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Stability Switches in a Logistic Population Model with Mixed Instantaneous and Delayed Density Dependence

Xiangping Yan · Junping Shi

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Abstract The local asymptotic stability and stability switches of the positive equilibrium in a logistic population model with mixed instantaneous and delayed density dependence is analyzed. It is shown that when the delayed dependence is more dominant, either the positive equilibrium becomes unstable for all large delay values, or the stability of equilibrium switches back and force several times as the delay value increases. Compared with the logistic model with the instantaneous term and a delayed term, our finding here is that the incorporation of another delayed term can lead to the occurrence of multiple stability switches.

Keywords Logistic model · Instantaneous and delayed density dependence · Stability switches · Hopf bifurcation

Mathematics Subject Classification 34K08 · 34K18 · 34K20 · 35R10 · 92E20

1 Introduction

Delay differential equations have been used as models for various natural phenomena and engineering controlled events [7,10,14,25,30]. The most significant dynamical behavior for many delayed differential equations is that a large delayed negative feedback can give rise to sustained oscillations [10,30]. The emergence of time-periodic dynamical behavior can usually be explained by the stability change of an equilibrium of the system and associated Hopf bifurcation which generates a small amplitude periodic orbit. Typically when using the value of delay (let's call it τ) as a bifurcation parameter and as the value of τ increase, an

X. Yan
Department of Mathematics, Lanzhou Jiaotong University, Lanzhou 730070, Gansu, China
e-mail: xpyan72@163.com

J. Shi (✉)
Department of Mathematics, College of William and Mary, Williamsburg, VA 23187-8795, USA
e-mail: jxshix@wm.edu

equilibrium changes from a stable one to an unstable one at a threshold value (bifurcation point) $\tau = \tau_0$, and the system possesses a periodic orbit for τ slightly passing τ_0.

In a model with a single negative delayed feedback, the loss of stability of the equilibrium at $\tau = \tau_0$ is permanent as the equilibrium is unstable all all $\tau > \tau_0$. For example, for the Hutchinson's model

$$\dot{u}(t) = u(t)\left(1 - u(t-\tau)\right), \tag{1.1}$$

one can solve the bifurcation values

$$\tau_n = \frac{(2n+1)\pi}{2}, \quad n \in \mathbb{N} \cup \{0\}, \tag{1.2}$$

and at each $\tau = \tau_n$, one pair of complex-valued eigenvalues of the characteristic equation moves across the imaginary axis to enter the right half of the complex plane. Thus for $\tau > \tau_n$, the characteristic equation has n pairs of complex eigenvalues with positive real part, and in particular, the equilibrium $u_* = 1$ is stable for $\tau < \tau_0$ and it is unstable for all $\tau > \tau_0$. Thus the parameter range for stability of $u_* = 1$ is $\tau \in [0, \tau_0)$, and the one for instability is (τ_0, ∞).

This stability change scenario also occurs in many other models. However in some other systems, there is a different stability switch scheme as the delay τ increases. That is, there exist bifurcation values $\tau_n^{(1)}$ and $\tau_n^{(2)}$ for $n \in \mathbb{N} \cup \{0\}$ such that

$$0 < \tau_0^{(2)} < \tau_0^{(1)} < \tau_1^{(2)} < \tau_1^{(1)} < \cdots < \tau_{j_0-1}^{(2)} < \tau_{j_0-1}^{(1)} < \tau_{j_0}^{(2)} < \tau_{j_0+1}^{(2)} < \tau_{j_0}^{(1)} < \cdots. \tag{1.3}$$

For $0 \le j \le j_0 - 1$, at each $\tau = \tau_j^{(2)}$, one pair of complex-valued eigenvalues of the characteristic equation moves across the imaginary axis to enter the *right* half of the complex plane, while at each $\tau = \tau_j^{(1)}$, one pair of complex-valued eigenvalues of the characteristic equation moves across the imaginary axis to enter the *left* half of the complex plane. That is, if the stability is lost at $\tau = \tau_j^{(2)}$, then it is regained at $\tau = \tau_j^{(1)}$ so that the stability switches back and force for the first j_0 pairs of bifurcation points. This stability switching-back can only happen finitely many times, thus for $\tau > \tau_{j_0}^{(2)}$, the stability is lost for good and no more switching-back will occur. This is due to the algebraic form of $\tau_j^{(i)}$ for $i = 1, 2$:

$$\tau_j^{(1)} = \tau_0^{(1)} + \Delta\tau_1 \cdot j\pi, \quad \tau_j^{(2)} = \tau_0^{(2)} + \Delta\tau_2 \cdot j\pi. \tag{1.4}$$

Because $\Delta\tau_1 - \Delta\tau_2 > 0$, so eventually the sequences $\{\tau_j^{(2)}\}$ and $\{\tau_j^{(1)}\}$ stop to appear alternatively, that is where the switching-backs end and the stability is lost for all large τ.

Several examples of stability switches have been shown in recent studies. In [12], parameter ranges for the linear delay differential equation $u''(t) = au(t) + bu'(t) + cu(t-\tau) + du'(t-\tau)$ undergoing stability switches were given. In [31], multiple stability switches were found for a planar predator-prey model. In [17], for a delayed model of CTL Response to HTLV-I infection, it was shown that a stability switch occurs and multiple periodic orbits coexist in some parameter range. The bifurcation sequences in [17] are like the one in (1.3) with two subsequences. In [16], it was shown that the model in [17] can also produce three Hopf bifurcation sequences and more complicated dynamics is possible. Recently such switching-back is also found in an intraguild predation model [11], as well as for a model of host-pathogen interaction incorporating density-dependent prophylaxis [24]. The models in [11,17,24] are all with three equations and a single delay, while the model in [31] has two variables and a single delay. Stability switches are also observed in some models with two delays, see for example, [22,32].

In this paper, we consider the stability switches in a scalar delay differential equation which is a generalized Hutchinson's model with the form

$$\dot{u}(t) = u(t)\left[1 - au(t) - bu(t - \tau_1) - cu(t - \tau_2)\right]. \tag{1.5}$$

If $c = 0$, then the model (1.5) is reduced to the following modified Hutchinson's equation (see [8,25,30,33])

$$\dot{u}(t) = u(t)\left[1 - au(t) - bu(t - \tau)\right]. \tag{1.6}$$

The model (1.6) has been studied extensively by many authors and it has been shown that if the instantaneous dependence is dominant, *i.e.* $a > b$, then the unique positive equilibrium $\bar{u} = 1/(a + b)$ of the model (1.6) is globally asymptotically stable for any $\tau \geq 0$, see for example, [5,6,15,21,25,29,30], and the global stability holds even for equation with more general type of delay term and diffusion term [13]. If the delayed dependence is more dominant, *i.e.* $a < b$, then it has been shown that [8,25,33] there exists a critical value $\tau_0 > 0$ given by

$$\tau_0 = \frac{a + b}{\sqrt{b^2 - a^2}} \arccos\left(-\frac{a}{b}\right),$$

such that the positive equilibrium $\bar{u}$ of the model (1.6) is locally asymptotically stable when $\tau \in [0, \tau_0)$ and it is unstable when $\tau > \tau_0$. In addition, the model (1.6) undergoes a Hopf bifurcation at $\bar{u}$ when τ increases across any critical value

$$\tau_n = \frac{a + b}{\sqrt{b^2 - a^2}} \left(\arccos\left(-\frac{a}{b}\right) + 2n\pi\right), \quad n \in \mathbb{N}.$$

While a quite complete analysis can be made for the single delay model (1.6), the analysis for a model with two distinct delays (1.5) is much more difficult. It is easy to see that the model (1.5) has two equilibria $u = 0$ and $u = u^* := 1/(a + b + c)$, where $u = 0$ is unstable for any $\tau_1, \tau_2 \geq 0$. Linearizing (1.5) at u^* gives the characteristic equation

$$\lambda + p + qe^{-\lambda\tau_1} + re^{-\lambda\tau_2} = 0, \tag{1.7}$$

where

$$p = au^* > 0, \;\; q = bu^* > 0, \;\; r = cu^* > 0. \tag{1.8}$$

Stability criteria on the parameters $(p, q, r, \tau_1, \tau_2)$ for (1.7) for various cases has been obtained in [2,9,18,20,23,27,28,34] and references therein.

