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Dynamical behavior for an eco-epidemiological model with discrete and distributed delay

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Abstract In this paper, the dynamical behavior of an eco-epidemiological model with discrete and distributed delay is studied. Sufficient conditions for the local asymptotical stability of the nonnegative equilibria are obtained. We prove that there exists a threshold value of the feedback time delay τ beyond which the positive equilibrium bifurcates towards a periodic solution. Using the normal form theory and center manifold argument, the explicit formulae which determine the stability, the direction and the periodic of bifurcating period solutions are derived. Numerical simulations are carried out to explain the mathematical conclusions.

Keywords Eco-epidemiological system · Asymptotical stability · Hopf bifurcation · Distributed delay

1 Introduction

Ecology and epidemiology are major fields of study in their own right but there are some common features between these system. It is very important both from the ecological and mathematical points of view to study ecological systems under the influence of epidemiological factors. The study of ecological systems with the influence of epidemiological parameters is termed as eco-epidemiology. The relevant literature on this field is now very rich [1–3]. Hadeler and Freedman [4] were probably the

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first to describe a predator-prey model where the prey is infected by a parasite, and in turn infects the predator with the parasite. After the pioneering work of Hadeler and Freedman [4] quite a large number of papers were published on the predator-prey system with infection in the prey [5–7]. Xiao and Chen [8] claimed that they were the first to formulate and analyze an eco-epidemiological model with time delay. But, to the best of our knowledge, very little attention has been paid so far to an eco-epidemiological model with distributed delay. In this paper, we will consider an eco-epidemiological model with discrete and distributed delay.

The following assumptions are made in formulating the eco-epidemiological model:

We have two populations:

1. The prey, whose total population density is denoted by N.
2. The predator, whose population density is denoted by P.

We make the following assumptions:

(A_1) In the absence of infection and predation, the prey population density grows logistically with carrying capacity K ($K > 0$), an intrinsic birth rate constant r ($r > 0$) and the feedback time delay of the prey to the growth of the species itself τ (> 0) [9–11]

$$\frac{dS}{dt} = rS\left(1 - \frac{S(t-\tau)}{K}\right). \tag{1.1}$$

It has been suggested that (1.1) can be used to model the dynamics of a single species population growing towards a saturation level K with a constant reproduction rate r; the term $1 - \frac{S(t-\tau)}{K}$ in (1.1) denotes a density dependent feedback mechanism which takes τ unites of time to respond to changes in the population density represented in (1.1) by $S(t)$.

(A_2) In the presence of disease, the total prey population N are divided into two distinct classes, namely, susceptible populations, S, and infected populations, I. Therefore, at any time t, the total density of prey population is

$$N(t) = S(t) + I(t). \tag{1.2}$$

(A_3) We assume that only susceptible prey S are capable of reproducing with logistic law (1.1); i.e., the infected prey I are removed by death (say its death rate is a positive constant c), or by predation before having the possibility of reproducing. However, the infective population I still contributes with S to population growth toward the carrying capacity.

(A_4) We assume that the force of infection at time t is given by bSI, where b is the average number of contacts per infective per day. Hence, the SI model of the infected prey is:

$$\begin{cases} \dot{S} = rS(1 - \frac{S(t-\tau)}{K}) - bSI, \\ \dot{I} = bSI - cI. \end{cases} \tag{1.3}$$

(A_5) It is assumed that predator can distinguish between infected and health prey. Since prey population are infected by a disease, infected preys are weakened and become easier to catch. For example, infected fish are much easier catch than healthy fish. We get a more realistic model if we take into account that the predators' growth rate at present depend on past quantities of prey and therefore a continuous weight (or density) function f introduced whose role is to weight moments of the past. Function f satisfies the requirements:

$$f(s \geq 0,)s \in (0, +\infty), \quad \int_0^{\infty} f(s)ds = 1, \tag{1.4}$$

and $I(t)$ is replaced in the growth rate of prey by its weighted average over the past

$$Q(t) = \int_{-\infty}^{t} I(s)f(t-s)ds. \tag{1.5}$$

This means that the time average of prey quantity over the past has the same fading influence on the present growth rates of different predators. The simplest choice is $f(s) = \delta e^{-\delta s}$, with $\delta > 0$. This function satisfies the condition (1.4) and now

$$Q(t) = \int_{-\infty}^{t} I(s)\delta e^{-\delta(t-s)}ds. \tag{1.6}$$

We call this choice of f exponentially fading memory, see in [12, 13]; later in [14]. (Since f is the probability density of an exponentially distributed random variable, the probabilistic interpretation is obvious.) The smaller $\delta > 0$ is the longer is the time interval in the past in which the values of $I(t)$ are taken into account, i.e. $\frac{1}{\delta}$ is the "measure of the influence of the past".

From the above assumptions we have the following model:

$$\begin{cases} \frac{dS}{dt} = rS(1 - \frac{S(t-\tau)}{K}) - bSI, \\ \frac{dI}{dt} = bSI - cI - aIP, \\ \frac{dP}{dt} = P(-d + h\int_{-\infty}^{t} \delta I(s)e^{-\delta(t-s)}ds), \end{cases} \tag{1.7}$$

where $S(t)$, $I(t)$ and $P(t)$ denote the quantities of sound prey, infected prey and predator, respectively. $K(> 0)$ is the carrying capacity, $r(> 0)$ is the intrinsic birth rate, $\tau \geq 0$ is the feedback time delay of the prey to the growth of the species itself, $b(> 0)$ is the transmission coefficient, $a(> 0)$ is the capturing rate, $h(> 0)$ denotes the product of the per-capita rate of predation and the rate of conversing prey into predator, $c(> 0)$ and $d(> 0)$ are the death rate of infected prey and predator respectively.

The integro-differential system (1.7) can be transformed [12, 13] into the system of differential equations on the interval $[0, +\infty)$

$$\begin{cases} \frac{dS}{dt} = rS(1 - \frac{S(t-\tau)}{K}) - bSI, \\ \frac{dI}{dt} = bSI - cI - aIP, \\ \frac{dP}{dt} = -dP + hPQ, \\ \frac{dQ}{dt} = \delta(I - Q). \end{cases} \tag{1.8}$$

We understand the relationship between the two systems as follows: If (S, I, P) : $[0, +\infty) \to R^3$ is the solution of (1.7) corresponding to continuous and bounded initial function $(\bar{S}, \bar{I}, \bar{P}) : (-\infty, 0] \to R^3$, then $(S, I, P, Q) : [0, +\infty) \to R^4$ is a solution of (1.8) with $S(\theta) = \bar{S}(\theta)$, $I(\theta) = \bar{I}(\theta)$, $P(\theta) = \bar{P}(\theta)$, and $Q(\theta) = \int_{-\infty}^{\theta} \delta \bar{I}(s) \exp(-\delta(\theta - s))ds$, $\theta \in [-\tau, 0]$. Especially,

$$Q(0) = \int_{-\infty}^{0} \delta \bar{I}(s) \exp(\delta s) ds.$$

Conversely, if (S, I, Q, P) is any solution of (1.8) defined on the entire real line and bounded on $(-\infty, 0]$, then Q is given by (1.1), and so (S, I, P) satisfies (1.7).

System (1.8) has to be analyzed with the initial conditions $\phi = (\phi_1, \phi_2, \phi_3, \phi_4)$ defined in the space

$$\begin{aligned} C^+ = \{\phi \in C([-\tau, 0], R^4_{0+}) : \phi_1(\theta) = S(\theta), \phi_2(\theta) = I(\theta),\\ \phi_3(\theta) = P(\theta), \phi_4(\theta) = Q(\theta)\}, \end{aligned}$$

where $S(\theta) > 0$, $I(\theta) > 0$, $P(\theta) > 0$, $Q(\theta) > 0$, $\theta \in C([-\tau, 0], R^4_{0+})$; $C([-\tau, 0], R^4_{0+})$ is the space of vector valued continuous functions and is a mapping from $[-\tau, 0]$ to R^4_{0+} ($R^4_{0+} = \{(S, I, P, Q) \in R^4 : S, I, P, Q \geq 0\}$). It can be shown that all solutions of the system in C^+, remain in C^+. Thus, C^+ is positively invariant and it is sufficient to consider solutions in C^+. In this region, the usual existence, uniqueness and continuation results hold for system (1.8).

