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ORIGINAL PAPER

Qualitative analysis of the chemostat model with variable yield and a time delay

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Abstract In this paper, we consider the chemostat model with inhibitory exponential substrate, variable yield and a time delay. A detailed qualitative analysis about existence and boundedness of its solutions and the local asymptotic stability of its equilibria are carried out. The Hopf bifurcation of solutions to the system is studied. Using Lyapunov–LaSalle invariance principle, we show that the washout equilibrium is global asymptotic stability for any time delay. Based on some known techniques on limit sets of differential dynamical systems, we show that, for any time delay, the chemostat model is permanent if and only if only one positive equilibrium exits.

Keywords Chemostat · Time delay · Stability · Lyapunov–LaSalle invariance principle · Hopf bifurcation · Permanence

1 Introduction and statement of improved model

The chemostat is an important laboratory apparatus used to culture microorganisms [1–3]. It is assumed that species grow in continuously stirred-tank fermenters which are fed continuously by a nutrient and the cells are drawn off continuously. Therefore, the chemostat is of both ecological and mathematical interest since its applicability

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in many areas, for example, waste water treatment and the operation of industrial fermenters etc [2,3].

It is well known that the basic chemostat model with single microorganism and nutrient takes the following form [2,3]

$$\begin{cases} \dot{S}(t) = D(S^0 - S) - \delta^{-1}\mu(S)X, \\ \dot{X}(t) = (\mu(S) - D)X, \end{cases} \tag{1.1}$$

where $S(t)$ and $X(t)$ denote concentrations of the nutrient and the microorganism at time t respectively, S_0 denotes the input concentration of nutrient, D denotes the volumetric dilution rate (flow rate/volume), δ is yield term, the function $\mu(S)$ denotes the microbial growth rate and a typical choice for $\mu(S)$ is $Monod$ kinetics function (Michaelis-Menten or Holling type II), which takes the form of $\mu(S) = \mu_m S/(k_m+S)$, and satisfies the following conditions: $\mu(0) = 0, \mu'(S) > 0, \lim_{S\to+\infty} \mu(S) = \mu_m < +\infty$. Here $\mu_m > 0$ is called the maximal specific growth rate; $k_m > 0$ is the half-saturation constant, such that $\mu(k_m) = \mu_m/2$. Clearly, $\mu(S)$ is an increasing function of S over the entire interval $[0, +\infty)$.

So far, the chemostat models with $Monod$ kinetics for nutrient uptake and its various modified versions have been studied sufficiently, because they could be used to account for various important phenomena that are relevant to the actual experiments in applications [3]. In most modified chemostat models, it is assumed that the nutrient uptake function $\mu(S)$ is increasing for any $S \geq 0$. On the other hand, in biology, there may be cases that very high substrate concentrations actually inhibit the growth of microorganisms, and that while the substrate concentrations increasing unlimitedly, some kind of microorganism will die eventually. Based on the above biological phenomenon, [4] introduced the so-called $Tissiet$ functional response, i.e., $\mu(S) = \mu_m \mathrm{S} e^{-S/k_i}/(k_m + S)$ [2,5–7], to the basic chemostat model (1.1), and got the following modified model:

$$\begin{cases} \dot{X}(t) = \frac{\mu_m S(t)}{k_m+S(t)} e^{-\frac{S(t)}{k_i}} X(t) - DX(t), \\ \dot{S}(t) = (S^0 - S(t))D - \frac{\mu_m S(t)}{k_m+S(t)} e^{-\frac{S(t)}{k_i}} X(t), \end{cases} \tag{1.2}$$

where, μ_m, k_m and k_i are positive constants. $Tissiet$ functional response has the properties that $\mu(S)$ is increasing on $[0, S^*]$ for some $S^* > 0$ and decreasing on $[S^*, +\infty)$ (of cause, the concentration of the nutrient can not attend to infinity in biology and the component $S(t)$ of any solution $(X(t), S(t))$ of (1.2) can not be unbounded in mathematics.). A detailed theoretical analysis on asymptotic properties of the equilibria of (1.1) is also carried out in [4].

Most of the models in chemostat assume that yield coefficient is a constant. But the experimental data indicate that a constant yield may fail to explain the observed oscillatory behavior in the vessel. And the fact that the yield coefficient may depend on the substrate concentration is now well established in experimental literature [8,9]. It is a function of nutrient density S, i.e. $\delta(S)$. The greater the nutrient density is, the lower the consuming rate. So the function $\delta(S)$ is a nondecreasing function of S and called the variable yield, which takes the form:

(1) $\delta(S) = A + BS^n, n = 1, 2, \ldots$ [9–20] and the references there in,
(2) $\delta(S) = (A + BS)^\gamma$ [21],
(3) $\delta(S) = A_0 + A_1 S + \cdots + A_n S^n$ [22,23],
(4) the case of general yield functions, $\delta(0) = 0$ and $\delta'(S) \geq 0$ [24–26].

These studies demonstrated that if the yield coefficient increases with substrate concentration, then in a suitable parameter range, the Hopf bifurcation, limit cycles or more complex dynamics may appear, which was useful to explain the phenomena of oscillations.

Furthermore, as pointed out in [3] that time delays occur naturally in chemostat. In recent years, chemostat models with time delays have been given much attention [27–34] and the references there in. It is shown that, for some models, time delays could destroy stability of the steady state of the models and result in periodical oscillation etc, and that for other models, time delays may be harmless for stability of the steady state and persistence of the models. So it is necessary to consider the time delays in a chemostat model.

As far as we know, there are almost no literatures to discuss the chemostat model with $Tissiet$ functional response, linear variable yield and time delay. In the paper, we shall further consider the chemostat model (1.2) with variable yield and a time delay, i.e., the chemostat model governed by the following nonlinear differential systems with time delay:

$$\begin{cases} \dot{X}(t) = \frac{\mu_m S(t-\tau)}{k_m + S(t-\tau)} e^{-\frac{S(t-\tau)}{k_i}} X(t-\tau) - DX(t), \\ \dot{S}(t) = (S^0 - S(t))D - \frac{\mu_m S(t)}{k_m + S(t)} e^{-\frac{S(t)}{k_i}} \frac{X(t)}{A + BS(t)}, \end{cases} \tag{1.3}$$

where $\tau \geq 0$ is time delay, and all other parameters in (1.3) are the same as that in (1.2). If $\tau = 0$, it will be the model of [5].

