Global dynamics of Nicholson's blowflies equation revisited: Onset and termination of nonlinear oscillations

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A B S T R A C T

We revisit Nicholson's blowflies model with natural death rate incorporated into the delay feedback. We consider the delay as a bifurcation parameter and examine the onset and termination of Hopf bifurcations of periodic solutions from a positive equilibrium. We show that the model has only a finite number of Hopf bifurcation values and we describe how branches of Hopf bifurcations are paired so the existence of periodic solutions with specific oscillation frequencies occurs only in bounded delay intervals. The bifurcation analysis and the Matlab package DDE-BIFTOOL developed by Engelborghs et al. guide some numerical simulations to identify ranges of parameters for coexisting multiple attractive periodic solutions.

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1. Introduction

Experimental data collected by the Australian entomologist Nicholson [23,24] has motivated much entomological, mathematical and statistical research. In particular, Gurney et al. [10] proposed a delay differential equation to explain the oscillatory behavior of the observed sheep blowfly *Lucilia cuprina* population in [23]. The model developed by Gurney et al. [10] takes the simple-looking form

$$N'(t) = f\big(N(t-\tau)\big) - \gamma N(t) \tag{1.1}$$

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with $f(N) = pNe^{-\alpha N}$. Here $N(t)$ denotes the population of sexually mature adults at time t, p is the maximum possible per capita egg production rate, $1/\alpha$ is the population size at which the whole population reproduces at its maximum rate. In the model, τ is the generation time, or the time taken from eggs to sexually mature adults, and γ is the per capita mortality rate of adults. Model (1.1) is called Nicholson's blowflies equation. It was used by Oster and Ipaktchi [25] for the development of an insect population, and its modifications have been intensively studied in the literature of theoretical biology and delay differential equations. Notably, it has been shown that a unique positive equilibrium of (1.1) is globally asymptotically stable (with respect to nonnegative and nontrivial initial conditions) for any $\tau \geqslant 0$ provided that $1 < p/\gamma < e^2$ (see, for example, [12,16,28]). In the case where $p/\gamma > e^2$, the positive equilibrium loses its local stability and Hopf bifurcations occur at an unbounded sequence of critical values. The existence of periodic solutions when the delay τ is not necessarily near the local Hopf bifurcation values was established by Wei and Li [33], using a global Hopf bifurcation theorem coupled with Bendixson's criterion for higher dimensional ordinary differential equations.

In the aforementioned work and much of the existing literature, the mortality of the population during the maturation process has been ignored. Consideration of the survival probability during the maturation period requires an additional multiplier, which is delay-dependent, to be incorporated into the nonlinear delayed feedback term. This leads to the delay differential equation with a delay-dependent coefficient as follows:

$$N'(t) = e^{-\delta\tau} f\big(N(t-\tau)\big) - \gamma N(t), \tag{1.2}$$

where $\delta > 0$ is the death rate of the immature population. One can of course derive this model, as did in [3,22], from a structured population model for $u(t,a)$ (the population density at age a and time t) as below

$$\partial_t u(t,a) + \partial_a u(t,a) = -\mu(a)u(t,a),$$

with the stage-specific mortality rate

$$\mu(a) = \begin{cases} \gamma, & a > \tau, \\ \delta, & a < \tau. \end{cases}$$

A simple application of the integration along characteristic lines leads to the model equation for the matured population $N(t) = \int_\tau^\infty u(t,a)\,da$ with Ricker's type birth function f.

The additional term $e^{-\delta\tau}$ is the probability of immature population surviving τ time units before becoming mature. This addition, as we shall show, leads to rather different dynamics for model (1.2). More specifically, as the delay τ increases, the positive equilibrium loses its stability and undergoes local Hopf bifurcations at a *finite even number* of critical values, and as τ passes a critical threshold, the positive equilibrium regains its stability. As τ keeps increasing and passes another threshold value, the positive equilibrium disappears and the species becomes extinct (the zero solution is globally asymptotically stable). We also observe the coexistence of multiple stable periodic solutions. We note that the coexistence of stable periodic solutions has been a remarkable phenomena in biological systems [2,11,18,26] and our work seems to be the first result for the simple-looking blowflies delay differential equation.

The rest of this paper is organized as follows. Section 2 collects some preliminary results on the structure of equilibria, and the global stability of the trivial equilibrium. We then, in Section 3, focus on the (local) stability and Hopf bifurcation analysis about the positive equilibrium. The global continuation of Hopf bifurcations is examined in Section 4, and numerical simulations based on the bifurcation analysis are reported in Section 5. We then conclude the paper with a summary and some discussions in Section 6.

2. Preliminaries

For any $\tau > 0$, let $\mathcal{C} := C([-\tau, 0], \mathbb{R})$ be the Banach space of continuous functions on $[-\tau, 0]$ with the norm defined as $\|\phi\| = \sup_{-\tau \leqslant \theta \leqslant 0} |\phi(\theta)|$ for $\phi \in \mathcal{C}$. Initial conditions, as inspired by the biological applications are taken from the nonnegative cone $\mathcal{C}^+ := C([-\tau, 0], \mathbb{R}_+)$. For a nontrivial solution, we always assume that the initial condition is given in the form of $N_0 = \phi$, $\phi \in \mathcal{C}^+$ and $\phi(0) > 0$. It can then be shown that for any such nontrivial initial value $N_0 = \phi$, system (1.2) admits a unique solution N_t through ϕ [13], and $N(t) > 0$ for $t > 0$.

Next, we show that all solutions of (1.2) are ultimately bounded. It follows from (1.2) and

$$f(x) = pxe^{-\alpha x} \leqslant f\left(\frac{1}{\alpha}\right) = \frac{p}{\alpha e}$$

for all $x \geqslant 0$ that

$$N'(t) \leqslant -\gamma N(t) + \frac{pe^{-\delta\tau}}{\alpha e}.$$

Thus

$$\limsup_{t\to\infty} N(t) \leqslant \frac{pe^{-\delta\tau}}{\alpha e \gamma}.$$

Summarizing the discussion above, we arrive at the following preliminary result.

Proposition 2.1. *For system* (1.2) *with nontrivial initial conditions, all solutions are positive and ultimately uniformly bounded in $\mathcal{C}^+$.*

Let

$$R_0 = \frac{pe^{-\delta\tau}}{\gamma}. \tag{2.1}$$

It is clear that if $R_0 \leqslant 1$, then model (1.2) admits only the trivial equilibrium $N = 0$, and if $R_0 > 1$, then, in addition to the trivial equilibrium, there is a unique positive equilibrium

$$N^* = \frac{1}{\alpha}\left(\ln\frac{p}{\gamma} - \delta\tau\right). \tag{2.2}$$

As R_0 is really the basic reproduction ratio of the system, the following result for the global attractivity of the trivial equilibrium is anticipated.

Theorem 2.2. *If $R_0 \leqslant 1$, then the trivial equilibrium 0 of (1.2) is globally asymptotically stable in $\mathcal{C}^+$. If $R_0 > 1$, then 0 is unstable and there exists a unique positive equilibrium N^*, which is given by (2.2).*

Proof. The characteristic equation associated with the linearization of model (1.2) at 0 is

$$\lambda + \gamma - e^{-\delta\tau} pe^{-\lambda\tau} = 0.$$

It is well known that all roots of this equation have negative real parts if and only if $R_0 < 1$, i.e., $0 < e^{-\delta\tau} p < \gamma$, and there exists at least one positive root if $R_0 > 1$ ([14, Theorem A.5] or [27]). This

shows that the trivial equilibrium is locally asymptotically stable provided that $R_0 < 1$, and is unstable if $R_0 > 1$.

Next we establish the global attractivity of the trivial equilibrium by using a Lyapunov functional $L : \mathcal{C}^+ \to \mathbb{R}$,

$$L(N_t) = N_t(0) + e^{-\delta\tau} \int_{-\tau}^{0} p N_t(s) e^{-\alpha N_t(s)} \, ds.$$

Calculating the time derivative of L along solutions of model (1.2), we obtain

$$L'|_{(1.2)} = -\gamma N(t) + e^{-\delta\tau} p N(t) e^{-aN(t)} \leqslant \gamma (R_0 - 1) N(t) \leqslant 0$$

if $R_0 \leqslant 1$, and $L'|_{(1.2)} = 0$ if and only if $N(t) = 0$. Thus, the global stability of the trivial equilibrium follows from the Lyapunov–LaSalle invariance principle [13]. $\square$

3. Stability and Hopf bifurcation of the positive equilibrium

In this section we assume that $R_0 > 1$, which ensures the existence of the positive equilibrium N^*. We investigate the stability of N^* and identify the parameter range in which the time delay can destabilize N^*, leading to Hopf bifurcations.

Let $\tau_{\max} = (1/\delta) \ln(p/\gamma)$. Then $R_0 > 1$ if and only if $p/\gamma > 1$ and $0 \leqslant \tau < \tau_{\max}$. Therefore, throughout this section, we assume that $p/\gamma > 1$. Next we investigate the dynamics of model (1.2) for $\tau \in [0, \tau_{\max})$. Linearizing (1.2) around N^* we obtain

$$N'(t) = -\gamma N(t) + b(\tau) N(t - \tau), \tag{3.1}$$

where

$$b(\tau) = \gamma \left(1 - \ln \frac{p}{\gamma} + \delta\tau \right). \tag{3.2}$$

The characteristic equation of (3.1) is

$$\lambda + \gamma - b(\tau) e^{-\lambda\tau} = 0. \tag{3.3}$$

We use the delay $\tau > 0$ as a bifurcation parameter and investigate the stability changes at N^* and the existence of periodic oscillations. First we note that when $\tau = 0$, the characteristic equation (3.3) gives

$$\lambda = b(0) - \gamma = -\gamma \ln \frac{p}{\gamma} < 0.$$

Thus a stability change at N^* can only happen when there are characteristic roots crossing the imaginary axis to the right. We thus look for a pair of purely imaginary roots $\lambda = \pm i\omega$ with $\omega > 0$ for $\tau > 0$. Substituting $\lambda = i\omega$ into (3.3) and separating the real and imaginary parts, we obtain

$$\omega + b(\tau) \sin \omega\tau = 0, \qquad \gamma - b(\tau) \cos \omega\tau = 0.$$

Equivalently,

$$\sin \omega\tau = -\frac{\omega}{b(\tau)}, \qquad \cos\omega\tau = \frac{\gamma}{b(\tau)}. \tag{3.4}$$

Squaring and adding both equations of (3.4) lead to

$$\omega^2 = b^2(\tau) - \gamma^2. \tag{3.5}$$

Therefore, Eq. (3.5) has a positive root if and only if $|b(\tau)| > \gamma$ or equivalently,

$$\frac{p}{\gamma} > e^2 \quad \text{and} \quad \tau < \frac{1}{\delta}\left(\ln\frac{p}{\gamma} - 2\right) =: \hat{\tau}. \tag{3.6}$$

This immediately gives the following result on the stability of N^*: if

$$1 < \frac{p}{\gamma} \leqslant e^2, \quad \text{and} \quad \tau \in [0, \tau_{\max}),$$

then model (1.2) has a unique positive equilibrium N^*, which is locally asymptotically stable.

