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Relative positions of limit cycles in the continuous culture vessel with variable yield

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To estimate the relative position of limit cycles for a continuous culture vessel is always useful in the qualitative study of the system. In this paper, we construct an annular region containing all the limit cycles for the chemostat with variable yield model that was studied by Huang (J. Math. Chem. 5, 151–166. 1990), and by Pilyugin and Waltman (Math. Biosci. 182, 151–166. 2003).

KEY WORDS: continuous culture, variable yield, limit cycles, relative position

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1. Introduction

Modeling microbial growth is an interesting problem in mathematical biology and theoretical ecology. One particular class of model is deterministic models of microbial growth in the continuous culture vessel (or bioreactor, or chemostat [1,2]). The model is

$$\begin{aligned} x' &= x(p(S) - D), \\ S' &= (S^0 - S)D - \frac{x}{\gamma} p(S), \end{aligned} \tag{1}$$

where $S(t)$ and $x(t)$ denote the concentrations of the nutrient and the microbial biomass, respectively; S^0 denotes the feed concentration of the nutrient and D the volumetric dilution rate (flow rate/volume). The function $p(S)$ denotes the microbial growth rate and a typical choice for p is the Monod kinetics, $p(S) = mS/(a + S)$. The stoichiometric yield coefficient γ denotes the ratio of microbial biomass produced to the mass of the nutrient consumed.

The dynamics of the model (1) was studied by many authors [3–10]. For example, Crooke et al. proved that the model could not exhibit any periodic solution if the stoichiometric yield coefficient in the model is constant [9]. There

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are also some experiments that indicate that the oscillatory behavior in the chemostat does exist [6,7,9]. The studies show that if the yield coefficient increases linearly with substrate concentration, then for certain parameter range, the stable rest state may undergo the Hopf bifurcation and a limit cycle may appear.

Now the fact that the yield coefficient may depend on the substrate concentration has been well established by experiments (see, for instance, Herbert [11], Panikov [12], Pirt [13], Caperon [14], Droop [15], Minkevich et al. [16], Powell [17], Tang et al. [18], Veldkamp [19], Matin and Veldkamp [20], Clark [21]). But, most of the authors model the constant yield by a linear function [9,10]

$$\gamma(S) = c_1 + c_2 S, \quad c_1, c_2 > 0.$$

Recently, Pilyugin and Waltman [22] introduced a more general class of functions, and derived the model:

$$\begin{aligned} \frac{\mathrm{d}S}{\mathrm{d}t} &= (S^0 - S)D - x\frac{p(S)}{\gamma(S)}, \quad S(0) \geqslant 0, \\ \frac{\mathrm{d}x}{\mathrm{d}t} &= x(p(S) - D_1), \quad x(0) \geqslant 0. \end{aligned} \tag{2}$$

Here as usual, the concentration is measured in units of S^0, and time in unites of $1/D$. If we rescale x by a factor $1/\gamma(0)$, and use a new $p(S)$ replaces $p(S^0 S)/D$, the new $\gamma(S)$ replaces $\gamma(S^0 S)/\gamma(0)$, and the new D replaces D_1/D, we then have the following generalized model:

$$\begin{aligned} \frac{\mathrm{d}x}{\mathrm{d}t} &= x(p(S) - D), \quad x(0) \geqslant 0, \\ \frac{\mathrm{d}S}{\mathrm{d}t} &= 1 - S - x\frac{p(S)}{\gamma(S)}, \quad S(0) \geqslant 0. \end{aligned} \tag{3}$$

Assuming

$$\begin{aligned} &p(S) \in C^1[0, +\infty), \quad p(0) = 0, \quad p'(S) > 0, \\ &\gamma(S) \in C^1[0, +\infty), \quad \gamma(S) > 0, \gamma(0) = 1, \end{aligned}$$

it was shown in ref. 22 that the model (3) exhibits sustained oscillations, and it may undergo a sub-critical Hopf bifurcation and feature at least two limit cycles.

It is interesting to notice that the model (3) was first studied 13 year ago by Huang in a continuous fermentation model [23]. The equations there are

$$\begin{aligned} \frac{\mathrm{d}x}{\mathrm{d}t} &= x(g(y) - 1), \\ \frac{\mathrm{d}y}{\mathrm{d}t} &= 1 - y - \frac{g(y)}{F(y)}x, \end{aligned} \tag{4}$$

where x and y are corresponding to S and x in (3), $g(y)$ and $F(y)$ to $p(S)$ and $\gamma(S)$.

