MICROBIAL DISEASE IN CORAL REEFS: AN ECOSYSTEM IN TRANSITION

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Abstract. Infectious disease outbreaks are considered an important factor for the degradation of coral reefs. Reef-building coral species are susceptible to the influences of black band disease (BBD), characterized by cyanobacteria-dominated microbial mat that migrates rapidly across infected corals, leaving empty coral skeletons behind. We investigate coral-macroalgal phase shift in presence of BBD infection by means of an eco-epidemiological model under the assumption that the transmission of BBD occurs through both contagious and non-contagious pathways. It is observed that in presence of low coral-recruitment rate on algal turf, reduced herbivory and high macroalgal immigration, the system exhibits hysteresis through a saddle-node bifurcation and a transcritical bifurcation. Also, the system undergoes a supercritical Hopf bifurcation followed by a saddle-node bifurcation if BBD-transmission rate crosses certain critical value. We examine the effects of incubation time lag of infectious agents develop in susceptible corals after coming in contact with infected corals and a time lag in the recovery of algal turf in response to grazing of herbivores by performing equilibrium and stability analyses of delay-differential forms of the ODE model. Computer simulations have been carried out to illustrate different analytical results.

1. Introduction. Coral diseases have been identified as among the most important contributors to the global degradation of coral reef ecosystems. Among all of the coral diseases, BBD is considered one of the most important contributors to the decline of coral reefs. Molecular studies by Richardson [25] reveal that cyanobacteria and a complex consortium of other bacteria are the main causative agents of BBD. This microbial community is responsible for creating a chemical environment that digests off and dissolves the coral tissue away from the skeleton [28]. Unlike other coral diseases, BBD is often found in low incidences but persists within a reef for long periods. Rutzler et al. [26] point out that healthy corals can become infected with BBD by direct contact. However, field observations by Antonelli [2] suggested that apart from direct contact, injured corals may become infected with BBD when placed at a distance apart. As observed by Aeby and Santavy [1], the transmission of BBD on injured corals is vector-mediated, capable of spreading by vectors such as via corallivorous fish.

In coral reef ecosystems, macroalgae and corals compete for space and in the absence of herbivory by reef fishes, the faster growing macroalgae often overgrow
corals, depriving them of essential sunlight and causing their decline [17, 20, 23]. The combinations of outbreak of BBD and proliferation of macroalgae is detrimental to coral reef ecosystem. As observed by Done [11] and Bellwood et al. [4], degradation of coral reefs often exhibits phase shifts in community structure for which corals decline with an increase in abundance of macroalgae [7]. Researchers observe that coral disease together with the reduction in herbivory can lead to a permanent shift in regime in which macroalgae, once dominant, inhibit coral settlement [8, 9]. The grazing of macroalgae by herbivores contributes to the resilience of the coral-dominated reef [18, 21, 22]. BBD-induced death of corals provides the space required for macroalgae to settle, and reduction in herbivory due to overfishing of reef-fish proliferates macroalgal biomass in seabed [10]. A catastrophic shift of regime occurs when the grazing rate of herbivores and the transmission rate of BBD cross some critical thresholds. As different sets of feedbacks stabilize each alternative regime, returning the system from macroalgae-dominated regime to coral-dominated regime becomes difficult [12]. Consequently, the threshold for a shift of regime and for its reversal can become different, a phenomenon known as hysteresis. The occurrence of hysteresis erodes the resilience of coral-dominated regime.

Mumby et al. [22] 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 sea bed is occupied by macroalgae, corals and turf algae with macroalgal vegetative growth on turf algae, macroalgal overgrowth on corals and grazing of herbivores. Blackwood et al. [6] have modified this model by introducing herbivores in the system and studied the grazing dynamics of herbivores. Our model originates from the models used in [6, 22] and is a direct extension of the model studied in [6] by subdividing coral population into susceptible and infected classes and by assuming that macroalgae recruits externally from the surrounding seascape. The tissue of corals after being infected by BBD are stripped from the coral surface and macroalgae rapidly colonize the naked skeleton, preventing any subsequent recovery of corals from the infection [30]. This prompts us to consider a model where the disease spreads among coral population according to a Susceptible→Infected (SI) type compartmental epidemiological model [3]. In the marine environment, corals are sessile for most of their lives [19]. Even in some coral reefs, coral larvae donot immigrate [29]. In our model, we have excluded the immigration of coral larvae on algal turf from other parts of seabed. BBD transmits through physical contact between susceptible and infected coral colonies and through the water column. This motivates us to consider the transmission of BBD of corals through both contagious and non-contagious pathways in our model. We examine the effects of a discrete time lag in the recovery of algal turf after macroalgae is grazed by herbivores. Also, we consider an incubation time lag of infectious agents develop inside susceptible corals after coming in contact with infected corals. We show that when the parameters representing time delays passes through a critical value, the interior equilibrium loses its stability and a Hopf bifurcation occurs.

In the present paper the main emphasis will be put in studying the dynamic behaviour of the system and to find out the long-term consequences of BBD and reduction in herbivory on coral resilience and persistence.

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. The coral population affected by BBD is subdivided into two classes viz. susceptible and infected. In formulating the model we assume that macroalgae are always present in coral reef ecosystem irrespective of the abundance of corals in seabed and BBD is assumed to be transmitted to corals through both contagious and non-contagious pathways. Let \( M(t) \) be the proportion of seabed covered by macroalgae, \( C_S(t) \) be the proportion of seabed covered by susceptible coral, \( C_I(t) \) be the proportion of seabed covered by infected coral and \( T(t) \) represent the fraction of seabed occupied by turf-algae so that \( M(t) + C_S(t) + C_I(t) + T(t) = c_0 \) (constant) at any instant \( t \). For simplicity, we have ignored the possibility of any empty space in the sea bed. We make the following assumptions in formulating the mathematical model:

\( H_1 \) Corals are overgrown by macroalgae at a rate \( \alpha \).

\( H_2 \) Macroalgae spread vegetatively over algal turfs at a rate \( a \).

\( H_3 \) Colonization rate of newly immigrated macroalgae on algal turf is \( b \).

\( H_4 \) Susceptible corals recruit to and overgrow algal turfs at a rate \( r \).

\( H_5 \) The rate of infection through contact is \( \lambda \) and the rate of infection through non-contagious pathway, independent of the density of infected corals, is \( \eta \).

\( H_6 \) Macroalgae and Corals have natural mortality rates \( d_1 \) and \( d_2 \) respectively.

\( H_7 \) Disease induced death rate of infected corals is \( \gamma \).

\( H_8 \) Grazing rate of herbivores on macroalgae is \( \frac{g}{M+T} \) per unit area of algal cover.

A schematic diagram of the system is given in Fig.1. Assuming that the grazing of herbivores as a dynamic process, the reef dynamics are thus described as a system of nonlinear differential equations:

\[
\begin{align*}
\frac{dM}{dt} &= M \left\{ \alpha(C_S + C_I) - \frac{g}{M+T} - d_1 \right\} + (aM + b)T \\
\frac{dC_S}{dt} &= C_S \left( rT - \alpha M - \lambda C_I - \eta - d_2 \right) \\
\frac{dC_I}{dt} &= C_I \left( \lambda C_S - \alpha M - d_2 - \gamma \right) + \eta C_S
\end{align*}
\] (1)

\textbf{Fig. 1.} Schematic representation of the eco-epidemiological model
proof. \[ \frac{dT}{dt} = \frac{gM}{M+T} + d_1M + d_2(C_S + C_I) + \gamma C_I - T(aM + b + rC_S) \]

where \( M(0) > 0, C_S(0) \geq 0, C_I(0) \geq 0 \) and \( T(0) > 0 \).

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

\[
\begin{align*}
\frac{dM}{dt} &= M \left\{ \alpha(C_S + C_I) - \frac{g}{1 - C_S - C_I} - d_1 \right\} + (aM + b)(1 - M - C_S - C_I) \equiv f^1 \\
\frac{dC_S}{dt} &= C_S \{ r(1 - M - C_S - C_I) - \alpha M - \lambda C_I - \eta - d_2 \} \equiv f^2 \\
\frac{dC_I}{dt} &= C_I(\lambda C_S - \alpha M - d_2 - \gamma) + \eta C_S \equiv f^3
\end{align*}
\]

where \( 0 < M(0) < 1, 0 \leq C_S(0) < 1 \) and \( 0 \leq C_I(0) < 1 \).

We observe that right-hand sides of the equations in the system (2) are smooth functions of the variables \( M, C_S, C_I \) and the parameters. As long as these quantities are non-negative, local existence and uniqueness properties hold in \( R^3_{+} = \{(M, C_S, C_I) : M > 0, C_S, C_I \geq 0 \} \).

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:

(i) Coral-free equilibrium \( E_0 = (M_0, 0, 0) \), where \( M_0 = \frac{a-b-d_1-g+\sqrt{(a-b-d_1-g)^2+4a\delta}}{2a} \).

\( E_0 \) always exists;

(ii) interior equilibrium \( E^* = (M^*, C_S^*, C_I^*) \), where \( C_I^* \) is a positive root of \( f_2(C_I) \)

\[
\begin{align*}
\alpha \{ f_1(C_I) + C_I - \frac{g}{1 - f_1(C_I)} - d_1 \} + (aM + b) \left\{ 1 - \sum_{i=1}^{2} f_i(C_I) - C_I \right\} &= 0, \\
C_S^* &= f_1(C_I^*) = \frac{M^*}{\lambda C_S - \alpha M - d_2 - \gamma} + \frac{1}{\gamma} \left[ \frac{M^*}{\lambda C_S - \alpha M - d_2 - \gamma} - \frac{\lambda C_S - \alpha M - d_2 - \gamma}{\eta} \right], \\
M^* &= f_2(C_I^*) = \frac{r(1 - M^* - C_S^*) - \lambda C_I^* - \eta - d_2}{\eta}.
\end{align*}
\]

At \( E_0 \) the eigenvalues of the Jacobian matrix of the system (2) are \( -\sqrt{(a-b-d_1-g)^2+4a\delta}, r - M_0(r + \alpha) - \eta - d_2 \) and \( -(aM_0 + d_2 + \gamma) \).

Therefore, all the eigenvalues of the Jacobian matrix are negative if \( r - M_0(r + \alpha) - \eta - d_2 < 0 \). This gives the following lemma:

Lemma 3.1. The system (2) is locally asymptotically stable at \( E_0 \) if \( \eta > \eta^* \), where \( \eta^* = (r - d_2) - M_0(r + \alpha) \).

Therefore, high BBD-infection rate through non-contagious pathway leads to the elimination of corals.

Lemma 3.2. If \( \alpha > a + \frac{b}{M_0} \) and \( g < \frac{(\alpha-a)M_0-b}{M_0} \), the system (2) undergoes a transcritical bifurcation at \( E_0 \) when \( \eta \) crosses \( \eta^* \).