In the sequel, we assume that

($\mathbf{H_1}$) $p/\gamma > e^2$ and $0 < \tau < \hat{\tau}$.

Then Eq. (3.5) has a unique positive real root

$$\omega = \omega(\tau) = \sqrt{b^2(\tau) - \gamma^2}. \tag{3.7}$$

Note that the existence of positive ω alone does not ensure that Eqs. (3.4) have a solution (ω, τ) as this is only a necessary condition for (3.3) to have a pair of purely imaginary roots $\pm i\omega$. It follows from ($\mathbf{H_1}$) that $\delta\tau + 1 < \ln(p/\gamma) - 1 < \ln(p/\gamma)$, which implies that $b(\tau) < 0$. Thus we have from (3.4) that $\sin\omega\tau > 0$ and $\cos\omega\tau < 0$, which implies that $\omega\tau \in (\pi/2 + 2n\pi, \pi + 2n\pi)$ for some nonnegative integer n. Substituting (3.7) into (3.4) gives

$$\sin\left(\tau\sqrt{b^2(\tau) - \gamma^2}\right) = -\frac{\sqrt{b^2(\tau) - \gamma^2}}{b(\tau)}, \qquad \cos\left(\tau\sqrt{b^2(\tau) - \gamma^2}\right) = \frac{\gamma}{b(\tau)}. \tag{3.8}$$

If (3.8) has a solution in $(0, \hat{\tau})$, then (3.3) has a pair of purely imaginary roots $\pm i\omega$ with ω given by (3.7). Therefore, we seek positive solutions of Eqs. (3.8) in $(0, \hat{\tau})$.

Let n be a nonnegative integer and $x = \theta_n(\tau)$ be the unique solution of the equation

$$\cos x = -\frac{\gamma\tau}{\sqrt{x^2 + \gamma^2\tau^2}}, \quad x \in \left(\frac{\pi}{2} + 2n\pi, \pi + 2n\pi\right).$$

It follows from the Implicit Function Theorem that for fixed n, $\theta_n(\tau)$ is continuous on $[0, \hat{\tau}]$ and differentiable on $(0, \hat{\tau})$, with $\theta_n(0) = \pi/2 + 2n\pi$. Note that $b(\hat{\tau}) = -\gamma$. Thus $\omega(\tau) \to 0$, $\sin\theta_n(\tau) \to 0$ and $\cos\theta_n(\tau) \to -1$ as $\tau \to \hat{\tau}$. As a consequence, $\theta_n(\hat{\tau}) = \pi + 2n\pi$. Moreover, using the fact that $\sin x = x/\sqrt{x^2 + \gamma^2\tau^2}$, we have

$$\theta'_n(\tau) = \frac{\gamma\theta_n(\tau)}{\theta_n^2(\tau) + \gamma^2\tau^2 + \gamma\tau} > 0 \tag{3.9}$$

and

$$\theta_n''(\tau) = -\frac{2\gamma\theta_n(\tau)(\theta_n(\tau)\theta_n'(\tau) + \gamma\tau)}{(\theta_n^2(\tau) + \gamma^2\tau^2 + \gamma\tau)^2} < 0$$

for all $\tau \in (0, \hat{\tau})$. Hence $\theta_n(\tau)$ is strictly increasing and concave down on $\tau \in [0, \hat{\tau}]$ for all n.

Define a function

$$S(\tau) = \tau\sqrt{b^2(\tau) - \gamma^2}, \quad \tau \in [0, \hat{\tau}].$$

We note that $S(\tau)$ is always nonnegative and

$$S'(\tau) = \frac{b^2(\tau) - \gamma^2 + \gamma\delta\tau b(\tau)}{\sqrt{b^2(\tau) - \gamma^2}}. \tag{3.10}$$

Denote $S_1(\tau) = b^2(\tau) - \gamma^2 + \gamma\delta\tau b(\tau)$. Substituting $b(\tau)$ into $S_1(\tau)$, we have

$$S_1(\tau) = 2\delta^2\gamma^2\tau^2 + 3\delta\gamma^2\left(1 - \ln\frac{p}{\gamma}\right)\tau + \gamma^2\ln\frac{p}{\gamma}\left(\ln\frac{p}{\gamma} - 2\right).$$

It is easy to check that $S_1(\tau)$ has two positive zeros c and $\bar{c}$ with

$$c = \frac{3(\ln\frac{p}{\gamma} - 1) - \sqrt{(\ln\frac{p}{\gamma})^2 - 2\ln\frac{p}{\gamma} + 9}}{4\delta},$$

$$\bar{c} = \frac{3(\ln\frac{p}{\gamma} - 1) + \sqrt{(\ln\frac{p}{\gamma})^2 - 2\ln\frac{p}{\gamma} + 9}}{4\delta}. \tag{3.11}$$

It is readily seen from ($\mathbf{H}_1$) that $c < \hat{\tau} < \bar{c}$. Thus $S_1(\tau) > 0$ on $[0, c)$ and $S_1(\tau) < 0$ on $(c, \hat{\tau}]$, which implies that $S(\tau)$ is strictly increasing on $[0, c)$ and strictly decreasing on $(c, \hat{\tau}]$. We further have

$$S''(\tau) = \frac{\gamma\delta}{(b^2(\tau) - \gamma^2)^{3/2}}\left(2b(\tau)\left(b^2(\tau) - \gamma^2\right) - \delta\gamma^2\tau\right) < 0$$

for $\tau \in (0, \hat{\tau})$. Therefore, $S(\tau)$ is strictly increasing on $[0, c)$ and strictly decreasing on $(c, \hat{\tau}]$. Moreover, $S(\tau)$ is concave down on $[0, \hat{\tau}]$ with its maximum value being $S(c) = c\sqrt{b^2(c) - \gamma^2}$, and $S(0) = S(\hat{\tau}) = 0$. Observe that $\tau = \tau^* > 0$ is a solution of (3.8) if and only if $\theta_n(\tau^*) = S(\tau^*)$ for some nonnegative integer n. Thus we arrive at the following result.

Lemma 3.1. *The function $\theta_n(\tau)$ is strictly increasing and concave down on $\tau \in [0, \hat{\tau}]$ satisfying $\theta_n(0) = \pi/2 + 2n\pi$ and $\theta_n(\hat{\tau}) = \pi + 2n\pi$ for all nonnegative integers n. The function $S(\tau)$ is concave down on $[0, \hat{\tau}]$ with its maximum value being $S(c) = c\sqrt{b^2(c) - \gamma^2}$, and $S(0) = S(\hat{\tau}) = 0$. Let K be the smallest integer such that $S(c) < \theta_K(c)$. Then we have the following:*

 (i) *For any nonnegative integer $j \geqslant K + 1$, $S(\tau) - \theta_j(\tau)$ has no zeros in $[0, \hat{\tau}]$;*
 (ii) *Eqs. (3.8) have at least K roots in $[0, c)$, and exactly K roots in $[c, \hat{\tau}]$.*

Proof. We are left to show (i) and (ii). Note that $S(\tau) \leqslant S(c) < \theta_K(c) < \pi + 2K\pi < \theta_j(\tau)$ for any $j \geqslant K + 1$, $\tau \in [0, \hat{\tau}]$, thus (i) follows.

For any $0 \leqslant j \leqslant K - 1$, we have $\theta_j(c) \leqslant \theta_{K-1}(c) \leqslant S(c)$ and $\theta_j(0) > 0 = S(0)$. Moreover, $\theta_j'(c) > 0 = S'(c)$, it follows from the Intermediate Value Theorem that $S(\tau) - \theta_j(\tau)$ has at least one zero in $[0, c)$. This implies that Eqs. (3.8) have at least K roots in $[0, c)$. Now, we show that Eqs. (3.8) have exactly K roots in $[c, \hat{\tau}]$. We note that $S(\tau) - \theta_j(\tau)$ is strictly decreasing in $(c, \hat{\tau}]$ for any nonnegative integer j. Furthermore, $S(\hat{\tau}) = 0 < \theta_j(\hat{\tau}) = \pi + 2j\pi$, it follows that $S(\tau) - \theta_j(\tau)$ has exactly one zero in $[c, \hat{\tau}]$ if and only if $S(c) \geqslant \theta_j(c)$, which happens if and only if $0 \leqslant j \leqslant K - 1$. The proof is complete. $\square$

In order to show that there are only a finite number of distinct positive solutions to (3.8), we require a generic transversality condition. By (3.9) and (3.10), at any τ such that $S(\tau) = \theta_j(\tau)$, we have

$$
\begin{aligned}
S'(\tau) - \theta_j'(\tau) &= \frac{b^2(\tau) - \gamma^2 + \delta\gamma\tau b(\tau)}{\sqrt{b^2(\tau) - \gamma^2}} - \frac{\gamma\theta_j(\tau)}{\theta_j^2(\tau) + \gamma^2\tau^2 + \gamma\tau} \\
&= \frac{b^2(\tau) - \gamma^2 + \delta\gamma\tau b(\tau)}{\sqrt{b^2(\tau) - \gamma^2}} - \frac{\gamma\tau\sqrt{b^2(\tau) - \gamma^2}}{\tau^2(b^2(\tau) - \gamma^2) + \gamma^2\tau^2 + \gamma\tau} \\
&= \frac{\tau b(\tau)}{\sqrt{b^2(\tau) - \gamma^2}(\tau b^2(\tau) + \gamma)}\left(b^3(\tau) - b(\tau)\gamma^2 + \delta\gamma^2 + \delta\gamma\tau b^2(\tau)\right). \quad (3.12)
\end{aligned}
$$

Define the function

$$
g(\tau) = b^3(\tau) - b(\tau)\gamma^2 + \delta\gamma^2 + \delta\gamma\tau b^2(\tau), \quad \tau \geqslant 0. \tag{3.13}
$$

