BIFURCATION ANALYSIS OF A DDE MODEL OF THE CORAL REEF

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ABSTRACT. In this paper, first we discuss a local stability analysis of model was
introduced by P. J. Mumby et. al. (2007), with $\frac{gM^2}{M+T}$ as the functional response
term. We conclude that the grazing intensity is the important parameter to
control the existence or extinction of the coral reef. Next, we consider this
model under the influence of the time delay as the bifurcation parameter. We
show that for small time delay, the stability type of the equilibria will not
change, however for large enough time delay, the interior equilibrium point
become unstable in contrast to the ODE case. Also for some critical grazing
intensity and the time delay, a Hopf bifurcation occur and a nontrivial periodic
orbit will appear. Further we discuss its corresponding stability switching
directions.

AMS Classification: 37N25, 37L10, 37L15, 35B10 .

Keywords: Ordinary differential equation, Delay differential equation, Stability,
Hopf bifurcation, periodic solution.

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1. Introduction

Coral reefs are extremely important as habitats for a range of marine species, natural buffers to severe wave actions and sites for recreation and cultural practices. Additionally, they contribute to the national economy of countries with coral reef ecosystems. However, the last several decades have demonstrated a decline in resilience that has often resulted in phase shifts to a degraded coral-depleted state with high levels of algal abundance. The deteriorating health of the world's coral reefs threatens global biodiversity, ecosystem function, and the livelihoods of millions of people living in tropical coastal regions [5]. Reefs in the Caribbean are among the most heavily affected [1, 4, 6, 7]. Declining reef health is characterized by increases in macroalgae. P. J. Mumby et. al. ([8]) introduced a system of ordinary differential equations to model the dynamics of the coral reef. Wang et. al. used and analysed this system in [9]. Authors of [2] suggested an alternative formulation to include the grazing term $\frac{gM^2}{M+T}$.

The paper is mainly concerned with a model of coral reef dynamics which is given by the following nonlinear system of ordinary differential equations:

(1)
$$\begin{cases} \frac{dM}{dt} = aMC - \frac{gM^2}{M+T} + \gamma MT, \\\\ \frac{dC}{dt} = rTC - dC - aMC, \\\\ \frac{dT}{dt} = \frac{gM^2}{M+T} - \gamma MT - rTC + dC. \end{cases}$$

Here C, T, and M represent the cover of corals, algal turfs and macroalgae respectively. Grazers are assumed not to discriminate between algal types. Algal turfs arise when macroalgae are grazed ($\frac{gM^2}{M+T}$) and as a result of natural coral mortality ($-dC$). Corals recruit to and overgrow algal turfs at a combined rate r, constrained by the existing cover of turfs. Corals can be overgrown by macroalgae ($-aMC$) but macroalgae usually colonize dead coral by spreading vegetatively over algal turfs (γMT). It was assumed that a particular region of the seabed is covered entirely by macroalgae (M), coral (C), and algal turfs (T) so that $M + C + T = 1$ at any given time. Then the fraction of algal turfs is defined by $T = 1 - M - C$ and consequently $\frac{dT}{dt} = -\frac{dM}{dt} - \frac{dC}{dt}$. This system is defined on the invariant region given by $0 < M + T < 1$ and $C, M, T \geq 0$. Therefore, in this case, only the first two equations of system (1) are needed. Let $x(t)$ and $y(t)$ denote the macroalgae (M)

and corals (C) at any time t, respectively. Then, from the aforementioned, we can rewrite the system (1) as

$$
(2) \quad
\begin{cases}
\frac{dx}{dt} = x[\gamma - \gamma x + (a - \gamma)y - \frac{gx}{1-y}] := xF(x,y), \\
\\
\frac{dy}{dt} = y[r - d - (r + a)x - ry] := yG(x,y).
\end{cases}
$$

The brief description of the parameter selection and parameter values can be found in [8], in which the authors listed the parameter values as follows:

$a = 0.1, \quad d = 0.44, \quad \gamma = 0.8, \quad r = 1, \quad 0 \leq g.$

For more detail the reader is referred to [8]. Here, it is sufficient to consider the following assumptions

$$
(3) \qquad\qquad\qquad 0 < a < d < \gamma < r, \quad 0 \leq g.
$$

Considering the biological background, we only care about the dynamics of system (2) in the closed first quadrant $\mathbb{R}^2_+$.

In this paper, first, we study the global stability of the ODE model (2) about the steady states. Then, we construct the DDE model and take the grazing intensity and the time delay as the parameters of interest and study the local stability of equilibria.

2. Stability analysis

In this section, first we give a qualitative analysis of system (2). From the standpoint of biology, we are only interested in the dynamics of model (2) in the closed first quadrant $\mathbb{R}^2_+$. Thus, we consider the biologically meaningful initial condition $x(0) = x_0 > 0$ and $y(0) = y_0 > 0$. We define

$$
\Omega = \{(x,y) \in \mathbb{R}^2_+ : 0 \leq x + y \leq 1\}.
$$

The vector field defined by system (2) is locally Lipschitz continuous in Ω, which guarantees the existence and uniqueness of solutions of system (2). To show that all orbits starting from Ω will remain in Ω, we state the following lemma.

