ON A STAGE-STRUCTURED POPULATION MODEL IN DISCRETE PERIODIC HABITAT: III. UNIMODAL GROWTH AND DELAY EFFECT

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Dedicated to Professor Sze-Bi Hsu
on the occasion of his 70th birthday and retirement

Abstract. For a stage-structured population model in periodic discrete habitat, with periodic initial values it reduces to a system of two differential equations with time delay. Assuming the birth rate is of unimodal type, we obtain the influence of time delay on the local and global dynamics. In particular, large delay leads to population vanishing. As delay decreases, we found three critical values of delay for the emergence of different dynamics, by appealing to a combination of monotone dynamical system theory, Hopf bifurcation theory and the fluctuation method. Numerical simulations are also performed to illustrate the results.

1. Introduction. In the companion paper [1], the authors proposed the following stage-structured population model in discrete periodic habitat to model the species invasion in spatially fragmental environment, such as corn and paddy field:

\[
\begin{align*}
    u'_i(t) &= \alpha(u_{i-1}(t) + u_{i+1}(t)) - 2\beta u_i(t) - \gamma u_i(t) + e^{-\gamma'\tau}b(u_i(t - \tau)), & \text{if } i \text{ is even}, \\
    u'_i(t) &= \beta(u_{i-1}(t) + u_{i+1}(t)) - 2\alpha u_i(t) - \eta u_i(t), & \text{if } i \text{ is odd},
\end{align*}
\]

(1.1)

where \(u_i(t)\) represents the density of the mature population at time \(t\) and location \(i\), \(\alpha\) is the dispersal rate from bad locations to their adjacent good locations, \(\beta\) is the dispersal rate from good locations to their adjacent bad locations, \(\gamma\) and \(\eta\) are the mortality rates for mature population, \(\gamma'\) is the mortality rate for immature population, \(\tau\) is the maturation age, and \(b\) is the birth rate for mature population in good locations. In [1], under the assumption that the recruitment \(b\) is nondecreasing and of KPP type, the unique optimal dispersal strategy for population spread is obtained in terms of \(\beta = \beta_1\), where \(\beta_1\) is uniquely determined, depending on other parameters in an implicit way.

In this paper, we consider another scenario that \(b\) is of unimodal type; it is increasing first and then decreasing. Without loss of generality, we assume that

\[b(u) = pue^{-qu}, \quad p > 0, q > 0,\]  

(1.2)
which is a typical unimodal type growth, known as the Ricker function. Unlike [1],
with the birth rate (1.2) the model (1.1) does not admit the comparison principle
in general and time delay may dramatically influence the global dynamics.

We further assume that the initial values has the spatial periodicity so that
the model reduces to a subsystem of two differential equations with time delay,
while leaving the whole model with general initial values for possible future study.
Consider the following initial values:

\[
\begin{align*}
  u_i(0) &= u_{i+2}(0), \quad i \text{ is odd}, \\
  u_i(\theta) &= u_{i+2}(\theta), \quad i \text{ is even, } \theta \in [-\tau, 0].
\end{align*}
\]  

(1.3)

For such type of initial values, by [1] we see that the solutions \(u_i(t)\) exist for \(t > 0\)
and \(i \in \mathbb{Z}\), and by the periodicity we further can infer that

\[
u_i(t) = u_{i+2}(t), \quad i \in \mathbb{Z}, t > 0.
\]

(1.4)

As such, we may define

\[
v(t) = u_{2k-1}(t), \quad w(t) = u_{2k}(t), \quad k \in \mathbb{Z}.
\]

(1.5)

Then model (1.1) reduces to a system consisting of an ordinary differential equation
and a delay differential equation:

\[
\begin{align*}
  v'(t) &= 2\beta w(t) - 2\alpha v(t) - \eta v(t), \\
  w'(t) &= 2\alpha v(t) - 2\beta w(t) - \gamma w(t) + \mu b(w(t - \tau)),
\end{align*}
\]

(1.6)

where

\[
\mu = e^{-\gamma t}.
\]

(1.7)

Here parameters \(\alpha\) and \(\beta\) measure the connectivity between good and bad habitats.
If \(\alpha = 0\) then (1.6) reduces to the classical Nicholson blowfly model. If \(\beta = 0\) then
(1.6) is asymptotic to the Nicholson blowfly model,

\[
\begin{align*}
  w'(t) &= -du(t) + \mu pu(t - \tau)e^{-qu(t-\tau)},
\end{align*}
\]

(1.8)

which was proposed by Gurney et al [7], hoping to explain the oscillatory phenomena
in Nicholson’s laboratory experiments [11]. As such, (1.6) may be regarded as a
generalized Nicholson blowfly model in two patches with directional dispersal.

The Nicholson’s blowfly model (1.8) has been widely studied. If the mortality
rate of the juveniles is small, then the delay effect in the initial net growth rate
\(\mu p\) might be ignorable. In this scenario, it has been shown that zero equilibrium is
globally stable if \(\frac{\mu}{\eta} \leq 1\), the unique positive equilibrium is globally asymptotically
stable if \(\frac{\mu}{\eta} \in (1, e^2]\) or \(\frac{\mu}{\eta} > e^2\) with small \(\tau\), see the book [15] by Smith and references
therein. When \(\frac{\mu}{\eta} > e^2\), Wei [21] obtained unbounded Hopf bifurcation branches as
\(\tau\) increases to infinity. If the mortality rate of the juveniles is not small, then the
delay effect in the initial growth rate \(p\) cannot be ignored. For such a scenario, Shu,
Wang and Wu [14] obtained bounded global Hopf bifurcation branches as \(\tau\) varies.
So, Wu and Zou [17] proposed a generalized two stage-structured population model
in two patches and performed interesting numerical analysis on periodic solutions,
pointing out that its global dynamics is far from completely understood. This
paper tries to make a step forward to this direction. Gourley and Wu [6] present
a survey about the modeling and analysis of diffusive stage-structured population.
Recently there are a number of studies about stage-structured population models,
for instance, [4, 5, 20, 18].
In this paper, we are interested in the question that how do the patchy environment and time delay $\tau$ jointly influence the population dynamics for model (1.6). Since $\mu$ depends on $\tau$ and $b$ is of unimodal type, one may expect rich dynamics induced jointly by $\tau$ and other parameters, including the directional dispersal rates $\alpha$ and $\beta$.

For the whole model (1.1) with monotone birth rate, the existence, uniqueness and continuity with respect to general initial values were studied in a companion paper [1], where the optimal dispersal strategy for maximizing the invasion speed is found. In another companion paper [2], the Allee effect for birth is taken into account and it is found that the diffusion strategy is essentially important for the propagation success or failure. For the whole model (1.1) with unimodal type birth rate, the propagation dynamics is much richer and is left for future study. The work on the subsystem (1.6) in this paper provides a basis for the study of propagation dynamics.

The rest of this paper is organized as follows. In section 2, we study the global stability of equilibria by appealing to appropriate tools, including the monotone dynamical system theory for delay differential equations, the fluctuation method and the comparison arguments. In section 3, we investigate the existence of Hopf bifurcation by computing the normal form in the center manifold. The direction and stability of the Hopf bifurcation are obtained. In section 5, some numerical simulations illustrate the results and a discussion concludes the paper.

2. Convergence to equilibrium. Since (1.6) consists of an ordinary differential equation and a delay differential equation, the initial value $\phi$ has two components, say $\phi = (\phi_1, \phi_2)$, where $\phi_1 \in R^+$ and $\phi_2 \in C([−\tau, 0], R^+)$. Let $u(t, \phi) = (w(t, \phi), v(t, \phi))$ be the solution of (1.6). Define

$$\delta = \gamma + \frac{2\beta}{1 + 2\alpha \eta - 1}.$$  

The main result of this section is as follows.

Theorem 2.1. Assume that $\phi \not\equiv 0$. Define

$$\tau^* := \max \left\{0, \frac{1}{\gamma} \ln \frac{p}{\delta} \right\}, \quad \tau_* := \max \left\{0, \frac{1}{\gamma} \left(\ln \frac{p}{\delta} - 2\right) \right\}$$

and

$$\tau_{**} = \min \left\{\tau_*, \frac{1}{p} e^{-2\beta - \gamma + 1}\right\}.$$  

(2.1)

Clearly, $\tau^* \geq \tau_* \geq \tau_{**}$. Then the following statements hold.

