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Dynamical analysis of a competition model in the turbidostat with discrete delay

Zuxiong Li^{1,2*}, Yong Yao², Hailing Wang² and Zhijun Liu²

*Correspondence: lizx0427@126.com ¹ School of Mathematics and Statistics, Huazhong University of Science and Technology, Wuhan, Hubei 430074, P.R. China ² Department of Mathematics, Hubei University for Nationalities, Enshi, Hubei 445000, P.R. China

Abstract

In this paper, the dynamic behaviors of a competition model in the turbidostat with discrete delay are investigated. The stability of the positive equilibrium and the existence of a Hopf bifurcation are discussed by choosing the delay of digestion as a bifurcation parameter. Furthermore, we determine the direction and stability of the bifurcating periodic solutions by the normal form and the center manifold theorem. Moreover, some examples are given to illustrate our main results.

Keywords: turbidostat; bifurcating periodic solutions; digestion delay; stability; competition

1 Introduction

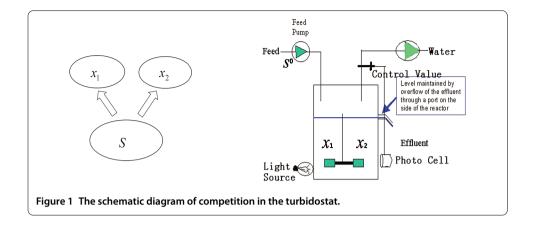
Chemostat models have been fruitful as a source of mathematical problems (see [1-11]). Generally, chemostat models lead to competitive exclusion results, which means that only one organism can survive in the competition at last. The phenomenon of coexistence of the organisms is a common thing in reality [3, 4, 12–14]. In a sense, coexistence reflects the ecological balance. The turbidostat as well as the chemostat is an important laboratory set for continuous cultivation of microorganisms, and also a very important medium between principle and application. Turbidostat model is one of the most important models in mathematical biology. Figure 1 [15] is the schematic diagram of the competition in the turbidostat. However, little work has been done in the study of mathematical models on the turbidostat, and the existing main studies can be listed as follows. Flegr [16] showed the coexistence of two organisms in the turbidostat by numerical analysis, De Leenheer and Smith [17] also verified Flegr's results by theoretical analysis. Li [18] and Cammarota and Miccio [19], respectively, established a mathematical model of competition in a turbidostat for an inhibitory nutrient, and one obtained sufficient conditions for coexistence solutions. Recently, to ensure the coexistence of the species, some scholars have considered turbidostat models by controlling the dilution rate of the turbidostat (see [20-22]).

De Leenheer and Smith [17] have considered the following system:

$$\begin{cases} \frac{dS(t)}{dt} = D(x(t))(S^0 - S(t)) - \frac{x_1(t)}{\gamma_1} f_1(S(t)) - \frac{x_2(t)}{\gamma_2} f_2(S(t)), \\ \frac{dx_1(t)}{dt} = x_1(t)[f_1(S(t)) - D(x(t))], \\ \frac{dx_2(t)}{dt} = x_2(t)[f_2(S(t)) - D(x(t))]. \end{cases}$$
(1.1)



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Here S(t) is the nutrient concentration and $x_i(t)$ (i = 1, 2) is the density of the *i*th organism at time *t*, respectively. $S^0 > 0$ represents the input concentration of the nutrient. $\gamma_i > 0$ (i = 1, 2) stands for the yield constant. $f_i(S(t)) = \frac{m_i S(t)}{a_i + S(t)}$ $(m_i > 0, a_i > 0, i = 1, 2)$ are uptakes functions. $D(x(t)) = d + k_1 x_1(t) + k_2 x_2(t)$ $(d > 0, k_i > 0, i = 1, 2)$ is the dilution of the turbidostat. k_i is the gain of the *i*th organism. System (1.1) is called 'turbidostat' by Li [18].

It was shown in [17] that a turbidostat with two organisms can be made coexistent if the dilution rate depends on the concentrations of two competing organisms. The authors showed that system (1.1) possessed a unique coexistence equilibrium under the specific conditions, and it is globally asymptotically stable. Yet people have recognized that time delay have a complex impact on the dynamics of a system in reality (see [23–25] and [26]). Yuan *et al.* [27] considered the effect of delay on the dilution rate D(x(t)) of system (1.1). The authors have investigated the stability of the positive equilibrium, the existence, and the stability of Hopf bifurcation. Further we note that the chemostat models with discrete delay due to the possibility that the organism digests (stores) the nutrient are natural and reasonable (see Bush and Cook [28], Freedman et al. [14] and Zhao [29]). Generally, different microorganisms have the different delays of digestion, but a single time delay is common in reality (see Lin et al. [30], Bender et al. [31] and Kharitonov [32]), so we assume that the two competitive microorganisms are homogeneous species and they have the same delay of digestion. Based on motivation from the work of Bush and Cook [28], Freedman et al. [14] and Zhao [29], in this study we focus on the dynamics of a turbidostat model with time delay of digestion which follows:

$$\begin{cases} \frac{dS(t)}{dt} = D(x(t))(S^0 - S(t)) - \frac{x_1(t)}{\gamma_1} f_1(S(t)) - \frac{x_2(t)}{\gamma_2} f_2(S(t)), \\ \frac{dx_1(t)}{dt} = x_1(t)[f_1(S(t - \tau)) - D(x(t))], \\ \frac{dx_2(t)}{dt} = x_2(t)[f_2(S(t - \tau)) - D(x(t))]. \end{cases}$$
(1.2)

Here S(t), $x_1(t)$, $x_2(t)$, D(x(t)), $f_i(S(t - \tau))$ (i = 1, 2) and the parameters play similar roles to system (1.1), $\tau > 0$ is the time delay of digestion.

The organization of this paper is as follows. We investigate the local stability and Hopf bifurcation of the positive equilibrium of system (1.2) in the next section. In Section 3, by using the normal form method and the center manifold theory introduced by Hassard *et al.* [33], we analyze the direction of Hopf bifurcation and the stability of bifurcating periodic solutions. In Section 4, some examples are given to illustrate our results.

2 Local stability and Hopf bifurcation

In the section, we focus on investigating the local stability of the positive equilibrium and the existence of local Hopf bifurcations for system (1.2).

For the sake of simplicity, we let

$$\bar{S}(t) = \frac{S(t)}{S^0}, \qquad \bar{k}_i = \gamma_i S^0 k_i, \qquad \bar{x}_i(t) = \frac{x_i(t)}{\gamma_i S^0}, \qquad \bar{f}_i(\bar{S}(t)) = f_i(\bar{S}(t)S^0), \quad i = 1, 2.$$

The bars dropped, system (1.2) becomes

$$\begin{cases} \frac{dS(t)}{dt} = (d + k_1 x_1(t) + k_2 x_2(t))(1 - S(t)) - x_1(t)f_1(S(t)) - x_2(t)f_2(S(t)), \\ \frac{dx_1(t)}{dt} = x_1(t)[f_1(S(t - \tau)) - (d + k_1 x_1(t) + k_2 x_2(t))], \\ \frac{dx_2(t)}{dt} = x_2(t)[f_2(S(t - \tau)) - (d + k_1 x_1(t) + k_2 x_2(t))]. \end{cases}$$
(2.1)

As in [17], we introduce the same hypothesis:

(H) The graphs of the functions f_1 and f_2 intersect once at S^* :

$$f_1(S^*) = f_2(S^*) = D^*,$$

where $S^* \in (0,1)$ and $f'_1(S^*) \neq f'_2(S^*)$.

Assume that $d \in (0, D^*)$ and

(H₁)
$$k_1 < \frac{D^* - d}{1 - S^*} < k_2$$
 or $k_2 < \frac{D^* - d}{1 - S^*} < k_1$,

then system (2.1) has a unique positive equilibrium $E^{\ast}=(S^{\ast},x_{1}^{\ast},x_{2}^{\ast}),$ where

$$S^* = \frac{m_2 a_1 - m_1 a_2}{m_1 - m_2},$$

$$x_1^* = \frac{D^* - k_2 (1 - S^*) - d}{k_1 - k_2},$$

$$x_2^* = \frac{k_1 (1 - S^*) - D^* + d}{k_1 - k_2}.$$

In the following, we will investigate the local stability of E^* and the existence of Hopf bifurcations induced by the time delay.

