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Dynamics of a Scalar Population Model with Delayed Allee Effect

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A scalar population model with delayed growth rate of Allee effect type is considered in this paper. The stability of equilibria and associated supercritical Hopf bifurcations are analyzed. The basins of attraction of the two locally stable equilibria are characterized in terms of parameter values. In particular, when the time delay is large, the basin of attraction of the persistence equilibrium and limit cycle shrinks to a single point, so a global extinction of population occurs as a combined result of Allee effect and time delay.

Keywords: Allee effect; time delay; Hopf bifurcation; basin of attraction; bistability.

1. Introduction

The Allee effect is a type of population growth for which the growth rate per capita is negative for both low density and high density, but is positive for intermediate density. It was first proposed by American biologist Warder Clyde Allee [Allee & Bowen, 1932; Courchamp *et al.*, 2008]. The Allee effect can be caused by mate limitation, cooperative feeding, cooperative defense, environmental conditioning, etc. [Kramer *et al.*, 2009; Stephens & Sutherland, 1999]. Empirical evidence of the Allee effect growth rates [Lidicker, 2010] has been reported in many natural populations including plants [Ferdy *et al.*, 1999; Groom, 1998], insects [Kuussaari *et al.*, 1998], marine invertebrates [Stoner & Ray-Culp, 2000], birds and mammals [Courchamp *et al.*, 2000].

There are many expressions describing the models of single species population dynamics subject to the Allee effect [Boukal & Berec, 2002]. Among them, the model with the simplest and most commonly used expression is [Allee & Bowen, 1932; Courchamp *et al.*, 2008]:

$$u' = ru\left(1 - \frac{u}{K}\right)\left(\frac{u}{\theta} - 1\right), \tag{1}$$

where u represents the density of the population; r is the intrinsic rate of increase; K is the carrying capacity of species; θ is the "measure" of the

Allee effect [Lewis & Kareiva, 1993], i.e. the Allee threshold. The Allee effect can be classified into two broad categories: weak Allee effect and strong Allee effect [Courchamp *et al.*, 2008; Wang & Kot, 2001]. In Eq. (1), the Allee effect is called weak when $-1 < \theta < 0$ and strong when $0 < \theta < K$ [Owen & Lewis, 2001; Wang & Kot, 2001]. In this paper, we only consider the strong Allee effect case. The term $(1 - u/K)(u/\theta - 1)$ represents the intrinsic growth rate of the species. The population has a negative growth rate for $0 < u < \theta$, and a positive growth rate for $\theta < u < K$. Expanding the intrinsic growth rate term of Eq. (1), then it becomes

$$\frac{1}{K\theta}(-K\theta + (K+\theta)u - u^2). \tag{2}$$

Here, the term $+(K+\theta)u$ represents the intraspecific cooperation as it apparently provides a positive feedback on the population growth, and the term $-u^2$ represents the case with the intraspecific competition as it provides a negative feedback [Jankovic & Petrovskii, 2014].

The impact of population density on the population growth rate could have a time delay. Then combining the effect of the time delay on both the intraspecific cooperation and the intraspecific competition in Eq. (1), the model becomes (see [Jankovic & Petrovskii, 2014]):

$$u'(t) = ru(t)\left(1 - \frac{u(t-\tau)}{K}\right)\left(\frac{u(t-\tau)}{\theta} - 1\right), \tag{3}$$

where the time delay τ accounts for maturation or gestation periods. Using nondimensionalized variables:

$$\tilde{u} = \frac{u}{K}, \quad \tilde{\theta} = \frac{\theta}{K}, \quad \tilde{t} = \frac{rK}{\theta}t, \quad \tilde{\tau} = \frac{rK}{\theta}\tau,$$

Eq. (3) becomes

$$u'(t) = u(t)(1 - u(t-\tau))(u(t-\tau) - \theta), \tag{4}$$

where we omit the symbol $\tilde{}$, when no confusion arises. In this paper, we focus on discussing the dynamical behavior of solutions to Eq. (5) with nonnegative initial condition $\phi(t)$, that is,

$$\begin{cases} u'(t) = u(t)(1 - u(t-\tau))(u(t-\tau) - \theta), \\ \hfill t > 0, \\ u(t) = \phi(t), \quad -\tau \le t \le 0, \end{cases} \tag{5}$$

where $\phi \in C([-\tau, 0], [0, +\infty))$.

To state our results, we recall some definitions introduced in Kuang [1993] as follows: we say a function $y(t)$, $t \ge a$ for some $a \in \mathbb{R}$, is oscillatory with respect to y^* if there is a sequence $t_n \ge a$, $t \to \infty$, as $n \to \infty$, $y(t_n) = y^*$; otherwise, we say it is nonoscillatory. Obviously, if the solution is nonoscillatory, then there exists a $\tilde{T} > 0$, such that for all $t > \tilde{T}$, $y(t) > y^*$ or $y(t) < y^*$, which implies that $y(t)$ is ultimately monotone.

Our main results in this paper can be summarized as follows:

(i) Equation (5) has exactly three non-negative equilibria: $u = 0$, $u = \theta$ and $u = 1$. Among them, $u = \theta$ is always unstable;

(ii) The dynamical behavior of equilibria $u = 0$ and $u = 1$ with respect to Eq. (5) depend on the initial condition $\phi(t)$:

(a) if $0 \le \phi(t) \le \theta$, for any $-\tau \le t < 0$, and $0 < \phi(0) < \theta$, then the solution $u(t)$ converges to 0 as t goes to ∞;
(b) if $\phi(t) \ge \theta$, for any $-\tau \le t < 0$, and $\phi(0) > \theta$, then the solution $u(t)$ must have one of the following asymptotical behaviors:
   - (b_1) there exists a $\tau_* = \tau_*(\theta)$, such that for each $0 < \tau < \tau_*$, the oscillatory solution $u(t)$ converges to 1 as t goes to ∞;
   - (b_2) if the solution $u(t)$ is ultimately monotonous in $[\theta, 1)$ or $[1, +\infty)$, then $u(t)$ converges to 1 as t goes to ∞;
   - (b_3) if the solution $u(t)$ is ultimately monotonous in $(0, \theta)$, then $u(t)$ converges to 0 as t goes to ∞;

(iii) There exists a constant $\tau_0 = \tau_0(\theta)$ $(\tau_0 > \tau_*)$, such that $u = 1$ is locally asymptotically stable when $\tau \in [0, \tau_0)$, whereas it is unstable when $\tau \in (\tau_0, +\infty)$. Furthermore, there exist a sequence of bifurcating values $\{\tau_k : \tau_k = \tau_k(\theta), 0 < \theta < 1, k \in \mathbb{N}^0 := \mathbb{N} \cup \{0\}\}$, such that a supercritical Hopf bifurcation occurs at $\tau = \tau_k$ near $u = 1$;

(iv) Numerical simulations show that the value of time delay τ plays an important role on the stability of Eq. (5), that is, as τ increases, the basin of attraction of $u = 1$ becomes smaller and the basin of attraction of $u = 0$ becomes larger. And there exists a $\tau^* > \tau_0$, such that for all $\tau > \tau^*$, almost all solutions of Eq. (5) converge to $u = 0$. Thus a global extinction occurs under a large time delay.

Note that the global extinction described above has been numerically found in [Jankovic & Petrovskii, 2014], and the single species model with Allee effect has been considered in [Boukal & Berec, 2002; Idlango *et al.*, 2014; Kang & Udiani, 2014]. In this paper, we obtain rigorous stability and Hopf bifurcation results for the model with Allee effect and delay, and we also obtain precise estimates of the basin of attraction of the persistence equilibrium $u = 1$. By combining analytic and numerical approaches, we show that the global extinction is a consequence of homoclinic bifurcation in the system tuned by the time delay.

The rest of this paper is organized as follows: we first study some basic properties of the solutions of Eq. (5) in Sec. 2, such as positivity and boundedness. In Sec. 3, we consider the stability and the basin of attractions of the equilibria of Eq. (5), including the existence of Hopf bifurcation. In Sec. 4, we prove the Hopf bifurcation is supercritical. In Sec. 5, we use some numerical simulations to illustrate our conclusions and further dynamic properties of the system.

