AN ANALYSIS APPROACH TO PERMANENCE OF A DELAY DIFFERENTIAL EQUATIONS MODEL OF MICROORGANISM FLOCCULATION

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Abstract. In this paper, we develop a delay differential equations model of microorganism flocculation with general monotonic functional responses, and then study the permanence of this model, which can ensure the sustainability of the collection of microorganisms. For a general differential system, the existence of a positive equilibrium can be obtained with the help of the persistence theory, whereas we give the existence conditions of a positive equilibrium by using the implicit function theorem. Then to obtain an explicit formula for the ultimate lower bound of microorganism concentration, we propose a general analysis method, which is different from the traditional approaches in persistence theory and also extends the analysis techniques of existing related works.

1. Introduction. Models of continuous culture of microorganism have drawn attentions of many authors (see, e.g. [5, 11, 27, 28, 40] for time-delayed models and [20, 23, 25, 39, 42, 43] for models without time delay). They studied the stability or permanence of the models by using the theory of delay differential equations

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(DDEs) (see, e.g., [24,31,34,45]). How to collect and extract microorganisms in continuous culture of microorganisms has always been a great practical and significant problem, which is from both industrial production and applications of microorganisms. Collection and extraction of microorganisms can be achieved by putting some suitable flocculants (e.g., aluminium salt or polyacrylamide) in the chemostat [6]. Flocculants can be used to precipitate microorganisms and then can also be used to precipitate pathogenic microorganisms in waste water (see [33]). Flocculation method has become very effective method in the chemostat and been widely used due to lower cost in the world.

Recently, [14] discussed the global dynamics of the following microorganism flocculation model

\[
\begin{aligned}
    \dot{x}(t) &= dx^0 - d x(t) - h_1 x(t) y(t), \\
    \dot{y}(t) &= h x(t - \tau) y(t - \tau) - d y(t) - h_2 y(t) z(t), \\
    \dot{z}(t) &= dz^0 - d z(t) - h_3 y(t) z(t),
\end{aligned}
\]

(1.1)

where \(x(t), y(t)\) and \(z(t)\) represent the concentrations of nutrient, microorganisms and flocculant at time \(t\), respectively. The positive constants \(x^0\) and \(z^0\) denote input concentrations of nutrient for cultivating microorganisms and flocculant for precipitating microorganisms, respectively. The positive constant \(d\) is the same velocities of inflow and outflow of nutrient and flocculant as well as the velocity of outflow of microorganisms. The positive constants \(h_1, h, h_2\) and \(h_3\) are the consumption rate of nutrient, the growth rate of microorganisms, the flocculating rate of microorganisms and the consumption rate of flocculant, respectively. The delay time \(\tau \geq 0\) embodies the effects of the storage of nutrients in the body of microorganism individual and metabolism of microorganisms (also see [3,4,15]).

Following discussions of [12,41,43], we consider the survival rate of microorganisms in the delay time \(\tau \geq 0\), then the growth rate of microorganisms \(h\) can be taken as \(h(\tau) = h_1 e^{-d \tau}\) (see [12,41,43]). In fact, some of nutrient, microorganisms and flocculant may be lost due to environmental factors in the continuous culture of microorganism with flocculation effect, and thus, they may exist a certain loss. For mathematical tractability, we assume that the lost rates of nutrient, microorganisms and flocculant are all \(a > 0\). In addition, for the growth and flocculating processes of microorganisms, the principle of mass action cannot account for the contributions of the interaction among nutrient, microorganisms and flocculant. To describe the contributions, the bilinear growth and flocculating rates of microorganisms can be replaced with nonlinear functional responses, i.e., the nonlinear terms instead of the terms \(x(t) y(t)\) and \(y(t) z(t)\).

Motivated by model (1.1) and those considerations, we develop the following DDEs model with more complex and general nonlinear growth and flocculating processes of microorganisms:

\[
\begin{aligned}
    \dot{x}(t) &= dx^0 - (d + a) x(t) - h_1 f(x(t),y(t)), \\
    \dot{y}(t) &= h(\tau) f(x(t - \tau),y(t - \tau)) - (d + a) y(t) - h_2 g(y(t),z(t)), \\
    \dot{z}(t) &= dz^0 - (d + a) z(t) - h_3 g(y(t),z(t)),
\end{aligned}
\]

(1.2)

where the functions \(f(x(t),y(t))\) and \(g(y(t),z(t))\) which satisfy some prescribed conditions, denote the growth and flocculating rate terms of microorganisms, respectively. All other parameters in (1.2) have completely the same biological meanings as that of (1.1).

We consider the functional response terms \(f(x, y)\) and \(g(y, z)\) are monotone separately increasing with respect to each corresponding variable on \(\mathbb{R}_+^2\) with \(\mathbb{R}_+ = \)
[0, \infty) \text{ (see condition (C1)), which can cover the bilinear functional response term [29, 37], the saturated functional response term [9], the ratio-dependent functional response term [1, 17], the Ivlev-type functional response term [21, 22], the Holling type II functional response term [18, 19], the Beddington-DeAngelis functional response term [2, 8], the Crowley-Martin functional response term [7], the more general functional response term [12, 26] and so on. We can find that } f(x(t), y(t)) = x(t)y(t) \text{ and } g(y(t), z(t)) = y(t)z(t) \text{ for the bilinear functional response terms of system (1.1), and the Beddington-DeAngelis functional response terms } f(x(t), y(t)) = x(t)y(t)/(1 + a_0x(t) + a_1y(t)) \text{ and } g(y(t), z(t)) = y(t)z(t)/(1 + b_0y(t) + b_1z(t)) \text{ can contain the saturated functional response terms of the improved version of system (1.1) in [15], where the constants } a_i, b_i \geq 0, i = 0, 1 \text{ are the measurements of the inhibitory effects.}

In this paper, we will propose a general analysis approach for proving the permanence of system (1.2). Due to the global dynamics of system (1.1) is more complicated than that of system (1.2) which undergoes a forward/backward bifurcation under some conditions, moreover, some analysis techniques for permanence in [13, 15, 38] cannot be put to good use, we will expand the techniques of [13, 15, 38] to prove the permanence of system (1.2), which can ensure the sustainable collection of microorganisms.

