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Asymptotic behavior of ratio-dependent chemostat model with variable yield

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Abstract: To make the theoretical analysis of the microbial continuous culture more close to the experimental results, a ratio-dependent chemostat model with variable yield is formulated. The model develops the classical Monod model and assumes that the yield is a linear function of the nutrient concentration and the microbial growth rate is a ratio-dependent type function. Qualitative analysis is implemented on this model. It is shown that the system is permanent if and only if it has a positive equilibrium. The sufficient conditions of existence of limit cycles and globally asymptotic stability of the positive equilibrium for the model are given.

Key words: chemostat model; continuous culture; ratio-dependent; permanence; limit cycle

0 Introduction

The chemostat is a good laboratory apparatus of microbial continuous culture. Moreover, investigating microbial growth is an especialy important problem in mathematical biology and theoretical ecology. A valuable reference for this subject is the recent book by Smith and Waltman[1]. The basic deterministic models of microbial growth in the continuous culture apparatus take the form[2]

$$\begin{cases} S' = (S^0 - S)Q - \dfrac{x}{\delta}p(S) \\ x' = x(p(S) - Q) \end{cases} \tag{1}$$

where $S(t)$ and $x(t)$ denote concentrations of the nutrient and the microbial biomass respectively; S^0 denotes the feed concentration of the nutrient and Q is the flow volume. The function $p(S)$ denotes the microbial growth rate and an especial choice is $p(S) = mS/(a+S)$[3], it is so-called "Monod growth rate". The stoichiometric yield coefficient δ is the ratio of microbial biomass produced to mass of nutrient consumed. The dynamical behaviors of the basic model (1) are simple. However, this basic model requires modification from the accumulation of experimental data. Especially, the basic model cannot explain the observed oscillatory behavior in the chemostat[4]. It can be more reasonable that the stoichiometric yield coefficient may be a function of nutrient concentration. Such hypothesis was studied theoretically in many chemical engineering literatures[5-7]. From these experiments, although the clear evidence for variability of the yield coefficient exists, its precise function form is still unknown.

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Pilyugin and Waltman[8] assumed that the yield coefficient $\delta(S)$ is a function of the substrate concentration S. They studied the Hopf bifurcation of the persistence rest point and showed that the bifurcation can be subcritical. At the same time, the fact that only supercritical bifurcation occurs when the yield varies linearly with S obtained. Thus, the previously published results in Lit. [5,6] were corrected.

Recently, there is a growing explicit biological and physiological evidence that when predators have to find food, a more reasonable functional response in a predator-prey model should be a function of the ratio of prey to predator. This is strongly supported by many fields and laboratory experiments and observations. A ratio-dependent predator-prey model, generally, takes the form[9]

$$\begin{cases} x' = xf(x) - yp(x/y) \\ y' = cyq(x/y) - dy \end{cases} \tag{2}$$

Here $p(x/y)$ is the so-called ratio-dependent functional response. Often, $q(x/y)$ is replaced by $p(x/y)$, in which case c is the conversion rate.

To make the theoretical analysis of the microbial continuous culture more close to the experimental results, the model in Lit. [8] will be modified in the present paper. That is, the microbial growth rate $p(S)$ is replaced by $p(S/x)$ and the growth yield coefficient $\delta(S)$ becomes a linear function of the nutrient concentration S. Thus, the chemostat model takes form

$$\begin{cases} S' = Q(S^0 - S) - \dfrac{\mu S}{(kx+S)} \dfrac{x}{(A+BS)} \\ x' = x\left(\dfrac{\mu S}{kx+S} - Q\right) \end{cases} \tag{3}$$

where all constant coefficients are positive. The function $p(S/x) = \dfrac{\mu S}{(kx+S)}$ denotes the microbial growth rate and the function $\delta(S) = A + BS$ is the yield coefficient. The objective of this paper is to study the global stability of the boundary equilibrium of the system (3) and show that under the positive equilibrium existence, the system is permanent. Finally, the existence of limit cycles and the global stability of the positive equilibrium are studied by the Poincaré-Bendixson theorem and Dulac criterion.

