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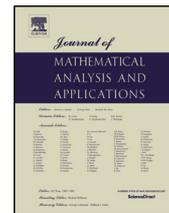
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Mathematical analysis of coral reef models

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ABSTRACT

It is acknowledged that coral reefs are globally threatened. P.J. Mumby et al. [10] constructed a mathematical model with ordinary differential equations to investigate the dynamics of coral reefs. In this paper, we first provide a detailed global analysis of the coral reef ODE model in [10]. Next we incorporate the inherent time delay to obtain a mathematical model with delay differential equations. We consider the grazing intensity and the time delay as focused parameters and perform local stability analysis for the coral reef DDE model. If the time delay is sufficiently small, the stability results remain the same. However, if the time delay is large enough, macroalgae only state and coral only state are both unstable, while they are both stable in the ODE model. Meanwhile, if the grazing intensity and the time delay are endowed some suitable values, the DDE model possesses a nontrivial periodic solution, whereas the ODE model has no nontrivial periodic solutions for any grazing rate. We study the existence and property of the Hopf bifurcation points and the corresponding stability switching directions.

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1. Introduction

Coral reefs have significant ecosystem functioning and commercial values. They are critically important for a marine ecosystem because of their ecosystem functions including coastal defence from storms, conservation of both fisheries and marine biodiversity [9]. Moreover, millions of people receive economic benefits from tourism or fisheries that rely on coral reefs.

However, it is acknowledged that coral reefs have suffered grave threats to abundance, diversity, habitat structure and functioning. For example, there was a massive region-wide decline of corals across the entire

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Caribbean basin, with the average hard coral cover on reefs being reduced from about 50% to 10% cover, in three decades. Assessments suggest that 11% of the historical extent of coral reefs is already lost, while a further 16% is severely damaged [5].

The degradation of coral reefs is due to a combination of human activities (e.g., overfishing, pollution) and natural disturbances (e.g., disease, hurricane, bleaching) [5,6,11]. The overall historical trajectory of reef degradation across all cultural periods provides a reasonable explanation for that earlier decline – overfishing. However, pollution from agriculture and land development could have acted synergistically with overfishing in some localities. Nevertheless, the reefs were substantially degraded before 1900 [11]. Hurricanes damage shallow-water branching species and increase the relative abundances of species with encrusting or massive-shaped colonies [6]. Increases in carbon dioxide and temperature over the next 50 years will exceed the conditions under which coral reefs have flourished over the past half-million years [7].

There is an urgent need, therefore, to identify how it is possible to cope with disturbances in the management and preservation of coral reefs. In the last decade, many studies have examined damages that may be occurring and the involved mechanisms [8]. However, most evidence is correlative or based on simple observations.

Although these are multiple threats to coral reefs, one serious cause is overfishing of grazing species. Fishing, particularly of herbivorous parrotfish and surgeonfish, affects more than just the size of harvestable stocks; it alters the entire dynamics of a reef [7]. Under the condition of heavy grazer depletion, coral cover was predicted to decline rapidly from an initial level of 30% to less than 1% within 40 years [9]. P.J. Mumby et al. used a fully parameterized simulation model in combination with a simple analytical model to show that the dynamical behavior of the system differs dramatically between high and low levels of grazing, which is primarily conducted by parrotfishes [10]. Subsequently, by including the control on fishing pressure, Blackwood et al. [3] extended the model and treated grazing as a dynamic process and consider two distinct scenarios of coral recovery, which identify critical fishing effort levels to allow coral recovery. It is assumed that grazing on macroalgae giving rise to algae turfs and grazing on algal turfs simply prevents macroalgae succession from the turf or the vegetative growth of macroalgae across the turf. Given the complexity of the simulation model, an ODE mean field model was introduced and analyzed in [3] and [10]. Other models include Singh et al. [12] and Wang et al. [13] which examine the refuge effects of a coral reef on fish biomass structure.

We focus on the impact of different grazing levels rather than other internal parameters due to extremes of grazing intensity have been shown to influence coral–algae interactions and the cover of living coral. Then several of the parameters, such as coral growth rate, are entered as constants rather than allowed to vary probabilistically. This approach avoids unnecessary variation from relatively well-established parameters and is consistent with other coral reef models [3,9,10].

The inherent delay effect has been considered to be important on Caribbean coral–algae interactions [2], in which the authors discussed the effect of time delays on transient dynamics. In this paper, we will focus on the impact of the inherent time delay on asymptotic dynamics. It takes a long period of time for algal turfs to arise after macroalgae are grazed. We construct a delay differential equation model to capture this fact.

The aim of this paper is to present a more complete mathematical analysis of the dynamics of the ODE model in [10], and to propose and analyze a more realistic model using DDEs. We discuss the dissipativity of the system, demonstrate the nonexistence of periodic solutions, and study the global stability in Section 2. In Section 3, we argue that action needs time to take effect in a natural system, and that algal turfs will not be recruited to macroalgae instantaneously after macroalgae are grazed, thus the corresponding coral reefs model should be described by a system of delay differential equations. We take the grazing intensity and the time delay as the parameters of interest and study the local stability of equilibria. If the time delay is sufficiently small, the stability results remain the same as the ODE case. However, if the time delay is

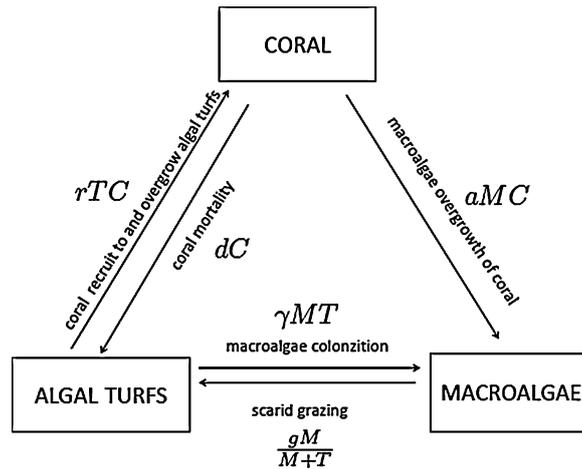


Fig. 1. Flowchart of model variables with their connections.

large enough, macroalgae only state and coral only state are both unstable, whereas they are both stable in the ODE case. Meanwhile, for some values of the grazing intensity and the time delay, the delay model possesses a nontrivial periodic solution, while the ODE model has no nontrivial periodic solutions for any grazing rate.

2. Mathematical analysis of the coral reef ODE model

We assume that (i) algal turfs arise from grazed macroalgae and natural coral mortality; (ii) corals recruit to and overgrow algal turfs, constrained by the turf cover; (iii) corals are overgrown by macroalgae; (iv) macroalgae colonize dead coral by spreading vegetatively over algal turfs [10] (see the flowchart in Fig. 1 for more details).

Denote C , T and M as the cover of corals, algal turfs, and macroalgae, respectively. The coral reef dynamics are described as a system of coupled nonlinear ordinary differential equations [3,10]:

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

where

- r is the rate that corals recruit to and overgrow algal turfs,
- d is the natural mortality rate of corals,
- a is the rate that corals are overgrown by macroalgae,
- γ is the rate that macroalgae spread vegetatively over algal turfs,
- g is the grazing rate that parrotfish graze macroalgae without distinction from algal turfs.

The brief description of the parameter selection and parameter values can be found in [3,10], in which the authors listed the parameter values as follows:

$$a = 0.1, \quad \gamma = 0.8, \quad r = 1, \quad d = 0.44, \quad 0 < g < 0.8. \quad (2)$$

In this paper, we only need the following assumptions

$$a < d < \gamma < r < 2\gamma, \quad 0 < g < \gamma, \tag{3}$$

satisfied by the above values, unless we particularly point out.

In this model, it is assumed that a particular region of the seabed is covered entirely by macroalgae (M), coral (C) and algal turfs (T), so that $M + C + T = 1$. Since the fraction of algal turfs is defined by $T = 1 - M - C$, and consequently $\frac{dT}{dt}$ is simply given by $-\frac{dM}{dt} - \frac{dC}{dt}$, only the first two equations of this model are needed:

$$\begin{cases} \frac{dM}{dt} = aMC - \frac{gM}{M+T} + \gamma MT, \\ \frac{dC}{dt} = rTC - dC - aMC. \end{cases} \tag{4}$$

Without loss of generality, let $x = M$, $y = C$, then we can rewrite the above system (4) as

$$\begin{cases} \frac{dx}{dt} = x \left[\gamma - \gamma x + (a - \gamma)y - \frac{g}{1-y} \right] := xF(x, y), \\ \frac{dy}{dt} = y[r - d - (a + r)x - ry] := yG(x, y). \end{cases} \tag{5}$$

First we focus on some basic properties of solutions of system (5), such as the dissipativity and the nonexistence of limit cycles. According to the biologic signification of the model described above, we define

$$\Omega = \{(x, y): 0 < x, 0 < y, x + y < 1\}.$$

Theorem 1. Ω is positively invariant for the semiflow generated by system (5), and system (5) has no periodic solutions in Ω .

Proof. It is clear that the positive x -axis and the positive y -axis are both invariant. To show that orbits starting from Ω cannot escape Ω from the upper boundary $\{(x, y): x > 0, y > 0, x + y = 1\}$, we define

$$z = x + y.$$

Then on the upper boundary, we have

$$\frac{dz}{dt} = \frac{dx}{dt} + \frac{dy}{dt} = -g - dy.$$

Hence, all orbits starting from Ω will stay in Ω for all forward time.