(i) If $\tau > \tau^*$, then $u(t, \phi) \to (0, 0)$ exponentially as $t \to \infty$.

(ii) If $\tau = \tau^*$, then $u(t, \phi) \to (0, 0)$ as $t \to \infty$.

(iii) If $\tau < \tau^*$, then a unique positive equilibrium $(v^*, w^*)$ appears, having the following explicit form

$$(v^*, w^*) = \left(\frac{\delta - \gamma}{\eta q} \ln \frac{p \mu}{\delta}, \frac{1}{q} \ln \frac{p \mu}{\delta}\right).$$

If, further, $\tau \in [0, \tau_*] \cup [\tau_*, \tau^*)$, then $u(t, \phi) \to (w^*, v^*)$ as $t \to \infty$.

Remark 1. With the distribution of eigenvalues as obtained in the proof of Lemmas 2.3 and 2.4, we can infer the following local stability results\footnote{Combining the attractivity in Theorem 2.1 and the local stability in Remark 1 one may obtain the related global stability.}. Indeed, if $\tau > \tau^*$, then
the principal eigenvalue at zero equilibrium is positive, and hence, zero is locally stable. When \( \tau \) decreases to \( \tau^* \) with \( \tau^* > 0 \), the principle eigenvalue becomes zero. In this critical case, since \( b(u) \leq pu \) for \( u \geq 0 \), we can infer by a direct calculation that \( (\bar{v}, \bar{w}) \equiv \sigma (1, \frac{2a+\eta}{2a}) \) with any \( \sigma > 0 \) and \((\bar{v}, \bar{w}) = (0, 0)\) are a pair of super and sub solutions of (1.6). This then implies that zero is still locally stable under small and nonnegative perturbations. When \( \tau \) continues to decrease, zero loses its stability and a unique positive equilibrium emerges and persists. Further, if \( \tau \in [0, \tau_{**}] \cup [\tau_{**}, \tau^*) \), the positive equilibrium is locally stable. When \( \tau \in (\tau_{**}, \tau^*) \neq \emptyset \), the local stability of the positive equilibrium is complicated and will be studied in section 3 by a Hopf bifurcation analysis.

To prove theorem 2.1, we start with the analysis of equilibria. Let \((v, w)\) be an equilibrium of (1.1), then it satisfies the following system of two algebraic equations:

\[
\begin{align*}
0 &= -\eta v + 2\beta w - 2\alpha v, \\
0 &= -\gamma w + 2\alpha v - 2\beta w + \mu b(w).
\end{align*}
\]

(2.2)

Recall that \( \mu = e^{-\gamma I} \) and \( b(s) = ps e^{-\eta s} \), where \( \gamma I, p, q \) are positive parameters.

Obviously, \( (0, 0) \) is always an equilibrium. As for the possible existence of positive equilibria we have the following result.

Lemma 2.2. If \( \tau \geq \tau^* \), then the only equilibrium is \( (0, 0) \); If \( \tau < \tau^* \), then there exists a unique positive equilibrium that reads

\[
(v^*, w^*) = \left( \frac{\delta - \gamma}{\eta q} \ln \frac{p\mu}{\delta}, \frac{1}{q} \ln \frac{p\mu}{\delta} \right).
\]

(2.3)

Proof. By direction computation, one can obtain the conclusion. The computation details are omitted. \( \square \)

For the stability of the zero equilibrium, we have the following result.

Lemma 2.3. The following statements hold:

(i) If \( \tau > \tau^* \), then for any \( \phi \), \((v(t, \phi), w(t, \phi))\) converges to \( (0, 0) \) exponentially as \( t \to +\infty \).

(ii) If \( \tau = \tau^* \), then for any \( \phi \), \((v(t, \phi), w(t, \phi))\) converges to \( (0, 0) \) as \( t \to +\infty \).

(iii) If \( \tau < \tau^* \), then \((0, 0)\) is unstable.

Proof. (i). We construct a super solution that converges to zero exponentially and then employ the comparison argument. Indeed, linearizing (1.6) at \((0, 0)\) gives a linear and monotone system:

\[
\begin{align*}
v' &= 2\beta w - 2\alpha v - \eta v, \\
w' &= 2\alpha v - 2\beta w - \gamma w + \mu w(t - \tau).
\end{align*}
\]

(2.4)

Since \( pse^{-\eta s} \leq ps, \forall s \geq 0 \), any positive solution of (2.4) provides a super solution of (1.6) due to the comparison principle. For (2.4), we seek for solutions having the form \((\xi e^{\lambda t}, e^{\lambda t})\) for some \( \xi > 0 \) and \( \lambda < 0 \). Substituting such a form in to (2.4) we obtain that \( \lambda \) solves

\[
\lambda + 2\beta + \gamma = \frac{4\alpha \beta}{\lambda + 2\alpha + \eta} + \mu e^{-\lambda \tau}.
\]

(2.5)

The left-hand side of (2.5) is an increasing function of \( \lambda \in \mathbb{R} \), while the right-hand side of (2.5) is a decreasing function of \( \lambda > -(2\alpha + \eta) \). Note that at \( \lambda = 0 \) the left-hand side is \( 2\beta + \gamma \) and the right-hand side is \( \frac{4\alpha \beta}{2\alpha + \eta} + \mu \). Since \( \tau > \tau^* \), we
have $2\beta + \gamma > \frac{4\alpha \beta}{\alpha + \gamma} + \mu \delta$. Consequently, it is not difficult to see that (2.5) admits a unique positive solution due to the fact that (2.5) is a cooperative and irreducible system of delay differential equations with $\sigma(1, \frac{2\alpha + \gamma}{\alpha + \gamma})$ converges to $(p, q)$ as $t \to \infty$.

(ii) We construct a nonlinear monotone system, any solution of which provides a super solution for (1.6). Indeed, define

$$h(z) := \begin{cases} pze^{-\gamma}z, & 0 < z < 1 \\ pe^{-1}, & z \geq 1 \end{cases} \quad (2.6)$$

Clearly, $h : \mathbb{R}^+ \to \mathbb{R}^+$ is a nondecreasing function. Consider

$$\begin{cases} v' = 2\beta w - 2\alpha v - \eta v, \\
w' = 2\alpha v - 2\beta w - \gamma w + \mu h(w(t - \tau)). \end{cases} \quad (2.7)$$

Clearly, (2.7) is a cooperative and irreducible system of delay differential equations. Meanwhile, since $\tau = \tau^*$, the only equilibrium of (2.7) is $(0, 0)$. For the same reason as in Remark 1 we see that $(\bar{v}, \bar{w}) = (0, 0)$ are a pair of super and sub solutions of (2.7). Then applying [15, page 3, Theorem 2.1] with $X = C([\tau, 0], \mathbb{R}^2)$, we obtain that (2.7) converges to $(0, 0)$ exponentially.

(iii) It suffices to analyze the eigenvalue problem at $(0, 0)$. By similar arguments to the case (i), we see that (2.5) admits a unique positive solution due to $\tau < \tau^*$. Therefore, $(0, 0)$ is unstable.

By Lemmas 2.2 and 2.3 we see that as delay $\tau$ decreases through $\tau^*$, the equilibrium $(0, 0)$ loses the global attractivity and a unique positive equilibrium $(\alpha^*, \beta^*)$ bifurcates from $(0, 0)$. Therefore, we investigate the local and global stability of $(\alpha^*, \beta^*)$. Recall that

$$\tau_* := \max \left\{ 0, \frac{1}{\gamma} \left( \frac{p}{\delta} - 2 \right) \right\}.$$  

Clearly, $\tau_* = 0$ when $p \in (0, \delta e^2]$ and $\tau_* > 0$ when $p > \delta e^2$. Moreover, $\tau_* < \tau^*$ when $p > \delta$ and $\tau_* = \tau^*$ when $p \in (0, \delta]$.}

**Lemma 2.4.** If $\tau \in [\tau_*, \tau^*)$, then $(v(t, \phi), w(t, \phi))$ converges to $(\alpha^*, \beta^*)$ exponentially as $t \to +\infty$.