Lemma 1. *The set $\Omega \subseteq \mathbb{R}^2_+$ is positively invariant for the system (2), and this system has no periodic solutions in Ω.*

Proof. On the boundary $\partial\Omega$, if $x = 0$, then $\frac{dx}{dt} = 0$, so the positive y-axis is invariant; likewise if $y = 0$, then $\frac{dy}{dt} = 0$, so the positive x-axis is invariant . In the following, we want to show that orbits starting from Ω cannot escape Ω from the upper boundary $\{(x, y) \in \mathbb{R}_+^2 : x + y = 1\}$ (system is not defined at $x = 0, y = 1$). Let $\xi := x + y$. Then on the upper boundary, we have

$$\frac{d\xi}{dt} = \frac{dx}{dt} + \frac{dy}{dt} = -dy - gx < 0.$$

Hence, all orbits starting from Ω will stay in Ω for all time and Ω is positively invariant. The vector field defined by system (2) is C^1, so the classical Dulacs criterion can be applied. Choose $B(x, y) = \frac{1}{xy}$. It is easy to verify

$$div(B(xF, yG)) = \frac{\partial}{\partial x}\left(\frac{1}{y}F\right) + \frac{\partial}{\partial y}\left(\frac{1}{x}G\right) = \frac{1}{y}F_x + \frac{1}{x}G_y = \frac{1}{y}\left(-\gamma - \frac{g}{1-y}\right) + \frac{1}{x}(-r) < 0.$$

Therefore, by the Dulacs criterion, the dynamical system (2) has no closed orbits wholly contained in Ω. Also there is no periodic orbit that partly contained in Ω. Assume otherwise and let Γ be a periodic orbit intersecting Ω. Any periodic orbit intersecting the line $x + y = 1$, will intersect at least at two points where the direction of the vector field about these two points are opposite to each other. But the direction of the vector field on the line $x + y = 1$ is inward. Also these periodic orbit can not intersect x-axis or y-axis, since these two lines are invariant. Therefore any periodic orbit that intersect Ω can not intersect its boundary. The proof of the lemma is completed. $\qquad\square$

In the following, we analyze the stability of the equilibria.
Equating the derivatives on the left hand sides to zero and solving the resulting algebraic equations we can find the nullclines of system (2) and possible equilibrium. The x-nullcline of system(2) is $x = 0$ and $F(x, y) = 0$, which $F(x, y) = 0$ implies

$$y =: f(x) = \frac{1}{2(\gamma - a)}[(2\gamma - a - \gamma x) - \sqrt{(\gamma x - a)^2 + 4gx(\gamma - a)}].$$

If $g > 0$, then the curve $y = f(x)$ is a monotone decreasing function and contained in the first quadrant, starts from the point $A = (0, 1)$, ends at the point $B = (\frac{\gamma}{g+\gamma}, 0)$. Therefore, the x-nullcline is the positive y-axis and a monotone decreasing smooth curve connecting the starting point A and the ending point B.
The y-nullcline of system (2) is $y = 0$ and $G(x, y) = 0$, which $G(x, y) = 0$ implies

$$y =: g(x) = -(1 + \frac{a}{r})x + (1 - \frac{d}{r}).$$

The curve $y = g(x)$ contained in the first quadrant, starts from the point $C = (0, 1 - \frac{d}{r})$, ends at the point $D = (\frac{r-d}{r+a}, 0)$. Under the assumption (3), $0 < y_C < 1$ and $0 < x_D < 1$, and $g(x)$ is monotone decreasing function. Hence, the y-nullcline is the positive x-axis and a monotone decreasing smooth curve connecting the starting point C and the ending point D.

From the above discussions, we recognize that the possible steady states of system (2) are

$O = (0, 0)$, the extinction equilibrium which always exists;

$C = (0, \frac{r-d}{r})$, the coral only state;

$B = (\frac{\gamma}{g+\gamma}, 0)$, the macroalgae only state; and

$E^* = (x^*, y^*)$, the interior equilibrium (the coexistence state).

Firstly, x^* and y^* are the positive solutions of

$$F(x, y) = \gamma - \gamma x + (a - \gamma)y - \frac{gx}{1 - y} = 0,$$

(4) $$G(x, y) = r - d - (r + a)x - ry = 0.$$

Eliminating x, we get

$$(\gamma a - ar - a^2)y^2 + (ar + a^2 - 2\gamma a - \gamma d + gr)y + \gamma a + \gamma d - g(r - d) = 0,$$

which is an equation for the variable y. Let

$$H(y) := (\gamma a - ar - a^2)y^2 + (ar + a^2 - 2\gamma a - \gamma d + gr)y + \gamma(a + d) - g(r - d).$$

Then

$$H(0) = (r - d)(\frac{\gamma(a + d)}{r - d} - g) = (r - d)(g_0 - g),$$

$$H(1) = gd,$$

where $g_0 := \frac{\gamma(a+d)}{r-d}$. From the assumption (3), we know that $H(1)$ is always positive. If $0 < g < g_0$, then $H(0) > 0$, $H(1) > 0$. Thus the above algebraic equations have no solutions whose y-coordinate belongs to the interval $[0, 1]$, which implies that the original system has no internal equilibrium in this case. However, if $g_0 < g$, $H(0) < 0$, $H(1) > 0$, then the above algebraic equations have a unique solution
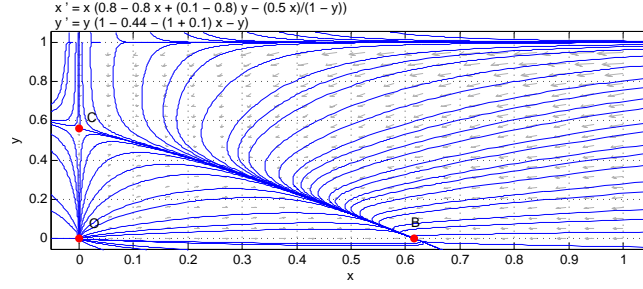
FIGURE 1. *The figure shows equilibrium covers of macroalgae(x) and corals(y) and trajectories over time. The grazing intensity $g = 0.5 < g_0$. In this case, there is no internal equilibrium in Ω, macroalgal bloom is the only stable node, and coral is an unstable saddle.*