Proof. At \( \eta = \eta^* \), we have

\[
J_0 = \begin{pmatrix}
-\sqrt{(a-b-d_1-g)^2+4a\delta} & (\alpha-g-a)M_0 - b & (\alpha-g-a)M_0 - b \\
0 & 0 & -\alpha M_0 - d_2 - \gamma \\
0 & \eta^* & -\alpha M_0 - d_2 - \gamma
\end{pmatrix}
\]

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 \( V = \begin{pmatrix} v_1 & v_2 & 1 \end{pmatrix}^T \) and \( W = \begin{pmatrix} 0 & 1 & 0 \end{pmatrix}^T \), where \( v_1 = \frac{(M_0 + d_2 + \gamma + \eta^*)((\alpha-g-a)M_0-b)}{\eta^* \sqrt{(a-b-d_1-g)^2+4a\delta}} \) and \( v_2 = \frac{\alpha M_0 + d_2 + \gamma}{\eta^*} \).
Let us express the system (2) in the form \( \dot{X} = f(X; \eta) \), where \( X = (M \ C_S \ C_I) \) and \( f(X; \eta) = (f_1 \ f_2 \ f_3) \). Then \( W^T f_3(M_0, 0; \eta^*) = 0 \) and so no saddle-node bifurcation occurs at \( E_0 \) when \( \eta \) crosses \( \eta^* \).

Also, \( Df_3(M_0, 0, 0; \eta^*)V = (0 \ -v_2 \ v_2)^T \) and so \( W^T[Df_3(M_0, 0, 0; \eta^*)V] = -v_2 < 0 \).

Now, we have

\[
D^2 f(M_0, 0, 0; \eta^*)(V, V) = \begin{pmatrix}
-2av_1^2 + 2v_1(1 + v_2)(\alpha - g - a) - 2gM_0(1 + v_2)^2 \\
-2v_2((r + \alpha)v_1 + rv_2 + r + \lambda) \\
-2(\alpha v_1 + \lambda v_2)
\end{pmatrix}
\]

This gives \( W^T[D^2 f(M_0, 0, 0; \eta^*)(V, V)] = -2v_2 \{(r + \alpha)v_1 + rv_2 + r + \lambda \}. \)

If \( \alpha > a + \frac{b}{M_0} \) and \( g < \frac{(\alpha-a)M_0-b}{M_0} \) hold, then we have \( v_1 > 0 \) and consequently \( W^T[D^2 f(M_0, 0, 0; \eta^*)(V, V)] < 0 \).

Therefore, if \( \alpha > a + \frac{b}{M_0} \) and \( g < \frac{(\alpha-a)M_0-b}{M_0} \) is satisfied, by Sotomayor theorem \[24\] it follows that the system (2) undergoes a transcritical bifurcation at \( E_0 \) when \( \eta \) crosses \( \eta^* \).

Thus, with high macroalgal overgrowth rate on corals and low grazing intensity of herbivores, the coexistence equilibrium and coral-free equilibrium exchange stability at \( \eta = \eta^* \). This threshold can be regarded as an invasion boundary of macroalgae.

The endemic equilibrium \( E^* \) is persistent if the boundary equilibrium \( E_0 \) repel interior trajectories. We see that the boundary equilibrium \( E_0 \) is unstable if \( \eta < \eta^* \). Also, the system is bounded. The following lemma gives the condition of persistence of the system (2):

**Lemma 3.3.** The system (2) is persistent at \( E^* \) if \( \eta < \eta^* \) and \( r > \frac{\alpha M_0 + d_2}{1 - M_0} \).

Therefore, if the recruitment rate of corals exceeds \( \frac{\alpha M_0 + d_2}{1 - M_0} \) and the rate of non-contagious infection of corals is less than \( \eta^* \), then the disease will persist in the population.

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

\[
J^* = \begin{pmatrix}
-aM^* - \frac{b}{M^*}(1 - C_S^* - C_I^*) & f_{C_S|E^*}^1 & f_{C_I|E^*}^1 \\
-(r + \alpha)C_S^* & -rC^* & -r(r + \lambda)C_S^* \\
-\alpha C_I^* & \lambda C_I^* & -\frac{rC_I^*}{C_I^*}
\end{pmatrix}
\]

where \( f_{C_S|E^*}^1 = f_{C_I|E^*}^1 = (\alpha - a - \frac{rg}{(1-C_S^*-C_I^*)^2})M^* - b \).

The characteristic equation of the Jacobian \( J^* \) of the system (2) evaluated at \( E^* \) is \( \mu^3 + \mu^2 + B\mu + C = 0 \), where

- \( A = aM^* + \frac{b}{M^*}(1 - C_S^* - C_I^*) + (r + \frac{\alpha}{C_I^*})C_S^* \),
- \( B = B_1 + \left\{ (\alpha - a)M^* - b - \frac{gM^*}{(1-C_S^*-C_I^*)} \right\}B_2 \), \( C = C_1 - \left\{ (\alpha - a)M^* - b - \frac{gM^*}{(1-C_S^*-C_I^*)} \right\}C_2 \),
- \( B_1 = \left( aM^* + \frac{b(1-C_S^*-C_I^*)}{M^*} \right)(r + \frac{\alpha}{C_I^*}) + (r + \lambda)(\lambda C_I^* + \eta) + \frac{rC_I^*}{C_I^*} \) \( C_S^* \), \( B_2 = (r + \alpha)C_S^* + \alpha C_I^* \),
- \( C_1 = (r + \lambda)(\lambda C_I^* + \eta) + \frac{rC_I^*}{C_I^*} \) \( aM^* + \frac{b(1-C_S^*-C_I^*)}{M^*} \) \( C_S^* \) and \( C_2 = (2a + r)\lambda C_I^* + (1 - \frac{C_I}{C_I^*})(r + \alpha)\eta \) \( C_S^* \).

Therefore, \( AB - C = P_1 + \left\{ (\alpha - a)M^* - b - \frac{gM^*}{(1-C_S^*-C_I^*)} \right\}P_2 \), where

- \( P_1 = \left( aM^* + \frac{b(1-C_S^*-C_I^*)}{M^*} \right)(r + \lambda)(\lambda C_I^* + \eta) + \frac{rC_I^*}{C_I^*} \) \( C_S^* \), \( P_2 = (r + \alpha)C_S^* + \alpha C_I^* \) \( (r + \alpha)(\lambda C_I^* + \lambda C^* + (r + 2a)(\eta + \lambda C_I^*)C_S^* \).

Also, we have \( A, C_1 > 0 \) and \( B_i, P_i > 0 \) for \( i = 1, 2 \).
Lemma 3.4. The system (2) is locally asymptotically stable at $E^*$ if $0 < b < \left\{ \alpha - a - \frac{g}{(1-C_S^2-C_I^2)^2} \right\} M^* + \min \left\{ \frac{b_1}{b_2}, \frac{b_2}{b_1} \right\}$. This gives the following lemma

Theorem 3.5. The system (2) undergoes a Hopf bifurcation at $g = g_{cr}$ if

(a) $\frac{b_1}{b_2} < \frac{b_2}{b_1}$ and $\lambda > \frac{m(\alpha + \eta)}{2(\alpha + \eta)C_S^2}$,

(b) $f_1(g_{cr}) = f_2(g_{cr})$,

(c) $\{M(g)K(g) + N(g)L(g)\}_{g=g_{cr}} \neq 0$, where $g_{cr} = \frac{(1-C_S^2-C_I^2)^2 \left\{ (\alpha - a)M^* + b \right\}}{M^*}$,

$f_1 = AB$ and $f_2 = C$.

Proof. We observe that $A(g_{cr})B(g_{cr}) = C(g_{cr})$ holds.

Also, for $\frac{b_1}{b_2} < \frac{b_2}{b_1}$ and $\lambda > \frac{m(\alpha + \eta)}{2(\alpha + \eta)C_S^2}$, we have $B(g_{cr}), C(g_{cr}) > 0$.

Therefore, at $g = g_{cr}$, the characteristic equation of the Jacobian of the system (2) at $E^*$ is $(\mu + A)(\mu^2 + B) = 0$, which gives $\mu = -A, \pm i\sqrt{B}$.

For $g \in (g_{cr} - \epsilon, g_{cr} + \epsilon)$, the roots are in general of the form: $\mu_1(g) = \beta_1(g) + i\beta_2(g), \mu_2(g) = \beta_1(g) - i\beta_2(g), \mu_3(g) = -A(g)$.

Therefore, $\frac{d}{dg} \left( \mu^3 + A\mu^2 + B\mu + C \right) = 0$ gives $(K + iL)\frac{dK}{dg} + (M + iN) = 0$, where $K(g) = 3\beta_1^2(g) - 3\beta_2^2(g) + 2A(g)\beta_1(g) + B(g)$, $L(g) = 6\beta_1(g)\beta_2(g) + 2A(g)\beta_2(g)$, $M(g) = C'(g) + \{\beta_1^2(g) - \beta_2^2(g)\}A'(g) + \beta_1 B'(g)$, $N(g) = 2\beta_1(g)\beta_2(g)A'(g) + \beta_2(g)B'(g)$.
Therefore, \( \frac{dn}{dg} = -\frac{\{M(g)K(g) + N(g)L(g)\} + \{N(g)K(g) - M(g)L(g)\}}{K^2(g) + L^2(g)} \) If \( \{M(g)K(g) + N(g)L(g)\}_{g=g_{cr}} \neq 0 \), then \( Re \left[ \frac{dn}{dg} \right]_{g=g_{cr}} \neq 0 \) and consequently, a Hopf bifurcation occurs when \( g \) crosses \( g_{cr} \) and also it is non-degenerate. \( \square \)

The condition \((ii)\) of Lemma 3.5 is equivalent to \( \frac{dn(g)}{dg} \) at \( g_{cr} \) \( \neq 0 \), where \( \phi(g) = f_1(g) - f_2(g) \). By using numerical methods, condition \((i)\) of Lemma 3.5 can be verified by showing that the curves \( y = f_1(g) \) and \( y = f_2(g) \) intersect at \( g = g_{cr} \), whereas the condition \((ii)\) can be verified by showing that the tangent to the curve \( y = \phi(g) \) at \( g = g_{cr} \) is not parallel to \( g \) axis \( [27] \).

Therefore, if the grazing intensity of herbivores goes below the threshold \( g = g_{cr} \), under the conditions \((a), (b)\) and \((c)\) of lemma 3.5, the extinction of coral population occurs due to natural fluctuations which drives the coral population to a smaller size.

**Corollary 3.1.** The period \( \tau \) of the bifurcating periodic orbits close to \( g = g_{cr} \) is given by \( \tau(g_{cr}) = \frac{2\pi}{\sqrt{B_{(g_{cr})}}} \).

Next we perform detailed analysis of the bifurcation solutions to study the nature of Hopf bifurcation.