In this paper we consider a special case of (1.5) with $\tau_2 = 2\tau_1$. In this case the model (1.5) reduces to

$$\begin{cases} \dot{u}(t) = u(t)\left[1 - au(t) - bu(t - \tau) - cu(t - 2\tau)\right], \\ u(s) = \phi(s) \geq 0, \qquad s \in [-2\tau, 0], \end{cases} \tag{1.9}$$

and the corresponding characteristic Eq. (1.7) has the form

$$\lambda + p + qe^{-\lambda\tau} + re^{-2\lambda\tau} = 0. \tag{1.10}$$

The distribution of roots of the transcendental polynomial equations similar to (1.10) has been discussed recently in [3,19]. In this paper we completely classify the local stability of the positive equilibrium u_* for all possible parameter (p, q, r) with $p, q, r > 0$ (or equivalently (a, b, c) with $a, b, c > 0$). We decompose the parameter space into parameter regions with following stability schemes:

(I) globally asymptotically stable for all $\tau \geq 0$.

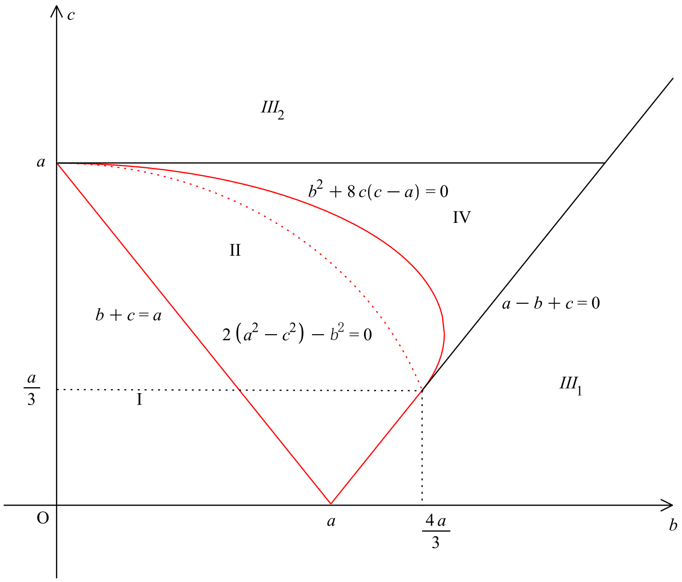


Fig. 1 Stability regions in the (b, c) plane when $a > 0$ is fixed

(II) locally asymptotically stable for all $\tau \geq 0$ (whether globally stable is not known).

(III) a single stability switch, that is, locally asymptotically stable for $\tau \in [0, \tau_0)$, and unstable for $\tau > \tau_0$.

(IV) possible multiple stability switches, that is, $u = u^*$ is locally asymptotically stable when

$$\tau \in \left[0, \tau_0^{(2)}\right) \cup \left(\tau_0^{(1)}, \tau_1^{(2)}\right) \cup \cdots \cup \left(\tau_{j_0-1}^{(1)}, \tau_{j_0}^{(2)}\right)$$

and it is unstable when

$$\tau \in \left(\tau_0^{(2)}, \tau_0^{(1)}\right) \cup \cdots \cup \left(\tau_{j_0-1}^{(2)}, \tau_{j_0-1}^{(1)}\right) \cup \left(\tau_{j_0}^{(2)}, \infty\right).$$

In particular we find that the region IV is not empty, thus two delayed negative feedbacks do not always produce oscillations when the delay value is increased. In some intermediate delay values, the stability can be regained with a proper combination of delay values of τ and 2τ. For any fixed $a > 0$, the regions I-IV are plotted in Fig. 1. Indeed these regions can be precisely described as follows:

$$\begin{aligned}
\text{I} &= \{(b, c) : b, c > 0, b + c < a\},\\
\text{II} &= \left\{(b, c) : 0 < c \leq \frac{a}{3}, a - c < b < a + c\right\}\\
&\quad \bigcup \left\{(b, c) : \frac{a}{3} < c < a, a - c < b < \sqrt{8c(a-c)}\right\},\\
\text{III} &= \{(b, c) : b > a, 0 < c < b - a\} \bigcup \{(b, c) : b > 0, c > \max\{a, b - a\}\},\\
\text{IV} &= \left\{(b, c) : \frac{a}{3} < c < a, \sqrt{8c(a-c)} < b < a + c\right\},
\end{aligned}$$

We remark that effort in some early work was to identify the "stable region", where the local stability holds for all $\tau \geq 0$. That stable region is $\text{I} \cup \text{II}$ in our notation, and the complement $\text{III} \cup \text{IV}$ would be unstable region. Our classification is more refined which also identifies more delicate properties of the system (1.9). In the unstable region III ∪ IV, a stability switch always happens, and in region IV, it is possible to have multiple stability switches (a condition to guarantee that is given in Sect. 3). Compared to earlier work in [11,17,22,24,31,32] for systems of equations, multiple stability switches as the delay value increases is shown for (1.9) which is scalar equation but with two (linearly dependent) delays. We consider (1.9) as a possibly minimal model for the occurrence of multiple stability switches in a delay differential equation.

In Sect. 2, we analyze the roots of characteristic Eq. (1.10), and in Sect. 3 we prove the stability switches in different cases. Some numerical simulations are given at the end of Sect. 3. Throughout this paper, we use $\mathbb{N}$ to denote the set of all positive integers and $\mathbb{N}_0 = \mathbb{N} \cup \{0\}$ to be the set of all nonnegative integers.

2 Transcendental Polynomial Characteristic Equation

In order to consider the local asymptotic stability of the positive equilibrium of (1.9), in this section we analyze the distribution of the roots of the characteristic equation

$$F(\lambda, \tau) := \lambda + p + qe^{-\lambda\tau} + re^{-2\lambda\tau} = 0 \tag{2.1}$$

on the complex plane while the parameter τ varies. If all the roots of (2.1) have negative real parts, then the positive equilibrium $u = u^*$ of (1.9) is locally asymptotically stable, and it is unstable if (2.1) has at least one root with positive real part.

We first consider the existence and number of the real-valued roots of (2.1) when $\tau > 0$. Let $\lambda \in \mathbb{R}$ and $e^{-\lambda\tau} = x$. Then $x > 0$ and when $\tau > 0$, solving λ in (2.1) is equivalent to solving x in an equation

$$f(x, \tau) := -\frac{\ln x}{\tau} + p + qx + rx^2 = 0. \tag{2.2}$$

Consequently the Eq. (2.1) has a real-valued negative (or positive) root λ if and only if the Eq. (2.2) has a real root $x > 1$ (or $0 < x < 1$). In what follows we analyze the existence and number of real positive roots of the Eq. (2.2).

It is easy to verify that for a fixed $\tau > 0$, the function $f(x, \tau)$ defined as in (2.2) has the properties

$$\lim_{x \to 0^+} f(x, \tau) = \infty, \quad f(1, \tau) > 0, \quad \lim_{x \to \infty} f(x, \tau) = \infty. \tag{2.3}$$

In addition, the equation

$$\frac{\partial f}{\partial x}(x, \tau) = 2rx + q - \frac{1}{\tau x} = 0$$

has a unique positive root

$$x_0(\tau) = \frac{-q + \sqrt{q^2 + 8r\tau^{-1}}}{4r}. \tag{2.4}$$

The following result gives the nonexistence, existence and number of positive real roots of the Eq. (2.2).

Proposition 1 *Suppose that $p, q, r > 0$. Then there exists $\tau^* \in (0, 1/(q + 2r))$ such that*

1. *when $0 < \tau < \tau^*$, the Eq. (2.2) has two positive real roots $x_1(\tau)$ and $x_2(\tau)$ with $1 < x_1(\tau) < x_2(\tau)$ and $\lim_{\tau \to 0^+} x_1(\tau) = 1$ and $\lim_{\tau \to 0^+} x_2(\tau) = \infty$;*
2. *the Eq. (2.2) has a unique positive real root $x_1 > 1$ when $\tau = \tau^*$;*
3. *the Eq. (2.2) has no positive real root when $\tau > \tau^*$.*

Proof From (2.3) and $f_x(x, \tau) = 0$ has a unique real positive root, one can conclude that the number of real positive roots of (2.2) is determined by the sign of $f(x_0(\tau), \tau)$: (2.2) has 0 (or 1, or 2) positive real root(s) if $f(x_0(\tau), \tau) > 0$ (or $= 0$, or < 0).