(x^*, y^*), where $y^* \in (0, 1)$, and

$$
\begin{cases}
x^* := \frac{r-d-ry^*}{r+a}, \\
\\
y^* := \frac{(ar+a^2-2a\gamma-\gamma d+gr)-\sqrt{(ar+a^2-2a\gamma-\gamma d+gr)^2-4(\gamma a-ar-a^2)(\gamma(a+d)-g(r-d))}}{2(ar+a^2-\gamma a)}.
\end{cases}
$$

Hence $E^* = (x^*, y^*)$ is a unique internal equilibrium for the system (2).

Let us now consider the stability analysis of the deterministic differential Eq. (2). For this we linearize system (2) about its equilibria. We find that the Jacobian matrix of (2) is

$$
J_{(x,y)} = \begin{pmatrix} F(x,y) + xF_x(x,y) & xF_y(x,y) \\ yG_x(x,y) & G(x,y) + yG_y(x,y) \end{pmatrix},
$$

where F and G are given in (4) and F_x, F_y, G_x and G_y are their partial derivatives with respect to x and y.

At the equilibrium point $O = (0, 0)$, the Jacobian matrix is

$$
J_{(0,0)} = \begin{pmatrix} \gamma & 0 \\ 0 & r-d \end{pmatrix}.
$$

The eigenvalues are $\lambda_1 = \gamma$ and $\lambda_2 = (r - d)$, which are positive under assumption (3). Then the boundary equilibrium point O is an unstable node.

The Jacobian matrix at $C = (0, \frac{r-d}{r})$ is

$$
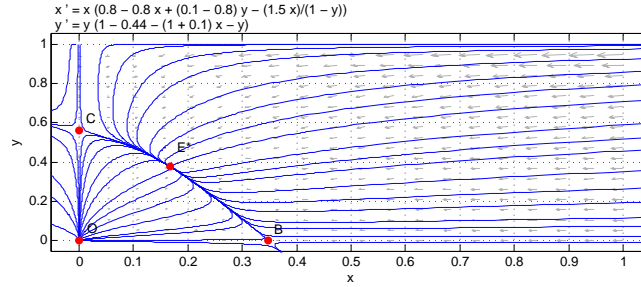J_C = \begin{pmatrix} \gamma + \frac{(a-\gamma)(r-d)}{r} & 0 \\ -(r+a)(\frac{r-d}{r}) & -(r-d) \end{pmatrix}.
$$

FIGURE 2. *The figure shows equilibrium covers of macroalgae(x) and corals(y) and trajectories over time. The grazing intensity $g = 1.5 > g_0$. In this case, there is stable internal equilibrium in Ω. Macroalgal bloom and coral bloom are both unstable saddle.*

The eigenvalues are $\lambda_1 = \gamma + \frac{(a-\gamma)(r-d)}{r}$ and $\lambda_2 = -(r-d)$, which are positive and negative respectively (under assumption (3)). Thus this equilibrium point is an unstable saddle.

At the boundary equilibrium point $B = (\frac{\gamma}{g+\gamma}, 0)$ the Jacobian matrix has the form

$$J_B = \begin{pmatrix} -\gamma & \frac{\gamma}{\gamma+g}(a - \gamma - \frac{g\gamma}{\gamma+g}) \\ 0 & r - d - \frac{\gamma(r+a)}{\gamma+g} \end{pmatrix}.$$

The eigenvalues are $\lambda_1 = -\gamma$ and $\lambda_2 = r - d - \frac{\gamma(r+a)}{\gamma+g} = \frac{(r-d)}{(g+\gamma)}(g - g_0)$. We know that under assumption (3), $\lambda_1 < 0$. Let $g_0 := \frac{\gamma(r+a)}{r-d} - \gamma = \frac{\gamma(a+d)}{r-d}$. Note that under assumption (3), $0 < g_0$. If $0 < g < g_0$, $\lambda_2 < 0$ and $B = (\frac{\gamma}{g+\gamma}, 0)$ is a stable node (Figure (1)). However, if $g_0 < g$, then $\lambda_2 > 0$, and B is an unstable saddle (Figure (2)). It can be easily seen when $g = g_0$ ($\lambda_2 = 0$) a transcritical bifurcation occurs (Figure (3)).

Next we study the stability of interior equilibrium point $E^* = (x^*, y^*)$. First of all, notice that for $g_0 < g$ this interior equilibrium point exist. Now we analyze the stability of E^*. At this point, the Jacobian matrix takes the form