The vector field defined by system (5) is locally Lipschitz continuous in Ω , which guarantees the existence and uniqueness of solutions of system (5). This vector field is C^1 , so the classical Dulac's criterion can be applied. Choose $\chi(x, y) = \frac{1}{xy}$. Easy computations yield that

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

Therefore, the Dulac's criterion can be applied to system (5) in Ω and thus the proof is completed. \square

Now we analyze the stability of the equilibria. For this purpose we first compute the nullclines of system (5). The x -nullcline of system (5) is $x = 0$ and $F(x, y) = 0$, where $F(x, y) = 0$ implies

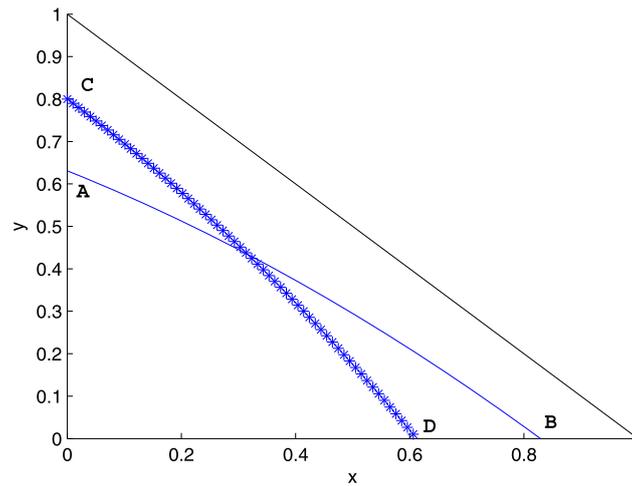


Fig. 2. The segment AB denotes x-nullcline and the segment CD denotes y-nullcline.

$$y \triangleq g(x) = \frac{1}{2(\gamma - a)} [(2\gamma - a - \gamma x) - \sqrt{\gamma^2 x^2 - 2a\gamma x + a^2 + 4\gamma g - 4ag}]$$

$$= \frac{1}{2(\gamma - a)} [(2\gamma - a - \gamma x) - \sqrt{(\gamma x - a)^2 + 4g(\gamma - a)}],$$

here we assume that $a < \gamma$. Denote the curve $y = g(x)$ contained in the first quadrant by l_1 . Then l_1 starts from the point $A(0, y_A)$, ends at the point $B(x_B, 0)$ (see Fig. 2), where

$$y_A = \frac{1}{2(\gamma - a)} [(2\gamma - a) - \sqrt{a^2 + 4g(\gamma - a)}],$$

$$x_B = 1 - \frac{g}{\gamma}.$$

If $a < \gamma, g > 0$, then $0 < y_A < 1$; if $0 < g < \gamma$, then $0 < x_B < 1$.

Now we discuss the monotonicity of the curve l_1 . Differentiating g yields that

$$y' = g'(x) = \frac{1}{2(\gamma - a)} [-\gamma - ((\gamma x - a)^2 + 4g(\gamma - a))^{-1/2} (\gamma x - a)\gamma]$$

$$= \frac{-\gamma}{2(\gamma - a)} \left[1 + \frac{\gamma x - a}{\sqrt{(\gamma x - a)^2 + 4g(\gamma - a)}} \right] < 0,$$

which implies that the curve l_1 starting from A ending at B is strictly monotone. That is, x -nullcline is the positive y -axis and a monotone decreasing smooth curve connecting the starting point $A(0, y_A)$ and the ending point $B(x_B, 0)$.

The y -nullcline of system (5) is $y = 0$ and $G(x, y) = 0$, where $G(x, y) = 0$ implies

$$y \triangleq h(x) = -\left(1 + \frac{a}{r}\right)x + \left(1 - \frac{d}{r}\right).$$

Denote the curve $y = h(x)$ contained in the first quadrant by l_2 . Then l_2 is a line starting from the point $C(0, y_C)$, ending at the point $D(x_D, 0)$, where

$$y_C = 1 - \frac{d}{r},$$

$$x_D = \frac{r - d}{r + a}.$$

If we assume that $d < r$, then $0 < y_C < 1, 0 < x_D < 1$.

Now we discuss the monotonicity of the curve l_2 . Differentiating h yields that

$$y' = h'(x) = -\left(1 + \frac{a}{r}\right) < 0,$$

which implies that the curve l_2 starting from C ending at D is strictly monotone. That is, y -nullcline is the positive x -axis and a monotone decreasing smooth curve connecting the starting point C and the ending point D (see Fig. 2).

From the above discussions about the nullclines of system (5), we know that system (5) has three boundary equilibria O , C and B . Now we analyze the stability of those boundary equilibria. To determine the local stability of those equilibria, we consider the Jacobian matrix of system (5):

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

At the equilibrium $O(0, 0)$, the Jacobian matrix takes the form

$$J_O = \begin{pmatrix} \gamma - g & 0 \\ 0 & r - d \end{pmatrix}.$$

The eigenvalues $\gamma - g$ and $r - d$ are positive under assumption (3), thus the origin is unstable node.

At the equilibrium $C(0, 1 - \frac{d}{r})$, the Jacobian matrix takes the form

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

The eigenvalues are $a + \frac{d}{r}(\gamma - a) - \frac{r}{d}g$ and $-(r - d)$. Let

$$g_0 = \frac{d}{r}a + \frac{d^2}{r^2}(\gamma - a).$$

If $0 < g < g_0$, $a + \frac{d}{r}(\gamma - a) - \frac{r}{d}g > 0$, then C is an unstable saddle; if $g_0 < g < \gamma$, $a + \frac{d}{r}(\gamma - a) - \frac{r}{d}g < 0$, then C is a stable node. In the below, we will see that when $g = g_0$, transcritical bifurcation occurs, and C is an unstable saddle-node.

Now we discuss the stability of the boundary equilibrium B . At the equilibrium $B(1 - \frac{g}{\gamma}, 0)$, the Jacobian matrix takes the form

$$J_B = \begin{pmatrix} -(\gamma - g) & (1 - \frac{g}{\gamma})(a - \gamma - g) \\ 0 & -(a + d) + \frac{g}{\gamma}(a + r) \end{pmatrix}.$$

The eigenvalues are $-(\gamma - g)$ and $-(a + d) + \frac{g}{\gamma}(a + r)$. Let

$$g_1 = \gamma \frac{a + d}{a + r}.$$

Note that if $a < \gamma$, $d < r$, then $0 < g_0 < g_1 < \gamma$. If $0 < g < g_1$, B is a stable node; if $g_1 < g < \gamma$, B is an unstable saddle. Also, in the below, we will see that when $g = g_1$, transcritical bifurcation occurs, and B is an unstable saddle-node.

Now we analyze the stability of the internal equilibrium, which is the intersection point of the curve l_1 and the line l_2 . If possible the coordinate of the internal equilibrium satisfies the following algebraic equations

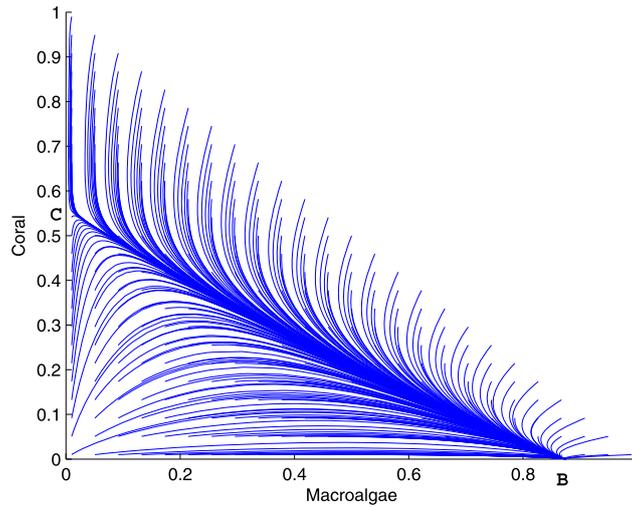


Fig. 3. This figure shows equilibrium covers of macroalgae and corals and trajectories over time. Trajectories may be thought of as arrows beginning at different initial covers and were plotted using numerical integration with 4th and 5th order Runge–Kutta formulae. The grazing intensity $g = 0.1 < g_0$. There is no internal equilibrium in Ω in this case. Macroalgal bloom is the only stable node.

$$\begin{cases} (a - \gamma)y + \gamma(1 - x) - \frac{g}{1 - y} = 0, \\ -(a + r)x - ry + r - d = 0. \end{cases}$$

Deleting the variable x , we obtain the equation for the variable y ,

$$(\gamma a - ra - a^2)y^2 + (ra + a^2 - 2a\gamma - \gamma d)y + \gamma(a + d) - g(a + r) = 0.$$

Let

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

Then

$$\begin{aligned} H(0) &= \gamma(a + d) - g(a + r) = (g_1 - g)(a + r), \\ H(y_C) &= H\left(1 - \frac{d}{r}\right) = (g_0 - g)(a + r). \end{aligned}$$

If we assume that $\gamma < r$, then $\gamma a - ra - a^2 < 0$. Therefore, if $0 < g < g_0$, $H(y_C) > 0$, $H(0) > 0$, then the above algebraic equations have no solutions whose y -coordinate belongs to the interval $[0, y_C]$, which implies that the original system has no internal equilibrium in Ω .

Thus, if $0 < g < g_0$, the dynamical behavior of system (5) is completely clear. That is, in this case, system (5) in Ω has no limit cycles, no internal equilibria, but only has three boundary equilibria O , C , B , and O is the unstable node, C is the unstable saddle, B is the only stable node (see Fig. 3).