We claim that $g(\tau)$ is a strictly increasing function on $[0, c]$ with $g(0) < 0$ and $g(c) > 0$. In fact, we have $g(c) = \delta\gamma^2 > 0$ and

$$
\begin{aligned}
g'(\tau) &= \delta\gamma\left(4b^2(\tau) + 2\delta\gamma\tau b(\tau) - \gamma^2\right) \\
&= \delta\gamma^3\left(6\delta^2\tau^2 - 10\left(\ln\frac{p}{\gamma} - 1\right)\delta\tau + 4\left(\ln\frac{p}{\gamma} - 1\right)^2 - 1\right),
\end{aligned}
$$

which is a quadratic polynomial of τ and has two positive roots with the smaller one given by

$$
\frac{5(\ln\frac{p}{\gamma} - 1) - \sqrt{(\ln\frac{p}{\gamma} - 1)^2 + 6}}{6\delta} > c,
$$

where c is defined in (3.11). Since the leading coefficient of $g'(\tau)$ is positive, we have $g'(\tau) > 0$ for any $\tau \in [0, c]$. Next, we show that $g(0) < 0$, which, from the definition of $b(\tau)$ in (3.2) and $g(\tau)$ in (3.13), is equivalent to the inequality

$$
\gamma\left(1 - \ln\frac{p}{\gamma}\right)^3 - \gamma\left(1 - \ln\frac{p}{\gamma}\right) + \delta < 0. \tag{3.14}
$$

Note that positive solutions of (3.8) exist only if $S(c) > \pi/2$, which is the same as

$$
(c\delta)^2\left(\left(1 - \ln\frac{p}{\gamma} + c\delta\right)^2 - 1\right) > \frac{\pi^2\delta^2}{4\gamma^2}.
$$

For simplicity, we denote $u = c\delta > 0$ and $a = \ln(p/\gamma) - 1 > 1$. The above inequality can be written as

$$\frac{\pi^2 \delta^2}{\gamma^2} < 2u^2 \big(2(u-a)^2 - 2\big). \tag{3.15}$$

On the other hand, we obtain from $S'(c) = 0$ that $2u^2 - 3au + a^2 - 1 = 0$ and

$$u = \frac{3a - \sqrt{a^2 + 8}}{4} < \frac{a^2 - 1}{3}$$

since $a > 1$. Substituting $2u^2$ by $3au - a^2 + 1$ and applying the above inequality for u into (3.15) yield

$$\frac{\pi^2 \delta^2}{\gamma^2} < \big(3au - a^2 + 1\big)\big(-au + a^2 - 1\big)$$

$$= -3a^2 u^2 + 4au\big(a^2 - 1\big) - \big(a^2 - 1\big)^2$$

$$< \frac{4a^2(a^2 - 1)^2}{3},$$

which implies

$$\frac{\delta}{\gamma} < \frac{2}{\sqrt{3}\pi} a\big(a^2 - 1\big) < a^3 - a = \left(\ln \frac{p}{\gamma} - 1\right)^3 - \left(\ln \frac{p}{\gamma} - 1\right).$$

Thus, (3.14) follows and we conclude that $g(0) < 0$. This proves our claim. Therefore, $g(\tau)$ has a unique root, denoted by c_0, in $[0, c]$. Furthermore, we have $g(\tau) < 0$ for $\tau \in [0, c_0)$ and $g(\tau) > 0$ for $\tau \in (c_0, c]$. Thus, it follows from (3.12) and the fact $b(\tau) < 0$ that if $\tau \in [0, c_0)$, then $S'(\tau) - \theta'_j(\tau) > 0$ for all integers $j \geqslant 0$; and if $\tau \in (c_0, c]$, then $S'(\tau) - \theta'_j(\tau) < 0$ for all integers $j \geqslant 0$.

For $\tau \in (c, \hat{\tau}]$, we have $S_1(\tau) = b^2(\tau) - \gamma^2 + \gamma \delta \tau b(\tau) < 0$, which together with the fact $b(\tau) < 0$ implies that $g(\tau) = b(\tau)S_1(\tau) + \delta \gamma^2 > 0$. This yields $S'(\tau) - \theta'_j(\tau) < 0$ for all integers $j \geqslant 0$ when $\tau \in (c, \hat{\tau}]$. Summarizing the above argument, we obtain the following lemma.

Lemma 3.2. *Assume that $S(c) > \pi/2$. Let c_0 be the unique root of $g(\tau) = 0$ on the interval $[0, c]$ with $g(\tau)$ defined in (3.13). Then for any integer $j \geqslant 0$,*

$$S'(\tau) - \theta'_j(\tau) \begin{cases} > 0, & \tau \in [0, c_0), \\ < 0, & \tau \in (c_0, \hat{\tau}]. \end{cases}$$

It can be observed from the above lemma that $S(\tau) - \theta_j(\tau)$ is strictly increasing in $(0, c_0)$ and strictly decreasing in $(c_0, \hat{\tau})$, which implies that it attains its maximum at $\tau = c_0$. We next use this fact to prove the following proposition.

Proposition 3.3. *Assume that $S(c_0) > \theta_0(c_0)$, where c_0 is defined in Lemma 3.2. Let K_1 be the smallest integer such that $S(c_0) \leqslant \theta_{K_1}(c_0)$. Then there are exactly $2K_1$ positive numbers $0 < \tau_0 < \tau_1 < \cdots < \tau_{2K_1-1} < \hat{\tau}$ such that $\tau_{K_1-1} < c_0 < \tau_{K_1}$ and $\theta_n(\tau_n) = S(\tau_n)$, $\theta_n(\tau_{2K_1-n-1}) = S(\tau_{2K_1-n-1})$ for $0 \leqslant n \leqslant K_1 - 1$. Moreover, $K_1 = K$ if $S(c_0) \leqslant \theta_K(c_0)$; and $K_1 = K + 1$ if $S(c_0) > \theta_K(c_0)$, where K is defined in Lemma 3.1.*

Proof. From the choice of K_1, we have $S(c_0) > \theta_j(c_0)$ for all $0 \leqslant j < K_1$ and $S(c_0) \leqslant \theta_j(c_0)$ for all $j \geqslant K_1$. Note that $S(c) > S(c_0) > \theta_0(c_0) > \theta_0(0) = \pi/2$. It then follows from Lemma 3.1 and Lemma 3.2 that for $j \geqslant K_1$, $S(\tau) - \theta_j(\tau)$ has no simple zero in $[0, \hat{\tau}]$, and for $0 \leqslant j < K_1$, $S(\tau) - \theta_j(\tau)$ has

exactly two distinct simple zeros; one in the interval $(0, c_0)$, denoted by τ_j, and the other in the interval $(c_0, \hat{\tau})$, denoted by τ_{2K_1-j-1}, respectively. Especially, by choosing $j = K_1 - 1$ we obtain $0 < \tau_{K_1-1} < c_0 < \tau_{K_1} < \hat{\tau}$. Moreover, from the monotonicity of $S(\tau) - \theta_j(\tau)$ with respect to j we have $\tau_0 < \tau_1 < \cdots < \tau_{2K_1-1}$.

Finally, from the definition of K in Lemma 3.1, we have $\theta_{K-1}(c) \leqslant S(c) < \theta_K(c)$. If $S(c_0) \leqslant \theta_K(c_0)$, it then follows from $S(c_0) - \theta_{K-1}(c_0) > S(c) - \theta_{K-1}(c) \geqslant 0$ that $K_1 = K$. Here we have made use of the fact that $S(\tau) - \theta_{K_1}(\tau)$ achieves its maximum at $\tau = c_0$ (Lemma 3.1). If $S(c_0) > \theta_K(c_0)$, then $\theta_j(\tau) \in [\pi/2 + 2j\pi, \pi + 2j\pi]$ and thus $\theta_K(c) < \theta_{K+1}(c)$. Therefore, we obtain from $S(c_0) < S(c) < \theta_K(c) < \theta_{K+1}(c)$ that $K_1 = K + 1$. This ends the proof. □

Lemma 3.4. *Let* $\lambda(\tau) = \xi(\tau) + i\omega(\tau)$ *be a root of the characteristic equation* (3.3) *near* $\tau = \tau^*$ *satisfying* $\xi(\tau^*) = 0$ *and* $\omega^* = \omega(\tau^*) > 0$. *Then we have the following transversality condition:*

$$\operatorname{sgn}\left(\frac{d\operatorname{Re}(\lambda(\tau^*))}{d\tau}\right) = \operatorname{sgn}\left(S'(\tau^*) - \theta_j'(\tau^*)\right)$$

for some integer $j \geqslant 0$.

Proof. Substituting $\lambda(\tau)$ into the characteristic equation (3.3) and taking the derivative with respective to τ, we obtain

$$\frac{d\lambda}{d\tau} - e^{-\lambda\tau}\frac{db(\tau)}{d\tau} + b(\tau)e^{-\lambda\tau}\left(\lambda + \tau\frac{d\lambda}{d\tau}\right) = 0.$$

Note that $b'(\tau) = \delta\gamma$ and $e^{-\lambda\tau} = (\lambda + \gamma)/(b(\tau))$. Then

$$\frac{d\lambda}{d\tau} = \frac{-b(\tau)\lambda^2 + \delta\gamma\lambda - b(\tau)\gamma\lambda + \delta\gamma^2}{\tau b(\tau)\lambda + b(\tau) + \tau\gamma b(\tau)}. \tag{3.16}$$

It follows from (3.16) that at $\tau = \tau^*$, $\lambda = i\omega^*$ and

$$\begin{aligned}
\frac{d\operatorname{Re}(\lambda(\tau^*))}{d\tau} &= \operatorname{Re}\left(\frac{b(\tau^*)\omega^{*2} + \delta\gamma^2 + (\delta - b(\tau^*))\gamma\omega^* i}{b(\tau^*) + \tau^*\gamma b(\tau^*) + \tau^* b(\tau^*)\omega^* i}\right) \\
&= \frac{b^4(\tau^*) - b^2(\tau^*)\gamma^2 + \delta\gamma\tau^* b^3(\tau^*) + \delta\gamma^2 b(\tau^*)}{(b(\tau^*) + \tau^*\gamma b(\tau^*))^2 + (\tau^* b(\tau^*)\omega^*)^2} \\
&= \frac{b(\tau^*)g(\tau^*)}{(b(\tau^*) + \tau^*\gamma b(\tau^*))^2 + (\tau^* b(\tau^*)\omega^*)^2}.
\end{aligned}$$

Therefore, by (3.12), we obtain

$$\operatorname{sgn}\left(\frac{d\operatorname{Re}(\lambda(\tau^*))}{d\tau}\right) = \operatorname{sgn}\left(b(\tau^*)g(\tau^*)\right) = \operatorname{sgn}\left(S'(\tau^*) - \theta_j'(\tau^*)\right). \qquad \square$$

Remark 3.5. Note that in the classical Hopf bifurcation theorem, the transversality condition is $\operatorname{sgn}(d\operatorname{Re}(\lambda(\tau^*))/d\tau) \neq 0$. Here, we provide a simple geometric method to check the conditions by determining whether the two curves $S(\tau)$ and $\theta_j(\tau)$ intersect transversally for some integer $j \geqslant 0$.