The organization of the paper is as follows: Section 2 is devoted to studying the dynamical behavior of the linearized system around each of the equilibria. In Sect. 3, we study the dynamical behavior of the endemic equilibrium, and we present the local stability of the endemic equilibrium and the existence of Hopf bifurcation around the endemic equilibrium. In Sect. 4, the direction of Hopf bifurcation and the stability and period of bifurcating periodic solutions on the center manifold are determined. In Sect. 5, some numerical simulations are performed to illustrate the analytical results found.

2 Equilibria

We now find all biologically feasible equilibria admitted by system (1.8) and study the dynamics of the system around each equilibrium.

If (H$_1$): $bK - c > 0$, $bKgr - b^2Kd - chr > 0$ holds, system (1.8) has the following nonnegative equilibria:

$$\begin{aligned} &E_0(0, 0, 0, 0), \quad E_1(K, 0, 0, 0),\\ &E_2\left(\frac{c}{b}, \frac{r(bK - c)}{b^2K}, 0, \frac{r(bK - c)}{b^2K}\right) \quad \text{and} \quad E_3(S^*, I^* < P^*, Q^*), \end{aligned}$$

where

$$S^* = \frac{K(hr - bd)}{hr}, \quad I^* = \frac{d}{h}, \quad P^* = \frac{bKhr - b^2Kd - chr}{ahr}, \quad Q^* = \frac{d}{h}.$$

Let $\bar{E}(\bar{S}, \bar{I}, \bar{P}, \bar{Q})$ be any arbitrary equilibrium. The Jacobian matrix evaluated at $\bar{E}$ leads to the following characteristic equation:

$$\begin{vmatrix} r - \frac{r\bar{S}}{K} - b\bar{I} - \frac{r\bar{S}}{K}e^{-\lambda\tau} - \lambda & -b\bar{S} & 0 & 0 \\ b\bar{I} & b\bar{S} - c - a\bar{P} - \lambda & -a\bar{I} & 0 \\ 0 & 0 & -d + h\bar{Q} - \lambda & h\bar{P} \\ 0 & \delta & 0 & -\delta - \lambda \end{vmatrix} = 0. \tag{2.1}$$

For equilibrium $E_0 = (0, 0, 0, 0)$, (2.1) reduces to

$$(r - \lambda)(-c - \lambda)(-d - \lambda)(-\delta - \lambda) = 0. \tag{2.2}$$

Clearly, $E_0(0, 0, 0, 0)$ is unstable.

For equilibrium $E_1(K, 0, 0, 0)$, (2.1) reduces to

$$(-re^{-\lambda\tau} - \lambda)(bK - c - \lambda)(-d - \lambda)(-\delta - \lambda) = 0. \tag{2.3}$$

Since $bK - c > 0$, $E_1(K, 0, 0, 0)$ is unstable.

For equilibrium $E_2(\frac{c}{b}, \frac{r(bK-c)}{b^2K}, 0, \frac{r(bK-c)}{b^2K})$, (2.1) reduces to

$$\left(-d + \frac{rh(bK - c)}{b^2K} - \lambda\right)(-\delta - \lambda)\left(\lambda^2 + \frac{rc}{bK}e^{-\lambda\tau}\lambda + \frac{rc(bK - c)}{bK}\right) = 0. \tag{2.4}$$

It is clear that (2.1) has the characteristic root $\lambda = \frac{bKhr - b^2Kd - chr}{b^2K} > 0$, E_2 is also unstable.

3 Dynamical behavior of endemic equilibrium E_3

In this section, we will consider the dynamical behavior of endemic equilibrium E_3. Some conditions for Hopf bifurcation around equilibrium E_3 to occur are obtained by using the time delay τ as a bifurcation parameter.

For endemic equilibrium $E_3(S^*, I^* < P^*, Q^*)$, (2.1) reduces to

$$\begin{vmatrix} -\frac{rS^*}{K}e^{-\lambda\tau} - \lambda & -bS^* & 0 & 0 \\ bI^* & -\lambda & -aI^* & 0 \\ 0 & 0 & -\lambda & hP^* \\ 0 & \delta & 0 & -\delta - \lambda \end{vmatrix} = 0,$$

i.e.,

$$\lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + (b_1\lambda^3 + b_2\lambda^2 + b_3)e^{-\lambda\tau} = 0, \tag{3.1}$$

where

$$
\begin{aligned}
a_1 &= \delta, \\
a_2 &= b^2 S^* I^*, \\
a_3 &= a\delta h I^* P^* + b^2 \delta S^* I^*, \\
b_1 &= \frac{rS^*}{K}, \\
b_2 &= \frac{rS^*\delta}{K}, \\
b_3 &= \frac{rS^*}{K} a\delta h I^* P^*.
\end{aligned}
$$

In addition, in view of Routh-Hurwitz criteria, we can easily know that all roots of (3.1) with $\tau = 0$ have negative real parts if the following condition holds:

(H_2): $a_2a_3 + b_2a_3 > a_1a_4$ and $b_1a_2 + b_1b_2 > a_3$.

Let us consider $\tau \neq 0$ and assume $\lambda(\tau) = u(\tau) + i\omega(\tau)$, where $u(\tau), \omega(\tau) \in R$. Substituting $\lambda(\tau) = u(\tau) + i\omega(\tau)$ and rewriting (3.1) in terms of its real and imaginary parts, we obtain

$$
\begin{aligned}
&u^4 + \omega^4 - 6u^2\omega^2 + a_1(u^3 - 3u\omega^2) + a_2(u^2 - \omega^2) + a_3 u \\
&\quad = e^{-\tau u}\{-b_1[(u^3 - 3u\omega^2)\cos(\tau u) + (3u^2\omega - \omega^3)\sin(\tau\omega)] \\
&\qquad - b_2[(u^2 - \omega^2)\cos(\tau\omega) + 2u\omega\sin(\tau\omega)] - b_3\cos(\tau\omega)\}, \qquad (3.2a)
\end{aligned}
$$

and

$$
\begin{aligned}
&4u\omega(u^2 - \omega^2) + a_1(3u^2\omega - \omega^3) + a_2(2u\omega) + a_3\omega \\
&\quad = e^{-\tau u}\{-b_1[(-u^3 + 3u\omega^2)\sin(\tau\omega) + (3u^2\omega - \omega^3)\cos(\tau\omega)] \\
&\qquad - b_2[(-u^2 + \omega^2)\sin(\tau\omega) + 2u\omega\cos(\tau\omega)] + b_3\sin(\tau\omega)\}. \qquad (3.2b)
\end{aligned}
$$

Let τ^* be such that $u(\tau^*) = 0$ and $\omega(\tau^*) = \omega(\tau^*)$, then (3.2a) and (3.2b) reduce to

$$
\omega^{*4} - a_2\omega^{*2} = (b_2\omega^{*2} - b_3)\cos(\tau^*\omega^*) + b_1\omega^*\sin(\tau^*\omega^*), \qquad (3.3a)
$$

and

$$
-a_1\omega^{*3} + a_3\omega^* = b_1\omega^{*3}\cos(\tau^*\omega^*) + (b_3 - b_2\omega_1^{*2})\sin(\tau^*\omega^*). \qquad (3.3b)
$$

By squaring and adding, it follows that

$$
\omega^{*8} + (a_1^2 - 2a_2 - b_1^2)\omega^{*6} + (a_2^2 - 2a_1a_3 - b_2^2)\omega^{*4} + (a_3^2 + 2b_2b_3)\omega^{*2} - b_3^2 = 0. \quad (3.4)
$$

Suppose that ω^* is the last positive simple root of (3.4). We shall now show that with this value of ω^*, there is a τ^* such that $u(\tau^*) = 0$ and $\omega(\tau^*) = \omega^*$. Given ω^*, (3.3a) and (3.3b) can be written as

$$U = \Phi \cos(\tau^*\omega^*) + \Psi \sin(\tau^*\omega^*), \tag{3.5a}$$

and

$$V = \Psi \cos(\tau^*\omega^*) - \Phi \sin(\tau^*\omega^*), \tag{3.5b}$$

where

$$\Phi = b_2\omega^{*2} - b_4, \qquad \Psi = b_1\omega^{*3},$$
$$U = \omega^{*4} - a_2\omega^{*2}, \qquad V = -a_1\omega^{*3} + a_3\omega^*,$$
$$\Phi^2 + \Psi^2 = U^2 + V^2 = H^2,$$

where $H > 0$.

