Hysteresis in coral reefs under macroalgal toxicity and overfishing

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Abstract Macroalgae and corals compete for the available space in coral reef ecosystems. While herbivorous reef fish play a beneficial role in decreasing the growth of macroalgae, macroalgal toxicity and overfishing of herbivores leads to proliferation of macroalgae. The abundance of macroalgae changes the community structure towards a macroalgae-dominated reef ecosystem. We investigate coral-macroalgal phase shifts by means of a continuous time model in a food chain. Conditions for local asymptotic stability of steady states are derived. It is observed that in the presence of macroalgal toxicity and overfishing, the system exhibits hysteresis through saddle-node bifurcation and transcritical bifurcation. We examine the effects of time lags in the liberation of toxins by macroalgae and the recovery of algal turf in response to grazing of herbivores on macroalgae by performing equilibrium and stability analyses of delay-differential forms of the ODE model. Computer simulations have been carried out to illustrate the different analytical results.

Keywords Macroalgal toxicity · Phase shifts · Hysteresis · Saddle-node bifurcation · Transcritical bifurcation

1 Introduction

Macroalgae play important roles in the ecology of coral reefs. Despite their recognized roles in coral reefs, macroalgal cover on reefs is increasingly related to coral

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reef decline [1, 2]. Reefs have shown a tendency to exist in alternate coral or algae-dominated states [3, 4]. As observed by Done [5] and Bellwood et al. [6], degradation of coral reefs often exhibits phase shifts in community structure for which corals decline with an increase in abundance of macroalgae. Phase shifts in coral reefs are mostly driven by the competition for light and space between corals and macroalgae [7]. Macroalgae encroach on coral basins by shading or abrasion and allelopathic chemical defenses [8]. Also, faster-growing macroalgae dominate coral reefs by reducing the available space for the successful settlement of coral larvae [9, 10]. Although corals grow in the range of approximately 2 – 185 mm per year, the collective growth of many colonies across a large area can return the area to coral dominance within a few years [11].

Coral reefs throughout the world have suffered substantial declines in coral cover due to rapid loss of herbivores [12]. In coral reef ecosystems, macroalgae and corals compete for space and when herbivores are not present, the faster growing macroalgae often overgrow corals, depriving them of essential sunlight and causing their decline [10, 13–15]. The grazing of macroalgae by herbivores contributes to the resilience of the coral-dominated reef. Researchers observe that overfishing of herbivores is one of the causes of proliferation of macroalgae on coral reefs that can lead to a permanent shift in regime in which macroalgae, once dominant, inhibit coral settlement [16–18]. A shift of regime occurs when the grazing rate of herbivores or the toxicity level of the macroalgae cross some critical threshold. As different sets of feedbacks stabilize each alternative regime, returning the system from the macroalgae-dominated regime to the coral-dominated regime becomes difficult. Consequently, the threshold for a shift of regime and for its reversal can become different, a phenomenon known as hysteresis.

Several algae species are known to produce allelopathic chemical compounds that are detrimental to corals [19]. The settlement and survival of coral larvae are known to be affected by the allelochemicals present on toxic macroalgae [20]. Field observations by [21, 22] demonstrate that numerous macroalgae species are particularly chemically toxic to corals, damaging coral tissues when in contact by transferring hydrophobic allelochemicals present on algal surfaces, and leading to reduced fecundity of corals and even coral mortality.

Mumby et al. [23] introduced a model on a coral reef ecosystem to analyze the effects of grazing on coral-macroalgal phase shifts. The model is based on the assumption that a fraction of the area of the seabed is occupied by macroalgae, corals, and turf algae with macroalgal vegetative growth on turf algae, macroalgal overgrowth on corals and grazing of herbivores on macroalgae. Blackwood et al. [24] modified this model by introducing herbivorous parrotfish into the system and studied the grazing dynamics of parrotfish. Our model originates from the models used in [23, 24] and is a direct extension of the model studied in [24] under the assumption that macroalgae recruits externally from the surrounding seascape and produce toxins that inhibit the growth of corals. We have also considered the natural mortality of macroalgae and examine the feedback resulting from toxin-induced mortality of corals on the dynamics of coral reef ecosystem. We examine the effects of a discrete time lag in the recovery of algal turf after macroalgae is grazed by herbivores. Also, we assume that macroalgae liberate toxins at some discrete time lag to account for the time required for maturation. In the present paper, the main emphasis will be placed on studying the dynamic behavior of the system and the role of macroalgal toxicity and herbivore-harvesting in coral-macroalgal phase shifts.

2 The basic model

We model three benthic groups: corals, turf algae, and toxic macroalgae, competing for space on the seabed by considering a fraction of seabed available for their growth. In formulating the model, we assume that macroalgae are always present in a coral reef ecosystem irrespective of the abundance of corals in a seabed. Let M be the fraction of seabed covered by macroalgae, C be the fraction of seabed covered by corals and T represent the fraction of seabed occupied by turf-algae so that $M + C + T = c_0$ (constant) at any instant t . For simplicity, we have ignored the possibility of any empty space in the seabed.

We make the following assumptions in formulating the mathematical model:

- (H_1) Corals are overgrown by macroalgae, at a rate α .
- (H_2) Macroalgae spread vegetatively over algal turfs at a rate a .
- (H_3) Colonization rate of newly immigrated macroalgae on algal turf is b .
- (H_4) Corals recruit to and overgrow algal turfs at a rate r .
- (H_5) Macroalgae and corals have natural mortality rates d_1 and d_2 respectively.
- (H_6) Death rate of corals from macroalgal toxicity [19] is γ .
- (H_7) The grazing rate of herbivorous fish on macroalgae is $\frac{g(1-\beta)}{M+T}$ per unit area of algal cover, where g is the maximal grazing rate of herbivorous fish in absence of harvesting and β represents the harvest-mediated reduction in grazing of herbivorous fish ($0 \leq \beta < 1$).

A schematic diagram of the system is given in Fig. 1. Parameters are listed in Table 1. The reef dynamics are thus described as a system of nonlinear differential equations:

$$\begin{aligned}\frac{dM}{dt} &= M \left\{ \alpha C - \frac{g(1-\beta)}{M+T} - d_1 \right\} + (aM + b)T \\ \frac{dC}{dt} &= C \{ rT - (\alpha + \gamma)M - d_2 \} \\ \frac{dT}{dt} &= M \left\{ \frac{g(1-\beta)}{M+T} + d_1 \right\} + d_2 C + \gamma MC - T(aM + rC + b)\end{aligned}\quad (1)$$

where $M(0) > 0$, $C(0) \geq 0$ and $T(0) > 0$.

Without any loss of generality, we assume that $c_0 = 1$. Then from (1) we obtain

$$\begin{aligned}\frac{dM}{dt} &= M \left\{ \alpha C - \frac{g(1-\beta)}{1-C} - d_1 \right\} + (aM + b)(1 - M - C) \equiv f^1 \\ \frac{dC}{dt} &= C \{ r(1 - M - C) - (\alpha + \gamma)M - d_2 \} \equiv f^2\end{aligned}\quad (2)$$

where $0 < M(0) < 1$, $0 \leq C(0) < 1$.

We observe that the right-hand sides of the equations in the system (2) are smooth functions of the variables M , C and the parameters. As long as these quantities are non-negative, local existence and uniqueness properties hold in the positive octant.

3 Equilibria and their stability

In this section, we determine biologically feasible equilibrium solutions of the model and investigate the dependence of their stability on several key parameters.

The system (2) possesses the following equilibria:

Fig. 1 Schematic diagram of coral-macroalgal competition for occupying turf algae

- (i) Coral-free equilibrium $E_0 = (M_0, 0)$, where $M_0 = \frac{a-b-d_1-g(1-\beta)+\sqrt{(a-b-d_1-g(1-\beta))^2+4ab}}{2a}$;
- (ii) interior equilibrium $E^* = (M^*, C^*)$, given by the intersections of the nullclines $M \left\{ \alpha C - \frac{g(1-\beta)}{1-C} - d_1 \right\} + (aM + b)(1 - M - C) = 0$ and $r(1 - M - C) = (\alpha + \gamma)M + d_2 = 0$ in the interior of the first quadrant. C^* is given by the equation $a_1 C^3 + a_2 C^2 + a_3 C + a_4 = 0$ and $M^* = p + q C^*$, where

$$\begin{aligned}
 a_1 &= q\{a(1+q) - \alpha\}, a_2 = q(\alpha + d_1) - \alpha p - aq(1-p) + (1+q)(b + ap - aq), \\
 a_3 &= p(\alpha + d_1) - q\{d_1 + g(1-\beta)\} + (1-p)(aq - ap - b) - (1+q)(ap + b), \\
 a_4 &= (ap + b)(1-p) - p\{d_1 + g(1-\beta)\}, p = \frac{r-d_2}{r+\alpha+\gamma} \text{ and } q = \frac{-r}{r+\alpha+\gamma}.
 \end{aligned}$$

We analyze the stability of system (2) by using eigenvalue analysis of the Jacobian matrix evaluated at the appropriate equilibrium.