1 The boundary equilibrium and permanence

For simplicity, the system (3) is rescaled with substitutions

$$S \to S^0\bar{s},\ x \to AS^0\bar{x},\ t \to \tau/Q$$

then the system (3) takes the following simpler form (note that $\bar{s}$, $\bar{x}$, $\bar{\tau}$ are still replaced by s, x, t, respectively)

$$\begin{cases} s' = 1 - s - \dfrac{asx}{bx+s}\dfrac{1}{1+cs} \\ x' = x\left(\dfrac{as}{bx+s} - 1\right) \end{cases} \tag{4}$$

where $a = \mu/Q$, $b = kA$, $c = BS^0/A$.

Lemma 1 The positive quadrant $\Omega = \{(s, x) \in \mathbf{R}^2 \mid s > 0, x > 0\}$ is positively invariant under the system (4). Moreover, the system (4) is dissipative in $\bar{\Omega}$.

Proof On the subset of $\partial\Omega = \{s = 0, x > 0\}$ the vector field is pointing strictly inside Ω since $s' \equiv 1 > 0$ there. The line $l = \{x = 0, s > 0\}$ is invariant under the system (4); thus Ω consists of positive semi-trajectories. The positive invariance of Ω is proved.

Since any solution $u(t) = (s(t), x(t))$ of the system (4) in Ω satisfies the differential inequality $s' \leqslant 1 - s$. Thus for every solution $u(t)$ in Ω, $\limsup\limits_{t\to\infty} s(t) \leqslant 1$. In particular, there is a $T \geqslant 0$ such that $s(t) \leqslant 2$ for all $t \geqslant T$. Let $q = \max\bar{\delta}(s)(s \in [0,2])$, where $\bar{\delta}(s) = 1 + cs$, let $z(t) = s(t) + x(t)/q$, then

$$z' = 1 - s - \frac{asx}{bx+s}\frac{1}{1+cs} + \frac{1}{q}\frac{asx}{bx+s} - \frac{x}{q} \leqslant 1 - s - \frac{x}{q} = 1 - z(t),\ t \geqslant T$$

Therefore

$$\limsup_{t\to\infty} x(t) \leqslant \limsup_{t\to\infty} qz(t) \leqslant q$$

It follows that the system (4) is dissipative in $\bar{\Omega}$. □

Theorem 1 The system (4) always has a boundary equilibrium $E_0=(1,0)$. When $a<1$, the equilibrium E_0 is a hyperbolically stable node. When $a=1$, the equilibrium E_0 is a saddle-node. When $a>1$, the equilibrium E_0 is a hyperbolically saddle. Moreover, if $a<1$, the equilibrium E_0 is globally asymptotically stable in $\overline{\Omega}$.

Proof Obviously, the point $E_0=(1,0)$ is an equilibrium of the system (4). Consider the Jacobian matrix $\boldsymbol{J}(E_0)$ of the system (4) at the equilibrium (1,0), which takes the form of

$$\boldsymbol{J}(E_0)=\begin{pmatrix}-1 & -\dfrac{a}{1+c}\\ 0 & a-1\end{pmatrix}$$

It is easy to see that the eigenvalues of the matrix $\boldsymbol{J}(E_0)$ are $\lambda_1=-1$ and $\lambda_2=a-1$. Consequently, when $a<1$, the equilibrium E_0 is a hyperbolically stable node. When $a=1$, the equilibrium E_0 is a saddle-node. When $a>1$, the equilibrium E_0 is a hyperbolically saddle.

Suppose that $a\leqslant 1$, then the boundary equilibrium E_0 is a unique equilibrium of the system (4). It follows that no solution $u(t)=(s(t),x(t))$ of the system (4) in Ω can have its ω-limit set different from E_0, since otherwise, the Poincaré-Bendixson theorem would imply the existence of a positive equilibrium. Together with Lemma 1 and the above-mentioned result, the globally asymptotic stability of the equilibrium E_0 in $\overline{\Omega}$ is proved. □

Theorem 2 When $a>1$, the system (4) has a unique positive equilibrium $E^*=(s^*,x^*)$ in Ω. Moreover, when $a>1$, the system (4) is permanent in Ω.