Let $E(x^*, y^*) = ((1 - y^*)F(y^*),\ g^{-1}(1))$. Assume $g(1) > 1$,then $E(x^*, y^*)$ is the only equilibrium point in the positive quadrant. By qualitative analysis of differential equations [23] proved the following theorem:

Theorem A. Assume $g(1) > 1$, if

$$1 + x^* \frac{\mathrm{d}}{\mathrm{d}y}\left(\frac{g}{F}\right)\bigg|_{y=y^*} > 0, \tag{5}$$

then the equilibrium point $E(x^*, y^*)$ of the system (4) is stable; if

$$1 + x^* \frac{\mathrm{d}}{\mathrm{d}y}\left(\frac{g}{F}\right)\bigg|_{y=y^*} < 0, \tag{6}$$

then $E(x^*, y^*)$ is unstable and there exists at least one limit cycle in (4) surrounding the equilibrium point.

Before we end this introduction we would like to emphasize the concept of limit cycles. The problem of limit cycles is always an attractive topic in mathematics since it was first appeared in the very famous papers of Poincare (1881, 1882, 1885, 1886). Even in the beginning of the 20th century, David Hilbert, at the Second International Congress of Mathematicians, Paris 1900, made the famous speech entitled: "Mathematical Problems." One of his 23 problems, the 16th, is on limit cycles – finding the maximum number of limit cycles of the differential equations:

$$\frac{\mathrm{d}x}{\mathrm{d}t} = X_n(x, y),$$

$$\frac{\mathrm{d}y}{\mathrm{d}t} = Y_n(x, y), \tag{E$_\mathrm{n}$}$$

where, $x_n(x, y)$ and $y_n(x, y)$are polynomials whose degrees are not greater than n. Then in the 1930s', van der Pol and Andronov showed that the closed orbit in the phase plane of a self-sustained oscillation occurring in a vacuum tube circuit was a limit cycle as considered by Poincaré. After that, the existence, nonexistence, uniqueness and other properties of limit cycles have been studied extensively by mathematicians and scientists (see, for example, Ye et al. [24]). Now, the existence of limit cycles in the models of microbial growth in the continuous culture vessel is another interesting example in sciences.

Usually, the study of limit cycles includes two aspects: one is the existence, stability and instability, number and relative positions of limit cycles, and the other is the creating and disappearing of limit cycles along with the varying of the parameters in the system (e.g. bifurcation). For the exact number of limit cycles and their relative positions, the known results are not many because determining the number and positions of limit cycles is not easy. That is the reason why the 16th Hilbert problem still remains open even for the case when $n = 2$ after 100 years, even some important progress has been made recently [25–28].

In this paper, we are going to construct an annular region containing all the limit cycles of the system (3). This region is different from the one of [23] both in the way it is constructed and in the relative position. The estimation of the relative position of the limit cycles in the model is obviously useful and important in analyzing the oscillation phenomenon in the continuous culture vessel with variable yield. For a further study on the topic of limit cycles, the references [29–37] are always useful.

2. Main theorems

Let $\Omega = \{(x, S) \in R^2 \,|\, x, S > 0\}$ be the positive quadrant, and assume

$$\begin{aligned} &p(S) \in C^1[0, \infty), \quad p(0) = 0, \quad p'(S) > 0, \\ &\gamma(S) \in C^1[0, \infty), \quad \gamma(0) = 1, \quad \gamma(S) > 0. \end{aligned}$$

The unique equilibrium point in Ω $E(x^*, y^*)$ is given with the condition $p(1) > D$, by

$$x^* = (1 - S^*)\gamma(S^*)/D, \quad S^* = p^{-1}(D).$$

In order to prove the main theorems, we need the following Lemma 1.

Lemma 1. Every solution in Ω of the following system

$$\begin{aligned} \frac{dx}{dt} &= x^*(p(S) - D), \\ \frac{dS}{dt} &= 1 - S^* - x\frac{p(S^*)}{\gamma(S^*)} \end{aligned} \tag{7}$$

is periodic.

Proof. Let $(x_0, S_0) \neq (x^*, S^*)$ be an initial point in Ω. The corresponding trajectory $\Gamma = (x(t), S(t))$ of the system (7) satisfies

$$\int_{x_0}^{x} \left(1 - S^* - x\frac{p(x^*)}{\gamma(S^*)}\right) \mathrm{d}x = \int_{S_0}^{S} x^*(p(S) - D)\mathrm{d}S. \tag{8}$$