If $g_0 < g < g_1$, then $H(0) > 0$, $H(y_C) < 0$. Thus the above algebraic equations have a unique solution (x^*, y^*) , where $0 < y^* < y_C$, and

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

Hence $E^* = (x^*, y^*)$ is a unique internal equilibrium for the original system (5) in Ω .

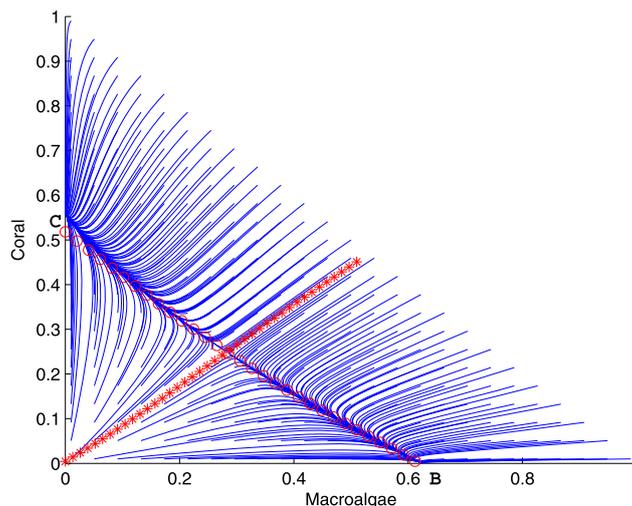


Fig. 4. The figure shows equilibrium covers of macroalgae and corals and trajectories over time. The grazing intensity is 0.3, which is in the interval $[g_0, g_1]$. There is unstable internal equilibrium in Ω . Corals bloom and macroalgal bloom are both stable. The trajectories shown in stars and circles stand for the invariant manifold of the internal equilibrium.

Now we analyze the stability of E^* . At E^* , the Jacobian matrix has the form

$$J_{E^*} = \begin{pmatrix} F + x^*F_x & x^*F_y \\ y^*G_x & G + y^*G_y \end{pmatrix} = \begin{pmatrix} x^*F_x & x^*F_y \\ y^*G_x & y^*G_y \end{pmatrix}.$$

The determinant of J_{E^*} is

$$x^*y^*F_xG_y - x^*y^*F_yG_x = x^*y^*F_yG_y \left(\frac{F_x}{F_y} - \frac{G_x}{G_y} \right).$$

Since at E^* , $F_y < 0$, $G_y < 0$ and $\frac{F_x}{F_y} - \frac{G_x}{G_y} < 0$, then the determinant of J_{E^*} is negative, which implies that one eigenvalue of J_{E^*} is positive, and the other eigenvalue is negative, hence the equilibrium E^* is an unstable saddle.

Thus, if $g_0 < g < g_1$, the dynamical behavior of system (5) is completely clear. That is, in this case, system (5) in Ω has no limit cycles, and has the unique internal equilibrium E^* , which is the unstable saddle, has three boundary equilibria O , C and B , and O is the unstable node, C and B are both stable (see Fig. 4).

If $g_1 < g < \gamma$, then $H(0) < 0$, $H(y_C) < 0$. If we assume that $r < 2\gamma$, $a < d$, then the symmetric axis is

$$y = \frac{ra + a^2 - 2a\gamma - \gamma d}{2(ra + a^2 - \gamma a)}.$$

Thus for all $y \in [0, y_C]$, $H(y) < 0$. Therefore the above algebraic equation has no solutions whose y -coordinates belong to the interval $[0, y_C]$, which implies that the original system has no internal equilibrium in Ω .

Thus, if $g_1 < g < \gamma$, the dynamical behavior of system (5) is completely clear. That is, in this case, system (5) in Ω has no limit cycles, no internal equilibria, but only three boundary equilibria O , C and B , and O is the unstable node, B is the unstable saddle, C is the only stable node (see Fig. 5).

If $g = g_0$, as mentioned before, when g tends to g_0 from the right, the internal equilibrium E^* will tend to the boundary equilibrium C , and when $g = g_0$, the unstable saddle E^* collides the stable node C , thus transcritical bifurcation appears, and C is a saddle-node.

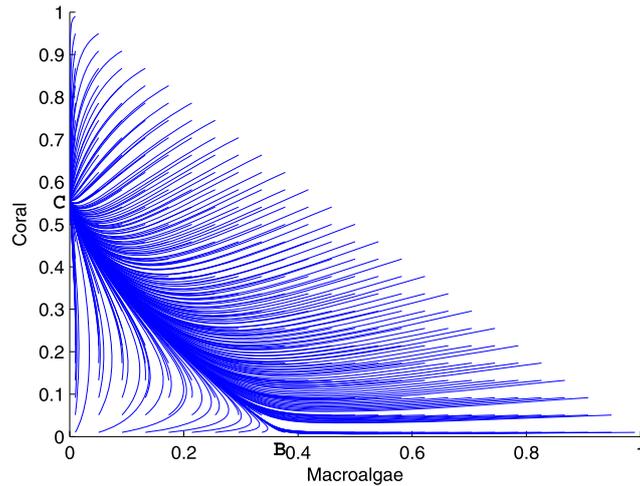


Fig. 5. The figure shows equilibrium covers of macroalgae and corals and trajectories over time. Here the grazing intensity $g = 0.5 > g_1$. There is no internal equilibrium in Ω . Corals bloom is stable node.

If $g = g_1$, also as mentioned before, when g tends to g_1 from the left, the internal equilibrium E^* will tend to the boundary equilibrium B . Therefore, when $g = g_1$, the unstable saddle E^* collides the stable node B , thus transcritical bifurcation appears, and B is a saddle-node.

Summarizing the above discussions, we obtain the following theorem and table.

Theorem 2. *If $0 < g < g_0$, system (5) has no internal equilibria 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 (5) has no internal equilibria in Ω but has three boundary equilibria O, C and B , which are unstable node, unstable saddle-node (transcritical bifurcation appears), and stable node, respectively.

If $g_0 < g < g_1$, system (5) has an unstable internal saddle E^ in Ω and three boundary equilibria O, C and B , which are unstable node, stable node, and stable node, respectively.*

If $g = g_1$, system (5) has no internal equilibria in Ω but has three boundary equilibria O, C and B , which are unstable node, stable node, and unstable saddle-node (transcritical bifurcation appears), respectively.

If $g_1 < g < \gamma$, system (5) has no internal equilibria in Ω but has three boundary equilibria O, C and B , which are unstable node, stable node, and unstable saddle, respectively.

	O	C	B	E^*
$0 < g < g_0$	unstable node	unstable saddle	stable node	not exist
$g = g_0$	unstable node	unstable saddle-node	stable node	not exist
$g_0 < g < g_1$	unstable node	stable node	stable node	unstable saddle
$g = g_1$	unstable node	stable node	unstable saddle-node	not exist
$g_1 < g < \gamma$	unstable node	stable node	unstable saddle	not exist

3. Mathematical analysis of the coral reef DDE model

It has been suggested by [2] that the inherent time delay has significant impact on transient dynamics of coral–algae interactions. Here we discuss its impact on asymptotic dynamics of coral reefs using the fact that it takes a long time for algal turfs to arise after macroalgae are grazed. To capture this fact, we construct the following delay model:

$$\begin{cases} \frac{dM}{dt} = aMC - \frac{gM(t-\tau)}{M(t-\tau) + T(t-\tau)} + \gamma MT, \\ \frac{dC}{dt} = rTC - dC - aMC, \\ \frac{dT}{dt} = \frac{gM(t-\tau)}{M(t-\tau) + T(t-\tau)} - \gamma MT - rTC + dC \end{cases} \quad (6)$$

which still follows the conservation law $M + C + T = 1$.

According to the conservation law, the system (6) can be simplified into the following two-dimensional system:

$$\begin{cases} \frac{dM}{dt} = aMC - \frac{gM(t-\tau)}{1 - C(t-\tau)} + \gamma M - \gamma M^2 - \gamma MC, \\ \frac{dC}{dt} = rC - rMC - rC^2 - dC - aMC. \end{cases} \quad (7)$$

Also, let $x = M, y = C$, then we can rewrite the above system (7) as

$$\begin{cases} \frac{dx}{dt} = x[\gamma - \gamma x + (a - \gamma)y] - \frac{gx(t-\tau)}{1 - y(t-\tau)} := H_1(x, y, x(t-\tau), y(t-\tau)), \\ \frac{dy}{dt} = y[r - d - (a + r)x - ry] := H_2(x, y, x(t-\tau), y(t-\tau)). \end{cases} \quad (8)$$

The possible equilibria of system (8) are $O(0, 0), B(1 - \frac{d}{\gamma}, 0), C(0, 1 - \frac{d}{r}), E^*(x^*, y^*)$ (if $g_0 < g < g_1$). The linearized system of system (8) 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

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

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

Now we will analyze the stability of these equilibria respectively. At the equilibrium $O(0, 0)$, A_1, A_2 take the form respectively

$$A_1 = \begin{pmatrix} \gamma & 0 \\ 0 & r - d \end{pmatrix}, \quad A_2 = \begin{pmatrix} -g & 0 \\ 0 & 0 \end{pmatrix}.$$

