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Global Hopf Bifurcation Analysis of a Nicholson's Blowflies Equation of Neutral Type

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Abstract We investigate Hopf bifurcations in a delayed Nicholson's blowflies equation of neutral type, derived from the Gurtin–MacCamy model. A key parameter that determines the direction of the Hopf bifurcation and the stability of the bifurcating periodic solutions is derived. Global extension of local Hopf branches is established by combining a global Hopf bifurcation theorem with a Bendixson criterion for higher dimensional ordinary differential equations. We show that a branch of slowly varying periodic solutions and a branch of fast oscillating periodic solutions coexist for all large delays.

Keywords NFDEs · Nicholson's blowflies equation · Hopf bifurcations

1 Introduction

Gurney [6] proposed the following delayed Nicholson blowflies equation to model the population $N(t)$ of Australian Sheep blowflies

$$N'(t)) = -\gamma N(t) + pN(t-\tau)e^{-aN(t-\tau)}. \tag{1.1}$$

Parameter p is the maximum per capita daily egg production rate, $1/a$ the size at which the blowfly population reproduces at its maximum rate, γ the per capita daily adult death rate and τ the generation time. Nicholson blowflies model (1.1) and its formulations using

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discrete, periodic, and diffusive equations have been extensively studied in the literature, see [12,14,16,15,20] and references therein.

In [1], Eq. (1.1) is reformulated from a generalized Gurtin–MacCamy model [7] for an age-structured population

$$\begin{aligned} u_t + u_a + \mu(a,\omega)u &= 0,\\ u(t,0) &= \int_0^\infty b(a,\omega)u(t,a)da,\\ \omega(t) &= \int_0^\infty \rho(a)u(t,a)da, \end{aligned} \tag{1.2}$$

with initial condition $u(0,a) = u_0(a)$. Here $u(t,a)$ is the age distribution at time t and with the following properties: $u(t,\tau) = u(0,\tau - t) = u_0(\tau - t)$, and $u(t,a) \to 0$ as $a \to \infty$, and function ω is a weighted average of the total population with weight function $\rho(a) \geq 0$. Parameters b and μ, depending on the age and the average ω, denote the birth and death rates, respectively. Let τ be the critical age that separates adults and juveniles. Then the total population of the mature individuals is

$$N(t) = \int_\tau^{+\infty} u(t,a)da.$$

Let $\rho(a) = 1$ and

$$\begin{aligned} b(a,\omega) &= pe^{-a\omega}H_\tau(a) + c\delta_\tau(a),\\ \mu(a,\omega) &= \gamma H_\tau(a), \end{aligned}$$

where $p,\ a,\ c,\ \gamma$ are positive numbers, $H_\tau(a)$ is the Heaviside function with jump at $a = \tau$ and $\delta_\tau(a)$ is the delta function with peak at $a = \tau$. Then, it can be verified that $N(t)$ satisfies

$$N'(t) + \gamma N(t) = u_0(\tau - t) \tag{1.3}$$

for $0 < t < \tau$, and

$$N'(t) - cN'(t-\tau) = -\gamma N(t) + c\gamma N(t-\tau) + pN(t-\tau)e^{-aN(t-\tau)} \tag{1.4}$$

for $t > \tau$. In particular, (1.1) can be derived from (1.4) by further assuming $c = 0$. For more details on the derivation of (1.3) and (1.4), we refer the readers to [1,4] and references therein.

Equation (1.4) is a neutral functional differential equations (NFDEs). Under the assumption $0 < c < 1$, the theory on the decomposition of the phase space for NFDEs applies [8], and (1.4) can be written as an abstract ODE in a suitable phase space [9]. The standard approach for investigating Hopf bifurcations for abstract ODEs can also be applied to (1.4) by studying the reduced bifurcation equations on the center manifold [2]. Using τ as a bifurcation parameter, we prove the occurrence of Hopf bifurcations at the positive equilibrium N^* when τ passes through a sequence of bifurcation values τ_k, $k = 1, 2, \ldots$. Following the development in [18], we also derive parameters that determine the direction of the Hopf bifurcations and the stability of bifurcating periodic solutions. Furthermore, we investigate global extensions of local Hopf branches when τ moves away from the bifurcation value τ_k. This is accomplished by combining global Hopf bifurcation theorems for NFDEs [10,24,23] with higher dimensional Bendixson-Dulac criteria for ordinary differential equations [13]. We show that a branch of slowly varying periodic solutions and a branch of fast oscillating periodic solutions coexist for all large delays. For arbitrary large delays, our numerical simulations show the existence of both stable slowly-varying periodic solutions and unstable fast-oscillating periodic solutions. Our results generalize the global Hopf bifurcation results in [20] for the delayed Nicholson blowflies equation (1.1).

Our study is mainly motivated by [19,20], and our analysis follows a general framework developed in [17,18]. An earlier study on local and global Hopf bifurcations for a transmission line equation was done in [21]. For NFDEs with symmetry, equivariant Hopf bifurcations are studied in [5] without using the center manifold reduction, and the global continuation problem is treated in [11] within this framework.

Our paper is organized as follows. In Sect. 2, we establish a positively invariant region in the positive cone of the phase space, in which model (1.4) is well defined in the sense that positive initial conditions give rise to positive solutions. In Sect. 3, we prove the occurrence of a sequence of local Hopf bifurcations using τ as the bifurcation parameter. In Sect. 4, the direction of the Hopf bifurcation and the stability of the bifurcating periodic solutions are investigated. In Sect. 5, we investigate global extension of local Hopf bifurcations and establish the existence of slowly-varying periodic solutions for all large delays.

2 Well-Posedness

For (1.4) to describe the dynamics of blowflies population, it is desirable that positive initial conditions lead to positive solutions. For neutral delay equations, this is not a trivial matter. Without loss of generality, we assume the initial time for (1.4) is zero. It is shown in [4] that, for (1.3) and (1.4), $N(t)$ remains non-negative provided initial values $u_0(a)$ for (1.2) are non-negative. This suggests that initial conditions for (1.4) need to be further restricted to ensure positivity of solutions.

One such restriction was given in [25]. Consider a subset

$$\Gamma_D = \{\phi \in C([-\tau, 0], \mathbb{R}) \mid \phi(0) - c\phi(-\tau) \geq 0, \text{ and } \phi(\theta) \geq 0, \ \theta \in [-\tau, 0]\}.$$

The following result is a special case of Lemma 3.1 in [25].