Now, applying Lemmas 3.2, 3.4 and Proposition 3.3 to the characteristic equation (3.3), and noting that 0 is a root if and only if $\ln(p/\gamma) = \delta\tau$, i.e., $R_0 = 1$, we have the following theorem concerning the stability of the positive equilibrium N^* of model (1.2) and Hopf bifurcation.

Theorem 3.6. *Consider model* (1.2).

(i) *If* $1 < p/\gamma \leqslant e^2$, *then* N^* *is asymptotically stable for all* $\tau \in [0, \tau_{\max})$.
(ii) *Assume* $p/\gamma > e^2$, *and let* $\hat{\tau}$, c_0, K_1 *be defined in* (**H**$_1$), *Lemma* 3.2 *and Proposition* 3.3, *respectively. Then we have the following results*:
    (a) *If* $S(c_0) \leqslant \theta_0(c_0)$, *then* N^* *is asymptotically stable for all* $\tau \in [0, \tau_{\max})$.
    (b) *If* $S(c_0) > \theta_0(c_0)$, *then there exist exactly* $2K_1$ *local Hopf bifurcation values, namely,* $0 < \tau_0 < \tau_1 < \cdots < \tau_{2K_1-1} < \hat{\tau}$ *such that model* (1.2) *undergoes a Hopf bifurcation at* N^* *when* $\tau = \tau_j$ *for* $0 \leqslant j \leqslant 2K_1 - 1$. *Given any* $n \in \{0, 1, \ldots, K_1 - 1\}$, *when* τ *is sufficiently close to* τ_n, *the period of the periodic solution is in the interval* $(2\tau_n/(2n+1), 4\tau_n/(4n+1))$; *when* τ *is sufficiently close to* τ_{2K_1-n-1}, *the period of the periodic solution is in the interval* $(2\tau_{2K_1-n-1}/(2n+1), 4\tau_{2K_1-n-1}/(4n+1))$. *Furthermore,* N^* *is asymptotically stable for* $\tau \in [0, \tau_0) \cup (\tau_{2K_1-1}, \tau_{\max})$, *and unstable for* $\tau \in (\tau_0, \tau_{2K_1-1})$.

Proof. (i) has been verified earlier.

(iia) If $S(c_0) < \theta_0(c_0)$, then $S(\tau) - \theta_0(\tau) \leqslant S(c_0) - \theta_0(c_0) < 0$ for all $\tau \in [0, \hat{\tau}]$, which implies that N^* is asymptotically stable for all $\tau \in [0, \hat{\tau}]$. When $\tau \in [\hat{\tau}, \tau_{\max})$, we have $|b(\tau)| < \gamma$, which excludes the existence of purely imaginary eigenvalues and thus implies that N^* is also asymptotically stable for all $\tau \in [0, \tau_{\max})$.

If $S(c_0) = \theta_0(c_0)$, then $S(\tau) - \theta_n(\tau)$ has no zero in $[0, \hat{\tau}]$ for $n \geqslant 1$ and $S(\tau) - \theta_0(\tau)$ has one double zero c_0 in $[0, \hat{\tau}]$, which imply that the transversality condition is not satisfied and all eigenvalues remain to the left of the pure imaginary axis. Therefore, N^* is still asymptotically stable for $\tau \in [0, \hat{\tau}]$. Similarly, we can extend the stable region to $[0, \tau_{\max})$ because $|b(\tau)| < \gamma$ for $\tau \in [\hat{\tau}, \tau_{\max})$.

(iib) If $S(c_0) > \theta_0(c_0)$, then it follows from Proposition 3.3 that there are exactly $2K_1$ positive simple roots, namely, $0 < \tau_0 < \tau_1 < \cdots < \tau_{2K_1-1} < \tau_{\max}$ such that $\tau_{K_1-1} < c_0 < \tau_{K_1}$ and

$$\theta_n(\tau_n) = S(\tau_n), \qquad \theta_n(\tau_{2K_1-n-1}) = S(\tau_{2K_1-n-1})$$

for $0 \leqslant n \leqslant K_1 - 1$. For any given $n \in \{0, 1, \ldots, K_1 - 1\}$, applying Lemma 3.4, we obtain

$$\text{sgn}\left(\frac{d\,\text{Re}(\lambda(\tau_n))}{d\tau}\right) = \text{sgn}\left(S'(\tau_n) - \theta_n'(\tau_n)\right) = 1,$$

$$\text{sgn}\left(\frac{d\,\text{Re}(\lambda(\tau_{2K_1-n-1}))}{d\tau}\right) = \text{sgn}\left(S'(\tau_{2K_1-n-1}) - \theta_n'(\tau_{2K_1-n-1})\right) = -1.$$

Therefore, this pair of simple conjugate purely imaginary eigenvalues $\pm i\omega(\tau_n)$ cross the imaginary axis from left to right, and the pair of simple conjugate purely imaginary eigenvalues $\pm i\omega(\tau_{2K_1-n-1})$ cross the imaginary axis from right to left. Thus, we can easily obtain the stability of N^* for $\tau \in [0, \hat{\tau}]$. Similar to (iia), we can obtain the stability of N^* for $\tau \in [\hat{\tau}, \tau_{\max})$. Note that

$$\frac{2\pi}{\omega(\tau_n)} = \frac{2\pi\tau_n}{\tau_n\sqrt{b^2(\tau_n) - \gamma^2}} = \frac{2\pi\tau_n}{\theta_n(\tau_n)},$$

$$\frac{2\pi}{\omega(\tau_{2K_1-n-1})} = \frac{2\pi\tau_{2K_1-n-1}}{\tau_{2K_1-n-1}\sqrt{b^2(\tau_{2K_1-n-1}) - \gamma^2}} = \frac{2\pi\tau_{2K_1-n-1}}{\theta_n(\tau_{2K_1-n-1})},$$

and $\theta_n \in (\frac{\pi}{2} + 2n\pi, \pi + 2n\pi)$. Therefore, we have

$$\frac{2\tau_n}{2n+1} < \frac{2\pi}{\omega(\tau_n)} < \frac{4\tau_n}{4n+1} \quad \text{and} \quad \frac{2\tau_{2K_1-n-1}}{2n+1} < \frac{2\pi}{\omega(\tau_{2K_1-n-1})} < \frac{4\tau_{2K_1-n-1}}{4n+1}.$$

The Hopf bifurcation theorem for delay differential equations [13,15] applies and there are small amplitude periodic solutions bifurcating at $\tau = \tau_n$ with periods between $2\tau_n/(2n+1)$ and $4\tau_n/(2n+1)$,

and at $\tau = \tau_{2K_1-n-1}$ with periods between $2\tau_{2K_1-n-1}/(2n+1)$ and $4\tau_{2K_1-n-1}/(4n+1)$ for $n \in \{0, 1, \ldots, K_1 - 1\}$. □

Remark 3.7.

(i) In case (iib) of Theorem 3.6, we notice that $K_1 \geqslant 1$ by the definition of K_1 in Proposition 3.3. Therefore, the necessary and sufficient condition for the occurrence of Hopf bifurcation is $p/\gamma > e^2$ and $S(c_0) > \theta_0(c_0)$.

(ii) It is noted that if $S(c) \leqslant \pi/2$, then $S(c_0) < \theta_0(c_0)$ is always satisfied. Thus we have a sufficient and easily verifiable condition for the nonexistence of Hopf bifurcations.

Let

$$\Gamma = \left\{ \phi \in C^+ : \|\phi\| \leqslant \frac{1}{\alpha}, \ \phi(0) > 0 \right\}$$

and

$$\bar{\tau} = \frac{1}{\delta}\left(\ln \frac{p}{\gamma} - 1 \right) \in (\hat{\tau}, \tau_{\max}).$$

Then by the method of Lyapunov functional, we obtain the following global stability result of N^*.

Theorem 3.8. *If either*

$$1 < \frac{p}{\gamma} \leqslant e, \quad and \quad \tau \in [0, \tau_{\max}) \tag{3.17}$$

or

$$\frac{p}{\gamma} > e, \quad and \quad \tau \in [\bar{\tau}, \tau_{\max}) \tag{3.18}$$

holds, then all solutions of model (1.2) *with nontrivial initial conditions converge to N^*.*

Proof. It follows from Eq. (1.2) that

$$N'(t) \leqslant -\gamma N(t) + \frac{p}{\alpha e^{\delta\tau+1}},$$

which, together with (3.17) and (3.18), implies that

$$\limsup_{t\to\infty} N(t) \leqslant \frac{p}{\alpha\gamma e^{\delta\tau+1}} \leqslant \frac{1}{\alpha} \quad and \quad N^* \in \left(0, \frac{1}{\alpha}\right].$$

Thus Γ is positively invariant and attracts all solutions of (1.2) with nontrivial initial conditions. This allows us to consider the solutions of (1.2) with initial conditions in Γ. Define a Lyapunov functional $V : \Gamma \to \mathbb{R}$,

$$V(N_t) = N_t(0) - N^* \ln N_t(0) + e^{-\delta\tau} \int_{-\tau}^{0} \left[f(N_t(s)) - f(N^*) \ln f(N_t(s)) \right] ds,$$

where $f(x) = pxe^{-\alpha x}$. Calculating the time derivative of L along the positive solutions of model (1.2), we obtain

$$V'|_{(1.2)} = -\gamma N(t) + \gamma N^* - \frac{N^*}{N(t)} e^{-\delta \tau} f\big(N(t-\tau)\big) + e^{-\delta \tau} f\big(N(t)\big)$$
$$- e^{-\delta \tau} f\big(N^*\big) \ln f\big(N(t)\big) + e^{-\delta \tau} f\big(N^*\big) \ln f\big(N(t-\tau)\big).$$

Using $e^{-\delta \tau} f(N^*) = \gamma N^*$ and denoting $h(x) = x - 1 - \ln x$ for $x > 0$, we obtain

$$V'|_{(1.2)} = -\gamma N(t) + e^{-\delta \tau} f\big(N(t)\big) - \gamma N^* \ln f\big(N(t)\big) + \gamma N^* \ln f\big(N(t-\tau)\big)$$
$$- \gamma N^* \ln \frac{N^* f(N(t-\tau))}{N(t) f(N^*)} - \gamma N^* h\left(\frac{N^* f(N(t-\tau))}{N(t) f(N^*)}\right)$$
$$= -\gamma N(t) + e^{-\delta \tau} f\big(N(t)\big) + \gamma N^* \ln \frac{N(t) f(N^*)}{N^* f(N(t))} - \gamma N^* h\left(\frac{N^* f(N(t-\tau))}{N(t) f(N^*)}\right).$$

