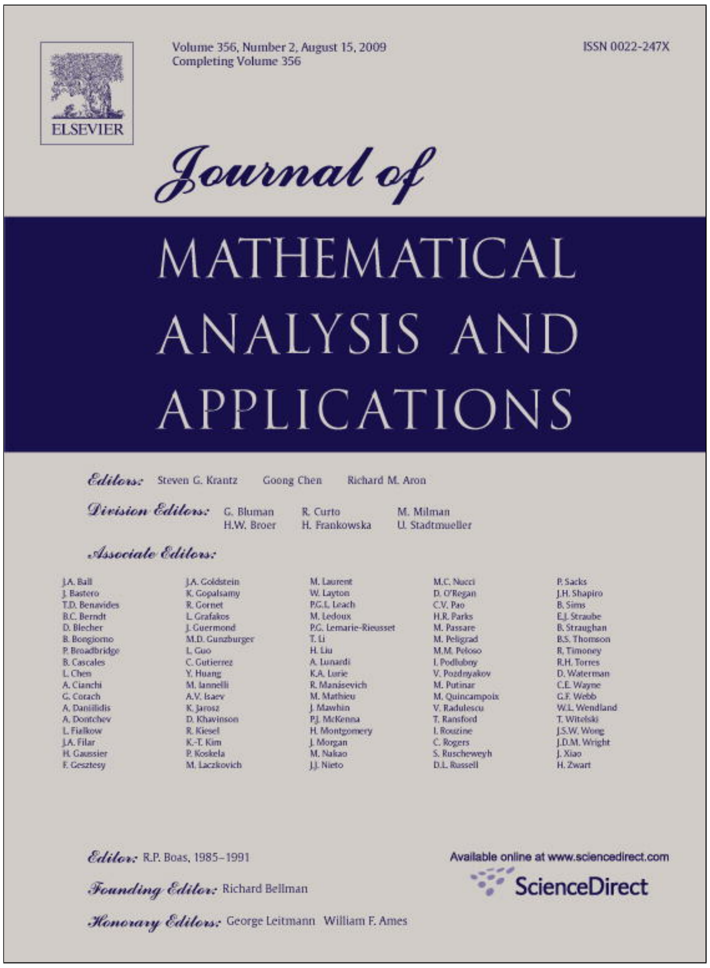
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Hopf bifurcation analysis for a model of genetic regulatory system with delay ☆

Aying Wan [a,c], Xingfu Zou [b,*]

[a] Department of Mathematics, Harbin Institute of Technology, Harbin 150001, PR China
[b] Department of Applied Mathematics, University of Western Ontario, London, Ontario, Canada N6A 5B7
[c] Department of Mathematics, Hulunbeir College, Hailar, Inner Mongolia, 021008, PR China

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ABSTRACT

This paper deals with a mathematical model that describe a genetic regulatory system. The model has a delay which affects the dynamics of the system. We investigate the stability switches when the delay varies, and show that Hopf bifurcations may occur within certain range of the model parameters. By combining the normal form method with the center manifold theorem, we are able to determine the direction of the bifurcation and the stability of the bifurcated periodic solutions. Finally, some numerical simulations are carried out to support the analytic results.

1. Introduction

In order to examine the capability of genetic regulatory systems for complex dynamic activity, Smolen [3] proposed a model in the form of two ordinary differential equations for the transcript factors (TFs). Denoting by TF–A the level of the transcriptional activators, and by TF–R the level of the protein that represses transcription by binding to TA–REs (the responsive elements of the TFs) the model is given by the following ode system:

$$\begin{cases} \dfrac{d[TF-A]}{dt} = \dfrac{k_{1,f}[TF-A]^2}{[TF-A]^2 + K_{1,d}(1+[TF-R]/K_{R,d})} - k_{1,d}[TF-A] + r_{1,bas}, \\ \dfrac{d[TF-R]}{dt} = \dfrac{k_{2,f}[TF-A]^2}{[TF-A]^2 + K_{2,d}(1+[TF-R]/K_{R,d})} - k_{2,d}[TF-R] \end{cases} \tag{1}$$

where $k_{1,f}$ is the maximal transcription rate of TF–A, $k_{2,f}$ is the maximal synthesis rate, $k_{1,d}$ and $k_{2,d}$ are degradation rates, $K_{1,d}$ and $K_{2,d}$ are the dissociation constants of TF–A dimer from TF–REs, $r_{1,bas}$ is a basal rate of synthesis of activator at negligible dimer concentration, $K_{R,d}$ is the dissociation constant of TF–R monomers from TF–REs. See [3] for detailed explanation for the model (2) and the parameters.

Using the numerical software AUTO, the authors of [3] numerically observed sustained oscillations for the model (2). They also suggested the oscillations could be generated by time delays which is ubiquitous in genetic regulatory systems. Indeed, in the same paper, the authors introduced a delay in to a scalar equation resulted from setting $TA - R = 0$ in (2), and also numerically observed oscillations, which partially confirmed their claim that time delays serves as another source

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* Corresponding author.
E-mail address: xzou@uwo.ca (X. Zou).

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to generate oscillations or complex transients. In a more recent work, Smolen et al. [4] modified (2) by incorporating a delay τ into (2) to obtain

$$\begin{cases} \dfrac{d[TF-A]}{dt} = \left(\dfrac{k_{1,f}[TF-A]^2}{[TF-A]^2 + K_{1,d}(1+[TF-R]/K_{R,d})}\right)(t-\tau) - k_{1,d}[TF-A] + r_{1,bas}, \\ \dfrac{d[TF-R]}{dt} = \left(\dfrac{k_{2,f}[TF-A]^2}{[TF-A]^2 + K_{2,d}(1+[TF-R]/K_{R,d})}\right)(t-\tau) - k_{2,d}[TF-R] \end{cases} \tag{2}$$

where τ is the time between changes in TF–A concentration and the resultant changes in the rate of formation of new TF–A due to TF–A transcription. Again, sustained oscillations were observed my numeric simulations of (2). No rigorous analysis has been given for (1) and (2), either in [3] or [4], and thus the simulations were in some sense based on lucks. On the other hand, Hopf bifurcation analysis on a system is a useful approaches that can provide much information about periodic solutions near a destabilized steady state, in terms of the system's parameters. This motivates us to perform a theoretical analysis on the modified model (2), aiming to obtain certain range for the model parameters within which Hopf bifurcations occur giving rise to some periodic solutions.

The rest of this paper is organized as below. In Section 2, we simplify the notations in (2), consider existence of a positive equilibrium and its stability, and show that Hopf bifurcation can occur for some parameter values. We use the delay τ as the bifurcation parameter, and thus, the obtained result confirms that the delay does cause oscillations in this model. In Section 3, by using the normal form theory and the center manifold argument presented in Hassard et al. [1], we derive some formulas that can determine the direction of the Hopf bifurcation and the stability of the bifurcated periodic solutions. We also perform some numeric simulations, guided by the results obtained in Section 2, to confirm the theoretical results.

In this section, we shall employ the result due to Ruan and Wei [2] to study the stability of the positive equilibrium and existence of local Hopf bifurcation.

2. Stability and Hopf bifurcation analysis

Through out this paper, we assume $K_{1,d} = K_{2,d}$. For convenience, we re-label the unknowns and parameters as below:

$$k_{1,f} = k_1, \quad k_{2,f} = k_2, \quad k_{1,d} = l_1, \quad k_{2,d} = l_2, \quad r_{1,bas} = r, \quad K_{R,d} = q, \quad K_{1,d} = K_{2,d} = p,$$
$$TF - A = x, \quad TF - R = y.$$

By the above re-labelling, system (2) is translated to

$$\begin{cases} \dot{x}(t) = \dfrac{k_1 x^2(t-\tau)}{x^2(t-\tau) + p(1 + y(t-\tau)/q)} - l_1 x(t) + r, \\ \dot{y}(t) = \dfrac{k_2 x^2(t-\tau)}{x^2(t-\tau) + p(1 + y(t-\tau)/q)} - l_2 y(t). \end{cases} \tag{3}$$

Let us firstly consider possible steady state (equilibrium) of system (3), which satisfies the following system of equations:

$$\begin{cases} \dfrac{k_1 x^2}{x^2 + p(1+y/q)} - l_1 x + r = 0, \\ \dfrac{k_2 x^2}{x^2 + p(1+y/q)} - l_2 y = 0. \end{cases} \tag{4}$$

For biological reasons, we are only interested in positive solutions of (4). It is very hard, if not impossible, to find an explicit expression for a positive solution of (4). Therefore, instead of looking for an explicit form of it, we shall prove the existence in an implicit way by some analysis.