Set $y_1(t) = S(t) - S^*$, $y_2(t) = x_1(t) - x_1^*$, $y_3(t) = x_2(t) - x_2^*$. Then system (2.1) can be written as

$$\begin{cases} \frac{dy_1(t)}{dt} = -ay_1(t) + (k_1 - k_1S^* - D^*)y_2(t) + (k_2 - k_2S^* - D^*)y_3(t) \\ + (-x_1^*b_{12} - x_2^*b_{22})y_1^2(t) + (-k_1 - b_{11})y_1(t)y_2(t) + (-k_2 - b_{21})y_1(t)y_3(t) \\ - b_{12}y_1^2(t)y_2(t) - b_{22}y_1^2(t)y_3(t) + (-b_{13}x_1^* - b_{23}x_2^*)y_1^3(t) + \cdots, \\ \frac{dy_2(t)}{dt} = -k_1x_1^*y_2(t) - k_2x_1^*y_3(t) + x_1^*b_{11}y_1(t - \tau) - k_1y_2^2(t) - k_2y_2(t)y_3(t) \\ + x_1^*b_{12}y_1^2(t - \tau) + b_{11}y_1(t - \tau)y_2(t) + b_{12}y_1^2(t - \tau)y_2(t) \\ + b_{13}x_1^*y_1^3(t - \tau) + \cdots, \\ \frac{dy_3(t)}{dt} = -k_1x_2^*y_2(t) - k_2x_2^*y_3(t) + x_2^*b_{21}y_1(t - \tau) - k_2y_3^2(t) - k_1y_2(t)y_3(t) \\ + x_2^*b_{22}y_1^2(t - \tau) + b_{21}y_1(t - \tau)y_3(t) + b_{22}y_1^2(t - \tau)y_3(t) \\ + b_{23}x_2^*y_1^3(t - \tau) + \cdots. \end{cases}$$

Here

$$a = d + k_1 x_1^* + k_2 x_2^* + b_{11} x_1^* + b_{21} x_2^*$$

= $D^* + b_{11} x_1^* + b_{21} x_2^*$,
 $b_{ij} = \frac{f_i^{(j)}(S^*)}{j!}, \quad i = 1, 2, j = 1, 2, 3, \dots$

So the linearized system of (2.1) at E^* is

$$\begin{cases} \frac{dy_1(t)}{dt} = -ay_1(t) + (k_1 - k_1S^* - D^*)y_2(t) + (k_2 - k_2S^* - D^*)y_3(t), \\ \frac{dy_2(t)}{dt} = -k_1x_1^*y_2(t) - k_2x_1^*y_3(t) + x_1^*b_{11}y_1(t - \tau), \\ \frac{dy_3(t)}{dt} = -k_1x_2^*y_2(t) - k_2x_2^*y_3(t) + x_2^*b_{21}y_1(t - \tau). \end{cases}$$
(2.3)

We obtain the characteristic equation from (2.3)

$$\lambda^{3} + p\lambda^{2} + q\lambda + r\lambda e^{-\lambda\tau} + ke^{-\lambda\tau} = 0, \qquad (2.4)$$

where

$$p = k_2 x_2^* + k_1 x_1^* + a,$$

$$q = a (k_2 x_2^* + k_1 x_1^*),$$

$$r = D^* x_2^* b_{21} + D^* x_1^* b_{11} - (x_1^* + x_2^*) (b_{11} k_1 x_1^* + b_{21} k_2 x_2^*),$$

$$k = x_1^* x_2^* D^* (k_2 - k_1) (b_{11} - b_{21}).$$

In order to study the distribution of the roots of (2.4), we consider the following two cases: $\tau = 0$ and $\tau > 0$.

For τ = 0, (2.4) becomes

$$\lambda^{3} + p\lambda^{2} + (q+r)\lambda + k = 0.$$
(2.5)

It is obvious that p > 0. According to the Routh-Hurwitz criterion, we immediately have the following lemma.

Lemma 2.1 If (H_2) k > 0, p(q + r) > k, then all roots of (2.5) have negative real parts.

For τ > 0, Beretta and Kuang [34] have studied the general characteristic equation with delay dependent parameters:

$$P_n(\lambda;\tau) + Q_m(\lambda;\tau)e^{-\lambda\tau} = 0,$$

where P_n and Q_m are, respectively, *n*-degree and *m*-degree polynomials in λ , with n > m and with delay dependent polynomial coefficients. In (2.4), the parameters are delay independent, so the stability switch of the (2.4) can be obtained as a particular case of the results in [34].

We set

$$P(\lambda) = P_n(\lambda;\tau) = \lambda^3 + p\lambda^2 + q\lambda, \qquad Q(\lambda) = Q_n(\lambda;\tau) = r\lambda + k.$$
(2.6)

We assume that $P_n(\lambda; \tau)$ and $Q_m(\lambda; \tau)$ cannot have imaginary roots. That is, for any real number *w*,

$$P_n(iw, \tau) + Q_m(iw, \tau) \neq 0.$$

We have

$$F(w) = |P(w;\tau)|^2 - |Q(w;\tau)|^2 = w^6 + (p^2 - 2q)w^4 + (q^2 - r^2)w^2 - k^2.$$
(2.7)

Hence, F(w) = 0 implies

$$w^{6} + (p^{2} - 2q)w^{4} + (q^{2} - r^{2})w^{2} - k^{2} = 0.$$
(2.8)

Set $v = w^2$, then (2.8) becomes

$$v^{3} + (p^{2} - 2q)v^{2} + (q^{2} - r^{2})v - k^{2} = 0.$$
(2.9)

Denote

$$f(\nu) = \nu^{3} + (p^{2} - 2q)\nu^{2} + (q^{2} - r^{2})\nu - k^{2}.$$
(2.10)

Since $f(0) = -k^2 < 0$, $\lim_{\nu \to +\infty} f(\nu) = +\infty$, it is obvious that (2.9) has at least one positive root. By (2.10), we get

$$f'(v) = 3v^2 + 2(p^2 - 2q)v + q^2 - r^2.$$
(2.11)

Denote $\Delta = 4(p^2 - 2q)^2 - 12(q^2 - r^2)$. If $\Delta \leq 0$, then the function f(v) is monotone increasing in $v \in [0, \infty)$. Thus, (2.9) has only a positive real root; on the other hand, when $\Delta > 0$, the equation $3v^2 + 2(p^2 - 2q)v + q^2 - r^2 = 0$ has two real roots $v_1 = \frac{-2(p^2 - 2q) + \sqrt{\Delta}}{6}$ and $v_2 = \frac{-2(p^2 - 2q) - \sqrt{\Delta}}{6}$. Since $p^2 - 2q > 0$, one can get $v_2 < 0$. We immediately know that f(v) has only a positive real root too, and f(v) is monotone increasing in $v \in (v_1, \infty)$. Thus, (2.9) has only a positive root denoted by v_0 . Furthermore, we have the fact that $v_0 > v_1$ is true when $\Delta > 0$. Then (2.8) has unique positive root $w_0 = \sqrt{v_0}$.

Furthermore, $P_R(iw_0, \tau) = -pw_0^2$, $P_I(iw_0, \tau) = -w_0^3 + qw_0$, $Q_R(iw_0, \tau) = k$, $Q_I(iw_0, \tau) = rw_0$. Hence, we have

$$\sin \theta = \frac{-P_R(iw_0, \tau)Q_I(iw_0, \tau) + P_I(iw_0, \tau)Q_R(iw_0, \tau)}{|Q(iw_0, \tau)|^2}$$

$$= \frac{prw_0^3 + (-w_0^2 + q)kw_0}{k^2 + r^2w_0^2},$$

$$\cos \theta = -\frac{P_R(iw_0, \tau)Q_R(iw_0, \tau) + P_I(iw_0, \tau)Q_I(iw_0, \tau)}{|Q(iw_0, \tau)|^2}$$

$$= -\frac{-pkw_0^2 + (-w_0^2 + q)rw_0^2}{k^2 + r^2w_0^2}.$$
(2.12)

We denote the corresponding critical value of time delay that is satisfied τ^* ,

$$S_n(\tau^*) = \tau^* - \tau_n(\tau^*) = 0, \quad n \in N_0.$$
(2.13)

Thus,

$$\tau^* = \tau_n = \frac{\theta + 2n\pi}{w_0}, \quad n \in N_0.$$
(2.14)