2. Preliminaries

In this section, we prove some basic properties of the solutions of Eq. (5). First the following lemma shows the positivity property and the convergence of the solutions of Eq. (5) with initial condition below the Allee threshold:

Lemma 1. *For Eq.* (5), *the following statements are true*:

(i) *If the initial condition satisfies*

$$\phi(t) \geq 0, \quad \text{for any } -\tau \leq t < 0 \text{ and } \phi(0) > 0, \tag{6}$$

then the solution of Eq. (5) *is positive for all* $t \in [0, +\infty)$;

(ii) *If the initial condition satisfies*

$$0 \leq \phi(t) \leq \theta, \quad \text{for any } -\tau \leq t < 0 \text{ and } 0 < \phi(0) < \theta, \tag{7}$$

then the solution of Eq. (5) *satisfies* $0 < u(t) < \theta$ *for all* $t \in [0, +\infty)$, *and*

$$\lim_{t\to\infty} u(t) = 0.$$

Proof. Define a function $f : \mathbb{R} \to \mathbb{R}$ by $f(u) = (1 - u)(u - \theta)$. Applying the variation of constants method, the solution of Eq. (5) can be written as

$$\begin{aligned} u(t) &= u(t_0) \exp\left\{\int_{t_0}^{t} (1 - u(s - \tau))(u(s - \tau) - \theta)\mathrm{d}s\right\} \\ &= u(t_0) \exp\left\{\int_{t_0-\tau}^{t-\tau} f(u(s))\mathrm{d}s\right\}. \end{aligned} \tag{8}$$

Choosing $t_0 = 0$ and $t \in (0, \tau]$ in Eq. (8), then for all $t \in (0, \tau]$,

$$u(t) = u(0) \exp\left\{\int_{-\tau}^{t-\tau} f(u(s))\mathrm{d}s\right\} > 0, \tag{9}$$

from (6). Choosing $t_0 = \tau$ and $t \in (\tau, 2\tau]$ in Eq. (8), then for all $t \in (\tau, 2\tau]$,

$$u(t) = u(\tau) \exp\left\{\int_{0}^{t-\tau} f(u(s))\mathrm{d}s\right\} > 0,$$

via (9). Repeating the above steps for any $t_0 = k\tau$ and $t \in (k\tau, (k + 1)\tau]$ for $k \in \mathbb{N}^0$, we obtain the conclusion (i).

Next we assume that the initial condition satisfies (7). Then for all $s \in [-\tau, 0]$ and $t \in (0, \tau]$, $f(u(s)) \leq 0$, and $0 < u(t) \leq u(0) < \theta$, from conclusion (i) and (8). Using the fact that $f(u(s)) < 0$, if $0 < u(s) < \theta$ and choosing $t_0 = \tau$ in the formula (8), we have

$$\begin{aligned} 0 < u(t) &= u(\tau) \exp\left\{\int_{0}^{t-\tau} f(u(s))\mathrm{d}s\right\} \\ &< u(\tau) < \theta, \end{aligned}$$

for all $t \in (\tau, 2\tau]$. Repeating the steps above for all $t_0 = k\tau$ and $t \in (k\tau, (k + 1)\tau]$ for $k \in \mathbb{N}$, we have $0 < u(t) < \theta$ for all $t \in [0, +\infty)$. Moreover, for all $t \in [\tau, +\infty)$, $u'(t) = u(t)f(u(t - \tau)) < 0$, which implies that $u(t)$ decreases strictly as t increases. Hence we can assume that $\lim_{t\to\infty} u(t) = c < \theta$. From Eq. (5), we obtain that $0 = c(1 - c)(c - \theta)$. That is $c = 0$. ■

Next we consider the dynamical behavior of solution $u(t)$ to (5) with the initial condition satisfying

$$\phi(t) \geq \theta, \quad \text{for any } -\tau \leq t < 0 \text{ and } \phi(0) > \theta. \tag{10}$$

The discussion can be divided into the following five cases:

(a) $u(t)$ is oscillatory with respect to $u = 1$;
(b) $u(t)$ is oscillatory with respect to $u = \theta$;
(c) $u(t)$ is ultimately monotonous in $(0, \theta)$;
(d) $u(t)$ is ultimately monotonous in $[\theta, 1)$;
(e) $u(t)$ is ultimately monotonous in $[1, +\infty)$.

For the ultimately monotonous solutions satisfying cases (c), (d) or (e), we have the following conclusion directly:

Lemma 2. *The following statements are true*:

(i) *If case* (c) *holds*, *then* $\lim_{t\to\infty} u(t) = 0$;
(ii) *If case* (d) *or case* (e) *holds*, *then* $\lim_{t\to\infty} \times u(t) = 1$.

Proof. The conclusion (i) is obtained directly by applying Lemma 1. Assume case (d) holds. Then there exists a $T_0 > 0$, such that for all $t \in (T_0, +\infty)$, $u(t) \in [\theta, 1)$. And $f(u(t-\tau)) \geq 0$ and $u'(t) \geq 0$ for all $t \in (T_0 + \tau, +\infty)$. That is, $u(t)$ is increasing as $t \in (T_0 + \tau, +\infty)$. Then there exists a $c \geq 1$ such that

$$\lim_{t\to\infty} u(t) = c \quad \text{and}$$

$$0 = \lim_{t\to\infty} u'(t) = c(1-c)(c-\theta),$$

which implies that $c = 1$, that is, $\lim_{t\to\infty} u(t) = 1$. The proof of case (e) is similar to case (d), which we omit here. ■

For the oscillatory solutions in case (a) or (b), we have

Lemma 3. *Assume $u(t)$ is the oscillatory solution in case* (a) *or case* (b). *Then there exists a $T > 2\tau$, such that for all $t \in [T, +\infty)$,*

$$\theta e^{-M\tau} < u(t) < e^{\frac{(1-\theta)^2}{4}\tau}, \tag{11}$$

where

$$M := e^{\frac{(1-\theta)^2}{2}\tau} + \theta. \tag{12}$$

Proof. Assume $u(t)$ is the oscillatory solution in case (a). Then there exist a $T_1 > 0$ and a sequence $\{t_n\}_{n=1}^{+\infty}$ satisfying $T_1 \leq t_1 < t_2 < \cdots$ and $\lim_{n\to\infty} t_n = \infty$, such that $u(t_n) = 1$ for all $n \in \mathbb{N}$. In addition, without loss of generality, assume for all $n \in \mathbb{N}$, $u(t) > 1$ for each $t \in (t_{2n-1}, t_{2n})$ and $u(t) < 1$ for each $t \in (t_{2n}, t_{2n+1})$. Then there exist two sequences denoted as $\{\xi_n\}_{n=1}^{+\infty}$ and $\{\zeta_n\}_{n=1}^{+\infty}$, such that for each $n \in \mathbb{N}$, $\xi_n \in (t_{2n-1}, t_{2n})$, $\zeta_n \in (t_{2n}, t_{2n+1})$ and

$$u(\xi_n) = \max_{t\in(t_{2n-1},t_{2n})} u(t), \quad u(\zeta_n) = \min_{s\in(t_{2n},t_{2n+1})} u(s).$$

Then we have $u'(\xi_n) = 0$, $u'(\zeta_n) = 0$. Choose $N_1 \in \mathbb{N}_0$, such that $\xi_n > \tau$ and $\zeta_n > \tau$ for all $n \geq N_1$. From Eq. (5),

$$0 = u'(\xi_n) = u(\xi_n)(1 - u(\xi_n - \tau))(u(\xi_n - \tau) - \theta),$$

$$0 = u'(\zeta_n) = u(\zeta_n)(1 - u(\zeta_n - \tau))(u(\zeta_n - \tau) - \theta),$$

which imply $u(\xi_n - \tau) = 1$ or $u(\xi_n - \tau) = \theta$ and $u(\zeta_n - \tau) = 1$ or $u(\zeta_n - \tau) = \theta$.

If $u(\xi_n - \tau) = 1$, then integrating both sides of Eq. (5) from $\xi_n - \tau$ to ξ_n leads to

$$\begin{aligned} \ln u(\xi_n) &= \ln u(\xi_n - \tau) \\ &\quad + \int_{\xi_n - 2\tau}^{\xi_n - \tau} (1 - u(s))(u(s) - \theta)\mathrm{d}s \\ &< \frac{(1-\theta)^2}{4}\tau, \end{aligned}$$

which means $u(\xi_n) < e^{\frac{(1-\theta)^2}{4}\tau}$ for all $n \geq N_1$. If $u(\xi_n - \tau) = \theta$, then we obtain the same result by using the similar method and the fact that $\ln u(\xi_n - \tau) = \ln\theta < 0$.