We note that

$$-\gamma N(t) + e^{-\delta \tau} f\big(N(t)\big) = -\gamma N(t) + \gamma N^* \frac{f(N(t))}{f(N^*)}$$
$$= \gamma N(t)\left(-1 + \frac{N^* f(N(t))}{N(t) f(N^*)} - \frac{N^*}{N(t)} + \frac{f(N^*)}{f(N(t))}\right) + \gamma N^* - \gamma N(t) \frac{f(N^*)}{f(N(t))}$$
$$= \gamma N(t)\left(\frac{f(N(t))}{f(N^*)} - 1\right)\left(\frac{N^*}{N(t)} - \frac{f(N^*)}{f(N(t))}\right) + \gamma N^* - \gamma N(t) \frac{f(N^*)}{f(N(t))}.$$

Therefore,

$$V'|_{(1.2)} = \gamma N(t)\left(\frac{f(N(t))}{f(N^*)} - 1\right)\left(\frac{N^*}{N(t)} - \frac{f(N^*)}{f(N(t))}\right)$$
$$- \gamma N^* h\left(\frac{N^* f(N(t-\tau))}{N(t) f(N^*)}\right) - \gamma N^* h\left(\frac{N(t) f(N^*)}{N^* f(N(t))}\right).$$

Since the function $f(N)$ is strictly increasing and concave down on $[0, 1/\alpha]$, we obtain that

$$\left(\frac{f(N(t))}{f(N^*)} - 1\right)\left(\frac{N^*}{N(t)} - \frac{f(N^*)}{f(N(t))}\right) \leqslant 0$$

for $N(t) \leqslant 1/\alpha$, and the equality holds only if $N(t) = N^*$. We further note that $h(x) \geqslant 0$ for $x > 0$ and $h(x) = 0$ if and only if $x = 1$. Hence, $V'|_{(1.2)} \leqslant 0$ for all $N \in \Gamma$, and thus the omega limit sets of the solutions are contained in U, the largest invariant subset of $\{V'|_{(1.2)} = 0\}$. It can be verified that $V'|_{(1.2)} = 0$ implies $N(t) = N^*$. Therefore, $U = \{N^*\}$. By the Lyapunov–LaSalle invariance principle [13], we can conclude that the positive equilibrium N^* is globally asymptotically stable if either (3.17) or (3.18) holds. □

4. Onset and termination of Hopf branches

Note that Theorem 3.6 states that if $p/\gamma > e^2$, $\tau < \hat{\tau}$ and $S(c_0) > \theta_0(c_0)$, then periodic solutions can bifurcate from N^* when τ is near the local Hopf bifurcation values τ_j, $j = 0, 1, 2, \ldots, 2K_1 - 1$. In this section, we study the global continuation of these local bifurcating periodic solutions by using the global Hopf bifurcation theorem for delay differential equations [6,34] and show that model (1.2) admits periodic solutions globally for the delay τ in a finite interval (τ_0, τ_{2K_1-1}) including the values that are not necessarily near the local Hopf bifurcation values. Let $z(t) = N(\tau t)$, model (1.2) can be rewritten as a general functional differential equation in the following form

$$z'(t) = F(z_t, \tau, T), \quad (t, \tau, T) \in \mathbb{R} \times I \times \mathbb{R}_+, \tag{4.1}$$

where $I = (0, \tau_{\max})$ and

$$F(z_t, \tau, T) = -\gamma \tau z(t) + \tau e^{-\delta \tau} p z(t-1) e^{-\alpha z(t-1)}. \tag{4.2}$$

Here $z_t(\theta) = z(t + \theta)$ for $\theta \in [-1, 0]$, and $z_t \in X := C([-1, 0], \mathbb{R}_+)$. Identifying the subspace of X consisting of all constant functions from $[-1, 0]$ to $\mathbb{R}_+$ with $\mathbb{R}_+$, we obtain a restricted function given by

$$\widetilde{F} := F|_{\mathbb{R}_+ \times I \times \mathbb{R}_+} : \mathbb{R}_+ \times I \times \mathbb{R}_+ \to \mathbb{R}.$$

It follows from (4.2) that, for $(z, \tau, T) \in \mathbb{R}_+ \times I \times \mathbb{R}_+$, $\widetilde{F}$ takes the form

$$\widetilde{F}(z, \tau, T) = -\tau \gamma z + \tau e^{-\delta \tau} p z e^{-\alpha z}.$$

Obviously, $\widetilde{F}$ is twice continuously differentiable, i.e., the assumption (**A1**) in [34] holds. We denote the set of stationary solutions of Eq. (4.1) by

$$\mathbf{O}(F) = \left\{ (\tilde{z}, \tilde{\tau}, \widetilde{T}) \in \mathbb{R}_+ \times I \times \mathbb{R}_+ : \widetilde{F}(\tilde{z}, \tilde{\tau}, \widetilde{T}) = 0 \right\}.$$

It follows from Theorem 2.2 that $\mathbf{O}(F) = \{(0, \tau, T), (N^*, \tau, T); \ (\tau, T) \in I \times \mathbb{R}_+\}$. For any stationary solution $(\tilde{z}, \tau, T)$, the characteristic function is

$$\begin{aligned}
\triangle_{(\tilde{z}, \tau, T)}(\lambda) &= \lambda - DF(\tilde{z}, \tau, T)(e^{\lambda \cdot}) \\
&= \lambda + \tau \gamma - \tau e^{-\delta \tau} p e^{-\alpha \tilde{z}} (1 - \alpha \tilde{z}) e^{-\lambda}.
\end{aligned}$$

Note that, for any $(\tilde{z}, \tilde{\tau}, \widetilde{T}) \in \mathbf{O}(F)$, if $R_0 \neq 1$, then

$$DF(\tilde{z}, \tilde{\tau}, \widetilde{T}) \neq 0.$$

This implies that if $R_0 > 1$, then $\lambda = 0$ is not a characteristic value of any stationary solution of (4.1) and hence the assumption (**A2**) in [34] holds. It can be checked easily from (4.2) that the smoothness condition (**A3**) in [34] is satisfied. As in [34], a stationary solution $(\tilde{z}, \tilde{\tau}, \widetilde{T})$ of (4.1) is called a center if $\det \triangle_{(\tilde{z}, \tilde{\tau}, \widetilde{T})}(im(2\pi/\widetilde{T})) = 0$ for some positive integer m. A center $(\tilde{z}, \tilde{\tau}, \widetilde{T})$ is said to be isolated if it is the only center in some neighborhood of $(\tilde{z}, \tilde{\tau}, \widetilde{T})$ and it has only finitely many purely imaginary characteristic values of the form $im(2\pi/\widetilde{T})$, where m is an integer.

Theorem 3.6 implies that if $p/\gamma > e^2$, $0 \leqslant \tau < \tau_{\max}$ and $S(c_0) > \theta_0(c_0)$, then for each $n = 0, 1, \ldots, 2K_1 - 1$ the stationary solution $(N^*, \tau_n, 2\pi/(\omega_n \tau_n))$ is an isolated center of (4.1) with

$$\omega_n = \sqrt{b^2(\tau_n) - \gamma^2}, \qquad b(\tau_n) = \gamma\left(1 - \ln\frac{p}{\gamma} + \delta\tau_n\right), \tag{4.3}$$

and there is only one purely imaginary characteristic value of the form $im(2\pi/\widetilde{T})$ with $m = 1$ and $\widetilde{T} = 2\pi/(\omega_n\tau_n)$. Thus, $J(N^*, \tau_n, 2\pi/(\omega_n\tau_n))$, the set of all such positive integers m, contains only one element $\{1\}$. Moreover, if follows from Lemma 3.4 that the crossing number $\zeta_1(N^*, \tau_n, 2\pi/(\omega_n\tau_n))$ at each of these centers is

$$\begin{aligned}
\zeta_1\left(N^*, \tau_n, \frac{2\pi}{\omega_n\tau_n}\right) &= -\operatorname{sgn}\left(\left.\frac{d(\operatorname{Re}\lambda(\tau))}{d\tau}\right|_{\tau=\tau_n}\right) \\
&= -\operatorname{sgn}\left(S'(\tau_n) - \theta'_j(\tau_n)\right) \\
&= \begin{cases} -1, & 0 \leqslant n \leqslant K_1 - 1, \\ 1, & K_1 \leqslant n \leqslant 2K_1 - 1, \end{cases}
\end{aligned} \tag{4.4}$$

where $j \in \{0, 1, \ldots, K_1 - 1\}$ is the unique integer such that $S(\tau_n) = \theta_j(\tau_n)$, and thus the condition (**A4**) in [34] holds.

Next we define a closed subset $\Sigma(F)$ of $X \times I \times \mathbb{R}_+$ by

$$\Sigma(F) = Cl\big\{(z, \tau, T) \in X \times I \times \mathbb{R}_+ : z \text{ is a nontrivial T-periodic solution of } (4.1)\big\},$$

and for each $n = 0, 1, \ldots, 2K_1 - 1$, let $\mathcal{C}(N^*, \tau_n, 2\pi/(\omega_n\tau_n))$ denote the connected component of $(N^*, \tau_n, 2\pi/(\omega_n\tau_n))$ in $\Sigma(F)$, where ω_n and τ_n are defined in (4.3) and Proposition 3.3, respectively. $\mathcal{C}(N^*, \tau_n, 2\pi/(\omega_n\tau_n))$ is a nonempty subset of $\Sigma(F)$ by Theorem 3.6. It follows from the global bifurcation theorem [34, Theorem 3.3] that either

(a) $\mathcal{C}(N^*, \tau_n, 2\pi/(\omega_n\tau_n))$ is unbounded in $X \times I \times \mathbb{R}_+$, or
(b) $\mathcal{C}(N^*, \tau_n, 2\pi/(\omega_n\tau_n))$ is bounded, $\mathcal{C}(N^*, \tau_n, \frac{2\pi}{\omega_n\tau_n}) \cap \mathbf{O}(F)$ is finite and

$$\sum_{(\tilde{z}, \tau, T) \in \mathcal{C}(N^*, \tau_n, \frac{2\pi}{\omega_n\tau_n}) \cap \mathbf{O}(F)} \zeta_m(\tilde{z}, \tau, T) = 0$$

for all $m = 1, 2, \ldots$, where $\zeta_m(\tilde{z}, \tau, T)$ is the mth crossing number of $(\tilde{z}, \tau, T)$ if $m \in J(\tilde{z}, \tau, T)$, otherwise, $\zeta_m(\tilde{z}, \tau, T)$ is zero.