From (2.4) one can obtain that $0 < x_0(\tau) < 1$ when $\tau > 1/(q + 2r)$, $x_0(\tau) = 1$ when $\tau = 1/(q + 2r)$ and $x_0(\tau) > 1$ when $0 < \tau < 1/(q + 2r)$. Accordingly, $(\ln x_0(\tau))/\tau \leq 0$ when $\tau \geq 1/(q + 2r)$. Moreover, notice that $p + qx + rx^2 > p > 0$ for all $x > 0$ since $p, q, r > 0$. Consequently, when $\tau \geq 1/(q + 2r)$, $f(x_0(\tau), \tau) > 0$ and thus (2.2) has no positive real root.

Now we restrict τ so that $0 < \tau < 1/(q + 2r)$. Since $\lim_{\tau\to 0^+} x_0(\tau) = \infty$, it follows that $\lim_{\tau\to 0^+} \ln x_0(\tau) = \infty$. In addition,

$$\lim_{\tau\to 0^+} \tau x_0(\tau) = \lim_{\tau\to 0^+} \frac{-q\tau + \sqrt{q^2\tau^2 + 8r\tau}}{4r} = 0, \tag{2.5}$$

$$\lim_{\tau\to 0^+} \tau x_0^2(\tau) = \lim_{\tau\to 0^+} \frac{2q^2\tau + 8r - 2q\sqrt{q^2\tau^2 + 8r\tau}}{16r^2} = \frac{1}{2r}. \tag{2.6}$$

From (2.5) and (2.6) we know that $\lim_{\tau\to 0^+} f(x_0(\tau), \tau) < 0$, and thus when $\tau > 0$ is small enough, the Eq. (2.2) has two positive real roots $x_1(\tau)$ and $x_2(\tau)$ with $1 < x_1(\tau) < x_0(\tau) < x_2(\tau)$ since $x_0(\tau) > 1$ and $f(1, \tau) > 0$. Meanwhile, this also implies that $\lim_{\tau\to 0^+} x_2(\tau) = \infty$ since $\lim_{\tau\to 0^+} x_0(\tau) = \infty$. On the other hand, when $\tau > 0$, the Eq. (2.2) is equivalent to

$$p\tau + q\tau x + r\tau x^2 - \ln x = 0. \tag{2.7}$$

It is clear that when $\tau = 0$, the Eq. (2.7) has only one root at $x = 1$. Therefore, we know that $\lim_{\tau\to 0^+} x_1(\tau) = 1$.

Finally we consider the monotonicity of $f(x_0(\tau))$ with respect to τ in $(0, 1/(q + 2r))$. We have

$$\frac{df(x_0(\tau), \tau)}{d\tau} = \frac{\partial f(x_0(\tau), \tau)}{\partial x}\frac{dx_0(\tau)}{d\tau} + \frac{\partial f(x_0(\tau), \tau)}{\partial \tau}.$$

Since $x_0(\tau) > 1$ when $0 < \tau < 1/(q + 2r)$, we have

$$\frac{\partial f(x_0(\tau), \tau)}{\partial \tau} = \frac{\ln x_0(\tau)}{\tau^2} > 0. \tag{2.8}$$

In addition, from (2.4) we know that

$$\frac{\partial f(x_0(\tau), \tau)}{\partial x} = 2rx_0(\tau) + q - \frac{1}{\tau x_0(\tau)} = 0. \tag{2.9}$$

Combining (2.8) and (2.9), we have that $df(x_0(\tau), \tau)/d\tau > 0$ and hence $f(x_0(\tau), \tau)$ is strictly increasing for $\tau \in (0, 1/(q + 2r))$. Together with the discussion above, we know that there exists a unique $\tau^* \in (0, 1/(q + 2r))$ such that $f(x_0(\tau), \tau) = 0$ when $\tau = \tau^*$, $f(x_0(\tau), \tau) > 0$ when $\tau > \tau^*$ and $f(x_0(\tau), \tau) < 0$ when $\tau < \tau^*$. This completes the proof. □

From Proposition 1, we can derive the following result on the existence and number of negative real roots of the Eq. (2.1).

Theorem 1 *Suppose that $p, q, r > 0$ and let $\tau^* \in (0, 1/(q + 2r))$ be given by Proposition 1. Then the Eq. (2.1) has no non-negative real-valued root for any $\tau \geq 0$, and the following results hold.*

1. *If* $0 < \tau < \tau^*$, *then* (2.1) *has exactly two negative real-valued roots* $\lambda_1(\tau)$ *and* $\lambda_2(\tau)$ *with* $\lambda_2(\tau) < \lambda_1(\tau)$, *and* $\lim_{\tau \downarrow 0} \lambda_1(\tau) = -(p+q+r)$, $\lim_{\tau \downarrow 0} \lambda_2(\tau) = -\infty$ *and* $\lim_{\tau \uparrow \tau^*} \lambda_1(\tau) = \lim_{\tau \uparrow \tau^*} \lambda_2(\tau)$.
2. *If* $\tau = \tau^*$, *then* (2.1) *has exactly one negative real-valued root.*
3. *If* $\tau > \tau^*$, *then* (2.1) *has no negative real-valued root.*

Next we analyze the existence of purely imaginary roots of the Eq. (2.1) and the crossing of complex-valued roots through the imaginary axis. In applications, if the Eq. (2.1) has no purely imaginary roots for any $\tau > 0$, then from a well-known result of roots of the characteristic equation (see [27]) and the fact that the Eq. (2.1) has only a real-valued negative root when $\tau = 0$, we know that all the roots of the Eq. (2.1) have negative real parts for any $\tau \geq 0$. On the other hand, if the Eq. (2.1) has a pair of purely imaginary roots for some $\tau = \tau_0$ and the complex conjugate pair of (2.1) cross through transversally the imaginary axis when $\tau = \tau_0$ from the left half complex plane to the right half complex plane, then (2.1) has a pair of conjugate complex roots with positive real part when $0 < \tau - \tau_0 \ll 1$.

Assume that $\pm i\omega(\omega > 0)$ are a pair of purely imaginary roots of the Eq. (2.1). Then we have

$$i\omega + p + qe^{-i\omega\tau} + re^{-2i\omega\tau} = 0,$$

or

$$e^{i\omega\tau}(i\omega + p) + q + re^{-i\omega\tau} = 0. \tag{2.10}$$

Separating the real and imaginary parts of the Eq. (2.10) yields

$$\begin{aligned} &(p+r)\cos\omega\tau - \omega\sin\omega\tau + q = 0, \\ &\omega\cos\omega\tau + (p-r)\sin\omega\tau = 0. \end{aligned} \tag{2.11}$$

One can obtain from Eq. (2.11) that

$$\begin{cases} (\omega^2 + p^2 - r^2)\cos\omega\tau + q(p-r) = 0, \\ (\omega^2 + p^2 - r^2)\sin\omega\tau - q\omega = 0. \end{cases} \tag{2.12}$$

Therefore, ω satisfies the following equation

$$\left(\omega^2 + p^2 - r^2\right)^2 = q^2\left[(p-r)^2 + \omega^2\right], \tag{2.13}$$

that is,

$$\omega^4 + \left[2\left(p^2 - r^2\right) - q^2\right]\omega^2 + (p-r)^2(p+q+r)(p-q+r) = 0. \tag{2.14}$$

Let

$$h(z) := z^2 + \left[2\left(p^2 - r^2\right) - q^2\right]z + (p-r)^2(p+q+r)(p-q+r). \tag{2.15}$$

Then from the analysis above one can see that the number of pairs of purely imaginary roots of the Eq. (2.1) is the same as the number of positive roots of the equation $h(z) = 0$. Notice that the discriminant of the quadratic function $h(z)$ is given by

$$\Delta := \left[2\left(p^2 - r^2\right) - q^2\right]^2 - 4(p-r)^2(p+q+r)(p-q+r) = q^2\left[q^2 + 8r(r-p)\right]. \tag{2.16}$$

Hence, for the positive roots of the equation $h(z) = 0$, we have the following observation.