$$J_{E^*} = \begin{pmatrix} F + x^* F_x & x^* F_y \\ y^* G_x & G + y^* G_y \end{pmatrix} = \begin{pmatrix} x^* F_x & x^* F_y \\ y^* G_x & y^* G_y \end{pmatrix}$$
$$= \begin{pmatrix} x^*(-\gamma - \frac{g}{1-y^*}) & x^*((a-\gamma) - \frac{gx^*}{(1-y^*)^2}) \\ -(r+a)y^* & -ry^* \end{pmatrix}.$$
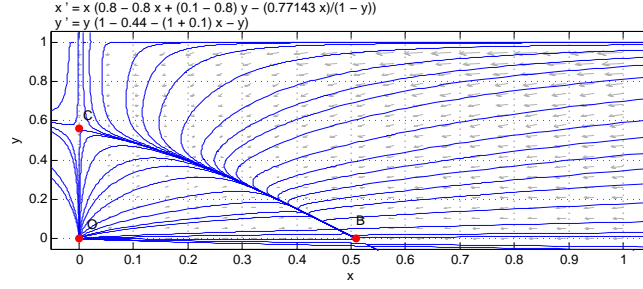
FIGURE 3. *The figure shows equilibrium covers of macroalgae(x) and corals(y) and trajectories over time. The grazing intensity $g = 0.77143 = g_0$. Here, there is no internal equilibrium in Ω, coral bloom is unstable saddle, and at equilibrium B transcritical bifurcation occurs.*

Obviously

$$Tr = \lambda_1 + \lambda_2 = -ry^* - x^*(\gamma + \frac{g}{1 - y^*}) < 0,$$

$$Det = \lambda_1.\lambda_2 = r(\gamma + \frac{g}{1 - y^*})y^*x^* + (r + a)y^*x^*((a - \gamma) - \frac{gx^*}{(1 - y^*)^2}) > 0.$$

Hence λ_1 and λ_2 have negative real parts. Also according to Lemma (1), in this case (for $g_0 < g$), the system (2) in Ω has no limit cycles, and E^* is an asymptotically stable node.

Therefore, we can summarize the above results as follows:

Theorem 1. *If $0 < g < g_0$, system (2) has no internal equilibrium point in Ω but has three boundary equilibria O,C and B, which are unstable node, unstable saddle, and stable node, respectively.*

If $g = g_0$, system (2) has no internal equilibrium point in Ω but has three boundary equilibria O,C and B, which are unstable node, unstable saddle, and unstable saddle-node (transcritical bifurcation occurs), respectively.

If $g_0 < g$, system (2) has the unique internal equilibrium point E^*, which is the stable node in Ω and three boundary equilibria O,C and B, which are unstable node, unstable saddle, and unstable saddle, respectively.

3. Mathematical analysis of the DDE model

It has been suggested by [8] that the inherent time delay has significant impact on dynamics of coral-algae interactions. Here we construct the following delay model by using the fact that it takes some time for algal turfs to arise after macroalgae are grazed by parrotfish:

(5)
$$
\begin{cases}
\frac{dM}{dt} = aMC - \frac{gM^2(t-\tau)}{M(t-\tau)+T(t-\tau)} + \gamma MT, \\[3mm]
\frac{dC}{dt} = rTC - dC - aMC, \\[3mm]
\frac{dT}{dt} = \frac{gM^2(t-\tau)}{M(t-\tau)+T(t-\tau)} - \gamma MT - rTC + dC
\end{cases}
$$

which still satisfies the assumptions of model (1). According to those assumptions, $M + C + T = 1$, and therefore the system (5) can be written as follow:

(6)
$$
\begin{cases}
\frac{dM}{dt} = aMC - \frac{gM^2(t-\tau)}{1-C(t-\tau)} + \gamma M(1 - M - C), \\[3mm]
\frac{dC}{dt} = r(1 - M - C)C - dC - aMC.
\end{cases}
$$

Let $M := x$, and $C := y$, then we can rewrite the system (6) as

(7)
$$
\begin{cases}
\frac{dx}{dt} = x[\gamma - \gamma x + (a - \gamma)y] - \frac{gx^2(t-\tau)}{1-y(t-\tau)} := H_1(x, y, x(t-\tau), y(t-\tau)), \\[3mm]
\frac{dy}{dt} = y[(r - d) - (r + a)x - ry] := H_2(x, y, x(t-\tau), y(t-\tau)).
\end{cases}
$$

The equilibrium of the system (7) are $O = (0,0)$, $C = (0, \frac{r-d}{r})$, $B = (\frac{\gamma}{g+\gamma}, 0)$, and $E^* = (x^*, y^*)$ (if $g_0 < g$). The linearized system of the above system (7) is

$$
\begin{pmatrix} \frac{dx}{dt} \\ \frac{dy}{dt} \end{pmatrix} = A_1 \begin{pmatrix} x(t) \\ y(t) \end{pmatrix} + A_2 \begin{pmatrix} x(t-\tau) \\ y(t-\tau) \end{pmatrix},
$$

where

$$
A_1 = \begin{pmatrix} \frac{\partial H_1}{\partial x} & \frac{\partial H_1}{\partial y} \\ \frac{\partial H_2}{\partial x} & \frac{\partial H_2}{\partial y} \end{pmatrix} = \begin{pmatrix} \gamma - 2\gamma x + (a - \gamma)y & (a - \gamma)x \\ -(r + a)y & (r - d) - 2ry - (r + a)x \end{pmatrix},
$$

$$
A_2 = \begin{pmatrix} \frac{\partial H_1}{\partial x(t-\tau)} & \frac{\partial H_1}{\partial y(t-\tau)} \\ \frac{\partial H_2}{\partial x(t-\tau)} & \frac{\partial H_2}{\partial y(t-\tau)} \end{pmatrix} = \begin{pmatrix} \frac{-2gx(t)}{1-y(t)} & -\frac{gx^2(t)}{(1-y(t))^2} \\ 0 & 0 \end{pmatrix}.
$$

Now we analyze the stability of these equilibria respectively. At the equilibrium $O = (0,0)$ and $C = (0, \frac{r-d}{r})$, A_2 is

$$A_2 = \begin{pmatrix} 0 & 0 \\ 0 & 0 \end{pmatrix}.$$

We know the characteristic equation is given by $\det(\lambda I - A_1 - A_2 e^{-\lambda \tau}) = 0$. However, in these cases $A_2 = [0]_{2\times 2}$. Hence the delay has no effect on the system and results hold as before. Therefore, for any $\tau \geq 0$, the equilibrium O and C are unstable node and a saddle, respectively.

