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A COMPETITION MODEL OF THE CHEMOSTAT WITH AN EXTERNAL INHIBITOR

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Abstract. A competition model of the chemostat with an external inhibitor is considered. This inhibitor is lethal to one competitor and results in the decrease of growth rate of this competitor. The existence and stability of the extinction equilibria are discussed by using Liapunov function. The necessary and sufficient condition guaranteeing the existence of the interior equilibrium is given. It is found by numerical simulation that the system may be globally stable or have a stable limit cycle if the interior equilibrium exists.

1. **Introduction.** The chemostat, a laboratory apparatus used for the continuous culture of microorganisms, has played an important role in microbiology and population [1, 2, 3, 4, 5]. It is the simplest idealization of a biological system where the parameters are measurable, the experiments are reasonable, and the mathematics is tractable [4]. Experiment verification of the match between theory and experiment in the chemostat can be found in [6]. A detailed mathematical description of competition in the chemostat may be found in [4].

Recently, the inhibitor has been introduced in the models for two competitors in a chemostat, and many authors have studied those models (see [7, 8, 9, 10, 11, 12], etc.). The inhibitor is assumed from the external resource and can inhibit the growth of one competitor that is not lethal or that is lethal to one competitor. In

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[8, 9], the mode with an external inhibitor was analyzed, and an attracting limit cycle was found by the theory of monotone flows or numerical simulation.

Hsu and Waltman [11] and Braselton and Waltman [12] assumed that the inhibitor for one competitor is produced by the other one and that the production of the inhibitor decreases its growth rate. Hsu and Waltman [11] assumed that the fraction of potential growth devoted to producing the inhibitor is a constant and they obtained the global asymptotic results. Braselton and Waltmann [12] assumed that the fraction of potential growth devoted to producing the inhibitor should depend on the concentration of the competitors, so the fraction is a function. In contrast to the former, the latter is with a much wider set of outcomes, which include possibly the interior, stable rest points and stable limit cycles.

In this paper, we consider a model of competition in the chemostat of two competitors for a single nutrient where there is an inhibitor from the external resource. This inhibitor is lethal to one competitor and can result in the decrease of growth rate of this competitor, but the other one can take it up with no deleterious effect.

The organization of this paper is as follows. In the next section, the model is presented. In section 3, the existence and the stability of boundary equilibria are obtained. In section 4, the existence of the interior equilibrium is discussed. In section 5, the dynamical behavior with interior equilibrium is analyzed, and some simulations are shown. Finally, a discussion appears in section 6.

2. **The model.** We use the standard chemostat notation [4]. Let $S(t)$ denote the nutrient concentration at time t, $x(t)$ and $y(t)$ denote the concentrations of the competitors, and $p(t)$ denote the concentration of the inhibitor against the competitor (x). From our assumption that the inhibitor acts only on the growth rate, the model takes the following form [7, 8]:

$$\begin{cases} S' = (S^{(0)} - S)D - e^{-\mu p}\frac{m_1 x S}{a_1+S} - \frac{m_2 y S}{a_2+S}, \\ x' = x(e^{-\mu p}\frac{m_1 S}{a_1+S} - D), \\ y' = y(\frac{m_2 S}{a_2+S} - D), \\ p' = (p^{(0)} - p)D - \frac{\delta y p}{k+p}. \end{cases} \tag{1}$$

Here, $S^{(0)}$ is the input concentration of the nutrient; $p^{(0)}$ is the input concentration of the inhibitor; D is the dilution rate of the chemostat. $S^{(0)}, p^{(0)}$ and D are under the control of the experimenter. The maximal growth rates of competitors without an inhibitor and the half saturation constants, respectively, are $m_i, a_i, i = 1, 2$. These parameters are measurable in the laboratory. The parameters δ and k play similar roles for the inhibitor, δ being the uptake by y and k being a half saturation parameter. Finally, $e^{-\mu p}$ represents the degree of inhibition of p on the growth rate of x.

For a case in which the inhibitor results only in the death of the competitor (x), the model takes the following form [9]:

$$\begin{cases} S' = (S^{(0)} - S)D - \frac{x}{\beta_1}\frac{m_1 S}{a_1+S} - \frac{y}{\beta_2}\frac{m_2 S}{a_2+S}, \\ x' = x(\frac{m_1 S}{a_1+S} - D - \gamma p), \\ y' = y(\frac{m_2 S}{a_2+S} - D), \\ p' = (p^{(0)} - p)D - \frac{\delta p y}{k+p}, \end{cases} \tag{2}$$

where the parameter γ represents the coefficient of the interaction between the inhibitor and the competitor (x), and $\beta_i, i = 1, 2$ represent the yield constants. The meanings of other parameters are the same as those in model (1).

We assume that the external inhibitor acts only on the competitor (x) and that it is lethal and can result in decrease of the growth rate. According to models (1) and (2), the model considered in this paper takes the form

$$\begin{cases} S' = (S^{(0)} - S)D - e^{-\mu p}\frac{m_1 S}{a_1+S}\frac{x}{\beta_1} - \frac{m_2 S}{a_2+S}\frac{y}{\beta_2}, \\ x' = x\left[e^{-\mu p}\frac{m_1 S}{a_1+S} - D - \gamma p\right], \\ y' = y\left[\frac{m_2 S}{a_2+S} - D\right], \\ p' = (p^{(0)} - p)D - \frac{\delta p}{k+p}y. \end{cases} \tag{3}$$

