Letters in Biomathematics

Taylor & Francis
Taylor & Francis Group

RESEARCH ARTICLE

ə OPEN ACCESS

Potential effects of invasive *Pterois volitans* in coral reefs

Banamali Maji[a], Joydeb Bhattacharyya[b] and Samares Pal[a] (ID)

[a]Department of Mathematics, University of Kalyani, Kalyani, India; [b]Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX, USA

ABSTRACT

The invasion of predatory lionfish (*Pterois volitans*) represents a major threat to the western Atlantic coral reef ecosystems. The proliferation of venomous, fast reproducing and aggressive *P. volitans* in coral reefs causes severe declines in the abundance and diversity of reef herbivores. There is also widespread cannibalism amongst *P. volitans* populations. A mathematical model is proposed to study the effects of predation on the biomass of herbivorous reef fishes by considering two life stages and intraguild predation of *P. volitans* population with harvesting of adult *P. volitans*. The system undergoes a supercritical Hopf bifurcation when the invasiveness of *P. volitans* crosses a certain critical value. It is observed that cannibalism of *P. volitans* induces stability in the system even with high invasiveness of adult *P. volitans*. The dynamic instability of the system due to higher invasiveness of *P. volitans* can be controlled by increasing the rate of harvesting of *P. volitans*. It is also proven that *P. volitans* goes extinct when the harvest rate is greater than some critical threshold value. These results indicate that the dynamical behaviour of the model is very sensitive to the harvesting of *P. volitans*, which in turn is useful in the conservation of reef herbivores.

1. Introduction

The invasion of *Pterois volitans* in the western Atlantic has brought a major change to the biodiversity of coral reefs (Morris et al., 2009). *P. volitans* are voracious in nature, spreading rapidly to new marine environments and driving down the populations of reef herbivores drastically (Benkwitt, 2015). The loss of herbivores results in the proliferation of algae, especially the brown algae *Lobophora variegata, Dictyota* spp. and *Sargassum* spp., which prevent the growth of corals (*Acropora* spp. and *Montastraea* spp.) on the seabed (Bhattacharyya & Pal, 2015). With venomous spines, *P. volitans* are the top-notch predators in the Atlantic and Caribbean regions. Since top predators like sharks and groupers typically avoid *P. volitans* and thus fail to keep the species population in check, commercial harvesting of the adult *P. volitans* species seems to be the only way to mitigate their impact on coral reef ecosystems (Morris & Whitfield, 2009).

CONTACT Samares Pal ✉ samareshp@klyuniv.ac.in

Parrotfish (*Sparisoma* spp.) play an important role in maintaining western Atlantic coral reef ecosystems by consuming algae to control its growth and promote coral recruitment (Fishelson, 1997; Rotjan & Lewis, 2006). *P. volitans* affect corals by overconsuming Parrotfish and other herbivorous fish that keep algae from overgrowing corals. As observed by Goreau and Hayes (1994), Hare and Whitfield (2003), and Albins and Hixon (2008), in the presence of predatory *P. volitans*, there is a rapid loss of herbivorous Parrotfish and subsequent loss of corals. Apart from preying on reef herbivores, adult *P. volitans* exhibit cannibalism, eating juveniles of their own species (Morris et al., 2009). Cannibalism has a strong impact on population dynamics because it reduces the predation pressure on reef herbivores (Rudolf, 2008).

Almost all organisms have a life history that takes them through multiple stages from juvenile to adult (Zhang, Chen, & Neumann, 2000) and cannibalistic interactions are very common in stage-structured populations (Rudolf, 2007). To model the effect of invasive *P. volitans*, we have considered a two-stage-structured system (Bhattacharyya & Pal, 2014), with Parrotfish and *P. volitans* following a Holling type III functional response (Luwig, Jones, & Holling, 1978). This response function is sigmoid, rising slowly when resources are rare, accelerating when resources become more abundant and finally reaching a saturated upper limit (Edwards & Brindley, 1999). The rate of loss from the prey population due to predation is defined as the uptake rate of the predator. In this formulation, the per capita uptake rate by the predator is given by

$$f(x) = \frac{mx^2}{a^2 + x^2},$$

where x is the prey abundance. This functional response is parameterized by the constants m and a, where m is the maximal prey uptake rate by the predator, and a is the value of the prey population level when the uptake rate per unit prey is half their maximum value, i.e. $f(x)_{|x=a} = m/2$.