Dividing the two quotient terms in (4), one can express y in terms of x by the following simpler formula:

$$y = \frac{k_2}{k_1 l_2}(l_1 x - r). \tag{5}$$

Substituting the above expression into the first equation of system (4) gives the following equation for x:

$$\frac{k_1 x^2}{x^2 + p(1 + \frac{k_2}{k_1 l_2 q}(l_1 x - r))} = l_1 x - r \tag{6}$$

which further leads to

$$x^3 + Ux^2 + Vx + R = 0 \tag{7}$$

where

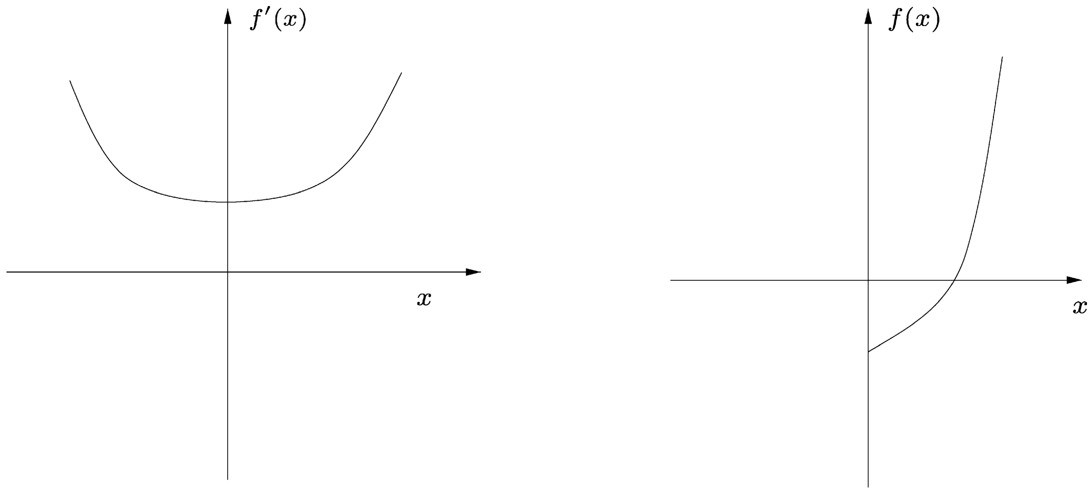

Fig. 1. $f(x)=0$ has a unique positive root under (A0)(i).

$$U=\frac{pl_1k_2}{k_1l_2q}-\frac{r+k_1}{l_1},\qquad V=p\left(1-\frac{2k_2r}{k_1l_2q}\right),\qquad R=\frac{-rp}{l_1}\left(1-\frac{k_2r}{k_1l_2q}\right). \tag{8}$$

The following lemma confirms establishes the existence of a unique positive root of (7) under some conditions.

Lemma 2.1. *System* (3) *has a unique positive equilibrium* $(\bar{x},\bar{y})$ *under the following assumption*:

(A0) $R<0$ *and one of the conditions holds*:
(i) $\Delta:=U^2-3V\leqslant 0$;
(ii) $\Delta:=U^2-3V>0$ *and* $-U-\sqrt{\Delta}<0$;
(iii) $\Delta:=U^2-3V>0$, $-U-\sqrt{\Delta}>0$ *and* $f(\frac{-U-\sqrt{\Delta}}{3})<0$.

Proof. Let $f(x)=x^3+Ux^2+Vx+R$. Since $f(0)=R<0$ and $f(+\infty)=+\infty$, by the intermediate value theorem, $f(x)=0$ has at least one positive root. Next we show that this root is unique under (A0), under either of the three conditions in (A0).

Notice that $f'(x)=3x^2+2Ux+V$. If (i) holds, then $f'(x)\geqslant \min f'(x)=(3V-U^2)/3\geqslant 0$ for all $x>0$, implying that the positive root is unique, as is demonstrated in Fig. 1. If (ii) holds, then $f'(x)$ has two zeros

$$x_1=\frac{-U-\sqrt{\Delta}}{3},\qquad x_1=\frac{-U+\sqrt{\Delta}}{3}$$

with $x_1<0$, meaning that the cubic function $f(x)$ attains its unique local maximum at left-hand side of the vertical axis. This together with $f(0)=R<0$ implies $f(x)$ only has one positive root (see Fig. 2). For case (iii), $f'(x)$ also has the two zeros but now with both being positive. Thus, the cubic function $f(x)$ attains its local maximum at $x_1>0$ with the value $f(\frac{-U-\sqrt{\Delta}}{3})<0$. Thus, $f(x)=0$ also only has one positive root, as is shown in Fig. 3.

We have seen that under (A0), $f(x)=0$ has a unique positive real root, denoting it by $\bar{x}$. Plugging $\bar{x}$ back either to (5) or to the first equation in (4) will give a value for y. But since there is no explicit formula for $\bar{x}$, one cannot confirm that this value of y is positive from either of these two equations. Thus, we need to seek alternative way to show this. Indeed, plugging $\bar{x}$ into the second equation in (4) and rewriting the resulting equation as

$$y^2+\frac{q}{p}\left(\bar{x}^2+p\right)y-\frac{k_2q}{l_2p}\bar{x}^2=0, \tag{9}$$

one immediately sees that this quadratic equation has two real roots, one is positive and the other is negative. Denoting the positive one by $\bar{y}$. This shows that under the assumption (A0), system (3) has a unique positive equilibrium $(\bar{x},\bar{y})$, completing the proof. □

In order to determine the stability of $(\bar{x},\bar{y})$, we linearize (3) at $(\bar{x},\bar{y})$ to obtain

$$\begin{cases}\dot{x}(t)=-l_1x(t)+k_1Mx(t-\tau)+k_1Ny(t-\tau),\\ \dot{y}(t)=-l_2y(t)+k_2Mx(t-\tau)+k_2Ny(t-\tau),\end{cases} \tag{10}$$

where

$$M=\frac{2p\bar{x}(1+\bar{y}/q)}{[\bar{x}^2+p(1+\bar{y}/q)]^2},\qquad N=\frac{(-p/q)\bar{x}^2}{[\bar{x}^2+p(1+\bar{y}/q)]^2}.$$