To reduce the number of parameters, let

$$\begin{array}{llll} \bar{S} = \frac{S}{S^{(0)}}, & \bar{x} = \frac{x}{\beta_1 S^{(0)}}, & \bar{y} = \frac{y}{\beta_2 S^{(0)}}, & \bar{p} = \frac{p}{p^{(0)}},\ \bar{t} = Dt, \\ \bar{\mu} = \mu p^{(0)}, & \bar{m}_1 = \frac{m_1}{D}, & \bar{a}_1 = \frac{a_1}{S^{(0)}}, & \bar{m}_2 = \frac{m_2}{D}, \\ \bar{a}_2 = \frac{a_2}{S^{(0)}}, & \bar{\gamma} = \frac{\gamma p^{(0)}}{D}, & \bar{\delta} = \frac{\delta \beta_2 S^{(0)}}{D p^{(0)}}, & \bar{k} = \frac{k}{p^{(0)}}, \end{array}$$

and make these changes for (3). Then, dropping the bars yields the nondimensional model

$$\begin{cases} S' = 1 - S - e^{-\mu p}\frac{m_1 S}{a_1+S}x - \frac{m_2 S}{a_2+S}y, \\ x' = x\left[e^{-\mu p}\frac{m_1 S}{a_1+S} - 1 - \gamma p\right], \\ y' = y\left[\frac{m_2 S}{a_2+S} - 1\right], \\ p' = 1 - p - \frac{\delta p}{k+p}y. \end{cases} \tag{4}$$

System (4) will be analyzed in the remainder part of this paper. We assume that the initial conditions satisfy

$$S(0) \geq 0, x(0) > 0, y(0) > 0, p(0) \geq 0.$$

Since both $x = 0$ and $y = 0$ are the solution surfaces of (4), and $S' = 1$ at $S = 0$, and $p' = 1$ at $p = 0$, the positive cone in R^4 is the positive invariant for (4).

From the first three equations of (4), we have

$$(S + x + y)' \leq 1 - (S + x + y);$$

then

$$S(t) + x(t) + y(t) \leq 1 + ce^{-t}.$$

Therefore, the coordinates of any omega limit point must satisfy $S + x + y \leq 1$.

From the last equation of (4), it follows that

$$p'(t) \leq 1 - p(t);$$

then

$$\lim_{t\to\infty} \sup p(t) \leq 1.$$

Our analysis for (4) will be restricted in the region

$$\Omega = \{(S, x, y, p) : S > 0, x \geq 0, y \geq 0, S + x + y \leq 1, 0 < p \leq 1\}.$$

For convenient notion, define $\lambda_1, \lambda_2, \bar{\lambda}_1$, and λ_p as solutions of

$$\begin{array}{ll} \frac{m_1\lambda_1}{a_1+\lambda_1} = 1, & \frac{m_2\lambda_2}{a_2+\lambda_2} = 1, \\ e^{-\mu}\frac{m_1\bar{\lambda}_1}{a_1+\bar{\lambda}_1} = 1 + \gamma, & e^{-\mu\bar{p}}\frac{m_1\lambda_p}{a_1+\lambda_p} = 1 + \gamma\bar{p}, \end{array}$$

respectively, where $\bar{p}$ is the positive root of equation $(1-z)(k+z)=\delta z(1-\lambda_2)$. Notice that $0<\bar{p}<1$ if and only if $0<\lambda_2<1$; then $\lambda_1<\lambda_p<\bar{\lambda}_1$ as $0<\lambda_2<1$. We define $\lambda_1=+\infty$ if $\frac{m_1}{a_1+1}<1$, $\lambda_2=+\infty$ if $\frac{m_2}{a_2+1}<1$, $\bar{\lambda}_1=+\infty$ if $e^{-\mu}\frac{m_1}{a_1+1}<1+\gamma$.

3. **Boundary equilibria: Existence and stability.**

The existence of the boundary equilibria of (4) is given in the following theorem.

THEOREM 3.1. *For system (4), the equilibrium $E_0(1,0,0,1)$ always exists. The equilibrium $E_1(\bar{\lambda}_1,\frac{1-\bar{\lambda}_1}{1+\gamma},0,1)$ exists if $0<\bar{\lambda}_1<1$; $E_2(\lambda_2,0,1-\lambda_2,\bar{p})$ exists if $0<\lambda_2<1$.*

The Jacobian matrices of (4) at the boundary equilibria E_0, E_1, and E_2 are respectively

$$J(E_0)=\begin{pmatrix} -1 & -e^{-\mu}\frac{m_1}{a_1+1} & -\frac{m_2}{a_2+1} & 0 \\ 0 & e^{-\mu}\frac{m_1}{a_1+1}-1-\gamma & 0 & 0 \\ 0 & 0 & \frac{m_2}{a_2+1}-1 & 0 \\ 0 & 0 & -\frac{\delta}{k+1} & -1 \end{pmatrix},$$

$$J(E_1) = \begin{pmatrix} -1-e^{-\mu}\frac{m_1a_1(1-\bar{\lambda}_1)}{(a_1+\bar{\lambda}_1)^2(1+\gamma)} & -e^{-\mu}\frac{m_1\bar{\lambda}_1}{a_1+\bar{\lambda}_1} & -\frac{m_2\bar{\lambda}_1}{a_2+\bar{\lambda}_1} & \mu e^{-\mu}\frac{m_1\bar{\lambda}_1}{a_1+\bar{\lambda}_1}\cdot\frac{1-\bar{\lambda}_1}{1+\gamma} \\ \frac{m_1a_1e^{-\mu}}{(a_1+\bar{\lambda}_1)^2}\cdot\frac{1-\bar{\lambda}_1}{1+\gamma} & 0 & 0 & -\left(\mu e^{-\mu}\frac{m_1\bar{\lambda}_1}{a_1+\bar{\lambda}_1}+\gamma\right)\frac{1-\bar{\lambda}_1}{1+\gamma} \\ 0 & 0 & \frac{m_2\bar{\lambda}_1}{a_2+\bar{\lambda}_1}-1 & 0 \\ 0 & 0 & -\frac{\delta}{k+1} & -1 \end{pmatrix},$$

and

$$J(E_2)=\begin{pmatrix} -1-\frac{m_2a_2(1-\lambda_2)}{(a_2+\lambda_2)^2} & -e^{-\mu\bar{p}}\frac{m_1\lambda_2}{a_1+\lambda_2} & -1 & 0 \\ 0 & e^{-\mu\bar{p}}\frac{m_1\lambda_2}{a_1+\lambda_2}-1-\gamma\bar{p} & 0 & 0 \\ \frac{m_2a_2(1-\lambda_2)}{(a_2+\lambda_2)^2} & 0 & 0 & 0 \\ 0 & 0 & -\frac{\delta\bar{p}}{k+\bar{p}} & -1-\frac{\delta k(1-\lambda_2)}{(k+\bar{p})^2} \end{pmatrix}.$$