At E_0 , the eigenvalues of the Jacobian matrix of the system (2) are $-\sqrt{(a-b-d_1-g(1-\beta))^2+4ab}$ and $r - M_0(r + \alpha + \gamma) - d_2$. Therefore, all the eigenvalues of the Jacobian matrix are negative if $r - M_0(r + \alpha + \gamma) - d_2 < 0$. This gives the following lemma:

Lemma 3.1 *The system (2) is locally asymptotically stable at E_0 if $\gamma > \gamma_*$, where $\gamma_* = \frac{r-d_2-M_0(r+\alpha)}{M_0}$.*

Therefore, with high macroalgal toxicity, corals are eliminated from the system. The system is persistent at E^* if the boundary equilibrium E_0 repels interior trajectories. We see that the boundary equilibrium E_0 is unstable if $\gamma \leq \gamma_*$. Also, the system is bounded. The following lemma gives the condition of persistence of the system (2):

Lemma 3.2 *The system (2) is persistent at E^* if $\gamma \leq \gamma_*$.*

The Jacobian $J^* \equiv J(E^*)$ of the system (2) evaluated at an interior equilibrium E^* is

$$J^* = \begin{pmatrix} -(M^*C^*\alpha + aM^* + b) - (1 - M^* - C^*)(aM^* + b - a) & M^*(\alpha - a) - b - \frac{gM^*(1-\beta)}{(1-C^*)^2} \\ -C^*(r + \alpha + \gamma) & -rC^* \end{pmatrix}$$

The characteristic equation of the Jacobian J^* of the system (2) evaluated at an interior equilibrium E^* is $\lambda^2 + \lambda \left(rC^* - f_{M|E^*}^1 \right) + C^*(r + \alpha + \gamma)f_{C|E^*}^1 - rC^*f_{M|E^*}^1 = 0$. Therefore, all the eigenvalues of the Jacobian matrix are negative if $rC^* > f_{M|E^*}^1$ and $(r + \alpha + \gamma)f_{C|E^*}^1 > rf_{M|E^*}^1$. This gives the following lemma:

Lemma 3.3 *If $r > \frac{f_{M|E^*}^1}{C^*}$ and $(r + \alpha + \gamma)f_{C|E^*}^1 > rf_{M|E^*}^1$, the system (2) is locally asymptotically stable at E^* .*

Corollary 3.1 *The system (2) is bistable at E_0 and E^* if $\gamma > \gamma_*$, $r > \frac{f_{M|E^*}^1}{C^*}$ and $(r + \alpha + \gamma)f_{C|E^*}^1 > rf_{M|E^*}^1$.*

We consider the Dulac function [25] $B(M, C) = \frac{1}{MC}$, where $M, C > 0$. Then at (M^*, C^*) , we have $\nabla \cdot (Bf^1, Bf^2) = -\frac{1}{C^*} \left\{ a + \frac{rC^*}{M^*} + \frac{b(1-C^*)}{M^{*2}} \right\} < 0$.

Since this divergence has constant sign throughout the first quadrant, by Dulac's criterion we get the following lemma:

Lemma 3.4 *The system (2) has no closed orbit contained in $\{(M, C) : 0 < M \leq 1, 0 < C < 1\}$.*

Since there is no periodic solution for the system (2) in the first quadrant, by Poincaré-Bendixon theorem, it follows that every trajectory of the system (2) approaches asymptotically to an equilibrium point of the system (2).

Lemma 3.5 *If $0 < g < \frac{M_0(\alpha-a)-b}{M_0(1-\beta)}$, the system (2) undergoes a transcritical bifurcation at E_0 when γ crosses γ_{lemma} .*

Proof At $\gamma = \gamma_*$, we have

$$J_0 = \begin{pmatrix} -\sqrt{\{a-b-d_1-g(1-\beta)\}^2 + 4ab} & M_0\{\alpha-a-g(1-\beta)\}-b \\ 0 & 0 \end{pmatrix}$$

Therefore, the zero eigenvalue of the Jacobian matrix is simple.

Let V and W be the eigenvectors corresponding to the zero eigenvalue for J_0 and J_0^T , respectively. Then we obtain $V = (1 \ v_1)^T$ and $W = (0 \ 1)^T$, where $v_1 = \frac{\sqrt{\{a-b-d_1-g(1-\beta)\}^2 + 4ab}}{M_0\{\alpha-a-g(1-\beta)\}-b}$. Let us express the system (2) in the form $\dot{X} = f(M, C; \gamma)$, where

$$X = (M \ C)^T \text{ and } f(M, C; \gamma) = \begin{pmatrix} f^1 & f^2 \end{pmatrix}^T$$

Then $W^T f_\gamma(M_0, 0; \gamma_*) = 0$ and so no saddle-node bifurcation occurs at E_0 when γ crosses γ_* .

Also, $Df_\gamma(M_0, 0; \gamma_*)V = \begin{pmatrix} 0 \\ -M_0v_1 \end{pmatrix}$ and so $W^T[Df_\gamma(M_0, 0; \gamma_*)(V, V)] = -M_0v_1 \neq 0$. Now, we have $D^2f(M_0, 0; \gamma_*)(V, V) = \begin{pmatrix} -2a + 2\{\alpha - g(1-\beta) - a\}v_1 - gM_0(1-\beta)v_1^2 \\ -2(r+\alpha+\gamma_*)v_1 - 2rv_1^2 \end{pmatrix}$. This gives $W^T[D^2f(M_0, 0; \gamma_*)(V, V)] = -2v_1(r+\alpha+\gamma_*+rv_1)$. Now, if $g < \frac{M_0(\alpha-a)-b}{M_0(1-\beta)}$ holds, then $v_1 > 0$ and consequently, $W^T[D^2f(M_0, 0; \gamma_*)(V, V)] < 0$. Therefore, if $0 < g < \frac{M_0(\alpha-a)-b}{M_0(1-\beta)}$ is satisfied, by the Sotomayor theorem [26] it follows that the system (2) undergoes a transcritical bifurcation at E_0 when γ crosses γ_* . $\square$

Lemma 3.6 *If $r > \frac{f_{M|E^*}^1}{C^*}$ and $\eta \neq 0$, the system (2) undergoes a saddle-node bifurcation at E^* when γ crosses γ^* , where $\gamma^* = \frac{rf_{M|E^*}^1}{f_{C|E^*}^1} - r - \alpha$ and $\eta = -2a - \left(\frac{r+\alpha+\gamma^*}{r}\right) \left[2(\alpha-a) - \frac{g(1-\beta)\{2r(1-C^*)-M^*(r+\alpha+\gamma^*)\}}{r(1-C^*)^3}\right]$.*

Proof If $r > \frac{f_{M|E^*}^1}{C^*}$ and $\gamma = \gamma^*$, then $Tr(J^*) \neq 0$ and $Det(J^*) = 0$ and so, the zero eigenvalue of the Jacobian matrix is simple.

$$\text{At } \gamma = \gamma^* \text{ we have } J^* = \begin{pmatrix} f_{M|E^*}^1 & f_{C|E^*}^1 \\ -\frac{rC^*f_{M|E^*}^1}{f_{C|E^*}^1} & -rC^* \end{pmatrix}$$