**Proof.** We divide the proof into two parts: (i) $\lim_{t \to +\infty} (v(t, \phi), w(t, \phi)) = (\alpha^*, \beta^*)$; (ii) all eigenvalues of the linearized system at $(\alpha^*, \beta^*)$ have negative real parts.

We will employ a fluctuation argument, which has been used in the study of global convergence to equilibria in reaction-diffusion models [10, 19, 22, 23]. Define

$$B = \begin{pmatrix} -(2\alpha + \eta) & 2\beta \\ 2\alpha & -(2\beta + \gamma) \end{pmatrix} \quad (2.8)$$

and $F : \mathbb{R}^2 \to \mathbb{R}^2$ by

$$F(z) = (0, f(z_1))^T$$

with $z = (z_1, z_2)^T$ and $f(s) = \mu p e^{-\alpha s}$.  

$$
Denote $u = (v, w)^T$. Then we may write (1.6) as the following integral form:

$$
\begin{align*}
\begin{cases}
u(t) = e^{Bt}u(0) + \int_0^t e^{Bs}F(u(t-s-\tau))ds, & t > 0, \\
u(t) = \phi(t), & t \in [-\tau, 0].
\end{cases}
\end{align*}
$$

(2.10)

Define

$$u^\infty = \limsup_{t \to \infty} u(t), \quad u_\infty = \liminf_{t \to \infty} u(t).$$

Clearly, $0 \leq u_\infty \leq u^\infty$. As $\tau \in [\tau_*, \tau^*)$, zero equilibrium of the auxiliary cooperative and irreducible system (2.7) is linearly unstable and there exists a unique positive equilibrium. Since $h(u)/u$ is decreasing to zero as $u \to \infty$, by direct computations we can infer that there exists $\sigma^* > 0$ such that $(\bar{\nu}, \bar{w}) \equiv \sigma(1, \frac{2\alpha+\beta}{2\alpha})$ is a super solution of (2.7) for $\sigma \geq \sigma^*$. By applying [15, page 3, Theorem 2.1], we obtain that starting from the initial value $\sigma(1, \frac{2\alpha+\beta}{2\alpha})$ with $\sigma \geq \sigma^*$ the solution $(v, w)$ of (2.7) converges to an equilibrium that has to be the positive one, since $(0, 0)$ is linearly unstable. Let $u(t; \phi)$ be the solution of (2.10). Choosing sufficiently large $\sigma$ and using the comparison principle again, we obtain that $0 \leq u(t; \phi) \leq ((v(t), w(t))$. Passing $t \to \infty$ we obtain that $u^\infty$ is non-negative and is not bigger than the positive equilibrium of (2.7). Since all eigenvalues of matrix $B$ are real and negative, it then follows that $\lim_{t \to \infty} e^{Bt}u(0) \to (0, 0)^T$. Hence, passing $t \to \infty$ in (2.10) we obtain

$$u^\infty = \limsup_{t \to \infty} \int_0^t e^{Bs}F(u(t-s-\tau))ds.$$ 

(2.11)

Since $B$ is cooperative, all entries of matrix exponential $e^{Bs}$ are positive. Hence, we may infer that

$$u^\infty = \limsup_{t \to \infty} \int_0^t e^{Bs}F(u(t-s-\tau))ds.$$ 

(2.12)

Define $g : \mathbb{R}^2_+ \to \mathbb{R}_+$ by

$$g(x, y) = \begin{cases}
\inf_{z \in [x, y]} f(z), & \text{if } x < y, \\
\sup_{z \in [y, x]} f(z), & \text{if } y < x.
\end{cases}$$

Clearly, $g(x, y)$ is non-decreasing in $x$ and non-increasing in $y$. Moreover, $g(x, x) = f(x)$. We apply the Fatou lemma to (2.11) to obtain

$$\left( \begin{array}{c} v^\infty \\ w^\infty \end{array} \right) \leq \int_0^\infty e^{Bs} \left( \begin{array}{c} 0 \\ g(w^\infty, w^\infty) \end{array} \right) ds,$$

(2.13)

which is equivalent to

$$\left( \begin{array}{c} v^\infty \\ w^\infty \end{array} \right) \leq g(w^\infty, w^\infty) \int_0^\infty \left( \begin{array}{c} (e^{Bs})_{12} \\ (e^{Bs})_{22} \end{array} \right) ds,$$

(2.14)

where $(e^{Bs})_{ij}$ is the entry of matrix $e^{Bs}$ in the $i$-th row and $j$-th column. In virtue of the Cayley-Hamilton theorem, we compute to have $e^{Bs} = a_0(s)I + a_1(s)B$, where

$$a_0(s) = \frac{\lambda_1 e^{\lambda_2 s} - \lambda_2 e^{\lambda_1 s}}{\lambda_1 - \lambda_2}, \quad a_1(s) = \frac{e^{\lambda_1 s} - e^{\lambda_2 s}}{\lambda_1 - \lambda_2}$$

with $\lambda_1$ and $\lambda_2$ being the two distinct eigenvalues of matrix $B$. As such,

$$(e^{Bs})_{22} = a_0(s) - (2\beta + \gamma)a_1(s),$$

(2.15)
and hence,
\[\int_0^\infty (e^B s)_{22} ds = -\frac{\lambda_1 + \lambda_2}{\lambda_1 - \lambda_2} - (2\beta + \gamma) - \frac{1}{\lambda_1} + \frac{1}{\lambda_2} = \frac{1}{\delta}\]  
(2.16)
Therefore, from (2.14) we obtain
\[w^\infty < \frac{1}{\delta} g(w^\infty, w^\infty).\]  
(2.17)
Similarly, we can obtain
\[w_\infty \geq \frac{1}{\delta} g(w_\infty, w^\infty).\]  
(2.18)
By the definition of \(g\), and inequalities (2.17) and (2.18),
\[w^\infty \leq \sup_{s \in [w_\infty, w^\infty]} f(s), \quad w_\infty \geq \inf_{s \in [w_\infty, w^\infty]} f(s),\]  
(2.19)
Note that there exist \(x, y \in [w_\infty, w^\infty]\) such that
\[f(x) = \sup_{s \in [w_\infty, w^\infty]} f(s), \quad f(y) = \inf_{s \in [w_\infty, w^\infty]} f(s),\]  
and hence, \(w^\infty \leq \frac{1}{\delta} f(x)\) and \(w_\infty \geq \frac{1}{\delta} f(y)\). This implies that
\[\frac{1}{\delta} f(x) \geq 1 = \frac{1}{\delta} \frac{f(w^*)}{w^*} = 1 \geq \frac{1}{\delta} \frac{f(y)}{y}.\]  
Since \(\frac{f(x)}{x}\) is decreasing in \(s > 0\), it follows that \(w^\infty \geq y \geq w^* \geq x \geq w_\infty\). Then by the same arguments as in page 279 of [23], we can infer that \(w^\infty = w_\infty = w^*\) provided that \(\frac{\partial f}{\partial s} \in (1, e^2]\), that is, \(\tau \in [\tau_*, \tau^*]\). Now that \(\lim_{t \to \infty} w(t, \phi) = w^*\), we may use the first equation of (1.6) to conclude that \(\lim_{t \to \infty} u(t, \phi) = v^*\).
(ii) The linearization of (1.6) at \((v^*, w^*)\) reads
\[
\begin{aligned}
w' &= 2\alpha v - 2\beta w - \gamma w + c(p, \tau)w(t - \tau) \\
v' &= 2\beta w - 2\alpha v - \eta v,
\end{aligned}
\]  
(2.20)
where \(c(p, \tau) = \delta (1 - \ln \frac{p^2}{\delta})\). We proceed with two cases: (1) \(\tau \in [\tau_*, \tau^*]\) and (2) \(\tau \in [\tau_*, \frac{\tau^* + \tau}{2}]\).
(1) Inequality \(\tau \geq \frac{\tau^* + \tau}{2}\) implies that \(c(p, \tau) \geq 0\), and hence, by the standard theory we know that the eigenvalue problem of (2.20) admits a principal eigenvalue \(\lambda_1\) that is a zero of
\[K(\lambda, \tau) := (\lambda + 2\beta + \gamma) - \frac{4\alpha \beta}{\lambda + 2\alpha + \eta} - c(p, \tau)e^{-\lambda \tau}.\]  
(2.21)
Further, since \(\tau \leq \tau^*\), we infer that \(\lambda_1 < 0\) by geometrically analyzing the shapes of the monotone function \(K(\lambda, \tau)\) of \(\lambda\).
(2) For \(\tau \in [\tau_*, \frac{\tau^* + \tau}{2}]\), we employ a continuation method. Indeed, note that
\[K(\lambda_1, \frac{\tau^* + \tau}{2}) = 0\]  
with \(\lambda_1 < 0\) and
\[\frac{\partial}{\partial \lambda} K(\lambda, \tau)|_{(\lambda_1, \frac{\tau^* + \tau}{2})} = 1 + \frac{4\alpha \beta}{(\lambda_1 + 2\alpha + \eta)^2} > 0.\]  
(2.22)
It then follows from the implicit function theorem that there exists \(\epsilon_0 > 0\) such that \(K(\lambda, \tau) = 0\) admits a unique negative solution \(\lambda_1 = \lambda_1(\tau)\) for \(\tau \in (\frac{\tau^* + \tau}{2} - \epsilon_0, \frac{\tau^* + \tau}{2})\). We write \(\lambda = a + ib\) and then use the implicit function theorem again
to obtain that there exists \( \epsilon_1 \in (0, \epsilon_0) \) such that the obtained negative number \( \lambda_1 \) is the unique solution of \( K(\lambda, \tau) = 0 \) in \( \mathbb{C} \) whenever \( \tau \in (\frac{\tau_*}{2} - \epsilon_1, \frac{\tau_*}{2}) \).