Set
\[
t = \frac{\hat{t}}{d + a}, \quad \tau = \frac{\hat{\tau}}{d + a}, \quad h(\tau) = \hat{h}(\hat{\tau}),
\]
\[
x(t) = \frac{dx(\hat{t})}{d + a}, \quad y(t) = \frac{\hat{h}(\hat{\tau})\hat{y}(\hat{t})}{d + a},
\]
\[
z(t) = \frac{dz(\hat{t})}{d + a}, \quad f_0(\hat{x}, \hat{y}) = \frac{h_3 f(dx(\hat{t})/(d + a), \hat{h}(\hat{\tau})\hat{y}(\hat{t})/(d + a))}{d\hat{x}},
\]
\[
g_0(\hat{x}, \hat{y}) = \frac{\hat{h}_2 g(\hat{\tau})\hat{y}(\hat{t})/(d + a), d\hat{x}z(\hat{t})/(d + a))}{\hat{h}(\hat{\tau})},
\]
and we still use } x, y, z, t, \tau, h, f, g \text{ to denote } \hat{x}, \hat{y}, \hat{z}, \hat{t}, \hat{\tau}, \hat{h}, f_0, g_0 \text{ respectively. Then system (1.2) can be simplified as}
\[
\begin{align*}
\dot{x}(t) &= 1 - x(t) - f(x(t), y(t)), \\
\dot{y}(t) &= rf(x(t - \tau), y(t - \tau)) - y(t) - g(y(t), z(t)), \\
\dot{z}(t) &= 1 - z(t) - \delta g(y(t), z(t)),
\end{align*}
\]
\[
(1.3)
\]
where
\[
r = \frac{dx}{h_1}, \quad \delta = \delta(\tau) = \frac{h(\tau)h_3}{d\tau h_2}.
\]
Next, let \text{Int}(\mathbb{R}_+^2) \text{ denote the interior of } \mathbb{R}_+^2 \text{ and let us suppose that the functions } f(x, y) \text{ and } g(y, z) \text{ have the following properties.}

(C1) } f, g \in C^1(\mathbb{R}_+^2) \text{ and the partial derivatives } f_x(x, y) > 0, f_y(x, y) > 0, f_y(x, 0) > 0, g_y(y, z) > 0, g_y(0, z) > 0 \text{ and } g_z(y, z) > 0 \text{ on } \text{Int}(\mathbb{R}_+^2). \text{ Furthermore, } f(x, y) = 0 \text{ if and only if } xy = 0, \text{ and } g(y, z) = 0 \text{ if and only if } yz = 0.

The remaining parts of this paper are organized as follows. In Section 2, we give the well-posedness and dissipativeness of system (1.3). In Section 3, by using the implicit function theorem, we prove the existence of positive equilibria. In Section 4, the permanence of microorganism flocculation is proved. Furthermore, we obtain an explicit expression on the ultimate lower bound of any positive solution of system (1.3), i.e., a specific estimation on the ultimate lower bound of microorganism concentration. A brief discussion and conclusions section completes the paper.
2. Well-posedness and dissipativeness. Let $C$ be the Banach space of continuous functions $\phi = (\phi_1, \phi_2, \phi_3)^T$ mapping from $[-\tau, 0]$ to $\mathbb{R}^3$ with the norm $\|\phi\| = \sup_{\theta \in [-\tau, 0]} |\phi(\theta)|$. Then the phase space of system (1.3) can be given by the nonnegative cone $C^+ := \{\phi \in C : \phi \geq 0\}$. Let $u : [-\tau, \varepsilon_\phi] \to \mathbb{R}^3$ be a continuous function with $\varepsilon_\phi > 0$. Then we denote $u_t \in C$ for $t \in [0, \varepsilon_\phi]$ as $u_t(\theta) = u(t + \theta)$, $\theta \in [-\tau, 0]$. For a real function $g(t)$ defined on $[0, \infty)$, we define

$$g_\infty = \liminf_{t \to \infty} g(t) \text{ and } g^\infty = \limsup_{t \to \infty} g(t).$$

Now, we start with the well-posedness and the dissipativeness of system (1.3). We first have the following assumptions.

(C2) $\frac{f(x, y)}{x}$ is non-increasing with respect to $x$ for $x, y > 0$.

(C3) $\frac{g(y, z)}{z}$ is non-increasing with respect to $z$ for $y, z > 0$.