Proposition 2.1 *The subset Γ_D is positively invariant with respect to* (1.4).

In particular, if the initial condition $\phi \in \Gamma_D$, then the solution $N(t, \phi)$ is nonnegative for $t > 0$.

Motivated by results in [4] and relation (1.3) in particular, we give another set of restrictions on the initial condition to ensure positivity of solutions. Consider the set

$$\Gamma_u = \{\phi \in C([-\tau, 0], \mathbb{R}) \mid \text{the left derivative} D^-\phi(\theta) \text{ exists,}$$
$$D^-\phi(\theta) + \gamma\phi(\theta) \geq 0, \text{ and } \phi(\theta) \geq 0, \theta \in (-\tau, 0]\}.$$

We prove the following result.

Proposition 2.2 *For* (1.4), *Γ_u is a positively invariant set.*

Proof For any initial condition $\phi \in \Gamma_u$, $\theta \in [-\tau, 0]$, and $t \in (0, \tau]$, the solution $N(t)$ of (1.4) satisfies that $D^-N(t)$ exists,

$$D^-N(t) + \gamma N(t) = c(D^-\phi(\theta) + \gamma\phi(\theta)) + p\phi(\theta)e^{-a\phi(\theta)},$$

and

$$D^{-}N(t)+\gamma N(t)\geq 0.$$

Solving this inequality we obtain $N(t)\geq N(0)e^{-\gamma t}\geq 0,\ t\in(0,\tau]$. Therefore, $N(t,\phi)\in\Gamma_u$ for all $t\in(0,\tau]$. Similarly, for $t\in(\tau,2\tau]$,

$$D^{-}N(t)+\gamma N(t)=c(D^{-}N(t-\tau)+\gamma N(t-\tau))+pN(t-\tau)e^{-aN(t-\tau)}.$$

We can show that $N(t,\phi)\in\Gamma_u$ for $t\in(\tau,2\tau]$. This argument can be continued to all positive time, which completes the proof. □

In the remaining of the paper, we investigate the dynamics of (1.4) in a positively invariant region Γ with either $\Gamma=\Gamma_D$ or $\Gamma=\Gamma_u$, and formulate our results accordingly.

3 Local Hopf Bifurcations

Assume that $0<c<1$. Rewrite Eq. (1.4) as

$$\frac{d}{dt}[N(t)-cN(t-\tau)]=-\gamma N(t)+c\gamma N(t-\tau)+pN(t-\tau)e^{-aN(t-\tau)}. \tag{3.1}$$

Note that $1-c>0$. A unique positive equilibrium $N^{*}=\frac{1}{a}\log\frac{p}{(1-c)\gamma}$ exists if and only if $p>(1-c)\gamma$. The linearization of (3.1) at $N=N^{*}$ is given by

$$\frac{d}{dt}[N(t)-cN(t-\tau)]=-\gamma N(t)-\gamma((1-c)aN^{*}-1)N(t-\tau),$$

with its characteristic equation

$$\lambda(1-ce^{-\lambda\tau})+\gamma+\gamma((1-c)aN^{*}-1)e^{-\lambda\tau}=0. \tag{3.2}$$

Suppose that $i\omega_0,\ \omega_0>0$, is a root of (3.2), that is

$$i\omega_0(1-ce^{-i\omega_0\tau})+\gamma+\gamma((1-c)aN^{*}-1)e^{-i\omega_0\tau}=0.$$

Then, separating the real and imaginary parts, we have

$$\begin{aligned}\gamma-c\omega_0\sin\omega_0\tau+\gamma((1-c)aN^{*}-1)\cos\omega_0\tau&=0,\\ \omega_0-c\omega_0\cos\omega_0\tau-\gamma((1-c)aN^{*}-1)\sin\omega_0\tau&=0.\end{aligned} \tag{3.3}$$

Solving (3.3) we obtain a unique positive solution

$$\omega_0=\sqrt{\frac{\gamma^2[((1-c)aN^{*}-1)^2-1]}{1-c^2}}. \tag{3.4}$$

In particular, $\omega_0>0$ exists if and only if $(1-c)aN^{*}-2>0$, or equivalently, $p>(1-c)\gamma e^{\frac{2}{1-c}}$. Furthermore, $i\omega_0$ is a (simple) imaginary root of (3.2) if and only if $\tau=\tau_k$, where

$$\tau_k=\frac{1}{\omega_0}\left[\arcsin\left(\frac{\gamma\omega_0(c+(1-c)aN^{*}-1)}{c^2\omega_0^2+\gamma^2((1-c)aN^{*}-1)^2}\right)+2k\pi\right],\quad k=0,1,\ldots. \tag{3.5}$$

Let $\lambda=\alpha(\tau)+i\omega(\tau)$ denote the root of (3.2) near $\tau=\tau_k$ satisfying $\alpha(\tau_k)=0,\ \omega(\tau_k)=\omega_0$.

Proposition 3.1 $\frac{d\alpha}{d\tau}(\tau_k) > 0$.

Proof Differentiating (3.2) with respect to λ we obtain

$$\begin{aligned}\left.\frac{d\tau}{d\lambda}\right|_{\lambda=i\omega_0} &= -\left.\frac{1-ce^{-\lambda\tau}+\tau c\lambda e^{-\lambda\tau}-\gamma\tau((1-c)aN^*-1)e^{-\lambda\tau}}{c\lambda^2e^{-\lambda\tau}-\lambda\gamma((1-c)aN^*-1)e^{-\lambda\tau}}\right|_{\lambda=i\omega_0,\tau=\tau_k}\\ &= \frac{\cos\omega_0\tau_k+i\sin\omega_0\tau_k-c+ic\omega_0\tau_k-\gamma((1-c)aN^*-1)\tau_k}{c\omega_0^2+i\omega_0\gamma((1-c)aN^*-1)}.\end{aligned}$$

Therefore, using (3.3), we obtain

$$\begin{aligned}\frac{d\alpha}{d\tau}(\tau_k) &= \frac{c^2\omega_0^4+\omega_0^2\gamma^2((1-c)aN^*-1)^2}{(\cos\omega_0\tau_k-c-\gamma(aN^*-1)\tau_k)c\omega_0^2+(\sin\omega_0\tau_k+c\omega_0\tau_k)\omega_0\gamma((1-c)aN^*-1)}\\ &= \frac{c^2\omega_0^4+\omega_0^2\gamma^2((1-c)aN^*-1)^2}{\omega_0(1-c^2)} > 0,\end{aligned}$$

which completes the proof. □

When $\tau = 0$, the only root of (3.2) is $\lambda = -aN^*\gamma < 0$. Since the characteristic roots have continuous dependence on τ, and purely imaginary roots only occurs at $\tau = \tau_k$, $k = 0, 1, \ldots$, a continuation argument leads to the following result.