Suppose Γ is not a closed orbit. There must be two points $(x(t_1), S(t_1))$, $(x(t_2), S(t_2))$ with $t_1 < t_2$ such that $x(t_1) = x(t_2) = x^*$, and $S(t_1), S(t_2) < S^*$. Let us assume, without loss of generality, $S(t_1) < S(t_2)$. Then

$$\int_{S_0}^{S(t_2)} x^*(p(S) - D)\mathrm{d}S = \int_{S_0}^{S(t_1)} x^*(p(S) - D) + \int_{S(t_1)}^{S(t_2)} x^*(p(S) - D)\mathrm{d}S. \tag{9}$$

Since $x^*(p(S) - D) < 0$ for $S < S^*$,

$$\int_{S_0}^{S(t_2)} x^*(p(S) - D)\mathrm{d}S < \int_{S_0}^{S(t_1)} x^*(p(S) - D)\mathrm{d}S. \tag{10}$$

However, it follows

$$\begin{aligned} \int_{x_0}^{x^*} \left(1 - S^* - x\frac{p(S^*)}{\gamma(S^*)}\right)\mathrm{d}x &= \int_{S_0}^{S(t_2)} x^*(p(S) - D)\mathrm{d}S \\ < \int_{S_0}^{S(t_1)} x^*(p(S) - D)\mathrm{d}S &= \int_{x_0}^{x^*} \left(1 - S^* - x\frac{p(S^*)}{\gamma(S^*)}\right)\mathrm{d}x. \end{aligned} \tag{11}$$

This is a designed contradiction which ends the proof of Lemma 1.

Theorem 1. Let $\bar{S} = \min\{S|(1 - S)\frac{\gamma(S)}{p(S)} = (1 - S^*)\frac{\gamma(S^*)}{p(S^*)},\ S \geq S^*\}$, and

$$A = \{(x, S)|x^* \leqslant x \leqslant (1 - S)\tfrac{\gamma(S)}{p(S)}, \quad S^* \leqslant S \leqslant \bar{S}\}.$$

If, for $0 < S \leqslant \bar{S}$,

$$\left(1 - S - x\frac{p(S)}{\gamma(S)}\right) x^*(p(S) - D) \geqslant \left(1 - S^* - x\frac{p(S^*)}{\gamma(S^*)}\right) x(p(S) - D), \tag{12}$$

then A is inside of all the limit cycles of the system (3).

Proof. Suppose L is a limit cycle of the system (3) surrounding the equilibrium point $E(x^*, S^*)$. By the phase portrait analysis L intersects the curve $1 - S - x\,p(S)/\gamma(S) = 0$ exactly at two points. Consider the system (7) with the initial condition $x(0) = x_0$, $S(0) = S_0$. Lemma 1 implies that all the solutions of the system (7) are periodic. Since each closed orbit has two intersection points with $S = S^*$, suppose one is $Q_i(x_i, S_i)$and the other is

$$\sigma(Q_i) = Q_{i\sigma}(x_{i\sigma}, S_{i\sigma}),$$

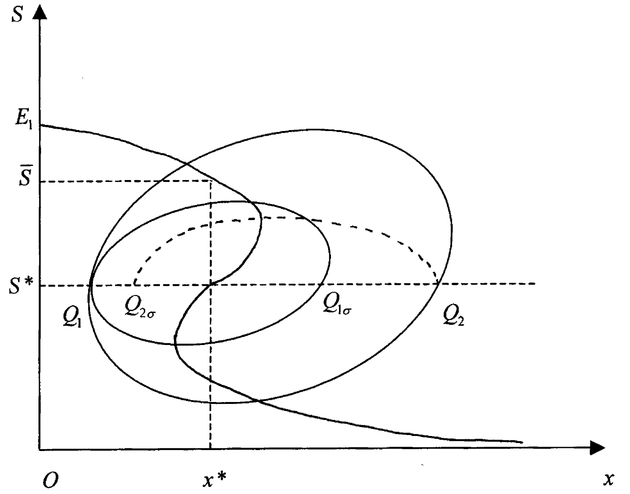

Figure 1. It is impossible that $l(Q_{2\sigma}) < l(Q_1)$.

where $S_i = S_{i\sigma} = S^*$. Clearly $\sigma(Q_{i\sigma}) = \sigma(\sigma(Q_i)) = Q_i$. It is easy to see that the distance from $Q_i(x_i, S_i)$ to $(0, S^*)$ is x_i, denoted as $l(Q_i)$. We can see that the bigger the $l(Q_i)$, the smaller the $l(\sigma(Q_i))$.