**Theorem 2.1.** Assume that the functions $f(x, y)$ and $g(y, z)$ satisfy conditions (C1)-(C3). Then the solution $u(t) = (x(t), y(t), z(t))^T$ of system (1.3) through any $\phi \in C^+$ exists, is unique and nonnegative on $[0, \infty)$, which satisfies

$$\begin{align*}
\omega \leq x(t) \leq x^\infty \leq 1, \\
0 \leq y(t) \leq y^\infty \leq \omega_1, \\
\omega_2 \leq z(t) \leq z^\infty \leq 1,
\end{align*}$$

(2.1)

where $\omega$ is the minimum root in $[1/(1 + f_x(0, r)), 1]$ of the following equation:

$$x + f(x, r(1 - x)) = 1,$$

(2.2)

$\omega_1 = r(1 - \omega)$ and $\omega_2 = 1/[1 + \delta g_z(r(1 - \omega), 0)]$. Moreover, the solution semi-flow $\Psi(t) := u_t(\cdot) : C^+ \to C^+ \ (t \geq 0)$ has a global attractor.

**Proof.** For any given $\phi \in C^+$, define

$$W(\phi) = (W_1(\phi), W_2(\phi), W_3(\phi))^T = \left(\begin{array}{c} 1 - \phi_1(0) - f(\phi_1(0), \phi_2(0)) \\
rf(\phi_1(-\tau), \phi_2(-\tau)) - \phi_2(0) - g(\phi_2(0), \phi_3(0)) \\
1 - \phi_3(0) - \delta g(\phi_2(0), \phi_3(0))\end{array}\right).$$

Note that $W(\phi)$ is continuous for $\phi \in C^+$ and Lipschitz in $\phi$ on each compact set of the closed set $C^+$. Thus, with the aid of the existence and uniqueness theorem of solutions of DDEs (see, e.g., [16, 24]), we have that the solution $u(t) = (x(t), y(t), z(t))^T$ of system (1.3) with any $\phi \in C^+$ is unique on its maximal interval $[0, \varepsilon_\phi)$ of existence. It follows from [30, Theorem 5.2.1] that the solution $u(t)$ is nonnegative on $[0, \varepsilon_\phi)$ on account of $W_1(\phi) \geq 0$ whenever $\phi \in C^+$ with $\phi_1(0) = 0$.

In the following, we will explore the boundedness of solutions of system (1.3) on $[0, \varepsilon_\phi)$. By the nonnegativity of the solution $u(t)$ on $[0, \varepsilon_\phi)$ and system (1.3), we have

$$\dot{x}(t) \leq 1 - x(t) \text{ for } t \in [0, \varepsilon_\phi).$$

It follows from the comparison principle that $x(t)$ is bounded on $[0, \varepsilon_\phi)$. Analogously, $z(t)$ is also bounded on $[0, \varepsilon_\phi)$. There exists a constant $B_\phi$ such that for $t \in [0, \tau] \cap [0, \varepsilon_\phi)$,

$$\dot{y}(t) \leq rf(x(t - \tau), y(t - \tau)) - y(t) \leq B_\phi - y(t).$$
Thus, \( y(t) \) is bounded on \([0, \tau] \cap [0, \varepsilon_\phi)\) and then \( \varepsilon_\phi > \tau \). Let \( p(t) = rx(t - \tau) + y(t) \) for \( t \in [0, \varepsilon_\phi) \). Then for \( t \in [\tau, \varepsilon_\phi) \), it holds
\[
\dot{p}(t) \leq r - p(t).
\] (2.3)

In consequence, \( p(t) \) is bounded on \([0, \varepsilon_\phi)\), which implies \( y(t) \) is also bounded on \([0, \varepsilon_\phi)\). It follows from the continuation theorem of solutions for DDEs (see, e.g., [16, 24]) that \( \varepsilon_\phi = \infty \). Further, the nonnegativity of solution \( u(t) \) on \([0, \infty)\) can be obtained.

Next, we will prove that (2.1) holds. By the first equation and the third equation of system (1.3), we have that \( x^\infty \leq 1 \) and \( z^\infty \leq 1 \). By (2.3), it holds
\[
y^\infty \leq r(1 - x^\infty) \leq r.
\] (2.4)

Let
\[
w_1 = \frac{1}{1 + f_x(0, r)}, \quad w_n = \frac{1}{1 + f(w_{n-1}, r(1 - w_{n-1}))/w_{n-1}}, n \geq 2.
\]
Then by conditions (C1) and (C2), it follows \( 0 < w_n \leq w_{n+1} < 1 \) for any \( n \geq 1 \). Thus, \( w_1 \leq \lim_{n \to \infty} w_n = w \leq 1 \), where \( w \) is a root in \([w_1, 1]\) of equation (2.2), which be equivalent to the equation
\[
x = \frac{1}{1 + f(x, r(1 - x))/x}.
\]
Obviously, 1 is the root of equation (2.2).

We can obtain that \( x(t) > 0 \) for \( t > 0 \). By (2.4), it holds that for any \( \varepsilon > 0 \), there can be found a \( K = K(\phi, \varepsilon) > 0 \) such that \( y(t) \leq r + \varepsilon \) for \( t \geq K \). In consequence, by the first equation of system (1.3) and conditions (C1) and (C2), we have that for \( t \geq K \),
\[
\dot{x}(t) = 1 - x(t) \left( 1 + \frac{f(x(t), y(t))}{x(t)} \right) \\
\geq 1 - x(t) \left( 1 + \frac{f(x(t), r + \varepsilon)}{x(t)} \right) \\
\geq 1 - x(t) \left( 1 + f_x(0, r + \varepsilon) \right).
\]
We thus have \( x_\infty \geq 1/(1 + f_x(0, r + \varepsilon)) \) and
\[
x_\infty = \lim_{\varepsilon \to 0^+} x_\infty \geq \lim_{\varepsilon \to 0^+} 1/(1 + f_x(0, r + \varepsilon)) = w_1 > 0.
\]
Hence, from (2.4) and the similar argument as above, it follows
\[
x_\infty \geq \frac{1}{1 + f(x_\infty, r(1 - x_\infty))/x_\infty}.
\] (2.5)

By a principle of mathematical induction and (2.5), we obtain \( x_\infty \geq w_n \) and then \( x_\infty \geq \omega \). Accordingly, from conditions (C1) and (C3) combining (2.4), there hold \( y^\infty \leq \omega_1 \) and \( z_\infty \geq \omega_2 \). Therefore, the solution semi-flow \( \Psi(t) \) is point dissipative.