As usual, in order to get dimensionless system, let us define

$$X = S^0 x, \quad S = S^0 y, \ t = T/D, \ m = \mu_m/D, \quad b = S^0/k_i, \ a = k_m/S^0, \ C = BS^0$$

and still denote T with t, then the system (1.3) becomes

$$\begin{cases} \dot{x}(t) = \frac{my(t-\tau)}{a + y(t-\tau)} e^{-by(t-\tau)} x(t-\tau) - x(t), \\ \dot{y}(t) = 1 - y(t) - \frac{my(t)}{a + y(t)} \frac{x(t)}{A + Cy(t)} e^{-by(t)}. \end{cases} \tag{1.4}$$

By biological meaning, the initial conditions of (1.4) are given as

$$x(t) = \varphi_1(t) \geq 0, \quad y(t) = \varphi_2(t) \geq 0, \quad t \in [-\tau, 0], \tag{1.5}$$

where $\varphi_1(t)$ and $\varphi_2(t)$ are all continuous functions on $[-\tau, 0]$. By a biological meaning, we further assume that $\varphi_i(0) > 0$ for $i = 1, 2$.

This paper is organized as follows. In the following section, we shall consider the existence and boundedness of solutions of (1.4) with the initial condition (1.4). Then, based on simple analysis on the characteristic equations of (1.4) about the equilibria, the local asymptotic stability of the equilibria shall be considered in Sect. 3. In Sect. 4, the global asymptotic stability of the washout equilibrium of (1.4) shall be discussed by Lyapunov–LaSalle invariance principle. In sect. 5, the permanence of (1.4) shall be discussed by some analytic techniques on limit sets of differential dynamical systems. Finally, some discussions are given in Sect. 6.

2 Existence and boundedness of solutions

In this section, we shall consider the existence and boundedness of solutions of (1.4) with the initial condition (1.5). It has the following

Theorem 2.1 *The solution* $(x(t), y(t))$ *of system* (1.4) *with the initial condition* (1.5) *exists and is positive on* $[0, +\infty)$. *Further,*

$$\limsup_{t\to+\infty} y(t) \le 1, \quad \limsup_{t\to+\infty} x(t) \le q, \quad \liminf_{t\to+\infty} y(t) \ge \nu$$

where $q = \max\{A + Cy\}$ $(y \in [0, 2])$, $\nu = \frac{aA}{aA+Mq}$.

Proof First, from theory of local existence of solutions of general functional differential equations (see, for example, [35]), it has that $x(t)$ and $y(t)$ are existent on $[0, b)$ for some positive constant b. Let us first show that $y(t) > 0$ for $t \in [0, b)$. In fact, if not so, by $\varphi_2(t) \ge 0$ and the continuity of $y(t)$, there must be $t_1 \ge 0$ such that

$$y(t_1) = 0, \quad \dot{y}(t_1) \le 0, \quad and \quad y(t) \ge 0(-\tau \le t \le t_1),$$

where $\dot{y}(t_1)$ denotes the right-hand derivative at $t = t_1$, if $t_1 = 0$. Hence, by the second equation of system (1.4), it has that

$$\dot{y}(t_1) = 1 - y(t_1) - \frac{mx(t_1)y(t_1)}{(a + y(t_1))(A + Cy(t_1))} e^{-by(t_1)} = 1 > 0.$$

This is a contradiction to $\dot{y}(t_1) \le 0$. This shows that $y(t) > 0$ for any $t \in [0, b)$.

We further show that $x(t) > 0$ for any $t \in [0, b)$. In fact, assume that there exists some $t_2 > 0$ such that

$$x(t_2) = 0, \quad x(t) > 0(-\tau \le t \le t_2)$$

Integrating the first equation of (1.4) from 0 to t_2, we see that

$$x(t_2) = x(0)e^{-t_2} + \int_0^{t_2} \frac{mx(u-\tau)y(u-\tau)e^{-by(u-\tau)}}{a + y(u-\tau)} e^{-(t_2-u)} du > 0,$$

which contradicts $x(t_2) = 0$. Therefore, it has that $x(t) > 0$ for any $t \in [0, b)$.

Next, let us prove that $x(t)$ and $y(t)$ are bounded on $[0, b)$. In fact, from (1.4) and the positivity of $x(t)$ and $y(t)$ on $[-\tau, b)$, it has that for any $t \in [0, b)$,

$$\begin{cases} \dot{x}(t) \le mx(t-\tau) - x(t), \\ \dot{y}(t) \le 1 - y(t). \end{cases} \tag{2.1}$$

Since any solution of the linear system with time delay

$$\begin{cases} \dot{u}(t) = mu(t-\tau) - u(t), \\ \dot{v}(t) = 1 - v(t) \end{cases} \tag{2.2}$$

is existent on $[0, +\infty)$, it has from well known comparison principle for delayed differential equations (see, for example, [36]) that for any $t \in [0, b)$,

$$x(t) \le u(t), \quad y(t) \le v(t), \tag{2.3}$$

where $(u(t), v(t))$ is unique solution of (2.2) with the initial condition $u(t) = \varphi_1(t) \ge 0$ and $v(t) = \varphi_2(t) \ge 0$ for $t \in [-\tau, 0]$. It is clear from (2.3) that the solution $(x(t), y(t))$ must be bounded on finite interval $[0, b)$. Therefore, it follows from theory of continuation of solutions for functional differential equations (see, for example, [35]) that the solution $(x(t), y(t))$ is existent and non-negative on $[0, +\infty)$. Furthermore, notice the second inequality of (2.1), it easily has that $\limsup_{t\to+\infty} y(t) \le 1$. In particular, there is a $T > 0$, such that $y(t) \le 2$ for all $t \ge T$. Let $q = \max\{A + Cy\}$ $(y \in [0, 2])$, $V(t) = \frac{x(t+\tau)}{q} + y(t)$, then

$$V'(t) \le 1 - y(t) - \frac{x(t+\tau)}{q} = 1 - V(t), \quad t \ge T.$$

Therefore

$$\limsup_{t\to+\infty} x(t) \le \limsup_{t\to+\infty} qV(t) \le q.$$

It is easily to see that for the system (1.4)

$$y'(t) \ge 1 - y(t) - \frac{mq}{aA} y(t) = 1 - \frac{mq + aA}{aA} y(t)$$

which implies that $\liminf_{t\to+\infty} y(t) \ge \frac{aA}{aA+mq} = \nu$. This completes the proof of Theorem 2.1.

3 Local asymptotic stability analysis

In this section, we shall consider the local asymptotic stability of the equilibria of system (1.4). Notice the proof of Theorem 4.1 in Sect. 4, it has that the subset

$$G = \{\phi = (\varphi_1, \varphi_2) \in C \mid \varphi_1 \ge 0, \nu \le \varphi_2 \le 1\}.$$

is positively invariant with respect to (1.4). Hence, it is enough to consider system (1.4) on G.