Proposition 3.2 *Assume that* $0 < c < 1$.

(1) *If* $(1-c)\gamma < p \le (1-c)\gamma e^{\frac{2}{1-c}}$ *and* $\tau > 0$ *or if* $p > (1-c)\gamma e^{\frac{2}{1-c}}$ *and* $\tau \in [0, \tau_0)$, *then all roots of the characteristic equation* (3.2) *have negative real parts.*
(2) *If* $p > (1-c)\gamma e^{\frac{2}{1-c}}$ *and* $\tau = \tau_0$, *there is a pair of simple imaginary roots* $\pm i\omega_0$ *of* (3.2), *and all the other roots have negative real parts.*
(3) *If* $\tau \in (\tau_k, \tau_{k+1})$, *then* (3.2) *has exactly* $2(k+1)$ *roots with positive real parts,* $k = 0, 1, \ldots$.

Based on the distribution of characteristic roots described in Proposition 3.2, and the transversality condition in Proposition 3.1, we can derive following results on the stability of N^* and Hopf bifurcation, using the standard linear NFDEs theory [8].

Theorem 3.3 *Assume that* $0 < c < 1$.

(1) *If* $(1-c)\gamma < p \le (1-c)\gamma e^{\frac{2}{1-c}}$, *then* N^* *is asymptotically stable for all* $\tau > 0$.
(2) *If* $p > (1-c)\gamma e^{\frac{2}{1-c}}$, *then* N^* *is asymptotically stable for* $\tau \in [0, \tau_0)$ *and unstable for* $\tau > \tau_0$.
(3) *For* $p > (1-c)\gamma e^{\frac{2}{1-c}}$, *Eq.* (3.1) *undergoes a Hopf bifurcation at* N^* *when* $\tau = \tau_k$, $k = 0, 1, \ldots$.

4 Properties of Hopf Bifurcations

A standard approach to study the direction and stability of Hopf bifurcations is to use normal form techniques. In [3], a method of obtaining normal forms is derived for FDEs without computing the center manifold. The method in [3] is extended to NFDEs in [17]. Explicit formula for calculating the normal forms for one dimensional NFDEs are derived in [18]. In this section, we apply the methods in [17,18] to analyze (3.1).

First, we formulate (3.1) as an abstract ODE in the Banach space

$$BC := \{\phi : [-1, 0] \to R \mid \phi \text{ is uniformly continuous on } [-1, 0)\}.$$

Rescaling the time by $t \to t/\tau$ so that the delay will be 1, we can rewrite (3.1) as

$$\frac{d}{dt}[N(t) - cN(t-1)] = -\tau\gamma N(t) + \tau c\gamma N(t-1) + \tau p N(t-1)e^{-aN(t-1)}. \tag{4.1}$$

Let $N(t) = N^* + y(t)$. Then (4.1) becomes

$$\frac{d}{dt}[y(t)-cy(t-1)] = -\tau\gamma(N^*+y(t)) + \tau\gamma(N^*+y(t-1))(c+(1-c)e^{-ay(t-1)}). \tag{4.2}$$

Set

$$\mu(\theta) = \begin{cases} -c, & \theta = -1 \\ 0, & \theta \in (-1, 0], \end{cases} \quad \eta(\tau, \theta) = \begin{cases} -\gamma\tau, & \theta = 0 \\ 0, & \theta \in (-1, 0) \\ \gamma\tau((1-c)aN^* - 1), & \theta = -1. \end{cases}$$

We can define linear functionals D and L on BC

$$D\phi = \phi(0) - \int_{-1}^{0} \phi(\theta) d\mu(\theta) = \phi(0) - c\phi(-1),$$

$$L(\tau)\phi = \int_{-1}^{0} \phi(\theta) d\eta(\theta) = -\gamma\tau\phi(0) - \gamma\tau((1-c)aN^* - 1)\phi(-1).$$

Introducing a new parameter $r = \tau - \tau_0$, we rewrite (4.2) as

$$\frac{d}{dt}[Dy_t] = L(\tau_0)y_t + F(r, y_t), \tag{4.3}$$

where

$$\begin{aligned} F(r, \phi) = &-\gamma r\phi(0) - \gamma r((1-c)aN^* - 1)\phi(-1) \\ &-\gamma(\tau_0 + r)[N^* - (N^* + \phi(-1)(c + (1-c)e^{-a\phi(-1)}) \\ &-((1-c)aN^* - 1)\phi(-1)]. \end{aligned} \tag{4.4}$$

Consider the linearization of (4.3)

$$\frac{d}{dt}Dy_t = L(\tau_0)y_t$$

in the phase space C, and let $\Lambda = \{-i\omega_0\tau_0, -i\omega_0\tau_0\}$. Using the formal adjoint theory for NFDEs [8], we decompose C as $C = P \oplus Q$. A basis of the center space P is given by $\Phi = (\phi_1, \phi_2)$ with $\phi_1 = e^{i\omega_0\tau_0\theta}$, $\phi_2 = e^{-i\omega_0\tau_0\theta}$. Choose a basis Ψ for the adjoint space P^*, such that $(\Psi, \Phi) = I$, where $(\cdot, \cdot)$ is the bilinear form on $C^* \times C$ defined by

$$(\psi, \phi) = \psi(0)\phi(0) - \int_{-1}^{0} d\left[\int_{0}^{\theta} \psi(\theta - \alpha) d\mu(\alpha)\right]\phi(\theta) - \int_{-1}^{0}\int_{0}^{\theta} \psi(\theta - \tau) d\eta(\tau)\phi(\theta) d\theta.$$

Thus $\Psi(s) = \text{col}(\psi_1, \psi_2) = \text{col}(\rho e^{-i\omega_0\tau_0 s}, \bar{\rho}e^{i\omega_0\tau_0 s})$, where

$$\rho = \frac{1}{1 - ce^{-i\omega_0\tau_0} - \gamma\tau_0((1-c)aN^* - 1)e^{-i\omega_0\tau_0}}.$$

Using the same process as in Sect. 2 of [17], we obtain the following result.