Proof By straightforward computation, $x^*=\dfrac{a-1}{b}s^*$ is obtained. When $a>1$, the sign of s^* determines the sign of x^*, thus it is sufficient to prove $s^*\in(0,1)$. After some computation, it can be seen that s^* is one of roots of the equation

$$f(s)=s^2-\frac{b(c-1)-(a-1)}{bc}s-\frac{1}{c}=0$$

Because

$$f(0)=-\frac{1}{c}<0,\ f(1)=\frac{a-1}{bc}>0\ (a>1)$$

Thus, the sign of two roots of the equation $f(s)=0$ is reverse and there must be a unique positive root in (0,1). The positive root is denoted by $s^*\in(0,1)$ and $s^*=\dfrac{\sigma+\sqrt{\sigma^2+4b^2c}}{2bc}$, where $\sigma\triangleq b(c-1)-(a-1)$. It follows that when $a>1$, the existence and uniqueness of the positive equilibrium E^* are proved completely.

It is easy to see that, for the system (4)

$$s'>1-s-\frac{asx}{bx+s}>1-s-\frac{a}{b}s=1-\frac{a+b}{b}s$$

which implies that $\liminf\limits_{t\to+\infty}s(t)\geqslant\dfrac{b}{a+b}\triangleq\underline{s}$. Hence, for large t, $s(t)>\underline{s}/2$, and

$$x'\geqslant x\left(\frac{a\underline{s}/2}{bx+\underline{s}/2}-1\right)$$

It follows that

$$x'\geqslant\frac{x[(a-1)\underline{s}-2bx]}{2bx+\underline{s}}$$

which yields that for $a>1$, $\liminf\limits_{t\to\infty}x(t)\geqslant\dfrac{(a-1)\underline{s}}{2b}\triangleq\underline{x}$.

It follows, together with the dissipativity of the system (4), that the system (4) is permanent in Ω. □

2 The local stability of the positive equilibrium and the existence of limit cycles

In this section, the existence of limit cycles of the system (4) in Ω will be discussed. It is known that the system (4) has a unique equilibrium E^* in Ω when $a>1$. Hence, in the rest of this section, it is assumed that the positive equilibrium always exists in Ω, that is $a>1$. In the following, the local stability of the equilibrium $E^*=(s^*,x^*)$ is studied.

Consider the Jacobian matrix $\boldsymbol{J}(E^*)$ of the system (4) at the equilibrium (s^*,x^*), which takes the form of

$\boldsymbol{J}(E^*)=$

$$\begin{pmatrix} -1-\dfrac{ax^*(bx^*-c(s^*)^2)}{(bx^*+s^*)^2(1+cs^*)^2} & -\dfrac{a(s^*)^2}{(bx^*+s^*)^2(1+cs^*)} \\ \dfrac{ab(x^*)^2}{(bx^*+s^*)^2} & -\dfrac{abs^*x^*}{(bx^*+s^*)^2} \end{pmatrix} \tag{5}$$

By substituting $x^*=\dfrac{a-1}{b}s^*$ into the system (5), and straightforward computation, it follows that

$$\det(\boldsymbol{J}(E^*))=\begin{vmatrix} -1-\dfrac{(a-1)[(a-1)-cs^*]}{ab(1+cs^*)^2} & -\dfrac{1}{a(1+cs^*)} \\ \dfrac{(a-1)^2}{ab} & -\dfrac{a-1}{a} \end{vmatrix}=$$

$$\frac{a-1}{a}\left[1+\frac{a-1}{b}\frac{1}{(1+cs^*)^2}\right]>0$$

Hence, E^* cannot be a saddle. Thus, the local stability of E^* is completely determined by the trace of $\boldsymbol{J}(E^*)$:

$$\mathrm{tr}(\boldsymbol{J}(E^*))=-1-[ax^*(bx^*-c(s^*)^2)+abs^*x^*(1+cs^*)^2]/[(bx^*+s^*)^2(1+cs^*)^2]=-1-\{(a-1)[b(1+cs^*)^2-(1+cs^*)+a]\}/[ab(1+cs^*)^2]\triangleq F^*$$

The above arguments imply that:

Theorem 3 When $a>1$, the positive equilibrium E^* is locally asymptotical stable for $F^*<0$; E^* is unstable for $F^*>0$; if $F^*=0$, then E^* is a nonhyperbolic equilibrium.