For the existence of the equilibria, it already has the following

Lemma 3.1 [4] (1.4) *always has a washout equilibrium* $E_0 = (0, 1)$. *For the existence of the positive equilibria, there are four cases:*

(1) If $0 < m \le 1$ *or* $m > 1,\ b < 2,\ me^{-b}(1-b) \ge 1,\ me^{-b} \le a+1$ *or* $m > 1,\ me^{-b}(1-b) < 1,\ me^{-b} < a+1,\ b\bar{y}^2 + ab\bar{y} - a < 0$, *then there does not exist any positive equilibrium, where* $\bar{y}$ *denotes the real root of* $f'(y) = me^{-by}(1-by) - 1 = 0$ *on* $[0, 1]$.

(2) If $m > 1, me^{-b} > a+1$ *or* $m > 1,\ me^{-b}(1-b) < 1,\ me^{-b} = a+1$, *then there exists a single positive equilibrium, denoted by* $E_1^+ = (A+(C-A)y_1^* - Cy_1^{*2}, y_1^*)$, *where* y_1^* *is unique real root of* $f(y) = mye^{-by} - a - y = 0$ *on* $[0, 1]$.

(3) If $m > 1, me^{-b} < a+1,\ me^{-b}(1-b) < 1,\ b\bar{y}^2 + ab\bar{y} - a = 0$, *then there exists a single positive equilibrium, denoted by* $E_3^+ = (A + (C-A)y_3^* - Cy_3^{*2}, y_3^*)$, *where* y_3^* *is unique real root of* $f(y) = mye^{-by} - a - y = 0$ *on* $[0, 1]$.

(4) If $m > 1, me^{-b} < a+1,\ me^{-b}(1-b) < 1,\ b\bar{y}^2 + ab\bar{y} - a > 0$, *then there exist two positive equilibria, denoted respectively, by* $E_{21}^+ = (A + (C-A)y_{21}^* - Cy_{21}^{*2}, y_{21}^*)$ *and* $E_{22}^+ = (A + (C-A)y_{22}^* - Cy_{22}^{*2}, y_{22}^*)$, *where* y_{21}^* *and* y_{22}^* *are only two real roots of* $f(y) = mye^{-by} - a - y = 0$ *on* $[0, 1]$.

Theorem 3.1 *If the case* (1) *of Lemma* 3.1 *holds, then, for any time delay* $\tau \ge 0$, E_0 *is locally asymptotically stable for* $me^{-b} < a+1$; E_0 *is unstable for* $me^{-b} > a+1$; *the trivial solution of the linearized system of* (1.4) *about* E_0 *is stable for* $me^{-b} = a+1$.

Proof The system (1.4) is centered on $E_i^+ = (x_i^*, y_i^*)$ $(i = 0, 1, 21, 22, 3)$ by introducing

$$\begin{cases} X = x - x_i^*, \\ Y = y - y_i^*, \end{cases}$$

and corresponding linearized system is of the form

$$\begin{cases} \dot{X}(t) = -X(t) + MX(t-\tau) + NY(t-\tau), \\ \dot{Y}(t) = PX(t) + QY(t), \end{cases} \tag{3.1}$$

where

$$M = \frac{my_i^*}{a+y_i^*}e^{-by_i^*},\ \ N = \frac{mx_i^*\left(-by_i^{*2} - aby_i^* + a\right)}{\left(a+y_i^*\right)^2}e^{-by_i^*},$$

$$P = -\frac{my_i^*e^{-by_i^*}}{\left(a+y_i^*\right)\left(A+Cy_i^*\right)},$$

$$Q = -\frac{mx_i^*\left[aA - abAy_i^* - (abC + bA + C)y_i^{*2} - bCy_i^{*3}\right]}{\left(a+y_i^*\right)^2\left(A+Cy_i^*\right)^2}e^{-by_i^*} - 1.$$

The associated characteristic equation of (3.1) is given by

$$\lambda^2 + (1 - Q)\lambda - M\lambda e^{-\lambda\tau} - Q + (MQ - NP)e^{-\lambda\tau} = 0. \tag{3.2}$$

We first consider local stability of $E_0 = (0, 1)$.

Now, $M = me^{-b}/(a+1)$, $N = 0$, $P = -me^{-b}/[(a+1)(A+C)]$, $Q = -1$. Hence, (3.2) becomes

$$(\lambda + 1)\left(\lambda + 1 - \frac{me^{-b}}{a+1}e^{-\lambda\tau}\right) = 0. \tag{3.3}$$

It is obviously that (3.3) has a negative characteristic root $\lambda = -1$. Next, we consider the roots of the transcendental equation

$$\lambda + 1 - \tfrac{me^{-b}}{a+1}e^{-\lambda\tau} = 0. \tag{3.4}$$

It follows from [35] that

(i) If $me^{-b} < a + 1$, then all roots of (3.4) have negative real parts for any time delay $\tau \geq 0$. Hence, E_0 is locally asymptotically stable for any time delay $\tau \geq 0$.
(ii) If $me^{-b} > a + 1$, then (3.4) has roots which have positive real roots for any time delay $\tau \geq 0$. Hence, E_0 is unstable for any time delay $\tau \geq 0$.
(iii) If $me^{-b} = a + 1$, this is a critical case and (3.4) is equivalent to

$$\lambda + 1 - e^{-\lambda\tau} = 0. \tag{3.5}$$

From [35], it has that except $\lambda = 0$, any root of (3.5) has negative real part for any time delay $\tau \geq 0$. Hence, the trivial solution of the linearized system of (1.4) about E_0 is stable for any time delay $\tau \geq 0$.

Theorem 3.2 *(1) If $\frac{1}{2}NP < Q < 0$, then E_1^+ is locally asymptotically stable for $\tau < \tau_0$, E_1^+ is unstable for $\tau > \tau_0$, there is a periodic solution around E_1^+ for $\tau = \tau_0$; If $Q > 0$ or $Q \leq \frac{1}{2}NP$, E_1^+ is unstable for any $\tau \geq 0$. (2) If $\frac{1}{2}NP < Q < 0$, then E_{21}^+ is locally asymptotically stable for $\tau < \bar{\tau}_0$, E_{21}^+ is unstable for $\tau > \bar{\tau}_0$, there is a periodic solution around E_{21}^+ for $\tau = \bar{\tau}_0$; If $Q > 0$ or $Q \leq \frac{1}{2}NP$, E_{21}^+ is unstable for any $\tau \geq 0$. (3) E_{22}^+ is unstable for any $\tau \geq 0$.* (4) *If $Q > 0$, then the trivial solution of the linearized system of* (1.4) *about E_3^+ is unstable for any $\tau \geq 0$; If $Q < 0$, then the trivial solution of the linearized system of* (1.4) *about E_3^+ is stable for any $\tau \geq 0$.*