According to the definition of A, if $S^* = \bar{S}$, then the set A has only one point (x^*, S^*), which is, of course, inside of L. Now suppose $S^* < \overline{S}$. By the fact that if $(x^*, \overline{S})$ is inside of L, then so is A, we suppose $(x^*, \overline{S})$ is not inside of L. Consider two vectors in the space:

$$\overline{V_1} = \left(1 - S - x\frac{p(S)}{\gamma(S)}, x(p(S) - D), 0\right),$$
$$\overline{V_2} = \left(1 - S^* - x\frac{p(S^*)}{\gamma(S^*)}, x^*(p(S) - D), 0\right) \tag{13}$$

and their vector product

$$\overline{V_1} \times \overline{V_2} = \left(0, 0, \left(\left(1 - S - x\frac{p(S)}{\gamma(S)}\right)x^* - \left(1 - S^* - x\frac{p(S^*)}{\gamma(S^*)}\right)x\right)(p(S) - D)\right). \tag{14}$$

Since $1 - S - x\ (p(S)/\gamma(S)) > 1 - S^* - x\ (p(S^*)/\gamma(S^*))$ for $S^* < S < \overline{S}$, thus $x^* \leqslant x$ for $(x, S) \in A$.

By (12), we have

$$\left(1 - S - x\frac{p(S)}{\gamma(S)}\right)x^*(p(S) - D) - \left(1 - S^* - x\frac{p(S^*)}{\gamma(S^*)}\right)x(p(S) - D) \geqslant 0 \tag{15}$$

for $0 < S \leqslant \overline{S}$. Hence the flow of the system (3) is always directed outwards with respect to the flow of the system (7).

Let $Q_1(x_1, S_1)$ and $Q_2(x_2, S_2)$ be the two intersection points of L with $S = S^*$. Consider the periodic orbit of the system (7) passing $Q_1(x_1, S_1)$, and the corresponding intersection point with $S = S^*$: $\sigma(Q_1) = Q_{1\sigma}(x_{1\sigma}, S_{1\sigma})$. (see figure 1)

Compare the trajectories of the two closed orbits for $S < S^*$.

$$l(Q_{1\sigma}) < l(Q_2). \tag{16}$$

Then, for the case when $S > S^*$, consider the trajectories of the closed orbits initiating at $Q_2(x_2, S_2)$. Since $\sigma(Q_1) = Q_{1\sigma}(x_{1\sigma}, S_{1\sigma})$, and we have

$$l(Q_{2\sigma}) < l(Q_1). \tag{17}$$

$Q_{2\sigma}$ is on the right of Q_1 on the line $S = S^*$. But it is impossible since two periodic orbits of the system (7) can not intersect with each other by the uniqueness of solutions. We can also think in this way. Consider the two periodic orbits of system (7) initiating at $Q_{2\sigma}$andQ_1, respectively. If the inequality (17) holds, then

$$l(\sigma(Q_{2\sigma})) > l(\sigma(Q_1)),$$

hence

$$l(Q_2) > l(Q_{1\sigma}). \tag{18}$$

This is a contradiction to (16), and the proof of Theorem 1 is completed.

Theorem 2. Let $\delta > 0$ be a constant such that

$$\frac{\mathrm{d}x}{\mathrm{d}t} + \delta \left.\frac{\mathrm{d}S}{\mathrm{d}t}\right|_{x=\delta(1-S)} \leqslant 0. \tag{19}$$

Then all the limit cycles of the system (3) are inside of the region B, where $B = B_1 \hbar B_2$, and

$$\begin{aligned} B_1 &= \left\{(x, S) | \, 0 \leqslant S \leqslant S^*, \quad 0 \leqslant x \leqslant \delta(1 - S^*)\right\}, \\ B_2 &= \left\{(x, S) | \, S^* \leqslant S \leqslant 1, \quad 0 \leqslant x \leqslant \delta(1 - S)\right\}. \end{aligned} \tag{20}$$

Proof. Define vectors $\overline{V}$and $\overline{T}$ as

$$\begin{aligned} \overline{V} &= \left(\frac{\mathrm{d}x}{\mathrm{d}t}, \frac{\mathrm{d}S}{\mathrm{d}t}, 0\right), \\ \overline{T} &= (t_1, -1, 0) = \begin{cases} (0, -1, 0) & \text{if } 0 \leqslant S \leqslant S^*, \quad x = \delta(1 - S^*), \\ (\delta, -1.0) & \text{if } S^* \leqslant S \leqslant 1, \quad x = \delta(1 - S). \end{cases} \end{aligned} \tag{21}$$

Since $\overline{T} \times \overline{V} = \left(0, 0, \frac{dx}{dt} + t_1 \frac{dS}{dt}\right)$, if we can prove, for $0 \leqslant S \leqslant 1$

$$\frac{dx}{dt} + t_1 \frac{dS}{dt} \leqslant 0, \tag{22}$$

then B is invariant under (3).