It is clear to obtain that all solutions of system (1.3) in \( C^+ \) are uniformly bounded on \([0, \tau]\). Since \( x(t) > 1 \) and \( p(t) > r \) for \( t \geq \tau \), there hold \( \dot{x}(t) < 0 \) and \( \dot{p}(t) < 0 \), which show that solutions of system (1.3) in \( C^+ \) are uniformly bounded on \([0, \infty)\).

By [16, Corollary 3.6.2], it holds that \( \Psi(t) \) is completely continuous for any \( t \geq \tau \). Thus, it follows from [16, Theorem 4.5.2] that there exists a global attractor for \( \Psi(t) \).

As a direct consequence of Theorem 2.1, we have the following corollary.
Corollary 2.2. If $\omega = 1$, then $\lim_{t \to \infty} u(t) = (1, 0, 1)^T \equiv E_0$, i.e., $E_0$ is global attractive.

Remark 1. It is clear that $E_0$ is a microorganism-free equilibrium (boundary equilibrium) of system (1.3).

3. Existence of positive equilibria. In this section, our key idea to prove the existence of positive equilibria is to use the implicit function theorem. By following a similar method in [36], we can define the following threshold of system (1.3):

$$R_0 = \frac{rf_y(1, 0)}{g_y(0, 1) + 1}.$$  

In Corollary 2.2, it is not difficult to check that $R_0 < 1$. In fact, let $\alpha(x) = x + f(x, r(1 - x)) - 1$, because $\alpha(0) = -1 < 0$, $\alpha(1) = 0$ and $\omega = 1$, it holds $\dot{\alpha}(1) \geq 0$, namely, $rf_y(1, 0) \leq 1$.

Usually, if $R_0 > 1$, there exists a microorganism equilibrium (positive equilibrium) $E^* = (x^*, y^*, z^*)^T$, which satisfies

$$\begin{cases} 0 = 1 - x^* - \frac{f(x^*, y^*)}{r}, \\ 0 = rf(x^*, y^*) - y^* - g(y^*, z^*), \\ 0 = 1 - z^* - \delta g(y^*, z^*). \end{cases}$$

For the existence of a positive equilibrium, we give the following result.

Theorem 3.1. Assume that the functions $f(x, y)$ and $g(y, z)$ satisfy conditions (C1). If $R_0 > 1$, then there exists a positive equilibrium $E^*$.

Proof. By the equilibrium equations of system (1.3), we have

$$1 - x = f(x, y) = \frac{y + g(y, z)}{r} = \frac{y}{r} + 1 - \frac{z}{r\delta}. $$

Further, 

$$F(y, z) \equiv g(y, z) - \frac{1 - z}{\delta} = 0, \quad (3.1)$$

$$x = 1 - \frac{y}{r} - \frac{1 - z}{r\delta}. \quad (3.2)$$

First, both partial derivatives $F_y(y, z) = g_y(y, z)$ and $F_z(y, z) = g_z(y, z) + \frac{1}{\delta}$ of the binary function $F(y, z)$ are continuous on $\mathbb{R}_+^2$. Second, $F(0, 1) = 0$ and $F_z(0, 1) = 1/\delta > 0$. Then by means of the implicit function theorem, there exists a unique implicit function $z \in C^1([0, \varepsilon), \mathbb{R}_+)$ which satisfies $F(y, z(y)) \equiv 0$ and $1 = z(0)$, where $[0, \varepsilon)$ is its maximal interval of existence. From (3.1), it follows $z(y) > 0$ for $y \in [0, \varepsilon)$. Inasmuch as

$$\dot{z}(y) = -\frac{g_y(y, z)}{g_z(y, z) + 1/\delta} < 0, \quad y \in (0, \varepsilon),$$

the limit $\lim_{y \to \varepsilon^-} z(y) \equiv z_\varepsilon$ exists and $0 < z_\varepsilon < z(y) \leq z(0) = 1$ for $y \in [0, \varepsilon)$. So in this case, we can claim $\varepsilon = \infty$. And then by (3.2), there is a positive constant $\bar{y} > 0$ such that $x = x(\bar{y}) > 0$, $y \in [0, \bar{y})$ and $x(\bar{y}) = 0$.