If $u(\zeta_n - \tau) = \theta$, then integrating both sides of Eq. (5) from $\zeta_n - \tau$ to ζ_n leads to

$$\begin{aligned} -\ln u(\zeta_n) &= -\ln u(\zeta_n - \tau) \\ &\quad - \int_{\zeta_n - 2\tau}^{\zeta_n - \tau} (1 - u(s))(u(s) - \theta)\mathrm{d}s \\ &= -\ln\theta + \int_{\zeta_n - 2\tau}^{\zeta_n - \tau} (u^2(s) - (1+\theta)u(s) + \theta)\mathrm{d}s \\ &< -\ln\theta + \int_{\zeta_n - 2\tau}^{\zeta_n - \tau} (u^2(s) + \theta)\mathrm{d}s \\ &< -\ln\theta + \tau(e^{\frac{(1-\theta)^2}{2}\tau} + \theta), \end{aligned}$$

which implies that $u(\zeta_n) > \theta\exp\{-\tau(e^{(1-\theta)^2\tau/2} + \theta)\} = \theta e^{-M\tau}$ for all $n \geq N_1$. If $u(\zeta_n - \tau) = 1$, then we obtain the similar result $u(\zeta_n) > e^{-M\tau}$ by using

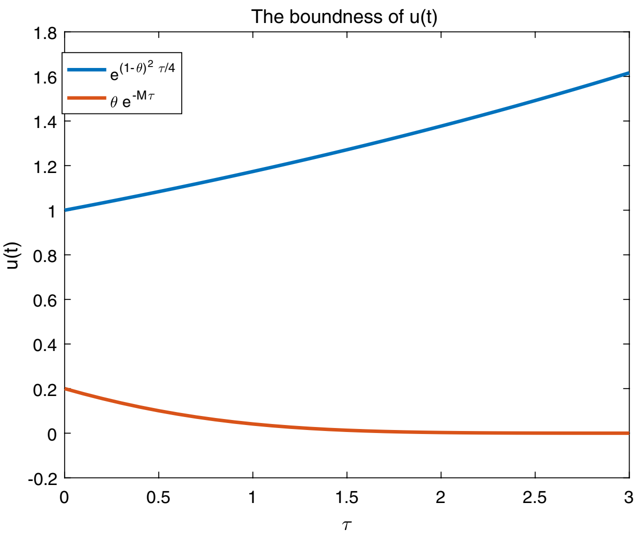

Fig. 1. Oscillation range for an oscillatory solution in case (a) or (b). Here $\theta = 0.2$.

the same method and the fact that $\ln u(\zeta_n - \tau) = 0$. To sum up, there exists a $T := \max\{\xi_{N_1}, \zeta_{N_1}\} > 2\tau$, such that (11) holds for all $t > T$, which completes the proof of case (a).

The proof of case (b) is similar to that of case (a), which we omit here. ■

Figure 1 shows the numerical simulation of the bounds of $u(t)$ obtained in Lemma 3. It is clear that as the time delay τ goes to infinity, the upper bound $e^{(1-\theta)^2\tau/4}$ goes to infinity and the lower bound $\theta e^{-M\tau}$ goes to 0. Also Lemma 3 holds for any $\tau > 0$, and in the next section, we show that under some conditions, the oscillatory solutions converge to $u = 1$.

3. Stability and Hopf Bifurcation

In this section, we consider the stability of the equilibria of Eq. (5), and possible Hopf bifurcation. Equation (5) has exactly three equilibria: $u = 0$, $u = \theta$ and $u = 1$. First, we establish the stability of the equilibria $u = 0$ and $u = \theta$ by analyzing the characteristic equation of the corresponding linearized equation.

Theorem 1. *For Eq. (5), the following statements are true:*

(i) *$u = 0$ is locally asymptotically stable for all $\tau \in [0, +\infty)$;*
(ii) *$u = \theta$ is unstable for all $\tau \in [0, +\infty)$.*

Proof. Denote u^* as an equilibrium of Eq. (5). A straightforward calculation leads to the characteristic equation

$$\lambda - A - Be^{-\lambda\tau} = 0, \tag{13}$$

where

$$\begin{aligned} A &= (u^* - \theta)(1 - u^*),\\ B &= u^*(1 + \theta - 2u^*). \end{aligned} \tag{14}$$

If $u^* = 0$, then $A = -\theta$, $B = 0$, and the unique eigenvalue of $u^* = 0$ is $\lambda = -\theta < 0$ for all $\tau \in [0, +\infty)$. Hence, $u^* = 0$ is locally asymptotically stable. If $u^* = \theta$, then $A = 0$, $B = \theta(1 - \theta)$, and the characteristic Eq. (13) becomes

$$\lambda - \theta(1 - \theta)e^{-\lambda\tau} = 0.$$

Note that, when $\tau = 0$, the unique eigenvalue is $\lambda = \theta(1 - \theta) > 0$, which means that $u^* = \theta$ is unstable. ■

Secondly we show that the stability of $u = 1$ depends on the time delay τ.

Theorem 2. *For the equilibrium $u = 1$ in Eq. (5), let $\tau_0 := \pi/(2(1-\theta))$ and $\tau_k := \tau_0 + 2k\pi/(1 - \theta)$.*

(i) *If $\tau \in [0, \tau_0)$, then $u = 1$ is locally asymptotically stable, and if $\tau > \tau_0$, then $u = 1$ is unstable;*
(ii) *When $\tau = \tau_k$ ($k \in \mathbb{N}^0$), Eq. (5) undergoes a supercritical Hopf bifurcation near $u = 1$, that is, the bifurcation is forward and bifurcating periodic solutions are stable.*

Proof. Considering (13) and (14) with $u^* = 1$, the characteristic equation becomes

$$\lambda + (1 - \theta)e^{-\lambda\tau} = 0. \tag{15}$$

It is not difficult to calculate that Eq. (15) has a negative root $\lambda = -(1 - \theta) < 0$, if $\tau = 0$. Also, $\lambda = 0$ is not a root of Eq. (15).

Assume that Eq. (15) has a simple pair of pure imaginary roots, denoted as $\lambda = \pm i\omega_0$ ($\omega_0 > 0$). Then we have

$$\cos(\omega_0\tau) = 0 \quad \text{and} \quad \sin(\omega_0\tau) = \frac{\omega_0}{1 - \theta},$$

which implies that $\omega_0 = 1 - \theta$, $\tau = \tau_k$, for any $k \in \mathbb{N}^0$.

Next we verify the transversality condition when there is a pair of purely imaginary roots.

Differentiating with respect to τ in Eq. (15), we get

$$\frac{\mathrm{d}\lambda}{\mathrm{d}\tau} - (1-\theta)e^{-\lambda\tau}\left(\lambda + \tau\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right) = 0,$$

that is,

$$\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)^{-1} = \frac{e^{\lambda\tau}}{\lambda(1-\theta)} - \frac{\tau}{\lambda}$$

and

$$\mathrm{Re}\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}(\tau_k)\right)^{-1} = \frac{1}{\omega_0^2} > 0,$$

which implies that the transversality condition holds at $\tau = \tau_k$. The proof of the properties of Hopf bifurcation is long and complicated, which we postpone to Sec. 4. ■

Finally we have the following result on the global dynamical behavior of equilibrium $u = 1$ of Eq. (5) by applying a Lyapunov functional argument adapted from [Gopalsamy & Ladas, 1990; Kuang, 1993].

Theorem 3. *Assume that $\tau > 0$ satisfies*

$$(3\theta^2 e^{-M\tau}(1-e^{-M\tau}) + e^{\frac{(1-\theta)^2}{4}\tau}(e^{\frac{(1-\theta)^2}{4}\tau} - \theta))\tau < \frac{1}{2}, \tag{16}$$

where M is defined in (12). Then any oscillatory solution of Eq. (5) with the initial condition satisfying (10) converges to $u = 1$ as $t \to \infty$.