Let V^* and W^* be the eigenvectors corresponding to the zero eigenvalue for J^* and J^{*T} , respectively. Then we obtain $V^* = \left(1 - \frac{r+\alpha+\gamma^*}{r}\right)^T$ and $W^* = \left(1 - \frac{f_{C|E^*}^1}{rC^*}\right)^T$. Therefore, $W^{*T}f_\gamma(M^*, C^*; \gamma^*) = -\frac{M^*f_{C|E^*}^1}{r} \neq 0$. We have $D^2f(M^*, C^*; \gamma^*)(V^*, V^*) = \begin{pmatrix} -2a - 2\left(\alpha - a - \frac{g(1-\beta)}{(1-C^*)^2}\right)\left(\frac{r+\alpha+\gamma^*}{r}\right) - \frac{gM^*(1-\beta)(r+\alpha+\gamma^*)^2}{r^2(1-C^*)^3} \\ 0 \end{pmatrix}$. Therefore, $W^{*T}[D^2f(M^*, C^*; \gamma^*)(V^*, V^*)] = -2a - \left(\frac{r+\alpha+\gamma^*}{r}\right) \left[2(\alpha-a) - \frac{g(1-\beta)\{2r(1-C^*)-M^*(r+\alpha+\gamma^*)\}}{r(1-C^*)^3}\right]$. Therefore, if $r > \frac{f_{M|E^*}^1}{C^*}$ and $\eta \neq 0$, the system (2) undergoes a saddle-node bifurcation at E^* when γ crosses γ^* , where $\eta = -2a - \left(\frac{r+\alpha+\gamma^*}{r}\right) \left[2(\alpha-a) - \frac{g(1-\beta)\{2r(1-C^*)-M^*(r+\alpha+\gamma^*)\}}{r(1-C^*)^3}\right]$. $\square$

Corollary 3.2 *Assume that the conditions of Lemma 3.4 and 3.5 are satisfied. If $\gamma_* < \gamma^*$ holds, a sharp transition with hysteresis occurs.*

By analyzing the system (2), we are now able to show that a sharp transition with hysteresis can be achieved by varying some of the parameter values.

To identify the impact of changes in macroalgal toxicity on coral cover, in Fig. 2a, we plot the solutions of the nullcline equations $M\left\{\alpha C - \frac{g(1-\beta)}{1-C} - d_1\right\} + (aM+b)(1-M-C) = 0 = C\{r(1-M-C) - (\alpha+\gamma)M - d_2\}$ in the $C-\gamma$ plane, yielding a bifurcation diagram. Coordinates of stable equilibria are shown in blue, and unstable equilibria are shown in red. The region I represents monostability at E^* for $0 \leq \gamma < \gamma_*$, representing the coral-dominated state for all non-negative initial conditions. In this region, the system will ultimately arrive at a coral-dominated state corresponding to low levels of

Fig. 2 **a** Bifurcation diagram of macroalgal toxicity (γ) versus the equilibrium value of coral cover, demonstrating the possibility of hysteresis ($\gamma_* < \gamma^*$) with the hysteresis loop depicted by arrows. Stable equilibria are indicated by blue lines, unstable equilibria by red lines. **b** Bifurcation diagram with $b = 0$ and γ as an active parameter. **c** The transcritical bifurcation is represented by (Det, Tr) diagram at $\gamma = 0.032 (= \gamma_*)$. **d** Saddle-node bifurcation at $\gamma = 0.3981 (= \gamma^*)$. Stable equilibria are indicated by blue lines, unstable equilibria by red lines

macroalgae. The bistable region is represented by the region II for $\gamma_* < \gamma < \gamma^*$. Hysteresis will result, with low macroalgal cover followed by an increase in the macroalgal cover above a critical threshold γ^* . Once the intensity of macroalgal toxicity surpasses the threshold γ^* , the system arrives at a macroalgae-dominated stable state, represented by region III of monostability at E_0 . Any perturbation in the system that has resulted in a subsequent decline in toxicity level below the threshold γ_* , returns the system to coral-dominated stable state in region I. Since $\gamma^* > \gamma_*$, returning to a coral-dominated state requires toxin intensity lower than the toxicity level at the latter stage that has forced the system to a macroalgae-dominated state. However, in the absence of external recruitment of macroalgae (i.e., for $b = 0$), choosing γ as an active bifurcation parameter, it is observed that the system exhibits a sudden change in transition from a coral-dominated stable regime to a coral-macroalgae bistable regime when γ crosses 0.175 (cf. Fig. 2b). Moreover, in the absence of macroalgal-immigration, the system exhibits no saddle-node bifurcation with high macroalgal toxicity and, consequently, no hysteresis is detected (cf. Fig. 2b).

From Fig. 2c, it follows that $Det(J_0)|_{\gamma=\gamma_*} = 0$ and $Tr(J_0)|_{\gamma=\gamma_*} < 0$ with instability at E_0 for $\gamma < \gamma_*$ and stability at E_0 for $\gamma > \gamma_*$, representing a transcritical bifurcation at E_0 when γ crosses γ_* . Figure 2d shows that $Det(J^*)|_{\gamma=\gamma^*} = 0$ and $Tr(J^*)|_{\gamma=\gamma^*} < 0$ with

Table 1 Parameter values used in the numerical analysis

Parameters	Description of Parameters	Value	Dimension	Reference
α	Growth rate of macroalgae over corals	0.1	$time^{-1}$	[24, 27]
r	Recruitment rate of corals on turf algae	0.55	$time^{-1}$	[27]
a	Growth rate of macroalgae over algal turfs	0.77	$time^{-1}$	[27]
b	Colonization rate of newly immigrated macroalgae on algal turf	0.005	$time^{-1}$	[27]
d_1	Natural mortality rate of macroalgae	0.1	$time^{-1}$	—
d_2	Natural mortality rate of corals	0.24	$time^{-1}$	[27]
γ	Toxin-induced death rate of corals	0.1	$time^{-1}$	—
g	Maximal grazing rate of herbivorous fish	0.4	$time^{-1}$	[27]
β	Parameter representing harvest-mediated grazing loss	0.05	—	—

stability at E^* for $\gamma < \gamma^*$ and non-existence of E^* for $\gamma > \gamma^*$, representing a saddle-node bifurcation at E^* when γ crosses γ^* .

Figure 3a represents a bifurcation diagram of γ versus the equilibrium value of coral cover for different grazing rates of herbivores. It is observed that an increase of the grazing rate increases the resilience of coral-dominated regime with high macroalgal toxicity, measured by taking the difference of the values of γ at the saddle-node bifurcation point (LP) and at transcritical bifurcating point (BP) for a particular value of g . Figure 3b gives a two-parameter bifurcation diagram with γ and a as active parameters, representing a cusp point (CP) at $(M, C, a, \gamma) = (0.1105, 0, 0.0873, 2.1544)$ with eigenvalues 0 and -0.4619 . The grazing rate g depends on the abundance of herbivores and is thus subject to variation with changes in available refuge and food abundance. To identify the impact of changes in grazing intensity on coral cover, in Fig. 4a, we plot the solutions of the nullcline equations in the $C - g$ plane, yielding a bifurcation diagram. The region IV represents monostability at E_0 for $0 \leq g < g_*$, representing macroalgae-dominated state for all non-negative initial conditions. In this region, the system will ultimately arrive at a coral-depleted state corresponding to high levels of macroalgae. The bistable region is represented by the region V for $g_* < g < g^*$. Hysteresis will result, with low coral cover followed by an increase in coral cover above a critical threshold g^* . The system arrives at a coral-dominated stable state, represented by region VI of monostability at E^* . Any perturbation in the system

Fig. 3 **a** Bifurcation diagram of γ versus the equilibrium value of coral cover for different values of g . **b** Two parameter bifurcation diagram with γ and a as active parameters

Fig. 4 **a** Bifurcation diagram of grazing intensity (g) versus the equilibrium value of coral cover, demonstrating the possibility of hysteresis ($g_* < g^*$) with the hysteresis loop depicted by arrows. Stable equilibria are indicated by blue lines, unstable equilibria by red lines. **b** The saddle-node bifurcation is represented by (Det, Tr) diagram at $g = 0.32102 (= g_*)$. **c** The transcritical bifurcation is represented by (Det, Tr) diagram at $g = 0.4445 (= g^*)$. Stable equilibria are indicated by blue lines, unstable equilibria by red lines

that has resulted in a subsequent decline in grazing below the threshold g_* , returns the system to macroalgae-dominated stable state in region IV. Since $g^* > g_*$, returning to coral-dominated state requires a grazing intensity higher than the initial grazing rate that has forced the system to a macroalgae-dominated state.

From Fig. 4b it follows that $Det(J^*)|_{g=g_*} = 0$ and $Tr(J^*)|_{g=g_*} < 0$ with stability at E^* for $g > g_*$ and non-existence of E^* for $g < g_*$, representing a saddle-node bifurcation at E^* when g crosses g_* . Figure 4c shows that $Det(J_0)|_{g=g^*} = 0$ and $Tr(J_0)|_{g=g^*} < 0$ with stability at E_0 for $g < g^*$ and instability at E_0 for $g > g^*$, representing a transcritical bifurcation at E_0 when g crosses g^* . The basin of attraction for E_0 and E^* corresponding to the bistable region V is given in Fig. 5a and b.