Therefore, E_0 is locally asymptotically stable if $e^{-\mu}\frac{m_1}{a_1+1}<1+\gamma$ and $\frac{m_2}{a_2+1}<1$ (that is, $\bar{\lambda}_1>1$ and $\lambda_2>1$); E_1 is locally asymptotically stable if $\frac{m_2\bar{\lambda}_1}{a_2+\bar{\lambda}_1}<1$ and $\bar{\lambda}_1<1$ (that is, $\bar{\lambda}_1<\lambda_2$ and $\bar{\lambda}_1<1$); and E_2 is locally asymptotically stable if $e^{-\mu\bar{p}}\frac{m_1\lambda_2}{a_1+\lambda_2}<1+\gamma\bar{p}$ and $0<\lambda_2<1$ (that is, $\lambda_2<\lambda_p$ and $\lambda_2<1$).

The stability of those boundary equilibria is summarized as follows.

THEOREM 3.2. *For system (4), E_0 is locally asymptotically stable if $\bar{\lambda}_1>1$ and $\lambda_2>1$; E_1 is locally asymptotically stable if $\bar{\lambda}_1<\lambda_2$ and $\bar{\lambda}_1<1$; and E_2 is locally asymptotically stable if $\lambda_2<\lambda_p$ and $\lambda_2<1$.*

From the third equation of (4), we have

$$y'\le y\left[\frac{m_2}{a_2+1}-1\right]$$

because $S\le 1$. Because $\lambda_2>1$ implies $\frac{m_2}{a_2+1}<1$, by the standard comparison theorem, $\lim_{t\to\infty}y(t)=0$ if $\lambda_2>1$. Further, from the fourth equation of (4), it is obtained that $\lim_{t\to\infty} p(t) = 1$ if $\lambda_2 > 1$. So we consider the limiting system

$$\begin{cases} S' = 1 - S - e^{-\mu}\frac{m_1 S x}{a_1+S}, \\ x' = x\left[e^{-\mu}\frac{m_1 S}{a_1+S} - 1 - \gamma\right]. \end{cases} \tag{5}$$

For system (5), we can easily obtain the following using the theory of asymptotic autonomous systems [13].

LEMMA 3.1. *Equilibrium* $(S, x) = (1, 0)$ *is globally asymptotically stable on the region* $\{(S, x) : S > 0, x \geq 0, S + x \leq 1\}$ *if* $\bar{\lambda}_1 > 1$*; equilibrium* $(S, x) = (\bar{\lambda}_1, 1 - \bar{\lambda}_1)$ *is globally asymptotically stable in the interior of the region* $\{(S, x) : S > 0, x \geq 0, S + x \leq 1\}$ *if* $\bar{\lambda}_1 < 1$.

By using the theory of asymptotic autonomous systems [13], we obtain the following theorems.

THEOREM 3.3. *Equilibrium* E_0 *is globally asymptotically stable if* $\bar{\lambda}_1 > 1$ *and* $\lambda_2 > 1$*; equilibrium* E_1 *is globally asymptotically stable if* $\bar{\lambda}_1 < 1$ *and* $\lambda_2 > 1$.

When $\lambda_2 < 1$, we have two theorems about the global stability of E_2 and E_1 as follows:

THEOREM 3.4. *When* $\lambda_2 < 1$ *and* $\lambda_2 < \lambda_p$, E_2 *is globally asymptotically stable.*

THEOREM 3.5. *When* $\bar{\lambda}_1 + \frac{\gamma}{1+\gamma} < \lambda_2 < 1$, E_1 *is globally asymptotically stable.*

To prove Theorem 3.4, the following lemmas are introduced:

LEMMA 3.2. *Let* α *be a finite number and* $f : [\alpha, \infty) \to R$ *a differential function. If* $\lim_{t\to\infty} f(t)$ *exists (finite) and the derivative function* f' *is uniformly continuous on* (α, ∞)*, then* $\lim_{t\to\infty} f'(t) = 0$.

Lemma 3.2 is cited from [14] and is used in proving the following lemma.

LEMMA 3.3. $\lim_{t\to\infty} \inf p(t) \geq \bar{p}$ *if* $\lambda_2 < 1$.

Proof. Because all of S, x, y, and p are bounded, the right-hand side of (4) is bounded. Moreover, the time derivative of the right-hand side of (4) is also bounded, so the right-hand side of (4) is uniformly continuous on $(0, \infty)$. From Lemma 3.2, $\lim_{t\to\infty} y'(t) = 0$ if $\lim_{t\to\infty} y(t)$ exists, and $\lim_{t\to\infty} p'(t) = 0$ if $\lim_{t\to\infty} p(t)$ exists.

If $\lim_{t\to\infty} p(t)$ exists, denoted $\lim_{t\to\infty} p(t) = \hat{p}$, then $\lim_{t\to\infty} y(t)$ exists, and $\lim_{t\to\infty} y(t) = \frac{(1-\hat{p})(k+\hat{p})}{\delta \hat{p}}$. Further, $\lim_{t\to\infty} S(t) = \lambda_2$ if $\hat{p} \neq 1$, so $\lim_{t\to\infty} y(t) \leq 1 - \lambda_2$ because $y(t) \leq 1 - S(t)$. This implies $\frac{(1-\hat{p})(k+\hat{p})}{\delta \hat{p}} \leq 1 - \lambda_2$. So we have $\hat{p} \geq \bar{p}$ from the definition of $\bar{p}$, since function $\frac{(1-u)(k+u)}{\delta u}$ is decreasing for u.