Proof. Assume $u(t)$ is an oscillatory solution of Eq. (5) with the initial condition satisfying (10). Firstly, we transform equilibrium $u = 1$ to the origin via a translation $u(t) = v(t) + 1$, then $v(t)$ satisfies

$$\begin{cases} v'(t) = -v(t-\tau)(v(t)+1)(v(t-\tau)+1-\theta), & t > 0, \\ v(t) = \varphi(t), \quad -\tau \le t < 0, \end{cases} \tag{17}$$

where $\varphi(t) := \phi(t) - 1 \in \mathbb{X}_\tau := C([-\tau,0],[-1,+\infty))$ satisfying

$$\varphi(t) \ge \theta - 1, \quad \text{for any } -\tau \le t < 0 \quad \text{and } \varphi(0) > \theta - 1,$$

from (10). Let $v(t)$ be an arbitrary solution of Eq. (17), then we have from Lemma 3, $v(t)$ is bounded on $[T,+\infty)$, where $T > 2\tau$ is defined in Lemma 3. Define a non-negative function $V : [T,+\infty) \to \mathbb{R}$ by

$$\begin{aligned} V(t) = &\left[v(t) - \int_{t-\tau}^{t} G(s+\tau)v(s)\mathrm{d}s\right]^2 \\ &+ 3\int_{t-\tau}^{t}\int_{s}^{t} G(s+2\tau)G(\xi+\tau)v^2(\xi)\mathrm{d}\xi\mathrm{d}s \\ &+ \int_{t}^{t+\tau}\int_{s}^{t+\tau} 3C_1\left(G(\xi)+\frac{1}{\tau}\right)v^2(s-\tau)\mathrm{d}\xi\mathrm{d}s, \end{aligned}$$

where

$$G(t) = (v(t)+1)(v(t-\tau)+1-\theta) + 3C_1,$$
$$C_1 = C_1(\theta,\tau) = \theta^2 e^{-M\tau}(1-e^{-M\tau})$$

and M is defined in (12). By using the conclusion of Lemma 3, we have

$$2C_1 < G(t) < 3C_1 + C_2,$$

for all $t > T$, where

$$C_2 = C_2(\theta,\tau) = e^{\frac{(1-\theta)^2}{4}\tau}(e^{\frac{(1-\theta)^2}{4}\tau} - \theta).$$

A direct calculation leads to

$$\begin{aligned} \frac{\mathrm{d}V(t)}{\mathrm{d}t} = &-2G(t+\tau)v^2(t) \\ &+ 2\int_{t-\tau}^{t} G(t+\tau)G(s+\tau)v(t)v(s)\mathrm{d}s \\ &+ 6C_1 v(t)v(t-\tau) \\ &- 6C_1\int_{t-\tau}^{t} G(s+\tau)v(s)v(t-\tau)\mathrm{d}s \\ &- 3\int_{t-\tau}^{t} G(t+\tau)G(s+\tau)v^2(s)\mathrm{d}s \\ &- 3C_1\int_{t}^{t+\tau}\left(G(s)+\frac{1}{\tau}\right)v^2(t-\tau)\mathrm{d}s. \end{aligned}$$

Using the inequalities $2v(s)v(t) \le v^2(t) + v^2(s)$ and the fact that

$$\int_{t}^{t+\tau}\left(G(s)+\frac{1}{\tau}\right)v^2(t-\tau)\mathrm{d}s = \int_{t-\tau}^{t}\left(G(s+\tau)+\frac{1}{\tau}\right)v^2(t-\tau)\mathrm{d}s,$$

we have

$$\frac{\mathrm{d}V(t)}{\mathrm{d}t} \le -A(t)v^2(t)$$
$$\le -G(t+\tau)\left(\frac{1}{2}-(3C_1+C_2)\tau\right)v^2(t)$$
$$\le 0, \tag{18}$$

where

$$A(t) := 2G(t+\tau) - 3C_1 - \int_{t-\tau}^{t} G(t+\tau)G(s+\tau)\mathrm{d}s$$
$$> G(t+\tau)\left(\frac{1}{2}-(3C_1+C_2)\tau\right)$$
$$> 0,$$

by (16). Integrating both sides of the second inequality of (18) from T to t, we have

$$V(t) + \left(\frac{1}{2}-(3C_1+C_2)\tau\right)\int_T^t G(s+\tau)v^2(s)\mathrm{d}s \le V(T).$$

Hence, $G(t+\tau)v^2(t) \in L^1[T,\infty)$, and

$$\left[v(t) - \int_{t-\tau}^{t} G(s+\tau)v(s)\mathrm{d}s\right]^2 \le V(t) \le V(T),$$

which yields

$$|v(t)| \le [V(T)]^{\frac{1}{2}} + \int_{t-\tau}^{t} G(s+\tau)|v(s)|\mathrm{d}s$$
$$\le [V(T)]^{\frac{1}{2}} + (3C_1+C_2)\int_{t-\tau}^{t} |v(s)|\mathrm{d}s.$$

Denote $\rho(t) = \max_{-\tau\le s\le t}|v(s)|$. Then

$$\rho(t) \le \frac{[V(T)]^{\frac{1}{2}}}{1-(3C_1+C_2)\tau}$$

and $v(t)$ is bounded. Since $G(t)$ is bounded, $v'(t)$ is bounded. Hence $G(t+\tau)v^2(t)$ is uniformly continuous. By Barbălat's lemma [Barbălat, 1959], we have

$$\lim_{t\to\infty} G(t+\tau)v^2(t) = 0 \quad \text{and} \quad \lim_{t\to\infty} v(t) = 0. \qquad \blacksquare$$

We remark that the range of τ satisfying (16) is clearly not empty and it is an interval $(0, \tau_*)$ where $\tau_* = \tau_*(\theta)$ can be numerically calculated.

4. Direction and Stability of Hopf Bifurcation

In Sec. 3, we have shown that Eq. (5) undergoes a Hopf bifurcation near $u = 1$ when $\tau = \tau_k$ $(k \in \mathbb{N}^0)$ in Theorem 2. In this section, we consider the direction of Hopf bifurcation and the stability of the bifurcating periodic solutions by applying the normal formal theory and the center manifold theorem (see [Hassard *et al.*, 1981]).

For fixed $k \in \mathbb{N}^0$, denote $\tilde{\tau} = \tau_k$, $\omega_0 = 1-\theta$, $\tilde{v}(t) = v(\tau t)$ and drop the symbol $\tilde{}$ as a matter of convenience. Then Eq. (17) becomes

$$v'(t) = -\tau v(t-1)(v(t)+1)(v(t-1)+\omega_0). \tag{19}$$

Set $\tau = \tilde{\tau}+\mu$, $\mu \in \mathbb{R}$, then $\mu = 0$ is a Hopf bifurcating value for Eq. (19). Denote

$$L_\mu\phi = -(\tilde{\tau}+\mu)\omega_0\phi(-1) \tag{20}$$

and

$$Y(\mu,\phi) = -(\tilde{\tau}+\mu)\phi(-1)[\phi(0)\phi(-1) + \omega_0\phi(0) + \phi(-1)], \tag{21}$$

for any $\phi \in \mathbb{X}_1 := C([-1,0],[-1,+\infty))$. Then Eq. (19) can be rewritten as

$$v'(t) = L_\mu v + Y(\mu, v). \tag{22}$$

Consider the linearized equation $v'(t) = L_\mu v$. By the Riesz representation theorem, there exists a function $\eta(\mu,\zeta)$ of the bounded variation for $\zeta \in [-1,0]$, such that

$$L_\mu\phi = \int_{-1}^{0} \mathrm{d}\eta(\mu,\zeta)\phi(\zeta),$$

for any $\phi \in \mathbb{X}_1$. In fact, we can choose $\eta(\mu,\zeta) = (\tilde{\tau}+\mu)\omega_0\delta(\zeta+1)$. For $\phi \in \mathbb{X}_1$, let

$$A(\mu)\phi = \begin{cases} \dfrac{\mathrm{d}\phi(\zeta)}{\mathrm{d}\zeta}, & \zeta \in [-1,0), \\ \displaystyle\int_{-1}^{0} \mathrm{d}\eta(\mu,\xi)\phi(\xi), & \zeta = 0, \end{cases}$$

$$N(\mu)\phi = \begin{cases} 0, & \zeta \in [-1,0), \\ Y(\mu,\phi), & \zeta = 0. \end{cases}$$

Then (22) can be rewritten as

$$v_t' = A(\mu)v_t + N(\mu)v_t,$$

where $v_t(\zeta) = v(t+\zeta)$ for $\zeta \in [-1,0]$. For $\psi \in C([0,1],\mathbb{R})$, define

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

For any $\phi \in \mathbb{X}_1$ and $\psi \in C([0,1],\mathbb{R})$, $A := A(0)$ and A^* are adjoint operators by using the following bilinear form

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

and $\pm i\tilde{\tau}\omega_0$ are eigenvalues of A and A^*. It is easy to verify that $q(\zeta) = e^{i\tilde{\tau}\omega_0\zeta}$ ($\zeta \in [-1,0]$) is an eigenvector of A corresponding to the eigenvalue $i\tilde{\tau}\omega_0$, and $q^*(s) = De^{i\tilde{\tau}\omega_0 s}$ is an eigenvector of A^* corresponding to the eigenvalue $-i\tilde{\tau}\omega_0$, where $1/D = 1 - i\tilde{\tau}\omega_0$, q and q^* satisfy $\langle q^*, q\rangle = 1$ and $\langle q^*, \overline{q}\rangle = 0$.