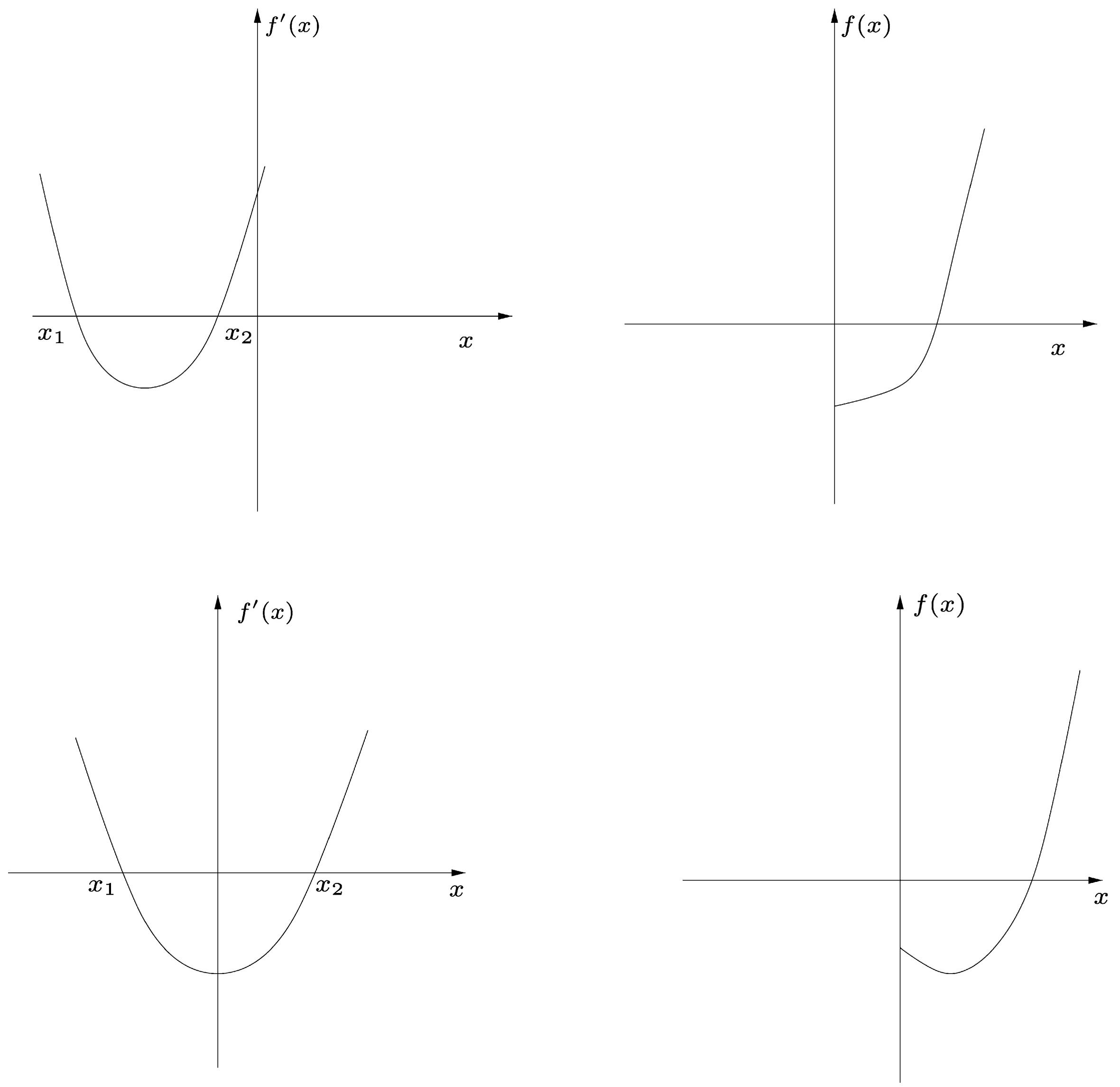

Fig. 2. $f(x) = 0$ has a unique positive root under (A0)(ii).

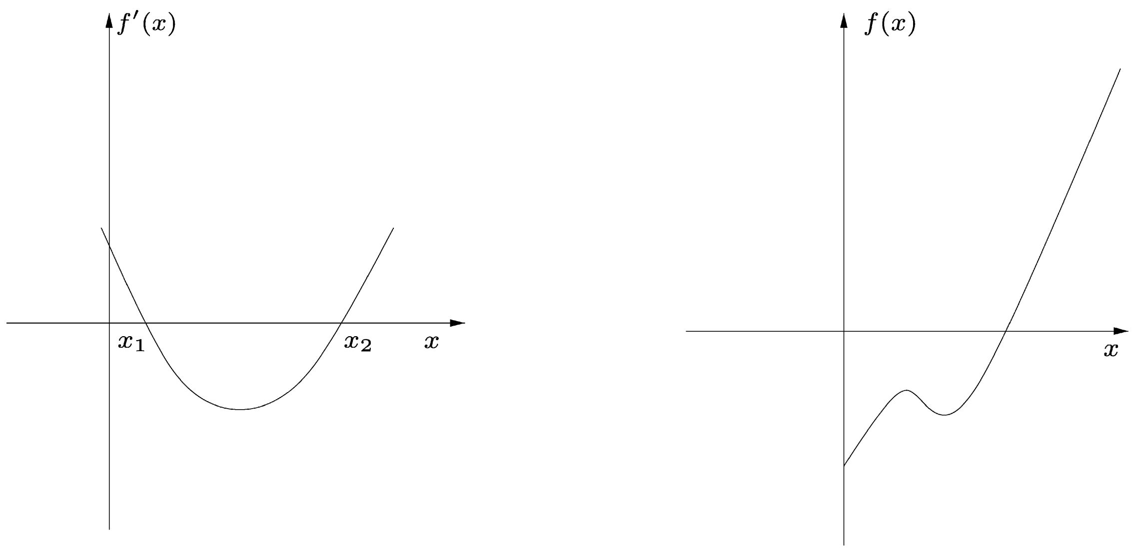

Fig. 3. $f(x) = 0$ has a unique positive root under (A0)(iii).

The characteristic equation of (10) is

$$\lambda^2 + \left(l_1 + l_2 - k_2 N e^{-\lambda\tau} - k_1 M e^{-\lambda\tau}\right)\lambda + l_1 l_2 - l_1 k_2 N e^{-\lambda\tau} - l_2 k_1 M e^{-\lambda\tau} = 0. \tag{11}$$

When $\tau = 0$, Eq. (11) becomes

$$\lambda^2 + \beta_1 \lambda + \beta_0 = 0, \tag{12}$$

where

$$\beta_0 = l_1 l_2 - l_1 k_2 N - l_2 k_1 M \quad \text{and} \quad \beta_1 = l_1 + l_2 - k_2 N - k_1 M.$$

The signs of β_0 and β_1 play an important role in determine the locations of the roots of (12). For β_0, we can show that $\beta_0 > 0$ as below. Consider the function

$$H(x) = \frac{k_1 x^2}{x^2 + p(1 + \frac{k_2}{k_1 l_2 q}(l_1 x - r))} - l_1 x + r.$$

Obviously, $H(x) = 0$ is equivalent to $f(x) = 0$, and hence $H(x) = 0$ also has the unique positive root $\bar{x}$. This, together with the fact that $H(0) = r > 0$ and $H(\infty) = -\infty$ implies that $H'(\bar{x}) < 0$. Now

$$H'(x) = \frac{\frac{p k_2 l_1}{l_2 q} x^2 + 2 k_1 p (1 - \frac{k_2 r}{k_1 l_2 q}) x}{[x^2 + p(1 + \frac{k_2}{k_1 l_2 q}(l_1 x - r))]^2} - l_1.$$

Substituting $\bar{x}$ into the above equation and noting that $\bar{y} = \frac{k_2}{k_1 l_2}(l_1 \bar{x} - r)$, we easily see that $H'(\bar{x}) < 0$ reduces to $\beta_0 > 0$.

The following lemma follows directly from the fact that $\beta_0 > 0$.

Lemma 2.2. *The following hold*:

(I) *If $\beta_1 > 0$, then all roots of* (12) *have negative real parts.*
(II) *If $\beta_1 < 0$, then all roots of* (12) *have positive real parts.*
(III) *If $\beta_1 = 0$,* (12) *has a pair of purely imaginary roots $\pm i\sqrt{\beta_0}$.*

Note that N and M depend on k_1 and k_2 via $\bar{x}$ and $\bar{y}$. Thus, the sign of β_1, in general, cannot be explicitly determined. The following numeric example shows that both cases of (I) and (II) are possible.

Example 1. Consider the same parameter values as used in Paul Smolen [3]:

$$k_2 = 0.3, \qquad l_1 = 1, \qquad l_2 = 0.2, \qquad p = 10, \qquad q = 0.2, \qquad r = 0.4.$$

When $\tau = 0$, the systems (3) becomes the following ordinary differential equations:

$$\begin{cases} \dot{x}(t) = \dfrac{k_1 x^2(t)}{x^2(t) + 10(1 + 5y(t))} - x(t) + 0.4, \\ \dot{y}(t) = \dfrac{0.3 x^2(t)}{x^2(t) + 10(1 + 5y(t))} - 0.3 y(t). \end{cases} \tag{13}$$

By numeric calculations, we can obtain $\beta_1 = l_1 + l_2 - k_2 N - k_1 M = 0$ at $k_1 = 9.9211$ or 10.8337. For $k_1 = 9.9211$, the equilibrium of system (13) is $(\bar{x}, \bar{y}) = (1.3638, 0.1457)$; for $k_1 = 10.8337$, the equilibrium of system (10) is $(\bar{x}, \bar{y}) = (3.1987, 0.3875)$. When $k_1 < 9.9211$ or $k_1 > 10.8337$, we have $\beta_1 > 0$; when $9.9211 < k_1 < 10.8337$, we have $\beta_1 < 0$. The conclusions (I)–(III) in Lemma 2.2 shows that Hopf bifurcation occurs when k_1 either increase to pass 9.9211 or decrease to pass 10.8337. These results are summarized in the following theorem.

Theorem 2.3. *Consider system* (13):

(i) *The unique positive equilibrium $(\bar{x}, \bar{y})$ is asymptotically stable when $k_1 < 9.9211$ or $k_1 > 10.8337$.*
(ii) *The equilibrium $(\bar{x}, \bar{y})$ is unstable when $9.9211 < k_1 < 10.8337$.*
(iii) *System* (13) *undergoes a Hopf bifurcation at $(\bar{x}, \bar{y})$ when k_1 increase to pass the value 9.9211 or decrease to pass the value 10.8337.*

The above results are numerically confirmed, as illustrated in Figs. 4–6.