Let \( p, q \in C^3 \) be the eigenvectors such that \( J^*q = i\omega q \) and \( J^*p = -i\omega p \) and \( \langle p, q \rangle = \sum_{i=1}^{3} \bar{p}_i q_i \), where \( \omega = \sqrt{B} \). Then we have \( p = \frac{1}{\bar{p}_1 + p_1 + p_2} \left( 1 \quad p_1 \quad p_2 \right)^T \) and \( q = \left( 1 \quad q_1 \quad q_2 \right)^T \), where

\[
\begin{align*}
p_1 &= \frac{\{f_{M1}(E^*) + i\omega\}(\lambda C_1^* + \eta + \alpha C_1 f_{C1}^{*}|E^*)}{\eta C_2^* - i\omega C_1} \left( \frac{\{f_{M1}(E^*) + i\omega\}(\lambda C_1^* + \eta + \alpha C_1 f_{C1}^{*}|E^*)}{\eta C_2^* - i\omega C_1} \right) \frac{\{f_{M1}(E^*) + i\omega\}(\lambda C_1^* + \eta + \alpha C_1 f_{C1}^{*}|E^*)}{\eta C_2^* - i\omega C_1} \right. \\
p_2 &= \frac{C_2}{\eta C_2^* - i\omega C_1} \left[ \left( \frac{\{f_{M1}(E^*) + i\omega\}(\lambda C_1^* + \eta + \alpha C_1 f_{C1}^{*}|E^*)}{\eta C_2^* - i\omega C_1} \right) \times \left( \frac{\{f_{M1}(E^*) + i\omega\}(\lambda C_1^* + \eta + \alpha C_1 f_{C1}^{*}|E^*)}{\eta C_2^* - i\omega C_1} \right) \right] \\
q_1 &= \frac{\{f_{M1}(E^*) + i\omega\}(r + \lambda)(r + \alpha)}{\eta C_2^* - i\omega C_1} \left( \frac{\{f_{M1}(E^*) + i\omega\}(r + \lambda)(r + \alpha)}{\eta C_2^* - i\omega C_1} \right) \frac{\{f_{M1}(E^*) + i\omega\}(r + \lambda)(r + \alpha)}{\eta C_2^* - i\omega C_1} \\
q_2 &= \frac{C_2}{\eta C_2^* - i\omega C_1} \left[ \left( \frac{\{f_{M1}(E^*) + i\omega\}(r + \lambda)(r + \alpha)}{\eta C_2^* - i\omega C_1} \right) \times \left( \frac{\{f_{M1}(E^*) + i\omega\}(r + \lambda)(r + \alpha)}{\eta C_2^* - i\omega C_1} \right) \right]
\end{align*}
\]

At \( E^* \) we obtain \( (J^* - 2i\omega I_3)^{-1} = \frac{1}{\Delta_\omega} \left( \lambda^i \right)_{3 \times 3} \), where \( \Delta_\omega = Det(J^* - 2i\omega I_3) \),

\[
\begin{align*}
A_{11} &= \frac{r \eta C_2^*}{C_1^2} - 4\omega^2 + 2i\omega C_2^* \left( r + \frac{\eta}{C_1^2} \right) \, , \\
A_{12} &= \left( \lambda C_1^* + \eta \right) f_{C1}^1 |E^*| + \left( \frac{\eta C_2}{C_1^2} + 2i\omega \right) f_{C1}^1 |E^*| , \\
A_{13} &= (r + \lambda) f_{C1}^1 |E^*| - (r + \lambda) C_1^* f_{C1}^1 |E^*| , \\
A_{14} &= \alpha (r + \lambda) C_1^* C_1 - (r + \alpha) \left( \frac{\eta C_2}{C_1^2} + 2i\omega \right) C_2^* , \\
A_{22} &= \alpha C_1^* f_{C1}^1 |E^*| + \left( 2i\omega - f_{M1}^{*1}|E^*| \right) \left( 2i\omega + \frac{\eta C_2}{C_1^2} \right) , \\
A_{23} &= (r + \lambda) C_1^* \left( f_{M1}^{*1}|E^*| - 2i\omega \right) - (r + \alpha) C_1^* f_{C1}^1 |E^*| , \\
A_{24} &= -\alpha (r + \lambda) \eta C_2^* - (r + \alpha) (r + \lambda) C_1^* C_1 , \\
A_{25} &= \alpha C_1^* f_{C1}^1 |E^*| - \alpha C_1^* f_{C1}^1 |E^*| , \\
A_{26} &= (r + \alpha) C_2^* f_{C1}^1 |E^*| + \left( f_{M1}^{*1}|E^*| - 2i\omega \right) (2i\omega + r C_2^*) .
\end{align*}
\]

Putting \( \omega = 0 \) in the above expressions we obtain \( J^* - 1 = \frac{1}{\Delta} \left( \lambda^{ij} \right)_{3 \times 3} \), where \( \Delta = Det(J^*) \).

Let \( u = \left( u_1 \quad u_2 \quad u_3 \right)^T \in \mathbb{R}^3 \) and \( v = \left( v_1 \quad v_2 \quad v_3 \right)^T \in C^3 \), satisfying \( J^* u = B(q, \bar{q}) \) and \( (J^* - 2i\omega I_3) v = B(q, \bar{q}) \) where
\[ B(q, p) = \begin{pmatrix} -2a + (p_1 + p_2 + q_1 + q_2)f_{MC}^I | E^* + (p_1 q_1 + p_2 q_2 + p_1 q_2 + p_2 q_1) f_{CS}^I | E^* \\ -(r + \alpha) (p_1 + q_1) - 2p_1 q_1 - (r + \lambda) (p_2 q_1 + p_2 q_2) \end{pmatrix} \].

\[ u_i = \left[ 2f_{MC}^| E^* Rl(q_1 + q_2) + f_{CS}^| E^* \left( |q_1|^2 + 2Rl(q_1 q_2) + |q_2|^2 \right) - 2a \right] A_i^1 + 2 \{ \lambda Rl(q_1 q_2) - \alpha Rl(q_2) \} A_i^3 - 2 \{ (r + \alpha) Rl(q_1) + (r + \lambda) Rl(q_1 q_2) + r |q_1|^3 \} A_i^2 \text{ and } \]

\[ v_i = \left[ 2f_{MC}^| E^*, (q_1 + q_2) + f_{MC}^I, (q_1 + q_2)^2 - 2a \right] A_i^1 - 2q_1 \{ (1 + q_1 + q_2) + \alpha q_1 + \lambda q_2 \} A_i^2 + 2q_2 (\alpha q_1 - \alpha) A_i^3, \ (i = 1, 2, 3). \]

Then the first Lyapunov number to determine the stability of limit cycle arising through Hopf-bifurcation is given by

\[ l_1 = \frac{1}{2} \text{Re} \left[ \left( q, C(q, q, \bar{q}) - 2(p, B(q, J^* - 2(\omega I_3))^{-1} B(q, q)) + (p, B(q, J^{* - 1} B(q, q))) \right) \right] , \] where

\[ C(q, p, u) = \left( \begin{array}{ccc} -2a [p_1 q_1 u_1 + (p_1 + p_2 + q_1)(u_2 + u_3)] & -q_1 [p_1 q_1 + p_2 q_2 + p_2 q_1] (u_2 + u_3) \\ \{1 - C_2 - C_3^2\} & \{1 - C_2 - C_3^2\} \end{array} \right) \]

If \( l_1 < 0 \) then \( E^* \) is destabilized through a supercritical Hopf-bifurcation, and if \( l_1 > 0 \) then the Hopf-bifurcation is subcritical.

Since the expression for the first Lyapunov number at the Hopf-bifurcation point is cumbersome, we use numerical simulations to examine the nature of Hopf bifurcation and it is found that the first Lyapunov number is always negative. Therefore, the Hopf-bifurcation is supercritical.

We investigate numerically the effect of the various parameters on the qualitative behavior of the system using parameter values given in Table 1 throughout, unless otherwise stated. By analyzing the system (2) we are able to show that a sharp transition with hysteresis can be achieved by varying some of the parameter values.

To identify the impact of non-contagious infection on coral cover, in Fig. 2(a), we plot the solutions of the nullcline equations in the \( C - \eta \) 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 \( 0 \leq \eta < \eta^* \), representing coral-macroalgae coexistent steady state for all non-negative initial conditions. Once the non-contagious infection rate surpasses the threshold \( \eta^* \), the system arrives at a macroalgae-dominated and coral-depleted stable state, represented by region \( II \) of monostability at \( E_0 \). Therefore, due to high contagious infection rate on corals, coexistence is not possible in the system.

From Fig. 2(b) we see that for \( 0 \leq \eta < \eta^* \) two eigenvalues of the Jacobian of the system at \( E_0 \) are negative and one eigenvalue is positive, i.e. the fixed point \( E_0 \) is unstable. The stability of the system changes when \( \eta \) crosses \( \eta^* \). All the

### Table 1. Parameter values used in the numerical analysis.

| Parameters | Description of Parameters | Value | Reference |
|------------|---------------------------|-------|-----------|
| \( \alpha \) | Macroalgal overgrowth rate on corals | 0.1 | [13] |
| \( r \) | Recruitment rate of susceptible corals on turf algae | 0.55 | [13] |
| \( a \) | Macroalgal vegetative growth rate on algal turfs | 0.77 | [13] |
| \( b \) | Immigration rate of macroalgae on algae turf | 0.005 | [13] |
| \( d_1 \) | Natural mortality rate of macroalgae | 0.1 | [6] |
| \( d_2 \) | Natural mortality rate of corals | 0.24 | [13] |
| \( \gamma \) | Disease induced death rate of infected corals | 0.1 | - |
| \( g \) | Maximal macroalgae-grazing rate of herbivores | 0.4 | [13] |
| \( \lambda \) | Rate of contagious infection | 3 | - |
| \( \eta \) | Rate of non-contagious infection | 0.001 | - |
eigenvalues becomes negative for \( \eta > \eta^* \), representing the stability of the system at \( E_0 \). To determine the nature of bifurcation at \( \eta = \eta^* \) and to verify the analytical results, we use numerical simulations.

At \( \eta = \eta^* = (r - d_2) - M_0(r + \alpha) = 0.0746 \), we have \( E_0 = (0.3621, 0, 0) \) and

\[
J_0 = \begin{pmatrix} -0.2926 & -0.3924 & -0.3924 \\ 0 & 0 & 0 \\ 0 & 0.0746 & -0.3762 \end{pmatrix}
\]

has a simple zero eigenvalue. Also, we obtain \( V = \begin{pmatrix} 8.1006 & 5.0402 & 1 \end{pmatrix}^T \), \( W = \begin{pmatrix} 0 & 1 & 0 \end{pmatrix}^T \), \( W^T f_\eta(E_0; \eta^*) = 0 \), \( W^T [D f_\eta(E_0; \eta^*)] V = -5.0402 < 0 \) and \( W^T [D^2 f(E_0; \eta^*)] (V, V) = -116.8061 < 0 \).

This implies, the system undergoes a transcritical bifurcation at \( E_0 \) when \( \eta \) crosses \( \eta^* = 0.0746 \).