Applying the notations and algorithms given by [Hassard *et al.*, 1981] and a similar calculation given in [Wei & Li, 2005] and [Wei, 2007], some formulas can be obtained as follows:

$$g_{20} = 2\overline{D}\tilde{\tau}(1+i\omega_0) = \frac{2\tilde{\tau}}{1+\tilde{\tau}^2\omega_0^2}[1+\tilde{\tau}\omega_0^2 + i\omega_0(1-\tilde{\tau})],$$

$$g_{11} = -2\tilde{\tau}\overline{D} = \frac{2\tilde{\tau}}{1+\tilde{\tau}^2\omega_0^2}(i\tilde{\tau}\omega_0 - 1),$$

$$g_{02} = 2\overline{D}\tilde{\tau}(1-i\omega_0) = \frac{2\tilde{\tau}}{1+\tilde{\tau}^2\omega_0^2}[1-\tilde{\tau}\omega_0^2 - i\omega_0(1+\tilde{\tau})],$$

$$\begin{aligned} g_{21} &= \overline{D}\tilde{\tau}[-2+\omega_0(2W_{11}(-1)+W_{20}(-1)) + i(2\omega_0 W_{11}(0) + 4W_{11}(-1) - \omega_0 W_{20}(0) - 2W_{20}(-1))] \\ &= \frac{-2\tilde{\tau}}{15\omega_0(1+\tilde{\tau}^2\omega_0^2)^2}[-12 + 9\omega_0^5\tilde{\tau}^3 + \omega_0(-2+6\tilde{\tau}) + 3\omega_0^4\tilde{\tau}^2(-1+7\tilde{\tau}) - 3\omega_0^2(1-7\tilde{\tau}+4\tilde{\tau}^2) \\ &\quad + \omega_0^3\tilde{\tau}(9-62\tilde{\tau}+66\tilde{\tau}^2) + i(-34+3\omega_0^5\tilde{\tau}^3 + 3\omega_0(7+4\tilde{\tau}) + \omega_0^4\tilde{\tau}^2(19+12\tilde{\tau}) \\ &\quad + 3\omega_0^3\tilde{\tau}(1+7\tilde{\tau}+4\tilde{\tau}^2) + \omega_0^2(19-48\tilde{\tau}+26\tilde{\tau}^2))], \end{aligned}$$

where

$$W_{20}(0) = \frac{-2}{15\omega_0(1+\tilde{\tau}^2\omega_0^2)}[3+\omega_0(4-10\tilde{\tau}) + 3\omega_0^2\tilde{\tau}^2 - 6\omega_0^3\tilde{\tau}^2 + i(-14+3\omega_0 - 20\omega_0^2\tilde{\tau} + 6\omega_0^2\tilde{\tau}^2 + 3\omega_0^3\tilde{\tau}^2)],$$

$$W_{20}(-1) = \frac{-2}{15\omega_0(1+\tilde{\tau}^2\omega_0^2)}[-13+6\omega_0 - 10\omega_0^2\tilde{\tau} - 3\omega_0^2\tilde{\tau}^2 + 6\omega_0^3\tilde{\tau}^2 - i(6+23\omega_0 - 20\omega_0\tilde{\tau} + 6\omega_0^2\tilde{\tau}^2 + 3\omega_0^3\tilde{\tau}^2)],$$

$$W_{11}(0) = \frac{-2(1-2\omega_0\tilde{\tau}+\omega_0^2\tilde{\tau}^2)}{\omega_0(1+\tilde{\tau}^2\omega_0^2)}, \quad W_{11}(-1) = \frac{2(1-\tilde{\tau}^2\omega_0^2)}{\omega_0(1+\tilde{\tau}^2\omega_0^2)}$$

and $E_1 = 2[2\omega_0 - 1 - i(\omega_0+2)]/(5\omega_0)$, $E_2 = -2/\omega_0$.

Hence,

$$\begin{aligned} c_1(0) &= \frac{i}{2\omega_0\tilde{\tau}}\left(g_{11}g_{20} - 2|g_{11}|^2 - \frac{|g_{02}|^2}{3}\right) + \frac{g_{21}}{2} \\ &= \frac{\tilde{\tau}}{15\omega_0(1+\omega_0^2\tilde{\tau}^2)}[3\omega_0^2(1-3\omega_0\tilde{\tau}) + \omega_0(32-21\omega_0\tilde{\tau}) + 3(4-22\omega_0\tilde{\tau})] \\ &\quad - \frac{\tau i}{15\omega_0(1+\omega_0^2\tilde{\tau}^2)}[66+3\omega_0^3\tilde{\tau} + 3\omega_0(7+4\tilde{\tau}) + \omega_0^2(29+12\tilde{\tau})], \end{aligned}$$

$$\mu_2 = -\frac{\mathrm{Re}(c_1(0))}{\mathrm{Re}(\lambda'(\tilde{\tau}))} = \frac{\omega_0\tilde{\tau}}{15}[3\omega_0^2(3\omega_0\tilde{\tau}-1)+\omega_0(21\omega_0\tilde{\tau}-32)+3(22\omega_0\tilde{\tau}-4)] > 0,$$

$$\beta_2 = 2\,\mathrm{Re}(c_1(0)) = \frac{2\tilde{\tau}}{15\omega_0(1+\omega_0^2\tilde{\tau}^2)}[3\omega_0^2(1-3\omega_0\tilde{\tau})+\omega_0(32-21\omega_0\tilde{\tau})+3(4-22\omega_0\tilde{\tau})] < 0,$$

$$\begin{aligned} T_2 &= -\frac{\mathrm{Im}(c_1(0))+\mu_2\,\mathrm{Im}(\lambda'(\tilde{\tau}))}{\omega_0\tilde{\tau}} \\ &= \frac{1}{15\omega_0^2(1+\omega_0^2\tilde{\tau}^2)^3}\left[\frac{494}{9}+21\omega_0+21\omega_0^3\tilde{\tau}^2+\left(3\omega_0^2\tilde{\tau}-\frac{10}{3}\right)^2+\omega_0^2(29+66\tilde{\tau}^2)\right] \\ &> 0, \end{aligned}$$

where using the fact that $\tilde{\tau}\omega_0 \geq \tau_0\omega_0 = \pi/2$. These calculations show that

(i) $\mu_2 > 0$ implies that the direction of the Hopf bifurcation is forward, that is, the bifurcating periodic orbit exists for $\tau \geq \tilde{\tau}$;
(ii) $\beta_2 < 0$ implies that the bifurcating periodic orbit is stable;
(iii) $T_2 > 0$ implies that the period of periodic orbit increases.

5. Numerical Simulations

In this section, we present some numerical simulations to demonstrate our theoretical results and enrich the conclusion of the stability of the equilibrium using the Matlab package DDE23.

We use the parameter value: $\theta = 0.2$. A straightforward calculation leads to

$$\tau_0 \approx 1.964, \quad M = e^{0.32\tau} + 0.2,$$

$$C_1 = \frac{1}{25}e^{-(e^{\frac{8}{25}\tau}+\frac{1}{5})\tau}(1-e^{-(e^{\frac{8}{25}\tau}+\frac{1}{5})\tau}),$$

$$C_2 = e^{\frac{4}{25}\tau}\left(e^{\frac{4}{25}\tau}-\frac{1}{5}\right).$$

Then (16) holds when $\tau < \tau_* \approx 0.5$, which implies that the solution of Eq. (5) with the initial condition satisfying (10) converges to $u = 1$, if the time delay $\tau < \tau_*$. Note that $\tau_* < \tau_0$, so between τ_* and τ_0, the global dynamics of Eq. (5) is not completely clear.

Figures 2 and 3 show the progression of the solution trajectory of (5) with the initial condition $\phi(t) = 0.3 > \theta = 0.2$. When $\tau < \tau_*$, by Theorems 2 and 3, the solution converges to $u = 1$. Numerical simulation shows that solutions with $\tau < \tau_0$ indeed converges to 1 monotonously, and when $\tau_* < \tau < \tau_0$, the convergence still appears to hold but the solution may be an oscillatory one (see Fig. 2). Using the formulas in Sec. 4, we can calculate the quantities representing the nature of the Hopf bifurcation:

$$\mu_2 \approx 10.429 > 0, \quad \beta_2 \approx -9.399 < 0,$$

$$T_2 = 8.855 > 0.$$

From Fig. 2, one can observe that as the time delay τ increases, the period of the periodic orbit increases and the amplitude also increases.

Figure 3 shows the solution for $\tau \approx 3.615$. For τ close to 3.615, the periodic orbit exhibits a relaxation oscillation profile with a large period (> 50) (see [Guckenheimer, 2004; van der Pol, 1926]). However when $\tau \geq \tau^* \approx 3.616$, the pulse cannot be sustained and it converges to $u = 0$ as $t \to \infty$. Testing other initial conditions gives the same result of converging to zero. Hence it appears that a global extinction occurs for $\tau > \tau^*$, so that no matter what initial condition is, the population goes to extinction.