Lemma 1 *Let the function* $h(z)$ *be defined by* (2.15). *If* $p = r$, *then the equation* $h(z) = 0$ *has only a positive root* $z = q^2$. *If* $p \neq r$, *then*

(i) *the equation* $h(z) = 0$ *has no positive root when one of the following conditions holds:*

$$q^2 + 8r(r-p) < 0, \quad or \tag{2.17}$$

$$p - q + r > 0, \quad and \quad 2(p^2 - r^2) - q^2 \geq 0; \tag{2.18}$$

(ii) *the equation* $h(z) = 0$ *has only a positive root when one of the following conditions holds:*

$$p - q + r < 0, \quad or \tag{2.19}$$

$$p - q + r > 0, \; 2(p^2 - r^2) - q^2 < 0, \quad and \quad q^2 + 8r(r-p) = 0. \tag{2.20}$$

(iii) *the equation* $h(z) = 0$ *has two positive roots when*

$$p - q + r > 0, \; 2(p^2 - r^2) - q^2 < 0, \quad and \quad q^2 + 8r(r-p) > 0. \tag{2.21}$$

Assume that $\omega^2 (\omega > 0)$ is a positive root of the equation $h(z) = 0$. Then from (2.13) we can observe that $\omega^2 + p^2 - r^2 \neq 0$. Therefore, we have from (2.12)

$$\cos \omega\tau = \frac{q(r-p)}{\omega^2 + p^2 - r^2} \text{ and } \sin \omega\tau = \frac{q\omega}{\omega^2 + p^2 - r^2}. \tag{2.22}$$

Thus, if $\pm i\omega (\omega > 0)$ are a pair of purely imaginary roots of the Eq. (2.1), then the corresponding values of τ are given by

$$\tau_j = \frac{1}{\omega} \left[\cos^{-1} \left(\frac{q(r-p)}{\omega^2 + p^2 - r^2} \right) + 2j\pi \right], \quad j \in \mathbb{N}_0. \tag{2.23}$$

Therefore for given $p, q, r > 0$, if one of the conditions (2.19), (2.20) or (2.21) is satisfied, then the Eq. (2.14) has a positive root $\omega > 0$, and the characteristic equation (2.1) has a pair of purely imaginary roots $\pm i\omega$ when $\tau = \tau_j$ defined as in (2.23).

In order to consider the way of the complex roots of the Eq. (2.1) crossing through the imaginary axis when $\tau = \tau_j$, we need the following result.

Lemma 2 *Let* $z = \omega^2 (\omega > 0)$ *be a simple positive root of the equation* $h(z) = 0$. *Then*

$$\omega^2 + p^2 + 3r^2 - 4pr \neq 0. \tag{2.24}$$

Proof It is clear that when $p = r$,

$$\omega^2 + p^2 + 3r^2 - 4pr = \omega^2 > 0.$$

If $p \neq r$, then from Lemma 1, $h(z) = 0$ has a simple positive root if (2.19) or (2.21) is satisfied, and $h(z) = 0$ has a non-simple positive root if (2.20) is satisfied.

Case 1: If $p \neq r$ and (2.19) is satisfied, then

$$q^2 + 8r(r-p) > (p+r)^2 + 8r(r-p) = (p-3r)^2 \geq 0. \tag{2.25}$$

It follows from (2.16) that $\Delta > 0$ and we have

$$\omega^2 = \frac{q^2 - 2(p^2 - r^2) + \sqrt{\Delta}}{2}. \tag{2.26}$$

From (2.16) and (2.26), one can obtain that

$$\omega^2 + p^2 + 3r^2 - 4pr = \frac{q^2 + 8r(r-p) + \sqrt{\Delta}}{2} = \frac{\sqrt{\Delta}}{2} \left(\frac{\sqrt{\Delta}}{q^2} + 1 \right) > 0. \tag{2.27}$$

Case 2: If $p \neq r$ and (2.21) is satisfied, then

$$\omega^2 = \omega_1^2 := \frac{q^2 - 2(p^2 - r^2) - \sqrt{\Delta}}{2}, \tag{2.28}$$

or

$$\omega^2 = \omega_2^2 := \frac{q^2 - 2(p^2 - r^2) + \sqrt{\Delta}}{2}. \tag{2.29}$$

From (2.27) we can get that $\omega_2^2 + p^2 + 3r^2 - 4pr > 0$. By (2.16) and (2.28), we have

$$\omega_1^2 + p^2 + 3r^2 - 4pr = \frac{\sqrt{\Delta}(\sqrt{\Delta} - q^2)}{2q^2} \neq 0, \tag{2.30}$$

since $\Delta - q^4 = 8q^2 r(r-p) \neq 0$ when $p \neq r$. □

By using Lemma 2, we can establish the existence of the complex-valued root for τ near τ_j.

Lemma 3 *Let $F(\lambda, \tau)$ be defined as in (2.1). Assume that $z = \omega^2 (\omega > 0)$ is a simple positive root of the equation $h(z) = 0$ and the Eq. (2.1) has the purely imaginary roots $\pm i\omega (\omega > 0)$ when $\tau = \tau_j (j \in \mathbb{N}_0)$. Then $F_\lambda(\pm i\omega, \tau_j) : \mathbb{C} \to \mathbb{C}$ is invertible. In particular, there are a neighborhood O of $\lambda = i\omega$ and an interval I containing τ_j such that when $\tau \in I$, the Eq. (2.1) has a complex root $\lambda(\tau) = \alpha(\tau) + i\beta(\tau)$ such that $\alpha(\tau_j) = 0$, $\beta(\tau_j) = \omega > 0$, and*

$$\lambda'(\tau_j) = \alpha'(\tau_j) + i\beta'(\tau_j) = \frac{i\omega\theta}{1 - \tau_j\theta} = \frac{i\omega\theta(1 - \tau_j\overline{\theta})}{|1 - \tau_j\theta|^2}, \tag{2.31}$$

where

$$\theta = qe^{-i\omega\tau_j} + 2re^{-2i\omega\tau_j}. \tag{2.32}$$

Proof For $F : \mathbb{C} \times \mathbb{R} \to \mathbb{C}$, one can calculate that

$$F_\lambda(\lambda, \tau)[\xi] = \left(1 - q\tau e^{-\lambda\tau} - 2r\tau e^{-2\lambda\tau}\right)[\xi], \quad \xi \in \mathbb{C}. \tag{2.33}$$

Hence

$$F_\lambda(i\omega, \tau_j)[\xi_1 + i\xi_2] = (1 \;\; i)\begin{pmatrix} \rho & -\mu \\ \mu & \rho \end{pmatrix}\begin{pmatrix} \xi_1 \\ \xi_2 \end{pmatrix} = (1 \;\; i)A(\omega, \tau_j)\begin{pmatrix} \xi_1 \\ \xi_2 \end{pmatrix}, \tag{2.34}$$

where

$$\rho = 1 - q\tau_j \cos\omega\tau_j - 2r\tau_j \cos 2\omega\tau_j, \quad \mu = q\tau_j \sin\omega\tau_j + 2r\tau_j \sin 2\omega\tau_j.$$

Then $F_\lambda(i\omega, \tau_j)$ is invertible if and only if the 2×2 matrix $A(\omega, \tau_j)$ is invertible, which is equivalent to $\rho^2 + \mu^2 \neq 0$. Indeed from Lemma 2,

$$\mu = \tau_j(q + 4r\cos\omega\tau_j)\sin\omega\tau_j = \frac{q^2\omega(\omega^2 + p^2 + 3r^2 - 4pr)}{(\omega^2 + p^2 - r^2)^2}\tau_j \neq 0.$$