Thus the characteristic equation is given by

$$\begin{aligned} \det[\lambda I - A_1 - A_2 e^{-\lambda\tau}] &= \begin{vmatrix} \lambda - \gamma + ge^{-\lambda\tau} & 0 \\ 0 & \lambda - r + d \end{vmatrix} \\ &= (\lambda - r + d)(\lambda - \gamma + ge^{-\lambda\tau}) = 0, \end{aligned}$$

and hence one eigenvalue $r - d$ is positive under assumption (3), other eigenvalues satisfy

$$\lambda = \gamma - ge^{-\lambda\tau}. \quad (9)$$

For $\tau = 0$, the eigenvalues are $r - d > 0$ and $\gamma - g > 0$, thus the equilibrium O is unstable. For $\tau > 0$, we need to analyze the movement of characteristic roots of Eq. (9) on the complex plane as the time delay τ increases. For the real parts of a pair of complex characteristic roots to change sign at some τ , the characteristic roots need to cross the imaginary axis at τ . We assume that $\lambda(\tau) = \alpha(\tau) + i\omega(\tau)$ is a root of Eq. (9) satisfying $\alpha(\tau^*) = 0$, $\lambda(\tau^*) = i\omega(\tau^*) = i\omega$ for some $\tau^* > 0$. Then

$$i\omega = \gamma - g \cos \omega\tau^* + ig \sin \omega\tau^*.$$

Separating the real and imaginary parts yields that

$$\begin{cases} \sin \omega\tau^* = \frac{\omega}{g}, \\ \cos \omega\tau^* = \frac{\gamma}{g}. \end{cases}$$

Adding up the squares of both equations, by $\cos^2 \omega\tau^* + \sin^2 \omega\tau^* = 1$, we obtain

$$\omega^2 = g^2 - \gamma^2.$$

Since $0 < g < \gamma$, Eq. (9) has no purely imaginary roots, and hence the number of roots with positive real parts of Eq. (9) does not change as the time delay τ increases [1,4]. Therefore, for any $\tau > 0$, the linearized equation of system (8) at the equilibrium O has two eigenvalues with positive real parts, all other eigenvalues have negative real parts, and the equilibrium O is unstable.

Summarizing the above discussions, we obtain the following theorem.

Theorem 3. *For any $\tau > 0$, the linearized equation of system (8) at the equilibrium O has two eigenvalues with positive real parts, all other eigenvalues have negative real parts, and the equilibrium O is unstable.*

Now we discuss the stability of the equilibrium $C(0, 1 - \frac{d}{r})$. At the equilibrium $C(0, 1 - \frac{d}{r})$, A_1, A_2 take the form respectively

$$A_1 = \begin{pmatrix} \gamma + (a - \gamma)(1 - \frac{d}{r}) & 0 \\ -(a + r)(1 - \frac{d}{r}) & d - r \end{pmatrix}, \quad A_2 = \begin{pmatrix} -\frac{gr}{d} & 0 \\ 0 & 0 \end{pmatrix}.$$

The characteristic equation is given by

$$\begin{aligned} \det[\lambda I - A_1 - A_2 e^{-\lambda\tau}] &= \begin{vmatrix} \lambda - \gamma - (a - \gamma)(1 - \frac{d}{r}) + \frac{gr}{d} e^{-\lambda\tau} & 0 \\ (a + r)(1 - \frac{d}{r}) & \lambda - (d - r) \end{vmatrix} \\ &= (\lambda + r - d) \left(\lambda - \gamma - (a - \gamma) \left(1 - \frac{d}{r} \right) + \frac{gr}{d} e^{-\lambda\tau} \right) = 0. \end{aligned}$$

Hence, one eigenvalue $d - r$ is negative under assumption (3), other eigenvalues satisfy

$$\lambda = a + (-a + \gamma) \frac{d}{r} - \frac{gr}{d} e^{-\lambda\tau} = \frac{r}{d} (g_0 - g e^{-\lambda\tau}). \tag{10}$$

Recall that for $\tau = 0$, the eigenvalues are $d - r < 0$ and $\frac{r}{d}(g_0 - g)$. Thus if $0 < g < g_0$, the equilibrium C is an unstable saddle; if $g = g_0$, the equilibrium C is an unstable saddle-node; if $g_0 < g < \gamma$, the equilibrium C is a stable node.

For $\tau > 0$, we assume that $\lambda(\tau) = \alpha(\tau) + i\omega(\tau)$ is a root of Eq. (10) satisfying $\alpha(\tau^*) = 0$, $\lambda(\tau^*) = i\omega(\tau^*) = i\omega$ for some $\tau^* > 0$. Then

$$i\omega = \frac{r}{d} [g_0 - g(\cos \omega\tau^* - i \sin \omega\tau^*)].$$

Separating the real and imaginary parts yields that

$$\begin{cases} \sin \omega\tau^* = \frac{\omega d}{gr}, \\ \cos \omega\tau^* = \frac{g_0}{g}. \end{cases}$$

Adding up the squares of both equations, by $\cos^2 \omega\tau^* + \sin^2 \omega\tau^* = 1$, we obtain

$$\omega^2 = \frac{g^2 - g_0^2}{(d/r)^2}.$$

Therefore, if $0 < g < g_0$, there exist no purely imaginary roots and hence the number of roots with positive real parts of Eq. (10) does not change as the time delay τ increases [1,4]. Therefore, if $0 < g < g_0$, for any $\tau > 0$, the linearized equation of system (8) at the equilibrium C has one eigenvalue with positive real part, all other eigenvalues have negative real parts, and the equilibrium C is unstable.

If $g = g_0$, 0 is a simple eigenvalue of the linearized equation of system (8) at the equilibrium C if $\frac{rg_0\tau}{d} \neq 1$.

If $g_0 < g < \gamma$, when

$$\tau = \tau_j = \frac{1}{\omega} (\arccos(g_0/g) + 2\pi j), \quad j = 0, 1, 2, \dots$$

Eq. (10) has a pair of purely imaginary roots $\pm i\omega$, where

$$\omega = \frac{\sqrt{g^2 - g_0^2}}{(d/r)}. \tag{11}$$

Now we are interested in the transversality condition when the time delay τ crosses τ_j . From (10) we obtain

$$\frac{d\tau}{d\lambda} = \frac{d}{g\lambda r e^{-\lambda\tau}} - \frac{\tau}{\lambda}.$$

The real part of $\frac{d\tau}{d\lambda}$ when $\lambda = \pm i\omega$ is

$$\left. \frac{d \operatorname{Re} \tau}{d\lambda} \right|_{\lambda=\pm i\omega} = \frac{d \sin \omega\tau}{g\omega r} = \left(\frac{d}{gr} \right)^2 > 0,$$

which implies that

$$\left. \frac{d \operatorname{Re} \lambda}{d\tau} \right|_{\tau=\tau_j} > 0$$

for $j = 0, 1, 2, \dots$

Next we consider the relationship between the first critical delay value τ_0 and the grazing intensity g . We compute $\frac{d\tau_0}{dg}$ and have

$$\begin{aligned} \frac{d\tau_0}{dg} &= \frac{d}{r} \cdot \frac{1}{g^2 - g_0^2} \cdot \left(\frac{g_0}{g} - \frac{g \arccos(g_0/g)}{\sqrt{g^2 - g_0^2}} \right) \\ &= \frac{d}{r} \cdot \frac{1}{g^2 - g_0^2} \cdot \frac{1}{g\sqrt{g^2 - g_0^2}} \cdot \left(g_0\sqrt{g^2 - g_0^2} - g^2 \arccos(g_0/g) \right). \end{aligned}$$

Denote

$$f(g) = g_0\sqrt{g^2 - g_0^2} - g^2 \arccos(g_0/g),$$

then differentiating $f(g)$ with respect to g , we obtain

$$f'(g) = -2g \arccos(g_0/g).$$

Since $f(g_0) = 0$ and $f'(g) < 0$, then $f(g) < 0$ when $g > g_0$, thus $d\tau_0/dg < 0$ when $g > g_0$.

Summarizing the above discussions, we obtain the following conclusions. If $g_0 < g < \gamma$ and $0 < \tau < \tau_0$, one eigenvalue $d-r$ is negative, all other eigenvalues also have negative real parts [1,4], and the equilibrium C is stable; if $g_0 < g < \gamma$ and $\tau = \tau_0$, there is a pair of purely imaginary roots and all other eigenvalues have negative real parts; if $g_0 < g < \gamma$ and $\tau_0 < \tau < \tau_1$, a pair of eigenvalues has positive real parts, all other eigenvalues have negative real parts, and the equilibrium C is unstable, and so on. If the time delay τ continues to increase, $g_0 < g < \gamma$ and $\tau = \tau_j$, there is a pair of purely imaginary roots; thus, if $g_0 < g < \gamma$ and $\tau_j < \tau < \tau_{j+1}$, $j + 1$ pair of eigenvalues has positive real parts, all other eigenvalues have negative real parts, and the equilibrium C is unstable.

Extracting the parts about the stability of the equilibrium C , we arrive at the following theorem.

Theorem 4. *If $0 < g < g_0$, the equilibrium C is unstable for all time delays $\tau \geq 0$; if $g_0 < g < \gamma$ and $0 < \tau < \tau_0$, the equilibrium C is stable; if $g_0 < g < \gamma$ and $\tau > \tau_0$, the equilibrium C is unstable. Moreover, with the increase of the grazing intensity g , the critical delay value τ_0 decreases.*

It is worth noting that when $\tau = \tau_j$, if C is an internal equilibrium, Hopf bifurcation will appear and a nontrivial periodic solution around the equilibrium C will arise; however, since C is a boundary equilibrium, we are not clear that system (8) possesses a nontrivial periodic solution around the equilibrium C or not. Also, if $g = g_0$ and $\tau = 0$, the equilibrium C is saddle-node (unstable); if $g = g_0$ and $\tau > 0$, 0 is an eigenvalue of the linearized equation of system (8) at the equilibrium C , which is a critical case, and the stability of the equilibrium C depends on high order terms of system (8). The dependence of τ_0 on g is graphically showed in Fig. 6.

