curve $S^{(0)} = F(D)$ which is determined by $\lambda_3 = 0$ or $\lambda_4 = 0$ in (3.2). We conjecture that E_1 is locally asymptotically stable.

In the future we shall investigate the bacteria wall attachment in a flow reactor with Droop type [11, 12].

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