This proves that $F_\lambda(\pm i\omega, \tau_j)$ is invertible. Now it follows from the implicit function theorem that there are a neighborhood O of $\lambda = i\omega$ and an interval I containing τ_j such that when $\tau \in I$, there exists a unique $\lambda(\tau) = \alpha(\tau) + i\beta(\tau)$ such that $F(\lambda(\tau), \tau) = 0, \alpha(\tau_j) = 0$ and $\beta(\tau_j) = \omega > 0$. Moreover, again from the implicit function theorem, $\lambda(\tau)$ is C^1, and $\lambda'(\tau_j) = -F_\lambda^{-1}(i\omega, \tau_j)[F_\tau(i\omega, \tau_j)]$. Since $F_\tau = -\lambda(qe^{-\lambda\tau} + 2re^{-\lambda\tau})$, then combining with (2.33), we obtain (2.31). □

Now let $z = \omega^2 (\omega > 0)$ be a simple positive root of the equation $h(z) = 0$ and $i\omega$ is a purely imaginary root of the Eq. (2.1). Then by (2.31), we know that

$$\frac{d\lambda(\tau)}{d\tau}\Big|_{\tau=\tau_j} = \frac{i\omega\theta - i\omega\tau_j|\theta|^2}{|1-\tau_j\theta|^2} = \frac{-\omega\mathrm{Im}(\theta) + i\omega(\mathrm{Re}(\theta) - \tau_j|\theta|^2)}{|1-\tau_j\theta|^2}. \tag{2.35}$$

According to (2.22), one can derive

$$\begin{aligned} -\mathrm{Im}(\theta) &= (q + 4r\cos\omega\tau_j)\sin\omega\tau_j \\ &= \frac{q^2\omega(\omega^2 + p^2 + 3r^2 - 4pr)}{(\omega^2 + p^2 - r^2)^2}. \end{aligned} \tag{2.36}$$

Thus from (2.35) and (2.36) we obtain that

$$\begin{aligned} \mathrm{Sign}\left[\frac{d\mathrm{Re}\lambda(\tau)}{d\tau}\right]_{\tau=\tau_j} &= \mathrm{Sign}\left[\frac{q^2\omega(\omega^2 + p^2 + 3r^2 - 4pr)}{(\omega^2 + p^2 - r^2)^2}\right] \\ &= \mathrm{Sign}(\omega^2 + p^2 + 3r^2 - 4pr) \\ &= \mathrm{Sign}[\omega^2 + (p-r)(p-3r)]. \end{aligned} \tag{2.37}$$

3 Stability Switches of the Positive Equilibrium

In this section, we shall discuss the stability switches of the positive equilibrium $u = u^*$ of (1.9) according to the analysis obtained in Sect. 3 for the corresponding characteristic Eq. (2.1).

3.1 Nonexistence of Stability Switch

If all the roots of the characteristic Eq. (2.1) have negative real parts for any $\tau \geq 0$, then the positive equilibrium $u = u^*$ of (1.9) is absolutely stable, *i.e.* $u = u^*$ has no stability switch for any $\tau > 0$.

From Lemma 1 we know that when (2.17) or (2.18) holds, the equation $h(z) = 0$ has no positive root and hence all the roots of the characteristic Eq. (2.1) have negative real parts for any $\tau \geq 0$. In addition, if (2.20) is satisfied, then the equation $h(z) = 0$ has a double root

$$\omega^2 = \frac{q^2 - 2(p^2 - r^2)}{2}.$$

It follows from (2.37) that

$$\mathrm{Sign}\left[\frac{d\mathrm{Re}\lambda(\tau)}{d\tau}\right]_{\tau=\tau_j} = \mathrm{Sign}(q^2 + 8r(r-p)) = 0.$$

Therefore, in this case we know that all the roots of the characteristic Eq. (2.1) have nonpositive real parts for any $\tau \geq 0$.

Based on the discussion above, we have the following result about the nonexistence of stability switch of $u = u^*$.

Theorem 2 *Assume that $p \neq r$, and one of* (2.17), (2.18) *or* (2.20) *holds. Then the positive equilibrium $u = u^*$ of* (1.9) *has no stability switch for all $\tau \geq 0$.*

3.2 Single Stability Switch

If there is a certain $\tau_0 > 0$ such that all the roots of the characteristic Eq. (2.1) have negative real parts when $0 \le \tau < \tau_0$, (2.1) has at least a root with positive real part when $\tau > \tau_0$, and one pair of complex roots of (2.1) crosses through the imaginary axis transversally at $\tau = \tau_0$ from the left half plane to the right half, then we say that the positive equilibrium $u = u^*$ of (1.9) has a single stability switch at $\tau = \tau_0$. Meanwhile, the model (1.9) undergoes a Hopf bifurcation at $u = u^*$ when $\tau = \tau_0$.

Here we give the conditions under which $u = u^*$ has only a single stability switch. We first consider the case when (2.15) has only one positive root.

Theorem 3 *Assume that p, q and r satisfy either $p = r$, or $p \ne r$ and (2.19). Let ω and τ_j be defined by (2.26) and (2.23), respectively. Then the positive equilibrium $u = u^*$ of (1.9) is locally asymptotically stable when $0 \le \tau < \tau_0$ and it is unstable when $\tau > \tau_0$. Furthermore, (1.9) undergoes a Hopf bifurcation at $u = u^*$ when $\tau = \tau_j$ for $j \in \mathbb{N}_0$.*

Proof From Lemma 1, the characteristic Eq. (2.15) has only one positive root ω which is given by (2.26), and at τ_j given by (2.23), a pair of complex-values roots of (2.1) crosses the imaginary axis transversally. Moreover from (2.27) and (2.37), we know that

$$\text{Sign}\left[\frac{d\text{Re}\lambda(\tau)}{d\tau}\right]_{\tau=\tau_j} > 0, \tag{3.1}$$

for $j \in \mathbb{N}_0$, which implies that $u = u^*$ is unstable for all $\tau > \tau_0$. □

Secondly we consider the case when p, q, r satisfy the condition (2.21). In this case, since $\Delta > 0$ and the equation $h(z) = 0$ has two different positive roots z_1 and z_2 with $z_1 < z_2$, where $z_k = \omega_k^2$ and $\omega_k^2 (k = 1, 2)$ are defined respectively by (2.28) and (2.29), then we can define $\tau_j^{(k)} (j \in \mathbb{N}_0)$ by

$$\tau_j^{(k)} = \frac{1}{\omega_k}\left[\cos^{-1}\left(\frac{q(r-p)}{\omega^2 + p^2 - r^2}\right) + 2j\pi\right], \quad j \in \mathbb{N}_0. \tag{3.2}$$

If in addition we assume that $p < r$, then

$$2\left(p^2 - 4pr + 3r^2\right) = 2(p-r)(p-3r) > 0,$$

and consequently from (2.37) one can see when $p < r$, we have (3.1) holds for both $\tau_j^{(1)}$ and $\tau_j^{(2)}$. In virtue of the analysis above, we have

Theorem 4 *Assume that p, q and $r > 0$ satisfy (2.21) and*

$$p < r. \tag{3.3}$$

Let ω_1 and ω_2 be defined by (2.28) and (2.29) respectively, and $\tau_j^{(k)} (k = 1, 2; j \in \mathbb{N}_0)$ be given by (3.2). Then the positive equilibrium $u = u^*$ of (1.9) is locally asymptotically stable when $0 \le \tau < \min\{\tau_0^{(1)}, \tau_0^{(2)}\}$ and it is unstable when $\tau > \min\{\tau_0^{(1)}, \tau_0^{(2)}\}$. Moreover (1.9) undergoes a Hopf bifurcation at $u = u^*$ when $\tau = \tau_j^{(k)}$ for $k = 1, 2, j \in \mathbb{N}_0$.

3.3 Multiple Stability Switches

In this subsection, we analyze possible multiple stability switches of the positive equilibrium $u = u^*$ of (1.9). To this end, throughout this subsection, we always assume that p, q and r satisfy (2.21) and $p > r$, or to be more explicit,

$$p > r,\ \ p - q + r > 0,\ \ 2(p^2 - r^2) - q^2 < 0 \text{ and } \Delta > 0. \tag{3.4}$$

In this case, the equation $h(z) = 0$ has two real positive roots $z_1 = \omega_1^2$ and $z_2 = \omega_2^2$ with $\omega_1 < \omega_2$ defined by (2.28) and (2.29) respectively, and $\tau_j^{(k)}$ with $k = 1, 2,\ j \in \mathbb{N}_0$ are defined by (3.2).