Proposition 4.1 (1) *Equation* (4.3) *can be written in the abstract form*

$$\frac{d}{dt}y_t = Ay_t + X_0 F(r, y_t), \tag{4.5}$$

where the operator $A : BC \to BC$ *is defined by*

$$A\phi(\theta) = \phi'(\theta) + X_0[L(\tau_0)\phi(\theta) - D\phi'(\theta)],$$

and the function $X_0 : [-1, 0] \to \mathbb{R}$ *is given by* $X_0(\theta) = 0$ *for* $\theta \in [-1, 0)$ *and* $X_0(0) = 1$.

(2) *Let* $y_t = \Phi x(t) + z,\ x(t) \in \mathbb{C}^2,\ z \in Q$. *Then* (4.5) *is decomposed as*

$$\begin{aligned} \dot{x} &= Bx + \Psi(0)F(r, \Phi x + z), \\ \dot{z} &= Az + (I - \pi)X_0 F(r, \Phi x + z), \end{aligned} \tag{4.6}$$

where

$$B = \begin{pmatrix} i\omega_0\tau_0 & 0 \\ 0 & -i\omega_0\tau_0 \end{pmatrix}$$

and $\pi : BC \to P$ *is defined as*

$$\pi(\phi + X_0\varsigma) = \Phi[(\Psi, \phi) + \Psi(0)\varsigma].$$

Next, we compute the normal forms of Eq. (4.6) up to the third order using formula provided in [18]. Let $F = \frac{1}{2}F_2 + \frac{1}{3!}F_3 + \frac{1}{4!}F_4 + \cdots$ be the Taylor expansion of F. Using (4.4) and (4.4), for each n, we can derive

$$F_n(\phi, r) = \sum_{|(k,l,m)|=n} a_{k,l,m}\phi(0)^k\phi(-1)^l r^m,$$

where the coefficients are given by

$$\begin{aligned} &a_{1,0,1} = -\gamma,\ a_{1,1,0} = 0,\ a_{0,1,1} = -\gamma((1-c)aN^* - 1), \\ &a_{2,0,0} = 0,\ a_{0,2,0} = a\gamma\tau_0((1-c)aN^* - 2), \\ &a_{2,0,1} = 0,\ a_{0,2,1} = a\gamma((1-c)aN^* - 2),\ a_{3,0,0} = 0, \\ &a_{0,3,0} = a^2\gamma\tau_0(-(1-c)aN^* + 3),\ a_{2,1,0} = 0,\ a_{1,2,0} = 0. \end{aligned} \tag{4.7}$$

The characteristic equation associated with the linearization of (4.2) at 0 is

$$\Delta(\lambda, \tau) = \lambda(1 - ce^{-\lambda}) - b(\tau) - c(\tau)e^{-\lambda} = 0,$$

where $b(\tau) = -\gamma\tau$ and $c(\tau) = -\gamma\tau((1-c)aN^* - 1)$. In order to simplify the notation, we define the operator ℓ by

$$\ell(cx_1^{q_1}x_2^{q_2}r^m) = \begin{bmatrix} cx_1^{q_1}x_2^{q_2}r^m, \\ \bar{c}x_1^{q_2}x_2^{q_1}r^m \end{bmatrix}, \quad c \in \mathbb{C}, \quad (q_1, q_2, m) \in \mathbb{N}^3, \quad |(q_1, q_2, m)| = j.$$

According to [18], the second order term $g_2^1(x, 0, r)$ and the third order term $g_3^1(x, 0, 0)$ in the normal form of (4.6) are given by

$$g_2^1(x, 0, r) = 2\ell(\rho(b'(\tau_0) + c'(\tau_0)e^{-i\omega_0\tau_0})x_1 r), \tag{4.8}$$

and

$$g_3^1(x, 0, 0) = \ell(K_{2,1,0})x_1^2 x_2, \tag{4.9}$$

respectively, where

$$K_{2,1,0} = \psi_1(0)\Big[A_{2,1,0} + \frac{3A_{2,0,0}}{\Delta(2i\omega_0\tau_0, \tau_0)}(2a_{2,0,0} + a_{1,1,0}(e^{-2i\omega_0\tau_0} + e^{i\omega_0\tau_0}) + 2a_{0,2,0}e^{-i\omega_0\tau_0}) - \frac{3A_{1,1,0}}{b(\tau_0) + c(\tau_0)}(2a_{2,0,0} + a_{1,1,0}(1+e^{-i\omega_0\tau_0})+2a_{0,2,0}e^{-i\omega_0\tau_0})\Big] \tag{4.10}$$

and

$$\begin{aligned} A_{2,1,0} &= 3a_{3,0,0} + 3a_{0,3,0}e^{-i\omega_0\tau_0} + a_{2,1,0}(e^{i\omega_0\tau_0} + 2e^{-i\omega_0\tau_0}) + a_{1,2,0}(2 + e^{-2i\omega_0\tau_0}) \\ &= 3a^2\gamma\tau_0(-(1-c)aN^* + 3)e^{-i\omega_0\tau_0}, \\ A_{2,0,0} &= a_{2,0,0} + a_{1,1,0}e^{-i\omega_0\tau_0} + a_{0,2,0}e^{-2i\omega_0\tau_0} = a\gamma\tau_0((1-c)aN^* - 2)e^{-2i\omega_0\tau_0}, \\ A_{1,1,0} &= 2a_{2,0,0} + a_{1,1,0}(e^{i\omega_0\tau_0} + e^{-i\omega_0\tau_0}) + 2a_{0,2,0} = 2a\gamma\tau_0((1-c)aN^* - 2). \end{aligned} \tag{4.11}$$

Using (4.7), (4.10) and (4.11), we obtain

$$K_{2,1,0} = 3a\gamma\tau_0\rho\Big[(-(1-c)aN^* + 3)e^{-i\omega_0\tau_0} + 2a\gamma\tau_0((1-c)aN^* - 2)e^{-i\omega_0\tau_0} \Big(\frac{((1-c)aN^* - 2e^{-2i\omega_0\tau_0})}{2i\omega_0\tau_0(1-ce^{-2i\omega_0\tau_0}) + \gamma\tau_0 + \gamma\tau_0((1-c)aN^* - 1)e^{-2i\omega_0\tau_0}} - \frac{2((1-c)aN^* - 2)}{(1-c)aN^*\gamma\tau_0}\Big)\Big]. \tag{4.12}$$

In summary, we have the following result.

Proposition 4.2 *A normal form of* (3.1) *on the center manifold of the origin is given by*

$$\dot{x} = Bx + \frac{1}{2}g_2^1(x, 0, r) + \frac{1}{3!}g_3^1(x, 0, r), \tag{4.13}$$

where g_2^1 and g_3^1 are given in (4.8), (4.9) *and* (4.12).