But at the equilibrium $B = (\frac{\gamma}{g+\gamma}, 0)$, A_1 and A_2 take the form

$$A_1 = \begin{pmatrix} \gamma - 2\gamma(\frac{\gamma}{\gamma+g}) & (a-\gamma)(\frac{\gamma}{\gamma+g}) \\ 0 & r - d - (r+a)(\frac{\gamma}{\gamma+g}) \end{pmatrix}, A_2 = \begin{pmatrix} -2g(\frac{\gamma}{\gamma+g}) & -g(\frac{\gamma}{\gamma+g})^2 \\ 0 & 0 \end{pmatrix}.$$

Then the characteristic equation is given by

$$\det(\lambda I - A_1 - A_2 e^{-\lambda \tau})$$

$$= \begin{vmatrix} \lambda - \gamma + 2\gamma(\frac{\gamma}{\gamma+g}) + 2g(\frac{\gamma}{\gamma+g})e^{-\lambda\tau} & -(a-\gamma)(\frac{\gamma}{\gamma+g}) + g(\frac{\gamma}{\gamma+g})^2 e^{-\lambda\tau} \\ 0 & \lambda - (r-d) + (r+a) \quad (\frac{\gamma}{\gamma+g}) \end{vmatrix}$$

$$= (\lambda - \gamma + 2\gamma(\frac{\gamma}{\gamma+g}) + 2g(\frac{\gamma}{\gamma+g})e^{-\lambda\tau})(\lambda - (r-d) + (r+a)(\frac{\gamma}{\gamma+g})) = 0.$$

Then one eigenvalue is

$$\lambda_2 = -\frac{(r-d)}{\gamma+g}(g_0 - g),$$

and the other eigenvalues satisfy

$$(8) \qquad \qquad \lambda = \gamma - 2\gamma(\frac{\gamma}{\gamma+g}) - 2g(\frac{\gamma}{\gamma+g})e^{-\lambda\tau}.$$

Recall that for $\tau = 0$, the eigenvalues are $\lambda_1 = -\gamma$ and $\lambda_2 = -\frac{(r-d)}{\gamma+g}(g_0 - g)$, for which λ_1 is negative. But sign of λ_2 depends on g. If $0 < g < g_0$, $\lambda_2 < 0$,then B is a stable node; if $g_0 < g$, $\lambda_2 > 0$, thus B is an unstable saddle. It can easily be seen when $g = g_0$ ($\lambda_2 = 0$) a transcritical bifurcation occurs and B is an unstable saddle-node.

For $\tau > 0$, we look for pure imaginary eigenvalue of (8) and we assume that $\lambda(\tau) = \alpha(\tau) + i\omega(\tau)$ is a root of Eq. (8) satisfying $\alpha(\tau^*) = 0$, $\lambda(\tau^*) = i\omega(\tau^*) = i\omega$ for some

$\tau^* > 0$. Then

$$i\omega = \gamma - 2\gamma(\frac{\gamma}{\gamma + g}) - 2g(\frac{\gamma}{\gamma + g})e^{-i\omega\tau^*}$$

$$= \frac{-\gamma(\gamma - g)}{\gamma + g} - (\frac{2g\gamma}{\gamma + g})(\cos\omega\tau^* - i\sin\omega\tau^*)$$

$$= \frac{-\gamma(\gamma - g + 2g\cos\omega\tau^*)}{\gamma + g} + i\frac{2g\gamma}{\gamma + g}\sin\omega\tau^*.$$

Therefore, separating the real and imaginary parts implies that

$$\begin{cases} \frac{-\gamma(\gamma - g + 2g\cos\omega\tau^*)}{\gamma + g} = 0, \\ \omega - \frac{2g\gamma}{\gamma + g}\sin\omega\tau^* = 0. \end{cases}$$

Thus by $\sin^2\omega\tau^* + \cos^2\omega\tau^* = 1$, we obtain

$$\omega^2 = \frac{\gamma^2}{\gamma + g}(3g - \gamma).$$

Thus, if $0 < g \le \frac{\gamma}{3}$, Eq. (8) has no purely imaginary roots. Also, under assumption (3), 0 is not a root of Eq. (8). If $g_0 < \frac{\gamma}{3}$, then when $0 < g < g_0 < \frac{\gamma}{3}$, Eq. (8) has no purely imaginary roots, and all roots have negative real parts for all time delays $\tau \ge 0$ [3], and the equilibrium B is stable. If $0 < g < \frac{\gamma}{3} < g_0$, Eq. (8) has no purely imaginary roots, and all roots have negative real parts for all time delays $\tau \ge 0$ [3], and the equilibrium B is stable; but, if $\frac{\gamma}{3} < g < g_0$, when

$$\tau = \tau_j = \frac{1}{\omega}\{\arccos(\frac{g - \gamma}{2g}) + 2\pi j\}, j = 0, 1, 2, ...$$

equation (8) has a pair of purely imaginary roots $\lambda = \pm i\omega$, where

(9)
$$\omega = \gamma\sqrt{\frac{3g - \gamma}{\gamma + g}}.$$

The quantity of interest is the sign of the derivative of $\text{Re}\,\lambda$ with respect to τ at the points where λ is purely imaginary. From Eq. (8), we have

$$(\frac{d\lambda}{d\tau})^{-1} = \frac{(\gamma + g)e^{\lambda\tau}}{2g\gamma\lambda} - \frac{\tau}{\lambda}.$$