From (2.7), we have

$$F'_{w}(w) = 2w \left(3w^{4} + 2\left(p^{2} - 2q\right)w^{2} + q^{2} - r^{2}\right) = 2wf'(v).$$
(2.15)

Differentiating (2.4) with respect to τ , we have

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{3\lambda^2 + 2p\lambda + q}{\lambda(-\lambda^3 - p\lambda^2 - q\lambda)} + \frac{r}{(r\lambda + k)\lambda} - \frac{\tau}{\lambda}.$$
(2.16)

Hence, a direct calculation shows that

$$\operatorname{Re}\left\{\left(\frac{d\lambda}{d\tau}\right)_{\lambda=iw_{0}}^{-1}\right\} = \operatorname{Re}\left\{\left(\frac{3\lambda^{2}+2p\lambda+q}{\lambda(-\lambda^{3}-p\lambda^{2}-q\lambda)}\right)_{\lambda=iw_{0}}\right\} + \operatorname{Re}\left\{\left(\frac{r}{(r\lambda+k)\lambda}\right)_{\lambda=iw_{0}}\right\} \\ = \frac{3w_{0}^{4}+(-4q+2p^{2})w_{0}^{2}+q^{2}}{(-w_{0}^{3}+qw_{0})^{2}+(pw_{0}^{2})^{2}} - \frac{r^{2}}{(rw_{0})^{2}+k^{2}}.$$
(2.17)

Also we have

$$\left(-w_0^3 + qw_0\right)^2 + \left(pw_0^2\right)^2 = (rw_0)^2 + k^2.$$
(2.18)

Hence,

$$\delta(\tau^{*}) = \operatorname{sign}\left\{ \left(\frac{d(\operatorname{Re} \lambda)}{d\tau} \right)_{\lambda = iw_{0}} \right\} = \operatorname{sign}\left\{ \operatorname{Re}\left(\frac{d\lambda}{d\tau} \right)_{\lambda = iw_{0}}^{-1} \right\}$$
$$= \operatorname{sign}\left\{ \frac{3w_{0}^{4} + (-4q + 2p^{2})w_{0}^{2} + q^{2} - r^{2}}{(rw_{0})^{2} + k^{2}} \right\}$$
$$= \operatorname{sign}\left\{ \frac{f'(w_{0}^{2})}{(rw_{0})^{2} + k^{2}} \right\}$$
$$= \operatorname{sign}\left\{ f'(w_{0}^{2}) \right\}.$$
(2.19)

We conclude that the sign of $(\frac{d(\mathbb{R}e\lambda)}{d\tau})_{\lambda=iw_0}$ is determined by that of $f'(w_0^2)$.

According to the above discussion, we know $f'(\nu_0) > 0$. Thus, $\delta(\tau^*) > 0$.

From Theorem 2.2 in [34], we have the following result.

Lemma 2.2 The characteristic equation (2.4) has a pair of simple and conjugate pure imaginary roots $\lambda = \pm iw_0$ at τ^* if $S_n(\tau^*) = \tau^* - \tau_n(\tau^*) = 0$ for some $n \in N_0$. Since $\delta(\tau^*) > 0$, this pair of simple conjugate pure imaginary roots crosses the imaginary axis from left to right. From Lemmas 2.1 and 2.2, we have the following lemma.

Lemma 2.3 If (H₂) holds, then (2.4) has a pair of simple imaginary roots $\pm iw_0$ when $\tau = \tau_n$, $n \in N_0$. Furthermore, when $\tau \in [0, \tau_0)$, all roots of (2.4) have negative real parts; when $\tau = \tau_0$, all roots of (2.4) except $\pm iw_0$ have negative real parts; when $\tau \in (\tau_n, \tau_{n+1}]$, (2.4) has 2(n + 1) roots with positive real parts.

Thus, from Lemmas 2.1-2.3 and Theorem 6.1 in [25], we have the following theorem.

Theorem 2.1 For system (2.1), assume that (H_1) and (H_2) hold, there exists a positive number τ_0 such that the positive equilibrium E^* is asymptotically stable when $\tau \in [0, \tau_0)$ and unstable when $\tau > \tau_0$. Furthermore, system (2.1) undergoes a Hopf bifurcation at E^* when $\tau = \tau_0$.

3 Direction and stability of the bifurcating periodic solutions

In Section 2, we have obtained the conditions under which system (2.1) undergoes Hopf bifurcation when $\tau = \tau_0$. In this section, by using the normal form and the center manifold theory that introduced by Hassard *et al.* [33], we will consider the direction of the Hopf bifurcation and the stability of bifurcating periodic solutions of system (2.1).

Set $\bar{y}_i(t) = y_i(\tau t)$, $\tau = \tau_0 + \mu$, where τ_0 is defined by (2.11), and drop the bars for convenience, then system (2.1) can be written as a FDE in $C = C([-1,0], R^3)$,

$$\dot{y}(t) = L_{\mu}(y_t) + h(\mu, y_t),$$
(3.1)

where $y(t) = (y_1(t), y_2(t), y_3(t))^T \in \mathbb{R}^3$, and $L_{\mu} : C \to \mathbb{R}^3$, $h : \mathbb{R} \times \mathbb{C} \to \mathbb{R}^3$ are, respectively, given by

$$L_{\mu}\varphi = (\tau_{0} + \mu) \begin{pmatrix} -a & k_{1} - k_{1}S^{*} - D^{*} & k_{2} - k_{2}S^{*} - D^{*} \\ 0 & -k_{1}x_{1}^{*} & -k_{2}x_{1}^{*} \\ 0 & -k_{1}x_{2}^{*} & -k_{2}x_{2}^{*} \end{pmatrix} \begin{pmatrix} \varphi_{1}(0) \\ \varphi_{2}(0) \\ \varphi_{3}(0) \end{pmatrix} + (\tau_{0} + \mu) \begin{pmatrix} 0 & 0 & 0 \\ x_{1}^{*}b_{11} & 0 & 0 \\ x_{2}^{*}b_{21} & 0 & 0 \end{pmatrix} \begin{pmatrix} \varphi_{1}(-1) \\ \varphi_{2}(-1) \\ \varphi_{3}(-1) \end{pmatrix}$$
(3.2)

and

$$h(\mu,\varphi) = (\tau_0 + \mu) \begin{pmatrix} h_1 \\ h_2 \\ h_3 \end{pmatrix}.$$
(3.3)

Here

$$\begin{split} h_1 &= \left(-x_1^* b_{12} - x_2^* b_{22} \right) \varphi_1^2(0) + (-k_1 - b_{11}) \varphi_1(0) \varphi_2(0) + (-k_2 - b_{21}) \varphi_1(0) \varphi_3(0) \\ &\quad - b_{12} \varphi_1^2(0) \varphi_2(0) - b_{22} \varphi_1^2(0) \varphi_3(0) + \left(-b_{13} x_1^* - b_{23} x_2^* \right) \varphi_1^3(0) + \cdots , \\ h_2 &= -k_1 \varphi_2^2(0) - k_2 \varphi_2(0) \varphi_3(0) + x_1^* b_{12} \varphi_1^2(-1) + b_{11} \varphi_1(-1) \varphi_2(0) + b_{12} \varphi_1^2(-1) \varphi_2(0) \\ &\quad + b_{13} x_1^* \varphi_1^3(-1) + \cdots , \end{split}$$

$$h_{3} = -k_{2}\varphi_{3}^{2}(0) - k_{1}\varphi_{2}(0)\varphi_{3}(0) + x_{2}^{*}b_{22}\varphi_{1}^{2}(-1) + b_{21}\varphi_{1}(-1)\varphi_{3}(0) + b_{22}\varphi_{1}^{2}(-1)\varphi_{3}(0) + b_{23}x_{2}^{*}\varphi_{1}^{3}(-1) + \cdots,$$

and $\varphi = (\varphi_1, \varphi_2, \varphi_3)^T \in C$.

By the Riesz representation theorem, there exists a function $\eta(\theta, \mu)$ of bounded variation for $\theta \in [-1, 0]$ such that

$$L_{\mu}\varphi = \int_{-1}^{0} d\eta(\theta,\mu)\varphi(\theta), \quad \text{for } \varphi \in C.$$
(3.4)

In fact, we can choose

$$\eta(\theta,\mu) = (\tau_0 + \mu) \begin{pmatrix} -a & k_1 - k_1 S^* - D^* & k_2 - k_2 S^* - D^* \\ 0 & -k_1 x_1^* & -k_2 x_1^* \\ 0 & -k_1 x_2^* & -k_2 x_2^* \end{pmatrix} \delta(\theta) \\ - (\tau_0 + \mu) \begin{pmatrix} 0 & 0 & 0 \\ x_1^* b_{11} & 0 & 0 \\ x_2^* b_{21} & 0 & 0 \end{pmatrix} \delta(\theta + 1),$$
(3.5)

where δ is the Dirac delta function.