The subsequent four lemmas exclude case (a) and thus case (b) must hold.

Lemma 4.1. *All non-constant and nonnegative periodic solutions of* (4.1) *are uniformly bounded, namely, there exist constants $\varepsilon, M > 0$ such that for any $t \in \mathbb{R}$, $\varepsilon \leqslant z(t) \leqslant M$. Consequently, the projection of $\mathcal{C}(N^*, \tau_n, 2\pi/(\omega_n\tau_n))$ onto X is bounded.*

Proof. From the proof of Proposition 2.1, we obtain an upper bound $M := p/(\alpha e\gamma)$. We are left to show that any periodic solution $z(t)$ is bounded from below. Let $z_{\min} := \min_{t \in \mathbb{R}} z(t) = z(t_{\min})$ for some $t_{\min} > 0$. It follows from $z'(t_{\min}) = 0$ that

$$\gamma z_{\min} = e^{-\delta\tau} f\big(z(t_{\min} - 1)\big),$$

where $f(x) = pxe^{-\alpha x}$. Note that $f(x) > \gamma e^{\delta \tau} x$ for all $x \in (0, N^*)$. We claim $z(t_{\min} - 1) > N^*$; otherwise $f(z(t_{\min} - 1)) > \gamma e^{\delta \tau} z(t_{\min} - 1)$, which, together with the above equation, implies $z_{\min} > z(t_{\min} - 1)$, a contradiction to the definition of $z_{\min}$. Therefore, we have

$$\gamma z_{\min} = e^{-\delta \tau} f\big(z(t_{\min} - 1)\big) \geqslant e^{-\delta \tau} pN^* e^{-aM} =: \gamma \varepsilon.$$

This completes the proof. $\quad\square$

Lemma 4.2. *The projection of* $\mathcal{C}(N^*, \tau_n, 2\pi/(\omega_n \tau_n))$ *onto* I *is bounded.*

Proof. Note that N^* is globally asymptotically stable when $\tau = 0$. This excludes the existence of periodic solutions at $\tau = 0$. Theorem 3.8 shows that N^* is also globally asymptotically stable, and thus no periodic solution exists when $\tau \in [\bar{\tau}, \tau_{\max})$. Therefore, periodic solutions are possible only when τ is bounded. This ends the proof. $\quad\square$

Lemma 4.3. *Assume that* $p/\gamma > e^2$. *Then Eq.* (4.1) *has no periodic solution of period 2.*

Proof. Let $u(t)$ be a periodic solution of (4.1) with period 2. Set $u_1(t) = u(t)$ and $u_2(t) = u(t - 1)$. Then $(u_1(t), u_2(t))$ is a periodic solution of the following system of ordinary differential equations:

$$\begin{aligned} u_1'(t) &= -\tau \gamma u_1(t) + \tau e^{-\delta \tau} p u_2(t) e^{-\alpha u_2(t)}, \\ u_2'(t) &= -\tau \gamma u_2(t) + \tau e^{-\delta \tau} p u_1(t) e^{-\alpha u_1(t)}. \end{aligned} \tag{4.5}$$

Let $(P(u_1, u_2), Q(u_1, u_2))$ denote the vector field of (4.5), then we have

$$\frac{\partial P}{\partial u_1} + \frac{\partial Q}{\partial u_2} = -2\tau \gamma < 0$$

for all (u_1, u_2). Thus, the nonexistence of periodic solutions for (4.5) follows from the classical Bendixson's negative criterion. This ends the proof. $\quad\square$

Using the general Bendixson's criterion developed by Li and Muldowney [17] and an argument similar to [33, Lemma 4.2], we can prove the following lemma.

Lemma 4.4. *If*

$$e^2 < p/\gamma < \sigma e^2, \tag{4.6}$$

where $\sigma > 1$ *is the largest real root of the equation* $xe^{3-xe} = 1$, *then Eq.* (4.1) *has no periodic solutions of period 4.*

Remark 4.5. We conjecture that the constant σ in (4.6) can be replaced by infinity, that is, Lemma 4.4 holds as long as $e^2 < p/\gamma$.

Note that Eq. (4.1) has no periodic solutions of period 2 or 4, and thus has no periodic solutions of period $2/k$ or $4/k$ for any positive integer k. It follows from Lemmas 4.3 and 4.4 that the period T of a periodic solution on the connected component $\mathcal{C}(N^*, \tau_j, 2\pi/(\omega_j \tau_j))$ satisfies

$$\frac{2}{2j + 1} < T < \frac{4}{4j + 1}$$

if $(z, \tau, T) \in \mathcal{C}(N^*, \tau_j, 2\pi/(\omega_j \tau_j)) \cup \mathcal{C}(N^*, \tau_{2K_1-j-1}, 2\pi/(\omega_{2K_1-j-1} \tau_{2K_1-j-1}))$ for any integer $0 \leqslant j \leqslant K_1 - 1$. Therefore, the projection of $\mathcal{C}(N^*, \tau_n, 2\pi/(\omega_n \tau_n))$ onto the T-space is bounded.

It follows from Lemma 4.1 that the periodic solutions are all bounded away from zero. Thus there is no need to consider the boundary equilibrium. We define

$$\mathbf{O}^*(F) := \left\{ (N^*, \tau, T) \colon (\tau, T) \in I \times \mathbb{R} \right\}.$$

It follows from the above four lemmas that for each $0 \leqslant n \leqslant 2K_1 - 1$, $\mathcal{C}(N^*, \tau_n, 2\pi/(\omega_n \tau_n))$ is bounded, $\mathcal{C}(N^*, \tau_n, 2\pi/(\omega_n \tau_n)) \cap \mathbf{O}^*(F)$ is finite and

$$\sum_{(\tilde{z}, \tau, T) \in \mathcal{C}(N^*, \tau_n, \frac{2\pi}{\omega_n \tau_n}) \cap \mathbf{O}^*(F)} \zeta_1(\tilde{z}, \tau, T) = 0. \tag{4.7}$$

We are now in the position to state our result concerning the properties of the global Hopf branches.

Theorem 4.6. *Assume that $R_0 > 1$, $S(c_0) > \theta_0(c_0)$, and $e^2 < p/\gamma < \sigma e^2$, where $\sigma > 1$ is given as in Lemma 4.4. Then for Eq. (4.1), we have the following results*:

(i) *All global Hopf branches are bounded for $n = 0, 1, \ldots, 2K_1 - 1$;*
(ii) *Each global Hopf branch connects a pair of Hopf bifurcation values τ_j and τ_{2K_1-j-1} for $j = 0, 1, \ldots, K_1 - 1$;*
(iii) *For each $\tau \in (\tau_j, \tau_{2K_1-j-1})$ with $0 \leqslant j \leqslant K_1 - 1$, Eq. (4.1) has at least one periodic solution with period in $(2/(2j+1), 4/(4j+1))$.*

Proof. The boundedness of global Hopf branches is a direct consequence of the four lemmas we have established above. It follows from (4.4) and (4.7) that any global Hopf branch must contain at least two Hopf bifurcation values, one is τ_j for some $j \in \{0, 1, \ldots, K_1 - 1\}$ and the other is τ_{2K_1-l-1} for some $l \in \{0, 1, \ldots, K_1 - 1\}$. Next, we claim that each global Hopf branch connects exactly a pair of Hopf bifurcation values τ_j and τ_{2K_1-j-1} for $j = 0, 1, \ldots, K_1 - 1$. Suppose, on the contrary, there exists a global Hopf branch connecting two Hopf bifurcation values τ_j and τ_{2K_1-l-1} with $j, l \leqslant K_1 - 1$ and $j \neq l$. Without loss of generality, we assume $j < l$. Note that, on the Hopf bifurcation branch near the Hopf bifurcation value $\tau = \tau_j$, the minimal period of a periodic solution is in the interval $(2/(2j+1), 4/(4j+1))$, and near the Hopf bifurcation value $\tau = \tau_{2K_1-l-1}$, the minimal period is in $(2/(2l+1), 4/(4l+1))$. By the continuity of Hopf bifurcation branch, there must exist a non-constant periodic solution of period $2/(2j+1)$. This contradicts to the nonexistence of period 2 solutions. Finally, for $0 \leqslant j \leqslant K_1 - 1$, the Hopf bifurcation branch $\mathcal{C}(N^*, \tau_j, 2\pi/(\omega_j \tau_j))$ is connected, thus its projection onto the I-space is also connected and contains two points τ_j and τ_{2K_1-j-1}. This implies that for each $\tau \in (\tau_j, \tau_{2K_1-j-1})$, there exists at least one periodic solution with period in $(2/(2j+1), 4/(4j+1))$. This completes the proof. $\quad\square$

5. Numerical simulations, and the coexistence of multiple stable periodic solutions

In this section, we present some numerical simulations to demonstrate our theoretical results and show that multiple stable periodic solutions can coexist. The global Hopf branches are computed by a Matlab package DDE-BIFTOOL developed by Engelborghs et al. [4,5].

We choose the following set of parameter values:

$$\gamma = 1, \qquad \delta = 0.01, \qquad p = 15, \qquad \alpha = 1. \tag{5.1}$$

It is easy to calculate $\hat{\tau} = 70.805 < \bar{\tau} = 170.805 < \tau_{\max} = 270.805$, and $R_0 > 1$ if and only if $0 \leqslant \tau < \tau_{\max}$. It can be verified that the conditions of case (iib) in Theorem 3.6 are satisfied only if
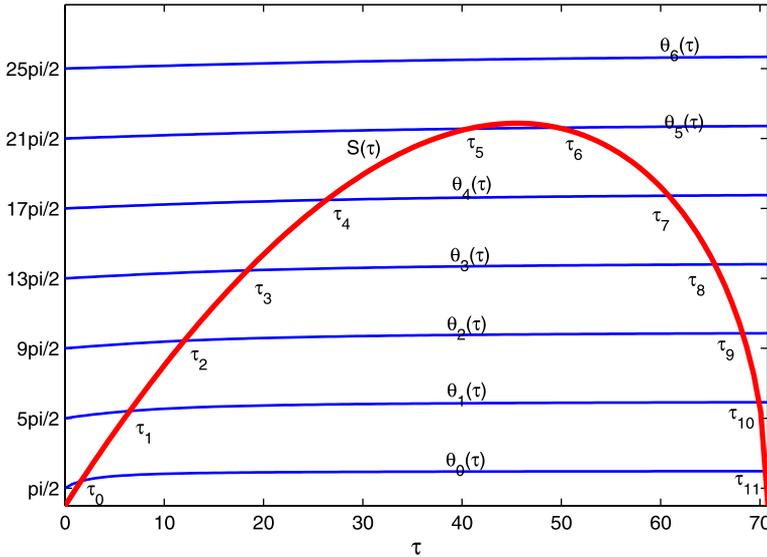
Fig. 1. The graphs of $S(\tau)$ and $\theta_i(\tau)$ for $i = 0, 1, \ldots, 6$. This gives the solution τ_n, $n = 0, 1, \ldots, 11$ of (3.8).