Now we are going to consider the stability of the equilibrium $B(1 - \frac{g}{\gamma}, 0)$. At the equilibrium $B(1 - \frac{g}{\gamma}, 0)$, A_1, A_2 take the form respectively

$$A_1 = \begin{pmatrix} 2g - \gamma & (a - \gamma)(1 - \frac{g}{\gamma}) \\ 0 & -d - a + (a + r)\frac{g}{\gamma} \end{pmatrix}, \quad A_2 = \begin{pmatrix} -g & -g + \frac{g^2}{\gamma} \\ 0 & 0 \end{pmatrix}.$$

Then the corresponding characteristic equation is

$$\begin{aligned} \det[\lambda I - A_1 - A_2 e^{-\lambda\tau}] &= \begin{vmatrix} \lambda + \gamma - 2g + g e^{-\lambda\tau} & -(a - \gamma)(1 - \frac{g}{\gamma}) + g e^{-\lambda\tau} - \frac{g^2}{\gamma} e^{-\lambda\tau} \\ 0 & \lambda + d + a - (a + r)\frac{g}{\gamma} \end{vmatrix} \\ &= \left[\lambda + d + a - (a + r)\frac{g}{\gamma} \right] (\lambda + \gamma - 2g + g e^{-\lambda\tau}) = 0. \end{aligned}$$

Hence one eigenvalue is

$$\lambda_1 = -d - a + (a + r)\frac{g}{\gamma} = \frac{a + r}{\gamma}(g - g_1),$$

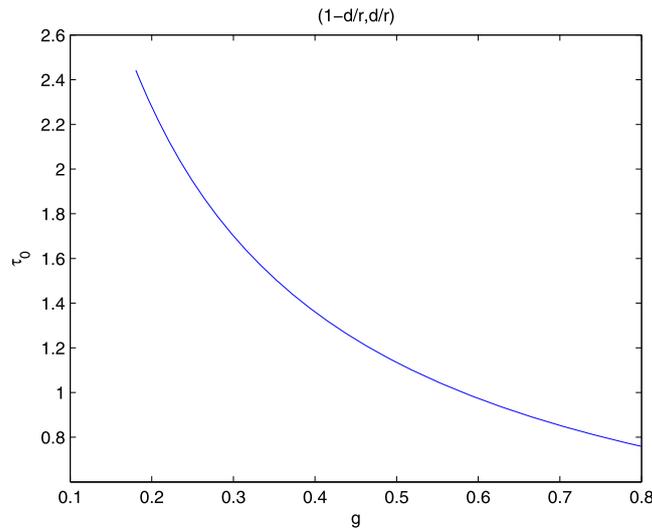


Fig. 6. τ_0 is a decreasing function of g .

and the other eigenvalues satisfy

$$\lambda = 2g - \gamma - ge^{-\lambda\tau}. \tag{12}$$

Let us recall the results when $\tau = 0$. For $\tau = 0$, the eigenvalues are $\lambda_1 = \frac{a+r}{\gamma}(g - g_1)$ and $\lambda_2 = g - \gamma$. Thus if $0 < g < g_1$, then $\lambda_1, \lambda_2 < 0$ and the equilibrium B is a stable node; if $g = g_1$, then $\lambda_1 = 0, \lambda_2 < 0$ and the equilibrium B is an unstable saddle-node; if $g_1 < g < \gamma$, then $\lambda_1 > 0, \lambda_2 < 0$ and the equilibrium C is an unstable saddle.

For $\tau > 0$, similar to the discussions about the equilibrium C , we assume that $\lambda(\tau) = \alpha(\tau) + i\omega(\tau)$ is a root of Eq. (12) satisfying $\alpha(\tau^*) = 0, \lambda(\tau^*) = i\omega(\tau^*) = i\omega$ for some $\tau^* > 0$. Then

$$i\omega = 2g - \gamma - g \cos \omega\tau^* + gi \sin \omega\tau^*.$$

Separating the real and imaginary parts, we have

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

Adding up the squares of both equations, by $\cos^2 \omega\tau^* + \sin^2 \omega\tau^* = 1$, we obtain

$$\left(\frac{\omega}{g}\right)^2 + \left(\frac{2g - \gamma}{g}\right)^2 = 1,$$

which implies that

$$\omega^2 = (\gamma - g)(3g - \gamma).$$

Thus, if $0 < g \leq \frac{\gamma}{3}$, Eq. (12) has no purely imaginary roots. Also, since $0 < g < \gamma$, 0 is not a root of Eq. (12).

If $g_1 \leq \frac{\gamma}{3}$, then when $0 < g < g_1$, Eq. (12) has no purely imaginary roots, and all roots have negative real parts for all time delays $\tau \geq 0$ [1,4], and the equilibrium B is stable.

If $g_1 > \frac{\gamma}{3}$, then when $0 < g \leq \gamma/3$, Eq. (12) has no purely imaginary roots, and all roots have negative real parts for all time delays $\tau \geq 0$ [1,4], and the equilibrium B is stable; if $\frac{\gamma}{3} < g < g_1$, when

$$\tau = \tau_j = \frac{1}{\omega} \left[\arccos \left(2 - \frac{\gamma}{g} \right) + 2j\pi \right], \quad j = 0, 1, 2, \dots,$$

Eq. (12) has a pair of purely imaginary roots $\pm i\omega$, where

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

Also we are interested in the transversality condition when the time delay τ crosses τ_j . Now we compute $\frac{d\tau}{d\lambda}$ from (12) and obtain

$$\frac{d\tau}{d\lambda} = \frac{e^{\lambda\tau}}{g\lambda} - \frac{\tau}{\lambda}.$$

The real part of $\frac{d\tau}{d\lambda}$ when $\lambda = \pm i\omega$ is

$$\left. \frac{d \operatorname{Re} \tau}{d\lambda} \right|_{\lambda = \pm i\omega} = \frac{\sin \omega\tau}{g\omega} = \frac{1}{g^2} > 0,$$

which implies that

$$\left. \frac{d \operatorname{Re} \lambda}{d\tau} \right|_{\tau = \tau_j} > 0$$

for $j = 0, 1, 2, \dots$

Therefore once τ crosses τ_j for every j , there exists a pair of eigenvalues which pass through the imaginary axis from the left to the right, and hence when $\tau > \tau_0$ the equilibrium B loses the stability and no longer gain. More precisely, if $\frac{\gamma}{3} < g < g_1$, when $0 < \tau < \tau_0$, all eigenvalues of the linearized equation at the equilibrium B have negative real parts, and the equilibrium B is stable; when $\tau = \tau_0$, the characteristic equation (12) has a pair of purely imaginary roots; according to the transversality condition, 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 B is unstable.

Similarly, differentiating τ_0 with respect to g gives

$$\frac{d\tau_0}{dg} = -\frac{1}{\omega^2} \left(\frac{2\gamma - 3g}{\omega} \arccos \left(2 - \frac{\gamma}{g} \right) + \frac{\gamma}{g} \right).$$

If $2d < r$, then $g_1 < 2\gamma/3$, thus $d\tau_0/dg < 0$ when $\gamma/3 < g < g_1$.

If $g = g_1$, when $\tau = 0$, the equilibrium B is an unstable saddle-node; when $\tau > 0$, $\lambda_1 = 0$, and other eigenvalues also satisfy Eq. (12). If $g_1 \leq \frac{\gamma}{3}$, for all $\tau > 0$ the roots of Eq. (12) have negative real parts, thus the eigenvalues of the linearized equation at the equilibrium B have negative real parts, except for zero root; if $g_1 > \frac{\gamma}{3}$, when $\tau = \tau_j$ ($j = 0, 1, 2, \dots$), Eq. (12) has a pair of purely imaginary roots, similarly when $\tau_j < \tau < \tau_{j+1}$, the linearized equation at the equilibrium B has $j + 1$ pair eigenvalues with positive real parts and zero root, others with negative real parts.

If $g_1 < g < \gamma$, for all $\tau \geq 0$, $\lambda_1 > 0$, and the equilibrium B is unstable. Similarly, if $g_1 > \frac{\gamma}{3}$, when $\tau = \tau_j$ ($j = 0, 1, 2, \dots$), Eq. (12) has a pair of purely imaginary roots, and when $\tau_j < \tau < \tau_{j+1}$, there exist a positive eigenvalue, $j + 1$ pair eigenvalues with positive real parts, the others with negative real parts. If $g_1 \leq \frac{\gamma}{3}$, when $g_1 < g \leq \frac{\gamma}{3}$, Eq. (12) has no purely imaginary roots, and thus all roots of Eq. (12) have

negative real parts, therefore the eigenvalues of the linearized equation at the equilibrium B have negative real parts, except for a positive eigenvalue. If $\frac{\gamma}{3} < g < \gamma$, Eq. (12) has a pair of purely imaginary roots, and when $\tau_j < \tau < \tau_{j+1}$, there exist a positive eigenvalue, $j + 1$ pair eigenvalues with positive real parts, the others with negative real parts.

Extracting the parts about the stability of the equilibrium B , we arrive at the following theorem and table.