Recall that the system (4) is permanent when $a>1$. However, the positive equilibrium E^* is unstable when $F^*>0$. It follows that there could be the limit cycles in Ω.

Theorem 4 When $a>1$ and $F^*>0$, the system (4) has at least one stable limit cycle in Ω which surrounds E^*.

Proof To prove the existence of limit cycle using the Poincaré-Bendixson theorem, first of all, an invariant set D which contains E^* needs to be constructed.

D is the region which consists of the positive s-axis, the positive x-axis and the lines l: $s=1$, m: $x=\dfrac{a-1}{b}s+1$. The points of intersection on the (s,x)-plane are $O(0,0)$, $A(0,1)$, $B\left(1,\dfrac{a+b-1}{b}\right)$, $C(1,0)$ respectively. Hence the region D is the part which is surrounded by the curve $OABCO$, obviously, $D\subset\Omega$.

Next, the tendency of the flow of the system (4) on the boundary of D is discussed. From the positive invariability of Ω, it is sufficient to analyze the tendency of the flow on the lines l and m. On the segment $AB\subset m$, $x'=-\dfrac{bx}{bx+s}<0$, the flow is tending to the interior of D. Similarly, the flow is tending to the interior of D on the segment $BC\subset l$ for $s'=-\dfrac{1}{1+c}\dfrac{ax}{bx+1}<0$. Thus, any trajectory which enters into the interior of D at some time cannot escape from D as time. But when $F^*>0$, the positive equilibrium E^* is unstable. Hence, it follows from the Poincaré-Bendixson theorem that the system (4) has at least one stable limit cycle in D. Theorem 4 is proved. □

Corollary 1 If $a>1$, then all positive solutions of the system (4) are ultimately bounded.

3 The global stability of the positive equilibrium

Firstly, assume $a>1$ in this section, that is to guarantee the existence of the positive equilibrium E^*. The globally asymptotic stability of the positive equilibrium E^* is proved by Dulac criterion together with Corollary 1 and the locally asymptotic stability of E^*.

Theorem 5 When $a>1$ and $F^*<0$, the positive equilibrium E^* is globally asymptotically stable in Ω if any one of the following conditions holds:

(1) $b(c+1)<1$ and $2bc-b-c+1>0$;

(2) $bc-2b+2<0$ and $2bc-b-c+1<0$.

Proof Choose a suitable Dulac function in

D. Obviously, D is a simply connected region. The Dulac function takes the form

$$B(s,x) = (1-s)^{-1}x^{-1}$$

Set

$$P(s,x) = 1 - s - \frac{asx}{bx+s}\frac{1}{1+cs}$$

$$Q(s,x) = x\left(\frac{as}{bx+s} - 1\right)$$

By straightforward computation, it follows that

$$\frac{\partial(BP)}{\partial s} + \frac{\partial(BQ)}{\partial x} = -\frac{a}{\Delta^2}[(bx+s)(1+cs^2) - s(1-s)(1+cs)(1-b-bcs)] \leqslant -\frac{as}{\Delta^2}f(s)$$

where

$$\Delta = (bx+s)(1+cs)(1-s)$$

$$f(s) = -bc^2s^3 + (bc^2 - 2bc + 2c)s^2 + (2bc - b - c + 1)s + b$$

If $f(s) > 0$ is true for some conditions, it implies that under these conditions $\frac{\partial(BP)}{\partial s} + \frac{\partial(BQ)}{\partial x} < 0$ is always tenable in D. It follows from the Dluac criterion and the proof of Theorem 4 that there cannot exist any closed trajectories in D. Thus, together with Corollary 1 and the locally asymptotic stability of E^*, the globally asymptotic stability of E^* is obtained immediately. Therefore, the next objective is to find the sufficient conditions which guarantee $f(s) > 0$.