Figure 6a represents a bifurcation diagram of g versus the equilibrium value of coral cover for different growth rates of macroalgae on algal turf. It is observed that with low macroalgal growth rate on turf algae (viz. $a = 0.17$), the system does not exhibit hysteresis. The increase of macroalgal growth rate on turf algae increases the resilience of the coral-dominated regime with high macroalgal grazing rate by herbivores, measured by taking the difference of the values of g at the saddle-node bifurcating point (LP) and at transcritical bifurcation point (BP) for a particular value of a . Figure 6b

gives a two-parameter bifurcation diagram with g and α as active parameters, representing two stable cusp points. The first stable cusp point is located at $(M, C, \alpha, g) = (0.0485, 0.2026, 1.2433, 0.8522)$ with eigenvalues 0 and -0.5724 . The other stable cusp point is located at $(M, C, \alpha, g) = (0.1805, 0, 1.0668, 0.7977)$ with eigenvalues 0 and -0.4159 . Figure 6c gives a two-parameter bifurcation diagram with g and r as active parameters, representing three stable cusp points. The first stable cusp point is located at $(M, C, r, g) = (0.1495, 0, 0.3173, 0.8834)$ with eigenvalues 0 and -0.4494 . The second stable cusp point is located at $(M, C, r, g) = (0.0885, 0.8749, 7.0598, 0.0047)$ with eigenvalues 0 and -6.3159 . The third stable cusp point is located at $(M, C, r, g) = (0.8245, 0, 2.3093, 0.0480)$ with eigenvalues 0 and -0.6958 .

The harvest-mediated grazing loss β depends on the rate of fishing of herbivores. To identify the impact of β on coral cover, in Fig. 7a we plot the solutions of the nullcline equations in the $C - \beta$ plane, yielding a bifurcation diagram. The region VII represents bistability for $0 < \beta < \beta^*$. For $\beta > \beta^*$, the system becomes monostable at E^* as depicted in region VIII.

From Fig. 7b it follows that $\text{Det}(J^*)|_{\beta=\beta^*} = 0$ and $\text{Tr}(J^*)|_{\beta=\beta^*} < 0$ with stability at E^* for $\beta < \beta^*$ and non-existence of E^* for $\beta > \beta^*$, representing a saddle-node bifurcation at E^* when β crosses β^* .

The basin of attraction for E_0 and E^* , corresponding to the bistable region VII, is shown in Fig. 8a and b.

4 Mathematical analysis of the system with delays

We analyze the dynamics of coral reefs by assuming that the recovery of algal turf after macroalgae is grazed by herbivores is not instantaneous, but will be mediated by some discrete time lag τ_1 . Further, we assume that macroalgae liberate toxic substances at a time

Fig. 5 **a** The basin of attraction for E^* (shaded) and E_0 (unshaded) with $g = 0.33$. **b** The basin of attraction for E^* (shaded) and E_0 (unshaded) with $g = 0.4$

Fig. 6 **a** Bifurcation diagram of g versus the equilibrium value of coral cover for different values of a . **b** Two-parameter bifurcation diagram with g and α as active parameters. **c** Two-parameter bifurcation diagram with g and r as active parameters

Fig. 7 **a** Bifurcation diagram of harvesting pressure (β) versus the equilibrium value of coral cover. Stable equilibria are indicated by blue lines, unstable equilibria by red lines. **b** The saddle-node bifurcation occurs at the intersection of Det and Tr with $\beta = 0.2378$ ($= \beta^*$)

Fig. 8 **a** The basin of attraction for E^* (shaded) and E_0 (unshaded) with $\beta = 0$. **b** The basin of attraction for E^* (shaded) and E_0 (unshaded) with $\beta = 0.2$

lag τ_2 , required for its maturity. By ignoring the possibility of any empty space in seabed, we construct the following delay model:

$$\begin{aligned}\frac{dM}{dt} &= M(\alpha C - d_1) + T(aM + b) - \frac{g(1-\beta)M(t-\tau_1)}{M(t-\tau_1) + T(t-\tau_1)} \\ \frac{dC}{dt} &= C\{rT - \alpha M - \gamma M(t-\tau_2) - d_2\} \\ \frac{dT}{dt} &= \frac{g(1-\beta)M(t-\tau_1)}{M(t-\tau_1) + T(t-\tau_1)} + d_1M + C\{d_2 + \gamma M(t-\tau_2)\} - T(aM + rC + b) \quad (3)\end{aligned}$$

Since $M + C + T = 1$, system (3) reduces to:

$$\begin{aligned}\frac{dM}{dt} &= M(\alpha C - d_1) + (aM + b)(1 - M - C) - \frac{g(1-\beta)M(t-\tau_1)}{1 - C(t-\tau_1)} \\ \frac{dC}{dt} &= C\{r(1 - M - C) - \alpha M - \gamma M(t-\tau_2) - d_2\} \quad (4)\end{aligned}$$

with the initial conditions $M(t) = \phi_1(t) > 0$, $C(t) = \phi_2(t) \geq 0$, $-\tau \leq t \leq 0$, where $\tau = \max\{\tau_1, \tau_2\}$, $\Phi = (\phi_1, \phi_2) \in C([-\tau, 0], R_{+0}^2)$, the Banach space of continuous functions, mapping the interval $(-\tau, 0)$ into R_{+0}^2 , where we define $R_{+0}^2 = \{(M, C) : M > 0, C \geq 0\}$.

For $0 \leq t \leq \min\{\tau_1, \tau_2\}$, we have

$$\begin{aligned}\frac{dM}{dt} &= M(t)\{\alpha C(t) - d_1\} + \{aM(t) + b\}\{1 - M(t) - C(t)\} - \frac{g(1-\beta)\phi_1(t-\tau_1)}{1 - \phi_2(t-\tau_1)} \\ \frac{dC}{dt} &= C(t)\{r\{1 - M(t) - C(t)\} - \alpha M(t) - \gamma\phi_1(t-\tau_2) - d_2\}\end{aligned}$$

Therefore, for $0 \leq t \leq \min\{\tau_1, \tau_2\}$, $\frac{dM}{dt} > 0$ implies $\phi_1(t-\tau_1) < l_1\{1 - \phi_2(t-\tau_1)\}$ and $\frac{dC}{dt} > 0$ implies $\phi_1(t-\tau_2) < l_2(t)$, where $l_1(t) = \frac{M(t)\{\alpha C(t) - d_1\} + a\{M(t) + b\}\{1 - M(t) - C(t)\}}{g(1-\beta)}$ and $l_2(t) = \frac{r\{1 - M(t) - C(t)\} - \alpha M(t) - d_2}{\gamma}$.

Thus, the system is well posed in $-\tau \leq s \leq 0$ if $0 \leq M(s) = \phi_1(s) \leq \max\{l_1(s + \tau_1)\{1 - \phi_2(s)\}, l_2(s + \tau_2)\}$ and $0 < C(s) = \phi_2(s)$.

The characteristic equation of the system (4) at E^* is

$$\begin{aligned} D(\lambda, \tau_1, \tau_2) &= \lambda^2 + \bar{A}\lambda + \bar{B} + \bar{C}\lambda e^{-\lambda\tau_1} + \bar{D}e^{-\lambda\tau_1} + \bar{E}e^{-\lambda\tau_2} + \bar{F}e^{-\lambda(\tau_1+\tau_2)} = 0, \text{ where } \bar{A} \\ &= -a_{11} - a_{22}, \bar{B} = a_{11}a_{22} - a_{12}a_{21}, \bar{C}_2 = -a_{13}, \bar{D} = a_{22}a_{13} - a_{14}a_{21}, \bar{E} = -a_{12}a_{23}, \bar{F} \\ &= -a_{14}a_{23}, a_{11} = \alpha C^* - d_1 - (aM^* + b) + a(1 - M^* - C^*), a_{12} = \alpha M^* - (aM^* + b), a_{13} \\ &= -\frac{g(1-\beta)}{1-C^*}, a_{14} = -\frac{g(1-\beta)M^*}{(1-C^*)^2}, a_{21} = -(r+\alpha)C^*, a_{22} = r(1 - M^* - 2C^*) \\ &\quad -(\alpha + \gamma)M^* - d_2 \text{ and } a_{23} = -\gamma C^*. \end{aligned}$$

In order to investigate the distribution of roots of this transcendental equation, we use the following Lemma by Ruan and Wei [28].