The equations

$$\Phi = H\cos\theta \quad \text{and} \quad \Psi = H\sin\theta \tag{3.6}$$

determine a unique $\theta \in [0, 2\pi)$. With this value of θ,

$$H\cos(\tau^*\omega^*)\cos\theta + H\sin(\tau^*\omega^*)\sin\theta = U, \tag{3.7a}$$

and

$$H\cos(\tau^*\omega^*)\sin\theta - H\sin(\tau^*\omega^*)\cos\theta = V. \tag{3.7b}$$

Hence,

$$H\cos(\tau^*\omega^* - \theta) = U, \tag{3.8a}$$

and

$$H\sin(\tau^*\omega^* - \theta) = -V. \tag{3.8b}$$

Equations (3.8) determine $\tau^*\omega^* - \theta$ uniquely in $[0, 2\pi)$, and hence, τ^* uniquely in $[\frac{\theta}{\omega^*}, \frac{\theta+2\pi}{\omega^*})$. To apply the Hopf bifurcation theorem as stated in [15], we state the following lemma.

Lemma 3.1 [16] *Suppose the equation (3.4) has at least one simple positive root and ω^* is the last such root. Then, $i\omega(\tau^*) = i\omega^*$ is a simple root of (3.1) and $u(\tau) + i\omega(\tau)$ is differentiable with respect to τ in a neighbourhood of $\tau = \tau^*$.*

Next, to establish Hopf bifurcation at $\tau = \tau^*$, we need to verify the transversality condition

$$\left.\frac{du}{d\tau}\right|_{\tau=\tau^*} \neq 0.$$

Differentiating equations (3.2) with respect to τ, setting $u = 0$ and $\omega = \omega^*$, solving for $\frac{du}{d\tau}|_{\tau=\tau^*}$ and $\frac{du}{d\tau}|_{\tau=\tau^*}$, and using (3.3) we obtain

$$\begin{cases} \Gamma_1 \frac{du}{d\tau}|_{\tau=\tau^*} + \Gamma_2 \frac{d\omega}{d\tau}|_{\tau=\tau^*} = -\Psi^5 + a_2\Psi^3, \\ \Gamma_2 \frac{du}{d\tau}|_{\tau=\tau^*} - \Gamma_1 \frac{d\omega}{d\tau}|_{\tau=\tau^*} = -a_1\Psi^4 + a_3\Psi^2. \end{cases} \tag{3.9}$$

Here

$$\Gamma_1 = -4\omega^{*3} + 2a_2\omega^* + \tau^*(-a_1\omega^{*3} + a_3\omega^*) + 3b_1\omega^{*2}\sin(\tau^*\omega^*) + 2b_2\omega^*\cos(\tau^*\omega^*),$$
$$\Gamma_2 = -3a_1\omega^{*2} + a_3 + \tau^*(\omega^{*4} - a_2\omega^{*2}) + 2b_2\omega^*\sin(\tau^*\omega^*) - 3b_1\omega^{*2}\cos(\tau^*\omega^*).$$

Hence

$$\left.\frac{du}{d\tau}\right|_{\tau=\tau^*} = \frac{1}{\Gamma_1^2+\Gamma_2^2}\{\omega^{*2}[4\omega^{*6} + 3\omega^{*4}(a_1^2 - 2a_2 - b_1^2) + 2\omega^{*2}(a_2^2 - 2a_1a_3 - b_2^2) + a_3^2 + 2b_2b_3]\}, \tag{3.10}$$

$$\left.\frac{d\omega}{d\tau}\right|_{\tau=\tau^*} = \frac{1}{\Gamma_1^2+\Gamma_2^2}\{\omega^{*3}[-\tau^*\omega^{*6} + \omega^{*4}(2a_2\tau^* - a_1^2\tau^* - a_1) + \omega^{*2}(3a_3 - a_2^2\tau^* + 2a_1a_3\tau^* + b_1b_2 - a_1a_2) - a_2a_3 - a_3^2 - 3b_1b_3]\}. \tag{3.11}$$

Clearly, $\Gamma_1^2 + \Gamma_2^2 > 0$ as $i\omega(\tau^*)$ is a simple root of (3.1). Let $\varsigma = \omega^{*2}$, then (3.4) reduce to $\nu(\varsigma) = 0$, where

$$\nu(\varsigma) = \varsigma^4 + (a_1^2 - 2a_2 - b_1^2)\varsigma^3 + (a_2^2 - 2a_1a_3 - b_2^2)\varsigma^2 + (a_3^2 + 2b_2b_3)\varsigma - b_3^2.$$

Hence,

$$\frac{d\nu}{d\varsigma} = 4\varsigma^3 + 3\varsigma^2(a_1^2 - 2a_2 - b_1^2) + 2\varsigma(a_2^2 - 2a_1a_3 - b_2^2) + (a_3^2 + 2b_2b_3). \tag{3.12}$$

If ω^{*2} is the first positive simple root of (3.4), then

$$\left.\frac{d\nu}{d\varsigma}\right|_{\varsigma=\omega^{*2}} > 0.$$

Hence, using (3.9) and (3.10) we deduce that

$$\left.\frac{du}{d\tau}\right|_{\tau=\tau^*} > 0.$$

Theorem 3.1 *Suppose that* (3.4) *has at least one simple positive root and ω^* is the last such root. Then, there is a Hopf bifurcation for the system* (1.8) *as τ passes upwards through τ^* leading to a periodic solution that bifurcates from E_3.*

Next, we shall give the sensible conditions that the Hopf bifurcation occurs around equilibrium E_3. Firstly, we need the following important lemma.

Define $f_1 = a_1^2 - 2a_2 - b_1^2,\ f_2 = a_2^2 - 2a_1a_3 - b_2^2,\ f_3 = a_3^2 + 2b_2b_3,\ f_4 = -b_3^2$ and $\varsigma = \omega_1^{*2}$ then (3.4) becomes

$$\varsigma^4 + f_1\varsigma^3 + f_2\varsigma^2 + f_3\varsigma + f_4 = 0.$$

Lemma 3.2 [16] *If* $f_4 < 0$, *then the quartic equation*

$$\nu(\varsigma) = \varsigma^4 + f_1\varsigma^3 + f_2\varsigma^2 + f_3\varsigma + f_4 = 0$$

has a strictly positive triple root β_1 *if and only if*

(1) $3f_1^2 \geq 8f_2$;
(2) $f_1 < 0$ *or* $f_2 < 0$;
(3) β_1 *satisfies the equation* $6\beta^2 + 3f_1\beta + f_2 = 0$;
(4) $f_3 = \beta_1^2(3f_1 + 8\beta_1)$; *and*
(5) $f_4 = \beta_1^3(-f_1 - 3\beta_1)$.

We also need the following mild condition.

Condition 1 Either

(i) $8f_2 > 3f_1^2$;
(ii) $f_1 \geq 0$ and $f_2 \geq 0$; or
(iii) if $3f_1^2 \geq 8f_2$ and also either $f_1 < 0$ or $f_2 < 0$, then if β_1 is a strictly positive root of the quadratic equation, $6\beta^2 + 3f_1\beta + f_2 = 0$, either $f_3 \neq \beta_1^2(3f_1 + 8\beta_1)$ or $f_4 \neq \beta_1^3(-f_1 - 3\beta_1)$.

Equation (3.4) has at least one positive real root for ω_1^{*2}. By Lemma 3.2, this is a simple root if Condition 1 is satisfied. Thus, from Lemma 3.1 and Theorem 3.1, we can get the following theorem.

Theorem 3.2 *Suppose that* (H_1), (H_2) *and Condition* 1 *hold. Then, there is a Hopf bifurcation for the system* (1.8) *as* τ *passes upwards through* τ_1^* *leading to a periodic solution that bifurcates from* E_3.

4 Direction and stability of the Hopf bifurcation

In Sect. 3, we obtain the conditions under which a family of periodic solutions bifurcate from the positive equilibrium E_3 at the critical value of τ^*. As pointed out in Hassard et al. [17], it is interesting to determine the direction, stability and period of the periodic solutions bifurcating from the positive equilibrium E_3. Following the ideas of Hassard et al., we derive the explicit formulaes for determining the properties of the Hopf bifurcation at the critical value of τ^* by using the normal form and the center manifold theory. Throughout this section, we always assume that system (1.8) undergoes Hopf bifurcation at the positive equilibrium $E_3(S^*, I^*, P^*, Q^*)$ for $\tau = \tau^*$, and then $\pm i\psi^*$ is corresponding purely imaginary roots of the characteristic equation at the positive equilibrium $E_3(S^*, I^*, P^*, Q^*)$.