Thus, we can have the following equation:

$$H(y) \equiv \frac{f(x, y)}{y} - \frac{1}{r} - \frac{g(y, z)}{ry} = 0, \quad y \in (0, \bar{y}).$$
Since $\mathcal{R}_0 > 1$,
\[
\lim_{y \to 0^+} H(y) = \lim_{y \to 0^+} \left( f_y (x(y), \xi_y) - \frac{1}{r} - \frac{g_y(\eta_y, z(y))}{r} \right) = f_y (1, 0) - \frac{1}{r} - \frac{g_y(0, 1)}{r} = \frac{(1 + g_y(0, 1)) (\mathcal{R}_0 - 1)}{r} > 0,
\]
where $\xi_y, \eta_y \in (0, y)$. Clearly, $\lim_{y \to 0^+} H(y) = -1/r - g(\tilde{y}, z(\tilde{y}))/r\tilde{y} < 0$. Thus, it follows from the intermediate value theorem that there exists at least one $y^* \in (0, \tilde{y})$ such that $H(y^*) = 0$. In consequence, $x^* = x(y^*) > 0$, $z^* = z(y^*) > 0$, which implies that there exists one positive equilibrium $E^*$.
\[
\square
\]
4. **Permanence.** In this section, we will give a general techniques of analysis for permanence of system (1.3) based on some techniques of [13, 15]. This qualitative analysis approach also generalizes that of [13, 15, 38, 43] for permanence of system (1.3). And then we will also obtain an explicit estimation on the ultimate lower bound of microorganism concentration. Let $X = \{ \phi \in C^+ : \phi(0) > 0 \}$ and $u_t = (x_t, y_t, z_t)^T$ be the solution of system (1.3) with any $\phi \in X$. We can check that $X$ is positively invariant for system (1.3). We have the following definition.

**Definition 4.1** ([24]). System (1.3) is said to be permanent if there exist positive constants $\nu_i$ and $m_i$ ($i = 1, 2, 3$) independent of the initial function $\phi$ such that

\[
\nu_1 \leq x_\infty \leq x^\infty \leq m_1,
\nu_2 \leq y_\infty \leq y^\infty \leq m_2,
\nu_3 \leq z_\infty \leq z^\infty \leq m_3.
\]

In particular, system (1.3) is said to be uniformly persistent if $\nu_1 \leq x_\infty$, $\nu_2 \leq y_\infty$ and $\nu_3 \leq z_\infty$ hold.

The permanence of system (1.3) has significant meaning in biology, which means that microorganism concentration $y(t)$ will ultimately exist and microorganisms can be collected on a continuous and long-term basis.

To start the permanence of system (1.3), we need the following assumptions and two lemmas.

(C4) $\frac{f(x, y)}{y}$ is non-increasing with respect to $y$ for $x, y > 0$.
(C5) $\frac{g(y, z)}{y}$ is non-increasing with respect to $y$ for $y, z > 0$.

**Lemma 4.2.** Suppose that conditions (C1)-(C2) are satisfied. If $\mathcal{R}_0 > 1$, then there is an $\varepsilon_0 > 1$ such that

\[
\frac{r f(\rho, y_1)}{y_1} - g_y(0, \varepsilon) - 1 > 0 \text{ for } \varepsilon \in (1, \varepsilon_0),
\]

where
\[
\rho = \frac{1}{b} + \left( \frac{\omega}{2} - \frac{1}{b} \right) e^{-T_0 b}, \quad b = 1 + \frac{f(x^*, y_1)}{x^*}, \quad T_0 = \frac{-1}{b} \ln \frac{f(1, y_1) R_0 - f_y(1, 0) y_1 b}{f(1, y_1) R_0}
\]

and $y_1$ satisfies
\[
0 < y_1 < y^*, \quad \frac{y_1 f_y(1, 0)}{f(1, y_1) R_0} < \frac{1}{b}.
\]
Thereupon, we have that 
\[ x \frac{y_1 f_y(1, 0)}{f(1, y_1) R_0} = \left( \frac{g_y(0, 1) + 1}{rf(1, y_1)} y_1 \right) < \frac{1}{b}. \]
Clearly, \( \rho > (1 - e^{-T_0 b}) / b = (g_y(0, 1) + 1) y_1 / rf(1, y_1) \). It is not difficult to verify \( \omega / 2 - 1 / b < 0 \). Thus, we have \( \rho < 1 \). Consequently, it follows from condition (C2) that
\[ \frac{rf(\rho, y_1)}{y_1} - g_y(0, 1) - 1 \geq \frac{\rho f(1, y_1)}{y_1} - g_y(0, 1) - 1 > 0. \]
Hence, there is an \( \varepsilon_0 > 1 \) such that
\[ \frac{rf(\rho, y_1)}{y_1} - g_y(0, \varepsilon) - 1 \geq \frac{\rho f(1, y_1)}{y_1} - g_y(0, \varepsilon) - 1 > 0 \text{ for } \varepsilon \in (1, \varepsilon_0). \]
\[ \square \]

Lemma 4.3. Suppose that conditions (C1), (C2), (C4) and (C5) are satisfied. If \( R_0 > 1 \), then there is a sequence \( \{t_n\} \) in \( R_+ \) and \( \lim_{n \to \infty} t_n = \infty \) such that \( y(t_n) > y_1 \) for \( n \geq 1 \).