We also point out that when the initial condition is sufficiently large enough, the corresponding solution does not converge to the periodic orbit observed in Figs. 2 and 3. For example, in Fig. 4, the solution converges to 1 when $\tau < \tau^{**} \approx 1.63$, but the solution converges to 0 when $\tau > \tau^*$.

Indeed, if we use $\phi(t) = c > 0$ as a constant initial condition, then a numerical bifurcation diagram of $\phi = c$ and τ is shown in Fig. 5 to illustrate the variation of the basins of attraction of the constant equilibria $u = 0$ and $u = 1$. There are four regimes in (τ, ϕ)-plane:

(I) The solution converges to $u = 0$ as $t \to \infty$, that is, the population becomes extinct;

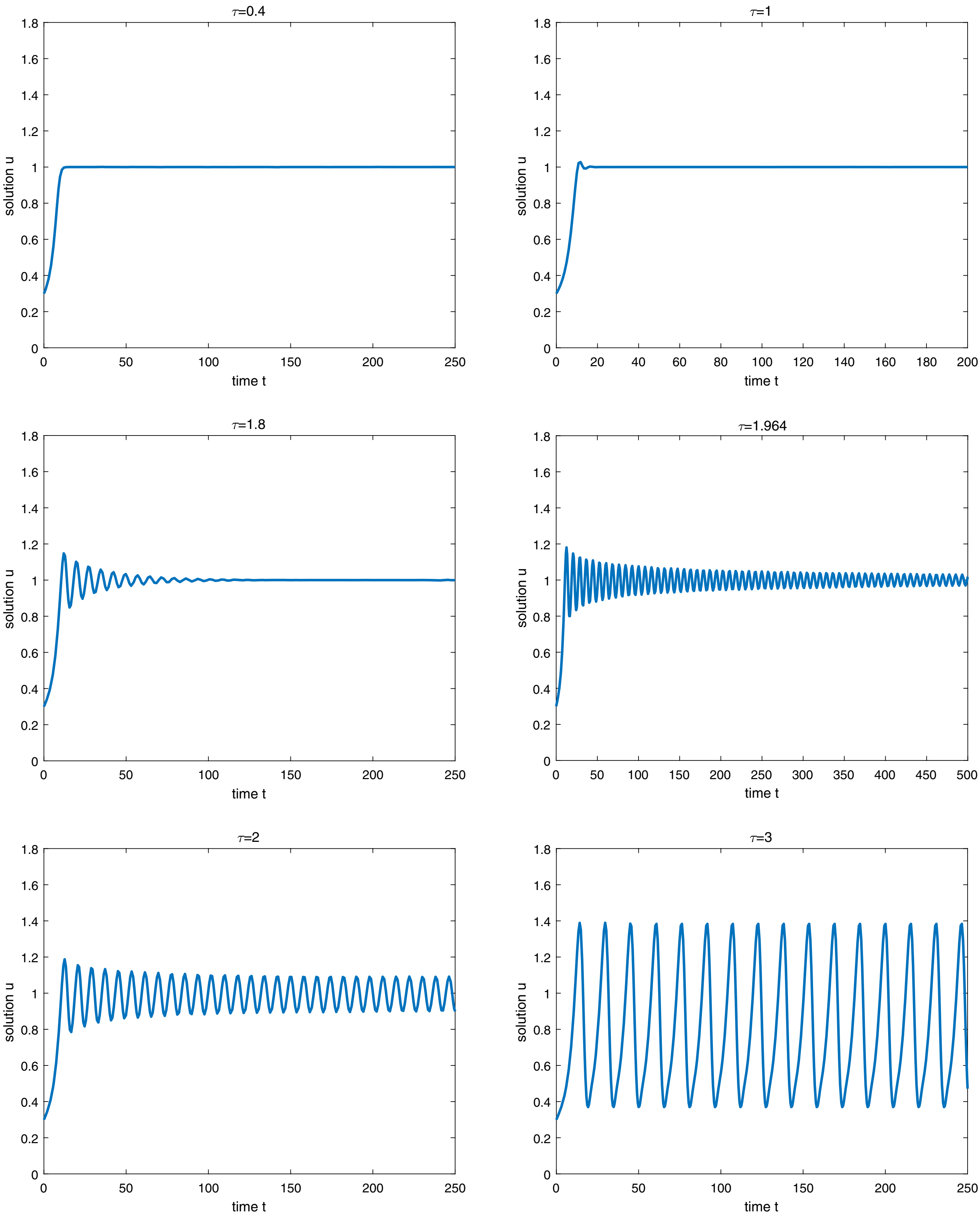

Fig. 2. Occurrence of the Hopf bifurcation near the positive equilibrium $u = 1$ in Eq. (5). Here the time series of the solutions to Eq. (5) with initial condition $\phi(t) = 0.3 > \theta = 0.2$ are plotted, and the values of τ are $\tau = 0.4, 1, 1.8, 1.964, 2$ and 3 respectively.

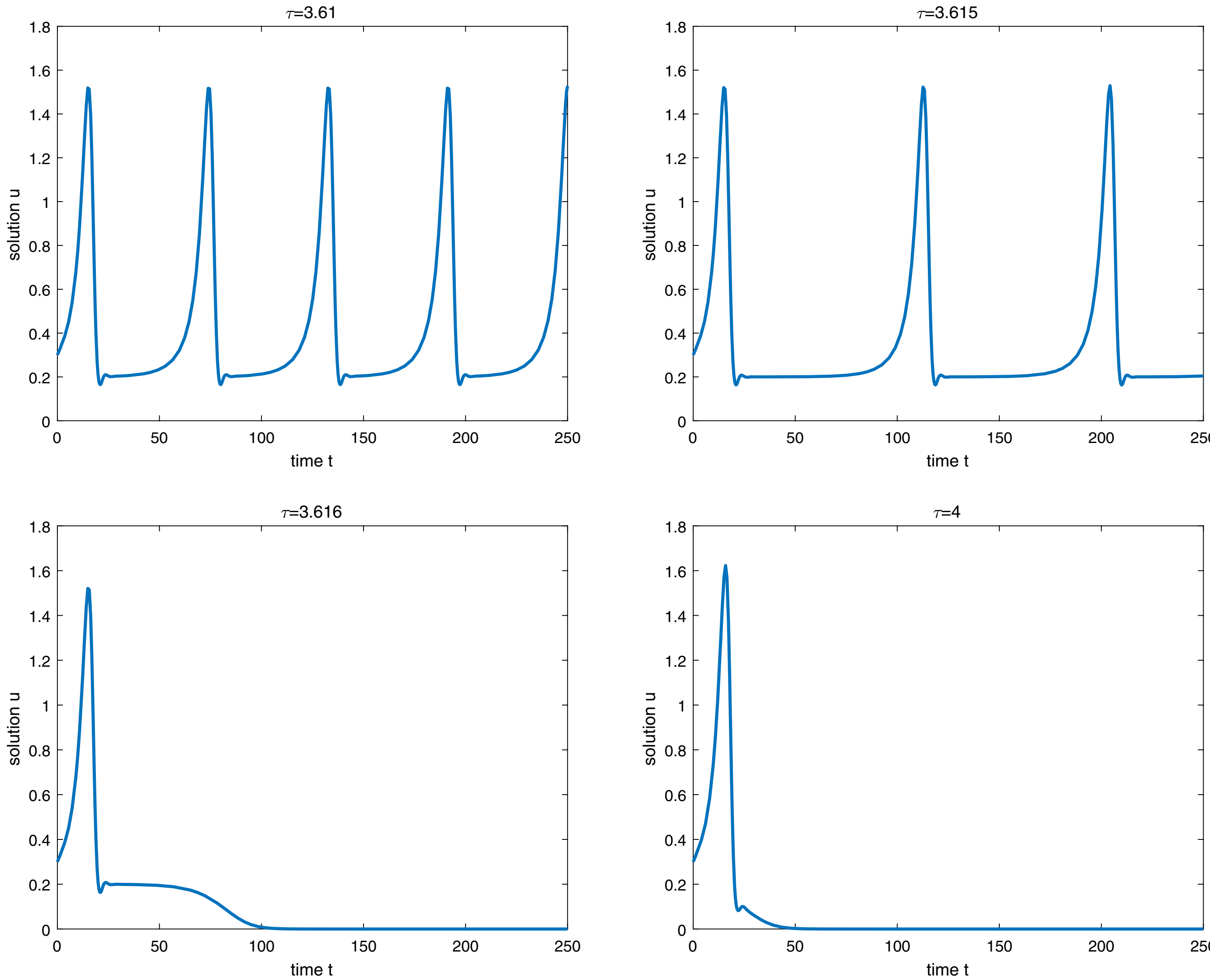

Fig. 3. From relaxation oscillation to global extinction in Eq. (5). Here the time series of the solutions to Eq. (5) with initial condition $\phi(t) = 0.3 > \theta = 0.2$ are plotted, and the values of τ are $\tau = 3.61, 3.615, 3.616$ and 4 respectively.