Through the change of variables $x_1 = w_1 - iw_2$, $x_2 = w_1 + iw_2$, $w_1 = \zeta\cos\xi$, $w_2 = \zeta\sin\xi$, Eq. (4.13) becomes

$$\begin{aligned} \dot{\zeta} &= r\tau_0\alpha'(\tau_0)\zeta + K\zeta^3 + O(r^2\zeta), \\ \dot{\xi} &= -\omega_0 + O(|(\zeta, r)|), \end{aligned} \tag{4.14}$$

where

$$K = \mathrm{Re}(K_{2,1,0}). \tag{4.15}$$

By the standard Hopf bifurcation theory for ODEs [22], and using $\alpha'(\tau_0) > 0$, we arrive at the following theorem.

Theorem 4.3 *In the case* (2) *of Theorem* 3.3*, the dynamics of equation* (4.1) *near the origin is governed by Eq.* (4.14)*. Moreover, if $K < 0$ (resp. $K > 0$), then the Hopf bifurcation at $\tau = \tau_0$ is supercritical (resp. subcritical), and the bifurcating periodic solutions are asymptotically stable (resp. unstable).*

We carry out numerical simulations to support our theoretical analysis. Consider (1.4) with $c = 0.1$, $a = 1$, $\gamma = 0.5$, $p = 5$. Using (3.5), (4.12) and (4.15), we have $\tau_0 = 7.29$, $K = -3.46$ and $N^* = 2.4$. By Theorem 3.3, we know that (1.4) undergoes a Hopf bifurcation at N^* when $\tau = \tau_0$. Furthermore, by Theorem 4.3, the Hopf bifurcation is supercritical and the bifurcating periodic solutions are orbitally asymptotically stable. Two Matlab simulations of asymptotically stable periodic solutions are shown in Fig. 1, using this set of parameter values and for different τ.

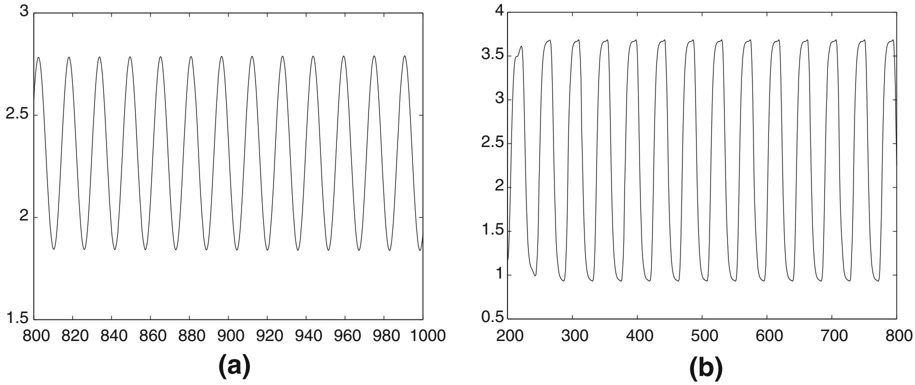

Fig. 1 **a** An asymptotically stable periodic solution bifurcating from the equilibrium $N^* = 2.4$ when $\tau = 7.5 > \tau_0$. **b** A stable periodic solution when $\tau = 20$

5 Global Hopf Bifurcation

Simulation results in previous section suggest that bifurcating periodic solutions may continue to exist for very large values of τ. In this section, we will establish that local Hopf branches can be globally extended to large values of bifurcation parameter τ.

Let $x = \alpha$ be the unique solution of $xe^x = e^{-1}$ and assume there exists real number $\beta > 1$ such that

$$\frac{3+c}{1-c} - \beta e^{\frac{1+c}{1-c}} > \log \frac{1-\alpha}{\beta^2} \tag{5.1}$$

and

$$\beta < \frac{2(1+c)}{\sqrt{2}+c} e^{\frac{-2c}{1-c}} \tag{5.2}$$

for $0 < c < 1$. Denote the set of β satisfying (5.1) and (5.2) by I_c. Then I_c is nonempty. In fact, it can be verified that there exists $\beta > 1$ that satisfies (5.1) and (5.2) when $c = 0$. Therefore, the two inequalities continue to hold for such a β for sufficient small $c > 0$.

Theorem 5.1 *Assume* $0 < c < 1$, $\beta \in I_c$ *and* $\gamma(1-c)e^{\frac{2}{1-c}} < p < \beta\gamma(1-c)e^{\frac{2}{1-c}}$. *Then the following statements hold.*

(1) *All Hopf branches bifurcating from* τ_k *can be globally extended to all* $\tau \geq \tau_k$, *for* $k = 0, 1, \ldots$.
(2) *The global Hopf branch based at* τ_0 *consists of slowly varying periodic solutions.*
(3) *Global Hopf branches based at* τ_k, $k > 1$ *consist of fast oscillating periodic solutions.*

The proof of Theorem 5.1 requires a series of lemmas.

Lemma 5.2 *All periodic solutions of* (4.1) *are uniformly bounded.*

Proof By Proposition 2.2, all periodic solutions of (4.1) in Γ are bounded below by 0. Let $y(t)$ be a nonconstant periodic solution to (4.1), and assume that $y(t) - cy(t-1)$ reaches its maximum at time t_1, that is,

$$y(t_1) - cy(t_1) = \max_{s\in\mathbb{R}}(y(s) - cy(s-1)).$$

Then

$$-\gamma y(t_1) + c\gamma y(t_1 - 1) + py(t_1 - 1)e^{-ay(t_1-1)} = 0, \tag{5.3}$$

and for any fixed s, we have

$$y(s) \le cy(s-1) + y(t_1) - cy(t_1 - 1).$$

Replacing s with $s - 1$ in the above equation, we get

$$y(s-1) \le cy(s-2) + y(t_1) - cy(t_1 - 1).$$

Similarly, for any integer m,

$$y(s) \le c^m y(s-m) + \frac{1-c^m}{1-c}(y(t_1) - cy(t_1 - 1)).$$

Letting $m \to \infty$ we obtain

$$y(s) \le \frac{y(t_1) - cy(t_1 - 1)}{1-c}. \tag{5.4}$$

Therefore, by (5.3)

$$y(s) \le \frac{\frac{p}{\gamma} y(t_1 - 1)e^{-ay(t_1-1)}}{1-c} \le \frac{pe^{-1}}{a\gamma(1-c)} := M. \tag{5.5}$$