For $\varphi \in C^1([-1, 0], \mathbb{R}^3)$, we define the operators A and \mathbb{R} as

$$A(\mu)\varphi = \begin{cases} \frac{d\varphi(\theta)}{d\theta}, & \theta \in [-1,0), \\ \int_{-1}^{0} d\eta(\theta,\mu)\varphi(\theta), & \theta = 0, \end{cases}$$
(3.6)

and

$$R(\mu)\varphi = \begin{cases} 0, & \theta \in [-1,0), \\ h(\mu,\varphi), & \theta = 0. \end{cases}$$
(3.7)

Then system (3.1) becomes

$$\dot{y}_t = A(\mu)y_t + R(\mu)y_t,$$
(3.8)

where $y_t(\theta) = y(t + \theta)$ for $\theta \in [-1, 0]$.

As in [35], the bifurcating periodic solutions $y(t, \mu)$ of system (3.1) are indexed by a small parameter ε . The solution $y(t, \mu(\varepsilon))$ has an amplitude $O(\varepsilon)$, a nonzero Floquet exponent $\beta(\varepsilon)$ with $\beta(0) = 0$ and a period $T(\varepsilon)$. Under the assumptions, μ , T, and β have expansions

$$\begin{cases} \mu = \mu_2 \varepsilon^2 + \mu_4 \varepsilon^4 + \cdots, \\ T = \frac{2\pi}{\omega} (1 + T_2 \varepsilon^2 + T_4 \varepsilon^4 + \cdots), \\ \beta = \beta_2 \varepsilon^2 + \beta_4 \varepsilon^4 + \cdots. \end{cases}$$
(3.9)

Here μ_2 determines the directions of the bifurcation: if $\mu_2 < 0$ (> 0), then the Hopf bifurcation is subcritical (supercritical); β_2 determines the stability of the bifurcating periodic solutions: the bifurcating periodic solutions are stable (unstable) if $\beta_2 < 0$ (> 0); and the period of the bifurcating periodic solutions is determined by T_2 : if $T_2 > 0$ (< 0), the period increases (decreases).

Next, we only need to compute the coefficients μ_2 , T_2 , β_2 in the above expansions. For $\psi \in C^1([0,1], (R^3)^*)$, we define the adjoint operator A^* of A as

$$A^*\psi = \begin{cases} \frac{-d\psi(s)}{ds}, & s \in (0,1], \\ \int_{-1}^0 d\eta^T(t,0)\psi(-t), & s = 0. \end{cases}$$
(3.10)

Meanwhile, we define a bilinear inner product as follows:

$$\left\langle \psi(s),\varphi(\theta)\right\rangle = \bar{\psi}^{T}(0)\varphi(0) - \int_{-1}^{0}\int_{\xi=0}^{\theta}\bar{\psi}^{T}(\xi-\theta)\,d\eta(\theta)\varphi(\xi)\,d\xi\,,\tag{3.11}$$

where $\eta(\theta) = \eta(\theta, 0)$.

From the discussion in Section 2, we know that $\pm iw_0\tau_0$ are eigenvalues of A(0). Thus, they are also eigenvalues of A^* , we first need to calculate the eigenvectors of A(0) and A^* corresponding to $iw_0\tau_0$ and $-iw_0\tau_0$, respectively.

Assume that $q(\theta) = (1, \alpha_1, \beta_1)^T e^{iw_0 \tau_0 \theta}$ is the eigenvector of A(0) corresponding to $iw_0 \tau_0$, then $A(0)q(\theta) = iw_0 \tau_0 q(\theta)$. By the definition of A(0) and (3.2), (3.4), and (3.5), we obtain

$$\tau_{0} \begin{pmatrix} iw_{0} + a & -k_{1} + k_{1}S^{*} + D^{*} & -k_{2} + k_{2}S^{*} + D^{*} \\ -x_{1}^{*}b_{11}e^{-iw_{0}\tau_{0}} & iw_{0} + k_{1}x_{1}^{*} & k_{2}x_{1}^{*} \\ -x_{2}^{*}b_{21}e^{-iw_{0}\tau_{0}} & k_{1}x_{2}^{*} & iw_{0} + k_{2}x_{2}^{*} \end{pmatrix} \begin{pmatrix} 1 \\ \alpha_{1} \\ \beta_{1} \end{pmatrix} = 0,$$

which yields

$$\alpha_{1} = \frac{e^{-iw_{0}\tau_{0}} [k_{2}x_{1}^{*}x_{2}^{*}(b_{11} - b_{21}) + iw_{0}x_{1}^{*}b_{11}]}{-w_{0}^{2} + iw_{0}(k_{1}x_{1}^{*} + k_{2}x_{2}^{*})},$$

$$\beta_{1} = \frac{e^{-iw_{0}\tau_{0}} [k_{1}x_{1}^{*}x_{2}^{*}(b_{21} - b_{11}) + iw_{0}x_{2}^{*}b_{21}]}{-w_{0}^{2} + iw_{0}(k_{1}x_{1}^{*} + k_{2}x_{2}^{*})}.$$
(3.12)

Similarly, set $q^*(s) = D(1, \alpha_2, \beta_2)e^{iw_0\tau_0 s}$ is the eigenvector of A^* corresponding to $-iw_0\tau_0$. It follows from the definition of A^* and (3.2), (3.4), and (3.5) that

$$\tau_0 \begin{pmatrix} iw_0 - a & x_1^* b_{11} e^{iw_0 \tau_0} & x_2^* b_{21} e^{iw_0 \tau_0} \\ k_1 - k_1 S^* - D^* & iw_0 - k_1 x_1^* & -k_1 x_2^* \\ k_2 - k_2 S^* - D^* & -k_2 x_1^* & iw_0 - k_2 x_2^* \end{pmatrix} \begin{pmatrix} 1 \\ \alpha_2 \\ \beta_2 \end{pmatrix} = 0,$$

we can easily obtain

$$\alpha_{2} = \frac{(ak_{1} - iw_{0}k_{1})e^{-iw_{0}\tau_{0}} + (D^{*} + k_{1}S^{*} - k_{1})b_{21}}{x_{1}^{*}k_{1}(b_{11} - b_{21}) + iw_{0}b_{21}},$$

$$\beta_{2} = \frac{(ak_{2} - iw_{0}k_{2})e^{-iw_{0}\tau_{0}} + (D^{*} + k_{2}S^{*} - k_{2})b_{11}}{x_{2}^{*}k_{2}(b_{21} - b_{11}) + iw_{0}b_{11}}.$$
(3.13)

From (3.11), we have

$$\begin{aligned} \left\langle q^*(s), q(\theta) \right\rangle &= \bar{D}(1, \bar{\alpha}_2, \bar{\beta}_2) (1, \alpha_1, \beta_1)^T \\ &- \int_{-1}^0 \int_{\xi=0}^{\theta} \bar{D}(1, \bar{\alpha}_2, \bar{\beta}_2) e^{-iw_0 \tau_0(\xi-\theta)} \, d\eta(\theta) (1, \alpha_1, \beta_1)^T e^{i\xi w_0 \tau_0} \, d\xi \end{aligned}$$

$$= \bar{D} \left\{ 1 + \alpha_1 \bar{\alpha}_2 + \beta_1 \bar{\beta}_2 - \int_{-1}^{0} (1, \bar{\alpha}_2, \bar{\beta}_2) \theta e^{i\theta w_0 \tau_0} d\eta(\theta) (1, \alpha_1, \beta_1)^T \right\}$$
$$= \bar{D} \left\{ 1 + \alpha_1 \bar{\alpha}_2 + \beta_1 \bar{\beta}_2 + \tau_0 (\bar{\alpha}_2 x_1^* b_{11} + \bar{\beta}_2 x_2^* b_{21}) e^{-iw_0 \tau_0} \right\}.$$