Proof We consider the local stability of

$$E_i^+ = \left(x_i^*, y_i^*\right) = \left(A + (C - A)y_i^* - Cy_i^{*2}, y_i^*\right), \quad (i = 1, 21, 22, 3).$$

Consider the transcendental equation (3.2). Now,

$$M = 1, N = \frac{\left(1 - y_i^*\right)\left(A + Cy_i^*\right)\left(-by_i^{*2} - aby_i^* + a\right)}{\left(a + y_i^*\right)y_i^*},\ \ P = -\frac{1}{A + Cy_i^*},$$
$$Q = -\frac{aA - abAy_i^* + (A + abA - bA + aC - C - abC)y_i^{*2} + (bA + 2C + abC - bC)y_i^{*3} + bCy_i^{*4}}{\left(a + y_i^*\right)y_i^*\left(A + Cy_i^*\right)}.$$

when $\tau = 0$, (3.2) becomes

$$\lambda^2 - Q\lambda - NP = 0. \tag{3.6}$$

From the proof of Lemma 3.1, as long as E_1^+ exits, it must be $by_1^{*2} + aby_1^* - a < 0$, thus, $N > 0, NP < 0$; as long as E_{21}^+ exits, it must be $by_{21}^{*2} + aby_{21}^* - a < 0$, thus, $N > 0, NP < 0$; as long as E_{22}^+ exits, it must be $by_{22}^{*2} + aby_{22}^* - a > 0$, thus, $N < 0, NP > 0$; as long as E_3^+ exits, it must be $by_3^{*2} + aby_3^* - a = 0$, thus, $N = 0, NP = 0$. Hence, from *Routh-Hurwitz* theory, we have that if $Q < 0$, then E_1^+ and E_{21}^+ are locally asymptotically stable; if $Q > 0$, then E_1^+ and E_{21}^+ are unstable; if $Q = 0$, then E_1^+ and E_{21}^+ are nonhyperbolic equilibria; E_{22}^+ is unstable; $E_3^+$is a critical case.

Suppose $\lambda = i\omega$ $(\omega > 0)$ is a root of (3.2) for some τ. We have that

$$\begin{aligned} &Q + \omega^2 + \omega\sin\omega\tau + (NP - Q)\sin\omega\tau = 0,\\ &(1 - Q)\omega - \omega\cos\omega\tau + (NP - Q)\cos\omega\tau = 0. \end{aligned} \tag{3.7}$$

Thus,

$$(\omega^2 + Q)^2 + (1 - Q)^2\omega^2 = \omega^2 + (NP - Q)^2. \tag{3.8}$$

Hence,

$$\omega^4 + Q^2\omega^2 + Q^2 - (NP - Q)^2 = 0. \tag{3.9}$$

Its roots are

$$\omega_\pm^2 = \frac{1}{2}\left\{-Q^2 \pm \sqrt{Q^4 - 4NP(2Q - NP)}\right\} \tag{3.10}$$

(1) We consider the stability of $E_1^+ = (x_1^*, y_1^*)$.

(i) If $Q > \frac{1}{2}NP$, there is only one positive root, $\lambda = \omega_+, \omega_+ > 0$, such that

$$\omega_+^2 = \frac{1}{2}\left\{-Q^2 + \sqrt{Q^4 - 4NP(2Q - NP)}\right\},$$

i.e. (3.2) has one imaginary solution, $\lambda = i\omega_+$, $\omega_+ > 0$. From Eq. (3.7), we obtain the following set of values of τ for which there are imaginary roots:

$$\tau_n = \frac{\theta}{\omega_+} + \frac{2n\pi}{\omega_+}, \quad (n = 0, 1, 2, \ldots) \tag{3.11}$$

where $0 \leq \theta < 2\pi$, and

$$\cos\theta = \frac{(Q-1)\omega_+^2 + (NP-Q)\left(Q+\omega_+^2\right)}{\omega_+^2 + (Q-NP)^2},$$
$$\sin\theta = \frac{(1-Q)(Q-NP)\omega_+ - \omega_+\left(Q+\omega_+^2\right)}{\omega_+^2 + (Q-NP)^2}.$$

If $Q < 0$, when $\tau = 0$, E_1^+ is locally asymptotically stable. Hence, if $\tau < \tau_0$, $(n = 0, i = 1)$, E_1^+ is locally asymptotically stable.

Next, we prove $\lambda = i\omega_+$ is simple. Denote

$$F(\lambda) = \lambda^2 + (1-Q)\lambda - M\lambda e^{-\lambda\tau} - Q + (MQ - NP)e^{-\lambda\tau}, \tag{3.12}$$

We have that

$$\frac{dF(\lambda)}{d\lambda} = 2\lambda + (1-Q) - e^{-\lambda\tau} + \tau\lambda e^{-\lambda\tau} - Q - \tau(Q - NP)e^{-\lambda\tau}. \tag{3.13}$$

If $\lambda(\tau_0) = i\omega_+$ is not simple, then $\frac{dF}{d\lambda}|_{\lambda=i\omega_+} = 0$, $F(i\omega_+) = 0$. Therefore,

$$\left\{\tau\lambda^2 + [(1-Q)\tau + 2]\lambda + 1 - 2Q - Q\tau - e^{-\lambda\tau}\right\}|_{\lambda=i\omega_+} = 0 \tag{3.14}$$

We have

$$\begin{aligned} &-\tau\omega_+^2 + 1 - 2Q - Q\tau - \cos\omega_+\tau = 0,\\ &((1-Q)\tau + 2)\omega_+ + \sin\omega_+\tau = 0. \end{aligned} \tag{3.15}$$

From the second equation of (3.15), we have

$$(1-Q)\tau\omega_+ + 2\omega_+ + \sin\omega_+\tau > 2\omega_+ + \omega_+ + \sin\omega_+\tau > 0,$$

which is a contradiction. Therefore $\lambda = i\omega_+$ is simple.