In view of (2.16), (2.30) and (2.37), we obtain that

$$\text{Sign}\left[\frac{d\text{Re}\lambda(\tau)}{d\tau}\right]_{\tau=\tau_j^{(1)}} = \text{Sign}(\sqrt{\Delta} - q^2) = \text{Sign}(r - p).$$

Thus we know that when $p > r$,

$$\left.\frac{d\text{Re}\lambda(\tau)}{d\tau}\right|_{\tau=\tau_j^{(1)}} < 0, \tag{3.5}$$

while from (2.27) we have that

$$\left.\frac{d\text{Re}\lambda(\tau)}{d\tau}\right|_{\tau=\tau_j^{(2)}} > 0. \tag{3.6}$$

Under the assumption (3.4), the two sequences $\tau_j^{(k)}$ defined by (3.2) have the following properties:

Lemma 4 *Assume that* (3.4) *holds and* $\omega_1 < \omega_2$ *are defined by* (2.28) *and* (2.29) *respectively. Then* $\tau_j^{(2)} < \tau_j^{(1)}$ *for* $j \in \mathbb{N}_0$*, and* $\tau_j^{(k)} < \tau_{j+1}^{(k)}$ *for* $k = 1, 2$ *and* $j \in \mathbb{N}_0$.

Proof From (2.22) we can see that

$$\tan \omega_k \tau_j^{(k)} = \frac{\omega_k}{r - p},\ \ k = 1, 2.$$

Since $p > r$, it follows that the function $\tan \omega\tau$ is monotonically decreasing in ω. Thus from the condition $\omega_1 < \omega_2$ one can derive $\omega_1 \tau_j^{(1)} > \omega_2 \tau_j^{(2)}$, that is,

$$\frac{\tau_j^{(2)}}{\tau_j^{(1)}} < \frac{\omega_1}{\omega_2} < 1.$$

Therefore, $\tau_j^{(2)} < \tau_j^{(1)}$. The assertion that $\tau_j^{(k)} < \tau_{j+1}^{(k)}$ is obvious from (3.2). □

Let $\Delta\tau_k$, $k = 1, 2$, be defined by

$$\Delta\tau_k = \tau_{j+1}^{(k)} - \tau_j^{(k)} = \frac{2\pi}{\omega_k},\ \ k = 1, 2 \text{ and } j \in \mathbb{N}_0. \tag{3.7}$$

Hence $\Delta\tau_1 - \Delta\tau_2 > 0$ since $\omega_1 < \omega_2$. The following observation on the order of $\tau_j^{(2)}$ and $\tau_j^{(1)}$ lead to multiple stability switches.

Lemma 5 *Assume that* (3.4) *holds and* $\tau_1^{(2)} - \tau_0^{(1)} > 0$. *If for some* $j_0 \in \mathbb{N}$,

$$j_0 - 1 < \frac{\tau_1^{(2)} - \tau_0^{(1)}}{\Delta\tau_1 - \Delta\tau_2} < j_0, \tag{3.8}$$

then

$$\tau_j^{(1)} < \tau_{j+1}^{(2)} \quad \textit{for} \quad 0 \leq j \leq j_0 - 1, \quad \textit{and} \quad \tau_{j_0-1}^{(1)} < \tau_{j_0}^{(2)} < \tau_{j_0+1}^{(2)} < \tau_{j_0}^{(1)}. \tag{3.9}$$

Proof Notice from (3.7) that for $j \in \mathbb{N}$,

$$\tau_j^{(k)} = \Delta\tau_1 + \tau_{j-1}^{(k)} = (j - l)\Delta\tau_1 + \tau_l^{(k)}, \ k = 1, 2, \tag{3.10}$$

where $l \in \mathbb{N}$ and $l \leq j$. For $0 \leq j \leq j_0 - 1 < \frac{\tau_1^{(2)} - \tau_0^{(1)}}{\Delta\tau_1 - \Delta\tau_2}$, we have

$$\tau_j^{(1)} = \tau_0^{(1)} + j\Delta\tau_1 < \tau_1^{(2)} + j\Delta\tau_2 = \tau_{j+1}^{(2)}.$$

If $\frac{\tau_1^{(2)} - \tau_0^{(1)}}{\Delta\tau_1 - \Delta\tau_2} > j_0 - 1$, then we have

$$\tau_{j_0-1}^{(1)} = \tau_0^{(1)} + (j_0 - 1)\Delta\tau_1 < \tau_1^{(2)} + (j_0 - 1)\Delta\tau_2 = \tau_{j_0}^{(2)}.$$

Similarly, if $\frac{\tau_1^{(2)} - \tau_0^{(1)}}{\Delta\tau_1 - \Delta\tau_2} < j_0$, then we have $\tau_{j_0+1}^{(2)} < \tau_{j_0}^{(1)}$. □

To show the multiple stability switches of the positive equilibrium of (1.9) in a rigorous way, we first prove the following preliminary results.

Lemma 6 *Let* $F(\lambda, \tau)$ *be defined as in* (2.1).

(i) *For any* $\tau \geq 0$, $F(\cdot, \tau)$ *is an analytic function for* $\lambda \in \mathbb{C}$.
(ii) *Let* λ *be a nonzero root of* $F(\cdot, \tau) = 0$ *with* $Re\lambda \geq 0$. *Then* $|\lambda| \leq p + q + r$.
(iii) *Let* $M(\tau)$ *be the number of roots (counting multiplicity) of* $F(\cdot, \tau) = 0$ *with positive real parts. Then* $M(0) = 0$ *and if for* $\tau_1 \leq \tau \leq \tau_2$, $F(\cdot, \tau) = 0$ *has no purely imaginary roots, then* $M(\tau)$ *is a constant on* $[\tau_1, \tau_2]$.

Proof The analyticity of $F(\cdot, \tau)$ is clear from its form in (2.1) as it is well-known that polynomials and exponential functions are analytic. If Re$\lambda \geq 0$, then $|e^{-\lambda\tau}| \leq 1$ and thus we observe that when $|\lambda| > p + q + r$,

$$\left|\frac{F(\lambda, \tau)}{\lambda}\right| = \left|\frac{p + qe^{-\lambda\tau} + re^{-2\lambda\tau}}{\lambda}\right| \leq \frac{p + q + r}{|\lambda|} < 1.$$

Therefore $|\lambda| \leq p + q + r$. Finally $M(0) = 0$ since when $\tau = 0$, all roots of (2.1) have negative real parts, and the remaining result is well-known, see [4,10,26]. □

We also recall the Rouché's Theorem (see for example [1,30]).

Lemma 7 *Let* γ *be a simple closed curve (non-intersecting) in the complex plane and let* $f(z)$ *and* $g(z)$ *be functions analytic in the complex plane satisfying*

$$|f(z) - g(z)| < |f(z)|, \ z \in \gamma.$$

Then in the domain enclosed by γ, *the number of zeros (counting multiplicity) of* $f(z)$ *and* $g(z)$ *are same.*

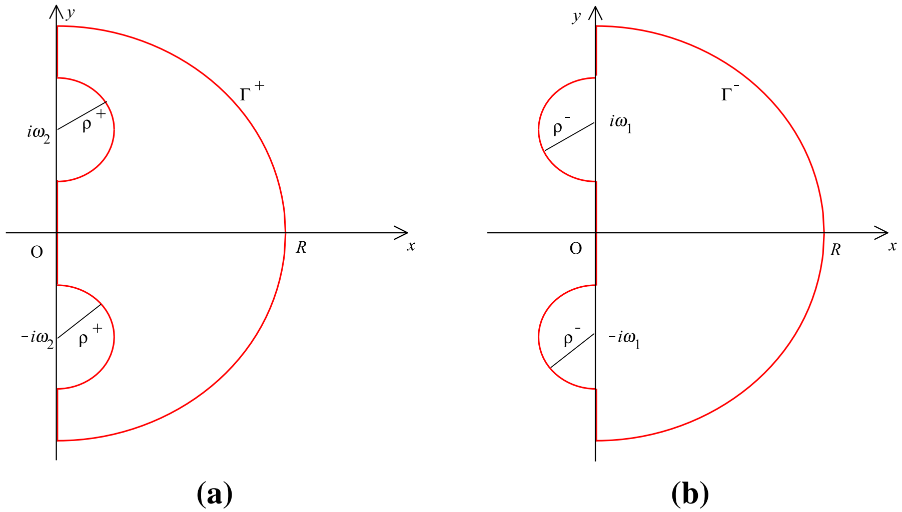


Fig. 2 Graphs of Jordan curves Γ^+ and Γ^-

Now we establish the stability of $u = u_*$ for different τ-values in terms of $M(\tau)$, the number of roots of (2.10) with positive real parts.