**Claim.** There exists \( \epsilon_2 \in (0, \epsilon_1) \) such that the negative eigenvalue \( \lambda_1 \) is the principal one.

We argue by the way of contradiction, assuming that there exists \( \tau_n \uparrow \frac{\tau_*}{2} \) and \( \mu_n \in \mathbb{C} \) such that \( K(\mu_n, \tau_n) = 0 \) with \( \Re\mu_n \geq \lambda_1(\tau_n) \) and \( \mu_n \neq \lambda_1(\tau_n) \). Substituting \( \lambda = \Re\mu_n + \Im\mu_n \) into \( K(\lambda, \tau_n) = 0 \) and separating real and imaginary parts yield

\[
\begin{align*}
0 &= \Re\mu_n + 2\beta + \gamma - \frac{4\alpha\beta(\Re\mu_n + 2\alpha + \eta)}{(\Re\mu_n + 2\alpha + \eta)^2 + (\Im\mu_n)^2} - c(p, \tau_n)e^{-\Re\mu_n\tau_n}\cos Im\mu_n \\
0 &= \Im\mu_n \left[ 1 + \frac{4\alpha\beta}{(\Re\mu_n + 2\alpha + \eta)^2 + (\Im\mu_n)^2} \right] + c(p, \tau_n)e^{-\Re\mu_n\tau_n}\sin Im\mu_n.
\end{align*}
\]

(2.23)

From the second equation of (2.23) we can infer that \( \{\Im\mu_n\}_{n \geq 1} \) are bounded, by which we can further infer from the first equation of (2.23) that \( \{\Re\mu_n\}_{n \geq 1} \) are bounded. Thus, \( \mu_n \), up to subsequence, converges to some \( \tilde{\mu} \) with \( \Re\tilde{\mu} \geq \lambda_1(\frac{\tau_*}{2}) \), and \( K(\tilde{\mu}, \frac{\tau_*}{2}) = 0 \). By the uniqueness of eigenvalues when \( \tau \in (\frac{\tau_*}{2} - \epsilon_1, \frac{\tau_*}{2}) \), we conclude that \( \mu_n = \lambda_1(\tau_n) \), leading to a contradiction. Therefore, the claim is proved.

By the continuity of eigenvalues in \( \tau \), we can infer that as \( \tau \) decreases to \( \tau_* \), there are eigenvalues with non-positive real parts emerging if and only if there are pure imaginary eigenvalues at some \( \hat{\tau} \geq \tau_* \). In the following we show such a pure imaginary eigenvalue does not exist when \( \tau \geq \tau_* \). Assume for the sake of contradiction that, \( \lambda = i\omega \) with \( \omega > 0 \) is an eigenvalue at \( \tau = \hat{\tau} \). Then we have

\[
\begin{align*}
0 &= 2\beta + \gamma - \frac{4\alpha\beta(2\alpha + \eta)}{(2\alpha + \eta)^2 + \omega^2} - c(p, \hat{\tau})\cos \omega \\
0 &= \omega \left[ 1 + \frac{4\alpha\beta}{(2\alpha + \eta)^2 + \omega^2} \right] + c(p, \hat{\tau})\sin \omega.
\end{align*}
\]

(2.24)

Define \( l(x) := \frac{4\alpha\beta}{(2\alpha + \eta)^2 + x} \), and consequently, \( x = \frac{4\alpha\beta}{l(x)} - (2\alpha + \eta)^2 \). Then we have

\[
(c(p, \hat{\tau}))^2 = [(2\beta + \gamma) - l(x)(2\alpha + \eta)]^2 + \left( \frac{4\alpha\beta}{l(x)} - (2\alpha + \eta)^2 \right)(1 + l(x))^2
\]

\[
= (2\beta + \gamma)^2 - (2\alpha + \eta)^2 + 8\alpha\beta + \frac{4\alpha\beta}{l(x)} + [4\alpha\beta - 2(2\alpha + \eta)^2 - 2(2\alpha + \eta)(2\beta + \gamma)]l(x)
\]

\[
:= H(l(x))
\]

(2.25)

Note that the coefficient of \( l(x) \) is negative. It then follows that a necessary condition for the existence of the solution for \( H(l(x)) = (c(p, \hat{\tau}))^2 \) is

\[
H \left( \frac{4\alpha\beta}{(2\alpha + \eta)^2} \right) > (c(p, \hat{\tau}))^2
\]

(2.26)

We compute to have \( H \left( \frac{4\alpha\beta}{(2\alpha + \eta)^2} \right) = \delta^2 \) and \( (c(p, \hat{\tau}))^2 < \delta^2 \) when \( \tau \geq \tau_* \). Therefore, no pure imaginary eigenvalue exists when \( \tau \geq \tau_* \), and hence, all eigenvalues have negative real parts when \( \tau \geq \tau_* \).

□

Lemmas 2.2-2.4 establish the global stability of equilibrium \((0,0)\) or \((v^*, w^*)\) when \( \tau \geq \tau_* \). On the other hand side, for delay differential equations there is a folklore that small delay is harmless for global dynamics. Clearly, when \( \tau = 0 \), the model (1.6) reduces to a cooperative and irreducible system of two ordinary differential equations. By standard theory on monotone dynamical systems we can
infer that all solutions converges to some equilibrium. Next we verify such a folklore for model (1.6). Recall that
\[ \tau_{ss} = \min \left\{ \tau_{s}, \frac{1}{p} e^{-2\beta - \gamma + 1} \right\}. \tag{2.27} \]
Note that \( \tau_s > 0 \) if and only if \( p > \delta e^2 \), so is \( \tau_{ss} \).

**Lemma 2.5.** Assume that \( p > \delta e^2 \) and \( \tau \leq \tau_{ss} \). Then \( v(t, \phi), w(t, \phi) \) converges to \( (v^*, w^*) \) as \( t \to \infty \).