The real part of $(\frac{d\lambda}{d\tau})^{-1}$ when $\lambda = \pm i\omega$ is

$$\alpha_1(\lambda) := \text{Re}(\frac{d\lambda}{d\tau})^{-1}|_{\lambda=\pm i\omega} = \frac{d\,\text{Re}\,\tau}{d\lambda}|_{\lambda=\pm i\omega} = \frac{(\gamma + g)^2}{4g^2\gamma^2} > 0,$$

which implies that $(\frac{d\,\text{Re}\,\lambda(\tau)}{d\tau})|_{\tau=\tau_j}$ is positive for $j = 0, 1, 2, ...$

Therefore if $\frac{\gamma}{3} < g < g_0$, when $0 < \tau < \tau_0$, all eigenvalues of the characteristic equation at the equilibrium B have negative real parts, and the equilibrium B is

stable; when $\tau = \tau_0$, the characteristic equation (8) has a pair of purely imaginary roots and $\alpha_1(\lambda)$ is positive; when $\tau_0 < \tau < \tau_1$, there exists a pair of eigenvalues whose real parts are positive, and other eigenvalues have negative real parts, the equilibrium B is unstable, and so on. With the continued increase of the time delay τ, once $\tau = \tau_j$ for every j, there exists a pair of purely imaginary roots; when $\tau_j < \tau < \tau_{j+1}$, the linearized equation at the equilibrium B has $j+1$ pair eigenvalues with positive real parts, others have negative real parts, and the equilibrium point B is unstable.

Now we suppose $g = g_0$. If $\tau = 0$, the equilibrium B is an unstable saddle-node; if $\tau > 0$, $\lambda_2 = 0$, and other eigenvalues also satisfy Eq. (8). If $g = g_0 \leq \frac{\gamma}{3}$, for all $\tau > 0$ the roots of Eq. (8) have negative real parts, thus the eigenvalues of the characteristic equation at the equilibrium B have negative real parts, except for zero root; if $g = g_0 > \frac{\gamma}{3}$, when $\tau = \tau_j$ (for $j = 0, 1, 2, ...$), equation (8) has a pair of purely imaginary roots and $\alpha_1(\lambda)$ is positive, similarly when $\tau_j < \tau < \tau_{j+1}$, the characteristic equation at the equilibrium B has $j+1$ pair eigenvalues with positive real parts and zero root, others with negative real parts.

If $g_0 < g$, for all $\tau \geq 0$, $\lambda_2 > 0$, and the equilibrium B is unstable. If $\frac{\gamma}{3} < g_0$, when $\tau = \tau_j$ (for $j = 0, 1, 2, ...$), Eq. (8) has a pair of purely imaginary roots and $\alpha_1(\lambda)$ is positive, and when $\tau_j < \tau < \tau_{j+1}$, there exist a positive eigenvalue ($\lambda_2 > 0$), $j + 1$ pair eigenvalues with positive real parts, the others with negative real parts. If $g_0 \leq \frac{\gamma}{3}$, when $g_0 < g \leq \frac{\gamma}{3}$, Eq. (8) has no purely imaginary roots, and thus all roots of this equation have negative real parts, therefore the eigenvalues of the linearized equation at the equilibrium B have negative real parts, except for λ_2, which is positive. If $g_0 \leq \frac{\gamma}{3} < g$, then Eq. (8) has a pair of purely imaginary roots (when $\tau = \tau_j$), and when $\tau_j < \tau < \tau_{j+1}$, there exist a positive eigenvalue, $j + 1$ pair eigenvalues with positive real parts, and the others with negative real parts. Therefore the system (7) is unstable around equilibrium B.

Summarizing the above discussions, we arrive at the following theorem.

Theorem 2. *If $g_0 \leq \frac{\gamma}{3}$, then when $0 < g < g_0$, the equilibrium B is stable for all $\tau \geq 0$; if $g_0 < g$, for all $\tau \geq 0$, the equilibrium B is unstable.*

If $g_0 > \frac{\gamma}{3}$, when $0 < g \leq \frac{\gamma}{3}$, the equilibrium B is stable for all time delays $\tau \geq 0$; when $\frac{\gamma}{3} < g < g_0$ and $0 < \tau < \tau_0$, the equilibrium B is stable; when $\tau > \tau_0$, B is unstable; if $g_0 < g$, the equilibrium B is unstable for all $\tau \geq 0$.