□

Lemma 5.3 *Under the assumptions of Theorem 5.1, (4.1) has no periodic solutions of period 4.*

Proof Suppose $y(t)$ is a nonconstant periodic solution of period 4 to (4.1). Set $u_j(t) = y(t - j + 1),\ j = 1, 2, 3, 4$. Then $u(t) = (u_1(t), u_2(t), u_3(t), u_4(t))$ is a periodic solution to the following system of ODEs

$$\frac{d}{dt}[u_i(t) - cu_{i+1}(t)] = -\gamma\tau u_i(t) + c\tau\gamma u_{i+1}(t) + \tau p u_{i+1}(t)e^{-au_{i+1}(t)}, \quad i = 1, 2, 3, 4, \tag{5.6}$$

where $u_5(t) = y(t-4) = u_1(t)$. System (5.6) can be rewritten as

$$\begin{aligned} u_i'(t) = \frac{\tau}{1-c^4}[&-\gamma u_i(t) + c^4\gamma u_i(t) + c^3 p u_i(t)e^{-au_i(t)} + pu_{i+1}(t)e^{-au_{i+1}(t)} \\ &+ cpu_{i+2}(t)e^{-au_{i+2}(t)} + c^2 pu_{i+3}(t)e^{-au_{i+3}(t)}], \end{aligned} \tag{5.7}$$

whose orbits belong to $G := \{u \in \mathbb{R}^4 \mid 0 < u_i < M,\ i = 1, 2, 3, 4\}$. Next, we will employ a general Bendixson's criterion in higher dimensions developed in [13] to exclude nonconstant periodic solutions of (5.7) in region G, which will guarantee that there are no 4-periodic solutions to (4.1). The Jacobian matrix $J(u)$ of (5.7), for $u \in \mathbb{R}^4$, is

$$J(u) = (-\gamma + c^4)I_{4\times 4} + \frac{\gamma\tau}{1-c^4}\begin{pmatrix} c^3pf_1 & pf_2 & cpf_3 & c^2pf_4 \\ c^2pf_1 & c^3pf_2 & pf_3 & cpf_4 \\ cpf_1 & c^2pf_2 & c^3pf_3 & pf_4 \\ pf_1 & cpf_2 & c^2pf_3 & c^3pf_4 \end{pmatrix},$$

where $f_i := f(u_i) = (1-au_i)e^{-au_i}$, $i = 1, 2, 3, 4$. The second additive compound matrix $J^{[2]}(u)$ of $J(u)$ is [13]

$$J^{[2]}(u) = \frac{\tau}{1-c^4} \times P,$$

where P is a 6×6 matrix, whose rows P_i are given in the following row vectors

$$\begin{aligned}
P_1 &= (-2\gamma + c^3p(f_1+f_2) + 2c^4\gamma, pf_3, cpf_4, -cpf_3, -c^2pf_4, 0),\\
P_2 &= (c^2pf_2, -2\gamma + c^3p(f_1+f_3) + 2c^4\gamma, pf_4, pf_2, 0, -c^2pf_4),\\
P_3 &= (cpf_2, c^2pf_3, -2\gamma + c^3p(f_1+f_4) + 2c^4\gamma, 0, pf_2, cpf_3),\\
P_4 &= (-cpf_1, c^2pf_1, 0, -2\gamma + c^3p(f_2+f_3) + 2c^4\gamma, pf_4, -cpf_4),\\
P_5 &= (-pf_1, 0, c^2pf_1, c^2pf_3, -2\gamma + c^3p(f_2+f_4) + 2c^4\gamma, pf_3),\\
P_6 &= (0, -pf_1, cpf_1, -cpf_2, c^2pf_2, -2\gamma + c^3p(f_3+f_4)) + 2c^4\gamma).
\end{aligned}$$

Choose l_∞ norm in $\mathbb{R}^6$, namely, $|x| = \max_{1\le i\le 6}|x_i|$. Let A be the diagonal matrix given by

$$A = \mathrm{diag}\{\sqrt{2}, 1, \sqrt{2}, \sqrt{2}, 1, \sqrt{2}\}. \tag{5.8}$$

Then the Lozinskiĭ measure of $AJ^{[2]}(u)A^{-1}$ [13] is

$$\mu(AJ^{[2]}(u)A^{-1}) = \frac{\tau\gamma}{1-c^4}\max\{\mu_1, \mu_2, \ldots, \mu_6\},$$

where

$$\begin{aligned}
\mu_1 &= [-2 + c^3\frac{p}{\gamma}(f_1+f_2) + 2c^4 + (\sqrt{2}+c)\frac{p}{\gamma}|f_3| + (\sqrt{2}c^2+c)\frac{p}{\gamma}|f_4|],\\
\mu_2 &= [-2 + c^3\frac{p}{\gamma}(f_1+f_3) + 2c^4 + \frac{\sqrt{2}}{2}(1+c^2)\frac{p}{\gamma}(|f_2|+|f_4|)],\\
\mu_3 &= [-2 + c^3\frac{p}{\gamma}(f_1+f_4) + 2c^4 + (\sqrt{2}+c)\frac{p}{\gamma}|f_2| + (\sqrt{2}c^2+c)\frac{p}{\gamma}|f_3|],\\
\mu_4 &= [-2 + c^3\frac{p}{\gamma}(f_2+f_3) + 2c^4 + (\sqrt{2}+c)\frac{p}{\gamma}|f_4| + (\sqrt{2}c^2+c)\frac{p}{\gamma}|f_1|],\\
\mu_5 &= [-2 + c^3\frac{p}{\gamma}(f_1+f_3) + 2c^4 + \frac{\sqrt{2}}{2}(1+c^2)\frac{p}{\gamma}(|f_1|+|f_3|)],\\
\mu_6 &= [-2 + c^3\frac{p}{\gamma}(f_3+f_4) + 2c^4 + (\sqrt{2}+c)\frac{p}{\gamma}|f_1| + (\sqrt{2}c^2+c)\frac{p}{\gamma}|f_2|].
\end{aligned} \tag{5.9}$$

It is shown in [13] that $\mu(AJ^{[2]}(u)A^{-1}) < 0$ for $u \in G$ is a Bendixson condition that rules out nonconstant periodic orbits of (5.7) in G. To prove $\mu(J^{[2]}(u)) < 0$, we first improve the lower bound of the periodic solutions of (4.1).