Let $x_1(t) = S(t) - S^*$, $x_2(t) = I(t) - I^*$, $x_3(t) = P(t) - P^*$, $x_4(t) = Q(t) - Q^*$, $\bar{x}_i(t) = x_i(\tau t)$, $(i = 1, 2, 3, 4)$, $\tau = \tau^* + \mu$, system (1.8) is transformed into an functional differential equation (FDE) in $C = C([-1, 0], R^4)$ as

$$\frac{dx}{dt} = L_\mu(x_t) + f(\mu, x_t), \tag{4.1}$$

where $x(t)=(x_1(t),x_2(t),x_3(t),x_4(t))^T\in R^4$ and $L\mu: C\to R$, $f: R\times C\to R$ are given respectively by

$$L_\mu(\phi)=(\tau^*+\mu)\begin{pmatrix}0 & -bS^* & 0 & 0\\ bI^* & 0 & -aI^* & 0\\ 0 & 0 & 0 & hP^*\\ 0 & \delta & 0 & -\delta\end{pmatrix}\begin{pmatrix}\phi_1(0)\\ \phi_2(0)\\ \phi_3(0)\\ \phi_4(0)\end{pmatrix}$$

$$+(\tau^*+\mu)\begin{pmatrix}-\frac{rS^*}{K} & 0 & 0 & 0\\ 0 & 0 & 0 & 0\\ 0 & 0 & 0 & 0\\ 0 & 0 & 0 & 0\end{pmatrix}\begin{pmatrix}\phi_1(-1)\\ \phi_2(-1)\\ \phi_3(-1)\\ \phi_4(-1)\end{pmatrix}, \tag{4.2}$$

$$f(\mu,\phi)=(\tau^*+\mu)\begin{pmatrix}-\frac{r}{K}\phi_1(0)\phi_1(-1)-b\phi_1(0)\phi_2(0)\\ b\phi_1(0)\phi_2(0)-a\phi_2(0)\phi_3(0)\\ h\phi_3(0)\phi_4(0)\\ 0\end{pmatrix}. \tag{4.3}$$

By the Riesz representation theorem, there exists a function $\eta(\theta,\mu)$ of bounded variation for $\theta\in[-1,0]$, such that

$$L_\mu\phi=\int_{-1}^{0}d\eta(\theta,0)\phi(\theta) \tag{4.4}$$

for $\phi\in C$.

In fact, we can choose

$$\eta(\theta,\mu)=(\tau^*+\mu)\begin{pmatrix}0 & -bS^* & 0 & 0\\ bI^* & 0 & -aI^* & 0\\ 0 & 0 & 0 & hP^*\\ 0 & \delta & 0 & -\delta\end{pmatrix}\delta(\theta)$$

$$-(\tau^*+\mu)\begin{pmatrix}-\frac{rS^*}{K} & 0 & 0 & 0\\ 0 & 0 & 0 & 0\\ 0 & 0 & 0 & 0\\ 0 & 0 & 0 & 0\end{pmatrix}\delta(\theta+1), \tag{4.5}$$

where δ is the Dirac delta function. For $\phi\in C^1([-1,0],R^4)$, define

$$A(\mu)\phi=\begin{cases}\frac{d\phi(\theta)}{d\theta}, & \theta\in[-1,0),\\ \int_{-1}^{0}d\eta(\mu,s)\phi(s), & \theta=0,\end{cases}$$

and

$$R(\mu)\phi=\begin{cases}0, & \theta\in[-1,0),\\ f(\mu,\phi), & \theta=0.\end{cases}$$

Then system (4.1) is equivalent to

$$\dot{x}_t = A(\mu)x_t + R(\mu)x_t, \tag{4.6}$$

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

For $\psi \in C^1([-1,0], (R^4)^*)$, define

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

and a bilinear inner product

$$\langle \psi(s), \phi(\theta)\rangle = \overline{\psi}(0)\phi(0) - \int_{-1}^{0}\int_{\zeta-\theta}^{\theta} \overline{\psi}(\zeta-\theta)d\eta(\theta)\phi(\zeta)d\zeta, \tag{4.7}$$

where $\eta(\theta) = \eta(\theta, 0)$. Then $A(0)$ and A^* are adjoint operators. By the discussion in Sect. 3, we know that $\pm i\omega^*\tau^*$ are eigenvalues of $A(0)$. Thus, they are also eigenvalues of A^*. We first need to compute the eigenvector of $A(0)$ and A^* corresponding to $+i\omega^*\tau^*$ and $-i\omega^*\tau^*$, respectively.

Suppose that $q(\theta) = (1, \alpha, \beta, \gamma)^T e^{i\omega^*\tau^*\theta}$ is the eigenvector of $A(0)$ corresponding to $+i\omega^*\tau^*$, then $A(0)q(\theta) = i\omega^*\tau^* q(\theta)$. It follows from the definition of $A(0)$ and (4.2), (4.4) and (4.5) that

$$\tau^* \begin{pmatrix} i\omega^* + \frac{rS^*}{K}e^{-i\omega^*\tau^*} & bS^* & 0 & 0 \\ -bI^* & i\omega^* & aI^* & 0 \\ 0 & 0 & i\omega^* & -hP^* \\ 0 & -\delta & 0 & i\omega^* + \delta \end{pmatrix} q(0) = \begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}.$$

Thus, we can easily obtain $q(0) = (1, \alpha, \beta, \gamma)^T$, where $\alpha = \frac{-i\omega^* - \frac{rS^*}{K}e^{-i\omega^*\tau^*}}{bS^*}$, $\gamma = \frac{\delta}{i\omega^*+\delta}\alpha$, $\beta = \frac{hP^*}{i\omega^*}\gamma$. Similarly, let $q^*(s) = D(1, \alpha^*, \beta^*, \gamma^*)e^{i\omega^*\tau^* s}$ be the eigenvector of A^* corresponding to $-i\omega^*\tau^*$. By the definition of A^* and (4.2)–(4.4), we can compute $\alpha^* = \frac{-i\omega^* + \frac{rS^*}{K}e^{-i\omega^*\tau^*}}{bI^*}$, $\beta^* = \frac{aI^*}{i\omega^*}\alpha^*$, $\gamma^* = \frac{-hP^*}{i\omega^*-\delta}\beta^*$. In order to assure $\langle q^*(s), q(\theta)\rangle = 1$, we need to determine the value of D. From (4.7), we have

$$\begin{aligned}
&\langle q^*(s), q(\theta)\rangle \\
&= \overline{D}(1, \overline{\alpha^*}, \overline{\beta^*}, \overline{\gamma^*})(1, \alpha, \beta, \gamma)^T \\
&\quad - \int_{-1}^{0}\int_{\zeta=0}^{\theta} \overline{D}(1, \overline{\alpha^*}, \overline{\beta^*}, \overline{\gamma^*})e^{-i\omega^*\tau^*(\zeta-\theta)}d\eta(\theta)(1, \alpha, \beta, \gamma)^T e^{i\omega^*\tau^*\zeta}d\zeta \\
&= \overline{D}\left\{1 + \alpha\overline{\alpha^*} + \beta\overline{\beta^*} + \gamma\overline{\gamma^*} - \int_{-1}^{0}(1, \overline{\alpha^*}, \overline{\beta^*}, \overline{\gamma^*})\theta e^{i\omega^*\tau^*\theta}d\eta(\theta)(1, \alpha, \beta, \gamma)^T\right\} \\
&= \overline{D}\left\{1 + \alpha\overline{\alpha^*} + \beta\overline{\beta^*} + \gamma\overline{\gamma^*} - \tau^* e^{-i\omega^*\tau^*}\frac{rS^*}{K}\right\}.
\end{aligned}$$

Thus, we can choose D as

$$D = \frac{1}{1 + \alpha\overline{\alpha^*} + \beta\overline{\beta^*} + \gamma\overline{\gamma^*} - \tau^* e^{-i\omega^*\tau^*}\frac{rS^*}{K}}.$$

In the remainder of this section, we use the same notations as in [18], we first compute the coordinates to describe the center manifold C_0 at $\mu = 0$. Let x_t be the solution of (4.6) when $\mu = 0$. Define

$$Z(t) = \langle q^*, x_t\rangle, \qquad W(t,\theta) = x_t(\theta) - 2\mathrm{Re}\{z(t)q(\theta)\}. \tag{4.8}$$