(II) The equilibrium $u = 1$ is unstable and the solution converges to the stable periodic solution;

(III) The equilibrium $u = 1$ is locally asymptotically stable but periodic solutions may exist due to the supercritical Hopf bifurcation;

(IV) The equilibrium $u = 1$ is locally asymptotically stable and the solution converges to $u = 1$ as $t \to \infty$ (Theorem 3).

We can observe that when $\tau < \tau^*$, the basin of attraction of $u = 0$ is "disconnected" with two connected components: $\{\phi < \theta = 0.2\}$ and a component with large ϕ. And as τ increases, the component with large ϕ expands as the basin of attraction of $u = 1$ or the limit cycle shrinks. The threshold value $\tau^*(\approx 3.616)$ is where the basin of attraction of the limit cycle collapses and the two components of the basin of attraction of $u = 0$ (extinction zone) join together, so a global extinction occurs when $\tau > \tau^*$ as shown in Fig. 3.

The sudden disappearance of the limit cycle at $\tau = \tau^*$ resembles the homoclinic bifurcation in a system of ordinary differential equations [Strogatz, 1994; Wiggins, 1988]. In Fig. 6, the "phase portraits" of (5) on the phase plane $(u(t), u(t - \tau))$ for different τ and $\theta = 0.2$ are shown. Again one can see the emergence of the limit cycle near $\tau_0 \approx 1.96$, and the cycle becomes larger as τ increases. When τ is close to $\tau^* \approx 3.616$, the lower edge of the cycle is near the equilibrium $(\theta, \theta) = (0.2, 0.2)$ on the phase plane; and when $\tau > \tau^*$, the orbits near the cycle

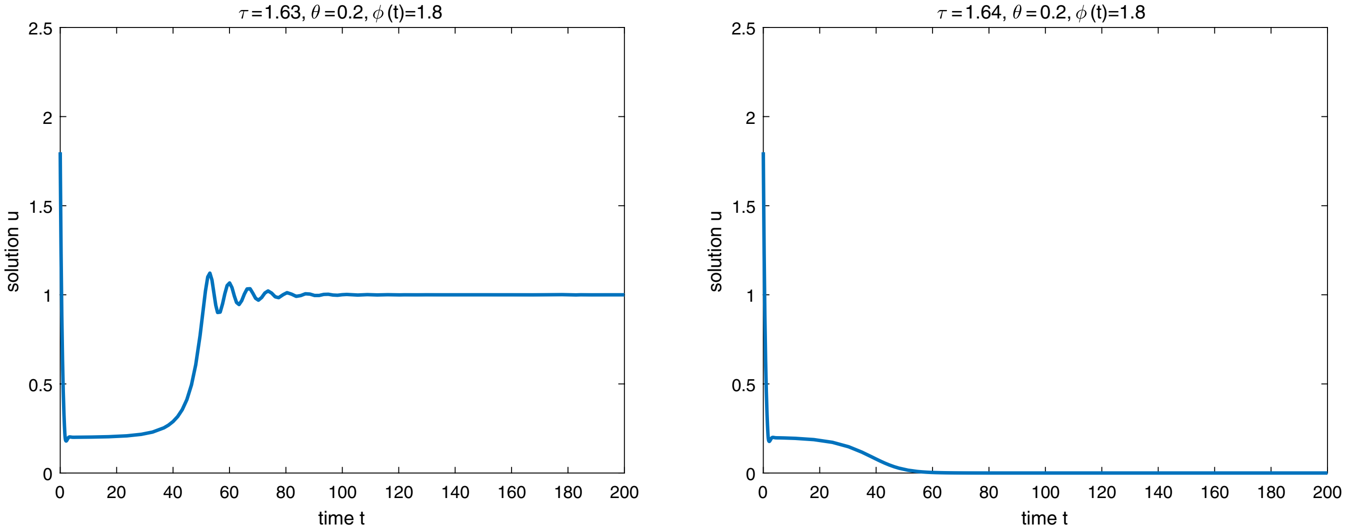

Fig. 4. From persistence to extinction in Eq. (5). Here the time series of the solutions to Eq. (5) with initial condition $\phi(t) = 1.8 > \theta = 0.2$ are plotted, and the values of τ are $\tau = 1.63$ and 1.64 respectively.

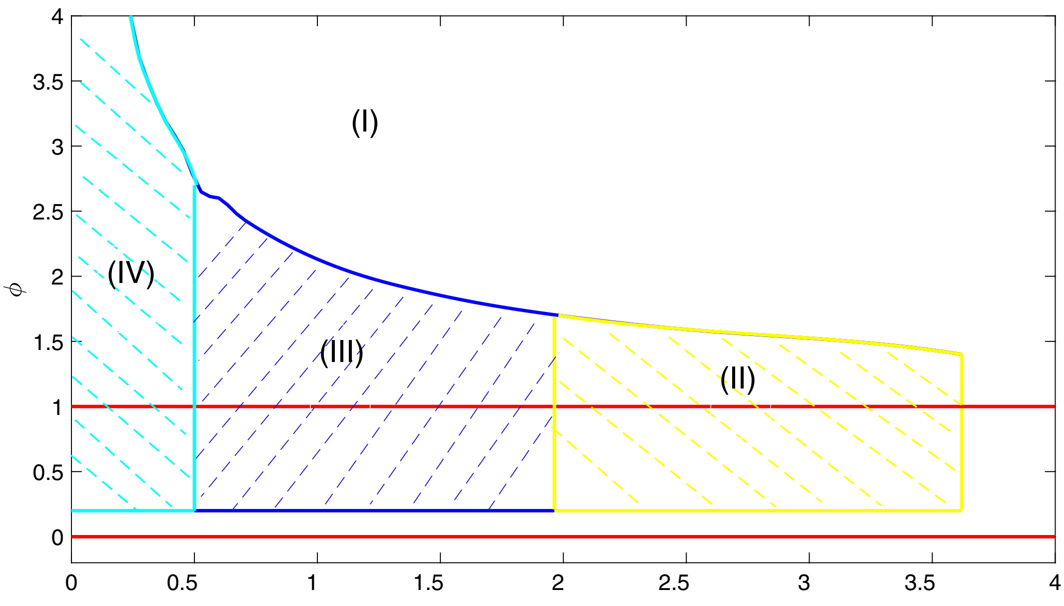

Fig. 5. Bifurcation diagram of Eq. (5) with the time delay τ and the constant initial condition ϕ as bifurcation parameters. Here $\theta = 0.2$.