If $\lim_{t\to\infty} p(t)$ does not exist, then there exist $t_n (n = 1, 2, ...)$, satisfying $\lim_{n\to\infty} t_n = \infty$, such that $p'(t_n) = 0$ and $\lim_{n\to\infty} p(t_n) = \lim_{t\to\infty} \inf p(t) =: p_*$. From $\frac{(1-p(t_n))(k+p(t_n))}{\delta p(t_n)} = y(t_n)$, we have $\frac{(1-p_*)(k+p_*)}{\delta p_*} = \lim_{n\to\infty} y(t_n) \leq \lim_{t\to\infty} \sup y(t)$.

We claim $\lim_{t\to\infty} \sup y(t) \leq 1 - \lambda_2$. If $\lim_{t\to\infty} y(t)$ does exist, then there exist $\tau_n (n = 1, 2, ...)$, satisfying $\lim_{n\to\infty} \tau_n = \infty$, such that $y'(\tau_n) = 0$, $\lim_{n\to\infty} y(\tau_n) = \lim_{t\to\infty} \sup y(t)$ and $S(\tau_n) = \lambda_2$. So $y(\tau_n) \leq 1 - \lambda_2$, then $\lim_{t\to\infty} \sup y(t) \leq 1 - \lambda_2$. Similarly, $\lim_{t\to\infty} y(t) \leq 1 - \lambda_2$ if $\lim_{t\to\infty} y(t)$ exists. Therefore, the claim holds.

Hence, if $\lim_{t\to\infty} p(t)$ does not exist, then $\frac{(1-p_*)(k+p_*)}{\delta p_*} \le 1-\lambda_2$. Moreover, $p_* \ge \bar{p}$, that is, $\lim_{t\to\infty} \inf p(t) \ge \bar{p}$. This completes the proof of Lemma 3.3. □

Proof of Theorem 3.4. Define the Liapunov function

$$V(S,x,y) = \int_{\lambda_2}^{S}\left(1-\frac{a_2+u}{m_2 u}\right)du + Bx + \int_{(1-\lambda_2)}^{y}\frac{u-(1-\lambda_2)}{u}du,$$

where $B = \frac{1}{2m_2a_1}\left[e^{-\mu\bar{p}}\cdot\frac{m_1a_2}{1+\gamma\bar{p}} + a_1(m_2-1)+a_2\right] > 0$ (since $\lambda_2<1$ implies $m_2 > 1$). By using $\frac{m_2\lambda_2}{a_2+\lambda_2}=1$, we have

$$\begin{aligned} V'|_{(4)} = \;& -\frac{(m_2-1)(S+m_2-1)(S-\lambda_2)^2}{m_2S(a_2+S)} \\ & +x\left[B\left(e^{-\mu p}\cdot\frac{m_1S}{a_1+S}-1-\gamma p\right) - e^{-\mu p}\frac{m_1S}{a_1+S}\left(1-\frac{a_2+S}{m_2S}\right)\right] \\ =: \;& -F(S)+xG(S,p), \end{aligned}$$

where $F(S)$ is positive definite with respect to $S=\lambda_2$, since $\lambda_2<1$.

$$G(S,p) = B\left(e^{-\mu p}\frac{m_1S}{a_1+S}-1-\gamma p\right) - e^{-\mu p}\frac{m_1(a_2+S)}{m_2(a_1+S)}\left(\frac{m_2S}{a_2+S}-1\right),$$

$$\begin{aligned} G'_S(S,p) &= \frac{m_1}{m_2}\cdot\frac{e^{-\mu p}}{(a_1+S)^2}\left[Bm_2a_1-(m_2-1)a_1-a_2\right] \\ &= \frac{m_1}{2m_2}\cdot\frac{e^{-\mu p}}{(a_1+S)^2}\left\{e^{-\mu\bar{p}}\frac{m_1a_2}{1+\gamma\bar{p}} - [(m_2-1)a_1+a_2]\right\}. \end{aligned}$$

By means of the definitions of λ_2 and λ_p, we have $e^{-\mu\bar{p}}\frac{m_1a_2}{1+\gamma\bar{p}} - [(m_2-1)a_1+a_2] = a_1a_2\left(\frac{1}{\lambda_p}-\frac{1}{\lambda_2}\right)$; then, $G'_S(S,p) = \frac{m_1a_1a_2}{2m_2}\cdot\frac{e^{-\mu p}}{(a_1+S)^2}\left(\frac{1}{\lambda_p}-\frac{1}{\lambda_2}\right)$.

Because $\lambda_2<\lambda_p$, it follows that $G'_S<0$. Moreover, $G(S,p)<G(0,p) = e^{-\mu p}\frac{m_1a_2}{m_2a_1} - B(1+\gamma p)$.

Define $f(\epsilon) = e^{-\mu(\bar{p}-\epsilon)}\frac{m_1a_2}{m_2a_1} - B[1+\gamma(\bar{p}-\epsilon)]$(where $\epsilon>0$). Since $f(0) = e^{-\mu\bar{p}}\frac{m_1a_2}{m_2a_1} - B(1+\gamma\bar{p}) = \frac{a_2(1+\gamma\bar{p})}{2m_2}\cdot\left(\frac{1}{\lambda_p}-\frac{1}{\lambda_2}\right)<0$, there exists $\epsilon>0$ small enough, such that $f(\epsilon)<0$. From Lemma 3.3, for this ϵ, there exists $T>0$ such that $p(t)>\bar{p}-\epsilon$ for $t>T$. Therefore, for $t>T$,

$$G(0,p) < e^{-\mu(\bar{p}-\epsilon)}\frac{m_1a_2}{m_2a_1} - B[1+\gamma(\bar{p}-\epsilon)] = f(\epsilon)<0.$$

Therefore, for $t>T$, $V'|_{(4)}\le 0$. So E_2 is globally asymptotically stable by LaSalle's Invariance Principle [15]. The proof of Theorem 3.4 is complete. □

For the proof of Theorem 3.5 we need following three propositions.