With high grazing rate of herbivores (viz. \( g = 0.4 \)), from Figs. 2(a)&3(a) it is observed that the system does not exhibit hysteresis when the rate of non-contagious infection is varied. Fig. 3(a) represents a bifurcation diagram of \( \eta \) versus equilibrium value of coral cover for different grazing rates of herbivores. It is observed that decrease of grazing rate of herbivores can lead to a pronounced hysteresis in response to non-contagious infection by eroding the resilience of coral-dominated regime. The increase of grazing rate of herbivores increases the tolerance of the coral-dominated steady state to non-contagious infection and therefore, increases the resilience of coral-dominated regime even with high rate of non-contagious infection. Also, the increase in grazing intensity decreases the threshold differences of saddle-node bifurcating point (LP) and a transcritical bifurcating point (BP). The emergence of LP and BP determines two possible steady states of the system, one is dominated by macroalgae with complete elimination of corals and the other is coexistence steady state. This emergence of LP and BP generates a zone of hysteresis where the resilience of the system is determined by means of ecological resilience having components latitude (L), resistance (R) and precariousness (Pr). Eventually, LP and BP merge on the \( \eta \)-axis, generating a cusp point (CP) where the system becomes monostable at coral-free equilibrium in a hysteresis-free zone. The coral-free
single attractor and the corresponding rate of recovery from small perturbations quantifies the engineering resilience of the system. From Fig. 3(a), we see that, for \( g = 0.315 \), a Hopf point emerges on the codimension one bifurcation curve together with a saddle-node bifurcating point (LP) and a transcritical bifurcating point. Fig. 3(b) gives a two-parameter bifurcation diagram with \( \eta \) and \( g \) as active parameters, representing a cusp point at \( (\eta, g) = (0.0419, 0.3595) \) with eigenvalues 0, –0.3812 and –0.3297, a Bogdanov-Takens (BT) point at \( (\eta, g) = (0.0002, 0.2738) \) with eigenvalues 0, 0, –0.3886 and a zero-Hopf (ZH) point at \( (\eta, g) = (0.0429, 0.1979) \) with eigenvalues 0 and \( \pm 0.4768i \) on the saddle-node curve. The Hopf curve intersects the saddle-node curve at BT which is a neutral saddle point. The absence of Bautin bifurcation point, on the Hopf curve, eliminates the chance of having an unstable limit cycle. Also, from Fig. 3(c) we see that the coral-dominated stable coexistence is not possible with low grazing rate of herbivores in presence of non-contagious infection of corals. With high rate of grazing, the system is coral-dominated and stable even with high non-contagious infection-rate.

From Fig 4(a) it is observed that with low recruitment rate of corals on turf algae, the system exhibits hysteresis when the rate of non-contagious infection is varied.
The increase of recruitment rate of corals on turf algae increases the tolerance of the coral-dominated steady state to non-contagious infection and therefore, increases the resilience of coral-dominated regime even with high rate of non-contagious infection. For \( r = 0.425 \), a Hopf point emerges on the codimension one bifurcation curve (cf. Fig. 4(a)) along with a saddle-node bifurcating point. Fig. 4(b) gives a two-parameter bifurcation diagram with \( \eta \) and \( r \) as active parameters, representing two cusp points (CP) at \((\eta, r) = (0.0426, 0.4998)\), \((\eta, r) = (0.0104, 0.3349)\) and a Bogdanov-Takens (BT) point at \((\eta, r) = (0.0001, 0.3867)\) on the saddle-node curve. The absence of Bautin bifurcation point, on the Hopf curve, eliminates the chance of having an unstable limit cycle.

To identify the impact of macroalgal immigration on coral cover, in Fig. 5(a), we plot the solutions of the nullcline equations in the \( C-b \) plane, yielding a bifurcation diagram. The region IIII represents monostability at \( E^* \) for \( 0 \leq b < b_\star = 0.087 \), representing coral-macroalgae coexistence steady 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 macroalgae. The bistable region is represented by the region IV for \( b_\star < b < b^* = 0.1035 \). Once the rate of macroalgal immigration surpasses the threshold \( b^* \), the system arrives at a macroalgae-dominated and coral-depleted stable state, represented by region \( V \) of monostability at \( E_0 \). Hysteresis will result, with low macroalgal cover followed by an increase in the macroalgal cover above a critical threshold \( b^* \). A backward shift occurs only if the macroalgal immigration rate is reduced far enough to reach the other bifurcation point \( b_\star \).

From Fig. 5(c) we see that for \( 0 \leq b < b_\star \), two eigenvalues of the Jacobian of the system at \( E_0 \) are negative and one eigenvalue is positive, i.e. the fixed point \( E_0 \) is unstable. All the eigenvalues becomes negative for \( b > b_\star \), representing the stability of the system at \( E_0 \). From Fig. 5(d) it follows that the system (2) has a stable focus at \( E^* \) for \( b < 0.1026 \) and has a stable node at \( E^* \) for \( 0.1056 < b < b^* \). Also, \( E^* \) ceased to exist for \( b > b^* \). Thus, there are changes in the stability of the system when \( b \) crosses \( b_\star \) and \( b^* \). We use numerical simulations to determine the nature of bifurcations at \( b = b_\star \) and \( b = b^* \).
Figure 5. (a) Bifurcation diagram of $b$ versus the equilibrium value of coral cover. (b) Change in the resilience of the system with $b$ as an active parameter. (c) Eigenvalues for the coral-free equilibrium $E_0$ as functions of $b$. (d) Eigenvalues for interior equilibrium $E^*$ as functions of $b$.

At $b = b_*$, we have $E_0 = (0.4754, 0, 0)$ and

$$J_0 = \begin{pmatrix}
-0.549 & -0.5956 & -0.5956 \\
0 & 0 & 0 \\
0 & 0.001 & -0.3875
\end{pmatrix}$$

has a simple zero eigenvalue. Also, we obtain $V = \begin{pmatrix} -421.5009 & 387.5353 & 1 \end{pmatrix}^T$, $W = \begin{pmatrix} 0 & 1 & 0 \end{pmatrix}^T$, $W^T f_0(E_0; b_*) = 0$ and $W^T [D^2 f(E_0; b_*) (V, V)] = 44397$, satisfying the conditions of transcritical bifurcation when $b$ crosses $b_*$.

At $b = b^*$, we have $E^* = (0.3906, 0.0939, 0.001)$ and

$$J^* = \begin{pmatrix}
-0.5406 & -0.556 & -0.556 \\
-0.0611 & -0.0517 & -0.3334 \\
-0.0001 & 0.0039 & -0.0973
\end{pmatrix}$$

with a simple zero eigenvalue. Also, we obtain $V = \begin{pmatrix} 0.7305 & -0.6823 & -0.0281 \end{pmatrix}^T$, $W = \begin{pmatrix} 0.038 & -0.3377 & 0.9405 \end{pmatrix}^T$, $W^T f_0(E^*; b^*) = 0.0195$ and $W^T [D^2 f(E^*; b^*) (V, V)] = 0.119$, satisfying the conditions of saddle-node bifurcation at $E^*$ when $b$ crosses $b^*$. 


To identify the resilience of the system at a particular point on the equilibrium curve in the bistable region IV, we consider an arbitrary point $A$ on the curve of stable interior equilibrium in the bistable region (cf. Fig. 5(a)). For a fixed value of $b$, if change in another parameter value is enough to move $A$ vertically downwards upto or just beyond the unstable coexistence state (in red), then there will be a shift of regime to the macroalgae-dominated and coral-depleted steady state. In this case, the latitude at $A$ is defined as the distance ($L$) between the stable coexistence state $A$ and its basin boundary. Also, due to the increase of macroalgal immigration rate beyond $b^*$, there will be a shift of regime by overcoming the resistance of the coexistence state and by eroding the size of its basin of attraction. The resistance of the system at $A$ can be defined as the minimum additional macroalgal-immigration level required for the complete elimination of corals and is denoted by $R$. The latitude ($L$) component of resilience is measured in terms of coral cover and the resistance ($R$) component of resilience is measured in terms of macroalgal-immigration level. The precariousness ($Pr$) of the system at $A$ is defined as the current position and trajectory of the system in the basin of attraction relative to the edge and can be measured as the linear distance from $A$ to the point of saddle node bifurcation. The resilience of the system at $A$ can be represented as a combination of the latitude

**Figure 6.** (a) Bifurcation diagram of $b$ versus the equilibrium value of coral cover for different values of $\lambda$. (b) Coexistence region in $\lambda - b$ parameter space. (c) Bifurcation diagram of $b$ versus the equilibrium value of coral cover for different values of $\eta$. 
component vector, the resistance component vector and the precariousness component vector at \( A \). Fig. 5(a) is a representation of the three aspects of resilience of our system at \( A \) in terms of macroalgal-toxicity and coral cover. From Fig. 5(b) it follows that the resilience of the system at the interior equilibrium is maximum when macroalgal immigration rate on algal turf is less than \( b^* \) and decreases in the bistable region \( IV \) due to the increase of macroalgal immigration on algal turf. The resilience becomes minimum when macroalgal immigration rate approaches the threshold value \( b^* \). In this case slight increase in \( b \) leads to a catastrophic shift of regime to a macroalgae-dominated and coral-depleted steady state.

From Figs. 6(a)&6(c) it follows that the coexistence equilibrium can tolerate high immigration rate of macroalgae if the transmission rates (contagious and non-contagious) of BBD are low. With the increase of transmission rates of BBD, the resilience of coexistence steady state decreases. Also, from Fig. 6(b) we can conclude that the system is coral-dominated and stable if the rate of macroalgal immigration and transmission rate of contagious infection is low.

\[ \phi(g) = f_1(g) - f_2(g) \]

**Figure 7.** (a) Bifurcation diagram of \( g \) versus the equilibrium value of coral cover. (b) The relative positions of \( f_1(g) \), \( f_2(g) \) and \( \phi(g) \) showing that Hopf bifurcation occurs when the two curves intersect at \( g = 0.2904 \) and \( g = 0.3107 \). (c) Bifurcation diagram of \( g \) versus the equilibrium value of coral cover for \( \lambda = 4 \). (d) Coexistence region in \( g - b \) parameter space.

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. 7(a), we plot the solutions of the nullcline equations in the $C - g$ plane, yielding a bifurcation diagram. Coordinates of stable equilibria are shown in blue, and unstable equilibria are shown in red. The region $VI$ represents monostability at $E_0$ for $0 \leq g < 0.2812$, representing macroalgae-dominated and coral-depleted state for all non-negative initial conditions. The bistable region is represented by the region $VII$ for $0.2812 < g < 0.2904$. For $0.2904 < g < 0.3095$, the system becomes monostable at $E_0$ in the region $VIII$. For $0.3095 < g < 0.3107$, the system becomes unstable at $E_0$ and $E^*$, represented by the region $IX$. Once the grazing intensity surpasses the threshold $g = 0.3107$, the system arrives at a coral-dominated stable state, represented by region $X$ of monostability at $E^*$.

From Fig. 7(b) we observe that $f_1(g)$ and $f_2(g)$ intersect at $g = 0.2904$ and $g = 0.3107$, indicating that the system changes its stability when the parameter crosses the thresholds $g = 0.2904$ and $g = 0.3107$. More specifically, for $g < 0.2904$ and $g > 0.3107$ we see that $f_1(g) > f_2(g)$, satisfying Routh Hurwitz condition and therefore the system is locally asymptotically stable at $E^*$. Moreover, we observe that the tangents to $\phi(g)$ at $g = 0.2904$ and $g = 0.3107$ respectively are not parallel to $g$ axis, satisfying the condition $\frac{d\phi}{dg}|_{g=0.2904,g=0.3107} \neq 0$. Thus, Hopf bifurcation occurs when the parameter $g$ crosses $g = 0.2904$ and $g = 0.3107$. The first Lyapunov number at $g = 0.2904$ is $l_1 = -6.9415 < 0$ and at $g = 0.3107$ is $l_1 = -1.625$. Hence the Hopf-bifurcation is supercritical. Fig. 7(c) represents a bifurcation diagram with $\lambda = 4$ and $g$ as a bifurcation parameter. It is observed that higher rate of harvesting of herbivores is required for the existence of the interior equilibrium and also the system does not exhibit Hopf bifurcation by varying the grazing intensity. From Fig. 7(d) we observe that with high immigration rate of macroalgae, the system is macroalgae-dominated and stable even with high grazing intensity of herbivores. But, stable coexistence is not possible with high immigration rate of macroalgae together with high contagious infection rate.