Since $\langle q^*(s), q(\theta) \rangle = 1$, we have

$$D = \frac{1}{1 + \bar{\alpha}_1 \alpha_2 + \bar{\beta}_1 \beta_2 + \tau_0 (\alpha_2 x_1^* b_{11} + \beta_2 x_2^* b_{21}) e^{i w_0 \tau_0}}.$$
(3.14)

In the following, we follow the ideas in Hassard *et al.* and use the same notations to compute the coordinates describing the center manifold C_0 at $\mu = 0$. Set y_t be the solution of (3.1) when $\mu = 0$. Define

$$z(t) = \langle q^*(s), y_t(\theta) \rangle, \qquad W(t, \theta) = y_t(\theta) - 2\operatorname{Re}\{z(t)q(\theta)\}.$$
(3.15)

On the center manifold C_0 , we have

$$W(t,\theta) = W(z(t),\bar{z}(t),\theta) = W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta)z\bar{z} + W_{02}(\theta)\frac{\bar{z}^2}{2} + \cdots,$$
(3.16)

where *z* and \bar{z} are local coordinates for center manifold C_0 in the direction of q^* and \bar{q}^* . Note that *W* is real if y_t is real. We consider only real solutions. For the solution $y_t \in C_0$ of (3.8), since $\mu = 0$, we have

$$\dot{z}(t) = iw_0 \tau_0 z + \langle \bar{q}^*(\theta), h(0, W(z, \bar{z}, \theta) + 2 \operatorname{Re}\{zq(\theta)\}) \rangle$$

= $iw_0 \tau_0 z + \bar{q}^*(0)h(0, W(z, \bar{z}, 0) + 2 \operatorname{Re}\{zq(0)\})$
$$\stackrel{\text{def}}{=} iw_0 \tau_0 z + \bar{q}^*(0)h_0(z, \bar{z}).$$
(3.17)

We rewrite the equation as

$$\dot{z}(t) = iw_0 \tau_0 z(t) + g(z, \bar{z}), \tag{3.18}$$

where

$$g(z,\bar{z}) = \bar{q}^*(0)h_0(z,\bar{z})$$

= $g_{20}\frac{z^2}{2} + g_{11}z\bar{z} + g_{02}\frac{\bar{z}^2}{2} + g_{21}\frac{z^2\bar{z}}{2} + \cdots$ (3.19)

The expressions of μ_2 , T_2 , and β_2 include the coefficients g_{20} , g_{11} , g_{02} , and g_{21} . Next, we need to compute g_{20} , g_{11} , g_{02} , and g_{21} .

By (3.15), we have $y_t(\theta) = (y_{1t}(\theta), y_{2t}(\theta), y_{3t}(\theta))^T = W(t, \theta) + zq(\theta) + \overline{zq(\theta)}$, and then

$$\begin{cases} y_{1t}(0) = W_{20}^{(1)}(0)\frac{z^2}{2} + W_{11}^{(1)}(0)z\bar{z} + W_{02}^{(1)}(0)\frac{\bar{z}^2}{2} + z + \bar{z} + O(|(z,\bar{z})|^3), \\ y_{2t}(0) = W_{20}^{(2)}(0)\frac{z^2}{2} + W_{11}^{(2)}(0)z\bar{z} + W_{02}^{(2)}(0)\frac{\bar{z}^2}{2} + \alpha_1 z + \bar{\alpha}_1 \bar{z} + O(|(z,\bar{z})|^3), \\ y_{3t}(0) = W_{20}^{(3)}(0)\frac{z^2}{2} + W_{11}^{(3)}(0)z\bar{z} + W_{02}^{(3)}(0)\frac{\bar{z}^2}{2} + \beta_1 z + \bar{\beta}_1 \bar{z} + O(|(z,\bar{z})|^3), \\ y_{1t}(-1) = W_{20}^{(1)}(-1)\frac{z^2}{2} + W_{11}^{(1)}(-1)z\bar{z} + W_{02}^{(1)}(-1)\frac{\bar{z}^2}{2} + ze^{-iw_0\tau_0} + \bar{z}e^{iw_0\tau_0} \\ + O(|(z,\bar{z})|^3). \end{cases}$$
(3.20)

From (3.19), we obtain

$$g(z,\bar{z}) = \bar{q}^{*}(0)h_{0}(z,\bar{z}) = \tau_{0}\bar{D}(1,\bar{\alpha}_{2},\bar{\beta}_{2})(h_{1},h_{2},h_{3})^{T} = \tau_{0}\bar{D}(h_{1}+\bar{\alpha}_{2}h_{2}+\bar{\beta}_{2}h_{3})$$

$$= \tau_{0}\bar{D}\Big[\Big(-x_{1}^{*}b_{12}-x_{2}^{*}b_{22}\Big)\varphi_{1}^{2}(0) + (-k_{1}-b_{11})\varphi_{1}(0)\varphi_{2}(0)$$

$$+ (-k_{2}-b_{21})\varphi_{1}(0)\varphi_{3}(0) - b_{12}\varphi_{1}^{2}(0)\varphi_{2}(0) - b_{22}\varphi_{1}^{2}(0)\varphi_{3}(0)$$

$$+ \Big(-b_{13}x_{1}^{*}-b_{23}x_{2}^{*}\Big)\varphi_{1}^{3}(0) + \dots + \bar{\alpha}_{2}\Big(-k_{1}\varphi_{2}^{2}(0) - k_{2}\varphi_{2}(0)\varphi_{3}(0)$$

$$+ x_{1}^{*}b_{12}\varphi_{1}^{2}(-1) + b_{11}\varphi_{1}(-1)\varphi_{2}(0) + b_{12}\varphi_{1}^{2}(-1)\varphi_{2}(0)$$

$$+ b_{13}x_{1}^{*}\varphi_{1}^{3}(-1) + \dots\Big) + \bar{\beta}_{2}\Big(-k_{2}\varphi_{3}^{2}(0) - k_{1}\varphi_{2}(0)\varphi_{3}(0) + x_{2}^{*}b_{22}\varphi_{1}^{2}(-1)$$

$$+ b_{21}\varphi_{1}(-1)\varphi_{3}(0) + b_{22}\varphi_{1}^{2}(-1)\varphi_{3}(0) + b_{23}x_{2}^{*}\varphi_{1}^{3}(-1) + \dots\Big)\Big].$$
(3.21)

By substituting (3.20) into (3.21) and comparing the coefficients with (3.19), we obtain