Proof. Let \( u_t = (x_t, y_t, z_t)^T \) be the solution of system (1.3) through any \( \phi \in X \). For any \( \varepsilon \in (1, \varepsilon_0) \), there exists \( T \equiv T(\phi, \varepsilon) > 0 \) such that \( x(t) \geq \omega / 2 \) and \( z(t) \leq \varepsilon \) for \( t \geq T \). Now, we provide the proof of Lemma 4.3 by contradiction. Suppose the lemma is false. That is, there exists a \( t_0 \geq T \) such that \( y(t) \leq y_1 \) for any \( t \geq t_0 \). Then we can claim that \( x(t) \geq x^* \) for \( t \geq t_0 + T_1 \), where
\[ T_1 = \frac{x^*}{1 - bx^*} > 0. \] (4.1)
Otherwise, if \( x(t_0) \geq x^* \), then it follows from (1.3) that there is a \( \bar{t} \in (t_0, \infty) \) such that
\[ x(\bar{t}) = x^* \text{ and } \bar{x}(\bar{t}) \leq 0. \] This contradicts
\[ \bar{x}(\bar{t}) \geq 1 - x^* - f(x^*, y_1) > 1 - x^* - f(x^*, y^*) = 0. \]
If \( x(t_0) < x^* \), by the argument of [13, Theorem 3.4], we have \( x(t) \geq x^* \) for \( t \geq t_0 + T_1 \). Thus, it holds that \( x(t) \geq x^* \) for \( t \geq t_0 + T_1 \).

From conditions (C1) and (C2) combining the first equation of system (1.3), it follows that for \( t \geq t_0 + T_1 \),
\[ \dot{x}(t) = 1 - \left( 1 + \frac{f(x(t), y(t))}{x(t)} \right) x(t) \geq 1 - bx(t), \]
which yields
\[ x(t) \geq \frac{1}{b} + \left( x(t_0 + T_1) - \frac{1}{b} \right) e^{-(t - t_0 - T_1)b} \geq \frac{1}{b} + \left( \frac{\omega}{2} - \frac{1}{b} \right) e^{-(t - t_0 - T_1)b}. \]
Thereupon, we have that \( x(t) \geq \rho \) for \( t \geq \bar{T} \equiv t_0 + T_0 + T_1 \).

Now, let us define the following functional:
\[ V(\phi) = \phi_2(0) + r \int_{-\tau}^{0} f(\phi_1(\theta), \phi_2(\theta)) d\theta, \phi \in X. \]
Then the derivative of $V(\phi)$ along this solution $u_t$ is taken by
\[
\dot{V}(u_t) = \left( \frac{rf(x(t), y(t))}{y(t)} - \frac{g(y(t), z(t))}{y(t)} - 1 \right) y(t). \tag{4.2}
\]
By conditions (C1), (C4) and (C5) combining (4.2), it holds that for $t \geq \hat{T}$,
\[
\dot{V}(u_t) \geq \left( \frac{rf(\rho, y_1)}{y_1} - g_\nu(0, \varepsilon) - 1 \right) \bar{y} \tag{4.3}
\]
Set
\[
\bar{y} = \min_{\theta \in [-\tau, 0]} y \left( \hat{T} + \tau + \theta \right).
\]
Next we will show that for all $t \geq \hat{T}$, $y(t) \geq \bar{y}$. By contradiction, suppose there exists some $T_2 \geq 0$ such that $y(t) \geq \bar{y}$ for $t \in [\hat{T}, \hat{T} + T_2]$, where $\bar{T} = \hat{T} + T_2 + \tau$, $y(\bar{T}) = \bar{y}$ and $\dot{y}(\bar{T}) \leq 0$. Then by virtue of the second equation of system (1.3) and Lemma 4.2, we have
\[
\dot{y}(\bar{T}) = \left( \frac{rf(x(\bar{T} - \tau), y(\bar{T} - \tau))}{\bar{y}} - \frac{g(\bar{y}, z(\bar{T}))}{\bar{y}} - 1 \right) \bar{y} \\
\geq \left( \frac{rf(\rho, \bar{y})}{\bar{y}} - g_\nu(0, \varepsilon) - 1 \right) \bar{y} \\
\geq \left( \frac{rf(\rho, y_1)}{y_1} - g_\nu(0, \varepsilon) - 1 \right) \bar{y} \\
> 0,
\]
which is a contradiction to $\dot{y}(\bar{T}) \leq 0$. In consequence, $y(t) \geq \bar{y}$ for $t \geq \hat{T}$ and it holds
\[
\dot{V}(u_t) \geq \left( \frac{rf(\rho, y_1)}{y_1} - g_\nu(0, \varepsilon) - 1 \right) \bar{y} \tag{4.3}
\]
for $t \geq \hat{T}$. Since $V(u_t)$ is bounded, this is a contradiction by (4.3). And thus the lemma is proved.

**Theorem 4.4.** Suppose that conditions (C1)-(C5) are satisfied. If $R_0 > 1$, then system (1.3) is permanent in $X$ and for the solution $u_t$ of system (1.3) there holds
\[
y_\infty \geq y_1 e^{-rf_\nu(1, 0)(T_0 + T_1 + \tau) / R_0} \equiv \nu, \tag{4.4}
\]
where $T_1$ is defined by (4.1).