$0 \leqslant \tau < \tau_{\max}$. By Theorem 3.6, we know that there are exactly 12 (with $K_1 = 6$) local Hopf bifurcation values, namely,

$$0 < \tau_0 = 1.614 < \tau_1 = 6.528 < \tau_2 = 12.013 < \tau_3 = 18.371$$

$$< \tau_4 = 26.349 < \tau_5 = 40.639 < \tau_6 = 49.664 < \tau_7 = 60.824$$

$$< \tau_8 = 65.469 < \tau_9 = 68.265 < \tau_{10} = 69.926 < \tau_{11} = 70.709 < \hat{\tau},$$

as shown in Fig. 1. Correspondingly,

$$\omega_0 = 1.365 > \omega_1 = 1.303 > \omega_2 = 1.233 > \omega_3 = 1.150$$

$$> \omega_4 = 1.042 > \omega_5 = 0.833 > \omega_6 = 0.864 > \omega_7 = 0.458$$

$$> \omega_8 = 0.331 > \omega_9 = 0.227 > \omega_{10} = 0.133 > \omega_{11} = 0.044.$$

All global Hopf branches of periodic solutions emanating from the Hopf bifurcation points are depicted in Fig. 2. It is seen from Fig. 2 that these branches are all bounded and each branch connects exactly a pair of bifurcation values τ_j and τ_{11-j} with integer $0 \leqslant j \leqslant 5$, respectively. DDE-BIFTOOL allows us to draw the associated principal Floquet multipliers in Fig. 3 (if the principal Floquet multiplier is larger than 1, then the corresponding periodic solution is unstable, otherwise, the bifurcated periodic solution is stable [13]). It is observed in Fig. 3 that the first branch is stable for small τ, and becomes unstable as τ increases, and regains its stability as τ is sufficiently large. On the contrary, the second branch is initially unstable and becomes stable later but eventually loses its stability as τ further increases. The other four branches are always unstable. In addition, the periods of periodic solutions on the $(j + 1)$th Hopf branch are in the interval $(2/(2j + 1), 4/(4j + 1))$ with the integer j satisfying $0 \leqslant j \leqslant 5$ (see Fig. 4). We can also easily verify that N^* is stable for $\tau \in [0, \tau_0) \cup (\tau_{11}, \tau_{\max})$ and is unstable for $\tau \in (\tau_0, \tau_{11})$.

It is interesting to note in Fig. 2 that when $\tau \in (\tau_j, \tau_{11-j})$, $1 \leqslant j \leqslant 5$, there are $j + 1$ associated Hopf branches. This makes the coexistence of multiple periodic solutions possible. Indeed, as shown
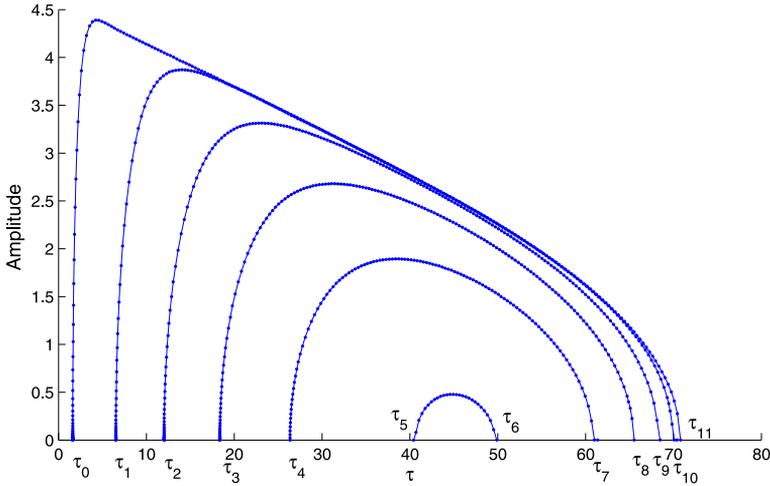
Fig. 2. The bifurcation diagram showing stability switch at positive equilibrium N^* and all global Hopf branches of model (1.2) with parameter values given in (5.1).
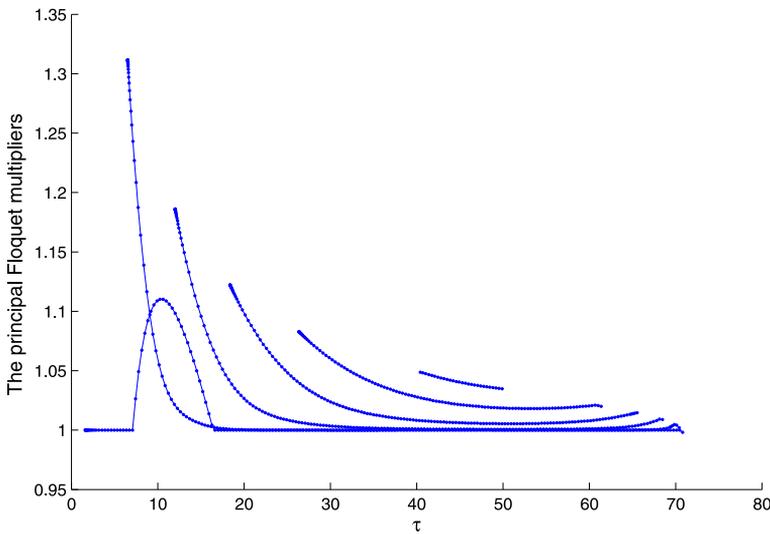

Fig. 3. The principal Floquet multipliers of periodic solutions on all Hopf branches of model (1.2) with parameter values given in (5.1).

in Fig. 3, there exists an interval of τ (for instance, $20 \leqslant \tau \leqslant 60$) on which more than one periodic solutions are stable. We take $\tau = 21$ and observe from Figs. 2 and 3 that there are two stable periodic solutions located on the first and second branches, respectively, and two unstable periodic solutions lying on the third and fourth branches. In Fig. 5, we observe two stable periodic solutions for the same τ value ($\tau = 21$). We observe that the periodic solution located on the first Hopf branch has period of 44 and is a slowly-oscillating periodic solution, while the periodic solution on the second Hopf branch has a period of 15 and is a fast-oscillating periodic solution. As shown in Figs. 6 and 7, there also exist two unstable periodic solutions which are the sources accounting for transient oscillations from cycles with small periods to a regular cycle with a larger period on the first Hopf branch. This suggests (numerically) that the slowly-oscillating periodic solution may have a larger basin of attraction.
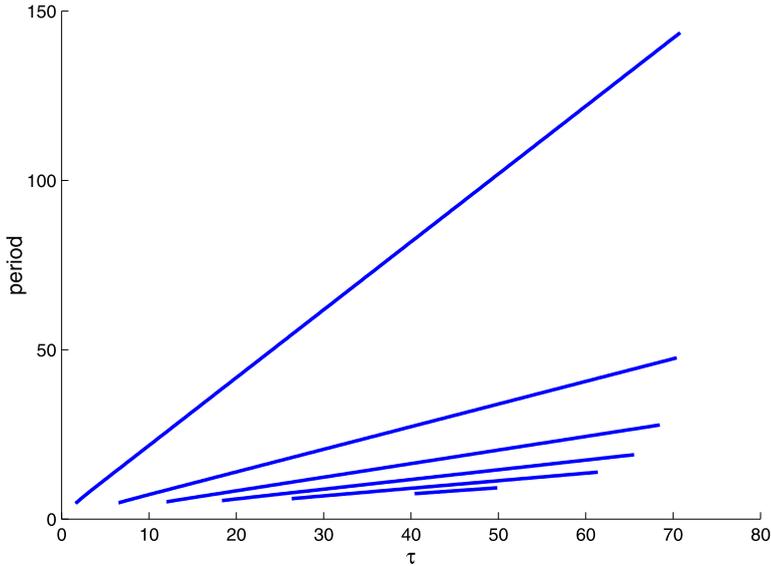
Fig. 4. The periods of periodic solutions on the Hopf branches of model (1.2) with parameter values given in (5.1).
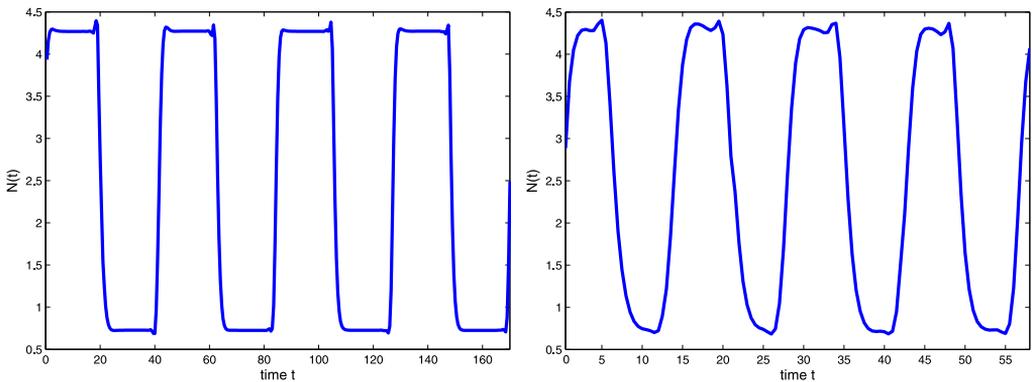

Fig. 5. Two coexisting stable periodic solutions for $\tau = 21$ with parameter values given in (5.1). Left: a stable periodic solution on the first branch with period 44. Right: a stable periodic solution on the second branch with period 15.