From Fig. 8(a) it is observed that with low transmission rate of contagious infection (viz. $\lambda = 0.95$), the system is coral-dominated and stable even with low grazing rate of herbivores. In this case the system undergoes a sudden change in transition when $g$ crosses $g = 0.2101$. The increase of contagious-infection rate decreases coral cover followed by an oscillatory state by the emergence of two Hopf points (H). Fig. 8(b) gives a two-parameter bifurcation diagram with $g$ and $\lambda$ as active parameters, representing two BT points at $(g, \lambda) = (0.2103, 0.952)$ and $(g, \lambda) = (0.237, 1.302)$ on the saddle-node curve. The Bogdanov-Takens points are common points for the saddle-node curve and the closed Hopf curve. The emergence of two BT points in Fig. 8(b) implies that Hopf bifurcation occurs in $0.2103 < g < 0.237$ and $0.952 < \lambda < 1.302$. From Fig. 8(c) we can conclude that the stable coexistence is not possible with low grazing rate of herbivores even with low BBD-transmission rate. Increase in grazing rate stabilizes the system at coral-dominated interior equilibrium. From Fig. 8(d) it follows that stable coexistence state is not possible for high transmission rate of BBD through non-contagious pathway.

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 $\tau_1$. Further, we assume that infectious agents develop in susceptible corals during its incubation period $\tau_2$ so that susceptible corals infected at time $t - \tau_2$ are able to spread the disease at time $t$. By ignoring the possibility of any empty space
in sea bed, we construct the following delay model:

\[
\begin{align*}
\frac{dM}{dt} &= M \{\alpha(C_S + C_I) - d_1\} + T(aM + b) - \frac{gM(t - \tau_1)}{M(t - \tau_1) + T(t - \tau_1)} \\
\frac{dC_S}{dt} &= C_S(rT - \alphaM - \eta - d_2) - \lambda M(t - \tau_2)C_S(t - \tau_2) \\
\frac{dC_I}{dt} &= \lambda M(t - \tau_2)C_S(t - \tau_2) + \eta C_S - C_I(\alphaM + d_2 + \gamma) \\
\frac{dT}{dt} &= \frac{g M(t - \tau_1)}{M(t - \tau_1) + T(t - \tau_1)} + d_1M + d_2(C_S + C_I) + \gamma C_I - T(aM + b + rC_S)
\end{align*}
\]

Since \(M(t) + C_S(t) + C_I(t) + T(t) = 1\), for all \(t \geq 0\), system (3) reduces to:

\[
\begin{align*}
\frac{dM}{dt} &= M \{\alpha(C_S + C_I) - d_1\} + (aM + b)(1 - M - C_S - C_I) - \frac{gM(t - \tau_1)}{1 - C_S(t - \tau_1) - C_I(t - \tau_1)} \\
\frac{dC_S}{dt} &= C_S \{r(1 - M - C_S - C_I) - \alphaM - \eta - d_2\} - \lambda M(t - \tau_2)C_S(t - \tau_2) \\
\frac{dC_I}{dt} &= \lambda M(t - \tau_2)C_S(t - \tau_2) + \eta C_S - C_I(\alphaM + d_2 + \gamma)
\end{align*}
\]

Figure 8. (a) Bifurcation diagram of \(g\) versus the equilibrium value of coral cover for different values of \(\lambda\). (b) Two parameter bifurcation diagram with \(g\) and \(\lambda\) as active parameters. (The saddle-node curve is in blue, Hopf curve is in red and codimension one bifurcation curve with \(\lambda = 3\) is in green) Coexistence region in (c) \(g - \lambda\) and (d) \(\lambda - \eta\) parameter space.
with the initial conditions $M(t) = \phi_1(t) > 0, C_2(t) \geq \phi_2(t) \geq 0, C_1(t) \geq \phi_3(t) \geq 0, -\tau \leq t \leq 0$, where $\tau = \text{max}\{\tau_1, \tau_2, \tau_3\}, \Phi = (\phi_1, \phi_2, \phi_3) \in C([-\tau, 0], R^{3+})$, the Banach space of continuous functions, mapping the interval $(-\tau, 0)$ into $R^{3+}$, where we define $R^{3+} = \{(M, C_S, C_I) : M > 0, C_S \geq 0, C_I \geq 0\}$.

For $0 \leq t < \min\{\tau_1, \tau_2, \tau_3\}, \frac{dC_2}{dt} > 0$ implies $\phi_1(t - \tau_1) < l_1(t) \{1 - \phi_2(t - \tau_1) - \phi_3(t - \tau_1)\}$ and $\frac{dC_1}{dt} > 0$ implies $\phi_2(t - \tau_2) \phi_2(t - \tau_2) < l_2(t), \text{where} \ l_1(t) = \frac{M(t)\{a(C_2(t)+C_I(t))-d_1\} + a(M(t)+b)\{1-M(t)-C_S(t)-C_I(t)\}}{\lambda \{1-M(t)-C_S(t)-C_I(t)\}-\alpha(M(t)-\eta-d_2)}$ and $l_2(t) = \frac{C_S(t)\{r\{1-M(t)-C_S(t)-C_I(t)\} - \alpha(M(t)-\eta-d_2)\}}{\lambda \}.

Thus, the system is well posed in $-\tau \leq s \leq 0$ if $\frac{l_1(s)}{\phi_2(s)} < M(s) < l_1(s + \tau_1) \{1 - \phi_2(s) - \phi_3(s)\}, 0 \leq C_S(s) = \phi_2(s) \text{ and } 0 \leq C_I(s) = \phi_3(s)$. The Jacobian of the system (4) evaluated at the boundary equilibrium $E_0$ is

$$
\begin{pmatrix}
(\alpha-2M_0) - b - d_1 - ge^{-\mu \tau_1} & (\alpha-a)M_0 - b - gM_0e^{-\mu \tau_1} \\
0 & -(r-M_0(r+\alpha) - \eta - d_2) \\
0 & -(\alpha M_0 + d_2 + \gamma)
\end{pmatrix}
$$

Two eigenvalues of the Jacobian matrix of the system (4) at $E_0$ are $r - M_0(r+\alpha) - \eta - d_2$ and $-(\alpha M_0 + d_2 + \gamma) < 0$. The third eigenvalue is given by the equation

$$
\mu - g (1 - e^{-\mu \tau_1}) + \sqrt{(a - b - d_1 - g)^2 + 4ab} = 0.
$$

Now, $r - M_0(r+\alpha) - \eta - d_2 < 0$ if $\eta > \eta^*$.

Also, $\mu = g (1 - e^{-\mu \tau_1}) - \sqrt{(a - b - d_1 - g)^2 + 4ab} < g - \sqrt{(a - b - d_1 - g)^2 + 4ab} < 0$ if $g < \frac{(a-b-d_1)^2+4ab}{a-b-d_1}$, where $a > b + d_1$. This gives the following lemma:

**Lemma 4.1.** The system (4) is locally asymptotically stable at $E_0$ if $\eta > \eta^*$ and $g < \frac{(a-b-d_1)^2+4ab}{a-b-d_1}$, where $a > b + d_1$.

The Jacobian $J^*$ of the system (4) evaluated at an interior equilibrium $E^*$ is

$$
\begin{pmatrix}
\bar{f}_{M|E^*} + \frac{g(1-e^{-\mu \tau_1})}{1-C_S-C_I} & \bar{f}_{C_2|E^*} - \frac{gM(1-e^{-\mu \tau_1})}{(1-C_S-C_I)} & \bar{f}_{C_1|E^*} - \frac{gM(1-e^{-\mu \tau_1})}{(1-C_S-C_I)} \\
\bar{f}_{M|E^*} & \bar{f}_{C_2|E^*} + \lambda C_I(1-e^{-\mu \tau_2}) & \bar{f}_{C_1|E^*} - \lambda C_I(1-e^{-\mu \tau_2}) \\
\bar{f}_{M|E^*} & \bar{f}_{C_2|E^*} - \lambda C_I(1-e^{-\mu \tau_2}) & \bar{f}_{C_1|E^*} + \lambda C_I(1-e^{-\mu \tau_2})
\end{pmatrix}
$$

The characteristic equation of the system (4) at $E^*$ is $D(\mu, \tau_1, \tau_2) = \mu^3 + (A + \bar{A})\mu^2 + (B + \bar{B})\mu + (C + \bar{C}) + e^{-\mu \tau_1}(P_1\mu^2 + Q_1\mu + R_1) + e^{-\mu \tau_2}(P_2\mu^2 + Q_1\mu + R_1) + e^{-\mu (\tau_1 + \tau_2)}(Q_3\mu + R_3) = 0$, where

$$
\begin{align*}
\bar{A} &= \lambda(C_S^0 - C_I^0) - \frac{g}{1-C_S^0-C_I^0}, \quad B = \frac{\sum_{i=2}^{\infty} f_{S_i|E^*} \lambda(C_S^0 - C_S^i)}{1-C_S^0-C_I^0} \\
&+ \lambda \left\{ (C_S^0 - C_S^i) f_{M|E^*} + C_I^0 \sum_{i=2}^{\infty} f_{C_i|E^*} - C_S^0 \sum_{i=2}^{\infty} f_{C_S|E^*} \right\}, \\
\bar{C} &= \lambda \left\{ (C_S^0 - C_S^i) f_{M|E^*} \sum_{i=2}^{\infty} f_{C_S|E^*} - C_I^0 \sum_{i=2}^{\infty} f_{C_i|E^*} + (C_S^0 - C_S^i) f_{S_i|E^*}, \sum_{i=2}^{\infty} f_{M|E^*} \right\} \\
+ \frac{g}{1-C_S^0-C_I^0} \left\{ \sum_{i=2}^{\infty} f_{S_i|E^*}, \sum_{i=2}^{\infty} f_{C_i|E^*}, - \lambda \left\{ \sum_{i=2}^{\infty} f_{S_i|E^*}, - C_I^0 \sum_{i=2}^{\infty} f_{C_i|E^*} \right\} \right\} ,
\end{align*}
$$

$$
\begin{align*}
R_1 &= \frac{g}{1-C_S^0-C_I^0} f_{S_i|E^*}, f_{C_i|E^*} - \lambda \left\{ \sum_{i=2}^{\infty} f_{S_i|E^*}, - C_I^0 \sum_{i=2}^{\infty} f_{C_i|E^*} \right\}, \\
Q_2 &= \lambda \left\{ (C_S^0 - C_S^i) \sum_{i=2}^{\infty} f_{C_S|E^*} - C_I^0 \sum_{i=2}^{\infty} f_{C_i|E^*} + (C_S^0 - C_S^i) f_{S_i|E^*}, \sum_{i=2}^{\infty} f_{M|E^*} \right\}, \\
Q_3 &= \frac{g}{1-C_S^0-C_I^0} \left\{ (C_S^0 - C_S^i) f_{M|E^*} - \lambda \left\{ \sum_{i=2}^{\infty} f_{S_i|E^*}, - C_I^0 \sum_{i=2}^{\infty} f_{C_i|E^*} \right\} \right\} ,
\end{align*}
$$