On the center manifold C_0 we have

$$W(t,\theta) = W(z(t), \bar{z}(t), \theta),$$

where

$$W(z,\bar{z},\theta) = W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta)z\bar{z} + W_{02}(\theta)\frac{\bar{z}^2}{2} + W_{30}(\theta)\frac{z^3}{6} + \cdots, \tag{4.9}$$

z and $\bar{z}$ are local coordinates for center manifold C_0 in the direction of q^* and $\overline{q^*}$. Note that W is real if x_t is real. We only consider real solutions. For solution $x_t \in C_0$ of (4.6), since $\mu = 0$, we have

$$\dot{z}(t) = i\omega^*\tau^* z + \overline{q^*}(0) f(0, W(z,\bar{z},\theta) + 2\mathrm{Re}\{zq(\theta)\}) = i\omega^*\tau^* z + \overline{q^*}(0) f_0(z,\bar{z}).$$

We rewrite this equation as

$$\dot{z}(t) = i\omega^*\tau^* z(t) + g(z,\bar{z}),$$

where

$$g(z,\bar{z}) = \overline{q^*}(0) f_0(z,\bar{z}) = g_{20}\frac{z^2}{2} + g_{11}z\bar{z} + g_{02}\frac{\bar{z}^2}{2} + g_{21}\frac{z^2\bar{z}}{2} + \cdots. \tag{4.10}$$

It follows from (4.8) and (4.9) that

$$\begin{aligned} x_t(\theta) &= W(t,\theta) - 2\mathrm{Re}\{z(t)q(t)\} \\ &= W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta)z\bar{z} + W_{02}(\theta)\frac{\bar{z}^2}{2} + (1,\alpha,\beta,\gamma)^T e^{i\omega^*\tau^*\theta} z \\ &\quad + (1,\bar{\alpha},\bar{\beta},\bar{\gamma})^T e^{-i\omega^*\tau^*\theta}\bar{z} + \cdots. \end{aligned} \tag{4.11}$$

It follows together with (4.3) that

$$\begin{aligned} g(z,\bar{z}) &= \overline{q^*}(0) f_0(z,\bar{z}) \\ &= \overline{q^*}(0) f(0, x_t) \end{aligned}$$

$$
\begin{aligned}
&= \tau_k \overline{D}(1, \overline{\alpha^*}, \overline{\beta^*}, \overline{\gamma^*}) \begin{pmatrix} -\frac{r}{K} x_{1t}(0) x_{1t}(-1) - b x_{1t}(0) x_{2t}(0) \\ b x_{1t}(0) x_{2t}(0) - a x_{2t}(0) x_{3t}(0) \\ h x_{3t}(0) x_{4t}(0) \\ 0 \end{pmatrix} \\
&= \tau^* \overline{D}\bigg[z + \bar{z} + W_{20}^{(1)}(0)\frac{z^2}{2} \\
&\quad + W_{11}^{(1)}(0) z\bar{z} + W_{02}^{(1)}(0)\frac{\bar{z}^2}{2} + o(|(z,\bar{z})^3|)\bigg] \\
&\quad \times \bigg\{ -\frac{r}{K}\bigg[e^{-i\omega^*\tau^*} z + e^{i\omega^*\tau^*}\bar{z} + W_{20}^{(1)}(-1)\frac{z^2}{2} + W_{11}^{(1)}(-1) z\bar{z} \\
&\quad + W_{02}^{(1)}(-1)\frac{\bar{z}^2}{2} + o(|(z,\bar{z})|^3)\bigg] \\
&\quad - b\bigg[\alpha z + \bar{\alpha}\bar{z} + W_{20}^{(2)}(0)\frac{z^2}{2} + W_{11}^{(2)}(0) z\bar{z} + W_{02}^{(2)}(0)\frac{\bar{z}^2}{2} + o(|(z,\bar{z})|^3)\bigg]\bigg\} \\
&\quad + \tau^* \overline{D}\bar{\alpha}^* \bigg[\alpha z + \bar{\alpha}\bar{z} + W_{20}^{(2)}(0)\frac{z^2}{2} \\
&\quad + W_{11}^{(2)}(0) z\bar{z} + W_{02}^{(2)}(0)\frac{\bar{z}^2}{2} + o(|(z,\bar{z})|^3)\bigg] \\
&\quad \times \bigg\{ b\bigg[z + \bar{z} + W_{20}^{(1)}(0)\frac{z^2}{2} + W_{11}^{(1)}(0) z\bar{z} + W_{02}^{(1)}(0)\frac{\bar{z}^2}{2} + o(|(z,\bar{z})|^3)\bigg] \\
&\quad - a\bigg[\beta z + \bar{\beta}\bar{z} + W_{20}^{(3)}(0)\frac{z^2}{2} + W_{11}^{(3)}(0) z\bar{z} + W_{02}^{(3)}(0)\frac{\bar{z}^2}{2} + o(|(z,\bar{z})|^3)\bigg]\bigg\} \\
&\quad + \tau^* \overline{D}\bar{\beta}^* h \bigg[\beta z + \bar{\beta}\bar{z} + W_{20}^{(3)}(0)\frac{z^2}{2} + W_{11}^{(3)}(0) z\bar{z} \\
&\quad + W_{02}^{(3)}(0)\frac{\bar{z}^2}{2} + o(|(z,\bar{z})|^3)\bigg] \\
&\quad \times \bigg[\gamma z + \bar{\gamma}\bar{z} + W_{20}^{(4)}(0)\frac{z^2}{2} + W_{11}^{(4)}(0) z\bar{z} \\
&\quad + W_{02}^{(4)}(0)\frac{\bar{z}^2}{2} + o(|(z,\bar{z})|^3)\bigg].
\end{aligned} \tag{4.13}
$$

Comparing the coefficients with (4.10), we have

$$
g_{20} = 2\tau^* \overline{D}\bigg[-\frac{r}{K} e^{-i\omega^*\tau^*} - \alpha b + \alpha\bar{\alpha}^* b - \alpha\bar{\alpha}^* a\beta + \beta\bar{\beta}^* hr \bigg],
$$

$$g_{11} = 2\tau^*\overline{D}\bigg[-\frac{r}{K}\mathrm{Re}\{e^{-i\omega^*\tau^*}\} - b\mathrm{Re}\{\alpha\} - \bar{\alpha^*}b\mathrm{Re}\{\alpha\}$$

$$- \bar{\alpha^*}a\mathrm{Re}\{\alpha\bar{\beta}\} + \bar{\beta^*}h\mathrm{Re}\{\beta\bar{\gamma}\}\bigg],$$

$$g_{02} = 2\tau^*\overline{D}\bigg[-\frac{r}{K}e^{i\omega^*\tau^*} - \bar{\alpha}b + \bar{\alpha}\bar{\alpha^*}b - \bar{\alpha}\bar{\alpha^*}a\beta + \bar{\beta}\bar{\beta^*}hr\bigg],$$

$$g_{21} = \tau^*\overline{D}\bigg[\bigg(-\frac{r}{K}e^{i\omega^*\tau^*} + \alpha\bar{\alpha^*}b\bigg)W_{20}^{(1)}(0) - \frac{\bar{\alpha}br}{K}W_{20}^{(1)}(0)W_{20}^{(1)}(-1)$$

$$+ (\bar{\alpha^*}b - b - \alpha\bar{\alpha^*}\bar{\beta})W_{20}^{(2)}(0)$$

$$+ (\bar{\beta^*}hr - \bar{\alpha}\bar{\alpha^*}a)W_{20}^{(3)}(0) + \bar{\beta}\bar{\beta^*}hW_{20}^{(4)}(0)$$

$$+ \bigg(-2\frac{r}{K}e^{-i\omega^*\tau^*} - 2b\alpha + 2\alpha\bar{\alpha^*}b\bigg)W_{11}^{(1)}(0)$$

$$+ 2W_{11}^{(1)}(-1) + (-2b + 2b\bar{\alpha^*} - 2\bar{\alpha^*}a\beta)W_{11}^{(2)}(0)$$

$$+ (-2\alpha\bar{\alpha^*}a + 2\bar{\beta^*}hr)W_{11}^{(3)}(0) + 2\beta\bar{\beta^*}W_{11}^{(4)}(0).$$