Lemma 4.1 *For the transcendental equation $P(\lambda, e^{-\lambda\tau_1}, \dots, e^{-\lambda\tau_m}) = \lambda^n + p_1^{(0)}\lambda^{n-1} + \dots + p_{n-1}^{(0)}\lambda + p_n^{(0)} + \left[p_1^{(1)}\lambda^{n-1} + \dots + p_{n-1}^{(1)}\lambda + p_n^{(1)}\right]e^{-\lambda\tau_1} + \dots + \left[p_1^{(m)}\lambda^{n-1} + \dots + p_{n-1}^{(m)}\lambda + p_n^{(m)}\right]e^{-\lambda\tau_m} = 0$, as $(\tau_1, \tau_2, \dots, \tau_m)$ vary, the sum of orders of the zeros of $P(\lambda, e^{-\lambda\tau_1}, e^{-\lambda\tau_2}, \dots, e^{-\lambda\tau_m})$ in the open right half plane can change only if a zero appears on or crosses the imaginary axis.*

4.1 System with $\tau_1 > 0$ and $\tau_2 = 0$

We consider the case in which the recovery of algal turf after macroalgae is grazed by herbivores is mediated by some discrete time lag τ_1 and an instantaneous macroalgal-toxic liberation. The system (4) reduces to

$$\begin{aligned} \frac{dM}{dt} &= M(\alpha C - d_1) + (aM + b)(1 - M - C) - \frac{g(1-\beta)M(t-\tau_1)}{1-C(t-\tau_1)} \\ \frac{dC}{dt} &= C\{r(1 - M - C) - (\alpha + \gamma)M - d_2\} \end{aligned} \quad (5)$$

with the initial conditions $M(t) = \phi_1(t) > 0$, $C(t) = \phi_2(t) \geq 0$, $-\tau_1 \leq t \leq 0$ and $\phi_i(0) > 0$ ($i = 1, 2$).

The characteristic equation of the system (5) at E^* is $\lambda^2 + \lambda A_1 + B_1 - e^{-\lambda\tau_1}(C_1 + \lambda D_1) = 0$, where $A_1 = \bar{A}$, $B_1 = \bar{B} - \bar{E}$, $C_1 = -\bar{F} - \bar{D}$ and $D_1 = -\bar{C}$.

Lemma 4.2 *Assume that the conditions of Lemma 3.2 are satisfied. For all $\tau_1 \in [0, \infty)$, the system (5) is locally asymptotically stable at E^* if either (a) $A_1^2 > 2B_1 + D_1^2$, $B_1^2 > C_1^2$ or (b) $(A_1^2 - 2B_1 - D_1^2)^2 < 4(B_1^2 - C_1^2)$ holds.*

Proof The system (5) is locally asymptotically stable at E^* for all $\tau_1 \geq 0$ if the following conditions given by Gopalsamy [29], Beretta and Kuang [30] hold:

- (i) the real parts of all the roots of $D(\lambda, 0, 0) = 0$ are negative,
- (ii) for all real ω and any $\tau_1 \geq 0$, $D(i\omega, \tau_1, 0) \neq 0$ where $i = \sqrt{-1}$.

Now, if the conditions of Lemma 3.2 are satisfied, the real parts of all the roots of $D(\lambda, 0, 0) = 0$ are negative.

Also, $D(i\omega, \tau_1, 0) = 0$ gives $-\omega^2 + B_1 = C_1 \cos \omega\tau_1 + \omega D_1 \sin \omega\tau_1$ and $\omega A_1 = \omega D_1 \cos \omega\tau_1 - C_1 \sin \omega\tau_1$. This gives $\omega^4 + \omega^2(A_1^2 - 2B_1 - D_1^2) + B_1^2 - C_1^2 = 0$.

If (a) $A_1^2 > 2B_1 + D_1^2$, $B_1^2 > C_1^2$ or (b) $(A_1^2 - 2B_1 - D_1^2)^2 < 4(B_1^2 - C_1^2)$ holds, then $\omega^4 + \omega^2(A_1^2 - 2B_1 - D_1^2) + B_1^2 - C_1^2 = 0$ has no positive root and so, for all real ω and for any $\tau_1 > 0$, $D(i\omega, \tau_1, 0) \neq 0$.

Hence, the system (5) is locally asymptotically stable at E^* . $\square$

Lemma 4.3 Assume that the conditions of Lemma 3.2 are satisfied. If either (i) $B_1^2 < C_1^2$ or (ii) $D_1^2 + 2B_1 - A_1^2 = 2\sqrt{B_1^2 - C_1^2} > 0$ holds, a Hopf bifurcation occurs as τ_1 crosses τ_1^+ , where $\tau_1^+ = \frac{1}{\omega_+} \tan^{-1} \left\{ \frac{\omega_+ D_1 (B_1 - \omega_+^2) - \omega_+ A_1 C_1}{\omega_+^2 A_1 D_1 + C_1 (B_1 - \omega_+^2)} \right\}$.

Proof Let $\lambda(\tau_1) = a(\tau_1) + ib(\tau_1)$ be a root of $D(\lambda, \tau_1, 0) = 0$.

For ease of notation, we denote $a(\tau_1) = a$ and $b(\tau_1) = \omega$. Separating the real and imaginary parts of $D(\lambda, \tau_1, 0) = 0$ and then putting $a = 0$, we get

$$-\omega^2 + B_1 = C_1 \cos \omega \tau_1 + \omega D_1 \sin \omega \tau_1 \quad (6)$$

$$A_1 \omega = \omega D_1 \cos \omega \tau_1 - C_1 \sin \omega \tau_1 \quad (7)$$

Eliminating τ_1 between (6) and (7) we get $\omega^4 + (A_1^2 - 2B_1 - D_1^2)\omega^2 + B_1^2 - C_1^2 = 0$. If either (i) $B_1^2 < C_1^2$ or (ii) $D_1^2 + 2B_1 - A_1^2 = 2\sqrt{B_1^2 - C_1^2} > 0$ holds, then $\omega^4 + (A_1^2 - 2B_1 - D_1^2)\omega^2 + B_1^2 - C_1^2 = 0$ has a unique positive root $\omega_+^2 = \frac{-A_1^2 + 2B_1 + D_1^2 + \sqrt{(A_1^2 - 2B_1 - D_1^2)^2 - 4(B_1^2 - C_1^2)}}{2}$.

Substituting ω_+^2 into (6) and (7) we get

$$\tau_{1n}^+ = \frac{1}{\omega_+} \tan^{-1} \left\{ \frac{\omega_+ D_1 (B_1 - \omega_+^2) - \omega_+ A_1 C_1}{\omega_+^2 A_1 D_1 + C_1 (B_1 - \omega_+^2)} \right\} + \frac{n\pi}{\omega_+}, n = 0, 1, 2, \dots$$

The smallest τ_{1n}^+ is given by $n = 0$ and we take it as $\tau_1^+ = \frac{1}{\omega_+} \tan^{-1} \left\{ \frac{\omega_+ D_1 (B_1 - \omega_+^2) - \omega_+ A_1 C_1}{\omega_+^2 A_1 D_1 + C_1 (B_1 - \omega_+^2)} \right\}$.

We are interested to know the change of stability at E^* which will occur at $\tau_1 = \tau_1^+$ for which $a(\tau_1^+) = 0$ and $b(\tau_1^+) = \omega_+ \neq 0$. Since $\lambda(\tau_1)$ is a root of $D(\lambda, \tau_1, 0) = 0$ near τ_1^+ , there exists $\epsilon > 0$ such that $\lambda(\tau_1)$ is continuously differentiable at $\tau_1 \in (\tau_1^+ - \epsilon, \tau_1^+ + \epsilon)$. Differentiating $D(\lambda, \tau_1, 0) = 0$ with respect to τ_1 we obtain

$$\left(\frac{d\lambda}{d\tau_1} \right)^{-1} = -\frac{2\lambda + A_1}{\lambda(\lambda^2 + A_1\lambda + B_1)} + \frac{D_1}{\lambda(C_1 + \lambda D_1)} - \frac{\tau_1}{\lambda} \text{ by using } e^{-\lambda\tau_1} = \frac{\lambda^2 + A_1\lambda + B_1}{C_1 + \lambda D_1}.$$

$$\text{Thus, } \text{sign} \left\{ \frac{d(Re\lambda)}{d\tau_1} \right\}_{\lambda=i\omega_+} = \text{sign} \left\{ \text{Re} \left(\frac{d\lambda}{d\tau_1} \right)^{-1} \right\}_{\lambda=i\omega_+} = \text{sign} \left\{ \frac{\sqrt{(A_1^2 - 2B_1 - D_1^2)^2 - 4(B_1^2 - C_1^2)}}{(\omega_+^2 - B_1)^2 + \omega_+^2 A_1^2} \right\}.$$