$$
\begin{align*}
R_1 &= \frac{gM(1-e^{-\mu \tau_1})}{(1-C_S-C_I)} f_{M|E^*} - \frac{gM(1-e^{-\mu \tau_1})}{(1-C_S-C_I)} f_{M|E^*} + \lambda \left\{ \sum_{i=2}^{\infty} f_{S_i|E^*}, - C_I^0 \sum_{i=2}^{\infty} f_{C_i|E^*} \right\} \sum_{i=2}^{\infty} f_{M|E^*} \\
&- \frac{g}{1-C_S-C_I} \left\{ \sum_{i=2}^{\infty} f_{S_i|E^*}, \sum_{i=2}^{\infty} f_{C_i|E^*}, - \lambda \left\{ \sum_{i=2}^{\infty} f_{S_i|E^*}, - C_I^0 \sum_{i=2}^{\infty} f_{C_i|E^*} \right\} \right\} .
\end{align*}
$$
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 $\tau_1$ and an instantaneous transmission of BBD through contact. The system (4) reduces to

$$\begin{align*}
\frac{dM}{dt} &= M \{\alpha(C_S + C_I) - d_1\} + (\alpha M + b)(1 - M - C_S - C_I) - \frac{gM(t - \tau_1)}{1 - C_S(t - \tau_1) - C_I(t - \tau_1)}, \\
\frac{dC_S}{dt} &= C_S \{\rho(1 - M - C_S - C_I) - \alpha M - \lambda C_I - \eta - d_2\}, \\
\frac{dC_I}{dt} &= C_I(\lambda C_S - \alpha M - d_2 - \gamma) + \eta C_S,
\end{align*}$$

with the initial conditions $M(t) = \phi_1(t) > 0$, $C_S(t) \geq \phi_2(t) \geq 0$ and $C_I(t) \geq \phi_3(t) \geq 0$, where $-\tau_1 \leq t \leq 0$.

The characteristic equation of the system (5) at $E^*$ is $D(\mu, \tau_1, 0)$ is $\mu^3 + (A + B)\mu^2 + (B + B)\mu + (C + \tilde{C}) + e^{-\rho\tau_1}(\tilde{P}_l\mu^2 + Q_l\mu + \tilde{R}_1) = 0$, where $A = \frac{\gamma - \rho}{1 - C_S - C_I}$, $B = \frac{gM(t - \tau_1)}{1 - C_S(t - \tau_1) - C_I(t - \tau_1)}$, $\tilde{C} = \frac{\gamma}{1 - C_S - C_I} f_{C_S}^{2, c_{1, g}} + f_{C_I}^{2, c_{1, g}} - \frac{M - c_{1, g} f_{I} f_{M|E^*}}{C_S - C_I}$, $\tilde{P}_l = \tilde{P}_1$, $\tilde{Q}_l = \tilde{Q}_1 + \tilde{Q}_3$, $\tilde{R}_1 = \tilde{R}_1 + \tilde{R}_3$.

**Lemma 4.2.** Assume that the conditions of Lemma 3.4 are satisfied. A sufficient condition that the system (5) is locally asymptotically stable at $E^*$ for all $\tau_1 \in [0, \infty)$ is that $Q_{11} > 0$ and $Q_{13} > \frac{Q_{11}^2}{4Q_{11}}$, where

- $Q_{11} = (A + \tilde{A})^2 - 2(B + \tilde{B}) - \tilde{P}_l^2$,
- $Q_{12} = (B + \tilde{B})^2 - 2(C + \tilde{C})(A + \tilde{A}) - 2\tilde{P}_l\tilde{R}_1 - \tilde{Q}_l^2$ and
- $Q_{13} = (C + \tilde{C})^2 - \tilde{R}_l^2$.

**Proof.** The system (5) is locally asymptotically stable at $E^*$ for all $\tau_1 \geq 0$ if the following conditions given by Gopalsamy [16], Beretta and Kuang [5] hold:

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

Since the conditions of Lemma 3.4 are satisfied, the real parts of the roots of $D(\mu, 0, 0)$ are negative.

Also, $D(i\omega, \tau_1, 0) = 0$ gives $-\omega^2(A + \tilde{A}) + C + \tilde{C} = (\omega^2\tilde{P}_1 - \tilde{R}_1)\cos\omega\tau_1 - \omega\tilde{Q}_1\sin\omega\tau_1 - \omega^3\tilde{A}_1 + \omega(B + \tilde{B}) = -\omega\tilde{Q}_1\cos\omega\tau_1 - (\omega^2\tilde{P}_1 - \tilde{R}_1)\sin\omega\tau_1$. This gives $\omega^6 + Q_{11}\omega^4 + Q_{12}\omega^2 + Q_{13} = 0$, where

- $Q_{11} = (A + \tilde{A})^2 - 2(B + \tilde{B}) - \tilde{P}_l^2$,
- $Q_{12} = (B + \tilde{B})^2 - 2(C + \tilde{C})(A + \tilde{A}) - 2\tilde{P}_l\tilde{R}_1 - \tilde{Q}_l^2$ and
- $Q_{13} = (C + \tilde{C})^2 - \tilde{R}_l^2$.

A sufficient conditions for the nonexistence of a real number $\omega$ satisfying $D(i\omega, \tau_1, 0) = 0$ can be written as: $\omega^6 + \omega^4Q_{11} + \omega^2Q_{12} + Q_{13} > 0 \Rightarrow \omega^6 + Q_{11}\left(\omega^2 + \frac{Q_{12}}{4Q_{11}}\right)^2 + \left(Q_{13} - \frac{Q_{11}^2}{4Q_{11}}\right) > 0$.

Thus for all real $\omega$ and for all $\tau_1 \geq 0$, $D(\mu, \tau_1, 0) \neq 0$ if $Q_{11} > 0$ and $Q_{13} > \frac{Q_{11}^2}{4Q_{11}}$.

Let $z = \omega^2$ and $F(z) = z^3 + z^2Q_{11} + zQ_{12} + Q_{13}$.
Then $\omega^6 + \omega^4 Q_{11} + \omega^2 Q_{12} + Q_{13} = 0$ takes the form $F(z) = 0$.

**Lemma 4.3.** Assume that the conditions of Lemma 3.4 are satisfied. Then the following results hold:

(i) If $Q_{13} \geq 0$ and $Q_{12}^2 \leq 3Q_{12}$, then the system (5) is locally asymptotically stable at $E^*$ for all $\tau_1 > 0$.

(ii) If (a) $Q_{13} < 0$ or (b) $Q_{13} \geq 0$ and $Q_{12}^2 > 3Q_{12}$, then $F(z_1^*) \leq 0$ hold, then the system (5) is locally asymptotically stable at $E^*$ for all $\tau_1 \in [0, \tau_{1o})$, where $\tau_{1o} = \min \{\tau_{1o}^1, \tau_{1o}^2, \tau_{1o}^3\}$, $\tau_{1o}^k = \frac{1}{\omega_k}$.

\[
F(z_1^*) = 0 \quad (k = 1, 2, 3). 
\]

(iii) If conditions in (ii) hold and $F'(z_1^*) \neq 0$, then the system (5) undergoes a Hopf bifurcation $E^*$ when $\tau_1$ crosses $\tau_{1o}^k$, where $F(z_1) = 0$ ($k = 1, 2, 3$).

**Proof.** Let $\mu(\tau_1) = \mu(\tau_1) + i\omega(\tau_1)$ be a root of $D(\lambda, \tau_1, 0) = 0$.

For ease of notation, we denote $p(\tau_1) = p$ and $\omega(\tau_1) = \omega$.

Now, $p = 0$ and $\omega \neq 0$ gives $F(z) = 0$, where $z = \omega^2$.

(i) If $Q_{13} \geq 0$ and $Q_{12}^2 \leq 3Q_{12}$, then $F(0) \geq 0$ and $F'(z) > 0$ for all $z$, and so $F(z) = 0$ has no positive root. Thus, in this case all the roots of $D(\mu, \tau_1, 0) = 0$ have negative real parts for all $\tau_1 > 0$.

Therefore, if $Q_{13} \geq 0$ and $Q_{12}^2 \leq 3Q_{12}$, the system (4) is locally asymptotically stable at $E^*$ for all $\tau_1 > 0$.

(ii) If (a) $Q_{13} < 0$, then as $F(0) < 0$ and $\lim_{z \to \infty} F(z) = \infty$, it follows that $F(z) = 0$ has at least one positive root. If (b) $Q_{13} \geq 0$ and $Q_{12}^2 > 3Q_{12}$, then $F'(z) = 0$ has the two roots, $z_1^* = -\frac{Q_{11} + \sqrt{Q_{11}^2 - 3Q_{12}}}{3}$ and $z_2^* = -\frac{Q_{11} - \sqrt{Q_{11}^2 - 3Q_{12}}}{3}$. Since $F''(z_1^*) > 0$ and $F''(z_2^*) < 0$, it follows that $F(z_1^*)$ and $F(z_2^*)$ are local minimum and local maximum of $F(z)$.

As $F(0) \geq 0$ and $\lim_{z \to \infty} F(z) = \infty$, it follows that $F(z) = 0$ has a positive root if $F(z_1^*) \leq 0$.

Conversely, let $F(z) = 0$ has a positive root. If $F(z_1^*) > 0$, then as $F(0) \geq 0$, it follows that $F(z) > 0$ for all $z > 0$, a contradiction. Therefore, if $Q_{13} \geq 0$ and $Q_{12}^2 > 3Q_{12}$, it follows that $F(z) = 0$ has positive roots if and only if $z_1^* = -\frac{Q_{11} + \sqrt{Q_{11}^2 - 3Q_{12}}}{3}$ and $F(z_1^*) \leq 0$.

Let either (a) or (b) holds. Without any loss of generality, we assume that equation $F(z) = 0$ has three positive roots, say, $z_1, z_2, z_3$. Consequently, $\omega^6 + \omega^4 Q_{11} + \omega^2 Q_{12} + Q_{13} = 0$ has three positive roots $\omega_1 = \sqrt{z_1}, \omega_2 = \sqrt{z_2}$ and $\omega_3 = \sqrt{z_3}$. This gives

\[
\tau_{1o}^k = \frac{1}{\omega_k} \tan^{-1} \left[ \frac{\omega_k \left( \omega_k^2 Q_{11} + \omega_k^2 (Q_{11} + A + A) - P_1(B + B) - R_1 \right) + R_1(B + B) - Q_1(C + C)}{\omega_k^2 Q_{11} + \omega_k^2 (Q_{11} + A + A) - P_1(B + B) - R_1 \left( Q_1(C + C) + R_1(A + A) - Q_1(B + B) - R_1(C + C) \right)} \right] + \pi k, \\
k = 1, 2, 3; n = 0, 1, 2, \ldots
\]

Then $\pm i \omega_k$ are a pair of purely imaginary roots of $D(\mu, \tau_1, 0) = 0$ with $\tau_1 = \tau_{1o}^k$, $k = 1, 2, 3; n = 0, 1, 2, \ldots$

The smallest $\tau_{1o}^k$ is given by $n = 0$. Let $\tau_{1o} = \min \{\tau_{1o}^1, \tau_{1o}^2, \tau_{1o}^3\}$.