Remark 1. *Notice that if B was an internal equilibrium, when $\tau = \tau_j$, Hopf bifurcation will appear and a nontrivial periodic solution around the equilibrium B will arise; however, we are not clear that system (7) has a nontrivial periodic solution around the equilibrium B or not. Also, if $g = g_0$ and $\tau = 0$, transcritical bifurcation occures; if $g = g_0$ and $\tau > 0$, 0 is a simple eigenvalue of Eq. (8), which is a critical case, and the stability of this equilibrium depends on high order terms of system (7).*

We shall now investigate the dynamics of the delay system (7) around the internal equilibrium $E^* = (x^*, y^*)$, which exists for $g_0 < g$, and when $\tau = 0$, E^* is stable. For $\tau > 0$, at E^*, A_1, A_2 are

$$A_1 = \begin{pmatrix} \gamma - 2\gamma x^* + (a - \gamma)y^* & (a - \gamma)x^* \\ -(r + a)y^* & r - d - 2ry^* - (r + a)x^* \end{pmatrix},$$

$$A_2 = \begin{pmatrix} \frac{-2gx^*}{1 - y^*} & \frac{-gx^{*2}}{(1 - y^*)^2} \\ 0 & 0 \end{pmatrix}.$$

From the linearized system, we obtain the characteristic equation

$$\det(\lambda I - A_1 - A_2 e^{-\lambda\tau}) =$$

$$\begin{vmatrix} \lambda - \gamma + 2\gamma x^* - (a - \gamma)y^* + \frac{2gx^*}{1 - y^*}e^{-\lambda\tau} & -(a - \gamma)x^* + \frac{gx^{*2}}{(1 - y^*)^2}e^{-\lambda\tau} \\ (r + a)y^* & \lambda + ry^* \end{vmatrix} =$$

(10) $$\lambda^2 + a\lambda + b\lambda e^{-\lambda\tau} + c + de^{-\lambda\tau} = 0$$

where

$$a := ry^* - \gamma + 2\gamma x^* - (a - \gamma)y^*,$$

$$b := \frac{2gx^*}{1 - y^*},$$

$$c := y^*[(r + a)(a - \gamma)x^* - \gamma r + 2\gamma rx^* - r(a - \gamma)y^*],$$

$$d := \frac{2grx^*y^*}{1 - y^*} - \frac{g(r + a)y^*x^{*2}}{(1 - y^*)^2}.$$

For $\tau = 0$, the characteristic equation (10) becomes

$$\lambda^2 + (a + b)\lambda + (c + d) = 0.$$

Since, in the absence of time delay, the system is locally asymptotically stable, then we can say $(a + b) > 0$ and $(c + d) > 0$. On the other hand, under assumption (3),

$c < 0$, then we have $d > 0$, $d > -c > 0$ and $d^2 > c^2$ (or $d^2 - c^2 > 0$).

Now for $\tau \neq 0$, if $\lambda = i\omega$ is a root of equation (10), then we have

$$-\omega^2 + ai\omega + bi\omega e^{-i\omega\tau^*} + c + de^{-i\omega\tau^*} = 0.$$

Separating real and imaginary parts, we get

$$c - \omega^2 + d\cos(\omega\tau^*) + b\omega\sin(\omega\tau^*) = 0,$$

(11) $$a\omega + b\omega\cos(\omega\tau^*) - d\sin(\omega\tau^*) = 0.$$

From (11), we obtain the fourth-order equation for ω as

(12) $$\omega^4 + \omega^2(a^2 - b^2 - 2c) + c^2 - d^2 = 0.$$

The roots are

(13) $$\omega_\pm^2 = \frac{1}{2}(b^2 - a^2 + 2c) \pm \{\frac{1}{4}(b^2 - a^2 + 2c)^2 - (c^2 - d^2)\}^{\frac{1}{2}}.$$

From (13) and $d^2 - c^2 > 0$, we see that there is a unique positive solution ω_+ for equation (12). Substituting ω_+ into (11) and solving for τ, we get

(14) $$\tau = \tau_n = \frac{1}{\omega_+}\left\{\arccos(\frac{d(\omega_+^2 - c) - ba\omega_+^2}{d^2 + b^2\omega_+^2})\right\} + \frac{2n\pi}{\omega_+}, n = 0, 1, 2, ...$$

Differentiating equation (10) with respect to τ, we obtain

$$\frac{d\lambda}{d\tau}[2\lambda + a + be^{-\lambda\tau} - b\lambda\tau e^{-\lambda\tau} - d\tau e^{-\lambda\tau}] = \lambda(d + b\lambda)e^{-\lambda\tau},$$

therefore we have

$$(\frac{d\lambda}{d\tau})^{-1} = \frac{(2\lambda + a)e^{\lambda\tau} + b}{\lambda(d + b\lambda)} - \frac{\tau}{\lambda}.$$

By using $e^{\lambda\tau} = \frac{-(d+b\lambda)}{\lambda^2 + a\lambda + c}$, we can obtain

$$\alpha_2(\lambda) := sign\left\{\frac{d(\text{Re }\lambda)}{d\tau}\right\}_{\tau = \tau_n} = sign\left\{\text{Re}(\frac{d\lambda}{d\tau})^{-1}\right\}_{\lambda = i\omega}$$

$$= sign\left\{\text{Re}[\frac{-(2\lambda + a)}{\lambda(\lambda^2 + a\lambda + c)}]_{\lambda = i\omega} + \text{Re}[\frac{b}{\lambda(d + b\lambda)}]_{\lambda = i\omega}\right\}$$

$$= sign\left\{\frac{a^2 - 2(c - \omega^2)}{a^2\omega^2 + (\omega^2 - c)^2} - \frac{b^2}{b^2\omega^2 + d^2}\right\}$$

$$= sign\left\{a^2 - b^2 - 2c + 2\omega^2\right\},$$

which is positive. Therefore, we can say that, when τ crosses τ_n ($\tau = \tau_n$) for every n, the characteristic equation (10) has a pair of purely imaginary roots $\pm i\omega_+$, and

$\alpha_2(\lambda)$ is positive, then the Hopf bifurcation occurs, and a nontrivial periodic solution appears; when $\tau_n < \tau < \tau_{n+1}$, the characteristic equation (10) has $n + 1$ pair of eigenvalues with positive real parts, the others with negative real parts. Therefore, the equilibrium E^* becomes unstable at the smallest value of τ for which an imaginary root exists and remains so as τ is increased.