**Proof.** We first construct an exponential ordering and then employ the monotone dynamical system theory in [16]. For \( \tau > 0 \), define a cooperative and irreducible matrix by
\[ D = \begin{pmatrix} -(2\alpha + \eta + \tau^{-1}) & 2\beta \\ 2\alpha & -(2\beta + \gamma + \tau^{-1}) \end{pmatrix}. \tag{2.28} \]
Define the set
\[ K_D := \{ \phi \in C([-\tau, 0], \mathbb{R}^2) : \phi(t) \geq e^{(t-s)D}\phi(s) \text{ for } -\tau \leq s \leq t \leq 0 \}. \tag{2.29} \]
Then one may check that \( K_D \) is a cone of \( C([-\tau, 0], \mathbb{R}^2) \).

By [16, Theorem 4.1], it suffices to show that for \( \phi \in C([-\tau, 0], \mathbb{R}^2) \) and \( \psi \in K_D \) with \( \psi \gg 0 \),
\[ \tau^{-1}\psi(0) + \left( p\mu e^{-q\phi_2(-\tau)}[1 - q\phi_2(-\tau)]\psi_2(-\tau) \right) \gg 0, \quad \forall \tau \leq \tau_{ss}, \tag{2.30} \]
where \( \phi_2 \) and \( \psi_2 \) are the second component of \( \phi \) and \( \psi \), respectively. Since the first component of (2.30) always holds due to \( \psi \gg 0 \). As for the second component, we first note that \( \psi(0) \geq e^{D\tau}\psi(-\tau) \), by which it remains to show that
\[ \tau^{-1}(e^{D\tau})_{22} + p\mu \min_{x \in \mathbb{R}} e^{-\tau}(1 - x) > 0, \quad \forall \tau \leq \tau_{ss}. \tag{2.31} \]
By the definition of \( D \) we can infer that \( (e^{D\tau})_{22} \geq e^{-(2\beta + \gamma + \tau^{-1})\tau} \). Meanwhile, \( \min_{x \in \mathbb{R}} e^{\tau}(1 - x) = -e^{-\tau} \). Hence, we only need to verify
\[ \tau^{-1}e^{-(2\beta + \gamma + \tau^{-1})\tau} - p\mu e^{-\tau} > 0, \quad \forall \tau \leq \tau_{ss}, \tag{2.32} \]
which is true due to \( \mu = \mu(\tau) < 1 \) and the definition of \( \tau_{ss} \) in (2.27). \( \square \)

**Proof of Theorem 2.1.** By Lemmas 2.2-2.5, we obtain all the conclusions in Theorem 2.1.

### 3. Hopf bifurcation analysis for \( \tau \in (\tau_{ss}, \tau_s) \).

For the sake of convenience, we define
\[ I := (\tau_{ss}, \tau_s). \]
Recall from Remark 1 that \( I \neq \emptyset \) is not empty if and only if \( p > p_1 \), where \( p_1 > \delta e^2 \).
So we always restrict our analysis in this section for the parameter region \( p > p_1 \) and \( \tau \in I \).

We first study the local stability of the positive equilibrium \( (v^*, w^*) \). By standard computations, we obtain the characteristic equation of (1.1) at \( (v^*, w^*) \):
\[ \Delta(\lambda, \tau) = \lambda^2 + a\lambda + b(\tau)e^{-\lambda \tau} + d(\tau)e^{-\lambda \tau} + c = 0, \tag{3.1} \]
where
\[ a = 2\alpha + \gamma + 2\beta + \eta, \quad b(\tau) = -\delta \left( 1 - \ln \frac{p_H}{\delta} \right), \quad c = 2\alpha\gamma + 2\beta\eta + \gamma\eta \]
and \[ d(\tau) = b(\tau)(2\alpha + \eta). \]

In the following, we apply the Beretta and Kuang’s results of [3] to study the distribution of eigenvalues. Rewrite (3.1) as the following standard form
\[ P(\lambda, \tau) + Q(\lambda, \tau)e^{-\lambda\tau} = 0 \]
with
\[ P(\lambda, \tau) = \lambda^2 + a\lambda + c, \quad Q(\lambda, \tau) = b(\tau)\lambda + d(\tau). \]

Denote
\[ E(\omega, \tau) := |P(i\omega, \tau)|^2 - |Q(i\omega, \tau)|^2. \]

Then \( E(\omega, \tau) = 0 \) implies
\[ \omega^4 - (b(\tau)^2 + 2c - a^2)\omega^2 + (c^2 - d(\tau)^2) = 0, \]
and its roots are given by
\[ \omega_+^2 = \frac{t_1(\tau) + \sqrt{[t_1(\tau)]^2 - 4t_2(\tau)}}{2} \quad \text{and} \quad \omega_-^2 = \frac{t_1(\tau) - \sqrt{[t_1(\tau)]^2 - 4t_2(\tau)}}{2}, \quad (3.3) \]
where
\[ t_1(\tau) = \delta^2(1 - \ln \frac{p_H}{\delta})^2 - (2\alpha + \eta)^2 - (2\beta + \gamma)^2 - 8\alpha\beta, \]
\[ t_2(\tau) = c^2 - d(\tau)^2 = c^2[1 - (1 - \ln \frac{p_H}{\delta})^2]. \]

We claim that only \( \omega_+ \) is the feasible root of \( E(\omega, \tau) = 0 \) with \( \omega > 0 \), and \( \omega_+ \) exists if and only if \( \tau \in [0, \tau_*) \). In fact, if \( t_1(\tau) > 0 \), we can get
\[ \frac{p_H}{\delta} < e^{1+\sqrt{\frac{(2\alpha+\eta)^2+(2\beta+\gamma)^2+8\alpha\beta}{\delta}}} . \]

Note that
\[ (2\alpha + \eta)^2[(2\alpha + \eta)^2 + (2\beta + \gamma)^2 + 8\alpha\beta] > (2\alpha\gamma + 2\beta\eta + \eta\gamma)^2 \]
i.e. \[ \frac{(2\alpha+\eta)^2+(2\beta+\gamma)^2+8\alpha\beta}{\delta^2} > 1. \] Therefore we obtain that \( \frac{p_H}{\delta} > e^2 \) which leads to \( t_2(\tau) < 0 \). Then \( \omega_+ \) exists; If \( t_1(\tau) < 0 \), \( \omega_- \) is not feasible, \( \omega_+ \) exists if and only if \( t_2(\tau) < 0 \) which is equivalent to \( \tau \in [0, \tau_*) \).

It is not difficult to verify that the following conditions in [3, page 1145] hold when \( \tau \in I \):

(i) \( P(0, \tau) + Q(0, \tau) \neq 0 \);
(ii) \( P(i\omega, \tau) + Q(i\omega, \tau) \neq 0, \omega \in \mathbb{R} \);
(iii) \( \lim \sup \{ |Q(\lambda, \tau)|: |\lambda| \to \infty, \Re \lambda \geq 0 \} < 1 \);
(iv) \( E(\omega, \tau) \) for each \( \tau \) has at most a finite number of zeros;
(v) Each positive root \( \omega(\tau) \) of \( E(\omega, \tau) \) is continuous and differentiable in \( \tau \) whenever it exists.

Denote
\[ S_n(\tau) = \tau - \frac{\theta(\tau) + 2n\pi}{\omega(\tau)}, \quad \tau \in I, n \in \mathbb{N}_0, \]
where \( \omega(\tau) \) satisfies \( E(\omega, \tau) = 0 \), \( \theta(\tau) \) is defined by the following equations
\[ \sin \theta(\tau) = \Im \left( \frac{P(i\omega(\tau), \tau)}{Q(i\omega(\tau), \tau)} \right), \quad \cos \theta(\tau) = -\Re \left( \frac{P(i\omega(\tau), \tau)}{Q(i\omega(\tau), \tau)} \right). \]
Then by applying [3, Theorem 4.1] we obtain the following lemma.