In the rest of the paper we assume that $\beta_1 > 0$ holds, hence $(\bar{x}, \bar{y})$ is stable when $\tau = 0$. We will explore how the time delay τ affects the dynamics of (3). It is well known (see, e.g. [2]) that a root $\lambda = \lambda(\tau)$ of (11) depends on τ continuously; if it will ever leave the left half plane and enter the right half plane on the complex plane as τ increases, it must cross the

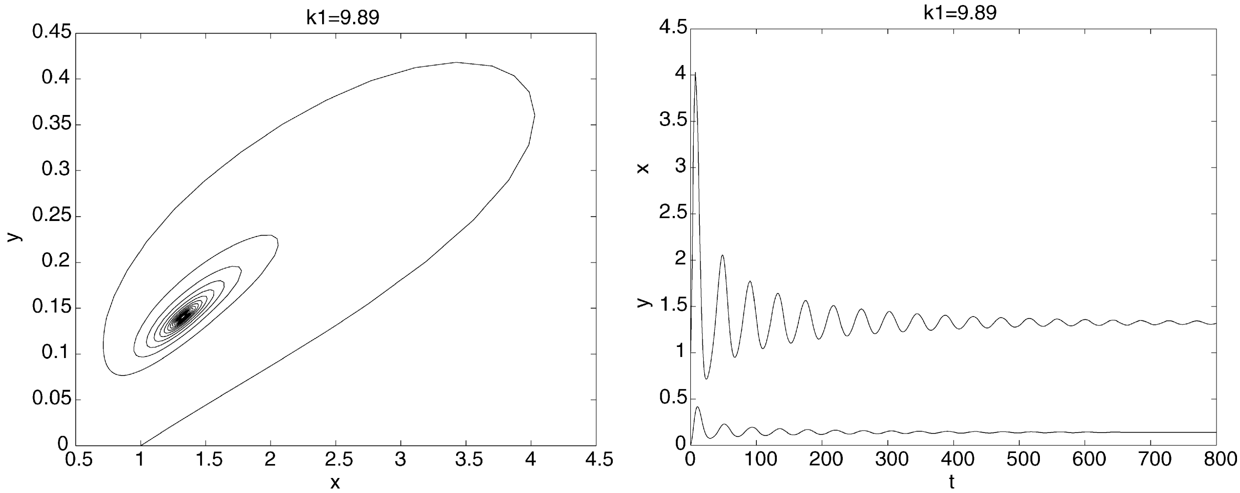

Fig. 4. Phase plots for system (13) with $k_1 = 9.89$, $k_2 = 0.3$, $l_1 = 1$, $l_2 = 0.2$, $p = 10$, $q = 0.2$, $r = 0.4$.

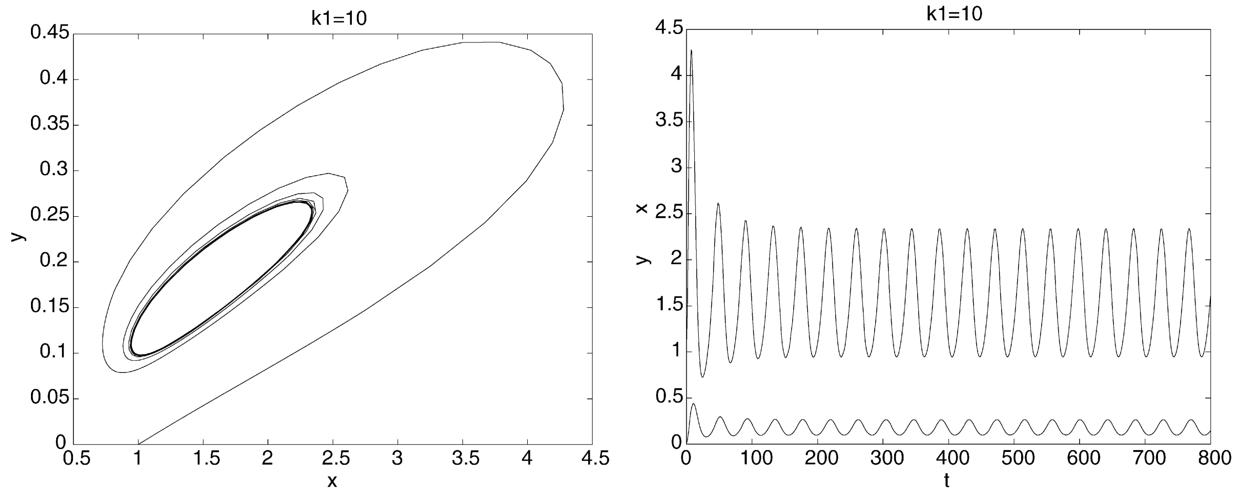

Fig. 5. Phase plots for system (13) with $k_1 = 10$, $k_2 = 0.3$, $l_1 = 1$, $l_2 = 0.2$, $p = 10$, $q = 0.2$, $r = 0.4$.

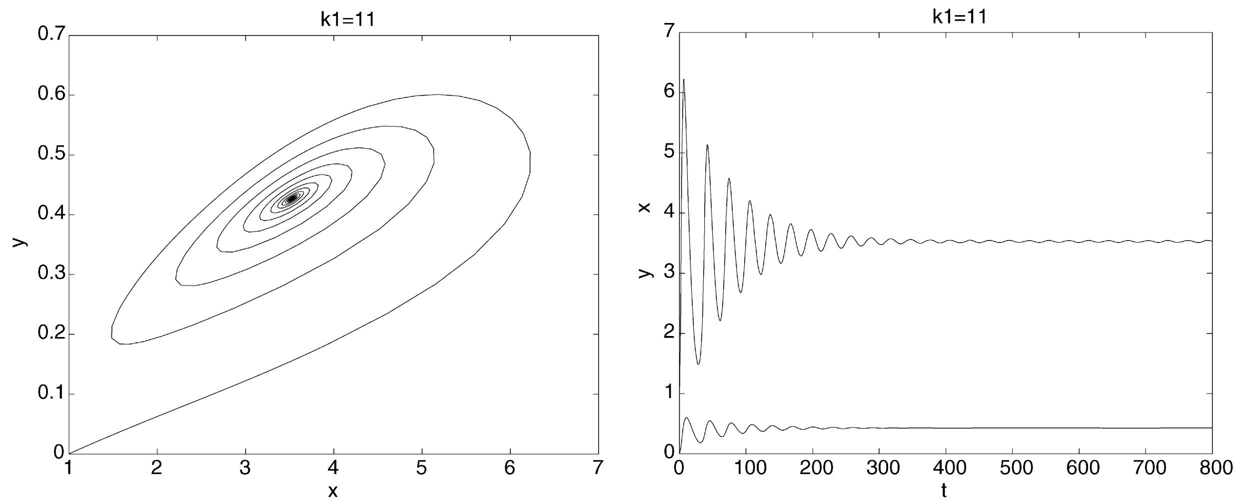

Fig. 6. Phase plots for system (13) with $k_1 = 11$, $k_2 = 0.3$, $l_1 = 1$, $l_2 = 0.2$, $p = 10$, $q = 0.2$, $r = 0.4$.

purely imaginary axis, and this is exactly the situation where Hopf bifurcation occurs. So, we need to explore the possibility of purely imaginary roots of (11) as τ increases. For convenience of notations, we denote

$$A = l_1^2 + l_2^2 - (k_2 N + k_1 M)^2, \qquad B = (l_1 l_2)^2 - (l_1 k_2 N + l_2 k_1 M)^2.$$

Lemma 2.4. *Assume that*

(A1) $A < 0$ *and* $A^2 - 4B > 0$

hold. Then Eq. (11) *has a pair of purely imaginary roots* $\pm i\omega_j$, $j = 1, 2$, *at* $\tau = \tau_n^j$, $j = 1, 2$ *and* $n = 0, 1, 2, \ldots,$ *where*

$$\tau_0^j = \begin{cases} -\frac{1}{\omega_j}\arctan\delta, & \text{if } \delta < 0,\\ \frac{1}{\omega_j}(\pi - \arctan\delta), & \text{if } \delta > 0, \end{cases}$$

$$\tau_n^j = \tau_0^j + \frac{n\pi}{\omega_j}, \quad n = 1, 2, \ldots, \ j = 1, 2,$$

$$\omega_1 = \sqrt{\frac{-A - \sqrt{A^2 - 4B}}{2}}, \qquad \omega_2 = \sqrt{\frac{-A + \sqrt{A^2 - 4B}}{2}},$$

$$\delta = \frac{k_2 N((\omega_j)^2 + l_1^2) + k_1 M((\omega_j)^2 + l_2^2)}{k_2 N l_2((\omega_j)^2 + l_1^2) + k_1 M l_1((\omega_j)^2 + l_2^2)}. \tag{14}$$