By (21) when $0 \leqslant S \leqslant S^*$, $t_1 = 0$, then

$$\frac{dx}{dt} + t_1 \frac{dS}{dt} = x\,(p(S) - D) < 0, \tag{23}$$

since $p(S) - D < 0$, for $0 \leqslant S \leqslant S^*$.
And, when $S^* < S \leqslant 1$, $t_1 = \delta$, by (17)

$$\frac{dx}{dt} + t_1 \frac{dS}{dt} = \left(\frac{dx}{dt} + \delta \frac{dS}{dt}\right)\bigg|_{x=\delta(1+S)} \leqslant 0. \tag{24}$$

Therefore, B contains all the limit cycles of the system (3) since B is invariant under (3).

Combine theorems 1 and 2, we have

Theorem 3. If $p(1) > D$, $1 + x^*(d/dS)\,(p(S)/\gamma(S))|_{S=S^*} < 0$, and if (12) and (19) hold, then all the limit cycles of the system (3) are in the annular region $B \backslash A$.

3. Discussion

Let us conclude the article by the following remarks.

Remark 1. The sets A and B are easily constructed and the region is explicitly computable. Thus, the theorems are practically useful.

Remark 2. It is not difficult to see that the set A can be extended to

$$A' = \{(x, S)|\; x^* \leqslant x \leqslant (1 - S_M)\frac{\gamma(S_M)}{p(S_M)}, \quad S^* \leqslant S \leqslant \overline{S}, p(S) - D > 0,$$
$$1 - S - x\frac{p(S)}{\gamma(S)} \geqslant 0 \text{ for } S_M \leqslant S \leqslant \overline{S}\}, \tag{25}$$

where

$$(1 - S_M)\frac{\gamma(S_M)}{p(S_M)} = \max_{S^* \leqslant S \leqslant \bar{S}} \left\{(1 - S)\frac{\gamma(S)}{p(S)}\right\}. \tag{26}$$

Remark 3. By a variable transformation, the system (3) can be rewritten as (4), then follow the same argument as in [23], the set B in Theorems 2 and 3 can be replaced by a Bendixson annular region.

Remark 4. If $p(S) = \dfrac{aS}{b+S}$, $\gamma(S) = A + CS$, then the system (3) is reduced to

$$\begin{aligned}\frac{dx}{dt} &= x\left(\frac{aS}{b+S} - 1\right),\\ \frac{dS}{dt} &= 1 - S - \frac{axS}{(b+S)(A+CS)},\end{aligned} \tag{27}$$

which was first studied in [8,9], and we have similar result as in Theorem A. It is also noticed that there are some typing mistake in ref. 23. For example, in both (3.4) (p. 290) and theorem 3.1 (p. 291) the condition for $g(1)$ should be > 1, not < 1.

Remark 5. The condition (10) in Theorem 1 is relevant to the condition (6) in theorem A. For example, if let

$$\begin{aligned}R(x, S) &= \left(1 - S^* - x\frac{p(S^*)}{\gamma(S^*)}\right)x - \left(1 - S - x\frac{p(S)}{\gamma(S)}\right)x^*\\ &= \left((S - S^*) + x\left(\frac{p(S)}{\gamma(S)} - \frac{p(S^*)}{\gamma(S^*)}\right)\right)x^* + \left(1 - S^* - x\frac{p(S^*)}{\gamma(S^*)}\right)(x - x^*).\end{aligned} \tag{28}$$

It is easy to see that

$$R(x, S^*) = \left(1 - S^* - x\frac{p(S^*)}{\gamma(S^*)}\right)(x - x^*) < 0, \tag{29}$$

and

$$\frac{dR}{dS} = 1 + x\frac{d}{ds}\left(\frac{p(S)}{\gamma(S)}\right). \tag{30}$$

If we assume that $dR/dS < 0$, for $S^* \leqslant S \leqslant \bar{S}$, then we have

$$R(x, S) \leqslant R(x, S^*) < 0. \tag{31}$$

Since $p(S) - D > 0$ for $S^* \leqslant S \leqslant \bar{S}$, we have

$$\left(1 - S - x\frac{p(S)}{\gamma(S)}\right)x^*(p(S) - D) - \left(1 - S^* - x\frac{p(S^*)}{\gamma(S^*)}\right)x(p(S) - D) > 0$$

for $S^* \leqslant S \leqslant \bar{S}$. The condition $dR/dS < 0$, for $S^* \leqslant S \leqslant \bar{S}$ is relevant to the condition (6), $1 + x^*(d/dS)\left(\dfrac{p}{\gamma}\right)\Big|_{S=S^*} < 0$. Similarly, we can analysis the case when $0 \leqslant S \leqslant S^*$.

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