**Proof.** By Theorem 2.1, we only need to prove (4.4) holds. From Lemma 4.3, we will consider (4.4) in two cases: $y(t) \geq y_1$ or $y(t)$ oscillates around $y_1$ for sufficiently large $t$. Hence, we only need to discuss $y(t)$ oscillates around $y_1$ for sufficiently large $t$. Consequently, we suppose that $t_1, t_2 \geq T$ are sufficiently large such that
\[
y(t) < y_1 \text{ for } t \in (t_1, t_2) \text{ and } y(t_1) = y(t_2) = y_1.
\]
From the second equation of system (1.3), it follows
\[
\dot{y}(t) \geq - (g_\nu(0, \varepsilon) + 1) y(t) \text{ for } t \geq T.
\]
When $t_2 \leq t_1 + T_0 + T_1 + \tau$ for $t \in [t_1, t_2]$, it holds
\[
y(t) \geq y_1 e^{-(g_\nu(0, \varepsilon) + 1)(t - t_1)} \geq y_1 e^{-(g_\nu(0, \varepsilon) + 1)(T_0 + T_1 + \tau)} \equiv \tilde{\nu}(\varepsilon) > 0.
\]
When $t_2 > t_1 + T_0 + T_1 + \tau$, $y(t) \geq \tilde{\nu}(\varepsilon)$ for $t \in [t_1, t_1 + T_0 + T_1 + \tau]$. For $t \in [t_1 + T_0 + T_1 + \tau, t_2]$, by the similar argument as in the proof of Lemma 4.3, we have $y(t) \geq \tilde{\nu}(\varepsilon)$.
In fact, if not, there exists some $T_3 \geq 0$ such that $y(t) \geq \tilde{\nu}(\varepsilon)$ for $t \in [t_1, \tilde{t}]$, where $\tilde{t} = t_1 + T_0 + T_1 + T_3 + \tau$, $y(\tilde{t}) = \tilde{\nu}(\varepsilon)$ and $\dot{y}(\tilde{t}) \leq 0$. By Lemma 4.2 and the second equation of system (1.3), it holds that

\[
\dot{y}(\tilde{t}) \geq \left( \frac{rf(x(\tilde{t} - \tau), \tilde{\nu}(\varepsilon))}{\tilde{\nu}(\varepsilon)} - g_y(0, \varepsilon) - 1 \right) \tilde{\nu}(\varepsilon)
\geq \left( \frac{rf(\rho, y_1)}{y_1} - g_y(0, \varepsilon) - 1 \right) \tilde{\nu}(\varepsilon)
> 0,
\]

which contradicts $\dot{y}(\tilde{t}) \leq 0$. Therefore, $y(t) \geq \tilde{\nu}(\varepsilon)$ for $t \in [t_1, t_2]$. Notice that this kind interval $[t_1, t_2]$ is chosen in an arbitrary way. Hence, for sufficiently large $t$, $y(t) \geq \tilde{\nu}(\varepsilon)$, which hints $y_\infty \geq \tilde{\nu}(\varepsilon)$. Consider that the choice of $\varepsilon$ is arbitrary, we thus have $y_\infty \geq \nu$. \qed

**Remark 2.** It is not difficult to find that Theorem 4.4 extends the related result in [15], and the proof method of Theorem 4.4 is also an extension of the analysis techniques for uniform persistence in [13, 15, 38, 43].

In Lemma 4.2, the conditions $0 < y_1 < y^*, y_1 \left( g_y(0, 1) + 1 \right) / rf(1, y_1) < 1 / b$ can ensure the positivity of both functions $T_0$ and $T_1$ with well-defined. To obtain $y_1$ simply, we have the following corollary.

**Corollary 4.5.** In Theorem 4.4, if the conditions

\[0 < y_1 < y^*, y_1 \left( g_y(0, 1) + 1 \right) / rf(1, y_1) < 1 / b\]

are replaced by the conditions $y_1 \in (0, y_0)$ and $y_0$ is a unique root in $(0, y^*)$ of the equation

\[
\frac{rf(1, y)}{y \left( g_y(0, 1) + 1 \right)} = f(x^*, y) = \frac{x^*}{y^*} + 1,
\]

then the conclusion of Theorem 4.4 still holds.

**Proof.** Let $\beta(y) = \frac{rf(1, y)}{y \left( g_y(0, 1) + 1 \right)} - \frac{f(x^*, y)}{x^*} - 1$ for $y \in (0, y^*)$. Then it follows from conditions (C1) and (C4) that $\beta(y)$ is a strictly decreasing function. By conditions (C1), (C2), (C5) and equilibrium equations of system (3), we have

\[
\frac{rf(1, y^*)}{y^*} x^* \leq \frac{rf(x^*, y^*)}{x^* y^*} x^* = \frac{rf(x^*, y^*)}{y^*} = 1 + \frac{g(x^*, y^*)}{y^*} \leq 1 + g_y(0, 1).
\]

Thus, $\frac{rf(1, y^*)}{y^* \left( 1 + g_y(0, 1) \right)} \leq \frac{1}{x^*} = \frac{f(x^*, y^*)}{x^*} + 1$, that is, $\beta(y^*) \leq 0$. Note that $\lim_{y \to y^*} \beta(y) = R_0 - 1 > 0$. Therefore, the intermediate value theorem implies that there is a unique positive constant $y_0 \in (0, y^*)$ such that $\beta(y_0) = 0$ and $y_1 \left( g_y(0, 1) + 1 \right) / rf(1, y_1) < 1 / b$ for $y_1 \in (0, y_0)$. \qed