**Lemma 3.1.** The characteristic equation (3.1) has a pair of simple and conjugate pure imaginary roots \( \lambda = \pm i \omega(\bar{\tau}) \), at \( \bar{\tau} \in I \) if \( S_n(\bar{\tau}) = 0 \) for some \( n \in N_0 \). Moreover, this pair of pure imaginary roots crosses the imaginary axis from left to right if \( \gamma(\bar{\tau}) > 0 \) and crosses the imaginary axis from right to left if \( \gamma(\bar{\tau}) < 0 \), where

\[
\gamma(\bar{\tau}) := \text{sign} \left\{ \frac{d \text{Re} \lambda}{d \tau} |_{\lambda = i \omega(\bar{\tau})} \right\} = \text{sign} \left\{ \frac{d S_n(\tau)}{d \tau} |_{\tau = \bar{\tau}} \right\}.
\]

Note that \( S_n > S_{n+1} \) for any \( n \in N_0 \) and \( \tau \in I \); \( S_n(\tau) \) is negative or it has an even number of zeros and \( S_n(\tau) < 0 \) when \( \tau = 0 \) or \( \tau \to \tau_* \). Moreover all solutions \( \omega(\tau) \) of \( E(\omega, \tau) = 0 \) are simple. Therefore we can obtain following result of Hopf bifurcations and stability switch.

**Theorem 3.2.** Assume \( S_0(\tau) = 0, \tau \in I \) has at least two roots. Let \( \tau_1 < \tau_2 \) be the first and last roots. Then \( \gamma(\tau_1) > 0 \) and \( \gamma(\tau_2) < 0 \), and Hopf bifurcations occur for (1.1) at \((v^*, w^*)\) when \( \tau = \tau_1 \) and \( \tau = \tau_2 \). Moreover, \((v^*, w^*)\) is locally asymptotically stable when \( \tau \in [0, \tau_1) \cup (\tau_2, \tau_*) \) and its stability switches when \( \tau \) crosses \( \tau_1 \) or \( \tau_2 \).

Before the proof, we mention that in the limiting case where \( \beta = 0 \), system (1.6) reduces to a scalar equation, i.e., the classical Nicholson blowflies model, for which a set of sufficient conditions to ensure that \( S_0(\tau) = 0 \) has exactly two roots in \( I \) was obtained in [13], see also [14] for a generalized scalar delay equation with unimodal feedback. While for \( \beta > 0 \) the model system has two coupled components, we are not able to give parameter regions such that \( S_0(\tau) = 0 \) has at least two roots in \( I \).

**Proof.** Firstly, we prove that when \( \tau = 0 \), all the roots of equation (3.1) have strictly negative real part. Note that (3.1) with \( \tau = 0 \) is

\[
\lambda^2 + (a + b(0))\lambda + c + d(0) = 0,
\]

here

\[
a + b(0) = \frac{4\alpha\beta + 4\alpha^2 + 4\alpha\eta + \eta^2}{2\alpha + \eta} + \delta \ln \frac{p}{\delta} > 0, \quad c + d(0) = \ln \frac{P}{\delta} > 0.
\]

It follows that the two roots of (3.1) with \( \tau = 0 \) have negative real parts. Note that for (3.1) there is no any eigenvalue with zero real part when \( \tau \in [0, \tau_1) \) and \( \gamma(\tau_1) > 0 \). Using [12, Corollary 2.4] we know all the eigenvalues of (3.1) have negative real parts when \( \tau \in [0, \tau_1) \). Similarly, we can prove that all the eigenvalues of (3.1) have negative real parts when \( \tau \in [\tau_2, \tau_*) \). The proof is completed.

**Remark 2.** When \( \tau \) varies in \((\tau_1, \tau_2)\) the local stability of \((v^*, w^*)\) may also switch at possible zeros of \( S_n(\tau), n \in N_0 \) when they exist.

Theorem 3.2 showed that at the first and last zeros \( \tau_1 \) and \( \tau_2 \) of \( S_0(\tau) \), then system (1.1) undergoes the Hopf bifurcations at \((v^*, w^*)\). In the following, we investigate the direction of these Hopf bifurcations and the stability of the periodic solutions bifurcated at \( \tau = \tau_1 \) and \( \tau = \tau_2 \), by appealing to the normal form theory in Hassard et al [9].

Normalizing the time delay and transforming the equilibrium \((v^*, w^*)\) to the origin, (1.1) is transformed to

\[
\begin{pmatrix}
v'(t) \\
w'(t)
\end{pmatrix} = \tau B \begin{pmatrix} v(t) \\ w(t) \end{pmatrix} + \tau C \begin{pmatrix} v(t-1) \\ w(t-1) \end{pmatrix} + \tau G(v(t), w(t)) \quad (3.4)
\]
where $B$ is defined by (2.8),

$$
C = \begin{pmatrix}
0 & 0 \\
0 & \delta (1 - \ln \frac{p_{\mu}}{\delta})
\end{pmatrix}
$$

and

$$
G(v(t), w(t)) = \begin{pmatrix}
0 \\
q_0^2 \delta^2 [w(t - 1)]^2 (\ln \frac{p_{\mu}}{\delta} - 2) + q_0^2 \delta^2 [w(t - 1)]^3 (3 - \ln \frac{p_{\mu}}{\delta}) + O(\delta^4)
\end{pmatrix}.
$$

Let $\tau = \tau^* + \sigma$, $\tau^* = \tau_1$ or $\tau_2$, $\sigma \in \mathbb{R}$, then $\sigma = 0$ is a Hopf bifurcation point for (1.1).

For $\phi = (\phi_1, \phi_2)^T \in C([-1, 0], \mathbb{R}^2)$, define

$$L_\sigma(\phi) = (\tau^* + \sigma)B\phi(0) + C\phi(-1),$$

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

$$L_\sigma(\phi) = \int_{-1}^{0} [d\eta(\theta, \sigma)]\phi(\theta), \text{ for } \phi \in C([-1, 0], \mathbb{R}^2).$$

In fact, we can choose

$$\eta(\theta, \sigma) = \begin{cases}
(\tau^* + \sigma)B, & \theta = 0 \\
0, & \theta \in (-1, 0) \\
-(\tau^* + \sigma)C, & \theta = -1
\end{cases}.$$