Proposition 3.1. *If $\lambda_2>\bar{\lambda}_1$ and $\lim_{t\to\infty} y(t)$ exists, then $\lim_{t\to\infty} y(t)=0$.*

Proof. If $\lim_{t\to\infty} y(t)=y^*>0$, then $\lim_{t\to\infty} S(t)=\lambda_2$ by Lemma 3.2. The limiting equation of the second equations in (4) is

$$\begin{aligned} x' &= x\left[e^{-\mu p}\frac{m_1\lambda_2}{a_1+\lambda_2}-1-\gamma p\right] \\ &\ge x\left[e^{-\mu}\frac{m_1\lambda_2}{a_1+\lambda_2}-1-\gamma\right], \end{aligned}$$

because $p(t)\le 1$. Since $\lambda_2>\bar{\lambda}_1$ implies $e^{-\mu}\frac{m_1\lambda_2}{a_1+\lambda_2}-1-\gamma>0$, then $\lim_{t\to\infty} x(t)=\infty$, which contradicts $0\le x(t)\le 1$. Hence, Proposition 3.1 is true. □

Proposition 3.2. *If $\lambda_2>\bar{\lambda}_1$ and $\lim_{t\to\infty} x(t)=\beta>0$, then $\lim_{t\to\infty} y(t)=0$.*

Proof. If $y(t)$ does not tend to a limit, then the following inequality holds:

$$0 \leq \lim_{t\to\infty} \inf y(t) < \lim_{t\to\infty} \sup y(t) = \alpha.$$

Choose a sequence $\{t_n\}(n = 1, 2, ...)$ satisfying $\lim_{n\to\infty} t_n = \infty$, such that $y'(t_n) = 0$ and $\lim_{n\to\infty} y(t_n) = \alpha$. Since $x(t)$ tends to a positive limit by hypothesis, then the limit of $x'(t)$ as t tends to infinity is zero by Lemma 3.2. So $\lim_{n\to\infty} x'(t_n) = 0$. Thus

$$\begin{aligned} 0 &= \lim_{\tau\to\infty} \left[e^{-\mu p(t_n)} \tfrac{m_1\lambda_2}{a_1+\lambda_2} - 1 - \gamma p(t_n) \right] \\ &\geq e^{-\mu} \tfrac{m_1\lambda_2}{a_1+\lambda_2} - 1 - \gamma, \end{aligned}$$

because $p(t) \leq 1$. This is a contradiction, because $\lambda_2 > \bar{\lambda}_1$. Thus, $y(t)$ tends to a limit as t tends to infinity. Further, this limit is zero by Proposition 3.1. This completes the proof of Proposition 3.2. □

Proposition 3.3. *If* $\bar{\lambda}_1 + \frac{\gamma}{1+\gamma} < \lambda_2 < 1$, *then* $\lim_{t\to\infty} y(t)$ *exists.*

Proof. We have already noted that

$$S(t) + x(t) + y(t) \leq 1 + ce^{-t}.$$

Adding the equations of S, x, and y in (2.4) yields

$$\begin{aligned} S'(t) + x'(t) + y'(t) &= 1 - S(t) - x(t) - y(t) - \gamma x(t)p(t) \\ &\geq 1 - S(t) - x(t) - y(t) - \gamma x(t) \\ &> 1 - (1+\gamma)(S(t) + x(t) + y(t)). \end{aligned}$$

The standard comparison theorem yields that

$$S(t) + x(t) + y(t) > \frac{1}{1+\gamma} + c'e^{-(1+\gamma)t}. \tag{6}$$

If the limits of $x(t)$ and $y(t)$ do not exist, then the following inequalities are true:

$$0 \leq \lim_{t\to\infty} \inf y(t) < \lim_{t\to\infty} \sup y(t) = \beta$$

and

$$\lim_{t\to\infty} \inf x(t) = \alpha < \lim_{t\to\infty} \sup x(t).$$

Choose a sequence, $\{t_n\}(n = 1, 2, ...)$ satisfying $\lim_{n\to\infty} t_n = \infty$, such that $y'(t_n) = 0$ and $\lim_{n\to\infty} y(t_n) = \beta$. Since $y(t_n) > 0, S(t_n) = \lambda_2$ and $\lambda_2 \leq 1 - \alpha - \beta$, i.e., $\alpha + \beta \leq 1 - \lambda_2$. Now choose a sequence, $\{\tau_n\}(n = 1, 2, ...)$ satisfying $\lim_{n\to\infty} \tau_n = \infty$, such that $x'(\tau_n) = 0$ and $\lim_{n\to\infty} x(\tau_n) = \alpha$. Because $p(t) \leq 1$,

$$e^{-\mu} \frac{m_1 S(\tau_n)}{a_1 + S(\tau_n)} - 1 - \gamma \leq e^{-\mu p(\tau_n)} \frac{m_1 S(\tau_n)}{a_1 + S(\tau_n)} - 1 - \gamma p(\tau_n) = 0.$$

Thus $S(\tau_n) \leq \bar{\lambda}_1$. Using (6) gives

$$\bar{\lambda}_1 + x(\tau_n) + y(\tau_n) > \frac{1}{1+\gamma} + c'e^{-(1+\gamma)\tau_n}.$$

Applying $\lim_{n\to\infty} x(\tau_n) = \alpha$ and $\lim_{t\to\infty} \sup y(t) = \beta$ yields $\bar{\lambda}_1 + \alpha + \beta \geq \frac{1}{1+\gamma}$. So we have

$$\frac{1}{1+\gamma} - \bar{\lambda}_1 \leq \alpha + \beta \leq 1 - \lambda_2,$$

which implies that

$$\frac{\gamma}{1+\gamma} + \bar{\lambda}_1 \geq \lambda_2.$$

This contradicts the hypothesis of the proposition. Therefore, Proposition 3.3 holds. □

By applying Propositions 3.1, 3.2, and 3.3 and the theory of asymptotic autonomous systems [13], it is easy to see that Theorem 3.5 is true.

4. **The existence of the interior equilibrium.**

The existence of the interior equilibrium of (4) is given in following theorem.