Proposition 2 *Assume that p, q, r satisfy (3.4), $\omega_1 < \omega_2$, and assume that (3.8) holds for some $j_0 \in \mathbb{N}$. Let $M(\tau)$ be defined as in Lemma 6.*

(i) *If $\tau \in [0, \tau_0^{(2)})$ or $\tau \in \left(\tau_{j-1}^{(1)}, \tau_j^{(2)}\right)$ for $1 \le j \le j_0$, then $M(\tau) = 0$.*

(ii) *If $\tau \in \left(\tau_j^{(2)}, \tau_j^{(1)}\right)$ for $0 \le j \le j_0 - 1$, then $M(\tau) = 2$.*

(iii) *If $\tau > \tau_{j_0}^{(2)}$, then $M(\tau) \ge 2$.*

Proof In virtue of $M(0) = 0$ and Lemma 6, one obtains that $M(\tau) = 0$ when $0 \le \tau < \tau_0^{(2)}$. If $\tau = \tau_0^{(2)}$, then from Lemma 3, there are disks $U_\pm$ centering respectively at $\pm i\omega_2$ with radius $\rho_+ \in (0, \omega_2/2)$ and an interval I_+ containing $\tau_0^{(2)}$ such that when $\tau \in I_+$, Eq. (2.1) has a unique pair of conjugate complex roots $\lambda = \alpha(\tau) \pm i\beta(\tau)$ in $U_\pm$ such that

$$\alpha\left(\tau_0^{(2)}\right) = 0,\ \ \alpha'\left(\tau_0^{(2)}\right) > 0 \text{ and } \beta\left(\tau_0^{(2)}\right) = \omega_2 > 0. \tag{3.11}$$

Therefore, when $0 < \tau - \tau_0^{(2)} \ll 1$, the Eq. (2.1) has at least one pair of complex roots with positive real parts.

We prove that when $\tau_0^{(2)} < \tau < \tau_0^{(1)}$, (2.1) has only one pair of complex roots with positive real parts so that $M(\tau) = 2$. Let $R = p + q + r + 1$ and take a Jordan curve Γ^+ (see Fig. 2(a)) in the complex plane as

$$\begin{aligned}\Gamma^+ = \{i\beta : \beta \in [-R, -\omega_2 - \rho_+] \cup [-\omega_2 + \rho_+, \omega_2 - \rho_+] \cup [\omega_2 + \rho_+, R]\}\\ \cup \{\mu \in \mathbb{C} : \mathrm{Re}\mu > 0, |\mu \pm i\omega_2| = \rho_+\} \cup \{\mu \in \mathbb{C} : \mathrm{Re}\mu > 0, |\mu| = R\}.\end{aligned}$$

Then we can see that, by shrinking I_+ if necessary, (i) for $\tau \in I_+$, the Eq. (2.1) has no roots on Γ^+; and (ii) for $\lambda \in \Gamma^+$ and $\tau \in I_+$,

$$\left|F(\lambda, \tau) - F\left(\lambda, \tau_0^{(2)}\right)\right| < \left|F\left(\lambda, \tau_0^{(2)}\right)\right|.$$

Therefore, by Lemma 6 and the Rouché's Theorem 7, we know that the sum of multiplicity of roots of (2.1) inside Γ^+ cannot change when $\tau \in I_+$. Notice that (2.1) has no roots inside Γ^+ when $\tau < \tau_0^{(2)}$ and $\tau \in I_+$. Thus, it follows that except the roots in $U_\pm$, the Eq. (2.1) has no other roots in the right half-plane when $\tau > \tau_0^{(2)}$ and $\tau \in I_+$, that is, $M(\tau) = 2$ when $\tau > \tau_0^{(2)}$ and $\tau \in I_+$. From Lemma 6, $M(\tau) = 2$ as long as $\tau_0^{(2)} < \tau < \tau_0^{(1)}$.

If $\tau = \tau_0^{(1)}$, then the transversality condition (3.5) and Lemma 3 again imply that there exist disks $V_\pm$ centering respectively at $\pm i\omega_1$ with radius $\rho_- \in (0, \omega_1/2)$ and the interval I_- containing $\tau_0^{(1)}$ such that when $\tau \in I_-$, the Eq. (2.1) has a unique pair of complex roots $\mu(\tau) = \alpha_*(\tau) \pm i\omega_*(\tau)$ in $V_\pm$ such that

$$\alpha_*\left(\tau_0^{(1)}\right) = 0,\ \alpha'_*\left(\tau_0^{(1)}\right) < 0 \text{ and } \beta_*\left(\tau_0^{(1)}\right) = \omega_1 > 0.$$

By shrinking I_- if necessary, we can assume that $\mu(\tau)$ does not lie on the boundary of $V_\pm$ for $\tau \in I_-$. Take the Jordan curve Γ^- (see Fig. 2 (b)) in the complex plane as

$$\begin{aligned}\Gamma^- &= \{i\beta : \beta \in [-R, -\omega_1 - \rho_-] \cup [-\omega_1 + \rho_-, \omega_1 - \rho_1] \cup [\omega_1 + \rho_-, R]\}\\ &\quad \cup \{\mu \in \mathbb{C} : \mathrm{Re}\mu < 0, |\mu \pm i\omega_1| = \rho_-\} \cup \{\mu \in \mathbb{C} : \mathrm{Re}\mu > 0, |\mu| = R\}.\end{aligned}$$

Again, by shrinking I_- if necessary, we can see that for $\lambda \in \Gamma^-$ and $\tau \in I_-$,

$$\left|F(\lambda, \tau) - F\left(\lambda, \tau_0^{(1)}\right)\right| < \left|F\left(\lambda, \tau_0^{(1)}\right)\right|.$$

Thus according to Lemma 3.6 and the Rouché's Theorem 7 we know that the number of roots (counting multiplicity) of (2.1) inside Γ^- is the same for all $\tau \in I_-$. For $\tau < \tau_0^{(1)}$ and $\tau \in I_-$, the number is 2 because $M(\tau) = 2$ and $\alpha_*(\tau) > 0$. Therefore it must also be 2 for $\tau > \tau_0^{(1)}$ and $\tau \in I_-$. But for such τ, $\alpha_*(\tau) < 0$, so $\mu(\tau)$ lies in the open left half-plane. It follows that $M(\tau) = 0$ for $\tau \in I_-$ and $\tau > \tau_0^{(1)}$ and thus from Lemma 6 we can derive that $M(\tau) = 0$ when $\tau_0^{(1)} < \tau < \tau_1^{(2)}$.

Similarly, one can show that $M(\tau) = 0$ when $\tau \in (\tau_{j-1}^{(1)}, \tau_j^{(2)})$ for $j = 1, 2, \cdots, j_0$ and $M(\tau) = 2$ when $\tau \in \left(\tau_j^{(2)}, \tau_j^{(1)}\right)$ for $j = 1, \cdots, j_0 - 1$. Thus we prove the conclusions (i) and (ii).