$$\begin{cases} g_{20} = 2\tau_0 \bar{D}[(-x_1^* b_{12} - x_2^* b_{22}) + \alpha_1(-k_1 - b_{11}) + \beta_1(-k_2 - b_{21}) \\ + \bar{\alpha}_2(-k_1 \alpha_1^2 - k_2 \alpha_1 \beta_1 + x_1^* b_{12} e^{-2iw_0 \tau_0} + b_{11} \alpha_1 e^{-iw_0 \tau_0}) \\ + \bar{\beta}_2(-k_2 \beta_1^2 - k_1 \alpha_1 \beta_1 + x_2^* b_{22} e^{-2iw_0 \tau_0} + b_{21} \beta_1 e^{-iw_0 \tau_0})], \\ g_{11} = \tau_0 \bar{D}[2(-x_1^* b_{12} - x_2^* b_{22}) + (-k_1 - b_{11})(\alpha_1 + \bar{\alpha}_1) + (-k_2 - b_{21})(\beta_1 + \bar{\beta}_1) \\ + \bar{\alpha}_2(-2k_1 \alpha_1 \bar{\alpha}_1 - k_2(\alpha_1 \bar{\beta}_1 + \bar{\alpha}_1 \beta_1) + 2x_1^* b_{12} + b_{11}(\alpha_1 e^{iw_0 \tau_0} + \bar{\alpha}_1 e^{-iw_0 \tau_0})) \\ + \bar{\beta}_2(-2k_2 \beta_1 \bar{\beta}_1 - k_1(\alpha_1 \bar{\beta}_1 + \bar{\alpha}_1 \beta_1) + 2x_2^* b_{22} + b_{21}(\beta_1 e^{iw_0 \tau_0} + \bar{\beta}_1 e^{-iw_0 \tau_0}))], \\ g_{02} = 2\tau_0 \bar{D}[(-x_1^* b_{12} - x_2^* b_{22}) + \bar{\alpha}_1(-k_1 - b_{11}) + \bar{\beta}_1(-k_2 - b_{21}) \\ + \bar{\alpha}_2(-k_1 \bar{\alpha}_1^2 - k_2 \bar{\alpha}_1 \bar{\beta}_1 + x_1^* b_{12} e^{2iw_0 \tau_0} + b_{11} \bar{\alpha}_1 e^{iw_0 \tau_0}) \\ + \bar{\beta}_2(-k_2 \bar{\beta}_1^2 - k_1 \bar{\alpha}_1 \bar{\beta}_1 + x_2^* b_{22} e^{2iw_0 \tau_0} + b_{21} \bar{\beta}_1 e^{iw_0 \tau_0}) \\ + \bar{\beta}_2(-k_2 \bar{\beta}_1^2 - k_1 \bar{\alpha}_1 \bar{\beta}_1 + x_2^* b_{22} e^{2iw_0 \tau_0} + b_{21} \bar{\beta}_1 e^{iw_0 \tau_0}) \\ + \bar{\beta}_2(-k_2 \bar{\beta}_1^2 - k_1 \bar{\alpha}_1 \bar{\beta}_1 + x_2^* b_{22} e^{2iw_0 \tau_0} + b_{21} \bar{\beta}_1 e^{iw_0 \tau_0}) \\ + \bar{\beta}_2(-k_2 \bar{\beta}_1^2 - k_1 \bar{\alpha}_1 \bar{\beta}_1 + x_2^* b_{22} e^{2iw_0 \tau_0} + b_{21} \bar{\beta}_1 e^{iw_0 \tau_0}) \\ + \frac{1}{2} W_{20}^{(2)}(0) + \frac{1}{2} W_{20}^{(1)}(0) \bar{\alpha}_1 + W_{11}^{(1)}(0) + (\lambda_1 - b_{21})(W_{11}^{(3)}(0) \\ + \frac{1}{2} W_{20}^{(2)}(0) + \frac{1}{2} W_{20}^{(2)}(0) \bar{\beta}_1 + W_{11}^{(2)}(0) \beta_1) + k_1^* b_{12} (2W_{11}^{(1)} - 1 e^{-iw_0 \tau_0} \\ + W_{20}^{(1)}(-1) e^{iw_0 \tau_0} + b_{12} (2\alpha_1 + e^{-2iw_0 \tau_0} \bar{\alpha}_1) + 3b_{13} x_1^* e^{-iw_0 \tau_0}) \\ + W_{20}^{(1)}(0) e^{-iw_0 \tau_0} + b_{12} (2\alpha_1 + e^{-2iw_0 \tau_0} \bar{\alpha}_1) + 3b_{13} x_1^* e^{-iw_0 \tau_0} \\ + \tilde{\beta}_2(-k_2 (\beta_1 W_{11}^{(3)}(0) + W_{20}^{(3)}(0) \bar{\beta}_1) - k_1 (\alpha_1 W_{11}^{(1)}(-1) + \frac{1}{2} \bar{\beta}_1 W_{20}^{(3)}(0) \\ + \frac{1}{2} \bar{\beta}_1 W_{20}^{(3)}(0) + \beta_1 W_{11}^{(2)}(0) + b_{21} (\beta_1 W_{11}^{(1)}(-1) + \frac{1}{2} \bar{\beta}_1 W_{20}^{(1)}(-1) \\ + \frac{1}{2} W_{20}^{(3)}(0) e^{iw_0 \tau_0} + W_{11}^{(3)}(0) e^{-iw_0 \tau_0$$

In order to determine g_{21} , we still need to compute $W_{20}(\theta)$ and $W_{11}(\theta)$. From (3.8) and (3.17), we get

$$\begin{split} \dot{W} &= \dot{y}_t - \dot{z}q - \dot{\bar{z}}\bar{q} \\ &= \begin{cases} AW - 2\operatorname{Re}\{\bar{q}^*(0)h_0(z,\bar{z})q(\theta)\}, & \theta \in [-1,0), \\ AW - 2\operatorname{Re}\{\bar{q}^*(0)h_0(z,\bar{z})q(\theta)\} + h_0(z,\bar{z}), & \theta = 0 \end{cases} \\ &\stackrel{\text{def}}{=} AW + H(z,\bar{z},\theta), \end{split}$$
(3.23)

where

$$H(z,\bar{z},\theta) = H_{20}(\theta)\frac{z^2}{2} + H_{11}(\theta)z\bar{z} + H_{02}(\theta)\frac{\bar{z}^2}{2} + H_{20}(\theta)\frac{z^3}{6} + \cdots$$
(3.24)

By comparing the coefficients (3.23), we get

$$\begin{cases} (A - 2iw_0\tau_0 I)W_{20}(\theta) = -H_{20}(\theta), \\ AW_{11}(\theta) = -H_{11}(\theta), \dots \end{cases}$$
(3.25)

From (3.23), we know that, for $\theta \in [-1, 0)$,

$$H(z,\bar{z},\theta) = -\bar{q}^{*}(0)h_{0}(z,\bar{z})q(\theta) - q^{*}(0)\bar{h}_{0}(z,\bar{z})\bar{q}(\theta)$$

$$= -g(z,\bar{z})q(\theta) - \bar{g}(z,\bar{z})\bar{q}(\theta)$$

$$= -\frac{1}{2}(g_{20}q(\theta) + \bar{g}_{02}\bar{q}(\theta))z^{2} - (g_{11}q(\theta) + \bar{g}_{11}\bar{q}(\theta))z\bar{z} + \cdots .$$
(3.26)

By comparing the coefficients with (3.24), we have

$$\begin{cases} H_{20}(\theta) = -g_{20}q(\theta) - \bar{g}_{02}\bar{q}(\theta), \\ H_{11}(\theta) = -g_{11}q(\theta) - \bar{g}_{11}\bar{q}(\theta). \end{cases}$$
(3.27)

It follows from (3.25), (3.27), and the definition of A that

$$\dot{W}_{20}(\theta) = 2iw_0\tau_0 W_{20}(\theta) + g_{20}q(\theta) + \bar{g}_{02}\bar{q}(\theta).$$

Notice $q(\theta) = (1, \alpha_1, \beta_1)^T e^{iw_0 \tau_0 \theta}$, then

$$W_{20}(\theta) = \frac{ig_{20}}{w_0\tau_0}q(0)e^{iw_0\tau_0\theta} + \frac{i\bar{g}_{02}}{3w_0\tau_0}\bar{q}(0)e^{-iw_0\tau_0\theta} + e^{2iw_0\tau_0\theta}E_1,$$
(3.28)

where $E_1 = (E_{11}, E_{12}, E_{13})^T \in \mathbb{R}^3$ is a constant vector. Similarly, from (3.25) and (3.27), it follows that

$$W_{11}(\theta) = \frac{-ig_{11}}{w_0\tau_0}q(0)e^{iw_0\tau_0\theta} + \frac{i\bar{g}_{11}}{w_0\tau_0}\bar{q}(0)e^{-iw_0\tau_0\theta} + E_2,$$
(3.29)

where $E_2 = (E_{21}, E_{22}, E_{23})^T \in \mathbb{R}^3$ is also a constant vector.

Next, we will search E_1 and E_2 . From (3.25) and the definition of A, we can obtain

$$\begin{cases} \int_{-1}^{0} d\eta(\theta) W_{20}(\theta) = 2iw_0 \tau_0 W_{20}(0) - H_{20}(0), \\ \int_{-1}^{0} d\eta(\theta) W_{11}(\theta) = -H_{11}(0), \end{cases}$$
(3.30)

where $\eta(\theta) = \eta(\theta, 0)$.