Theorem 3. *If $a + b > 0$, $c + d > 0$ and $d^2 - c^2 > 0$, then the equilibrium E^* is asymptotically stable for $\tau < \tau_0$ and unstable for $\tau > \tau_0$. Further, as τ increases through τ_0, (x^*, y^*) bifurcates into small amplitude periodic solutions, where $\tau_0 = \tau_n$.*

Example 1. *Now fix the following parameters:*

(15) $$a = 0.1, \quad d = 0.44, \quad g = 1.5, \quad \gamma = 0.8, \quad r = 1,$$

then we have the uniqe interior equilibrium $E^* = (0.16818, 0.37500)$. As mentioned in section 2, we conclude that the equilibrium E^* is stable. Now, we consider the system (7). By direct computation, we obtain $\tau_0 = 1.86828$. In other words, if $\tau < \tau_0$, E^* is stable; if $\tau = \tau_0$, the Hopf bifurcation occures, and if $\tau > \tau_0$, E^* is unstable. This is shown in Figure (4).

4. Discussion and Conclusion

Based on the model (1) and by considering assumptions in [8], we have obtained the system (2). The dynamics of the model (2) are investigated. The sufficient conditions are given to ensure that the positive equilibrium is locally asymptotically stable. In addition, also we have considered the effect of time delay on the stability of different equilibria and existence of periodic orbits and Hopf bifurcations from the internal equilibria. Also some numerical simulations are carried out for illustrating the analytic results.
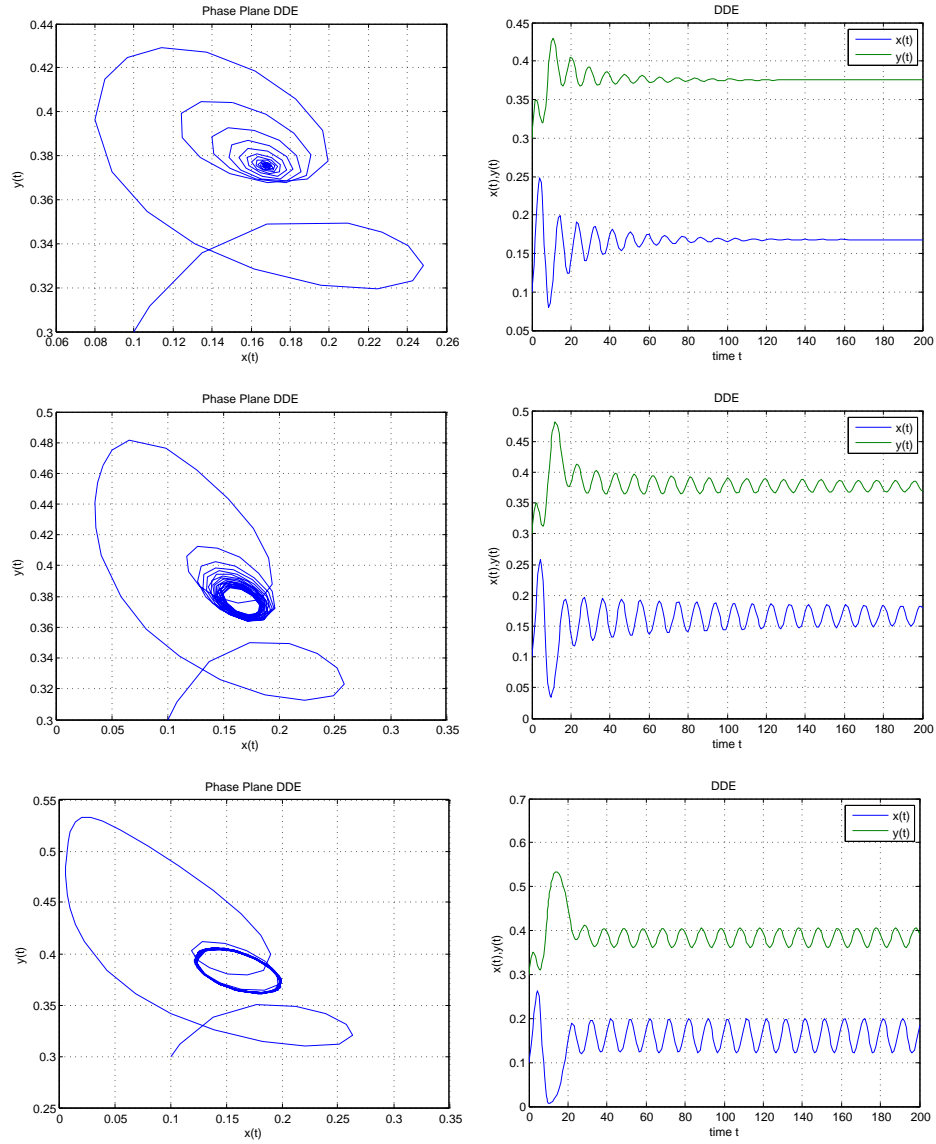
FIGURE 4. Figures are system (7), with initial condition $(0.1, 0.3)$ and with time delay $\tau = 1.75$, $\tau = 1.87$ and $\tau = 1.92$, respectively, around the interior equilibrium E^*.

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