THEOREM 4.1. *System (4) has a unique interior equilibrium $E^*(S^*, x^*, y^*, p^*)$ if and only if $0 < \lambda_2 < 1$ and $\lambda_p < \lambda_2 < \bar{\lambda}_1$.*

Proof. For the interior equilibrium $E^*(S^*, x^*, y^*, p^*)$ of (4), it is evident that $S^* = \lambda_2(0 < \lambda_2 < 1)$ and that x^*, y^* and p^* satisfy equations

$$1 - \lambda_2 - e^{-\mu p}\frac{m_1\lambda_2}{a_1+\lambda_2}x - \frac{m_2\lambda_2}{a_2+\lambda_2}y = 0, \tag{7}$$

$$e^{-\mu p}\frac{m_1\lambda_2}{a_1+\lambda_2} = 1 + \gamma p, \tag{8}$$

$$1 - p = \frac{\delta p}{k+p}y. \tag{9}$$

When $0 < \lambda_2 < 1$, (8) has only one positive root p^* in the interval (0, 1) if and only if $\frac{m_1\lambda_2}{a_1+\lambda_2} - 1 > 0 > e^{-\mu}\frac{m_1\lambda_2}{a_1+\lambda_2} - (1+\gamma)$; that is, $\lambda_1 < \lambda_2 < \bar{\lambda}_1$.

Substituting $p = p^*$ into (9) gets $y^* = \frac{(1-p^*)(k+p^*)}{\delta p^*} > 0$. Again, substituting $p = p^*$ and $y = y^*$ into (7) gets $x^* = \frac{1-\lambda_2-y^*}{1+\gamma p^*}$.

When $\lambda_p < \lambda_2 < \bar{\lambda}_1$, $p^* < 1$ due to $\lambda_1 < \lambda_p$. And, when $\lambda_2 > \lambda_p$, we have

$$e^{\mu p^*}(1+\gamma p^*) = \frac{m_1\lambda_2}{a_1+\lambda_2} > \frac{m_1\lambda_p}{a_1+\lambda_p} = e^{\mu\bar{p}}(1+\gamma\bar{p}).$$

So $p^* > \bar{p}$, and $y^* = \frac{(1-p^*)(k+p^*)}{\delta p^*} < \frac{(1-\bar{p})(k+\bar{p})}{\delta\bar{p}} = 1 - \lambda_2$. Thus $x^* > 0$.

$S^* + x^* + y^* = \lambda_2 + \frac{1-\lambda_2-y^*}{1+\gamma p^*} + y^* = \frac{1+\gamma p^*(\lambda_2+y^*)}{1+\gamma p^*} < 1$ because $\lambda_2 + y^* < 1$.

When $\lambda_1 < \lambda_2 \leq \lambda_p$, it follows that $e^{\mu p^*}(1+\gamma p^*) = \frac{m_1\lambda_2}{a_1+\lambda_2} \leq \frac{m_1\lambda_p}{a_1+\lambda_p} = e^{\mu\bar{p}}(1+\gamma\bar{p})$; then, $p^* \leq \bar{p}$, so $y^* = \frac{(1-p^*)(k+p^*)}{\delta p^*} \geq \frac{(1-\bar{p})(k+\bar{p})}{\delta\bar{p}} = 1 - \lambda_2$, and thus $x^* \leq 0$. Therefore, when $\lambda_1 < \lambda_2 \leq \lambda_p$, (4) has no interior equilibrium. Therefore, Theorem 4.1 is true. □

5. **Dynamical behavior and simulation with the interior equilibrium.**

Theorem 4.1 shows that the boundary equilibrium E_2 must exist and is unstable when the interior equilibrium E^* exists. We find by numerical simulation that its dynamical behavior is complex. Three examples are presented here to show its complexity. All of the computations in this section were performed with Maple.

In the first example, parameter values of (2.4) are as follows: $\mu = 0.002, m_1 = 4.5, a_1 = 0.02, m_2 = 4.5, a_2 = 1.0, \gamma = 4.0, k = 1.5, \delta = 5.0$. For this case, system (2.4) has two boundary equilibria: $E_0(1, 0, 0, 1), E_2 = (0.2857, 0, 0.7143, 0.3400)$, and the interior equilibrium $E^* = (0.2857, 0.1427, 0.1152, 0.7997)$. Since $\bar{\lambda}_1 = \infty, \lambda_2 = 0.2857$, and $\lambda_p = 0.0221$ (that is, $\lambda_p < \lambda_2 < 1 < \bar{\lambda}_1$), both E_0 and

E_2 are unstable. And the computation indicates that E^* is unstable. The numerical simulation shows that system (2.4) has an attracting limit cycle. The time course is shown in Figure 1 and Figure 2. The trajectory in (S, x, y) space is shown in Figure 3.

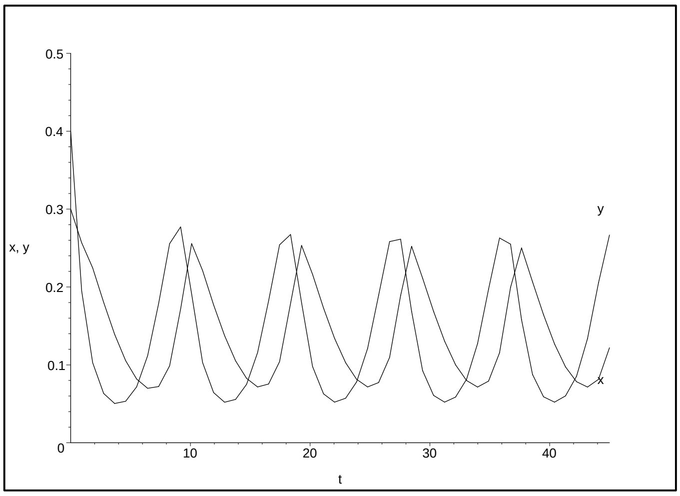

FIGURE 1. Plot of $x(t)$ and $y(t)$ in the case of oscillatory coexistence.