Noting that $q(\theta)$ is the eigenvector of A(0) and from (3.28) and the definition of A(0), we have

$$\int_{-1}^{0} d\eta(\theta) W_{20}(\theta) = \frac{ig_{20}}{w_0 \tau_0} \int_{-1}^{0} d\eta(\theta) q(\theta) + \frac{i\bar{g}_{02}}{3w_0 \tau_0} \int_{-1}^{0} d\eta(\theta) \bar{q}(\theta) + \int_{-1}^{0} d\eta(\theta) E_1 e^{2iw_0 \tau_0 \theta}$$
$$= \frac{ig_{20}}{w_0 \tau_0} (iw_0 \tau_0 q(0)) + \frac{i\bar{g}_{02}}{3w_0 \tau_0} (-iw_0 \tau_0 \bar{q}(0)) + \int_{-1}^{0} d\eta(\theta) E_1 e^{2iw_0 \tau_0 \theta}$$
$$= -g_{20} q(0) + \frac{\bar{g}_{02}}{3} \bar{q}(0) + \int_{-1}^{0} d\eta(\theta) E_1 e^{2iw_0 \tau_0 \theta}, \qquad (3.31)$$

and

$$2iw_0\tau_0 W_{20}(0) = -2g_{20}q(0) - \frac{2\bar{g}_{02}}{3}\bar{q}(0) + 2iw_0\tau_0 E_1.$$
(3.32)

Hence, the first equation of (3.30) becomes

$$H_{20}(0) = -g_{20}q(0) - \bar{g}_{02}\bar{q}(0) + \left(2iw_0\tau_0 - \int_{-1}^0 d\eta(\theta)e^{2iw_0\tau_0\theta}\right)E_1.$$
(3.33)

Similarly, from (3.29), it follows that

$$\int_{-1}^{0} d\eta(\theta) W_{11}(\theta) = g_{11}q(0) + \bar{g}_{11}\bar{q}(0) + \int_{-1}^{0} d\eta(\theta)E_2.$$
(3.34)

Thus, the second equation of (3.30) becomes

$$H_{11}(0) = -g_{11}q(0) - \bar{g}_{11}\bar{q}(0) - \int_{-1}^{0} d\eta(\theta)E_2.$$
(3.35)

From (3.23), it follows that

$$H_{20}(0) = -g_{20}q(0) - \bar{g}_{02}\bar{q}(0) + 2\tau_0(w_1, w_2, w_3)^T,$$
(3.36)

where

$$\begin{cases} w_1 = -x_1^* b_{12} - x_2^* b_{22} + \alpha_1 (-k_1 - b_{11}) + \beta_1 (-k_2 - b_{21}), \\ w_2 = -k_1 \alpha_1^2 - k_2 \alpha_1 \beta_1 + x_1^* b_{12} e^{-2iw_0 \tau_0} + b_{11} \alpha_1 e^{-iw_0 \tau_0}, \\ w_3 = -k_2 \beta_1^2 - k_1 \alpha_1 \beta_1 + x_2^* b_{22} e^{-2iw_0 \tau_0} + b_{21} \beta_1 e^{-iw_0 \tau_0}. \end{cases}$$

Also

$$H_{11}(0) = -g_{11}q(0) - \bar{g}_{11}\bar{q}(0) - 2\tau_0(\nu_1, \nu_2, \nu_3)^T, \qquad (3.37)$$

where

$$\begin{cases} \nu_1 = x_1^* b_{12} + x_2^* b_{22} + \operatorname{Re}\{(k_1 + b_{11})\alpha_1 + (k_2 + b_{21})\beta_1\}, \\ \nu_2 = k_1 \alpha_1 \bar{\alpha}_1 + k_2 \operatorname{Re}\{\alpha_1 \bar{\beta}_1\} - x_1^* b_{12} - b_{11} \operatorname{Re}\{\alpha_1 e^{iw_0 \tau_0}\}, \\ \nu_3 = k_2 \beta_1 \bar{\beta}_1 + k_1 \operatorname{Re}\{\alpha_1 \bar{\beta}_1\} - x_2^* b_{22} - b_{21} \operatorname{Re}\{\beta_1 e^{iw_0 \tau_0}\}. \end{cases}$$

From (3.33) and (3.36), we have

$$\left(2iw_0\tau_0 - \int_{-1}^0 d\eta(\theta)e^{2iw_0\tau_0\theta}\right)E_1 = 2\tau_0(w_1, w_2, w_3)^T,$$

which leads to

$$\begin{pmatrix} 2iw_0 + a & -k_1 + k_1S^* + D^* & -k_2 + k_2S^* + D^* \\ -x_1^*b_{11}e^{-2iw_0\tau_0} & 2iw_0 + k_1x_1^* & k_2x_1^* \\ -x_2^*b_{21}e^{-2iw_0\tau_0} & k_1x_2^* & 2iw_0 + k_2x_2^* \end{pmatrix} E_1 = 2 \begin{pmatrix} w_1 \\ w_2 \\ w_3 \end{pmatrix}.$$

Thus, we have

$$E_{1} = 2 \begin{pmatrix} 2iw_{0} + a & -k_{1} + k_{1}S^{*} + D^{*} & -k_{2} + k_{2}S^{*} + D^{*} \\ -x_{1}^{*}b_{11}e^{-2iw_{0}\tau_{0}} & 2iw_{0} + k_{1}x_{1}^{*} & k_{2}x_{1}^{*} \\ -x_{2}^{*}b_{21}e^{-2iw_{0}\tau_{0}} & k_{1}x_{2}^{*} & 2iw_{0} + k_{2}x_{2}^{*} \end{pmatrix}^{-1} \begin{pmatrix} w_{1} \\ w_{2} \\ w_{3} \end{pmatrix}.$$
 (3.38)

Similarly, from (3.35) and (3.37), we have

$$\begin{pmatrix} -a & k_1 - k_1 S^* - D^* & k_2 - k_2 S^* - D^* \\ x_1^* b_{11} & -k_1 x_1^* & -k_2 x_1^* \\ x_2^* b_{21} & -k_1 x_2^* & -k_2 x_2^* \end{pmatrix} E_2 = 2 \begin{pmatrix} v_1 \\ v_2 \\ v_3 \end{pmatrix}.$$

Then we have

$$E_{2} = 2 \begin{pmatrix} -a & k_{1} - k_{1}S^{*} - D^{*} & k_{2} - k_{2}S^{*} - D^{*} \\ x_{1}^{*}b_{11} & -k_{1}x_{1}^{*} & -k_{2}x_{1}^{*} \\ x_{2}^{*}b_{21} & -k_{1}x_{2}^{*} & -k_{2}x_{2}^{*} \end{pmatrix}^{-1} \begin{pmatrix} \nu_{1} \\ \nu_{2} \\ \nu_{3} \end{pmatrix}.$$
 (3.39)

Hence, we can determine $W_{20}(\theta)$ and $W_{11}(\theta)$ from (3.28) and (3.29). Furthermore, g_{21} can be expressed explicitly. Next, we can compute the following values:

$$\begin{cases} c_1(0) = \frac{i}{2w_0\tau_0} (g_{11}g_{20} - 2|g_{11}|^2 - \frac{1}{3}|g_{02}|^2) + \frac{g_{21}}{2}, \\ \mu_2 = \frac{-\operatorname{Re}(c_1(0))}{\operatorname{Re}(\lambda'(\tau_0))}, \\ \beta_2 = 2\operatorname{Re}(c_1(0)), \\ T_2 = -\frac{\operatorname{Im}(c_1(0)) + \mu_2\operatorname{Im}(\lambda'(\tau_0))}{w_0\tau_0}. \end{cases}$$
(3.40)

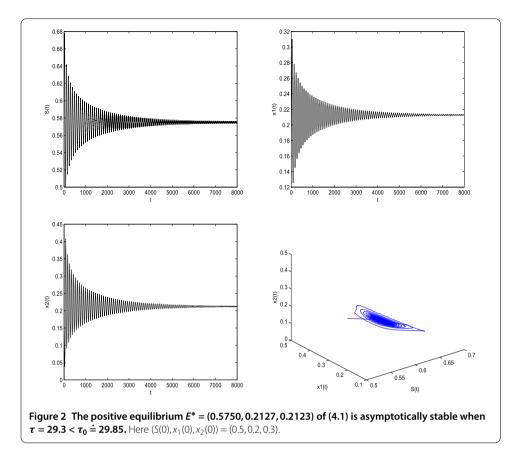
It follows that $\operatorname{Re}(\lambda'(\tau_0)) > 0$ from Lemma 2.3. Thus, $\operatorname{Re}(c_1(0))$ determines the signs of μ_2 and β_2 . We have the following theorem.

Theorem 3.1 If $\operatorname{Re}(c_1(0)) < 0$ (> 0), then the direction of the Hopf bifurcation of the system (2.1) at the positive equilibrium $E^*(S^*, x^*)$ when $\tau = \tau_0$ is supercritical (subcritical) and the bifurcating periodic solutions are stable (unstable).

4 Numerical simulation and discussion

It was shown in [17] that the coexistence of two organisms was achieved in the turbidostat. While it was also shown in [27] that the coexistence was achieved if we consider system (1.1) with the delay on the dilution rate. In this paper, system (1.1) with the time delay of digestion was investigated. By choosing the time delay as the bifurcation parameter and analyzing the characteristic equation, we obtained sufficient conditions for the local stability of the positive equilibrium and the existence of a Hopf bifurcation. The direction, stability, and the other properties of the bifurcating periodic solutions were determined by the normal form theory and the center manifold theorem. These results show that it is possible to make the two organisms in the turbidostat coexist.