Similar to the proof of Lemma 5.2, letting $y(t)$ be any nonconstant periodic solution to (4.1) and assuming that $y(t) - cy(t-1)$ reaches its minimum at t_2, we can also derive

$$y(t_2) = \frac{p}{\gamma}y(t_2-1)e^{-ay(t_2-1)} + cy(t_2-1),$$

and

$$y(s) \geq \frac{y(t_2) - cy(t_2 - 1)}{1 - c} = \frac{\frac{p}{\gamma} y(t_2 - 1) e^{-ay(t_2-1)}}{1 - c} := h(y(t_2 - 1)) \tag{5.10}$$

for any $s \in \mathbb{R}$. In particular, $y(t_2) \leq y(t_2 - 1)$, which lead to $y(t_2 - 1) > N^* > \frac{1}{a}$. Since h is decreasing when $y(t_2 - 1) > \frac{1}{a}$, combining with (5.1), (5.5) and (5.10), we can get

$$y(s) \geq \frac{\frac{p}{\gamma} M e^{-aM}}{1 - c} \geq \frac{1 - \alpha}{a}.$$

Hence,

$$-e^{-2} < f_i = (1 - au)e^{-au} < \alpha e^{\alpha - 1} < e^{-2} \quad \text{for } i = 1, 2, 3, 4. \tag{5.11}$$

This allows the following estimates of terms in (5.9)

$$\begin{aligned}
\mu_1 &= -2 + c^3 \frac{p}{\gamma}(f_1 + f_2) + 2c^4 + (\sqrt{2} + c)\frac{p}{\gamma}|f_3| + (\sqrt{2}c^2 + c)\frac{p}{\gamma}|f_4| \\
&\leq -2 + 2c^4 + (2c^3 + \sqrt{2}c^2 + 2c + \sqrt{2})\frac{p}{\gamma}e^{-2} \\
&\leq -2 + 2c^4 + \beta(2c^3 + \sqrt{2}c^2 + 2c + \sqrt{2})(1 - c)e^{\frac{2c}{1-c}}
\end{aligned}$$

and

$$\begin{aligned}
\mu_2 &= -2 + c^3 \frac{p}{\gamma}(f_1 + f_3) + 2c^4 + \frac{\sqrt{2}}{2}(1 + c^2)\frac{p}{\gamma}(|f_2| + |f_4|) \\
&\leq -2 + 2c^4 + (2c^3 + \sqrt{2}c^2 + \sqrt{2})\frac{p}{\gamma}e^{-2} \\
&\leq -2 + 2c^4 + \beta(2c^3 + \sqrt{2}c^2 + \sqrt{2})(1 - c)e^{\frac{2c}{1-c}}.
\end{aligned}$$

By assumption (5.2), we see $\mu_1 < 0$ and $\mu_2 < 0$. Similarly, we can show that $\mu_i < 0$ for $i \geq 3$. Therefore, $\mu(AJ^{[2]}(u)A^{-1}) < 0$. Applying Theorem 3.4 of [13] with $D_0 = G$ and A as in (5.8), we can conclude that system (5.7) has no nonconstant periodic solutions in G. □

Lemma 5.4 *Under the assumptions of Theorem 5.1, Eq. (4.1) has no periodic solutions of period 1 or 2.*

Proof Using phase-line analysis, it is obvious that

$$(1 - c)u'(t) = -(1 - c)\gamma u(t) + pu(t)e^{-au(t)}$$

has no nonconstant periodic solutions. Therefore, equation (4.1) has no 1-periodic solutions.

As shown in Lemma 5.3, if (4.1) has a 2-periodic solution, then $u(t) = (u_1(t), u_2(t)) := (y(t), y(t - 1))$ is a periodic solution of the following system

$$\begin{aligned}
\frac{d}{dt}[u_1(t) - cu_2(t)] &= -\tau\gamma u_1(t) + c\tau\gamma u_2(t) + p\tau u_2(t)e^{-au_2(t)}, \\
\frac{d}{dt}[u_2(t) - cu_1(t)] &= -\tau\gamma u_2(t) + c\tau\gamma u_1(t) + p\tau u_1(t)e^{-au_1(t)},
\end{aligned}$$

or equivalently,

$$\begin{aligned}
u_1'(t) &= \frac{\tau}{1 - c^2}[-(1 - c^2)\gamma u_1(t) + pu_2(t)e^{-au_2(t)} + cpu_1(t)e^{-au_1(t)}] := P(u_1, u_2), \\
u_2'(t) &= \frac{\tau}{1 - c^2}[-(1 - c^2)\gamma u_2(t) + pu_1(t)e^{-au_1(t)} + cpu_2(t)e^{-au_2(t)}] := Q(u_1, u_2).
\end{aligned} \tag{5.12}$$

By (5.11) and (5.2), we have

$$\begin{aligned}\frac{\partial P}{\partial u_1}+\frac{\partial Q}{\partial u_2} &= \frac{\tau}{(1-c^2)\gamma}[-2(1-c^2)+c\frac{p}{\gamma}(f_1+f_2)]\\ &< \frac{2\tau}{\gamma(1+c)}(-(1+c)+c\beta e^{\frac{2c}{1-c}})<0.\end{aligned}$$

The classical Bendixson's negative criterion implies that system (5.12) has no nonconstant periodic solutions, and thus (4.1) has no nonconstant 2-periodic solutions. □

We will apply a global Hopf bifurcation result, Theorem 5.14, in [10] to prove our Theorem 5.1.

Proof of Theorem 5.1 Let

$$F(y_t,\tau,1):=-\gamma\tau y(t)+c\gamma\tau y(t-1)+p\tau y(t-1)e^{-ay(t-1)}.$$

Then $F(y_t,\tau,1)$ satisfies the assumptions of Theorem 5.14 in [10] with

$$\begin{aligned}(\hat{y_0},\alpha_0,p_0) &= (N^*,\tau_k,\frac{2\pi}{\tau_k\omega_0}),\\ \Delta_{(N^*,\tau_k,\frac{2\pi}{\tau_k\omega_0})}(z) &= z\tau(1-ce^{-z})+\tau\gamma+\tau\gamma((1-c)aN^*-1)e^{-z}.\end{aligned}$$