Finally, we prove the conclusion (iii). Similar to the previous proof, we can demonstrate that $M(\tau) = 2$ when $\tau \in \left(\tau_{j_0}^{(2)}, \tau_{j_0+1}^{(2)}\right)$ and $M(\tau) = 4$ when $\tau \in \left(\tau_{j_0+1}^{(2)}, \tau_{j_0}^{(1)}\right)$. Indeed from (3.8) and (3.9), every time τ increases across τ_j^2, then $M(\tau)$ increases by 2, while every time τ increases across τ_j^1, then $M(\tau)$ decreases by 2. But when $\tau > \tau_{j_0}^{(2)}$, the number of $\tau_j^{(2)}$ in $(0, \tau)$ is larger than the number of $\tau_j^{(1)}$. Hence $M(\tau) \geq 2$ when $\tau > \tau_{j_0}^{(2)}$, and (2.1) has at least a pair of complex roots with positive real parts. □

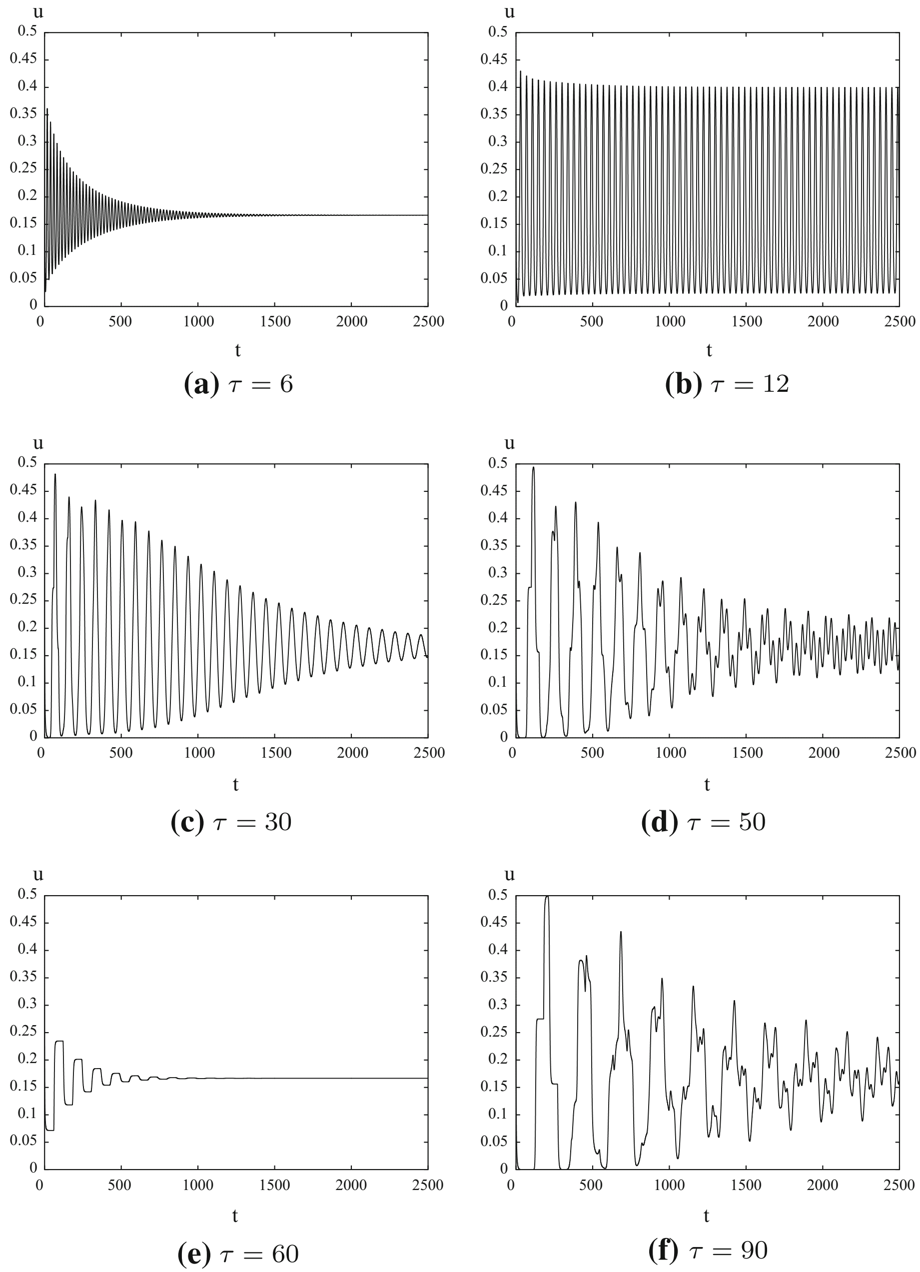
The results in Proposition 2 directly imply the following main theorem in this section.

Theorem 5 *Assume that p, q, r satisfy (3.4), $\omega_1 < \omega_2$, and assume that (3.8) holds for some $j_0 \in \mathbb{N}$. Then the positive equilibrium $u = u^*$ of (1.9) has $2j_0 + 1$ times stability switches and then becomes eventually unstable, that is, $u = u^*$ is locally asymptotically stable when*

$$\tau \in \left[0, \tau_0^{(2)}\right) \cup \left(\tau_0^{(1)}, \tau_1^{(2)}\right) \cup \cdots \cup \left(\tau_{j_0-1}^{(1)}, \tau_{j_0}^{(2)}\right)$$

and it is unstable when

$$\tau \in \left(\tau_0^{(2)}, \tau_0^{(1)}\right) \cup \cdots \cup \left(\tau_{j_0-1}^{(2)}, \tau_{j_0-1}^{(1)}\right) \cup \left(\tau_{j_0}^{(2)}, \infty\right).$$



(a) $\tau = 6$ **(b)** $\tau = 12$

(c) $\tau = 30$ **(d)** $\tau = 50$

(e) $\tau = 60$ **(f)** $\tau = 90$

Fig. 3 Time series of the model (1.9), $a = 2$, $b = 2.5$ and $c = 1.5$, with different values of τ and initial data $\phi(s) = 0.3$ for $s \in [-2\tau, 0]$

Finally to verify our theoretical prediction in Theorem 5, we use a specific example for (1.9) to demonstrate the stability switches. In (1.9), we take $a = 2$, $b = 2.5$ and $c = 1.5$, then $u^* = 1/6$ and

$$p = \frac{1}{3},\ q = \frac{5}{12},\ r = \frac{1}{4}.$$

It is easy to verify that p, q and r satisfy the condition (3.4). Therefore, from (2.28) and (2.29) we have

$$\omega_1 = \sqrt{\frac{q^2 - 2(p^2 - r^2) - \sqrt{\Delta}}{2}} \approx 0.1443,$$

$$\text{and } \omega_2 = \sqrt{\frac{q^2 - 2(p^2 - r^2) + \sqrt{\Delta}}{2}} \approx 0.2357.$$

Thus $\Delta\tau_1 = 13.8564\pi$, $\Delta\tau_2 = 8.4853\pi$ and

$$\tau_j^{(1)} = 14.5104 + 13.8564 j\pi \text{ and } \tau_j^{(2)} = 8.1061 + 8.4853 j\pi,\ \ j \in \mathbb{N}_0. \tag{3.12}$$

Now we can get

$$\frac{\tau_1^{(2)} - \tau_0^{(1)}}{\Delta\tau_1 - \Delta\tau_2} \approx 1.2003 \in (1, 2).$$

In fact, from (3.12) one obtains that

$$\tau_0^{(2)} < \tau_0^{(1)} < \tau_1^{(2)} < \tau_1^{(1)} < \tau_2^{(2)} < \tau_3^{(2)} < \tau_2^{(1)} < \cdots$$

as the bifurcation values can be calculated as

$\tau_0^{(2)}$	$\tau_0^{(1)}$	$\tau_1^{(2)}$	$\tau_1^{(1)}$	$\tau_2^{(2)}$	$\tau_3^{(2)}$	$\tau_2^{(1)}$
8.1061	14.5104	34.7634	58.0416	61.4207	88.0780	101.5728

Therefore, from Theorem 5 one can get that the positive equilibrium $u = 1/6$ of (1.9) has 5 stability switches, that is, $u = 1/6$ is locally asymptotically stable for

$$\tau \in \left[0, \tau_0^{(2)}\right) \cup \left(\tau_0^{(1)}, \tau_1^{(2)}\right) \cup \left(\tau_1^{(1)}, \tau_2^{(2)}\right)$$

and it is unstable when

$$\tau \in \left(\tau_0^{(2)}, \tau_0^{(1)}\right) \cup \left(\tau_1^{(2)}, \tau_2^{(1)}\right) \cup \left(\tau_2^{(2)}, \infty\right).$$

Numerical simulation for various τ values are shown in Fig. 3.

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