Proof. Substituting $\lambda = i\omega$ $(\omega > 0)$ into Eq. (11) yields

$$-\omega^2 + \big[l_1 + l_2 - (k_2 N + k_1 M)(\cos\omega\tau - i\sin\omega\tau)\big]i\omega + l_1 l_2 - (l_1 k_2 N + l_2 k_1 M)(\cos\omega\tau - i\sin\omega\tau) = 0.$$

Separating the real and imaginary parts leads to

$$\begin{aligned} &\omega(k_2 N + k_1 M)\cos\omega\tau - (l_1 k_2 N + l_2 k_1 M)\sin\omega\tau = \omega(l_1 + l_2),\\ &\omega(k_2 N + k_1 M)\sin\omega\tau + (l_1 k_2 N + l_2 k_1 M)\cos\omega\tau = -\omega^2 + l_1 l_2. \end{aligned} \tag{15}$$

Squaring and adding both equations of (12) results in the equation,

$$\omega^4 + A\omega^2 + B = 0. \tag{16}$$

Obviously, if (16) has no positive solution for ω^2, then (11) cannot have purely imaginary roots. Now, under the assumption (A1), (16) has two positive solutions for ω:

$$\omega_1 = \sqrt{\frac{-A - \sqrt{A^2 - 4B}}{2}}, \qquad \omega_2 = \sqrt{\frac{-A + \sqrt{A^2 - 4B}}{2}}$$

with $\omega_1 < \omega_2$. Let

$$\tau_0^j = \begin{cases} -\frac{1}{\omega_j}\arctan\delta, & \text{if } \delta < 0,\\ \frac{1}{\omega_j}(\pi - \arctan\delta), & \text{if } \delta > 0, \end{cases}$$

and define

$$\tau_n^j = \tau_0^j + \frac{n\pi}{\omega_j}, \quad n = 1, 2, \ldots, \ j = 1, 2,$$

then (τ_n^j, ω_j) solves Eq. (15). This means that $i\omega_j$ is a root of Eq. (11) when $\tau = \tau_n^j$ $(n = 0, 1, 2, \ldots, \ j = 1, 2)$. This completes the proof. □

The following lemma verifies the transversality condition.

Lemma 2.5. *Let* $\lambda(\tau) = \alpha(\tau) + i\omega(\tau)$ *be the root of Eq.* (11) *satisfying* $\alpha(\tau_n^j) = 0$ *and* $\omega(\tau_n^j) = \omega_j$. *If*

(A2) $\frac{1}{(\omega_j)^2 + l_2^2} + \frac{1}{(\omega_j)^2 + l_1^2} > \frac{(k_1 M + k_2 N)^2}{(k_1 M + k_2 N)^2(\omega_j)^2 + (k_1 l_2 M + k_2 l_1 N)^2}$

holds, then

$$\alpha'(\tau_n^j) > 0.$$

Proof. Substituting $\lambda(\tau)$ into (11) and differentiating both sides with respect to τ gives

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = -\frac{1}{\lambda(\lambda+l_2)} - \frac{1}{\lambda(\lambda+l_1)} + \frac{k_1M+k_2N}{\lambda[\lambda(k_1M+k_2N)+(k_2l_1N+k_1l_2M)]} - \frac{\tau}{\lambda}.$$

At $\tau = \tau_n^j$, $\lambda = i\omega_j$ and hence,

$$\left(\frac{d\lambda}{d\tau}\right)^{-1}\bigg|_{\lambda=i\omega_j,\tau=\tau_n^j} = \frac{1}{(\omega_j)^2 - i\omega_j l_2} + \frac{1}{(\omega_j)^2 - i\omega_j l_1} + \frac{k_1M+k_2N}{(-\omega_j)^2(k_1M+k_2N)+i\omega_j(k_2l_1N+k_1l_2M)} - \frac{\tau_n^j}{i\omega_j}.$$

Taking out the real part, one then obtains

$$\left(\alpha'(\tau_n^j)\right)^{-1} = \frac{1}{(\omega_j)^2+l_2^2} + \frac{1}{(\omega_j)^2+l_1^2} - \frac{(k_1M+k_2N)^2}{(k_1M+k_2N)^2(\omega_j)^2+(k_1l_2M+k_2l_1N)^2}$$

which is positive by (A2). This completes the proof. □

Summarizing the above analysis and applying the Hopf bifurcation theorem for functional differential equations (see, e.g., [1]), we obtain the following theorem.

Theorem 2.6. *Assume that $\beta_1 > 0$, and (A1) and (A2) hold. Then $(\bar{x}, \bar{y})$ is asymptotically stable for $\tau \in [0, \tau_0)$ with $\tau_0 = \min\{\tau_0^1, \tau_0^2\}$, and it becomes unstable for $\tau > \tau_0$. System (3) undergoes Hopf bifurcations around $(\bar{x}, \bar{y})$ as τ increases to pass $\tau = \tau_n^j$ for $j = 1, 2$ and $n = 0, 1, 2, \ldots$, where τ_n^j, $j = 1, 2$ and $n = 0, 1, 2, \ldots$, are defined by (14).*

Although there is a sequence of critical values for the bifurcation parameter τ, only at the smallest one $\tau_0 = \min\{\tau_0^1, \tau_0^2\}$ it is possible for the bifurcated periodic solution to be stable and hence numerically observable. In the next section, we will investigate the direction of the Hopf bifurcation and the stability of the bifurcated periodic solution near the first critical value τ_0.

3. Direction and stability of the Hopf bifurcation

In this section we shall study the direction of the Hopf bifurcation and the stability of the bifurcated periodic solutions near τ_0, by using the algorithm developed in Hassard et al. [1] which is based on the normal form and center manifold theory.

Let $\tau = \tau_0 + \mu$. Then $\mu = 0$ is the Hopf bifurcation value for system (3) in terms of the new bifurcation parameter μ. Let $X(t) = x(t) - \bar{x}$, $Y(t) = y(t) - \bar{y}$, $t = s\tau$ and still denote $X(t), Y(t)$ by $x(t), y(t)$, $s\tau$ by t. System (3) can be written as

$$\begin{aligned}
\dot{x}(t) &= \tau\left[\frac{k_1(x(t-1)+\bar{x})^2}{(x(t-1)+\bar{x})^2 + p(1+(y(t-1)+\bar{y})/q)} - l_1\big(x(t)+\bar{x}\big) + r\right],\\
\dot{y}(t) &= \tau\left[\frac{k_2(x(t-1)+\bar{x})^2}{(x(t-1)+\bar{x})^2 + p(1+(y(t-1)-\bar{y})/q)} - l_2\big(y(t)+\bar{y}\big)\right].
\end{aligned} \tag{17}$$

Choose the phase space as $C = C([-1, 0], R^2)$. For any $\phi \in C$ let

$$\begin{aligned}
L_\mu(\phi) &= (\tau_0+\mu)\begin{bmatrix} -l_1 & 0 \\ 0 & -l_2 \end{bmatrix}\begin{bmatrix} \phi_1(0) \\ \phi_2(0) \end{bmatrix} + (\tau_0+\mu)\begin{bmatrix} k_1M & k_1N \\ k_2M & k_2N \end{bmatrix}\begin{bmatrix} \phi_1(-1) \\ \phi_2(-1) \end{bmatrix}\\
&\overset{\text{def}}{=} (\tau_0+\mu)B\phi(0) + (\tau_0+\mu)C\phi(-1)
\end{aligned}$$

and

$$F(\mu,\phi) = (\tau_0+\mu)\begin{bmatrix} \frac{k_1}{2}(M_1x^2(t-1) + 2Q_1x(t-1)y(t-1) + N_1y^2(t-1)) + \frac{k_1}{6}(M_2x^3(t-1) \\ \quad + 3Q_2x^2(t-1)y(t-1) + 3R_2x(t-1)y^2(t-1) + N_2y^3(t-1)) + O(x^4(t-1), y^4(t-1)) \\ \frac{k_2}{2}(M_1x^2(t-1) + 2Q_1x(t-1)y(t-1) + N_1y^2(t-1)) + \frac{k_2}{6}(M_2x^3(t-1) \\ \quad + 3Q_2x^2(t-1)y(t-1) + 3R_2x(t-1)y^2(t-1) + N_2y^3(t-1)) + O(x^4(t-1), y^4(t-1)) \end{bmatrix}$$