Theorem 5. *If $g_1 \leq \frac{\gamma}{3}$, then when $0 < g < g_1$, the equilibrium B is stable for all time delays $\tau \geq 0$; if $g_1 > \frac{\gamma}{3}$, when $0 < g \leq \gamma/3$, the equilibrium B is stable for all time delays $\tau \geq 0$; if $g_1 > \frac{\gamma}{3}$, when $\frac{\gamma}{3} < g < g_1$ and $0 < \tau < \tau_0$, the equilibrium B is stable; if $g_1 > \frac{\gamma}{3}$, when $\frac{\gamma}{3} < g < g_1$ and $\tau > \tau_0$, the equilibrium B is unstable; if $g_1 < g < \gamma$, the equilibrium B is unstable for all time delays $\tau \geq 0$. Moreover, with the increase of the grazing intensity g , the critical delay value τ_0 decreases.*

$g_1 \leq \frac{\gamma}{3} \begin{cases} 0 < g < g_1, & B \text{ is stable} \\ g_1 < g < \gamma, & B \text{ is unstable} \end{cases}$
$g_1 > \frac{\gamma}{3} \begin{cases} 0 < g \leq \frac{\gamma}{3}, & B \text{ is stable} \\ \frac{\gamma}{3} < g < g_1 \begin{cases} 0 < \tau < \tau_0, & B \text{ is stable} \\ \tau > \tau_0, & B \text{ is unstable} \end{cases} \\ g_1 < g < \gamma, & B \text{ is unstable} \end{cases}$

Also when $\tau = \tau_j$, we are not clear that system (8) possesses a nontrivial periodic solution around the equilibrium B or not. At the same time, if $g = g_1$ and $\tau = 0$, the equilibrium B is saddle-node (unstable); if $g = g_1$ and $\tau > 0$, 0 is a simple eigenvalue of the linearized equation of system (8) at the equilibrium B , we do not know whether the equilibrium B is stable or not.

The another possible equilibrium is the internal equilibrium $E^*(x^*, y^*)$. According to Section 2, we know that if $g_0 < g < g_1$, E^* exists, and when $\tau = 0$, E^* is an unstable saddle.

For $\tau > 0$, at $E^*(x^*, y^*)$, A_1, A_2 take the form respectively

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

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

The corresponding characteristic equation is

$$\det[\lambda I - A_1 - A_2 e^{-\lambda\tau}] = \begin{vmatrix} \lambda - \gamma + 2\gamma x^* - (a - \gamma)y^* + \frac{g}{1-y^*} e^{-\lambda\tau} & -(a - \gamma)x^* + \frac{gx^*}{(1-y^*)^2} e^{-\lambda\tau} \\ (a + r)y^* & \lambda + ry^* \end{vmatrix}$$

$$= \lambda^2 + \lambda \left(ry^* + \gamma x^* - \frac{g}{1-y^*} \right) + \lambda e^{-\lambda\tau} \frac{g}{1-y^*}$$

$$+ y^* \left(ra - ad + d\gamma - \frac{2rg}{1-y^*} \right) + e^{-\lambda\tau} \frac{dgy^*}{(1-y^*)^2}$$

$$= 0.$$

Let $\bar{a} = ry^* + \gamma x^* - \frac{g}{1-y^*}$, $\bar{b} = \frac{g}{1-y^*}$, $\bar{c} = y^*(ra - ad + d\gamma - \frac{2rg}{1-y^*})$, $\bar{d} = \frac{dgy^*}{(1-y^*)^2}$, then the characteristic equation becomes

$$\lambda^2 + \bar{a}\lambda + \bar{b}\lambda e^{-\lambda\tau} + \bar{c} + \bar{d}e^{-\lambda\tau} = 0. \tag{13}$$

When $\tau = 0$, the characteristic equation (13) is

$$\lambda^2 + (\bar{a} + \bar{b})\lambda + \bar{c} + \bar{d} = 0. \tag{14}$$

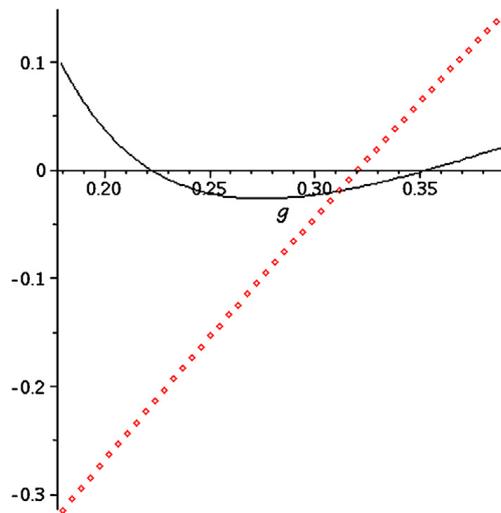


Fig. 7. The line denotes Δ , the points display $s(g)$. Denote the intersection points of the line and the horizontal axis by g_2 and g_3 (where $g_2 < g_3$).

According to the conclusion in Section 2, there are one positive eigenvalue and one negative eigenvalue for Eq. (14), which implies that $\bar{c} + \bar{d} < 0$. Since $\bar{d} > 0$, then $\bar{c} < -\bar{d} < 0$, and hence yields $\bar{c}^2 > \bar{d}^2$.

When $\tau > 0$, we suppose that $\lambda(\tau) = \alpha(\tau) + i\omega(\tau)$ is a root of Eq. (13) satisfying $\lambda(\tau^*) = i\omega(\tau^*) = i\omega$, $\alpha(\tau^*) = 0$ for some $\tau^* > 0$. Then

$$-\omega^2 + \bar{a}i\omega + \bar{b}i\omega e^{-i\omega\tau^*} + \bar{c} + \bar{d}e^{-i\omega\tau^*} = 0.$$

Separating the real and imaginary parts, we get

$$\begin{cases} \bar{c} - \omega^2 + \bar{b}\omega \sin \omega\tau^* + \bar{d} \cos \omega\tau^* = 0, \\ \bar{a}\omega + \bar{b}\omega \cos \omega\tau^* - \bar{d} \sin \omega\tau^* = 0. \end{cases} \tag{15}$$

Adding up the squares of both equations, by $\cos^2 \omega\tau^* + \sin^2 \omega\tau^* = 1$, we obtain

$$\omega^4 - (\bar{b}^2 - \bar{a}^2 + 2\bar{c})\omega^2 + \bar{c}^2 - \bar{d}^2 = 0. \tag{16}$$

Denote $s = s(g) = \bar{b}^2 - \bar{a}^2 + 2\bar{c}$, $t = t(g) = \bar{c}^2 - \bar{d}^2 > 0$, and $\Delta = \Delta(g) = s^2 - 4t$ (see Fig. 7). Then Eq. (16) becomes

$$\omega^4 - s\omega^2 + t = 0.$$

Now we are going to discuss the stability of the internal equilibrium E^* according to the number of positive roots for Eq. (16).

Case 1. $\Delta < 0$ (if we fix the other parameters except for g , then this case corresponds to that $g \in (g_2, g_3)$ in Fig. 7, here we assume that $g_0 < g_2 < g_3 < g_1$ without loss of generality). Now Eq. (16) has no positive roots. Thus, the characteristic equation (13) has no purely imaginary roots, the number of eigenvalues with positive real parts of the characteristic equation (13) does not depend on the time delay τ [1,4], and for all time delays $\tau \geq 0$, the linearized equation at the equilibrium E^* has one eigenvalue with positive real part, the others with negative real parts. Therefore the equilibrium E^* is unstable.

Case 2. $\Delta = 0$, $s < 0$, which corresponds to $g = g_2$ in Fig. 7. Similar to Case 1, Eq. (16) has no any positive roots. Then for all time delays $\tau \geq 0$, the linearized equation at the equilibrium E^* has one eigenvalue with positive real part, the others with negative real parts, and hence the equilibrium E^* is unstable.

Case 3. $\Delta = 0, s > 0$, which corresponds to $g = g_3$ in Fig. 7. Now Eq. (16) has a pair of positive roots with double multiplicity. Thus, when the time delay

$$\tau = \tau_n = \frac{1}{\omega} \cos^{-1} \left\{ \frac{\bar{d}(\omega^2 - \bar{c}) - \omega^2 \bar{a}\bar{b}}{\bar{b}^2 \omega^2 + \bar{d}^2} \right\} + \frac{2\pi n}{\omega} \quad (n = 0, 1, \dots),$$

the characteristic equation (13) has a pair of purely imaginary roots with double multiplicity $\pm i\omega$, where $\omega^2 = \frac{s}{2}$. If there exist purely imaginary roots, we need to know that when τ crosses to τ_n , how real parts of eigenvalues change. Differentiating (13) with respect to τ yields that

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

which implies that

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{(2\lambda + \bar{a})e^{\lambda\tau} + \bar{b}}{\lambda(\bar{b}\lambda + \bar{d})} - \frac{\tau}{\lambda}, \quad e^{\lambda\tau} = \frac{-(\bar{b}\lambda + \bar{d})}{\lambda^2 + \bar{a}\lambda + \bar{c}}.$$

Therefore,

$$\begin{aligned} \operatorname{Re} \left\{ \frac{d\lambda}{d\tau} \right\}_{\lambda=i\omega_{\pm}} &= \left\{ \operatorname{Re} \left[\frac{-(2\lambda + \bar{a})}{\lambda(\lambda^2 + \bar{a}\lambda + \bar{c})} \right]_{\lambda=i\omega_{\pm}} + \operatorname{Re} \left[\frac{\bar{b}}{\lambda(\bar{b}\lambda + \bar{d})} \right]_{\lambda=i\omega_{\pm}} \right\} \\ &= \left\{ \frac{\bar{a}^2 - 2(\bar{c} - \omega^2)}{\bar{a}^2 \omega^2 + (\omega^2 - \bar{c}^2)} - \frac{\bar{b}^2}{\bar{b}^2 \omega^2 + \bar{d}^2} \right\} \\ &= \{ \bar{a}^2 - \bar{b}^2 - 2\bar{c} + 2\omega^2 \} \\ &= 0, \end{aligned}$$

and the transversality condition does not hold. Thus, the direction of movement of eigenvalue with the increase τ depends on the higher derivative, and we omit the detail.