Furthermore, we need to determine the sign of the derivative of $Re\lambda(\tau)$ at $\lambda = i\omega_+$. For convenience, we study $(d\lambda/d\tau)^{-1}$ instead of $d\lambda/d\tau$. We have

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{(2\lambda + 1 - Q)e^{\lambda\tau} - 1}{\lambda(-\lambda + Q - NP)} - \frac{\tau}{\lambda},$$

and

$$e^{\lambda\tau} = \frac{\lambda + NP - Q}{\lambda^2 + (1-Q)\lambda - Q}.$$

Therefore,

$$\begin{aligned} sign\left\{\frac{d(Re\lambda)}{d\tau}\right\}_{\lambda=i\omega_+} &= sign\left\{Re\left(\frac{d\lambda}{d\tau}\right)^{-1}\right\}_{\lambda=i\omega_+} \\ &= sign\left\{Re\left[\frac{-(2\lambda+1-Q)}{\lambda(\lambda^2+(1-Q)\lambda-Q)}\right]_{\lambda=i\omega_+}+Re\left[\frac{1}{\lambda(\lambda+NP-Q)}\right]_{\lambda=i\omega_+}\right\} \\ &= sign\left\{\frac{(1-Q)^2+2\left(Q+\omega_+^2\right)}{\left(Q+\omega_+^2\right)^2+(1-Q)^2\omega_+^2}-\frac{1}{(NP-Q)^2+\omega_+^2}\right\} \\ &= sign\left\{(1-Q)^2+2Q-1+2\omega_+^2\right\} \\ &= sign\left\{Q^2+2\omega_+^2\right\} > 0. \end{aligned}$$

Hence, there is a Hopf bifurcation at $\omega = \omega_+, \tau = \tau_0$. Therefore, if $Q < 0$, $Q > \frac{1}{2}NP$, then E_1^+ is locally asymptotically stable for $\tau < \tau_0$, E_1^+ is unstable for $\tau > \tau_0$, there is a periodic solution around E_1^+ for $\tau = \tau_0$. If $Q > 0$, when $\tau = 0$, E_1^+ is unstable. Hence, if $Q > 0$, then, E_1^+ is unstable for any $\tau \geq 0$.

(ii) If $Q \leq \frac{1}{2}NP$, then (3.9) has no positive root, i.e. (3.2) does not have imaginary solution. Therefore, if $Q \leq \frac{1}{2}NP$, then E_1^+ is locally asymptotically stable for any $\tau \geq 0$.

(2) We consider the stability of $E_{21}^+ = (x_{21}^*, y_{21}^*)$.
Using the same method as the proof of E_1^+, if $Q \leq \frac{1}{2}NP$, then E_{21}^+ is locally asymptotically stable for any $\tau \geq 0$; if $Q < 0$, $Q > \frac{1}{2}NP$, then E_{21}^+ is locally asymptotically stable for $\tau < \bar{\tau}_0$, E_{21}^+ is unstable for $\tau > \bar{\tau}_0$, there is a periodic solution around E_{21}^+ for $\tau = \bar{\tau}_0$; where $\bar{\tau}_0 = \frac{\theta}{\omega_+}$, $(i = 21)$. If $Q > 0$, then, E_1^+ is unstable for any $\tau \geq 0$.

(3) We consider the stability of $E_{22}^+ = (x_{22}^*, y_{22}^*)$.

(i) If $Q > \frac{1}{2}NP$, there is only one positive root. From the proof of E_1^+, $\frac{dRe(\lambda(\tau))}{d\tau}|_{\lambda=i\omega_+} > 0$. Hence, E_{22}^+ is unstable for any $\tau \geq 0$.

(ii) If $Q \leq \frac{1}{2}NP$, then (3.9) has no positive root, i.e. (3.2) does not have imaginary solution. When $\tau = 0$, E_{22}^+ is unstable. Therefore, if $Q \leq \frac{1}{2}NP$, then E_{22}^+ is unstable for any $\tau \geq 0$.

Therefore, E_{22}^+ is unstable for any $\tau \geq 0$.

(4) We consider the stability of $E_3^+ = (x_3^*, y_3^*)$.

Consider the characteristic equation (3.2). $\lambda(\tau) = 0$ is a root of (3.2) for all $\tau \geq 0$. Assume $\lambda = u + iv$ is a root of (3.2), then, we have

$$\begin{aligned} u^2 - v^2 + 2iuv + (1-Q)u + i(1-Q)v - (u+iv)e^{-u\tau}(cosv\tau - isinv\tau) - Q \\ +Qe^{-u\tau}(cosv\tau - isinv\tau) = 0. \end{aligned}$$

Therefore,

$$u^2 - v^2 + (1-Q)u - Q + (-u+Q)e^{-u\tau}cosv\tau - ve^{-u\tau}sinv\tau = 0 \quad (3.16)$$

$$2uv + (1-Q)v - ve^{-u\tau}cosv\tau + (u-Q)e^{-u\tau}sinv\tau = 0 \quad (3.17)$$

From (3.12) and (3.13), we have

$$[u^2-v^2+(1-Q)u-Q]^2+[2uv+(1-Q)v]^2 = e^{-2u\tau}[(u-Q)^2+v^2] \quad (3.18)$$

(i) Assume $Q \le 0$. Suppose (3.2) has a root $\lambda = u + iv, u > 0$, for some $\tau \ge 0$. Then, from (3.14), we have

$$(u^2 - v^2)^2 + 4u^2v^2 + 2(1-Q)(u^3+uv^2)+(Q^2-2Q)u^2+Q^2v^2+2Q^2u < 0.$$

This is impossible, since we are assuming $Q \le 0$ and $u > 0$. Hence, all roots of (3.2) have non-positive real parts; this implies that the trivial solutions of the linearized system of (1.4) about E_3^+ is stable.

(ii) Assume $Q > 0$. Consider the following real function

$$f(\lambda, \tau) = \lambda^2 + (1-Q)\lambda - \lambda e^{-\lambda\tau} - Q + Qe^{-\lambda\tau}.$$

We observe

$$f(0, \tau) = 0$$

and

$$\lim_{\lambda \to +\infty} f(\lambda, \tau) = +\infty.$$

There exists a $M > 0$ such that, if $\lambda \ge M$, $f(\lambda, \tau) \ge 0$, we also have

$$\frac{\partial f(\lambda, \tau)}{\partial \tau} = 2\lambda + (1-Q) + (-1 + \tau\lambda - Q\tau)e^{-\lambda\tau},$$
$$\frac{\partial f(0, \tau)}{\partial \lambda} = -Q(1+\tau) < 0, (\tau \ge 0).$$

Hence, there exists a $\delta(\tau) > 0$ such that when $0 < \lambda \le \delta(\tau)$, $f(\lambda, \tau) < 0$. Therefore , there must exist at least a $\bar{\lambda}$, $\delta(\tau) < \bar{\lambda} \le M$, such that $f(\bar{\lambda}, \tau) = 0$, i.e. (3.2) has at least a positive root. Hence, the trivial solution of the linearized system of (1.4) about E_3^+ is unstable.

4 Global asymptotic stability analysis of E_0

In Sect. 3, we have considered local asymptotical stability of E_0 in details. In the section, we shall further consider global asymptotical stability of E_0 by means of Liapunov–LaSalle invariance principle. The following theorem is main result in the section.

Theorem 4.1 *If the case* (1) *of Theorem* (3.1) *holds, then, for any time delay* τ, *the washout equilibrium* E_0 *is globally asymptotically stable for* $me^{-b} < a+1$, *and globally attractive for* $me^{-b} = a+1$.