where

$$M_1 = \frac{2}{\bar{x}^2 + \frac{p(1+\bar{y})}{q}} - \frac{10\bar{x}^2}{[\bar{x}^2 + \frac{p(1+\bar{y})}{q}]^2} + \frac{8\bar{x}^4}{[\bar{x}^2 + \frac{p(1+\bar{y})}{q}]^3},$$

$$N_1 = \frac{2\bar{x}^2 p^2}{[\bar{x}^2 + \frac{p(1+\bar{y})}{q}]^3 q^2},$$

$$Q_1 = -\frac{2\bar{x}p}{[\bar{x}^2 + \frac{p(1+\bar{y})}{q}]^2 q} + \frac{4\bar{x}^3 p}{[\bar{x}^2 + \frac{p(1+\bar{y})}{q}]^3 q},$$

$$M_2 = -\frac{24\bar{x}}{[\bar{x}^2 + \frac{p(1+\bar{y})}{q}]^2} + \frac{72\bar{x}^3}{[\bar{x}^2 + \frac{p(1+\bar{y})}{q}]^3} - \frac{48\bar{x}^5}{[\bar{x}^2 + \frac{p(1+\bar{y})}{q}]^4},$$

$$N_2 = -\frac{6\bar{x}^2 p^3}{[\bar{x}^2 + \frac{p(1+\bar{y})}{q}]^4 q^3},$$

$$R_2 = \frac{4\bar{x}p^2}{[\bar{x}^2 + \frac{p(1+\bar{y})}{q}]^3 q^2} - \frac{12\bar{x}^3 p^2}{[\bar{x}^2 + \frac{p(1+\bar{y})}{q}]^4 q^2},$$

$$Q_2 = -\frac{2p}{[\bar{x}^2 + \frac{p(1+\bar{y})}{q}]^2 q} + \frac{20\bar{x}^2 p}{[\bar{x}^2 + \frac{p(1+\bar{y})}{q}]^3 q} - \frac{24\bar{x}^4 p}{[\bar{x}^2 + \frac{p(1+\bar{y})}{q}]^4 q}.$$

By the Riesz representation theorem, there exists a matrix whose components are bounded variation function $\eta(\theta,\mu) : [-1,0] \to R^{2^2}$ in $\theta \in [-1,0]$ such that

$$L_\mu \phi = \int_{-1}^{0} d\eta(\theta,\mu)\phi(\theta) \quad \text{for } \phi \in C. \tag{18}$$

In fact, if we choose

$$\eta(\theta,\mu) = \begin{cases} (\tau_0+\mu)B, & \theta = 0, \\ 0, & \theta \in (-1,0), \\ -(\tau_0+\mu)C, & \theta = -1, \end{cases}$$

then (18) is realized.

For $\phi \in C^1([-1,0], R^2)$, define

$$A(\mu)\phi = \begin{cases} d\phi(\theta)/d\theta, & \theta \in [-1,0), \\ \int_{-1}^{0} d\eta(t,\mu)\phi(t), & \theta = 0, \end{cases} \qquad R(\mu)\phi = \begin{cases} 0, & \theta \in [-1,0), \\ F(\mu,\phi), & \theta = 0. \end{cases}$$

Then system (17) can be rewritten in the following form:

$$\dot{u}_t = A(\mu)u_t + R(\mu)u_t, \tag{19}$$

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

For $\psi \in C^1([0,1], (C^2)^*)$, define

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

For $\phi \in C([-1,0], C^2)$ and $\psi \in C([0,1], (C^2)^*)$, define

$$\langle \psi, \phi \rangle = \bar{\psi}(0)\phi(0) - \int_{-1}^{0}\int_{0}^{\theta} \bar{\psi}(\xi - \theta)\, d\eta(\theta)\phi(\xi)\, d\xi$$

where $\eta(\theta) = \eta(\theta,0)$. Then A^* and $A(0)$ are adjoint operators. Let $q(\theta)$ and $q^*(s)$ are eigenvector of A and A^* corresponding to $i\tau_0\omega_0$ and $-i\tau_0\omega_0$, respectively. By direct computation, we obtain that

$$q(\theta) = (1,E)^T e^{i\omega_0\tau_0\theta}, \qquad q^*(s) = \frac{1}{\bar{D}}(1,F)e^{i\omega_0\tau_0 s},$$

where

$$E=\frac{i\omega_0\tau_0+l_1-k_1Me^{-i\omega_0\tau_0}}{k_1Ne^{-i\omega_0\tau_0}},\qquad F=\frac{k_1Ne^{i\omega_0\tau_0}}{-i\omega_0\tau_0+l_2-k_2Ne^{i\omega_0\tau_0}},$$
$$D=1+E\bar F+(k_1M+\bar Fk_2M+Ek_1N+E\bar Fk_2N)\tau_0e^{-i\omega_0\tau_0}.$$

Moreover, $\langle q^*(s),q(\theta)\rangle=1$ and $\langle q^*(s),\bar q(\theta)\rangle=0$.

Using the same notation as in Hassard et al. [1], we first compute the coordinates for describing the center manifold $\mathcal{L}_0$ at $\mu=0$. Let u_t be the solution of Eq. (17) when $\mu=0$. Define $z(t)=\langle q^*,u_t\rangle$ and $W(t,\theta)=u_t(\theta)-2\,\mathrm{Re}\{z(t)q(\theta)\}$. On the center manifold $\mathcal{L}_0$, we have $W(t,\theta)=w(z,\bar z,\theta)$, where

$$W(z,\bar z,\theta)=W_{20}(\theta)\frac{z^2}{2}+W_{11}(\theta)z\bar z+W_{02}(\theta)\frac{\bar z^2}{2}+W_{30}(\theta)\frac{z^3}{6}+\cdots,$$

z and $\bar z$ are local coordinates for center manifold $\mathcal{L}_0$ in the direction of q^* and $\bar q^*$. Noticing that W is real, if u_t is real, we only need to consider real solutions. For a solution $u_t\in\mathcal{L}_0$ of (17), since $\mu=0$, we have

$$\dot z(t)=i\omega_0\tau_0z(t)+\bar q^*(0)F_0(z,\bar z).\tag{20}$$

We rewrite this equation as

$$\dot z(t)=i\omega_0\tau_0z(t)+g(z,\bar z),\tag{21}$$

where

$$g(z,\bar z)=\bar q^*(0)F_0(z,\bar z)=g_{20}\frac{z^2}{2}+g_{11}z\bar z+g_{02}\frac{\bar z^2}{2}+g_{21}\frac{z^2\bar z}{2}+\cdots.\tag{22}$$

By (18) and (20), we have

$$\begin{aligned}\dot W&=\dot u_t-\dot zq-\dot{\bar z}\bar q=\begin{cases}AW-2\,\mathrm{Re}\{\bar q^*(0)F_0q(\theta)\}, & \theta\in[-1,0),\\ AW-2\,\mathrm{Re}\{\bar q^*(0)F_0q(\theta)\}+F_0, & \theta=0,\end{cases}\\ &:=AW+H(z,\bar z,\theta),\end{aligned}$$

where $F_0\overset{\text{def}}{=}F_0(z,\bar z)$, and

$$H(z,\bar z,\theta)=H_{20}\frac{z^2}{2}+H_{11}z\bar z+H_{02}\frac{\bar z^2}{2}+\cdots.\tag{23}$$

Expanding the above series and comparing the corresponding coefficients, we obtain

$$(A-2i\omega_0\tau_0)W_{20}(\theta)=-H_{20}(\theta),\qquad AW_{11}(\theta)=-H_{11}(\theta),\ldots.\tag{24}$$

Note that $u_t=W(t,\theta)+zq(\theta)+\bar z\bar q(\theta)$ and $q(\theta)=(1,E)^Te^{i\omega_0\tau_0\theta}$, we get

$$x(t-1)=ze^{-i\omega_0\tau_0}+\bar ze^{i\omega_0\tau_0}+W^{(1)}(-1),\qquad y(t-1)=zEe^{-i\omega_0\tau_0}+\bar z\bar Ee^{i\omega_0\tau_0}+W^{(2)}(-1),$$

where

$$W^{(1)}(-1)=W^{(1)}_{20}(-1)\frac{z^2}{2}+W^{(1)}_{11}(-1)z\bar z+W^{(1)}_{02}(-1)\frac{\bar z^2}{2}+\cdots,$$
$$W^{(2)}(-1)=W^{(2)}_{20}(-1)\frac{z^2}{2}+W^{(2)}_{11}(-1)z\bar z+W^{(2)}_{02}(-1)\frac{\bar z^2}{2}+\cdots.$$