Therefore, $\left[\frac{d(Re\lambda)}{d\tau_1} \right]_{\tau_1=\tau_1^+, \lambda=i\omega_+} > 0$ and hence the system (5) undergoes a Hopf bifurcation when τ_1 crosses τ_1^+ . $\square$

Lemma 4.4 Assume that the conditions of Lemma 3.2 are satisfied. If $D_1^2 + 2B_1 - A_1^2 > 2\sqrt{B_1^2 - C_1^2} > 0$ holds, then there exists a positive integer k such that there are k

switches from stability to instability and from instability to stability. Therefore, Hopf bifurcation occurs as τ_1 crosses $\tau_{1_n}^\pm$, where $\tau_{1_n}^\pm = \frac{1}{\omega_\pm} \tan^{-1} \left\{ \frac{\omega_\pm D_1 (B_1 - \omega_\pm^2) - \omega_\pm A_1 C_1}{\omega_\pm^2 A_1 D_1 + C_1 (B_1 - \omega_\pm^2)} \right\} + \frac{n\pi}{\omega_\pm}$, ($n = 0, 1, 2, \dots, k$).

Proof If $D_1^2 + 2B_1 - A_1^2 > 2\sqrt{B_1^2 - C_1^2} > 0$ holds, then $\omega^4 + (A_1^2 - 2B_1 - D_1^2)\omega^2 + B_1^2 - C_1^2 = 0$ has two positive roots, $\omega_\pm^2 = \frac{-A_1^2 + 2B_1 + D_1^2 \pm \sqrt{(A_1^2 - 2B_1 - D_1^2)^2 - 4(B_1^2 - C_1^2)}}{2}$.

In this case, $D(\lambda, \tau_1, 0) = 0$ has purely imaginary roots when τ_1 takes certain critical values $\tau_{1_n}^\pm$, where $\tau_{1_n}^\pm = \frac{1}{\omega_\pm} \tan^{-1} \left\{ \frac{\omega_\pm D_1 (B_1 - \omega_\pm^2) - \omega_\pm A_1 C_1}{\omega_\pm^2 A_1 D_1 + C_1 (B_1 - \omega_\pm^2)} \right\} + \frac{n\pi}{\omega_\pm}$, ($n = 0, 1, 2, \dots$).

Let $D(\lambda, \tau_1, 0) = 0$ has k positive roots, $\lambda_j^\pm(\tau_1) = a_j^\pm(\tau_1) + ib_j^\pm(\tau_1)$, ($j = 0, 1, 2, \dots, k$) satisfying $a_j^\pm(\tau_{1_j}^\pm) = 0$ and $b_j^\pm(\tau_{1_j}^\pm) = \omega_\pm \neq 0$.

Differentiating $D(\lambda, \tau_1, 0) = 0$ with respect to τ_1 we obtain

$$\begin{aligned} \operatorname{sign} \left\{ \frac{d(\operatorname{Re} \lambda)}{d\tau_1} \right\}_{\lambda=i\omega_+} &= \operatorname{sign} \left\{ \frac{\sqrt{(A_1^2 - 2B_1 - D_1^2)^2 - 4(B_1^2 - C_1^2)}}{(\omega_+^2 - B_1)^2 + \omega_+^2 A_1^2} \right\} \quad \text{and} \\ \operatorname{sign} \left\{ \frac{d(\operatorname{Re} \lambda)}{d\tau_1} \right\}_{\lambda=i\omega_-} &= \operatorname{sign} \left\{ \frac{-\sqrt{(A_1^2 - 2B_1 - D_1^2)^2 - 4(B_1^2 - C_1^2)}}{(\omega_-^2 - B_1)^2 + \omega_-^2 A_1^2} \right\}. \end{aligned}$$

Therefore, $\left[\frac{d(\operatorname{Re} \lambda)}{d\tau_1} \right]_{\tau_1=\tau_{1_j}^+, \lambda=i\omega_+} > 0$ and $\left[\frac{d(\operatorname{Re} \lambda)}{d\tau_1} \right]_{\tau_1=\tau_{1_j}^-, \lambda=i\omega_-} < 0$.

Thus, if $D_1^2 + 2B_1 - A_1^2 > 2\sqrt{B_1^2 - C_1^2} > 0$ holds, the system (5) undergoes Hopf bifurcations as τ_1 crosses $\tau_{1_j}^\pm$, ($j = 0, 1, 2, \dots, k$).

Further, when $\tau_1 \in [0, \tau_{1_0}^+)$, $(\tau_{1_0}^-, \tau_{1_1}^+)$, $\dots$, $(\tau_{1_{k-1}}^-, \tau_{1_k}^+)$, all roots of $D(\lambda, \tau_1, 0) = 0$ will have negative real parts and when $\tau_1 \in [\tau_{1_0}^+, \tau_{1_1}^-)$, $[\tau_{1_1}^+, \tau_{1_2}^-)$, $\dots$, $[\tau_{1_{k-1}}^+, \tau_{1_k}^-)$, $(\tau_{1_k}^+, \infty)$, at least one root of $D(\lambda, \tau_1, 0) = 0$ will have positive real part. $\square$

4.2 System with $\tau_1 = 0$ and $\tau_2 > 0$

We now consider the case of instantaneous recovery of algal turf after macroalgae is grazed by herbivores but a discrete time lag τ_2 for macroalgal-toxic liberation.

The system (4) reduces to

$$\begin{aligned} \frac{dM}{dt} &= M \left\{ \alpha C - \frac{g(1-\beta)}{1-C} - d_1 \right\} + (aM + b)(1 - M - C) \\ \frac{dC}{dt} &= C \{ r(1 - M - C) - \alpha M - \gamma M(t - \tau_2) - d_2 \} \end{aligned} \quad (8)$$

with the initial conditions $M(t) > 0$, $C(t) = \phi_2(t) \geq 0$, $-\tau_2 \leq t \leq 0$ and $\phi_2(0) > 0$.

The characteristic equation of the system (8) at E^* is $\lambda^2 + \lambda A_2 + B_2 - C_2 e^{-\lambda \tau_2} = 0$, where $A_2 = \bar{A} + \bar{C}$, $B_2 = \bar{B} + \bar{D}$ and $C_2 = -(\bar{E} + \bar{F})$.

Lemma 4.5 Assume that the conditions of Lemma 3.2 are satisfied. For all $\tau_2 \in [0, \infty)$, the system (8) is locally asymptotically stable at E^* if either (a) $A_2^2 > 2B_2$, $B_2^2 > C_2^2$ or (b) $(A_2^2 - 2B_2)^2 < 4(B_2^2 - C_2^2)$ holds.

Proof $D(i\omega, 0, \tau_2) = 0$ implies $-\omega^2 + B_2 = C_2 \cos \omega\tau_2$ and $\omega A_2 = -C_2 \sin \omega\tau_2$.

This gives $\omega^4 + \omega^2(A_2^2 - 2B_2) + B_2^2 - C_2^2 = 0$.

If (a) $A_2^2 > 2B_2$, $B_2^2 > C_2^2$ or (b) $(A_2^2 - 2B_2)^2 < 4(B_2^2 - C_2^2)$ holds, then $\omega^4 + \omega^2(A_2^2 - 2B_2) + B_2^2 - C_2^2 = 0$ has no positive root and so, for all real ω and for any $\tau_2 > 0$, $D(i\omega, 0, \tau_2) \neq 0$.

Hence, the system (8) is locally asymptotically stable at E^* . $\square$

Lemma 4.6 Assume that the conditions of Lemma 3.2 are satisfied. If either (i) $B_2^2 < C_2^2$ or (ii) $2B_2 - A_2^2 = 2\sqrt{B_2^2 - C_2^2} > 0$ holds, a Hopf bifurcation occurs as τ_2 crosses τ_2^+ , where $\tau_2^+ = \frac{1}{b_+} \tan^{-1} \left(\frac{b_+ A_2}{b_+^2 - B_2} \right)$.

Proof Let $\lambda(\tau_2) = a(\tau_2) + ib(\tau_2)$ be a root of $D(\lambda, 0, \tau_2) = 0$.