Note that $s \in [0,1]$, it follows from straightforward computation that the derivatives of $f(s)$ and their values at the end points are as follows:

$$f(0) = b > 0,\ f(1) = 1 + c > 0$$

$$\begin{cases} f'(s) = -3bc^2s^2 + 2(bc^2 - 2bc + 2c)s + (2bc - b - c + 1) \\ f'(0) = 2bc - b - c + 1 \\ f'(1) = -bc^2 - 2bc + 3c - b + 1 \end{cases} \tag{6}$$

$$\begin{cases} f''(s) = -6bc^2s + 2(bc^2 - 2bc + 2c) \\ f''(0) = 2c(bc - 2b + 2) \\ f''(1) = 4c[1 - b(c+1)] \end{cases} \tag{7}$$

$$f'''(s) = -6bc^2 < 0 \tag{8}$$

From Eq. (8), $f''(s)$ is monotonically decreasing in $[0,1]$, which implies that $f''(0) > f''(s) > f''(1)$. Thus, the following cases are got.

Case 1 When $f''(1) > 0$, it implies that $f'(s)$ is monotonically increasing in $[0,1]$, which implies that $f'(0) < f'(s) < f'(1)$.

Case 1.1 When $f'(0) > 0$, it implies that $f(s)$ is monotonically increasing in $[0,1]$, which implies that $f(s) > f(0) = b > 0$. Thus, under these conditions, $f(s) > 0$ is true in $[0,1]$.

Case 1.2 When $f'(1) < 0$, by observation, it is contrary to $f''(1) > 0$.

Consequently, from Eqs. (6) and (7), when $b(c+1) < 1$ and $2bc - b - c + 1 > 0$, $f(s)$ is always positive in $[0,1]$.

Case 2 When $f''(0) < 0$, it implies that $f'(s)$ is monotonically decreasing in $[0,1]$, which implies that $f'(0) > f'(s) > f'(1)$.

Case 2.1 When $f'(0) < 0$, it implies that $f(s)$ is monotonically decreasing in $[0,1]$, which implies that $f(s) > f(1) = 1 + c > 0$. Thus, under these conditions, $f(s) > 0$ is right in $[0,1]$.

Case 2.2 When $f'(1) > 0$, by observation, it is contrary to $f''(0) < 0$.

Consequently, from Eqs. (6) and (7), when $bc - 2b + 2 < 0$ and $2bc - b - c + 1 < 0$, $f(s)$ is always positive in $[0,1]$.

Thus, the proof of Theorem 5 is finished. □

4 Conclusion

In this paper, the ratio-dependent chemostat model with variable yield is considered. The results of the permanence of the system and the existence of limit cycles are obtained, these results are interesting. The analysis of the globally asymptotic stability of the positive equilibrium of this model is more difficult for the microbial growth rate of the ratio-dependent type and the variable yield.

However, the microbial growth rate of the microbial continuous culture models in the previous literatures is mostly Monod type, say, $p(S)=\frac{\mu S}{k+S}$, thus, the analysis of the global stability of the positive equilibrium is easy. On the other hand, the yield of some microbial continuous culture models is a constant, it can reduce the models. But, the ratio-dependent chemostat model with variable yield is more realistic and interesting, therefore, it is very significant to further consider the ratio-dependent chemostat model with variable yield in the future.

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具有变消耗率的比率确定型chemostat模型渐近行为

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摘要:为了使微生物培养的理论研究更接近于实验,建立了一个具有变消耗率的比率确定型chemostat模型.这个模型推广了经典的Monod模型,而且假定了消耗率是一个营养基的线性函数,微生物增长率是比率确定型函数.对该模型作了定性分析,证明了只要正平衡点存在系统就是持续生存的.同时也给出了系统极限环存在和正平衡点全局渐近稳定的充分条件.

关键词:chemostat模型;连续培养;比率确定;持续生存;极限环

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