In our model, we have considered the stage structure of the juvenile and adult *P. volitans* under the assumption that the adult *P. volitans* prey on Parrotfish and have reproductive ability. For effective, widespread control of *P. volitans*, a non-constant harvesting policy, introduced by Lenzini and Rebaza (2010), is used in our model. We will examine the interactions of algae, Parrotfish and *P. volitans* to determine effective strategies for controlling the growth of *P. volitans* in coral reefs. We have studied the model analytically as well as numerically, with all proofs relegated to the Appendix 1.

2. The model

We consider a mathematical model consisting of algae at the first trophic level with concentration $P(t)$ at time t, and Parrotfish at the second trophic level with concentration $x(t)$, feeding on the algae. We also consider a two-stage structure for the top predator *P. volitans*, with $y(t)$ and $z(t)$ as the concentrations of juvenile and adult *P. volitans*, respectively. In our proposed model, it is assumed that adult *P. volitans* prey both on Parrotfish and juvenile *P. volitans*, whereas juvenile *P. volitans* do not attack Parrotfish, and have no reproductive ability (Wang & Chen, 1997). Adult *P. volitans* are harvested with a non-constant harvesting policy that provides diminishing marginal returns of

the harvesting organization (Leard, Lewis, & Rebaza, 2008). We make the following assumptions in formulating the mathematical model:

(H1) In the absence of Parrotfish, macroalgae have only intraspecic competition, and grow according to the logistic equation with intrinsic growth rate r and carrying capacity K.

(H2) The death rate of Parrotfish is proportional to the existing Parrotfish population with a proportionality constant D_1.

(H3) The death rate of juvenile *P. volitans* and the transformation rate from juvenile to adult *P. volitans* are proportional to the existing juvenile population with proportionality constants D_2 and μ, respectively.

(H4) The death rate of adult *P. volitans* is proportional to the existing adult population with a proportionality constant D_3.

(H5)

$$\frac{m_3 y^2 z}{a_3^2 + y^2}$$

represents the rate of cannibalism of adult *P. volitans* (z) by consuming juvenile *P. volitans* (y) leading to the growth of new juveniles. The growth rate of new juveniles is

$$\frac{\alpha m_3 y^2 z}{a_3^2 + y^2}, \quad 0 < \alpha < 1.$$

Thus,

$$\frac{(1 - \alpha) m_3 y^2 z}{a_3^2 + y^2}$$

represents the reduction in growth rate of juvenile *P. volitans* due to cannibalism.

The basic equations with all the parameters are

$$\frac{dP}{dt} = rP \left(1 - \frac{P}{K} \right) - \frac{m_1 P^2 x}{a_1^2 + P^2}$$

$$\frac{dx}{dt} = x \left(\frac{\alpha_1 m_1 P^2}{a_1^2 + P^2} - D_1 - \frac{m_2 xz}{a_2^2 + x^2} \right)$$

$$\frac{dy}{dt} = \frac{\alpha_2 m_2 x^2 z}{a_2^2 + x^2} - (\mu + D_2) y - \frac{(1 - \alpha) m_3 y^2 z}{a_3^2 + y^2}$$

$$\frac{dz}{dt} = \mu y - D_3 z - \frac{hz}{c + z}, \tag{1}$$

where $P(0) \geq 0, x(0) \geq 0, y(0) \geq 0$ and $z(0) \geq 0$. Here $1/\mu$ represents the total time spent by *P. volitans* in its juvenile stage, h is the maximum harvesting rate of adult *P. volitans*, c is the concentration of adult *P. volitans* for which the rate of harvesting is exactly half the maximal harvesting rate, m_1 is the maximal uptake rate of algae by Parrotfish, m_2 is the maximal uptake rate of Parrotfish by the adult *P. volitans*, m_3 is the maximal uptake rate of juvenile *P. volitans* by the adult *P. volitans* and a_i are the corresponding half saturation constants ($i = 1, 2, 3$). The parameters α and α_i represent the growth efficiency ($0 < \alpha, \alpha_i < 1, i = 1, 2$) of the organisms; all of these are positive quantities. The parameters

K, h, c are environmental variables, while r, μ, m_i, a_i, D_i, α and α_i are properties of the organisms.