Moreover define

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

and

$$R(\sigma)\phi(\theta) = \begin{cases}
0, & \theta \in [-1, 0) \\
(\tau^* + \sigma)G(\sigma, \phi(0)), & \theta = 0
\end{cases}.$$
\( q(\theta) := (q_1, q_2)^T e^{i\omega^* \tau^* \theta} \) is the eigenvector of \( A(0) \) with respect to eigenvalue \( i\omega^* \tau^* \),
\( q^*(s) := \frac{(q_1 q_2)}{D} \) is the eigenvector of \( A^*(0) \) with respect to eigenvalue \(-i\omega^* \tau^* \),
then
\[
\langle q^*, q \rangle = 1, \quad \langle q^*, \overline{q} \rangle = 0.
\]
By the direct calculation, we
\[
(q_1, q_2)^T = \left( \frac{2\beta}{2\alpha + \eta + i\omega^*}, 1 \right)^T, \quad (q_1^*, q_2^*) = \left( \frac{2\beta}{2\alpha + \eta - i\omega^*}, 1 \right)
\]
and
\[
D = (\overline{q_1}^* q_1 + \overline{q_2}^* q_2) - \int_{t-1}^{t} \int_{0}^{\theta} \overline{q}_1^*(\xi - \theta) \eta(q)(\xi) d\xi
d\xi
= \overline{q}_1^*(q_1 + \tau^* e^{-i\omega^* \tau^*} \sum_{j=1}^{2} c_{1j} q_j) + \overline{q}_2^*(q_2 + \tau^* e^{-i\omega^* \tau^*} \sum_{j=1}^{2} c_{2j} q_j)
= 1 + \tau^* \delta(1 - \ln \frac{p \mu}{\delta}) e^{-i\omega^* \tau^*}
\]
where \( c_{ij} (i=1, 2) \) represents the element of row \( i \) and column \( j \) in matrix \( A \).
Using the same notations as in Hassard et al [9], we now compute the center manifold [8]. Let \( x_t \) be the solution of (3.5) when \( \sigma = 0 \). Define
\[
z(t) = \langle q^*, x_t \rangle, \quad W(t, \theta) = x_t - 2\text{Re}\{z(t)q(\theta)\}. \tag{3.7}
\]
On the center manifold \( C_0 \), we have
\[
W(t, \theta) = W(z(t), \overline{z}(t), \theta).
\]
\( W(z(t), \overline{z}(t), \theta) \) can be expanded to the power series form of \( z \) and \( \overline{z} \):
\[
W(z(t), \overline{z}(t), \theta) = W_{20}(\theta) \frac{z^2}{2} + W_{11}(\theta) z \overline{z} + W_{02}(\theta) \frac{\overline{z}^2}{2} + W_{30}(\theta) \frac{z^3}{6} + \cdots,
\]
and we denote \( W_{2j}(\theta) = (W_{i,j}^{(1)}(\theta), W_{i,j}^{(2)}(\theta)) \). Abstraction of ordinary differential equations for equation systems \( x_t \in C_0 \), since
\[
\langle q^*, W \rangle = \langle q^*, x_t - zq - \overline{z}q \rangle = \langle q^*, x_t \rangle - z\langle q^*, q \rangle - \overline{z}\langle q^*, \overline{q} \rangle = z - z = 0.
\]
So,
\[
z'(t) = i\omega^* \tau^* z + \overline{q}_1^*(0) f_0(z, \overline{z}) = i\omega^* \tau^* z(t) + g(z, \overline{z}),
\]
where
\[
f_0(z, \overline{z}) = f_{zz} \frac{z^2}{2} + f_{z\overline{z}} \frac{\overline{z}^2}{2} + f_{zz\overline{z}} + f_{zzz} \frac{z^2 \overline{z}}{2}
\]
and
\[
g(z, \overline{z}) = \overline{q}_1^*(0) f_0(z, \overline{z}) = g_{20} \frac{z^2}{2} + g_{02} \frac{\overline{z}^2}{2} + g_{11} z \overline{z} + g_{21} \frac{z^2 \overline{z}}{2}.
\]
Comparing the coefficients of the above two formulas, we have
\[
g_{20} = \overline{q}_1^*(0) f_{zz}, \quad g_{11} = \overline{q}_1^*(0) f_{z\overline{z}}, \quad g_{02} = \overline{q}_1^*(0) f_{\overline{z}^2}, \quad g_{21} = \overline{q}_1^*(0) f_{zz\overline{z}}.
\]
Calculated below \( g_{20}, g_{11}, g_{02}, g_{21} \), use
\[
f_0 = \begin{pmatrix} f_1^1 \\ f_2^1 \\ f_1^2 \\ f_2^2 \end{pmatrix} = \begin{pmatrix} \phi_1(-1)^2 [\ln \frac{\mu}{\delta} - 2] + \phi_1^2 [\phi_1(-1)] e^{(3 - \ln \frac{\mu}{\delta})} \end{pmatrix}.
We obtain that
\[ g_0 = \frac{2\tau^*}{D}(q_1^*, q_2^*) \left( \begin{array}{c} 0 \\ \frac{m_2 q_2 e^{-2\omega^* \tau^*}}{2m_2 q_2} \end{array} \right) = \frac{2\tau^* m}{D} e^{-2\omega^* \tau^*}, \]
\[ g_1 = \frac{\tau^*}{D}(q_1^*, q_2^*) \left( \begin{array}{c} 0 \\ \frac{m_2 q_2}{2m_2 q_2} \end{array} \right) = \frac{2\tau^* m}{D}, \]
\[ g_2 = \frac{\tau^*}{D}(q_1^*, q_2^*) \left( \begin{array}{c} 0 \\ \frac{m_2 q_2 e^{-2\omega^* \tau^*}}{2m_2 q_2} \end{array} \right) = \frac{2\tau^* m}{D} e^{-2\omega^* \tau^*}, \]
\[ g_1 = \frac{\tau^*}{D}(q_1^*, q_2^*) e^{-2\omega^* \tau^*} \left( \begin{array}{c} 0 \\ \frac{2m_2 q_2 W_1^{(2)}(\theta) + m_2 q_2 W_1^{(1)}(\theta)}{2m_2 q_2} \end{array} \right), \]
where
\[ m = \frac{q_0}{2}(\ln 2 - 2), n = \frac{q_0^2}{6}(3 - \ln 2). \]

By (3.5) and (3.7) we have
\[ W' = x' + z' q - \bar{z} \bar{q} = \begin{cases} AW - g q(\bar{\theta}) - \bar{g} q(\bar{\theta}), & \theta \in [-1, 0) \\ AW - g q(\bar{\theta}) - \bar{g} q(\bar{\theta}) + f_0, & \theta = 0 \end{cases} \]
(3.10)

On the central manifold,
\[ W' = W_{zz'} + W_{\bar{z} \bar{z}} \]
\[ = [W_{11}(\theta) + W_{11}(\theta) + W_{11}(\theta) + W_{20}(\theta)] + \bar{g}(z, \bar{z}) + W_{11}(\theta) + W_{20}(\theta) \bar{z}[\bar{\omega} + \bar{\omega}(t) + g(z, \bar{z})] + [W_{11}(\theta) + W_{20}(\theta)] \]
Comparing the coefficients of the terms \( z^2/2 \) and \( z \bar{z} \) we have
\[ (2i\omega + I - A)W_{20}(\theta) = \begin{cases} -g_{20} q(\bar{\theta}) - \bar{g}_{20} q(\bar{\theta}), & \theta \in [-1, 0), \\ -g_{20} q(\bar{\theta}) - \bar{g}_{20} q(\bar{\theta}) + f_{zz}, & \theta = 0 \end{cases} \]
and
\[ -AW_{11}(\theta) = \begin{cases} -g_{11} q(\bar{\theta}) - \bar{g}_{11} q(\bar{\theta}), & \theta \in [-1, 0), \\ -g_{11} q(\bar{\theta}) - \bar{g}_{11} q(\bar{\theta}) + f_{zz}, & \theta = 0. \end{cases} \]
When \( \theta \in [-1, 0), \)
\[ W_{20}(\theta) = 2i\omega + \tau^* W_{20}(\theta) + g_{20} q(\bar{\theta}) + \bar{g}_{20} q(\bar{\theta}). \]
We have
\[ W_{20}(\theta) = \frac{ig_{20}}{\omega + \tau^*} q(0) e^{i\omega^* \tau^*} + \frac{i\bar{g}_{20}}{3\omega + \tau^*} \bar{q}(0) e^{-i\omega^* \tau^*} + E_1 e^{2i\omega^* \tau^*}. \]
When \( \theta = 0, \)
\[ \int_{-1}^{0} d\eta(\sigma_0, \theta) W_{20}(\theta) = 2i\omega + \tau^* W_{20}(\theta) + g_{20} q(\bar{\theta}) + \bar{g}_{20} q(\bar{\theta}) - f_{zz} \]
and
\[ E_1 = [2i\omega + I - \int_{-1}^{0} e^{2i\omega + \theta} d\eta(\sigma_0, \theta)]^{-1} f_{zz}. \]
When \( \theta \in [-1, 0), \)
\[ W_{11}(\theta) = -\frac{ig_{11}}{\omega + \tau^*} q(0) e^{i\omega^* \tau^*} + \frac{i\bar{g}_{11}}{\omega + \tau^*} \bar{q}(0) e^{-i\omega^* \tau^*} + E_2. \]
When \( \theta = 0 \),
\[
\int_{-1}^{0} d\theta \eta(\sigma_0, \theta) W_{11}(\theta) = g_{11} q(0) + \overline{g_{11}} \bar{q}(0) - f z \tau
\]
and
\[
E_2 = -\left[ \int_{-1}^{0} d\theta \eta(\sigma_0, \theta) \right]^{-1} f z \tau.
\]
Note that
\[
\int_{-1}^{0} e^{2i\omega_+ \tau^*} d\theta \eta(\sigma_0, \theta) = \int_{-1}^{0} \tau^* B + \tau^* C e^{-2i\omega_+ \tau^*} d\theta
\]
\[
= \begin{pmatrix} -(2\alpha + \eta) & 2\beta \\ 2\alpha & -(2\beta + \gamma) \end{pmatrix} + e^{-2i\omega_+ \tau^*} \begin{pmatrix} 0 & 0 \\ 0 & \delta(1 - \ln \frac{p\mu}{\delta}) \end{pmatrix}.
\]
Let
\[
N = \begin{pmatrix} -(2\alpha + \eta) & 2\beta \\ 2\alpha & -(2\beta + \gamma) + \delta(1 - \ln \frac{p\mu}{\delta}) e^{-2i\omega_+ \tau^*} \end{pmatrix},
\]
\[
M = \begin{pmatrix} 2i\omega_+ \tau^* + (2\alpha + \eta) & -2\beta \\ -2\alpha & 2i\omega_+ \tau^* + (2\beta + \gamma) - \delta(1 - \ln \frac{p\mu}{\delta}) e^{-2i\omega_+ \tau^*} \end{pmatrix}.
\]
Then we obtain
\[
\begin{cases}
E_1 = 2M^{-1} f z = 2\tau^* M^{-1} \left( \frac{0}{mq_2 e^{-2i\omega_+ \tau^*}} \right) \\
E_2 = -N^{-1} f z = -\tau^* N^{-1} \left( \frac{0}{2mq_2 \overline{q_2}} \right)
\end{cases} \tag{3.11}
\]
Based on the above calculations, we can compute \( g_{20}, g_{11}, g_{02}, g_{21} \) explicitly by the parameters. Substituting those expressions into the following relation
\[
C_1(0) = \frac{i}{2\omega^* \tau^*} \left( g_{11} g_{20} - 2g_{11} |g_{02}|^2 - \frac{|g_{02}|^2}{3} \right) + g_{21} \frac{2}{3},
\]
we have
\[
C_1(0) = \frac{-2\tau^* m^2 i}{D^2 \omega_+} e^{-2i\omega_+ \tau^*} + \frac{14\tau^* m^2 i}{3D^2 \omega_+} + \frac{2m \tau^* E_1^{(2)}}{D} e^{-i\omega_+ \tau^*}
\]
\[
+ \frac{4m \tau^* E_2^{(2)}}{D} e^{-2i\omega_+ \tau^*} + \frac{6m \tau^*}{D} e^{-i\omega_+ \tau^*}, \tag{3.12}
\]
where \( m, n \) and \( D \) are just defined by (3.9) and (3.6), \( E_1^{(2)} \) and \( E_2^{(2)} \) are the elements of second row in \( E_1 \) and \( E_2 \) defined by (3.11).