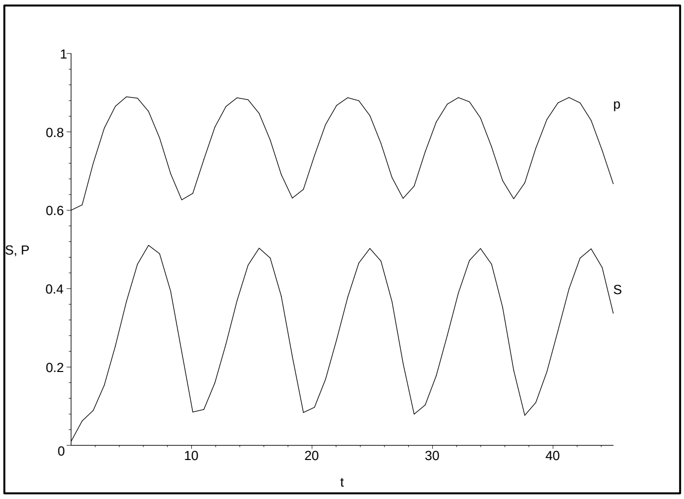

FIGURE 2. Plot of $S(t)$ and $p(t)$ in the case of oscillatory coexistence.

In the second example, the parameters are as above, except that $\gamma = 3.45$. For this case, system (2.4) has two boundary equilibria that are the same as above, and the interior equilibrium $E^* = (0.2857, 0.1610, 0.0383, 0.9269)$. Because $\bar{\lambda}_1 = 2.1703, \lambda_2 = 0.2857$, and $\lambda_p = 0.1870$ (that is, $\lambda_p < \lambda_2 < 1 < \bar{\lambda}_1$), both E_0 and E_2 are unstable. And the computation indicates that E^* is stable. The numerical simulation shows that E^* is globally asymptotically stable. The time course is shown in Figure 4. The trajectory in (S, x, y) space is shown in Figure 5.

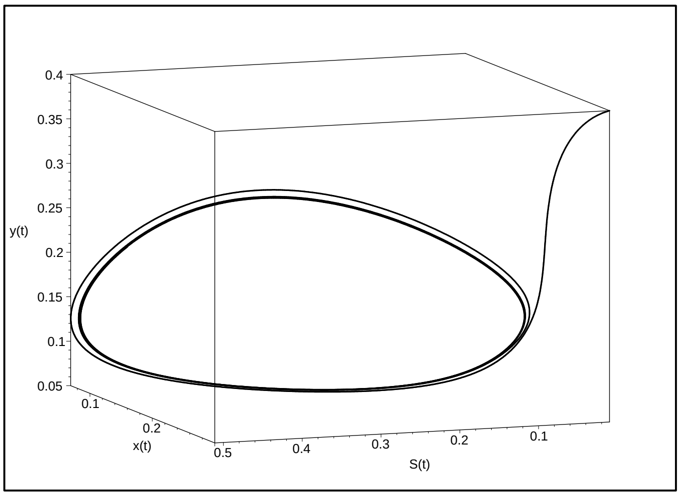

FIGURE 3. Plot in R^3 of the limit cycle in Figures 1 and 2.

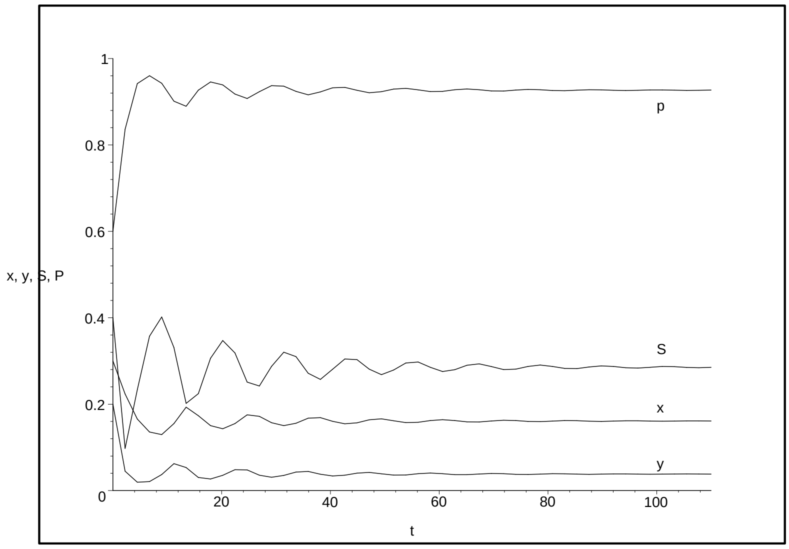

FIGURE 4. Plot in time course.

In the third example, the parameters are taken to be $\mu = 0.002, m_1 = 4.5, a_1 = 0.02, m_2 = 26, a_2 = 2.5, \gamma = 3.2, k = 1.5, \delta = 5.0$. In this case, system (2.4) has three boundary equilibria: $E_0(1, 0, 0, 1), E_1 = (0.2887, 0.1694, 0, 1), E_2 = (0.1, 0, 0.9, 0.2839)$, and the interior equilibrium $E^* = (0.1, 0.2195, 0.0784, 0.8574)$. Since $\bar{\lambda}_1 = 0.2887, \lambda_2 = 0.1$, and $\lambda_p = 0.0147$ (that is, $\lambda_p < \lambda_2 < \bar{\lambda}_1 < 1$), all of the boundary equilibria E_0, E_1 and E_2 are unstable. And the computation indicates that E^* is stable. The numerical simulation shows that system (2.4) is globally asymptotically stable. The time course is shown in Figure 6. The trajectory in (S, x, y) space is shown in Figure 7.

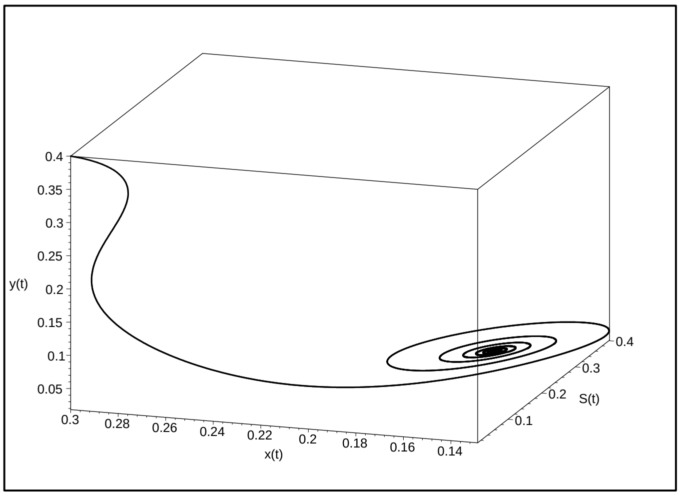

FIGURE 5. Plot in R^3 of location of the spiral.