It follows that

$$F_0=\tau_0\times\begin{pmatrix}
\frac{k_1}{2}\{M_1[ze^{-i\omega_0\tau_0}+\bar{z}e^{i\omega_0\tau_0}+W_{20}^{(1)}(-1)\frac{z^2}{2}+W_{11}^{(1)}(-1)z\bar{z}+W_{02}^{(1)}(-1)\frac{\bar{z}^2}{2}+\cdots]^2\\
\quad+2Q_1[ze^{-i\omega_0\tau_0}+\bar{z}e^{i\omega_0\tau_0}+W_{20}^{(1)}(-1)\frac{z^2}{2}+W_{11}^{(1)}(-1)z\bar{z}+W_{02}^{(1)}(-1)\frac{\bar{z}^2}{2}\\
\quad+\cdots][zEe^{-i\omega_0\tau_0}+\bar{z}\bar{E}e^{i\omega_0\tau_0}+W_{20}^{(2)}(-1)\frac{z^2}{2}+W_{11}^{(2)}(-1)z\bar{z}+W_{02}^{(2)}(-1)\frac{\bar{z}^2}{2}+\cdots]\\
\quad+N_1[zEe^{-i\omega_0\tau_0}+\bar{z}\bar{E}e^{i\omega_0\tau_0}+W_{20}^{(2)}(-1)\frac{z^2}{2}+W_{11}^{(2)}(-1)z\bar{z}+W_{02}^{(2)}(-1)\frac{\bar{z}^2}{2}+\cdots]^2\}\\
\quad+\frac{k_1}{6}\{M_2[ze^{-i\omega_0\tau_0}+\bar{z}e^{i\omega_0\tau_0}+W_{20}^{(1)}(-1)\frac{z^2}{2}+W_{11}^{(1)}(-1)z\bar{z}+W_{02}^{(1)}(-1)\frac{\bar{z}^2}{2}+\cdots]^3\\
\quad+3Q_2[ze^{-i\omega_0\tau_0}+\bar{z}e^{i\omega_0\tau_0}+W_{20}^{(1)}(-1)\frac{z^2}{2}+W_{11}^{(1)}(-1)z\bar{z}+W_{02}^{(1)}(-1)\frac{\bar{z}^2}{2}\\
\quad+\cdots]^2[zEe^{-i\omega_0\tau_0}+\bar{z}\bar{E}e^{i\omega_0\tau_0}+W_{20}^{(2)}(-1)\frac{z^2}{2}+W_{11}^{(2)}(-1)z\bar{z}+W_{02}^{(2)}(-1)\frac{\bar{z}^2}{2}+\cdots]\\
\quad+3R_2[ze^{-i\omega_0\tau_0}+\bar{z}e^{i\omega_0\tau_0}+W_{20}^{(1)}(-1)\frac{z^2}{2}+W_{11}^{(1)}(-1)z\bar{z}+W_{02}^{(1)}(-1)\frac{\bar{z}^2}{2}\\
\quad+\cdots][zEe^{-i\omega_0\tau_0}+\bar{z}\bar{E}e^{i\omega_0\tau_0}+W_{20}^{(2)}(-1)\frac{z^2}{2}+W_{11}^{(2)}(-1)z\bar{z}+W_{02}^{(2)}(-1)\frac{\bar{z}^2}{2}+\cdots]^2\\
\quad+N_2[zEe^{-i\omega_0\tau_0}+\bar{z}\bar{E}e^{i\omega_0\tau_0}+W_{20}^{(2)}(-1)\frac{z^2}{2}+W_{11}^{(2)}(-1)z\bar{z}+W_{02}^{(2)}(-1)\frac{\bar{z}^2}{2}+\cdots]^3\}\\
\quad+O(x^4(t-1),y^4(t-1))\\
\frac{k_2}{2}\{M_1[ze^{-i\omega_0\tau_0}+\bar{z}e^{i\omega_0\tau_0}+W_{20}^{(1)}(-1)\frac{z^2}{2}+W_{11}^{(1)}(-1)z\bar{z}+W_{02}^{(1)}(-1)\frac{\bar{z}^2}{2}+\cdots]^2\\
\quad+2Q_1[ze^{-i\omega_0\tau_0}+\bar{z}e^{i\omega_0\tau_0}+W_{20}^{(1)}(-1)\frac{z^2}{2}+W_{11}^{(1)}(-1)z\bar{z}+W_{02}^{(1)}(-1)\frac{\bar{z}^2}{2}\\
\quad+\cdots][zEe^{-i\omega_0\tau_0}+\bar{z}\bar{E}e^{i\omega_0\tau_0}+W_{20}^{(2)}(-1)\frac{z^2}{2}+W_{11}^{(2)}(-1)z\bar{z}+W_{02}^{(2)}(-1)\frac{\bar{z}^2}{2}+\cdots]\\
\quad+N_1[zEe^{-i\omega_0\tau_0}+\bar{z}\bar{E}e^{i\omega_0\tau_0}+W_{20}^{(2)}(-1)\frac{z^2}{2}+W_{11}^{(2)}(-1)z\bar{z}+W_{02}^{(2)}(-1)\frac{\bar{z}^2}{2}+\cdots]^2\}\\
\quad+\frac{k_2}{6}\{M_2[ze^{-i\omega_0\tau_0}+\bar{z}e^{i\omega_0\tau_0}+W_{20}^{(1)}(-1)\frac{z^2}{2}+W_{11}^{(1)}(-1)z\bar{z}+W_{02}^{(1)}(-1)\frac{\bar{z}^2}{2}+\cdots]^3\\
\quad+3Q_2[ze^{-i\omega_0\tau_0}+\bar{z}e^{i\omega_0\tau_0}+W_{20}^{(1)}(-1)\frac{z^2}{2}+W_{11}^{(1)}(-1)z\bar{z}+W_{02}^{(1)}(-1)\frac{\bar{z}^2}{2}\\
\quad+\cdots]^2[zEe^{-i\omega_0\tau_0}+\bar{z}\bar{E}e^{i\omega_0\tau_0}+W_{20}^{(2)}(-1)\frac{z^2}{2}+W_{11}^{(2)}(-1)z\bar{z}+W_{02}^{(2)}(-1)\frac{\bar{z}^2}{2}+\cdots]\\
\quad+3R_2[ze^{-i\omega_0\tau_0}+\bar{z}e^{i\omega_0\tau_0}+W_{20}^{(1)}(-1)\frac{z^2}{2}+W_{11}^{(1)}(-1)z\bar{z}+W_{02}^{(1)}(-1)\frac{\bar{z}^2}{2}\\
\quad+\cdots][zEe^{-i\omega_0\tau_0}+\bar{z}\bar{E}e^{i\omega_0\tau_0}+W_{20}^{(2)}(-1)\frac{z^2}{2}+W_{11}^{(2)}(-1)z\bar{z}+W_{02}^{(2)}(-1)\frac{\bar{z}^2}{2}+\cdots]^2\\
\quad+N_2[zEe^{-i\omega_0\tau_0}+\bar{z}\bar{E}e^{i\omega_0\tau_0}+W_{20}^{(2)}(-1)\frac{z^2}{2}+W_{11}^{(2)}(-1)z\bar{z}+W_{02}^{(2)}(-1)\frac{\bar{z}^2}{2}+\cdots]^3\}\\
\quad+O(x^4(t-1),y^4(t-1))
\end{pmatrix}.$$