Then by Theorem 3.2 and the general results for the direction and stability of in [9], we have the following results.

**Theorem 3.3.** Assume that \( \tau_1 < \tau_2 \) are the first and last roots of \( S_0(\tau) = 0, \tau \in I \). Let \( C_1(0) \) be given in (3.12). Then we have

(i) The Hopf bifurcation occurs when \( \tau \) crosses from \( \tau_1 \) to its right if \( \text{Re} C_1(0) < 0 \) with \( \tau^* = \tau_1 \), and to its left if \( \text{Re} C_1(0) < 0 \) with \( \tau^* = \tau_1 \); The Hopf bifurcation occurs when \( \tau \) crosses \( \tau_2 \) to its left if \( \text{Re} C_1(0) < 0 \) with \( \tau^* = \tau_2 \), and to its right if \( \text{Re} C_1(0) > 0 \) with \( \tau^* = \tau_2 \);

(ii) The periodic solutions bifurcated from \( \tau = \tau_1 \) is stable if \( \text{Re}(C_1(0)) < 0 \) with \( \tau^* = \tau_1 \) and unstable if \( \text{Re}(C_1(0)) > 0 \) with \( \tau^* = \tau_1 \); The periodic solutions bifurcated from \( \tau = \tau_2 \) is stable if \( \text{Re}(C_1(0)) < 0 \) with \( \tau^* = \tau_2 \) and unstable if \( \text{Re}(C_1(0)) > 0 \) with \( \tau^* = \tau_2 \).
4. **Numerical simulations and discussions.** For the reduced model (1.6), we have studied the influence of time delay on the local and global dynamics. Three critical values of time delay $\tau^*(p) \geq \tau_*(p) \geq \tau_{**}(p)$, depending on $p$, and some implicit curves in $(\tau, p)$ plane are found. As delay decreases from a large value (greater than $\tau^*$) to zero, then one may observe the change of the global dynamics.

We use Figure 1 to summarize what we have obtained in this paper.

![Figure 1. Parameter regions for different dynamics in $(\tau, p)$ plane.](image)

For $\tau \geq \tau^*(p)$, there is no positive equilibrium. By a comparison argument we show that zero is globally stable. For $\tau \in \left[ \frac{\tau^*(p) + \tau_*(p)}{2}, \tau^* \right)$, the model system has the comparison principle. By the monotone dynamical system theory we prove that the positive equilibrium is globally stable. For $\tau \in \left[ \tau_*, \frac{\tau^*(p) + \tau_*(p)}{2} \right)$, the comparison principle is lost but a fluctuation method can be used to prove the global stability of the positive equilibrium. For $\tau \in [0, \tau_{**}]$, we use the idea of experiential ordering to cast the problem into the abstract framework of monotone dynamical systems and then prove the globally stability of the positive equilibrium. The curve $S_n(\tau) = 0, n \in \mathbb{N}$ are the Hopf bifurcation points of $\tau$. For fixed $p$, there are only finitely many points. The direction of Hopf bifurcation and the stability of bifurcated periodic solutions at $S_0(\tau) = 0$ are analyzed by the normal form theory in the center manifold, yielding some useful formulas for determining these properties, including $\text{Re}(C_1(0))$.

To illustrate the bifurcation results, we use the following example:

$\alpha = 0.12, \quad \beta = 0.1, \quad \gamma = 0.016, \quad \eta = 0.062, \quad \gamma^f = 0.03, \quad p = 7, \quad q = 0.05.$

Then $S_0(\tau)$ can be draw in Figure 2. With the above values for these parameters, numerically we solve $S_0(\tau) = 0$ to obtain only two solutions $\tau_1 < \tau_2$ with

$\tau_1 = 16.1941, \quad \tau_2 = 83.7885.$

Consequently, we compute to have

$\tau^* = 152.1, \quad \tau_* = 85.44, \quad \tau_{**} = 0.30.$

It then confirms that $\tau_{**} < \tau_1 < \tau_2 < \tau_*$. Further computations yields that

$\text{Re}(C_1(0)) = -0.1561 < 0 \quad \text{at} \quad \tau = \tau_1$

and

$\text{Re}(C_1(0)) = 0.0148 > 0 \quad \text{at} \quad \tau = \tau_2.$
By Theorem 3.3 we obtain the following dynamics: (i) as delay increases from 0 to $\tau_1$, the stable positive equilibrium alter its stability at $\tau = \tau_1$ and a bifurcated periodic solution occurs as $\tau$ is close to $\tau_1$ from right; (ii) as delay continues to increase to $\tau_2$, the positive equilibrium alters the stability at $\tau = \tau_2$, becoming stable. The following numerics in Figure 4 confirms the theoretical results.

Figure 3. (a) $\tau = 15 \leq \tau_1$ and the solution converges to the positive equilibrium; (b) $\tau = 20 > \tau_1$ but close to $\tau_1$, and the solution converges to a periodic solution; (c) $\tau = 80 < \tau_2$ but close to $\tau_2$, and the solution still converges to periodic solution which has a larger period than in (b); (d) $\tau = 90 \in (\tau_2, \tau^*)$, the solution converges to the positive equilibrium.
Remark 3.  
(i) In the above simulations, when increasing $\tau$ from $\tau_1$ to $\tau_2$, we see that there is a periodic solution. But it is not known whether such a periodic solution is the continuation of the periodic solution bifurcated from the positive equilibrium at $\tau = \tau_1$.

(ii) We did not find parameter values such that $\text{Re}(C_1(0))$ is positive at $\tau_1$ or negative at $\tau_2$. It then remains an interesting question to prove or disprove that $\text{Re}(C_1(0))$ does not change sign for all meaningful parameters at $\tau_i, i = 1, 2$.

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