Proof We shall also use Liapunov–LaSalle invariance principle (see, for example, [35] and [37]) to prove Theorem 4.1 Define the subset

$$G = \{\varphi = (\varphi_1, \varphi_2) \in C \mid \varphi_1 \geq 0, \nu \leq \varphi_2 \leq 1\}.$$

We first show that G is positively invariant with respect to (1.4).

For any $\varphi = (\varphi_1, \varphi_2) \in G$, let $(x(t), y(t))$ be the solution of (1.3) with the initial function φ. From the proof of Theorem 2.1 it has that $(x(t), y(t))$ is non-negative for any $t \geq 0$. We further show that $y(t) \leq 1$ for any $t \geq 0$. In fact, if there is a $t_3 > 0$ such that $y(t_3) > 1$, it has from *Lagrange mean value theorem* that $\dot{y}(t_4) > 0$ for some $t_4 \in (0, t_3)$ and $y(t_4) = 1$. Hence, it has from the second equation of (1.3) that

$$\dot{y}(t_4) = 1 - y(t_4) - \frac{mx(t_4)y(t_4)}{(a + y(t_4))(A + Cy(t_4))}e^{-by(t_4)} < 0,$$

which is a contradiction to $\dot{y}(t_4) > 0$.

Let us show that $y(t) \geq \nu$ for all $t \geq 0$. If not, we can find some $t_5 \geq 0$ such that $y(t_5) = \nu$, $y(t) \geq \nu$ for all $-\tau \leq t \leq t_5$ and $\dot{y}(t_5) \leq 0$. On the other hand, it follows from (1.4) that

$$\dot{y}(t_5) = 1 - y(t_5) - \tfrac{my(t_5)x(t_5)}{(a+y(t_5))(A+Cy(t_5))}e^{-by(t_5)} > 1 - \nu - \tfrac{qm}{aA}\nu = 0.$$

Thus, we again have a contradiction. Therefore, G is positively invariant with respect to (1.4).

Let us define a functional V on G as follows,

$$V(\varphi) = \varphi_1(0) + \int_{-\tau}^{0} \varphi_1(\theta)d\theta. \tag{4.1}$$

It is clear that $V(\varphi)$ is continuous on the subset G and that the derivative of $V(\varphi)$ along the solution of (1.4) satisfies

$$\begin{aligned}
\dot{V}(\varphi)|_{(1.4)} &= \dot{\varphi}_1(0) + \varphi_1(0) - \varphi_1(-\tau) \\
&= \dot{x}(t) + x(t) - x(t-\tau) \\
&= \frac{my(t-\tau)}{a + y(t-\tau)}e^{-by(t-\tau)}x(t-\tau) - x(t) + x(t) - x(t-\tau) \\
&= \frac{my(t-\tau)}{a + y(t-\tau)}e^{-by(t-\tau)}x(t-\tau) - x(t-\tau) \\
&= \frac{f(y(t-\tau))}{a + y(t-\tau)}x(t-\tau) \\
&= \frac{f(\varphi_2(-\tau))}{a + \varphi_2(-\tau)}\varphi_1(-\tau),
\end{aligned} \tag{4.2}$$

for $t \geq 0$, where

$$f(y) = mye^{-by} - a - y.$$

Since (1.4) has unique equilibrium E_0, it has that $f(y) \leq 0$ for any $y \in [0, 1]$. Hence, it has that for any $t \geq 0$,

$$\dot{V}(\varphi)|_{(1.4)} \leq 0.$$

This shows that $V(\varphi)$ is a *Lyapunov* functional of (1.4) on the subset G.

Define $E = \{\varphi \in G \mid \dot{V}(\varphi)|_{(1.4)} = 0\}$. From (4.2), it has that

$$E = \{\varphi \in G \mid \varphi_1(-\tau) = 0 \quad or \quad f(\varphi_2(-\tau)) = 0\}. \tag{4.3}$$

Let M be the largest set in E which is invariant with respect to (1.4). Clearly, M is not empty since $E_0 = (0, 1) \in M$. We have two cases to be discussed.

(1) If $me^{-b} < a + 1$, it has that $f(y) < 0$ for any $y \in [0, 1]$. Hence,

$$E = \{\varphi \in G \mid \varphi_1(-\tau) = 0\}.$$

For any $\varphi \in M$, let $(x(t), y(t))$ be the solution of (1.4) with the initial function φ. From the invariance of M, it has that $(x_t, y_t) \in M \subset E$ for any $t \in R$. Thus, $x(t - \tau) = 0$ for any $t \in R$, which implies that $x(t) \equiv 0$ and $\varphi_1 \equiv 0$ for any $t \in R$. From the second equation of system (1.4), it has that $\dot{y}(t) = 1 - y(t)$ for any $t \in R$. Since $y(t) \to 1$ as $t \to +\infty$. Hence, $\varphi_2 \equiv 1$. Therefore,

$$M = \{(0, 1)\} = \{E_0\}.$$

The classical Liapunov–LaSalle invariance principle (see, for example, [35]) shows that E_0 is globally attractive for any $\tau \geq 0$. It follows from Theorem 3.1 that the washout equilibrium E_0 of (1.4) is globally asymptotically stable for any time delay $\tau \geq 0$.

(2) If $me^{-b} = a + 1$, it has that $f(y) = 0$ is equivalent to $y = 1$. Hence, while $f(\varphi_2(-\tau)) = 0$, it must have that $\varphi_2(-\tau) = 1$. Thus,

$$E = \{\varphi \in G \mid \varphi_1(-\tau) = 0 \quad or \quad \varphi_2(-\tau)) = 1\}.$$

For any $\varphi \in M$, let $(x(t), y(t))$ be the solution of (1.4) with the initial function φ. From the invariance of M, it has that $(x_t, y_t) \in M \subset E$ for any $t \in R$. Thus for any $t \in R$, it has that $x(t - \tau) = 0$ or $y(t - \tau) = 1$. If $y(t - \tau) = 1$ for some $t \in R$, it has from the invariance of G that the function $y(t)$ takes local maximum at $t - \tau$. Hence, it must have that $\dot{y}(t - \tau) = 0$. From the second equation of system (1.4), it has that

$$\dot{y}(t - \tau) = 1 - y(t - \tau) - \frac{mx(t - \tau)y(t - \tau)}{(a + y(t - \tau))(A + Cy(t - \tau))} e^{-by(t-\tau)} = 0.$$

Since $y(t-\tau)=1$, we have that $x(t-\tau)=0$. Therefore, for any $\varphi=(\varphi_1,\varphi_2)\in E$, it always has that $x(t-\tau)=0$ for any $t\in R$, i.e., $\varphi_1(-\tau)=0$. By repeating the proof of case (1), it also has that $M=\{E_0\}$. It again follows from the Liapuynov–LaSalle invariance principle that E_0 is globally attractive for any $\tau\geq 0$. This completes the proof of Theorem 4.1.