**Example 4.1** In system (1.3), taking

\[
f(x, y) = \frac{\theta x y}{1 + a_1 x + b_1 y}, \quad g(y, z) = \frac{\epsilon y}{1 + a_2 y} \frac{z}{1 + b_2 z},
\]

where the parameters $\theta, \epsilon, a_1, a_2, b_1, b_2$ are positive and the other parameters are also positive. Then system (1.3) becomes

\[
\begin{align*}
\dot{x}(t) &= 1 - x(t) - \frac{\theta z(t) y(t)}{1 + a_1 x(t) + b_1 y(t)}, \\
\dot{y}(t) &= r - \frac{\theta z(t - \tau) y(t - \tau)}{1 + a_1 x(t - \tau) + b_1 y(t - \tau)} - y(t) - \epsilon \frac{y(t)}{1 + a_2 y(t)} - \frac{z(t)}{1 + b_2 z(t)}, \\
\dot{z}(t) &= 1 - z(t) - \delta \frac{y(t)}{1 + a_2 y(t)} \frac{z(t)}{1 + b_2 z(t)}.
\end{align*}
\]
We can easily verify that Beddington-DeAngelis type functional response \( f(x, y) \) and Crowley-Martin type functional response \( g(y, z) \) meet the conditions (C1)-(C5) and compute the threshold
\[
R_0 = \frac{r\theta(b_2 + 1)}{(a_1 + 1)(b_2 + \epsilon + 1)}.
\]
Let \( y_0 = \frac{-B + \sqrt{B^2 - 4AC}}{2A} \), where
\[
A = b_1(b_2 + \epsilon + 1)(b_1 + \theta),
B = b_1(a_1 + 1)(b_2 + \epsilon + 1)\left(\frac{a_1x^* + 1}{a_1 + 1} + \frac{\theta}{b_1} + 1 - R_0\right),
C = (a_1 + 1)(b_2 + \epsilon + 1)(a_1x^* + 1)(1 - R_0).
\]
Then Corollary 4.5 yields the following sharp result.

**Corollary 4.6.** If \( R_0 > 1 \), then system (4.5) is permanent in \( X \) and for the solution \( u_t \) of system (4.5) there holds
\[
y\infty \geq y_1 e^{-\frac{(b_2 + \epsilon + 1)(T_0 + T_1 + \tau)}{(b_2 + 1)}}, \quad (4.6)
\]
where \( y_1 \in (0, y_0) \), and
\[
T_0 = \frac{-1}{b} \ln \left(\frac{(a_1 + 1)R_0 - b(1 + a_1 + b_1y_1)}{(a_1 + 1)R_0}\right),
T_1 = \frac{x^*}{1 - bx^*},
\]
\[
b = \frac{1 + a_1x^* + (b_1 + \theta)y_1}{1 + a_1x^* + b_1y_1}.
\]

5. **Discussion and conclusions.** As is well-known, two traditional approaches in persistence theory are Morse decompositions and acyclic coverings (see, e.g., [10, 35, 45] for details). In this paper, we discuss the permanence of system (1.3) by using a general analysis method which is a generalization of methods in [13, 15, 38, 43]. From the point of view in mathematics, the traditional methods and Theorem 4.4 can get fully the same conclusion for the uniform persistence of system (1.3). In addition, comparing Theorem 4.4 with the traditional methods, an explicit ultimate lower bound of each positive solution of system (1.3) can be obtained in Theorem 4.4, especially, the lower bound \( \nu \) of \( y\infty \) is given. Thus both in mathematics and biology, Theorem 4.4 gives more practical meaning and reference. The proof of Theorem 4.4 also provides a theoretical basis for permanence of a dissipative biological system.

Usually, to establish the existence of the microorganism equilibrium \( E^* \) of system (1.3) with general monotonic functional responses, the persistence theorem [32, Theorem 3] (also see [45, Theorem 1.3.2]) and the existence theorem of coexistence steady states for uniformly persistent systems [44, Theorem 2.4] (also see [45, Theorem 1.3.11]) are applied. Whereas we give a more simple method to ensure the existence of the equilibrium \( E^* \). To obtain the global attractivity of the equilibrium \( E^* \), \( \nu \) in Theorem 4.4 may also be used to ease its conditions, e.g., see [15, Theorem 5.2].

Next, we use numerical computation via MATLAB to illustrate the validity of our results. In system (4.5), we take
\[
\begin{align*}
  r &= 14.65, \delta = 10, \tau = 0.03, \theta = 60, \epsilon = 0.1, a_1 = 0.11, a_2 = 45, b_1 = 0.1, b_2 = 56.
\end{align*}
\]
By calculation, we get $R_0 \approx 790.505 > 1$. Further, we obtain a unique microorganism equilibrium with microorganic load $y^* \approx 14.609$ and $y_0 \approx 13.944$. Choosing the initial function $\phi = (1, 2, 3)^T$, it holds $y_\infty > \nu \approx 11.896$ and the accuracy of $\nu$ is about 81.429%. This indicates that Corollary 4.5 is valid and numerical simulations suggest that microorganism equilibrium may be globally attractive under some conditions. In the given some parameters, there can be found a $y_1 \in (0, y_0)$ such that $\nu = \nu(y_1)$ is a better estimation of the lower bound on $y_\infty$. Thus, $\nu$ is not only a good explicit estimation of $y_\infty$, but also it has much practical use.

In this study, the global dynamics of system (1.3) is investigated in terms of the threshold parameter $R_0$. The monotonic functional responses includes some usual functional responses said in Introduction. First of all, the well-posedness and dissipativeness of system (1.3) are proved, and then the existence conditions of a positive equilibrium are given with the help of the implicit function theorem. A mathematical result has shown that system (1.3) is permanent for $R_0 > 1$, particularly, microorganism concentration $y(t)$ is uniformly persistent. This means that the collection of microorganisms is sustainable for $R_0 > 1$. System (1.3) may undergo a forward bifurcation or backward bifurcation. Although $E_0$ is global attractive if $\omega = 1$ (which implies $R_0 < 1$) in Corollary 2.2, the condition $\omega = 1$ is conservative. Thus, the global stability of equilibria of system (1.3) under some conditions still is a very interesting and challenging problem. We thus leave this problem for future work.

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