6. Summary and discussion

We have revisited Nicholson's blowflies model by incorporating the mortality of the population during the maturation process into the delayed feedback, which has been ignored in the literature. Regarding the delay as the bifurcation parameter, we have shown that the revised model (1.2) possesses very different dynamics compared with model (1.1) in which the mortality rate of the immature individuals is not explicitly incorporated into the model system. Especially, we have proven that if $p/\gamma > e^2$ and $S(c_0) > \theta_0(c_0)$, then four threshold values $\tau_0 < \tau_{2K_1-1} < \bar{\tau} < \tau_{max}$ characterize the dynamics. The positive equilibrium N^* of (1.2) is locally asymptotically stable when $\tau \in [0, \tau_0) \cup (\tau_{2K_1-1}, \tau_{max})$, and is globally asymptotically stable when $\tau \in [\bar{\tau}, \tau_{max})$, and when $\tau \geqslant \tau_{max}$, model (1.2) admits only the trivial equilibrium resulting in the extinction of the species. It has been shown that the model has only a finite even number of Hopf bifurcation values. We have also described how branches of Hopf bifurcations are paired indicating that periodic solutions with specific oscillation frequencies can exist only in bounded delay intervals.
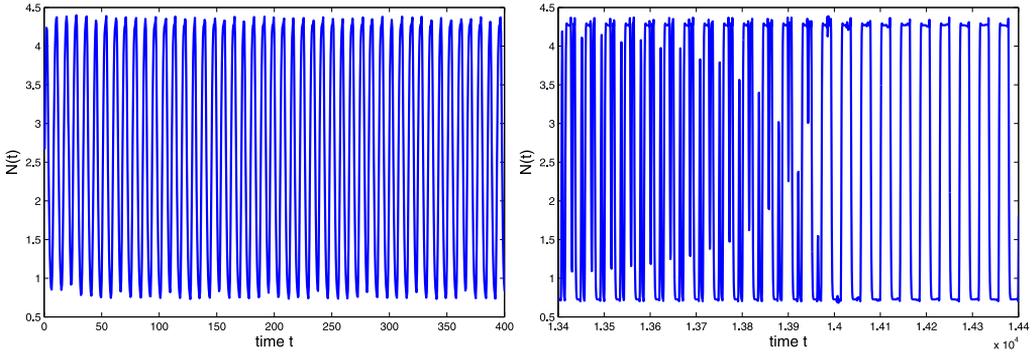
Fig. 6. An unstable periodic solution with period 9 on the third branch is observed when $\tau = 21$. The solution undergoes some transient oscillations and eventually converges to the stable slowly-oscillating periodic solution on the first branch.
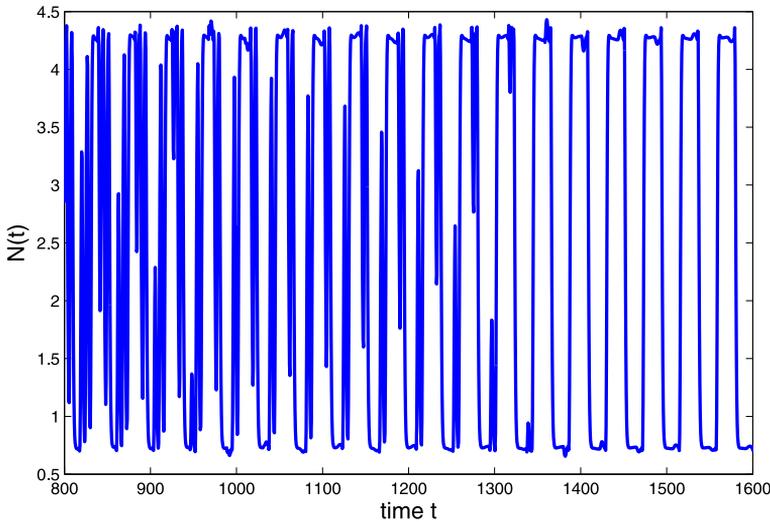
Fig. 7. An unstable periodic solution with period 6 on the fourth branch.

To the best of our knowledge, this is the very first paper proving that the global Hopf branches are all bounded, and each branch connects exactly two local Hopf bifurcation values resulting in multiplicity of periodic solutions and coexistence of multiple stable periodic solutions. The techniques we used in this paper can also be employed to explore the global Hopf branch structure for other models with age-structures, and in particular, for diffusive Nicholson's blowflies equations considered in [7–9,19–21,29–32,35] and the references therein. It would be interesting to see what kind of new oscillatory patterns may emerge for the non-autonomous version of the model we considered [1].

We should point out that the proof of Theorem 4.6 utilized a global Hopf bifurcation theorem due to Wu [34] and a general Bendixson's criterion developed by Li and Muldowney [17]. In particular, we applied the general Bendixson's criterion to exclude the existence of a periodic solution of period 4 (Lemma 4.4). To relax our conditions, a new approach is needed to prove the nonexistence of periodic solutions for a four-dimensional ordinary differential equation system. We conjecture that Eq. (4.1) has no periodic solutions of period 4 provided $p/\gamma > e^2$.

Acknowledgments

References

[1] L. Berezansky, E. Braverman, L. Idels, Nicholson's blowfiles differential equations revisited: main results and open problems, Appl. Math. Model. 34 (2010) 1405–1417.
[2] L.H. Clark, P.M. Schlosser, J.F. Selgrade, Multiple stable periodic solutions in a model for hormonal control of the menstrual cycle, Bull. Math. Biol. 65 (2003) 157–173.
[3] O. Diekmann, S.A. van Gils, S.M.V. Lunel, H.-O. Walther, Delay Equations: Functional-, Complex-, and Nonlinear Analysis, Springer, New York, 1995.
[4] K. Engelborghs, T. Luzyanina, G. Samaey, DDE-BIFTOOL v. 2.00: A Matlab package for bifurcation analysis of delay differential equations, Technical Report TW-330, KU Leuven, Belgium, 2001.
[5] K. Engelborghs, T. Luzyanina, D. Roose, Numerical bifurcation analysis of delay differential equations using DDE-BIFTOOL, ACM Trans. Math. Software 28 (2002) 1–21.
[6] L.H. Erbe, W. Krawcewicz, K. Geba, J. Wu, S^1-degree and global Hopf bifurcation theory of functional differential equations, J. Differential Equations 98 (1992) 198–277.
[7] T. Faria, S. Trofimchuk, Nonmonotone travelling waves in a single species reaction–diffusion equation with delay, J. Differential Equations 228 (2006) 357–376.
[8] S.A. Gourley, Traveling fronts in the diffusive Nicholson's blowflies equation with distributed delays, Math. Comput. Modelling 32 (2000) 843–853.
[9] S.A. Gourley, S. Ruan, Dynamics of the diffusive Nicholson's blowflies equation with distributed delay, Proc. Roy. Soc. Edinburgh Sect. A 130 (2000) 1275–1291.
[10] M.S. Gurney, S.P. Blythe, R.M. Nisbee, Nicholson's blowflies revisited, Nature 287 (1980) 17–21.
[11] M. Gyllenberg, P. Yan, Four limit cycles for a three-dimensional competitive Lotka–Volterra system with a heteroclinic cycle, Comput. Math. Appl. 58 (2009) 649–669.
[12] I. Györi, S.I. Trofimchuk, On the existence of rapidly oscillatory solutions in the Nicholson blowflies equation, Nonlinear Anal. 48 (2002) 1033–1042.
[13] J.K. Hale, S.M.V. Lunel, Introduction to Functional Differential Equations, Springer-Verlag, New York, 1993.
[14] J.K. Hale, Theory of Functional Differential Equations, Springer, Berlin, 1977.
[15] B.D. Hassard, N.D. Kazarinoff, Y.H. Wan, Theory and Applications of Hopf Bifurcation, Cambridge University Press, Cambridge, 1981.
[16] Y. Kuang, Global attractivity and periodic solutions in delay-differential equations related to models in physiology and population biology, Japan J. Indust. Appl. Math. 9 (1992) 205–238.
[17] M.Y. Li, J.S. Muldowney, On Bendixson's criterion, J. Differential Equations 106 (1994) 27–39.
[18] M.Y. Li, H. Shu, Multiple stable periodic oscillations in a mathematical model of CTL-response to HTLV-I infection, Bull. Math. Biol. 73 (2011) 1774–1793.
[19] W.T. Li, S. Ruan, Z.C. Wang, On the diffusive Nicholson's blowflies equation with nonlocal delay, J. Nonlinear Sci. 17 (2007) 505–525.
[20] D. Liang, J.W.-H. So, F. Zhang, X. Zou, Population dynamic models with nonlocal delay on bounded fields and their numeric computations, Differential Equations Dynam. Systems 11 (2003) 117–139.
[21] M. Mei, J.W.-H. So, M.Y. Li, S. Shen, Asymptotic stability of travelling waves for Nicholson's blowflies equation with diffusion, Proc. Roy. Soc. Edinburgh Sect. A 134 (2004) 579–594.
[22] J.A. Metz, O. Diekmann, The Dynamics of Physiologically Structured Populations, Springer, New York, 1986.
[23] A.J. Nicholson, An outline of the dynamics of animal populations, Aust. J. Zool. 2 (1954) 9–65.
[24] A.J. Nicholson, Compensatory reactions of populations to stresses, and their evolutionary significance, Aust. J. Zool. 2 (1954) 1–8.
[25] G. Oster, A. Ipaktchi, Population cycles, in: H. Eyring (Ed.), Periodicities in Chemistry and Biology, Academic Press, New York, 1978, pp. 111–132.
[26] S.S. Pilyugin, P. Waltman, Multiple limit cycles in the chemostat with variable yield, Math. Biosci. 132 (2003) 151–166.
[27] H. Smith, Monotone semiflows generated by functional differential equations, J. Differential Equations 66 (1987) 420–442.
[28] J.W.-H. So, J.S. Yu, Global attractivity and uniform persistence in Nicholson's blowflies, Differential Equations Dynam. Systems 2 (1994) 11–18.
[29] J.W.-H. So, Y. Yang, Dirichlet problem for the diffusive Nicholson's blowflies equation, J. Differential Equations 150 (1998) 317–348.
[30] J.W.-H. So, J. Wu, Y. Yang, Numerical steady state and Hopf bifurcation analysis on the diffusive Nicholson's blowflies equation, Appl. Math. Comput. 111 (2000) 33–51.
[31] J.W.-H. So, J. Wu, X. Zou, A reaction diffusion model for a single species with age structure, I. Traveling wave fronts on unbounded domains, Proc. R. Soc. Lond. Ser. A 457 (2001) 1841–1854.
[32] Y. Su, J. Wei, J. Shi, Bifurcation analysis in a delayed diffusive Nicholson's blowflies equation, Nonlinear Anal. 11 (2010) 1692–1703.

[33] J. Wei, M.Y. Li, Hopf bifurcation analysis in a delayed Nicholson blowflies equation, Nonlinear Anal. 60 (2005) 1351–1367.
[34] J. Wu, Symmetric functional differential equations and neural networks with memory, Trans. Amer. Math. Soc. 350 (1998) 4799–4838.
[35] T. Yi, X. Zou, Global attractivity of the diffusive Nicholson blowflies equation with Neumann boundary condition: a non-monotone case, J. Differential Equations 245 (2008) 3376–3388.