Comparing the coefficients with (21), we have

$$\begin{aligned}
g_{20}&=\frac{\tau_0(k_1+k_2\bar{F})}{D}\big(M_1+2Q_1E+N_1E^2\big)e^{-2i\omega_0\tau_0},\\
g_{11}&=\frac{\tau_0(k_1+k_2\bar{F})}{D}(M_1+Q_1\bar{E}+Q_1E+N_1E\bar{E}),\\
g_{02}&=\frac{\tau_0(k_1+k_2\bar{F})}{D}\big(M_1+2Q_1\bar{E}+N_1\bar{E}^2\big)e^{2i\omega_0\tau_0},\\
g_{21}&=\frac{\tau_0(k_1+k_2\bar{F})}{D}\big[M_1\big(W_{20}^{(1)}(-1)e^{i\omega_0\tau_0}+2W_{11}^{(1)}(-1)e^{-i\omega_0\tau_0}\big)\\
&\quad+Q_1\big(2W_{11}^{(2)}(-1)e^{-i\omega_0\tau_0}+W_{20}^{(2)}(-1)e^{i\omega_0\tau_0}+W_{20}^{(1)}(-1)\bar{E}e^{i\omega_0\tau_0}+2W_{11}^{(1)}(-1)Ee^{-i\omega_0\tau_0}\big)\\
&\quad+N_1\big(2EW_{11}^{(2)}(-1)e^{-i\omega_0\tau_0}+\bar{E}W_{20}^{(2)}(-1)e^{i\omega_0\tau_0}\big)+M_2e^{-i\omega_0\tau_0}+Q_2(\bar{E}+2E)e^{-i\omega_0\tau_0}\\
&\quad+R_2\big(E^2+2E\bar{E}\big)e^{-i\omega_0\tau_0}+N_2E^2\bar{E}e^{-i\omega_0\tau_0}\big],
\end{aligned}\tag{25}$$

where

$$W_{20}(\theta)=\frac{ig_{20}}{\omega_0\tau_0}q(\theta)+\frac{i\bar{g}_{02}}{3\omega_0\tau_0}\bar{q}(\theta)+E_1e^{2i\omega_0\tau_0\theta},\tag{26}$$

$$W_{11}(\theta)=-\frac{ig_{11}}{\omega_0\tau_0}q(\theta)+\frac{i\bar{g}_{11}}{\omega_0\tau_0}\bar{q}(\theta)+E_2,\tag{27}$$

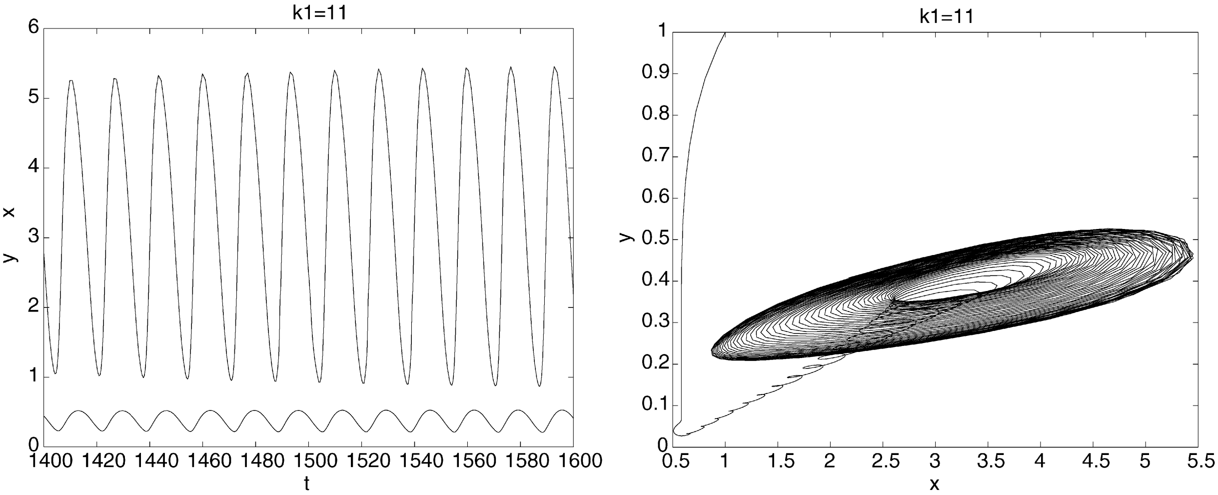

Fig. 7. Delay induced sustained oscillations: numeric simulations of system (3) with $k_1 = 11$, $k_2 = 0.3$, $l_1 = 1$, $l_2 = 0.2$, $p = 10$, $q = 0.2$, $r = 0.4$ and $\tau = 12 > \tau_0 = 2.3026$.

$$E_1 = \begin{bmatrix} 2i\omega_0 + l_1 - k_1 M e^{-2i\omega_0\tau_0} & -k_1 N e^{-2i\omega_0\tau_0} \\ -k_2 M e^{-2i\omega_0\tau_0} & 2i\omega_0 + l_2 - k_2 N e^{-2i\omega_0\tau_0} \end{bmatrix}^{-1} \times \begin{bmatrix} k_1(M_1 e^{-2i\omega_0\tau_0} + 2Q_1 E e^{-2i\omega_0\tau_0} + N_1 E^2 e^{-2i\omega_0\tau_0}) \\ k_2(M_1 e^{-2i\omega_0\tau_0} + 2Q_1 E e^{-2i\omega_0\tau_0} + N_1 E^2 e^{-2i\omega_0\tau_0}) \end{bmatrix},$$

$$E_2 = -\begin{bmatrix} -l_1 + k_1 M & k_1 N \\ k_2 M & -l_2 + k_2 N \end{bmatrix}^{-1} \times \begin{bmatrix} k_1(M_1 + Q_1\bar{E} + Q_1 E + N_1 E\bar{E}) \\ k_2(M_1 + Q_1\bar{E} + Q_1 E + N_1 E\bar{E}) \end{bmatrix}.$$

Solving the above equations to obtain E_1 and E_2, and substituting them into (26) and (27), respectively, we can get $W_{20}(\theta)$ and $W_{11}(\theta)$. Then g_{21} can be expressed by the parameters and delay in Eq. (17) Consequently, g_{ij} in (25) can be expressed by the parameters and delays in (17). Thus, we can compute the following quantities:

$$c_1(0) = \frac{i}{2\omega_0}\left(g_{11}g_{20} - 2|g_{11}|^2 - \frac{|g_{02}|^2}{3}\right) + \frac{g_{21}}{2}, \qquad \mu_2 = -\frac{\operatorname{Re}(c_1(0))}{\operatorname{Re}(\lambda'(\tau_0))},$$
$$\gamma_2 = 2\operatorname{Re}\big(c_1(0)\big), \qquad T_2 = -\frac{\operatorname{Im}(c_1(0)) + \mu_2 \operatorname{Im}(\lambda'(\tau_0))}{\omega_0}, \tag{28}$$

which determine the properties of bifurcating periodic solutions at the critical value τ_0 as below:

(i) μ_2 determines the directions of the Hopf bifurcation: if $\mu_2 > 0$ ($\mu_2 < 0$), then the Hopf bifurcation is supercritical (subcritical) and the bifurcating periodic solutions exist for $\tau > \tau_0$ ($\tau < \tau_0$);
(ii) γ_2 determines the stability of bifurcating periodic solutions: the bifurcating periodic solutions are stable (unstable) if $\gamma_2 < 0$ ($\gamma_2 > 0$);
(iii) T_2 determines the period of the bifurcating periodic solutions: the period increases (decreases) if $T_2 > 0$ ($T_2 < 0$).

4. Numeric simulations

To illustrate the analytical results obtained in Section 3, we will choose parameter values as

$$k_2 = 0.3, \qquad l_1 = 1, \qquad l_2 = 0.2, \qquad p = 10, \qquad q = 0.2, \qquad r = 0.4.$$

When $k_1 = 11$, the equilibrium is given by $(\bar{x}, \bar{y}) \doteq (3.5268, 0.4263)$, and (A_0), (A_1) and (A_3) are all satisfied. Furthermore, we have $\omega_0 \doteq 0.6656$, $\tau_0 \doteq 2.3026$, $g_{20} \doteq 0.6165 - 0.5428i$, $g_{11} \doteq -0.6120 + 0.3759i$, $g_{02} \doteq 0.7630 - 0.3044i$, and $g_{21} \doteq -6.6747 - 2.8357i$, $\lambda'(\tau_0) = 3.7758 - 6.8184$. By (23), we can further compute to obtain

$$c_1(0) \doteq -3.5250 - 1.8938i, \qquad \mu_2 \doteq 0.9335, \qquad \gamma_2 \doteq -7.0501, \qquad T_2 \doteq 12.4083.$$

Hence we conclude that the bifurcation occurs when τ increases to pass τ_0, the bifurcated periodic solution is orbitally asymptotically stable, and the period increases as well as τ increase. These are illustrated in Fig. 7. Note that values of all parameters are taken the same as in Fig. 6, except $\tau = 12$, showing the sustained oscillations are induced by delay.

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