Since there are $W_{20}(\theta)$ and $W_{11}(\theta)$ in g_{21}, we still need to compute them. From (4.6) and (4.8), we have

$$\dot{W} = \dot{x}_t - \dot{z}q - \dot{\bar{z}}\bar{q}$$
$$= \begin{cases} AW - 2\mathrm{Re}\{\overline{q^*}(0)f_0q(\theta)\}, & \theta \in [-1, 0), \\ AW - 2\mathrm{Re}\{\overline{q^*}(0)f_0q(\theta)\} + f_0, & \theta = 0, \end{cases} \triangleq AW + H(z, \bar{z}, \theta), \tag{4.14}$$

where

$$H(z, \bar{z}, \theta) = H_{20}(\theta)\frac{z^2}{2} + H_{11}(\theta)z\bar{z} + H_{02}(\theta)\frac{\bar{z}^2}{2} + \cdots. \tag{4.15}$$

Substituting the corresponding series into (4.14) and comparing the coefficients, we obtain

$$(A - 2i\omega^*\tau^*)W_{20}(\theta) = -H_{20}, \quad AW_{11}(\theta) = -H_{11}, \quad \ldots. \tag{4.16}$$

From (4.14), we know that for $\theta \in [-1, 0)$,

$$H(z, \bar{z}, \theta) = -\overline{q^*}(0)f_0q(\theta) - q^*(0)\bar{f_0}\bar{q}(\theta) = -g(z, \bar{z})q(\theta) - g(z, \bar{z})\bar{q}(\theta). \tag{4.17}$$

Comparing the coefficients with (4.15) gives that

$$H_{20}(\theta) = -g_{20}q(\theta) - \bar{g}_{02}\bar{q}(\theta), \tag{4.18}$$

and

$$H_{11}(\theta) = -g_{11}q(\theta) - \bar{g}_{11}\bar{q}(\theta). \tag{4.19}$$

From (4.16), (4.18) and the definition of A, it follows that

$$\dot{W}_{20} = 2i\omega^*\tau^* W_{20}(\theta) + g_{20}q(\theta) + \bar{g}_{02}\bar{q}(\theta).$$

Notice that $q(\theta) = (1, \alpha, \beta, \gamma)^T e^{i\omega^*\tau^*\theta}$, hence

$$W_{20}(\theta) = \frac{ig_{20}}{\omega^*\tau^*} q(0)e^{i\omega^*\tau^*\theta} + \frac{i\bar{g}_{02}}{3\omega^*\tau^*}\bar{q}(0)e^{-i\omega^*\tau^*\theta} + E_1 e^{2i\omega^*\tau^*\theta}, \tag{4.20}$$

where $E_1 = (E_1^{(1)}, E_1^{(2)}, E_1^{(3)}, E_1^{(4)}) \in R^4$ is a constant vector. Similarly, from (4.16) and (4.19), we obtain

$$W_{11}(\theta) = -\frac{ig_{11}}{\omega^*\tau^*} q(0)e^{i\omega^*\tau^*\theta} + \frac{i\bar{g}_{11}}{\omega^*\tau^*}\bar{q}(0)e^{-i\omega^*\tau^*\theta} + E_2, \tag{4.21}$$

where $E_2 = (E_2^{(1)}, E_2^{(2)}, E_2^{(3)}, E_2^{(4)}) \in R^4$ is also a constant vector.

In what follows, we shall seek appropriate E_1 and E_2. From the definition of A and (4.16), we obtain

$$\int_{-1}^{0} d\eta(\theta) W_{20}(\theta) = 2i\omega^*\tau^* W_{20}(\theta) - H_{20}(\theta), \tag{4.22}$$

and

$$\int_{-1}^{0} d\eta(\theta) W_{11}(\theta) = -H_{11}(\theta), \tag{4.23}$$

where $\eta(\theta) = \eta(0, \theta)$. By (4.14), we have

$$H_{20}(\theta) = -g_{20}q(0) - \bar{g}_{20}\bar{q}(0) + 2\tau^* \begin{pmatrix} -\frac{r}{K}e^{-i\omega^*\tau^*} - \alpha b \\ \alpha b - \alpha a\beta \\ \beta h r \\ 0 \end{pmatrix}, \tag{4.24}$$

and

$$H_{11}(\theta) = -g_{11}q(0) - \bar{g}_{11}\bar{q}(0) + 2\tau^* \begin{pmatrix} -\frac{r}{K}\mathrm{Re}\{e^{-i\omega^*\tau^*}\} - b\mathrm{Re}\{\alpha\} \\ -b\mathrm{Re}\{\alpha\} - a\mathrm{Re}\{\alpha\bar{\beta}\} \\ h\mathrm{Re}\{\beta\bar{\gamma}\} \\ 0 \end{pmatrix}. \tag{4.25}$$

Substituting (4.20) and (4.24) into (4.22), we obtain

$$\left(2\omega^*\tau^* I - \int_{-1}^{0} e^{2i\omega^*\tau^*\theta} d\eta(\theta)\right) E_1 = 2\tau^* \begin{pmatrix} -\frac{r}{K}e^{-i\omega^*\tau^*} - \alpha b \\ \alpha b - \alpha a\beta \\ \beta h r \\ 0 \end{pmatrix},$$

which leads to

$$\begin{pmatrix} 2i\omega^* + \frac{rS^*}{K}e^{-i\omega^*\tau^*} & bS^* & 0 & 0 \\ -bI^* & 2i\omega^* & aI^* & 0 \\ 0 & 0 & 2i\omega^* & -hP^* \\ 0 & -\delta & 0 & 2i\omega^* + \delta \end{pmatrix} E_1 = 2 \begin{pmatrix} -\frac{r}{K}e^{-i\omega^*\tau^*} - \alpha b \\ \alpha b - \alpha a \beta \\ \beta h r \\ 0 \end{pmatrix},$$

where

$$\Delta = \begin{vmatrix} 2i\omega^* + \frac{rS^*}{K}e^{-i\omega^*\tau^*} & bS^* & 0 & 0 \\ -bI^* & 2i\omega^* & aI^* & 0 \\ 0 & 0 & 2i\omega^* & -hP^* \\ 0 & -\delta & 0 & 2i\omega^* + \delta \end{vmatrix}.$$

It follows that

$$E_1^{(1)} = \frac{2}{\Delta} \begin{vmatrix} -\frac{r}{K}e^{-i\omega^*\tau^*} - \alpha b & bS^* & 0 & 0 \\ \alpha b - \alpha a \beta & 2i\omega^* & aI^* & 0 \\ \beta h r & 0 & 2i\omega^* & -hP^* \\ 0 & -\delta & 0 & 2i\omega^* + \delta \end{vmatrix},$$

$$E_1^{(2)} = \frac{2}{\Delta} \begin{vmatrix} 2i\omega^* + \frac{rS^*}{K}e^{-i\omega^*\tau^*} & -\frac{r}{K}e^{-i\omega^*\tau^*} - \alpha b & 0 & 0 \\ -bI^* & \alpha b - \alpha a \beta & aI^* & 0 \\ 0 & 0 & 2i\omega^* & -hP^* \\ 0 & -\delta & 0 & 2i\omega^* + \delta \end{vmatrix},$$

$$E_1^{(3)} = \frac{2}{\Delta} \begin{vmatrix} 2i\omega^* + \frac{rS^*}{K}e^{-i\omega^*\tau^*} & bS^* & -\frac{r}{K}e^{-i\omega^*\tau^*} - \alpha b & 0 \\ -bI^* & 2i\omega^* & \alpha b - \alpha a \beta & 0 \\ 0 & 0 & \beta h r & -hP^* \\ 0 & -\delta & 0 & 2i\omega^* + \delta \end{vmatrix},$$

$$E_1^{(4)} = \frac{2}{\Delta} \begin{vmatrix} 2i\omega^* + \frac{rS^*}{K}e^{-i\omega^*\tau^*} & bS^* & 0 & -\frac{r}{K}e^{-i\omega^*\tau^*} - \alpha b \\ -bI^* & 2i\omega^* & aI^* & \alpha b - \alpha a \beta \\ 0 & 0 & 2i\omega^* & \beta h r \\ 0 & -\delta & 0 & 0 \end{vmatrix}.$$