5 Permanence

In this section, we will use the same method as [38] to prove the permanence of system (1.4). The following theorem is main result in the section.

Theorem 5.1 *For any time delay $\tau\geq 0$, $m>1$ and $me^{-b}>a+1$ are necessary and sufficient for the permanence of* (1.4).

Proof Note that the washout equilibrium E_0 is globally asymptotically stable or globally attractive if $m>1$ and $me^{-b}>a+1$ are not valid. We only need to prove the sufficiency. It follows from the definition of permanence and Theorem 2.1, we only need to show

$$\liminf_{t\to\infty} x(t)\geq \upsilon. \tag{5.1}$$

Here υ is some positive constant which does not depend on the initial function φ. The proof is divided into two steps.

Step 1. Let us first show

$$\liminf_{t\to\infty} x(t)>0. \tag{5.2}$$

From the invariance of G, it is enough to consider the solution $(x(t),y(t))$ $(t\geq 0)$ with the initial function $\varphi\in G$. From Theorems 2.1 and 4.1, we see that the omega limit set $\omega(\varphi)$ of $(x(t),y(t))$ $(t\geq 0)$ is nonempty, compact, invariant and $\omega(\varphi)\subset G$.

If $\liminf_{t\to+\infty} x(t)=0$, we shall show that there is a contradiction.

In fact, from $\liminf_{t\to+\infty} x(t)=0$, we see that there exists a positive time sequence $\{t_n\}:t_n\to+\infty(n\to+\infty)$ such that

$$\lim_{t_n\to+\infty} x(t_n)=0,\quad \dot{x}(t_n)\leq 0,\quad x(t)\geq x(t_n)\quad (t_n-\tau\leq t\leq t_n).$$

Note that the solution $(x(t),y(t))$ is bounded on $[0,+\infty)$ by Theorem 2.1. It follows from (1.4) that is $(x(t),y(t))$ uniformly continuous on $[0,+\infty)$. Hence, it follows from Ascoli's theorem that there is a subsequence of $\{t_n\}$, still denoted by $\{t_n\}$, such that

$$\lim_{t_n\to+\infty}(x(t_n),y(t_n))=(\tilde{x}(t),\tilde{y}(t))$$

holds uniformly on R in the wider sense. From Theorem 4.1, we have that $(\tilde{x}_t,\tilde{y}_t)\in G$ for any $t\in R$, and that for any $\tau\in R$, the function $(\tilde{x}(t+\tau),\tilde{y}(t+\tau))$ of t is the solution of (1.4) with the initial function $(\tilde{x}_\tau, \tilde{y}_\tau)$. Here we note that $\tilde{x}(0) = 0$ and $\nu \le \tilde{y}(t) \le 1$ for any $t \in R$.

We claim that $(\tilde{x}(t), \tilde{y}(t)) = (0, 1)$ for any $t \in R$. Note that if $\varphi_1(0) > 0$, then the solution $(x(t), y(t))$ of (1.4) exists and $x(t) > 0$ and $y(t) > 0$ $(t \ge 0)$. Thus, from $\tilde{x}(0) = 0$, we have that $\tilde{x}(t) = 0$ for any $t < 0$. Thus, it follows from (1.4) that $x(t) \equiv 0$ for any $t \in R$, and that $\tilde{y}'(t) = 1 - \tilde{y}(t)$ for any $t \ge \tau$. Hence,

$$\tilde{y}(t) = \tilde{y}(0)\mathrm{e}^{-t} + (1 - \mathrm{e}^{-t}), (t \ge \tau).$$

Note that from the arbitrariness of τ, we have that

$$\tilde{y}(t) = 1 + (\tilde{y}(0) - 1)\mathrm{e}^{-t}.$$

Since $\tilde{y}(t)$ is bounded for $t \in R$, we must have that $\tilde{y}(0) = 1$, which implies that $\tilde{y}(t) = 1$ for any $t \in R$. It follows from (1.4) and the invariance of G that $(\tilde{x}(t), \tilde{y}(t)) = (0, 1)$ for any $t \in R$. This shows that the above claim holds. Specially, we have that

$$\lim_{n\to+\infty} x(t_n - \tau) = \tilde{x}(-\tau) = 0, \lim_{n\to+\infty} y(t_n - \tau) = \tilde{y}(-\tau) = 1,$$
$$\lim_{n\to+\infty} \frac{my(t_n - \tau)}{a + y(t_n - \tau)} e^{-by(t_n-\tau)} = \frac{me^{-b}}{a+1} > 1.$$

For sufficiently small $\epsilon > 0$ and sufficiently large N, $n > N$, we have

$$\frac{my(t_n - \tau)}{a + y(t_n - \tau)} e^{-by(t_n-\tau)} > \frac{me^{-b}}{a+1} - \epsilon > 1.$$

Hence

$$\begin{aligned}\dot{x}(t_n) &= \frac{my(t_n - \tau)}{a + y(t_n - \tau)} e^{-by(t_n-\tau)} x(t_n - \tau) - x(t_n)\\ &\ge \left(\frac{my(t_n - \tau)}{a + y(t_n - \tau)} e^{-by(t_n-\tau)} - 1\right) x(t_n)\\ &> \left(\frac{me^{-b}}{a+1} - \epsilon - 1\right) x(t_n) > 0.\end{aligned}$$

which is a contradiction to $\dot{x}(t_n) \le 0$. This completes the proof of $\liminf_{t\to\infty} x(t) > 0$.

Step 2. Let us show that

$$\liminf_{t\to\infty} x(t) \ge \upsilon > 0.$$

For any initial functions sequence $\varphi_n = \{(\varphi_1^{(n)}, \varphi_2^{(n)})\} \subset G$, let $(x^{(n)}(t), y^{(n)}(t))$ be the solution of (1.4) with the initial function φ_n. Let $\omega_n(\varphi_n)$ be the omega limit set of $(x^{(n)}(t), y^{(n)}(t))$. We have that there exits some compact and invariant set $\omega^* \subset G$ such that $dist(\omega_n(\varphi_n), \omega^*) \to 0$ as $n \to +\infty$. Here, $dist(\omega_n(\varphi_n), \omega^*)$ means $Hausdorff$ distance.