Therefore, if either (a) or (b) is satisfied, all the roots of $D(\mu, \tau_1, 0) = 0$ have negative real parts for all $\tau_1 \in [0, \tau_{1o})$ and consequently, the system (5) is locally asymptotically stable at $E^*$ for all $\tau_1 \in [0, \tau_{1o})$.

(iii) Let the conditions in (ii) hold. We are interested to know the change of stability at $E^*$ which will occur at $\tau_1 = \tau_{1o}^k$ for which $p(\tau_{1o}^k) = 0$ and $\omega(\tau_{1o}^k) \neq 0$, $k = 1, 2, 3$. 
Since \( \mu(\tau_1) \) is a root of \( D(\mu_1, \tau_1, 0) = 0 \) near \( \tau_1^k \), there exists \( \epsilon > 0 \) such that \( \mu(\tau_1) \) is continuously differentiable at \( \tau_1 \in (\tau_{10}^k - \epsilon, \tau_{10}^k + \epsilon) \), \( k = 1, 2, 3 \).

Differentiating \( D(\mu_1, \tau_1, 0) = 0 \) with respect to \( \tau_1 \) and using \( e^{-\mu_{12} \tau_1} = \mu^2 + \mu^2(A + \dot{A}) + \mu(B + \dot{B}) + C + \dot{C} \) we obtain

\[
\left( \frac{d\mu}{d\tau_1} \right)^{-1} = -\frac{3\mu^2 + 2\mu(A + \dot{A}) + B + \dot{B}}{\mu^2 + \mu^2(A + \dot{A}) + \mu(B + \dot{B}) + C + \dot{C}} - \frac{\tau_1}{\mu^2 + \mu^2(A + \dot{A}) + \mu(B + \dot{B}) + C + \dot{C}}
\]

Thus,

\[
sign \left\{ \text{Re} \left( \frac{d\mu}{d\tau_1} \right)^{-1} \right\}_{\mu = i\omega_k} = \text{sign} \left\{ \frac{3\omega_k^4 + 2\omega_k^2 Q_{11} + Q_{12}}{(\omega_k^2 P_1 - R_1)^2 + \omega_k^2 Q_{12}} \right\}, \quad k = 1, 2, 3.
\]

Therefore, if \( F'(z_k) \neq 0 \) holds, then \( \left[ \frac{d(\text{Re}(\mu))}{d\tau_1} \right]_{\tau_1 = \tau_{10}, \lambda = i\omega_k} \neq 0 \) and so the system (5) undergoes a Hopf bifurcation at \( \tau_{10}^k \), \( k = 1, 2, 3 \). \( \square \)

**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 and by assuming that susceptible corals infected through contagious pathway at time \( t - \tau_2 \) becomes infected at time \( t \). Then system (4) reduces to

\[
\begin{align*}
\frac{dM}{dt} &= M \left\{ \alpha(C_S + C_I) - \frac{9}{1 - C_S - C_I} - d_1 \right\} + (aM + b)(1 - M - C_S - C_I) \\
\frac{dC_S}{dt} &= C_S \left\{ r(1 - M - C_S - C_I) - \alpha M - \eta - d_2 \right\} - \lambda M(t - \tau_2) C_S(t - \tau_2) \\
\frac{dC_I}{dt} &= \lambda M(t - \tau_2) C_S(t - \tau_2) + \eta C_S - C_I(\alpha M + d_2 + \gamma)
\end{align*}
\]

with the initial conditions \( M(0) = \phi_1(t) > 0 \), \( C_S(0) \geq \phi_2(t) \geq 0 \) and \( C_I(0) \geq 0 \).

The characteristic equation of the system (6) at \( E^* \) is

\[
D(\mu, 0, \tau_2) = \mu^4 + (A + \dot{A}) \mu^2 + (B + \dot{B}) \mu + (C + \dot{C}) + e^{-\mu \tau_2}(\dot{P}_0 \mu^2 + \dot{Q}_0 \mu + \dot{R}_0) = 0,
\]

where \( \dot{A} = \lambda(C_S - C_I) \),

\[
\dot{B}_0 = \lambda \left\{ \frac{i(C_I - C_S) f_{1|M|E^*} + f_{1|C|E^*} f_{1|C|E^*} + f_{1|C|E^*} f_{1|C|E^*}}{C_S} \right\} - C_I f_{1|M|E^*} - C_I f_{1|C|E^*} - C_I f_{1|C|E^*} + C_I f_{1|C|E^*} + C_I f_{1|C|E^*} - C_I f_{1|C|E^*} + C_I f_{1|C|E^*} + (C_I + C_S) f_{1|M|E^*} f_{1|M|E^*},
\]

\[
\dot{C}_0 = \lambda \left\{ \frac{i(C_I - C_S) f_{1|M|E^*} + f_{1|C|E^*} f_{1|C|E^*} + f_{1|C|E^*} f_{1|C|E^*}}{C_S} \right\} - C_I f_{1|M|E^*} - C_I f_{1|C|E^*} - C_I f_{1|C|E^*} + C_I f_{1|C|E^*} + C_I f_{1|C|E^*} - C_I f_{1|C|E^*} + C_I f_{1|C|E^*} + (C_I + C_S) f_{1|M|E^*} f_{1|M|E^*},
\]

\[
\dot{P}_0 = \dot{P}_2, \quad \dot{Q}_0 = \dot{Q}_2 + \dot{Q}_3, \quad \dot{R}_0 = \dot{R}_2 + \dot{R}_3.
\]

Then similar to Lemma 4.2 and Lemma 4.3 we get the following results

**Lemma 4.4.** Assume that the conditions of Lemma 3.4 are satisfied. A sufficient condition that the system (6) is locally asymptotically stable at \( E^* \) for all \( \tau_2 \in [0, \infty) \) is that \( \dot{Q}_{11} > 0 \) and \( \dot{Q}_{13} > \frac{Q_{12}}{Q_{11}} \), where \( \dot{Q}_{11} = (A + \dot{A}) \dot{P}_0 + 2(B + \dot{B}) \dot{P}_0 + \dot{Q}_{12}^2 \), \( \dot{Q}_{13} = (B + \dot{B})^2 - 2(C + \dot{C})(A + \dot{A}) - 2\dot{P}_0 \dot{R}_0 - \dot{Q}_0^2 \), and \( \dot{Q}_{12} = (C + \dot{C}) \dot{P}_0 - 2\dot{P}_0 \dot{R}_0 - \dot{Q}_0^2 \).

Let \( z = \omega^2 + iP_{11} + iQ_{12} \). Then \( \omega^2 + \omega^2 Q_{11} + \omega^2 Q_{12} + \dot{Q}_{13} = 0 \) takes the form \( \dot{F}(z) = 0 \).

**Lemma 4.5.** Assume that the conditions of Lemma 3.4 are satisfied. Then the following results hold:

(i) If \( \dot{Q}_{13} \geq 0 \) and \( \dot{Q}_{12}^2 \leq 3 \dot{Q}_{12} \), then the system (6) is locally asymptotically stable at \( E^* \) for all \( \tau_2 > 0 \).

(ii) If (a) \( \dot{Q}_{13} < 0 \) or (b) \( \dot{Q}_{13} \geq 0 \) and \( \dot{Q}_{12}^2 > 3 \dot{Q}_{12} \), \( \dot{z} = \frac{-Q_{11} + \sqrt{Q_{11}^2 - 3Q_{12}}}{3} \) and \( \dot{F}(\dot{z}) \leq 0 \) hold, then the system (6) is locally asymptotically stable at \( E^* \) for all
$\tau_2 \in [0, \tau_{20})$, where $\tau_{20} = \min \{\tau_{20}^1, \tau_{20}^2, \tau_{20}^3\}$,

$\tau_{20}^i = \frac{1}{\omega_i} \arctan \left[ \frac{\omega_i}{1 - \omega_i^2 (Q_0(A + A_0) - \bar{Q}_0(A + \bar{A}_0) - \bar{Q}_0(B + \bar{B}_0) - \bar{Q}_0(C + \bar{C}_0))} \right] \quad \text{and} \quad \tilde{F}(\omega_k^i) = 0 \quad (k = 1, 2, 3).

(iii) If conditions in (ii) hold and $\tilde{F}'(\bar{z}_k) \neq 0$, then the system (6) undergoes a Hopf bifurcation $E^*$ when $\tau_2$ crosses $\tau_{20}^i$ where $\tilde{F}(z_k) = 0 \quad (k = 1, 2, 3)$.

**System with $\tau_1 > 0$ and $\tau_2 > 0$.** We consider $D(\mu, \tau_1, \tau_2) = 0$ in its stable interval and regard $\tau_1$ as a parameter.

Without any loss of generality, we assume that the conditions of Lemma 3.4 and Lemma 4.5(ii) are satisfied. Then the system (6) is stable for $\tau_2 \in [0, \tau_{20}^+)$. Let $i\omega (\omega > 0)$ be a root of $D(\mu, \tau_1, \tau_2) = 0$. Then $D(\mu, \tau_1, \tau_2) = 0$ gives

$\omega = 0$ where $H(\omega) = \omega^6 + k_1 \omega^5 + k_2 \omega^4 + k_3 \omega^3 + k_4 \omega^2 + k_5 \omega + k_6$, $k_1 = -2P_2 \sin \omega_2$, $k_2 = P_2^2 - P_1^2 + (A + \bar{A})^2 - 2(B + \bar{B}) + 2(P_2(A + \bar{A}) - \bar{Q}_2) \cos \omega_2$, $k_3 = 2(P_2 + P_3 + P_3(B + \bar{B}) - \bar{Q}_2(A + \bar{A})) \sin \omega_2$, $k_4 = P_2^2 - Q_2^2 - Q_2^2 + (B + \bar{B})^2 + 2P_1R_1 - 2P_3 \bar{R}_2 - 2(A + \bar{A})(C + \bar{C})$, $k_5 = 2(Q_1 R_3 - Q_2 R_1 + Q_2(C + \bar{C}) - 2\bar{R}_2(B + \bar{B}) \sin \omega_2$ and $k_6 = R_2^2 - R_1^2 + R_3^2 + (C + \bar{C})^2 + 2(\bar{R}_2(C + \bar{C}) - \bar{R}_1 \bar{R}_3) \cos \omega_2$

If $k_6 < 0$, then $H(0) < 0$ and as $\lim_{\omega \to \infty} H(\omega) = \infty$ it follows that $H(\omega) = 0$ has finite positive roots, say, $\omega_1, \omega_2, \ldots, \omega_m$.

For every fixed $\omega_i, i = 1, 2, \ldots, m$, there exists a sequence $\{\tau_1^i : j = 1, 2, 3, \ldots\}$ such that $H(\omega_i) = 0$ holds.

Let $\tau_1^i = \min \{\tau_1^i \quad : i = 1, 2, \ldots, m; j = 1, 2, 3, \ldots\}$. When $\tau_1 = \tau_1^i$, the equation $D(\mu, \tau_1, \tau_2) = 0$ has a pair of purely imaginary roots $\pm i\omega^* \quad \text{for} \quad \tau_2 \in [0, \tau_{20}^i]$.