For ease of notation, we denote $a(\tau_2) = a$ and $b(\tau_2) = b$. Separating the real and imaginary parts of $D(\lambda, 0, \tau_2) = 0$ and then putting $a = 0$, we get $-\omega^2 + B_2 = C_2 \cos \omega\tau_2$ and $A_2\omega = -C_2 \sin \omega\tau_2$. Eliminating τ_2 we get $\omega^4 + (A_2^2 - 2B_2)\omega^2 + B_2^2 - C_2^2 = 0$. If either (i) $B_2^2 < C_2^2$ or (ii) $2B_2 - A_2^2 = 2\sqrt{B_2^2 - C_2^2} > 0$ holds, then $\omega^4 + (A_2^2 - 2B_2)\omega^2 + B_2^2 - C_2^2 = 0$ has a unique positive root $b_+^2 = \frac{-A_2^2 + 2B_2 + \sqrt{(A_2^2 - 2B_2)^2 - 4(B_2^2 - C_2^2)}}{2}$.

This gives $\tau_{2n}^+ = \frac{1}{b_+} \tan^{-1} \left(\frac{b_+ A_2}{b_+^2 - B_2} \right) + \frac{n\pi}{b_+}$, $n = 0, 1, 2, \dots$.

The smallest τ_{2n}^+ is given by $n = 0$ and we take it as $\tau_2^+ = \frac{1}{b_+} \tan^{-1} \left(\frac{b_+ A_2}{b_+^2 - B_2} \right)$.

We are interested to know the change of stability at E^* which will occur at $\tau_2 = \tau_2^+$ for which $a(\tau_2^+) = 0$ and $b(\tau_2^+) = b_+ \neq 0$.

We obtain $\left(\frac{d\lambda}{d\tau_2} \right)^{-1} = -\frac{2\lambda + A_2}{\lambda(\lambda^2 + A_2\lambda + B_2)} - \frac{\tau_2}{\lambda}$ by using $e^{-\lambda\tau_1} = \frac{\lambda^2 + A_2\lambda + B_2}{C_2}$.

Thus, $\text{sign} \left\{ \frac{d(Re\lambda)}{d\tau_2} \right\}_{\lambda=ib_+} = \text{sign} \left\{ Re \left(\frac{d\lambda}{d\tau_2} \right)^{-1} \right\}_{\lambda=ib_+} = \text{sign} \left\{ \frac{\sqrt{(A_2^2 - 2B_2)^2 - 4(B_2^2 - C_2^2)}}{(b_+^2 - B_2)^2 + b_+^2 A_2^2} \right\}$.

Therefore, $\left[\frac{d(Re\lambda)}{d\tau_2} \right]_{\tau_2=\tau_2^+, \lambda=ib_+} > 0$ and hence the system (8) undergoes a Hopf bifurcation when τ_2 crosses τ_2^+ . $\square$

Lemma 4.7 Assume that the conditions of Lemma 3.2 are satisfied. If $2B_2 - A_2^2 > 2\sqrt{B_2^2 - C_2^2} > 0$ holds, then there exists a positive integer r such that there are r switches from stability to instability and from instability to stability. Therefore, a Hopf bifurcation occurs as τ_2 crosses $\tau_{2n}^\pm$, where $\tau_{2n}^\pm = \frac{1}{b_\pm} \tan^{-1} \left(\frac{b_\pm A_2}{b_\pm^2 - B_2} \right) + \frac{n\pi}{b_\pm}$, ($n = 0, 1, 2, \dots, r$).

Proof If $2B_2 - A_2^2 > 2\sqrt{B_2^2 - C_2^2} > 0$ holds, then $\omega^4 + (A_2^2 - 2B_2)\omega^2 + B_2^2 - C_2^2 = 0$ has two positive roots, $b_\pm^2 = \frac{-A_2^2 + 2B_2 \pm \sqrt{(A_2^2 - 2B_2)^2 - 4(B_2^2 - C_2^2)}}{2}$.

In this case, $D(\lambda, 0, \tau_2) = 0$ has purely imaginary roots when τ_2 takes certain critical values $\tau_{2_n}^\pm$, where $\tau_{2_n}^\pm = \frac{1}{b_\pm} \tan^{-1} \left(\frac{b_\pm A_2}{b_\pm^2 - B_2} \right) + \frac{n\pi}{b_\pm}$, ($n = 0, 1, 2, \dots$).

Let $D(\lambda, 0, \tau_2) = 0$ has r positive roots, $\lambda_j^\pm(\tau_2) = a_j^\pm(\tau_2) + ib_j^\pm(\tau_2)$, ($j = 0, 1, 2, \dots, r$) satisfying $a_j^\pm(\tau_{2_j}^\pm) = 0$ and $b_j^\pm(\tau_{2_j}^\pm) = b_\pm \neq 0$.

Differentiating $D(\lambda, 0, \tau_2) = 0$ with respect to τ_2 we obtain

$$\begin{aligned} \operatorname{sign} \left\{ \frac{d(\operatorname{Re} \lambda)}{d\tau_2} \right\}_{\lambda=ib_+} &= \operatorname{sign} \left\{ \frac{\sqrt{(A_2^2 - 2B_2)^2 - 4(B_2^2 - C_2^2)}}{(b_+^2 - B_2)^2 + b_+^2 A_2^2} \right\} \quad \text{and} \\ \operatorname{sign} \left\{ \frac{d(\operatorname{Re} \lambda)}{d\tau_2} \right\}_{\lambda=ib_-} &= \operatorname{sign} \left\{ \frac{-\sqrt{(A_1^2 - 2B_2)^2 - 4(B_2^2 - C_2^2)}}{(b_-^2 - B_2)^2 + b_-^2 A_2^2} \right\}. \end{aligned}$$

Therefore, $\left[\frac{d(\operatorname{Re} \lambda)}{d\tau_2} \right]_{\tau_2=\tau_{2_j}^+, \lambda=ib_+} > 0$ and $\left[\frac{d(\operatorname{Re} \lambda)}{d\tau_2} \right]_{\tau_2=\tau_{2_j}^-, \lambda=ib_-} < 0$.

Thus, if $2B_2 - A_2^2 > 2\sqrt{B_2^2 - C_2^2} > 0$ holds, the system (8) undergoes Hopf bifurcations as τ_2 crosses $\tau_{2_j}^\pm$, ($j = 0, 1, 2, \dots, r$).

Further, when $\tau_2 \in [0, \tau_{2_0}^+)$, $(\tau_{2_0}^-, \tau_{2_1}^+)$, $\dots$, $(\tau_{2_{r-1}}^-, \tau_{2_r}^+)$, all roots of $D(\lambda, 0, \tau_2) = 0$ will have negative real parts and when $\tau_2 \in [\tau_{2_0}^+, \tau_{2_0}^-)$, $[\tau_{2_1}^+, \tau_{2_1}^-)$, $\dots$, $[\tau_{2_{r-1}}^+, \tau_{2_{r-1}}^-)$, $(\tau_{2_r}^+, \infty)$, at least one root of $D(\lambda, 0, \tau_2) = 0$ will have positive real part. $\square$

4.3 System with $\tau_1 > 0$ and $\tau_2 > 0$

We consider $D(\lambda, \tau_1, \tau_2) = 0$ in its stable interval and regard τ_1 as a parameter.