Lemma 3.1 implies that there exist $\varepsilon,\delta>0$ and a smooth curve $z:(\tau_k-\delta,\tau_k+\delta)\to\mathbb{C}$ such that $\Delta(z(\tau))=0$, $z(\tau_k)=i\tau_k\omega_0$, and $|z(\tau)-i\tau_k\omega_0|<\varepsilon$. Denote $T_k=\dfrac{2\pi}{\tau_k\omega_0}$ and let

$$\Omega_\varepsilon=\{(v,T):0<v<\varepsilon,|T-T_k|<\varepsilon\}.$$

Then, on $(\tau_k-\delta,\tau_k+\delta)\times\partial\Omega_\varepsilon$, $\det\Delta_{(N^*,\tau,T)}(v+\frac{2\pi i}{T})=0$ if and only if $\tau=\tau_k$, $v=0$ and $T=T_k$. Let

$$H^{\pm}(N^*,\tau_k,\frac{2\pi}{\tau_k\omega_0})(v,T)=\Delta_{(N^*,\tau_k\pm\delta,T)}(v+\frac{2\pi i}{T}).$$

Then the crossing number

$$\begin{aligned}\gamma_1(N^*,\tau_k,\frac{2\pi}{\tau_k\omega_0}) &= \deg_B(H^-(N^*,\tau_k,\frac{2\pi}{\tau_k\omega_0}),\Omega_\varepsilon)\\ &\quad -\deg_B(H^+(N^*,\tau_k,\frac{2\pi}{\tau_k\omega_0}),\Omega_\varepsilon)=-1,\end{aligned}$$

and

$$\Sigma_{(\hat{y},\tau,T)\in C(N^*,\tau_k,\frac{2\pi}{\tau_k\omega_0})\cap N(F)}\gamma_1(\hat{y},\tau,T)<0,$$

where

$$\begin{aligned}\Sigma(F) &:= Cl\{(y,\tau,T): y \text{ is a T-periodic solution of 4.1 }\},\\ N(F) &:= \{(\hat{y},\tau,T):F(\hat{y},\tau,T)=0\}.\end{aligned}$$

Therefore, the connected component $C(N^*,\tau_k,\frac{2\pi}{\tau_k\omega_0})$ through $(N^*,\tau_k,\frac{2\pi}{\tau_k\omega_0})$ in $\Sigma(F)$ is unbounded.

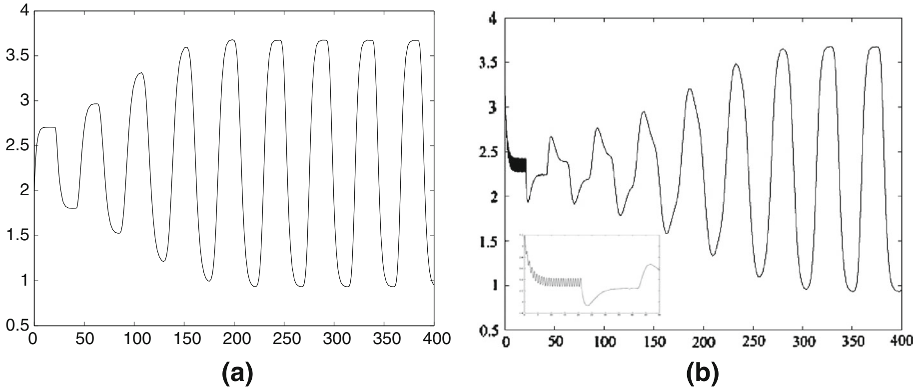

Fig. 2 **a** A solution converges to a slowly-varying periodic solution. **b** A solution first approaches a fast-oscillating unstable periodic solution before it converges to the slowly-varying periodic solution. The *inset* in (**b**) zooms in on the solution for $t \in [0, 50]$

From (5.2), we have $\beta < \sqrt{2} < e^{\frac{1}{c}}$, which leads to $(1-c)aN^* < 1 + \frac{1}{c}$. Therefore, by (3.3) and (3.4), we get $\sin \tau_k\omega_0 > 0$ and

$$\cos \tau_k\omega_0 = \frac{-\gamma^2((1-c)aN^*-1) + c\omega_0^2}{\gamma^2((1-c)aN^*-1)^2 + c^2\omega_0^2}$$
$$= \frac{-(1-c^2)((1-c)aN^*-1) + c(((1-c)aN^*-1)^2-1)}{(1-c^2)((1-c)aN^*-1)^2 + c^2(((1-c)aN^*-1)^2-1)} < 0,$$

which implies that

$$\frac{\pi}{2} < \tau_0\omega_0 < \pi, \quad \text{and} \quad 2\pi < \tau_k\omega_0 < (2k+1)\pi, \ k \geq 1.$$

Hence,

$$2 < \frac{2\pi}{\tau_0\omega_0} < 4, \quad \text{and} \quad \frac{1}{k+1} < \frac{2\pi}{\tau_k\omega_0} < 1, \ k \geq 1. \tag{5.13}$$

By Lemmas 5.3 and 5.4, we know that the projection of each $C(N^*, \tau_k, \frac{2\pi}{\tau_k\omega_0})$ onto T space is bounded, since $2 < T < 4$ if $(y, \tau, T) \in C(N^*, \tau_0, \frac{2\pi}{\tau_0\omega_0})$ and $\frac{1}{k+1} < T < 1$ if $(y, \tau, T) \in C(N^*, \tau_k, \frac{2\pi}{\tau_k\omega_0})$. Meanwhile, by Lemma 5.2, we know that the projection of $C(N^*, \tau_k, \frac{2\pi}{\tau_k\omega_0})$ onto the y space is bounded. Moreover, using the phase-line analysis, it can be verified that (4.1) has no periodic solutions when $\tau = 0$. Consequently, the projection of $C(N^*, \tau_k, \frac{2\pi}{\tau_k\omega_0})$ onto the τ space must be unbounded. From (5.13), periodic solutions on the first Hopf branch based at τ_0 have periods bounded between 2 and 4, and thus are slowly varying (note that the delay τ is scaled to 1 in (4.1)), while periodic solutions on other Hopf branches have periods smaller than 1, and thus are fast oscillating. Because of the separation of periods between the first Hopf branch with the remaining ones, and the nonexistence of 2-periodic solutions, the first Hopf branch will not intersect other branches when globally extended. This shows that slowly varying periodic solutions and fast oscillating periodic solutions coexist for all $\tau \geq \tau_1$. This completes the proof of Theorem 5.1. □

We demonstrate the results of Theorem 5.1 using Matlab simulations. In Fig. 2, we show the coexistence of a slowly-varying periodic solution and a fast-oscillating periodic solution for $\tau = 21$. Other parameter values are the same as in Fig. 1.

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