Case 4. $\Delta > 0, s < 0$, which corresponds to $g_0 < g < g_2$ in Fig. 7. Similar to Case 1, Eq. (16) has no any positive roots. Then for all time delays $\tau \geq 0$, the linearized equation at the equilibrium E^* has one eigenvalue with positive real part, the others with negative real parts, and hence the equilibrium E^* is unstable.

Case 5. $\Delta > 0, s > 0$, which corresponds to $g_3 < g < g_1$ in Fig. 7. Now Eq. (16) has two positive roots

$$\omega_{\pm}^2 = \frac{1}{2}(s \pm \Delta^{1/2}),$$

when τ takes the following values (see Fig. 8)

$$\begin{aligned} \tau_{n,1} &= \frac{1}{\omega_+} \cos^{-1} \left\{ \frac{\bar{d}(\omega_+^2 - \bar{c}) - \omega_+^2 \bar{a}\bar{b}}{\bar{b}^2 \omega_+^2 + \bar{d}^2} \right\} + \frac{2\pi n}{\omega_+} \quad (n = 0, 1, \dots) \\ \tau_{n,2} &= \frac{1}{\omega_-} \cos^{-1} \left\{ \frac{\bar{d}(\omega_-^2 - \bar{c}) - \omega_-^2 \bar{a}\bar{b}}{\bar{b}^2 \omega_-^2 + \bar{d}^2} \right\} + \frac{2\pi n}{\omega_-} \quad (n = 0, 1, \dots). \end{aligned}$$

Similar to Case 3, we have

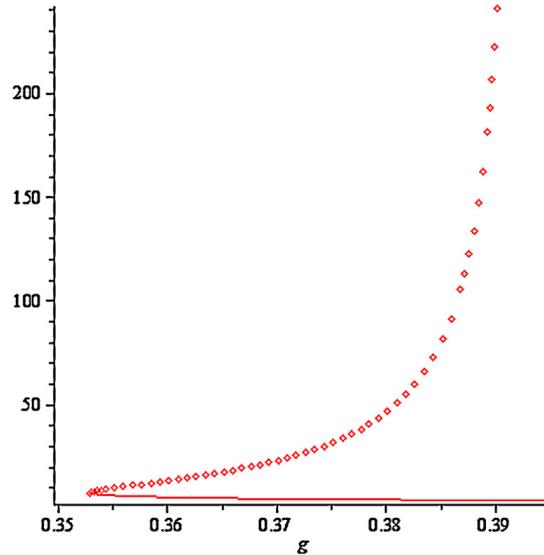


Fig. 8. The line denotes $\tau_{0,1}$, the points denote $\tau_{0,2}$.

$$\begin{aligned} \operatorname{Re}\left\{\frac{d\lambda}{d\tau}\right\}_{\lambda=i\omega_{\pm}} &= \left\{ \operatorname{Re}\left[\frac{-(2\lambda + \bar{a})}{\lambda(\lambda^2 + \bar{a}\lambda + \bar{c})}\right]_{\lambda=i\omega_{\pm}} + \operatorname{Re}\left[\frac{\bar{b}}{\lambda(\bar{b}\lambda + \bar{d})}\right]_{\lambda=i\omega_{\pm}} \right\} \\ &= \left\{ \frac{\bar{a}^2 - 2(\bar{c} - \omega^2)}{\bar{a}^2\omega^2 + (\omega^2 - \bar{c}^2)} - \frac{\bar{b}^2}{\bar{b}^2\omega^2 + \bar{d}^2} \right\} \\ &= \{\bar{a}^2 - \bar{b}^2 - 2\bar{c} + 2\omega^2\} \\ &= \left\{ \pm 2 \left\{ \frac{1}{4}(\bar{b}^2 - \bar{a}^2 + 2\bar{c})^2 - (\bar{c}^2 - \bar{d}^2) \right\}^{1/2} \right\}. \end{aligned}$$

Therefore,

$$\operatorname{Re}\left\{\frac{d\lambda}{d\tau}\right\}_{\lambda=i\omega_{+}} > 0, \quad \operatorname{Re}\left\{\frac{d\lambda}{d\tau}\right\}_{\lambda=i\omega_{-}} < 0.$$

Since the characteristic equation (13) with $\tau = 0$ has one positive eigenvalue and one negative eigenvalue, and $\tau_{0,1} < \tau_{0,2}$ (see Fig. 8), then when $0 < \tau < \tau_{0,1}$, the characteristic equation (13) has one positive eigenvalue and the others with negative real parts, thus the equilibrium E^* is unstable; when $\tau = \tau_{0,1}$, the characteristic equation (13) has a pair of purely imaginary roots $\pm i\omega_{+}$, and the transversality sign is positive, thus Hopf bifurcation occurs, and a nontrivial periodic solution appears; when $\tau_{0,1} < \tau < \tau_{0,2}$, the characteristic equation (13) has one positive eigenvalue, a pair of eigenvalues with positive real parts, the others with negative real parts, hence the equilibrium E^* is unstable; when $\tau = \tau_{0,2}$, the characteristic equation (13) has a pair of purely imaginary roots $\pm i\omega_{-}$, and the transversality sign is negative, thus Hopf bifurcation occurs, and a nontrivial periodic solution appears; when $\tau_{0,2} < \tau < \tau_{1,1}$, the characteristic equation (13) has one positive eigenvalue and the others with negative real parts, thus the equilibrium E^* is unstable; when $\tau = \tau_{1,1}$, the characteristic equation (13) has a pair of purely imaginary roots $\pm i\omega_{+}$, and the transversality sign is positive, thus Hopf bifurcation occurs, and a nontrivial periodic solution appears, and so on. It is interesting that the transversality sign at $\pm i\omega_{+}$ is positive, the transversality sign at $\pm i\omega_{-}$ is negative, which leads to that after one cycle, the number of eigenvalues with positive real parts does not change.

Summarizing the above discussions, we obtain the following theorem.

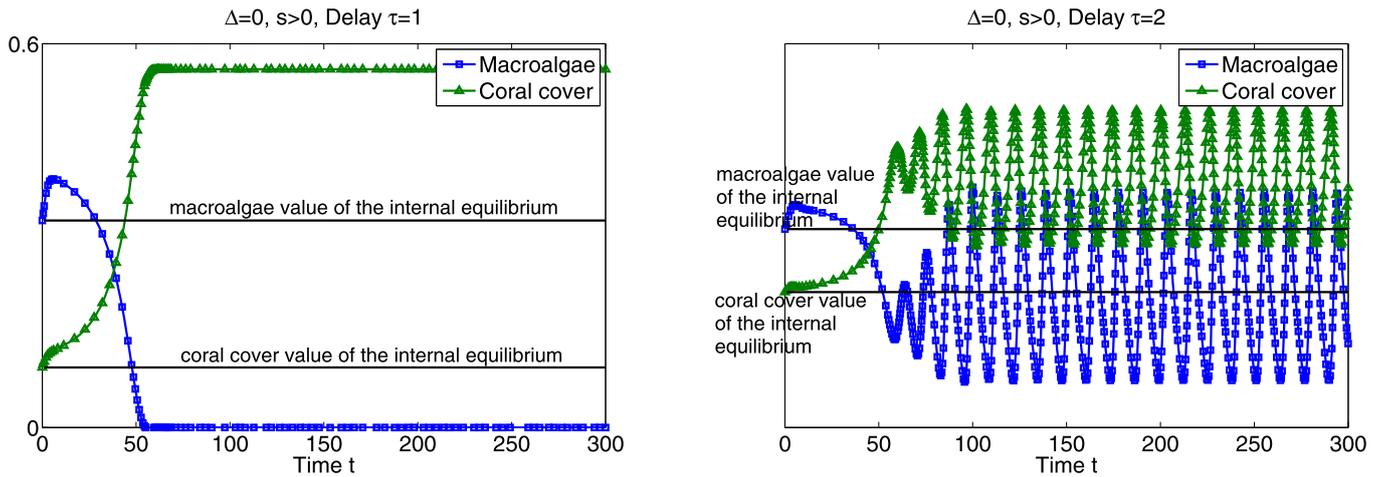


Fig. 9. Sample solutions starting from the neighborhood of E^* for the special case $\Delta = 0, s > 0$.

Theorem 6. *If $\Delta < 0$, or $\Delta = 0, s < 0$, or $\Delta > 0, s < 0$, for all time delays $\tau \geq 0$, the linearized equation at the internal equilibrium E^* has one positive eigenvalue, the others with negative real parts, thus the internal equilibrium E^* is unstable; if $\Delta > 0, s > 0$, for all time delays $\tau \geq 0$, the internal equilibrium E^* is unstable, moreover there exist two sequences $\tau_{n,1}, \tau_{n,2}$ ($n = 0, 1, 2, \dots$), when the time delay τ takes these values, Hopf bifurcations occur, and nontrivial periodic solutions appear.*

We remark that when $\Delta = 0, s > 0$, we do not know the dynamical behavior around the internal equilibrium E^* . Numerical simulations in Fig. 9 show that the internal equilibrium E^* is unstable in the case $\Delta = 0, s > 0$.