Without any loss of generality, we assume that the conditions of Lemma 3.2 are satisfied and either (i) $B_2^2 < C_2^2$ or (ii) $2B_2 - A_2^2 = 2\sqrt{B_2^2 - C_2^2} > 0$ hold. Then the system (8) is stable for $\tau_2 \in [0, \tau_2^+)$. Let $i\omega$ ($\omega > 0$) be a root of $D(\lambda, \tau_1, \tau_2) = 0$. Then $D(i\omega, \tau_1, \tau_2) = 0$ gives $-\omega^2 + \bar{B} + \bar{E} \cos \omega \tau_2 = -(\bar{F} \cos \omega \tau_2 + \bar{D}) \cos \omega \tau_1 + (\bar{F} \sin \omega \tau_2 - \omega \bar{C}) \sin \omega \tau_1$ and $\omega \bar{A} - \bar{E} \sin \omega \tau_2 = (\bar{F} \cos \omega \tau_2 + \bar{D}) \sin \omega \tau_1 + (\bar{F} \sin \omega \tau_2 - \omega \bar{C}) \cos \omega \tau_1$. Squaring and adding these equations we get $\omega^4 + k_1 \omega^2 + k_2 \omega + k_3 = 0$, where $k_1 = \bar{A}^2 - \bar{C}^2 - 2\bar{B} - 2\bar{E} \cos \omega \tau_2$, $k_2 = 2(\bar{C}\bar{F} - \bar{A}\bar{E}) \sin \omega \tau_2$ and $k_3 = \bar{E}^2 + \bar{B}^2 - \bar{F}^2 - \bar{D}^2 + 2(\bar{B}\bar{E} - \bar{D}\bar{F}) \cos \omega \tau_2$. Let $G(\omega) = \omega^4 + k_1 \omega^2 + k_2 \omega + k_3$. Then if $(\bar{B} + \bar{E})^2 < (\bar{D} + \bar{F})^2$, then $G(0) < 0$. Also, $\lim_{\omega \rightarrow \infty} G(\omega) = \infty$. We can obtain that $G(\omega) = 0$ has finite positive roots $\omega_1, \omega_2, \dots, \omega_m$. For every fixed ω_i , $i = 1, 2, \dots, m$, there exists a sequence $\{\tau_{1_i}^j : j = 1, 2, 3, \dots\}$ such that $G(\omega) = 0$ holds. Let $\tau_1^* = \min\{\tau_{1_i}^j : i = 1, 2, \dots, m; j = 1, 2, 3, \dots\}$. When $\tau_1 = \tau_1^*$, the equation $D(\lambda, \tau_1, \tau_2) = 0$ has a pair of purely imaginary roots $\pm i\omega^*$ for $\tau_2 \in [0, \tau_2^+)$. We assume that $\zeta = \left[\frac{d(\operatorname{Re} \lambda)}{d\tau_1} \right]_{\lambda=i\omega^*} \neq 0$. Therefore, by the general Hopf bifurcation theorem for functional differential equations, we get the following result:

Lemma 4.8 Assume that the conditions of Lemma 3.2 are satisfied. Let $\zeta \neq 0$, $(\bar{B} + \bar{E})^2 < (\bar{D} + \bar{F})^2$ and either (i) $B_2^2 < C_2^2$ or (ii) $2B_2 - A_2^2 = 2\sqrt{B_2^2 - C_2^2} > 0$ hold for all

Fig. 9 **a** For $r = 1$, other parameter values as in Table 1, the system (2) is stable at coral-dominated E^* . **b** For $r = 1$, $\tau_1 = 1.06$, $\tau_2 = 0.1$, other parameter values as in Table 1, the system (4) undergoes a Hopf bifurcation as γ is increased through $\gamma_{cr} = 0.6$

$\tau_2 \in [0, \tau_2^+)$. Then E^* is locally asymptotically stable when $\tau_1 \in [0, \tau_1^*)$ and the system (4) undergoes a Hopf bifurcation at E^* as τ_1 crosses τ_1^* .

From Fig. 9a it follows that for $r = 1$, the system (2) remains stable at coral-dominated E^* , whereas, with $r = 1$, $\tau_1 = 1.06$ and $\tau_2 = 0.1$, the system (4) undergoes a Hopf bifurcation when γ crosses $\gamma_{cr} = 0.6$ (cf. Fig. 9b). From Fig. 10 it follows that the system (2) is macroalgae-dominated and stable for $r = 1$ and $\gamma = 2.5$, whereas, for $r = 1$ and $\gamma = 2.5$, the system (4) with time lags becomes coral-dominated and stable ($\tau_1 = 1.06$, $\tau_2 = 0.1$). Further, for $r = 1$, $\gamma = 0.1$ and $\tau_2 = 0.1$, the system (4) undergoes a Hopf bifurcation when τ_1 crosses $\tau_1^* = 1.03$ (cf. Fig. 11).

Fig. 10 **a** For $r = 1$ and $\gamma = 1.3$, the system (2) is stable at macroalgae-dominated E_0 , whereas, the system (4) with $\tau_1 = 1.06$, $\tau_2 = 0.1$, is stable at coral-dominated E^* (solid lines). **b** For $r = 1$ and $\gamma = 2.5$, the system (2) and the system (4) with $\tau_1 = 1.06$, $\tau_2 = 0.1$, both are stable at macroalgae-dominated E_0 (dotted lines)

Fig. 11 For $r = 1$ and $\tau_2 = 0.1$, other parameter values as in Table 1, the system (4) undergoes a Hopf bifurcation as τ_1 is increased through $\tau_1^* = 1.03$

5 Discussion

We have considered a model to study the dynamics of the coral reef benthic system in which macroalgae and corals compete to occupy turf algae. In our model, the immigration of algae from other areas of the seabed is taken into account. Underwood et al. [31] examined coral larvae dispersal in three coral reef systems in Northwest Australia, for the brooding coral *Seriatopora hystrix* and the spawning coral *Acropora tenuis*. Underwood et al. found that many reefs or reef patches are demographically independent and the hydrodynamics associated with these reefs restrict the movement of coral larvae. The study also found that there was no major genetic divergence for *Acropora tenuis* between Scott Reef and Rowley Shoals, two of the coral reef systems that are separated by hundreds of kilometers. Thus, for some reefs, it may be appropriate to exclude the immigration of coral larvae. We model a coral reef ecosystem in which coral larvae do not immigrate. We first perform equilibrium and stability analysis on our 2D non-linear ODE model and found that the model is capable of exhibiting the existence of two stable configurations of the community under the same environmental conditions by allowing saddle-node bifurcations and associated hysteresis effects with changing parameter values. This supports the observations from previous modeling analyses by Blackwood et al. [24], Mumby et al. [23] and Fung et al. [32, 33]. A study by Chattopadhyay et al. [34] reveal that the liberation of toxic substances by algae species is not an instantaneous process but is mediated by some time lag required for maturity of the species. This motivates us to consider toxin-liberation time lag of macroalgae in our model. We observe that, with macroalgal-toxicity below a certain threshold, the system exhibits two alternative stable states. When the toxicity level exceeds the threshold, the system becomes locally asymptotically stable at a coral-free equilibrium following a sudden change of transition and hysteresis, justifying the observations of [19] that allelopathy can suppress coral resilience by preventing coral recovery. It is noteworthy that in the absence of macroalgal-immigration, no hysteresis is observed. This too justifies the consideration of macroalgal dispersal in our model. Also, the low grazing intensity of herbivores can lead to a sudden

change of regime from a coral-dominated regime to one that is dominated by macroalgae. Moreover, a high level of harvest-mediated grazing loss marks the transition from a coral-macroalgae bistable regime to a macroalgae-dominated regime. This supports the reviews by Dudgeon et al. [35] and Cruz et al. [36] that the existence of multiple stable states in coral reefs is necessary for the occurrence of phase shifts. We have studied the dynamic behavior of the system with a discrete time lag in macroalgal recovery after grazing and a time-lag of microalgal-toxin-liberation. Further, analytical and numerical simulations demonstrate the following conclusions:

- (i) With low microalgal toxicity, the system becomes stable at the coral-dominated regime. Increase of the toxicity level beyond a certain threshold determines two possible stable regimes depending upon the initial conditions. With high macroalgal toxicity, coral depletes completely and the system becomes stable at the coral-free equilibrium, consistent with the experimental observations of Bonaldo and Hay [19] that toxic-macroalgae can exhibit significant negative impact on coral species.
- (ii) With high macroalgal-toxicity level, increase of grazing rate of herbivores increases the resilience of the coral-dominated regime, signifying the importance of grazers in coral reefs affected by seaweed allelopathy.
- (iii) With high macroalgal grazing rate by herbivores, increase of macroalgal growth rate on algal turf increases the resilience of the coral-dominated regime.
- (iv) The system without time delay becomes stable with high growth rate of corals on turf algae even with high macroalgal toxicity level, whereas, the system with delays becomes oscillatory when the microalgal toxicity level crosses a certain threshold.
- (v) With high microalgal toxicity, the system without time delay becomes macroalgae-dominated and stable, whereas with the same toxicity level below some certain threshold, the system with delays becomes coral-dominated and stable. Thus, by considering the macroalgal-recovery time lag and toxin-liberation delay, the coral-dominated system becomes more tolerant to higher toxicity level of macroalgae.

Throughout the article an attempt is made to search for a suitable way to control the growth of macroalgae and corals and maintain stable coexistence. From analytical and numerical observations, it is seen that an increase of the harvesting of herbivores can lead to a sudden shift from coral-dominated regime to macroalgae-dominated regime. Moreover, we observe that a higher grazing rate of herbivores reduces macroalgal cover and increases the resilience of the coral-dominated regime.

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