We next take an example to illustrate our main results. Setting $a_1 = 0.25$, $a_2 = 0.8$, $m_1 = 3$, $m_2 = 5$, $k_1 = 2.2$, $k_2 = 1.05$, and d = 1.4, we consider the following example of sys-



tem (2.1):

$$\begin{cases} \frac{dS(t)}{dt} = (1.4 + 2.2x_1(t) + 1.05x_2(t))(1 - S(t)) - \frac{3x_1(t)S(t)}{0.25 + S(t)} - \frac{5x_2(t)S(t)}{0.8 + S(t)}, \\ \frac{dx_1(t)}{dt} = x_1(t) [\frac{3S(t-\tau)}{0.25 + S(t-\tau)} - 1.4 - 2.2x_1(t) - 1.05x_2(t)], \\ \frac{dx_2(t)}{dt} = x_2(t) [\frac{5S(t-\tau)}{0.8 + S(t-\tau)} - 1.4 - 2.2x_1(t) - 1.05x_2(t)]. \end{cases}$$
(4.1)

It is easy to verify that the conditions (H₁) and (H₂) hold, and then we can obtain the positive equilibrium $E^* = (S^*, x_1^*, x_2^*) = (0.5750, 0.2127, 0.2123)$. By a simple calculation, we have $w_0 \doteq 0.0670$, $\tau_0 \doteq 29.85$, and $(\frac{d(\operatorname{Re}\lambda)}{d\tau})_{\tau=\tau_0} = 9.8772 \times 10^{-4} > 0$. By Theorem 2.1, the positive equilibrium E^* is asymptotically stable when $\tau = 29.3$ (or 29.6) < τ_0 (see Figure 2 and Figure 3). The positive equilibrium E^* is unstable and a Hopf bifurcation occurs, *i.e.*, a bifurcating periodic solution occurs from E^* when $\tau = 29.9$ (or 31) > τ_0 (see Figure 4 and Figure 5).

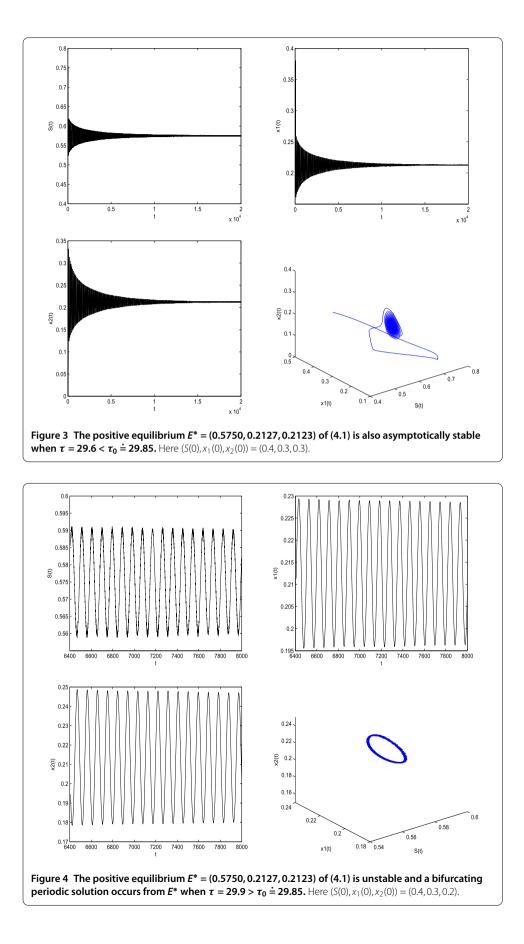
According to (3.22), we can compute

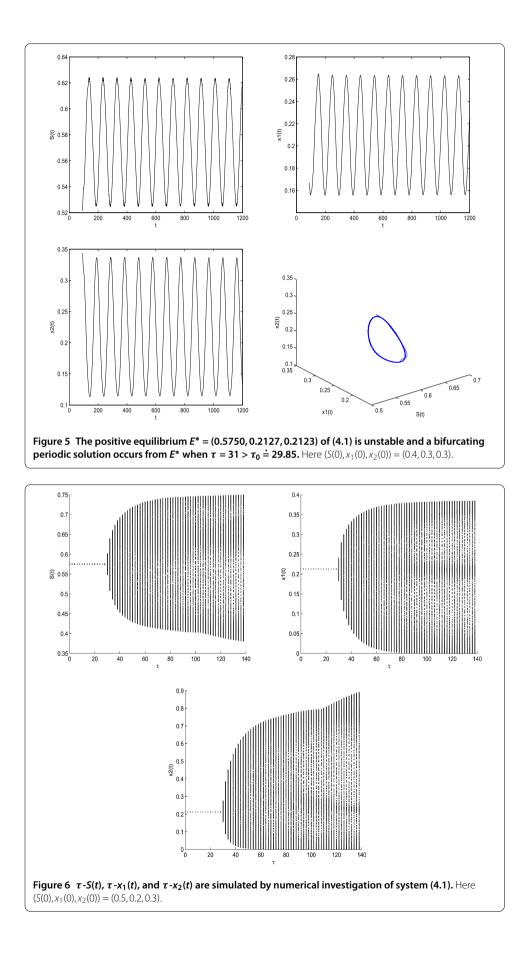
$$g_{20} \doteq -11.3349 - 0.5847i,$$

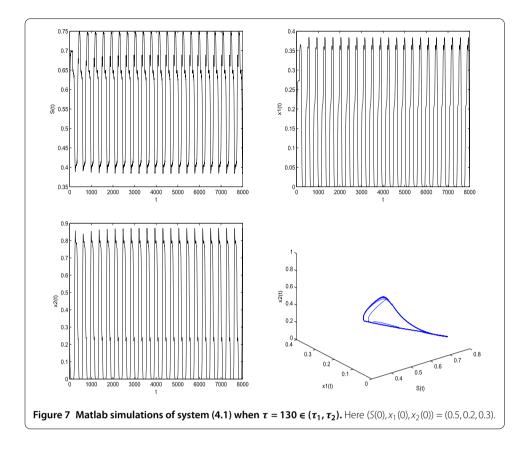
$$g_{11} \doteq 4.8196 + 1.4763i,$$

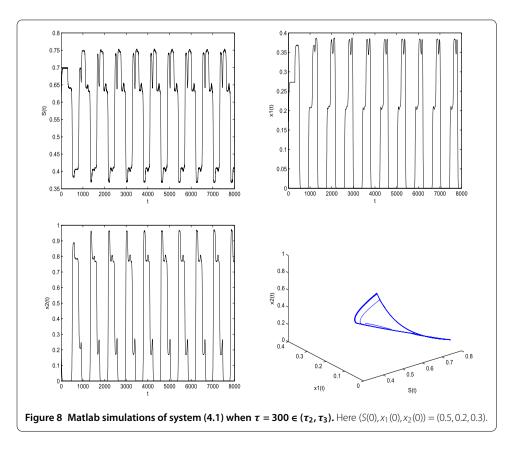
$$g_{02} \doteq 12.1356 + 8.7657i,$$

$$g_{21} \doteq -119.4956 + 102.3496i.$$









Hence, from (3.40), we can obtain

$$c_1(0) \doteq -54.8623 + 6.3751i,$$

 $\mu_2 \doteq 55544.4951 > 0,$
 $\beta_2 \doteq -109.7245 < 0,$
 $T_2 \doteq 59.2812 > 0.$

Therefore, when $\tau = 29.9$ (or 31) $\in (\tau_0, \tau_1)$, $\mu_2 > 0$, and $\beta_2 < 0$, then the Hopf bifurcation for system (4.1) is supercritical, and the stable bifurcating periodic solutions can occur from the positive equilibrium $E^*(0.5750, 0.2127, 0.2123)$. From Figure 3 and Figure 4, we can find that the dynamics of system (4.1) changes when τ is located near τ_0 . Comparing Figure 2 and Figure 3, we can see that the size of τ affects the dynamical behaviors of the turbidostat model. These are also shown by Figure 6. By Figures 7 and 8, we see that the bifurcating periodic solutions increase.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

All authors read and approved the manuscript.

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