If (5.1) does not hold, for some initial function sequence $\varphi_n = \{(\varphi_1^{(n)}, \varphi_2^{(n)})\} \subset G$ such that $\varphi_1^{(n)}(0) > 0$, we have that there is some $\bar{\varphi} = (\bar{\varphi}_1, \bar{\varphi}_2) \in \omega^*$ such that $\bar{\varphi}_1(\theta_0) = 0$ for some $\theta_0 \in [-\tau, 0]$. Now, let $(\bar{x}(t), \bar{y}(t))$ be the solution of (1.4) with the initial function $\bar{\varphi}$. Then, by the invariance of ω^*, we have that $(\bar{x}_t, \bar{y}_t) \in \omega^*$ for all $t \in R$. Note $\bar{\varphi}_1(\theta_0) = 0$ and the positivity of all solutions, we easily have that $\bar{x}(t) = 0$ for all $t \leq \theta_0$. Hence, it follows from (1.4) that $\bar{\varphi}_1(\theta) = 0(-\tau \leq \theta \leq 0)$ and $\bar{x}(t) = 0(t \in R)$. This implies that $\bar{x}(t) = 0, \bar{y}(t) = \bar{g}(t)$ for all $t \in R$, where $\bar{g}(t) = 1 - (1 - \bar{\varphi}_2(0))\mathrm{e}^{-t}$. If $\bar{\varphi}_2(0) < 1$, we see that the negative semi-orbit $(\bar{x}_t, \bar{y}_t)(t \leq 0)$ is unbounded. This is a contradiction.

If $\bar{\varphi}_2(0) = 1$, we have that $\bar{x}(t) = 0, \bar{y}(t) = 1$ for all $t \in R$. This shows that $\bar{\varphi} = (0, 1) = E_0 \in \omega^*$. Let us show that E_0 is factually isolated [39,40]. That is, there exists some neighborhood U of E_0 in G such that E_0 is the largest invariant set in U. In fact, let us choose

$$U = \left\{\varphi \mid \varphi = (\varphi_1, \varphi_2) \in \bar{G}, \parallel \varphi - E_0 \parallel < \varepsilon\right\}$$

for some sufficiently small positive constant ε and $\varepsilon < \frac{me^{-b}-(a+1)}{me^{-b}-1}$. We shall show that E_0 is the largest invariant set in U for some ε.

If not, for any sufficiently small ε there exists some invariant set $W(W \subset U)$ such that $W \backslash E_0$ is not empty. Let $\varphi = (\varphi_1, \varphi_2) \in W \backslash E_0$ and (x_t, y_t) be the solution of (1.4) with the initial function φ. Then, $(x_t, y_t) \in W$ for all $t \in R$.

If $\varphi_1(0) = 0$, by the invariance of W and Theorem 2.1, we also have the contradiction that $\varphi = E_0$ or that the negative semi-orbit $(x_t, y_t)(t < 0)$ of (1.4) through φ is unbounded.

If $\varphi_1(0) > 0$, from the Theorem 2.1, we see that $x(t) > 0$ for all $t \geq 0$. Now, let us consider the continuous function

$$P(t) = x(t) + \rho \int_{t-\tau}^{t} x(\theta) d\theta, \tag{5.3}$$

for some constant $\rho > 1$. Because of $(x_t, y_t) \in U(t \in R)$, we have $1 - \varepsilon \leq y(t) \leq 1$, $(t \in R)$. The time derivative of $P(t)$ along the solution $(x(t), y(t))$ satisfies

$$\begin{aligned} \dot{P}(t) &= \dot{x}(t) + \rho(x(t) - x(t-\tau)) \\ &= (\rho - 1)x(t) + \left(\frac{my(t-\tau)}{a+y(t-\tau)} e^{-by(t-\tau)} - \rho\right) x(t-\tau) \\ &\geq (\rho - 1)x(t) + \left(\frac{me^{-b}(1-\varepsilon)}{a+(1-\varepsilon)} - \rho\right) x(t-\tau) \end{aligned} \tag{5.4}$$

Since $\varepsilon < \frac{me^{-b}-(a+1)}{me^{-b}-1}$ and $\frac{me^{-b}}{a+1} > 1$, we have that $\frac{me^{-b}(1-\varepsilon)}{a+(1-\varepsilon)} > 1$. We can choose $\rho > 1$, such that $1 < \rho < \frac{me^{-b}(1-\varepsilon)}{a+(1-\varepsilon)}$. From (5.2), we have that $x(t) \geq \eta > 0$ for some constant η and all large $t \geq t_1 > 0$. Hence, it follows from (5.4),

$$\dot{P}(t) \geq (\rho - 1)x(t) > 0. \tag{5.5}$$

Thus, $P(t) \to +\infty$ as $t \to +\infty$. This contradicts Theorem 2.1, and shows that E_0 is isolated.

We easily see that the semigroup defined by the solution of (1.4) satisfies the conditions of Lemma 4.3 in [40] with $M = E_0$. Thus, by Lemma 4.3 in [40] , we have that there is some $\xi = (\xi_1, \xi_2)$, such that $\xi \in \omega^* \cap (W^s(E_0) \backslash E_0)$. Here, $W^s(E_0)$ denotes the stable set of E_0.

If $\xi_1(0) = 0$, again by the invariance of M and Theorem 2.1, we also have the contradiction that $\xi = E_0$ or that the negative semi-orbit $(\hat{x}_t, \hat{y}_t)(t < 0)$ of (1.4) through ξ is unbounded.

If $\xi_1(0) > 0$, from Theorem 2.1, we see that $\hat{x}(t) > 0, \hat{y}(t) > 0$ for all $t > 0$. It follows from $\xi \in \omega^* \cap (W^s(E_0) \backslash E_0)$ that $\lim_{t \to +\infty} \hat{x}(t) = 0,\ \lim_{t \to +\infty} \hat{y}(t) = 1$, which contradicts (5.2). This shows that (5.1) holds. Thus, (1.4) is permanent. This proves our theorem.

6 Discussion

In this paper, based on some biological meanings, we introduce variable yield and time delay to a class of chemostat model with inhibitory exponential substrate uptake which was considered in [4], and get an improved chemostat model (1.3) with time delay, which accounts for the natural phenomenon more reasonably. Then, by using comparison principle for functional differential equations and traditional analysis technique for transcendental equations [35], we give a detailed analysis on global existence and boundedness of solutions of (1.4) and local asymptotic stability of the equilibria of (1.4). Finally, based on Lyapunov–LaSalle principle for functional differential equations, we completely obtain global asymptotic stability and global attraction of the washout equilibrium of (1.4). Our results show that time delay is factually *harmless* for the local and global asymptotic stability of the washout equilibrium of (1.4), but it is not always harmless for the stability of the positive equilibrium, that is to say, because of the time delay the positive equilibrium becomes unstable (Theorem 3.2). Based on some known techniques on limit sets of differential dynamical systems, we show that, for any time delay, the chemostat model is permanent if and only if only one positive equilibrium exits. Unfortunately, we cannot give a complete proof to the global asymptotic stability of the positive equilibrium E_1^+. We shall leave the problems as future work.

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