We assume that $\zeta = \left[ \frac{d(D(\mu, \tau_1, \tau_2))}{d\tau_2} \right]_{\mu = i\omega^*} \neq 0$.

By the general Hopf bifurcation theorem for functional differential equations, we get the following result:

**Lemma 4.6.** For the system (2), assume that Lemma 3.4 and 4.5(ii) are satisfied for all $\tau_2 \in [0, \tau_{20})$. Then, if $k_6 < 0$ and $\zeta \neq 0$ hold, $E^*$ is locally asymptotically stable when $\tau_1 \in [0, \tau_{20}^*)$ and the system (4) undergoes a Hopf bifurcation at $E^*$ as $\tau_1 \to \tau_{20}^*$. Considering $\tau_2$ as a parameter, $D(\mu, \tau_1, \tau_2) = 0$ gives

$\omega = 0$ where $H(\omega) = \omega^6 + k_1 \omega^5 + k_2 \omega^4 + k_3 \omega^3 + k_4 \omega^2 + k_5 \omega + k_6 = 0$, where $k_1 = -2P_2 \sin \omega_1$, $k_2 = P_2^2 - P_1^2 + (A + \bar{A})^2 - 2(B + \bar{B}) + 2(P_2(A + \bar{A}) - \bar{Q}_2) \cos \omega_1$, $k_3 = 2(P_2 + P_3 + P_3(B + \bar{B}) - \bar{Q}_2(A + \bar{A})) \sin \omega_2$, $k_4 = P_2^2 - Q_2^2 - Q_2^2 + (B + \bar{B})^2 + 2P_1R_1 - 2P_3 \bar{R}_2 - 2(A + \bar{A})(C + \bar{C})$, $k_5 = 2(Q_1 R_3 - Q_2 R_1 + Q_2(C + \bar{C}) - 2\bar{R}_2(B + \bar{B}) \sin \omega_2$ and $k_6 = R_2^2 - R_1^2 + R_3^2 + (C + \bar{C})^2 + 2(\bar{R}_2(C + \bar{C}) - \bar{R}_1 \bar{R}_3) \cos \omega_2$.
\[ \dot{k}_3 = 2 (\hat{R}_1 + \hat{P}_2 \hat{Q}_3 + \hat{P}_1 (B + \hat{B}) - \hat{Q}_1 (A + \hat{A})) \sin \omega \tau_1, \]
\[ \dot{k}_4 = \hat{Q}_1^2 - \hat{Q}_2^2 - \hat{Q}_3^2 + (B + \hat{B})^2 + 2 \hat{P}_2 \hat{R}_2 - 2 \hat{P}_1 \hat{R}_1 - 2 (A + \hat{A}) (C + \hat{C}) \]
\[ + 2 (\hat{P}_2 \hat{R}_3 - \hat{Q}_2 \hat{R}_3 - \hat{P}_1 (C + \hat{C}) - \hat{R}_1 (A + \hat{A})) \cos \omega \tau_1, \]
\[ \dot{k}_5 = 2 (\hat{Q}_2 \hat{R}_3 - \hat{Q}_3 \hat{R}_2 + \hat{Q}_1 (C + \hat{C}) - \hat{R}_1 (B + \hat{B})) \sin \omega \tau_1 \] and
\[ \dot{k}_6 = \hat{R}_1^2 - \hat{R}_3^2 - \hat{R}_2^2 + (C + \hat{C})^2 + 2 (\hat{R}_1 (C + \hat{C}) - \hat{R}_2 \hat{R}_3) \cos \omega \tau_1. \]

If \( k_6 < 0 \), then \( \hat{H}(\omega) = 0 \) has finite positive roots, say, \( \omega_1, \omega_2, \ldots, \omega_r \).

For every fixed \( \omega_i \) (\( i = 1, 2, \ldots, r \)), there exists a sequence \( \{\tau_{2i}^j : j = 1, 2, 3, \ldots\} \)
such that \( \hat{H}(\omega) = 0 \).

Let \( \tau_{2i}^* = \min\{\tau_{2i}^j : i = 1, 2, \ldots, r; j = 1, 2, 3, \ldots\} \).

When \( \tau_2 = \tau_{2i}^* \), the equation \( D(\mu, \tau_1, \tau_2) = 0 \) has a pair of purely imaginary roots
\( \pm i \omega^* \) for \( \tau_1 \in [0, \tau_{10}) \).

We assume that \( \hat{\zeta} = \left[ \frac{d(Rc\mu)}{d\tau_2} \right]_{\mu = i\omega^*} \neq 0 \). Then similar to Lemma 4.6 we get the following result

**Lemma 4.7.** For the system (2), assume that Lemma 3.4 and 4.3(ii) are satisfied
for all \( \tau_1 \in [0, \tau_{10}) \). Then, if \( k_6 < 0 \) and \( \hat{\zeta} \neq 0 \) hold, \( E^* \) is locally asymptotically
stable when \( \tau_2 \in [0, \tau_{2i}^*] \) and the system (6) undergoes a Hopf bifurcation at \( E^* \) as
\( \tau_2 \) crosses \( \tau_{2i}^* \). We take \( \tau_1 = 0.5, \tau_2 = 0.5 \) and other parameter values as given in

\[ \begin{array}{c}
\text{Figure 9. Bifurcation diagrams for populations corresponding to} \\
(\text{a) } b \text{ as bifurcation parameter, } (b) \lambda \text{ as bifurcation parameter and} \\
(c) \eta \text{ as bifurcation parameter, indicating the presence of Hopf} \\
bifurcations. The splitted curves indicate the minima and maxima of periodic} \\
occurrences. \\
\end{array} \]

Table 1 for numerical simulation of the system (4) with both delays. From Fig. 5(a) it follows that the system (2) is stable at \( E^* \) for \( b < 0.1035 \), whereas, from Fig. 9(a) it follows that system (4) is stable at \( E^* \) for \( b < 0.003 \) and undergoes a Hopf bifurcation when \( b \) is increased through \( b_{cr} = 0.003 \). From Fig. 9(b) it follows that the system (4) is stable at \( E^* \) for \( \lambda < 2.7 \) and the decrease in the value of \( \lambda \) increases coral-dominance of the system. Also, the system (4) undergoes a Hopf bifurcation when \( \lambda \) is increased through \( \lambda_{cr} = 2.7 \). From Fig. 9(c) it is observed that the system (4) becomes oscillatory for low value of \( \eta \) and by a Hopf bifurcation occurs at \( E^* \) when \( \eta \) crosses \( \eta_{cr} = 0.0043 \). From Fig. 8(a) we see that the system (2) undergoes Hopf bifurcations at \( g = 0.2904 \) and \( g = 0.3107 \), whereas, from Fig. 10(a) we see that the system (4) undergoes a catastrophic Hopf bifurcation at \( E^* \) when \( g \) crosses \( g_{cr1} = 0.31 \) followed by two Hopf bifurcations at \( g_{cr2} = 0.425 \) and \( g_{cr3} = 0.45 \). Figs. 10(b) and 10(c) represent bifurcation diagrams of the system.
We have considered a eco-epidemiological model to study the dynamics of coral reef benthic system in which macroalgae and corals are competing to occupy turf algae in presence of a microbial infection, BBD on corals. In our model the immigration of algae from other areas of the seabed is taken into account. Underwood et al. [29] observed that for some coral 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. Also, in our model, we have assumed that the transmission of BBD occurs through both contagious and non-contagious pathways. Firstly, we analyze the system in the absence of time delays. We first perform equilibrium and stability analysis on our 3D non-linear ODE model and found that the model is capable of exhibiting of the existence of two stable configurations of the community under the same environmental conditions with saddle-node bifurcations and associated hysteresis effects when the grazing rate of herbivores and disease-transmission rates cross some certain thresholds. The effect of grazing on hysteresis supports the observations from previous modeling analyses by Blackwood et al. [6], Mumby et al. [22] and Fung et al. [14, 15]. It is noteworthy that in absence of macroalgal-immigration, no hysteresis is observed. This too justifies the consideration of macroalgal dispersal in our model. The system exhibits a sudden change of transition associated with saddle-node bifurcations and hysteresis effects when the immigration rate of macroalgae cross some certain threshold. Moreover, it is observed that with high microbial infection rate, the system undergoes a Hopf bifurcation followed by a sudden change of transition from coexistence state to coral-depleted state, when the grazing intensity is lowered below some critical thresholds. In this case, the extinction of coral population is due to natural fluctuations which become very likely when the oscillation drives the coral population to small size. We have studied the dynamic behaviour of the system with a discrete time lag in macroalgal recovery after grazing and an incubation time lag of the infecting agents. It is observed that when macroalgal recovery lag and incubation time lag cross some critical thresholds, the interior equilibrium loses its stability and a Hopf bifurcation occurs. Further, analytical and numerical simulations demonstrate the following.

Figure 10. Bifurcation diagrams for populations corresponding to (a) $g$ as bifurcation parameter, (b) $\tau_1$ as bifurcation parameter and (c) $\tau_2$ as bifurcation parameter, indicating the presence of Hopf bifurcations. The splitted curves indicate the minima and maxima of periodic oscillations.
conclusions:

(i) The system is macroalgae-dominated with low macroalgal grazing rate by herbivores. Increase of grazing intensity by herbivores increases the resilience of the coral-dominated regime, justifying the observations of Blackwood et al. [6] and Mumby et al. [22]. In presence of discrete time delays, the system exhibits a catastrophic Hopf bifurcation when the grazing intensity is increased from a low threshold level, resulting in sudden jump from macroalgae-dominated stable state to an oscillatory coexistence state.

(ii) In the absence of delays, the system becomes macroalgae-dominated when the macroalgal immigration on algal turfs becomes high. In this case higher rate of herbivory is necessary to stabilize the system at coral-dominated state. In presence of delays, increase of macroalgal immigration leads to a Hopf bifurcation followed by the depletion of corals.

(iii) The system becomes macroalgae-dominated with the increase of BBD transmission on corals. In this case, increase of herbivory increases the resilience of the coral-dominated regime. With low rate of contagious infection, the system is coral-dominated and stable even with moderately high non-contagious infection rate. The system with delays becomes oscillatory followed by the elimination of corals when the rate of contagious infection becomes high. But due to the increase of the rates of contagious and non-contagious infection, the system becomes macroalgae-dominated followed by the elimination of corals.

(iv) Increase of macroalgal immigration together with BBD infection increases the resilience of macroalgae-dominated regime.

(v) With low recruitment rate of corals on turf algae, the system is macroalgae-dominated with complete elimination of corals. Increase in the recruitment rate of corals on turf algae can generate a coral-dominated regime even with moderately high rate of BBD infection on corals.

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 the reduction in herbivory can lead to a sudden shift of transition from BBD-infected coral-dominated regime to macroalgae-dominated regime. With low grazing rate of herbivores, due to the increase of contagious infection rate, the system exhibit dynamic instability followed by a sudden change of transition from coexistence state to coral-depleted state. Moreover, we observe that higher grazing rate of herbivores reduces macroalgal cover and increases the resilience of the coral-dominated regime. Further, with macroalgal-recovery time lag and incubation time lag of infectious agents, the coral-dominated stable coexistence state is less tolerant to higher transmission rate of BBD infection and high macroalgal immigration rate of turf algae.

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