4. Summary and discussion

We provide global stability analysis of the coral reef ODE model (5), thus the dynamical behaviors are completely clear. First, we have found the attracting region for this model which is ecologically meaningful. At the same time, we have proved that this model has no limit cycles. Second, this model has three boundary equilibria: extinction state, macroalgae only state, coral only state. The extinction state is an unstable node, which implies that macroalgae and coral do not go extinct together. If we vary the grazing intensity only and fix the other parameters, the grazing intensity on the dynamics of the system has a decisive role: when the grazing intensity is lower ($0 < g < g_0$), macroalgae only state is a globally attracting node, which implies that macroalgae blooms; when the grazing intensity is higher ($g_1 < g < \gamma$), coral only state is a globally attracting node, which implies that coral blooms; when the grazing intensity is in some intermediate range ($g_0 < g < g_1$), the system has an unstable coexistence state, and macroalgae only state and coral only state are both stable, in this case bistability phenomenon appears, moreover there exists a heteroclinic orbit connecting the coexistence state with the three other states; when $g = g_0$ ($g = g_1$), transcritical bifurcation occurs, and coral only state (or macroalgae only state) is an unstable saddle-node.

In reality it takes a long time for algal turfs to arise after macroalgae are grazed. To capture this fact, we construct the delay model (8). Here the grazing intensity and the time delay are treated as varying parameters at the same time. The stability of the extinction state is the same as that in the ODE model (5). However, the stabilities of macroalgae only state and coral only state are changed; they depend not only on the grazing intensity but also on the time delay.

Let us restate the stability results of coral only state in the delay model (8). If the grazing intensity is less than g_0 , coral only state is unstable for all time delays $\tau \geq 0$; if the grazing intensity is large than g_0 , then there exists a critical delay value τ_0 such that if the delay is smaller than τ_0 , coral only state is stable, if the delay is larger than τ_0 , coral only state is unstable. Moreover, with the increase of the grazing intensity g ,

the critical delay value τ_0 decreases. For reef health, we need a high grazing rate and a short delay such that the coral only state is stable. In Caribbean reefs, researchers have observed macroalgal bloom, in which case the grazing rate is low. The ODE model is sufficient for Caribbean reefs, but for the current healthy reefs in which the grazing rate is usually large, the delay effect can play an important role in determining the coral reef in an equilibrium way or in an oscillatory way. The latter would make field data collection and health control much harder.

For simplicity, except for the grazing intensity and the time delay, we adopt the particular values given in (2) for the other parameters, then

$$0 < g_0 = 0.1795 < g_2 = 0.2223 < \frac{\gamma}{3} = 0.2667 < g_3 = 0.3529 < g_1 = 0.3927 < \gamma = 0.8.$$

Now we are in a position to state the stability results of macroalgae only state in the delay model (8): if the grazing intensity is larger than g_1 , macroalgae only state is unstable for all time delays $\tau \geq 0$; if the grazing intensity is less than $\gamma/3$, macroalgae only state is stable for all time delays $\tau \geq 0$; if $\frac{\gamma}{3} < g < g_1$, then there exists a critical delay value τ_0^* such that if the delay is smaller than τ_0^* , macroalgae only state is stable, if the delay is larger than τ_0^* , macroalgae only state is unstable. Moreover, with the increase of the grazing intensity g , the critical delay value τ_0^* decreases. These mathematical results can aid to answer the question for the reversibility of the unhealthy Caribbean reefs to healthy status. If we could increase the grazing rate and/or increase the delay effect, then the current Caribbean reefs can switch from the algae-dominant status to a more healthy status.

As for the internal equilibrium E^* , for all time delays $\tau \geq 0$, it is unstable. However, if $g_3 < g < g_1$, there exist two sequences $\tau_{n,1}, \tau_{n,2}$ ($n = 0, 1, 2, \dots$), when the time delay τ takes these values, Hopf bifurcations occur, and nontrivial periodic solutions appear. This result implies that a status between healthy and unhealthy can only exist in an oscillatory way. This phenomenon can only appear with the delay effect.

As a conclusion, if $0 < g < g_0$, the delay model (8) has no internal equilibria, but has three boundary equilibria, macroalgae only state is a unique locally stable equilibrium for all time delays $\tau \geq 0$; if $g_1 < g < \gamma$, the delay model (8) has no internal equilibria, but has three boundary equilibria, coral only state is a unique locally stable equilibrium for time delays $\tau < \tau_0$; if $g_0 < g < g_1$, the delay model (8) has an unstable internal equilibrium, and has three boundary equilibria. Moreover, among these, when $g_0 < g < \gamma/3$, macroalgae only state is stable for all time delays $\tau \geq 0$ and coral only state is stable for time delays $\tau < \tau_0$; when $\gamma/3 < g < g_1$, macroalgae only state and coral only state are stable for $\tau < \tau_0^*$ and $\tau < \tau_0$ respectively; especially, when $g_3 < g < g_1$, there exist two sequences $\tau_{n,1}, \tau_{n,2}$ ($n = 0, 1, 2, \dots$), when the time delay τ takes these values, Hopf bifurcations occur.

Indeed, the coral reef ODE model (5) is a special case of the delay model (8) ($\tau = 0$), if the time delay is sufficiently small, for example, the time delay is smaller than τ_0 and τ_0^* , the stability results of the equilibria remain the same, however, if the time delay is larger than τ_0 and τ_0^* and $\gamma/3 < g < g_1$, macroalgae only state and coral only state are both unstable. Meanwhile, if $g_3 < g < g_1$ and $\tau = \tau_{n,1}, \tau_{n,2}$ ($n = 0, 1, 2, \dots$), the delay model (8) has a nontrivial periodic solution, but the ODE model (5) has no nontrivial periodic solutions for all g values.

Certainly, mathematical analysis of the delay model (8) is not complete, more precisely, we only discussed the local stability of these equilibria. Compare the delay model (8) with the ODE model (5), we have not known the dynamical behaviors in some critical cases and whether there exists a heteroclinic orbit connecting the coexistence state with the three other states. In order to keep the conservation law in the delay model, we put the delay in both M and T equations, in which case the positivity of M is not guaranteed. We can show that C and T are nonnegative but M can be negative for nonnegative initial functions. Hence, we need to find conditions to guarantee M is nonnegative. When the delay is large enough, then the oscillations have large amplitudes, in which case M can be negative for some time intervals. Actually this scenario never occurs

in real coral reefs, and of course our delay model cannot be applied. Numerically, when M can be negative, that is, $M = 0$ at some \bar{t} , then we should terminate the model simulation, and this means a perfectly healthy reef. If we only put the delay in T equation but not in M equation, then we can easily gain nonnegativity of all variables and the forward invariant set $\Omega_{\text{delay}} = \{(M, C, T): M \geq 0, C \geq 0, T \geq 0, M + C + T = 1\}$ or $\{(x, y): x \geq 0, y \geq 0, x + y \leq 1\}$, however, the conservation law disappears in this case. We welcome any idea to combine these two delay models together.

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References

- [1] E. Beretta, Y. Kuang, Geometric stability switch criteria in delay differential systems with delay dependent parameters, *SIAM J. Math. Anal.* 33 (2002) 1144–1165.
- [2] J.C. Blackwood, A. Hastings, The effect of time delays on Caribbean coral–algal interactions, *J. Theoret. Biol.* 273 (2011) 37–43.
- [3] J.C. Blackwood, A. Hastings, P.J. Mumby, The effect of fishing on hysteresis in Caribbean coral reefs, *Theor. Ecol.* 5 (2012) 105–114.
- [4] K.L. Cooke, Z. Grossman, Discrete delay, distributed delay and stability switches, *J. Math. Anal. Appl.* 86 (1982) 592–627.
- [5] T.A. Gardner, I.M. Cote, J.A. Gill, Long-term region-wide declines in Caribbean corals, *Science* 301 (2003) 958–960.
- [6] T.P. Hughes, Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reefs, *Science* 265 (1994) 1547–1551.
- [7] T.P. Hughes, A.H. Baird, D.R. Bellwood, Climate change, human impacts, and the resilience of coral reefs, *Science* 301 (2003) 929–933.
- [8] L.J. McCook, J. Jompa, G. Diaz-pulido, Competition between corals and algae on coral reefs: a review of evidence and mechanisms, *Coral Reefs* 19 (2001) 400–417.
- [9] P.J. Mumby, The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs, *Ecol. Appl.* 16 (2006) 747–769.
- [10] P.J. Mumby, A. Hastings, H.J. Edwards, Thresholds and the resilience of Caribbean coral reefs, *Nature* 450 (2007) 98–101.
- [11] J.M. Pandolfi, R.H. Bradbury, E. Sala, Global trajectories of the long-term decline of coral reef ecosystems, *Science* 301 (2003) 955–958.
- [12] A. Singh, H. Wang, W. Morrison, H. Weiss, Modeling fish biomass structure at near pristine coral reefs and degradation by fishing, *J. Biol. Syst.* 20 (2012) 21–36.
- [13] H. Wang, W. Morrison, A. Singh, H. Weiss, Modeling inverted biomass pyramids and refuges in ecosystems, *Ecol. Model.* 220 (2009) 1376–1382.