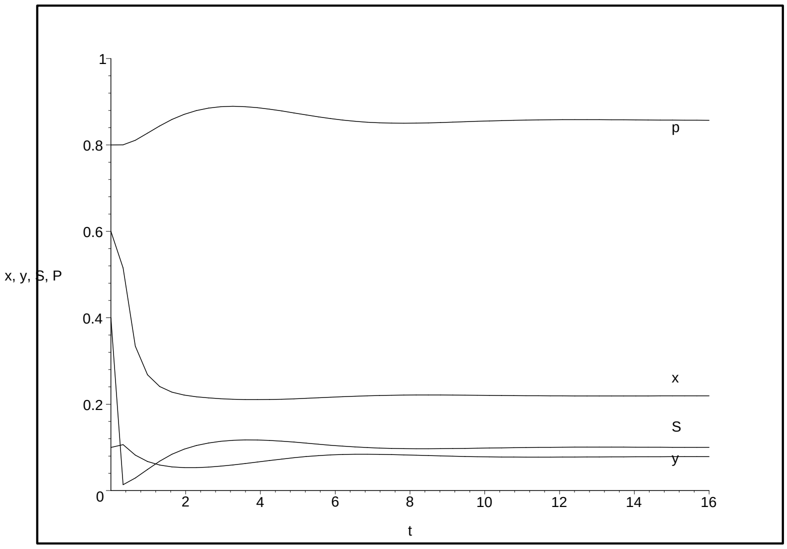

FIGURE 6. Plot in time course.

6. **Discussion.** This paper has considered a competition model for a single nutrient in a chemostat with an external inhibitor. This inhibitor is lethal to one competitor and can result in a decreased growth rate for this competitor, but the other one can take it up with no deleterious effect. By some changes of variables and parameters, the basic model is transferred to a new system, which contains fewer parameters, and is investigated throughout this paper.

The boundary equilibria are located, and their stabilities are obtained by Liapunov function and the theory of asymptotic autonomous systems. The existence and stability results are summarized in Table 6.

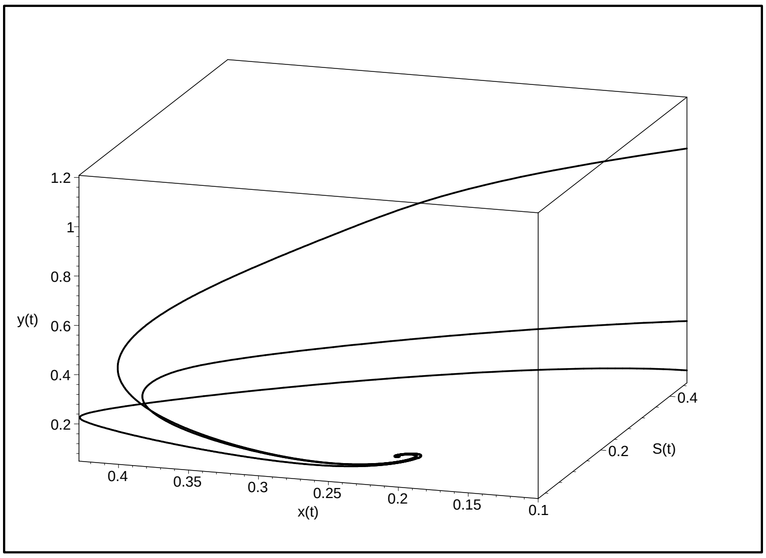

Figure 7. Plot in R^3 of asymptotic behavior.

Table 1. US-unstable; LAS-locally asymptotically stable; GAS-globally asymptotically stable

<table>
<tr><td rowspan="2">$\lambda_2 > 1$</td><td colspan="3">$\bar{\lambda}_1 > 1$</td><td>E_0(GAS)</td></tr>
<tr><td colspan="3">$\bar{\lambda}_1 < 1$</td><td>E_0(US), E_1(GAS)</td></tr>
<tr><td rowspan="6">$\lambda_2 < 1$
($\bar{p} < 1$)</td><td rowspan="3">$\bar{\lambda}_1 > 1$</td><td colspan="2">$\lambda_p > 1$</td><td>E_0(US), E_2(GAS)</td></tr>
<tr><td rowspan="2">$\lambda_p < 1$</td><td>$\lambda_2 < \lambda_p$</td><td>E_0(US), E_2(GAS)</td></tr>
<tr><td>$\lambda_2 > \lambda_p$</td><td>E_0(US), E_2(US), E^*</td></tr>
<tr><td rowspan="3">$\bar{\lambda}_1 < 1$</td><td rowspan="2">$\lambda_2 < \bar{\lambda}_1$</td><td>$\lambda_2 < \lambda_p < \bar{\lambda}_1$</td><td>$E_0$(US), E_1(US), E_2(GAS)</td></tr>
<tr><td>$\lambda_p < \lambda_2 < \bar{\lambda}_1$</td><td>$E_0$(US), E_1(US), E_2(US), E^*</td></tr>
<tr><td colspan="2">$\lambda_2 > \bar{\lambda}_1$</td><td>$E_0$(US), E_1(LAS), E_2(US)</td></tr>
</table>

The results obtained show that the system demonstrates the complex dynamical behavior. When the interior equilibrium exists, the computation indicates that it may be stable or unstable. Moreover, we find by numerical simulation that the system may be globally stable or have an attracting limit cycle. For this case, the system is uniformly persistent, that is, the competitors may coexist. Therefore, for this model, the competitive exclusion principle does not hold.

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