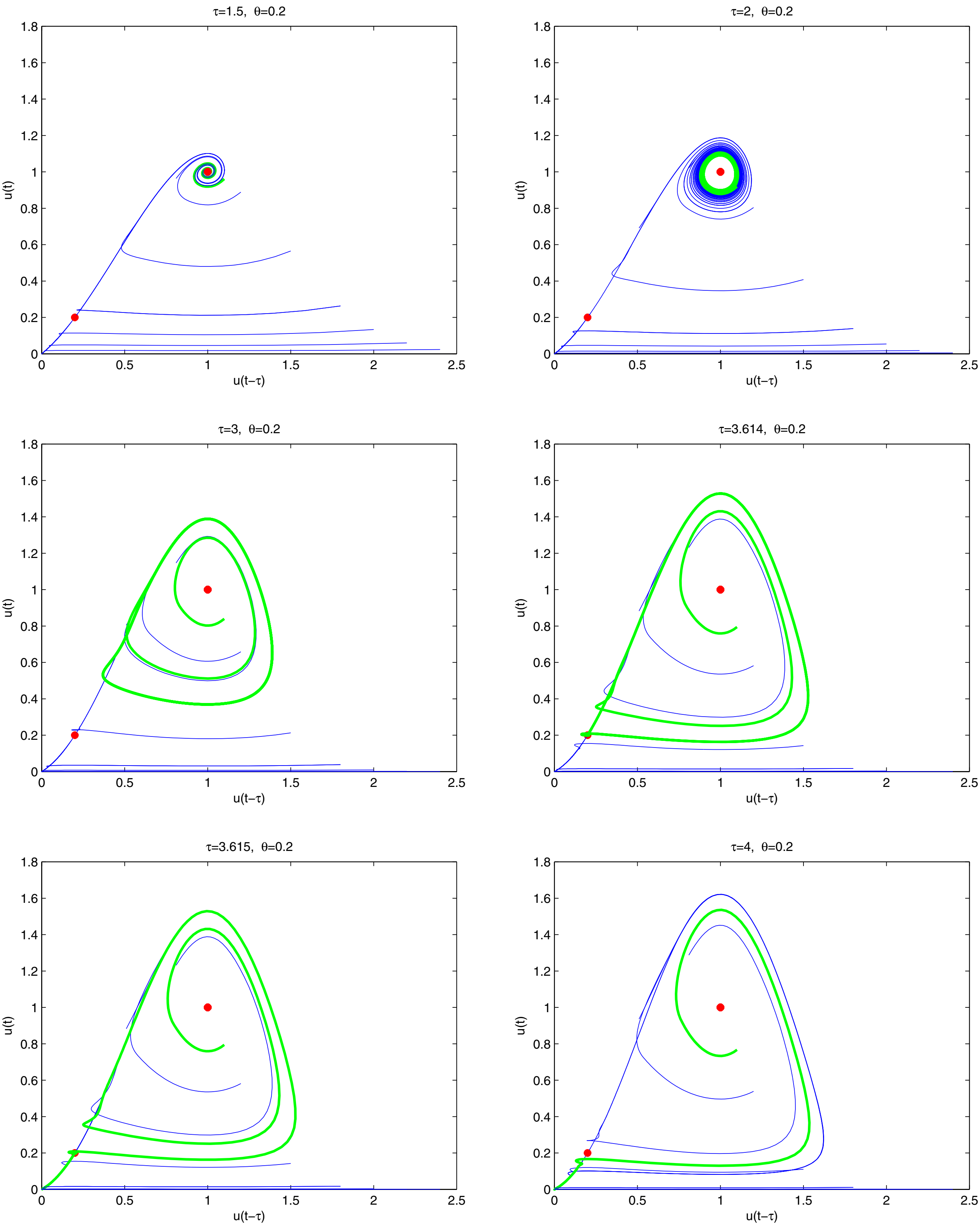

Fig. 6. The solution orbit $u(t)$ of system (5) in $(u(t), u(t-\tau))$-plane for varying τ. In each graph, the green curve is the solution curve with the initial condition $\phi(t) = 1.1$. Here $\theta = 0.2$, and $\tau = 1.5, 2, 3, 3.614, 3.615$ and 4.

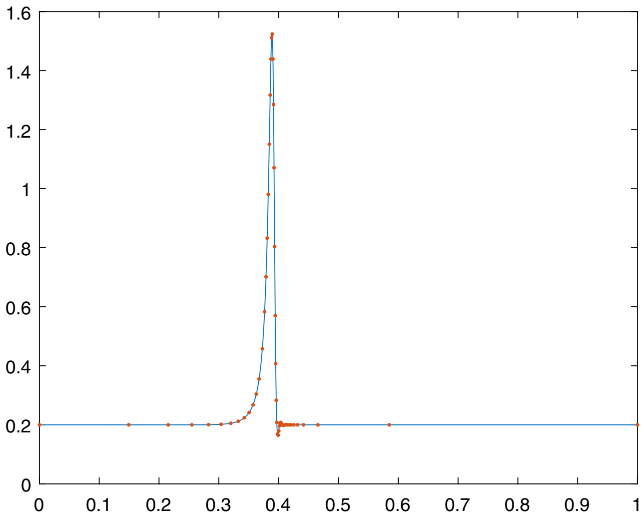

Fig. 7. The homoclinic orbit of Eq. (5) when $\theta = 0.2$ and $\tau = 3.616$.

follow the unstable manifold of $(\theta, \theta) = (0.2, 0.2)$ to go to the extinction state $(0, 0)$. At the bifurcation point τ^*, a homoclinic orbit based on $u = \theta$ exists as shown in the numerical simulation in Fig. 7. Notice that the profile of the homoclinic orbit in Fig. 7 is similar to the action potential pulse in the well-known Hodgkin–Huxley model and FitzHugh–Nagumo model.

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References

Allee, W. C. & Bowen, E. S. [1932] "Studies in animal aggregations: Mass protection against colloidal silver among goldfishes," *J. Exp. Zool.* **61**, 185–207.

Barbălat, I. [1959] "Systèmes d'équations différentielles d'oscillations non linéaires," *Rev. Math. Pures Appl.* **4**, 267–270.

Boukal, D. S. & Berec, L. [2002] "Single-species models of the Allee effect: Extinction boundaries, sex ratios and mate encounters," *J. Theoret. Biol.* **218**, 375–394.

Courchamp, F., Grenfell, B. T. & Clutton-Brock, T. H. [2000] "Impact of natural enemies on obligately cooperative breeders," *Oikos* **91**, 311–322.

Courchamp, F., Berec, L. & Gascoigne, J. [2008] *Allee Effects in Ecology and Conservation* (Oxford University Press, Oxford).

Ferdy, J. B., Austerlitz, F., Moret, J., Gouyon, P. H. & Godelle, B. [1999] "Pollinator-induced density dependence in deceptive species," *Oikos* **87**, 549–560.

Gopalsamy, K. & Ladas, G. [1990] "On the oscillation and asymptotic behavior of $\dot{N}(t) = N(t)[a + bN(t-\tau) - cN^2(t-\tau)]$," *Quart. Appl. Math.* **48**, 433–440.

Groom, M. J. [1998] "Allee effects limit population viablity of an annual plant," *Am. Nat.* **151**, 487–496.

Guckenheimer, J. [2004] "Bifurcations of relaxation oscillations," *Normal Forms, Bifurcations and Finiteness Problems in Differential Equations* (Kluwer, Dordrecht, The Netherlands), pp. 295–316.

Hassard, B. D., Kazarinoff, N. D. & Wan, Y. H. [1981] *Theory and Applications of Hopf Bifurcation* (Cambridge University Press, Cambridge, NY).

Idlango, M. A., Shepherd, J. J. & Gear, J. A. [2014] "Multiscaling analysis of a slowly varying single species population model displaying an Allee effect," *Math. Meth. Appl. Sci.* **37**, 1561–1569.

Jankovic, M. & Petrovskii, S. [2014] "Are time delays always destabilizing? Revisiting the role of time delays and the Allee effect," *Theor. Ecol.* **7**, 335–349.

Kang, Y. & Udiani, O. [2014] "Dynamics of a single species evolutionary model with Allee effects," *J. Math. Anal. Appl.* **418**, 492–515.

Kramer, A. M., Dennis, B., Liebhold, A. M. & Drake, J. M. [2009] "The evidence for Allee effects," *Popul. Ecol.* **51**, 341–354.

Kuang, Y. [1993] *Delay Differential Equations with Applications in Population Dynamics* (Academic Press, Inc., Boston, MA).

Kuussaari, M., Saccheri, I., Camara, M. & Hanski, I. [1998] "Allee effect and population dynamics in the glanville fritillary butterfly," *Oikos* **82**, 384–392.

Lewis, M. A. & Kareiva, P. [1993] "Allee dynamics and the spread of invading organisms," *Theor. Popul. Biol.* **43**, 141–158.

Lidicker, W. Z. [2010] "The Allee effect: Its history and future importance," *Open Ecol. J.* **3**, 71–82.

Owen, M. R. & Lewis, M. A. [2001] "How predation can slow, stop or reverse a prey invasion," *Bull. Math. Biol.* **63**, 655–684.

Stephens, P. A. & Sutherland, W. J. [1999] "Consequences of the Allee effect for behaviour, ecology and conservation," *Trends Ecol. Evol.* **14**, 401–405.

Stoner, A. W. & Ray-Culp, M. [2000] "Evidence for Allee effects in an over-harvested marine gastropod: Density dependent mating and egg production," *Mar. Ecol. Prog. Ser.* **202**, 297–302.

Strogatz, S. H. [1994] *Nonlinear Dynamics and Chaos*: *With Applications to Physics*, *Biology*, *Chemistry*, *and Engineering* (Perseus Books).

van der Pol, B. [1926] "On relaxation oscillations," *Philos. Mag.* **2**, 978–992.

Wang, M. & Kot, M. [2001] "Speeds of invasion in a model with strong or weak Allee effects," *Math. Biosci.* **171**, 83–97.

Wei, J. & Li, M. Y. [2005] "Hopf bifurcation analysis in a delayed Nicholson blowflies equation," *Nonlin. Anal.*: *Th. Math. Appl.* **60**, 1351–1367.

Wei, J. [2007] "Bifurcation analysis in a scalar delay differential equation," *Nonlinearity* **20**, 2483–2498.

Wiggins, S. [1988] *Global Bifurcations and Chaos*, Applied Mathematical Sciences, Vol. 73 (Springer-Verlag, NY).