Similarly, substituting (4.21) and (4.25) into (4.23), we can get

$$\begin{pmatrix} \frac{rS^*}{K} & bS^* & 0 & 0 \\ -bI^* & 0 & aI^* & 0 \\ 0 & 0 & 0 & -hP^* \\ 0 & -\delta & 0 & \delta \end{pmatrix} E_2 = \begin{pmatrix} -\frac{r}{K}\mathrm{Re}\{e^{-i\omega^*\tau^*}\} - b\mathrm{Re}\{\alpha\} \\ -b\mathrm{Re}\{\alpha\} - a\mathrm{Re}\{\alpha\bar{\beta}\} \\ h\mathrm{Re}\{\beta\bar{\gamma}\} \\ 0 \end{pmatrix},$$

and hence

$$E_2^{(1)} = \frac{2}{\Delta_1}\begin{vmatrix} -\frac{r}{K}\mathrm{Re}\{e^{-i\omega^*\tau^*}\} - b\mathrm{Re}\{\alpha\} & bS^* & 0 & 0 \\ -b\mathrm{Re}\{\alpha\} - a\mathrm{Re}\{\alpha\bar{\beta}\} & 0 & aI^* & 0 \\ h\mathrm{Re}\{\beta\bar{\gamma}\} & 0 & 0 & -hP^* \\ 0 & -\delta & 0 & \delta \end{vmatrix},$$

$$E_2^{(2)} = \frac{2}{\Delta_1}\begin{vmatrix} \frac{rS^*}{K} & -\frac{r}{K}\mathrm{Re}\{e^{-i\omega^*\tau^*}\} - b\mathrm{Re}\{\alpha\} & 0 & 0 \\ -bI^* & -b\mathrm{Re}\{\alpha\} - a\mathrm{Re}\{\alpha\bar{\beta}\} & aI^* & 0 \\ 0 & h\mathrm{Re}\{\beta\bar{\gamma}\} & 0 & -hP^* \\ 0 & 0 & 0 & \delta \end{vmatrix},$$

$$E_2^{(3)} = \frac{2}{\Delta_1}\begin{vmatrix} \frac{rS^*}{K} & bS^* & -\frac{r}{K}\mathrm{Re}\{e^{-i\omega^*\tau^*}\} - b\mathrm{Re}\{\alpha\} & 0 \\ -bI^* & 0 & -b\mathrm{Re}\{\alpha\} - a\mathrm{Re}\{\alpha\bar{\beta}\} & 0 \\ 0 & 0 & h\mathrm{Re}\{\beta\bar{\gamma}\} & -hP^* \\ 0 & -\delta & 0 & \delta \end{vmatrix},$$

$$E_2^{(4)} = \frac{2}{\Delta_1}\begin{vmatrix} \frac{rS^*}{K} & bS^* & 0 & -\frac{r}{K}\mathrm{Re}\{e^{-i\omega^*\tau^*}\} - b\mathrm{Re}\{\alpha\} \\ -bI^* & 0 & aI^* & -b\mathrm{Re}\{\alpha\} - a\mathrm{Re}\{\alpha\bar{\beta}\} \\ 0 & 0 & 0 & h\mathrm{Re}\{\beta\bar{\gamma}\} \\ 0 & -\delta & 0 & 0 \end{vmatrix},$$

where

$$\Delta_1 = \begin{vmatrix} \frac{rS^*}{K} & bS^* & 0 & 0 \\ -bI^* & 0 & aI^* & 0 \\ 0 & 0 & 0 & -hP^* \\ 0 & -\delta & 0 & \delta \end{vmatrix}.$$

Thus, we can determine $W_{20}(\theta)$ and $W_{11}(\theta)$ from (4.20) and (4.21). Furthermore, g_{21} in (4.13) can be expressed by the parameters and delay. Then, we can compute the following values:

$$\begin{aligned} c_1(0) &= \frac{i}{2\omega^*\tau^*}\left(g_{20}g_{11} - 2|g_{11}|^2 - \frac{|g_{02}|^2}{3}\right) + \frac{g_{21}}{2}, \\ \mu_2 &= -\frac{\mathrm{Re}\{c_1(0)\}}{\mathrm{Re}\{\lambda'(\tau^*)\}}, \\ \beta_2 &= 2\mathrm{Re}\{c_1(0)\}, \\ T_2 &= -\frac{\mathrm{Im}\{c_1(0)\} + \mu_2\mathrm{Im}\{\lambda'(\tau^*)\}}{\omega^*\tau^*}. \end{aligned} \tag{4.26}$$

By the result of Hassard et al. [17], we have the following:

Theorem 4.1 *In* (4.26), *the sign of* μ_2 *determined the direction of Hopf bifurcation*: *if* $\mu_2 > 0$ ($\mu_2 < 0$), *then the Hopf bifurcation is supercritical* (*subcritical*) *and the* *bifurcating periodic solution exist for* $\tau > \tau^*$ ($\tau < \tau^*$). β_2 *determines the stability of the bifurcating periodic solution*: *the bifurcating periodic solution is stable* (*unstable*) *if* $\beta_2 < 0$ ($\beta_2 > 0$) *and* T_2 *determines the period of the bifurcating periodic solution*: *the period increase* (*decrease*) *if* $T_2 > 0$ ($T_2 < 0$).

5 Numerical simulations

From Theorems 3.2 and 4.1, it follows that the feedback time delay τ may lead to oscillatory behaviors of the prey and predator populations. When the feedback time delay τ crosses τ^* left ($\beta_2 > 0$), the prey and predator populations will periodically oscillate near τ^*, while the populations will be stabilized at τ^* when τ crosses τ^* from right ($\beta_2 < 0$).

In order to check our computation for Theorem 4.1, we perform some numerical simulations. Let $r = 2$, $b = 0.5$, $K = 100$, $c = 0.9$, $a = 2$, $d = 0.3$, $h = 0.4$, $\delta = 2$. We consider the following system:

$$\begin{cases} \frac{dS}{dt} = 2S(1 - \frac{S(t-\tau)}{100}) - 0.5SI, \\ \frac{dI}{dt} = 0.5SI - 0.9I - 2IP, \\ \frac{dP}{dt} = -0.3P + 0.4PQ, \\ \frac{dQ}{dt} = 2(I - Q). \end{cases} \tag{5.1}$$

The initial conditions are $S(0) = 60$, $I(0) = 1$, $P(0) = 20$, $Q(0) = 1$. By computing, we get the positive equilibrium $E_3(81.25, 0.75, 19.8625, 0.75)$. The parameters satisfy the conditions indicated in Theorem 3.2. We also can know $\omega^* = 4.017622584$ and $\tau^* = 0.2383864215$. Hence, we can say that as τ increases, stability switch may occur. The value of τ where stability switch occurs is $\tau^* = 0.2383864215$, which can be easily calculated using (3.1). Hence, by Butler's lemma, E_3 remains stable for $\tau < \tau^*(= 0.2383864215)$. In the following, we mainly consider the direction and stability of Hopf bifurcation at $\tau = \tau^*$.

From Lemma 3.1 and Theorem 3.1, we can obtain that the characteristic equation of (5.1) at $E_3(81.25, 0.75, 19.8625, 0.75)$ has two simple roots $\pm i\omega^*$ for $\tau = \tau^*$ and the other roots $\lambda \neq \pm i\omega^*$ have non-zero real parts. Furthermore, if $\tau \in [0, \tau^*)$, all the characteristic equation of (5.1) at $E_3(81.25, 0.75, 19.8625, 0.75)$ is locally asymptotically stable. At $\tau = \tau^*$, Hopf bifurcation occurs for system (5.1). We also obtain $\lambda'(\tau^*) = 0.54729415 - 1.56842451i$, $c_1(0) = 0.84276562 - 2.54815512i$. From the formulaes (4.26) in Sect. 4, $\mu_2 < 0$, $\beta_2 > 0$ and $T_2 > 0$. Therefore, we conclude that the bifurcation occuring at critical value τ^* takes place when τ crosses τ^* to the left (subcritical) and the bifurcating periodic solution are unstable. We obtain the numerical results by meas of the software Matlab (See Figs. 1 and 2).

Last, we will perform some numerical simulations to show the importance of parameter δ. Let $r = 2$, $K = 100$, $b = 0.5$, $c = 0.9$, $a = 2$, $d = 0.3$, $h = 0.6$, $\tau = 0.25$. The initial conditions are $S(0) = 60$, $I(0) = 1$, $P(0) = 20$, $Q(0) = 1$. From the Figs. 3 and 4, We can observe that when $\delta = 1.8$ the three species coexist, i.e., E_3 is asymptotically stable (Fig. 3); when $\delta = 2.65$ the three species periodically oscillate, i.e.,

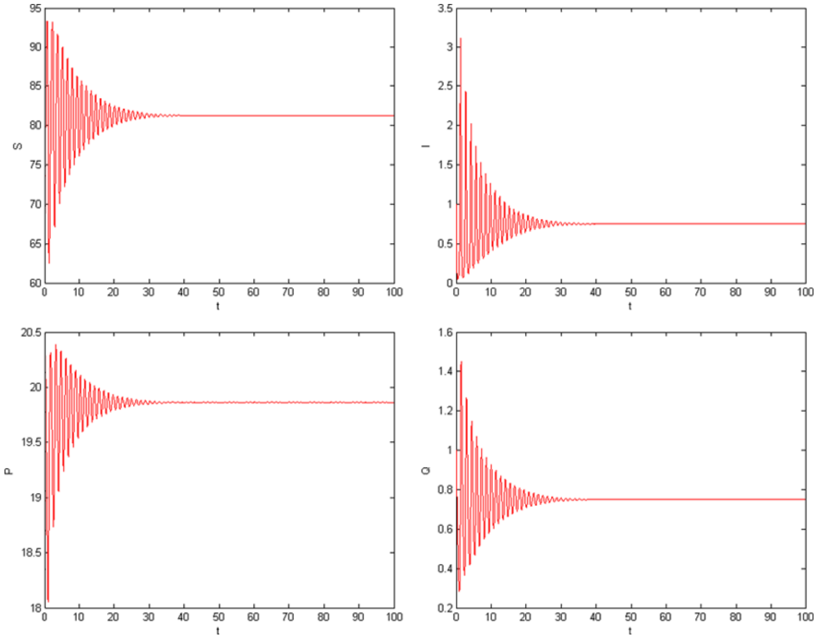

Fig. 1 When $\tau = 0.21$, the positive equilibrium E_3 is asymptotically stable

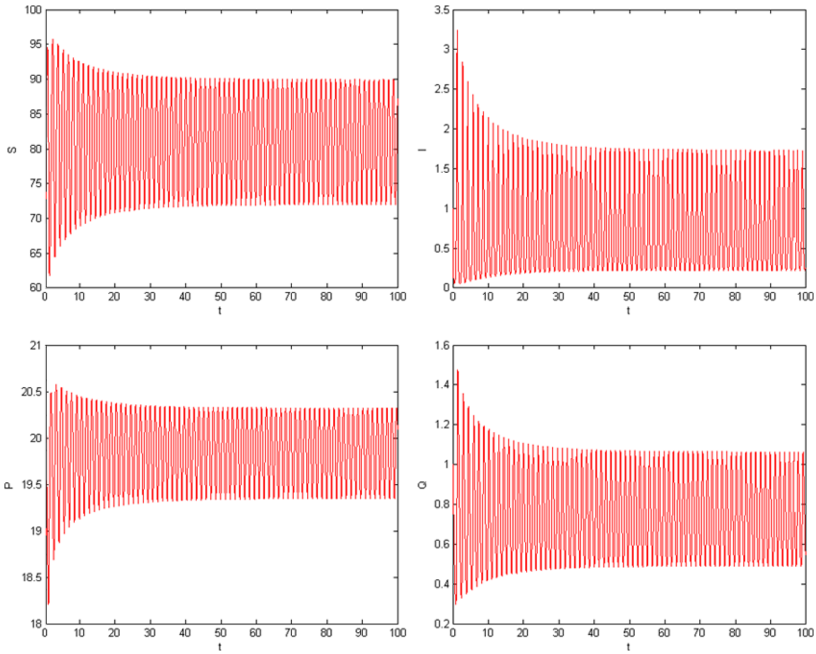

Fig. 2 When $\tau = 0.25$ and is sufficiently near to τ^*, the bifurcating periodic solutions from the positive equilibrium E_3 occur and are unstable

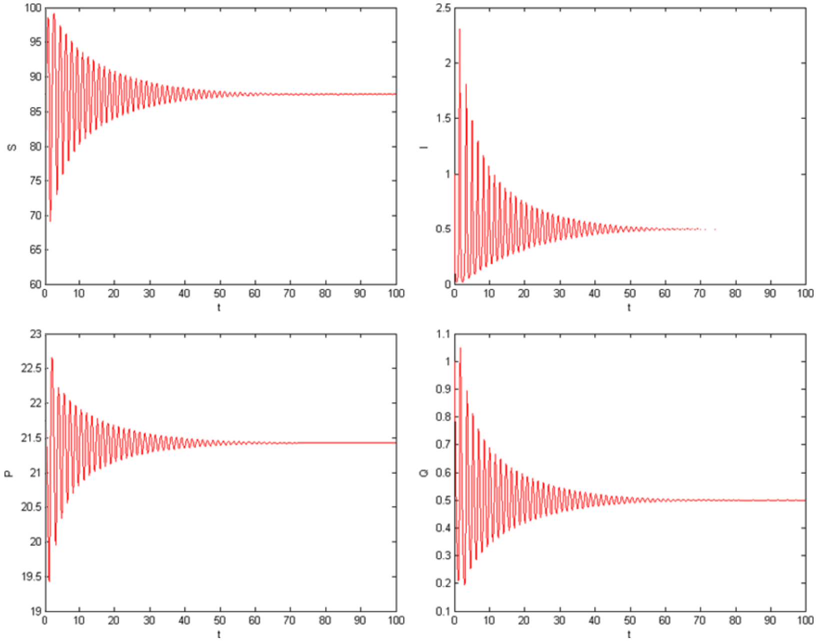

Fig. 3 When $r = 2$, $K = 100$, $b = 0.5$, $c = 0.9$, $a = 2$, $d = 0.3$, $h = 0.6$, $\tau = 0.25$ and $\delta = 1.8$, the positive equilibrium E_3 is asymptotically stable

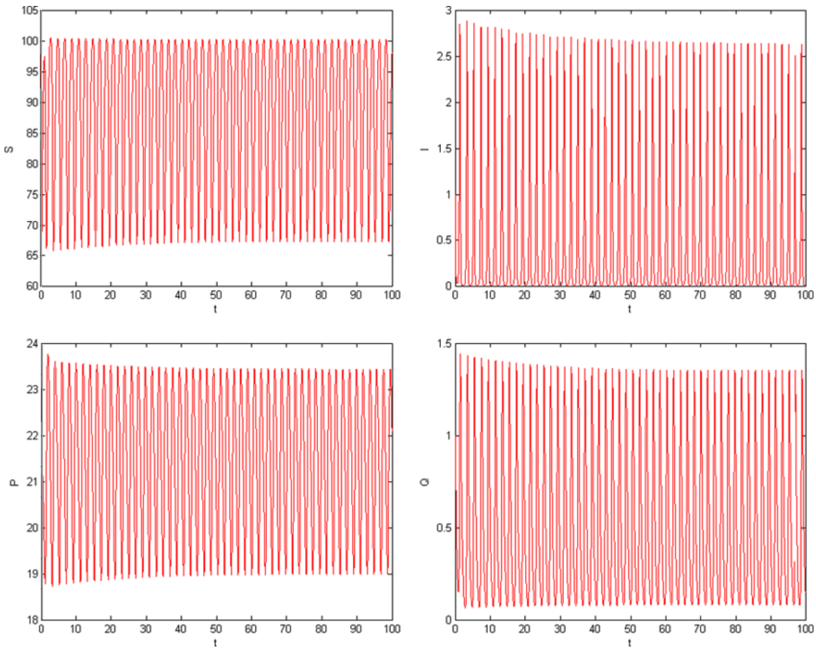

Fig. 4 When $r = 2$, $K = 100$, $b = 0.5$, $c = 0.9$, $a = 2$, $d = 0.3$, $h = 0.6$, $\tau = 0.25$ and $\delta = 2.65$, the bifurcating periodic solutions from the positive equilibrium E_3 occur

Hopf bifurcation occurs around E_3 (Fig. 4). That is to say that, there is an critical value δ^*, when $\delta < \delta^*$ the positive equilibrium is stable; when $\delta > \delta^*$ the positive equilibrium is unstable and Hopf bifurcation occurs. How to get the critical value δ^*? We leave it in the future.

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