3. Non-dimensionalization of the system

Let us change the variables of the system (1) to non-dimensional ones by substituting

$$\bar{P} = \frac{P}{K}, \quad \bar{x} = \frac{x}{\alpha_1 K}, \quad \bar{y} = \frac{y}{\alpha_1 \alpha_2 K}, \quad \bar{z} = \frac{z}{\alpha_1 \alpha_2 K}, \quad \bar{t} = rt,$$

and defining non-dimensional parameters

$$\bar{a}_1 = \frac{a_1}{K}, \quad \bar{a}_2 = \frac{a_2}{\alpha_1 K}, \quad \bar{a}_3 = \frac{a_3}{\alpha_1 \alpha_2 K}, \quad \bar{m}_1 = \frac{\alpha_1 m_1}{r}, \quad \bar{m}_2 = \frac{\alpha_2 m_2}{r}, \quad \bar{m}_3 = \frac{(1-\alpha)m_3}{r},$$

$$\bar{D}_1 = \frac{D_1}{r}, \quad \bar{D}_2 = \frac{D_2}{r}, \quad \bar{D}_3 = \frac{D_3}{r}, \quad \bar{\mu} = \frac{\mu}{r}, \quad \bar{h} = \frac{h}{\alpha_1 \alpha_2 rK}, \quad \bar{c} = \frac{c}{\alpha_1 \alpha_2 K}.$$

After we make the substitutions above and drop the bars for simplicity, the system (1) is reduced to

$$\frac{dX}{dt} = f(X), \tag{2}$$

where $X = \begin{bmatrix} P & x & y & z \end{bmatrix}^T$ and $f(X) = \begin{bmatrix} F^1 & F^2 & F^3 & F^4 \end{bmatrix}^T$ with

$$F^1(P, x) = P(1 - P) - \frac{m_1 x P^2}{a_1^2 + P^2},$$

$$F^2(P, x, z) = x\left(\frac{m_1 P^2}{a_1^2 + P^2} - \frac{m_2 xz}{a_2^2 + x^2} - D_1\right),$$

$$F^3(x, y, z) = \frac{m_2 x^2 z}{a_2^2 + x^2} - \frac{m_3 y^2 z}{a_3^2 + y^2} - (\mu + D_2)y,$$

$$F^4(y, z) = \mu y - \frac{hz}{c + z} - D_3 z.$$

We assume that all initial values are non-negative. The right-hand sides of the equations in the system (2) are smooth functions of the variables P, x, y, z and the parameters. The following lemma gives the condition for which the solutions of the system (2) are positive.

Lemma 3.1: *If $y(t)$ and $z(t)$ are always positive, then all possible solutions of the system (2) are positive.*

Therefore, as long as $y(t) > 0$ and $z(t) > 0$ for all t, local existence and uniqueness properties hold in the region $\Omega = \{(P, x, y, z) : P > 0, \ x > 0, \ y > 0, \ z > 0\}$.

4. Boundedness and permanence of the system

We first prove that the solutions of Equation (2) with initial values in Ω are bounded, so that Equation (2) represents a biologically meaningful system. The proofs of all the lemmas are given in the Appendix 1.

Lemma 4.1: *For all $\epsilon > 0$, there exists $t_\epsilon > 0$ such that all the solutions of (2) with positive initial values fall into the set $\{(P, x, y, z) \in \Omega : P(t) + x(t) + y(t) + z(t) < 1/D + \epsilon, \epsilon > 0\}$ whenever $t \geq t_\epsilon$, where $D = \min\{1, D_1, D_2, D_3\}$.*

Since $P(t) + x(t) + y(t) + z(t) < 1/D$ as $t \to \infty$ it follows that there exist positive numbers M_1, M_2, M_3 with $M_1 + M_2 + M_3 < 1/D$ such that $x(t) \leq M_1, y(t) \leq M_2$ and $z(t) \leq M_3$ for large values of t.

Let us define

$$\lambda = \sqrt{\frac{a_1^2 D_1}{m_1 - D_1}}, \quad m_1 > D_1.$$

Then λ denotes the break-even concentration of algae for which the Parrotfish population is constant in the absence of *P. volitans*. The following lemma states the condition under which neither Parrotfish nor *P. volitans* can survive in the system:

Lemma 4.2: *If (i) $m_1 \leq D_1$ or (ii) $m_1 > D_1$ and $\lambda > 1/D$ hold, then*

$$\lim_{t \to \infty} x(t) = \lim_{t \to \infty} y(t) = \lim_{t \to \infty} z(t) = 0.$$

According to Lemma 4.2, we have

 (i) If the maximal uptake rate of Parrotfish is less than or equal to its death rate, then Parrotfish and *P. volitans* will not survive in the system.
 (ii) If the maximal uptake rate of Parrotfish is greater than its death rate and the break-even concentration λ is greater than $1/D$, then Parrotfish and *P. volitans* will not survive in the system.

The system (2) will be permanent (Ruan, 1993) if there exists $u_{1_i}, M_i \in (0, \infty)$ such that

$$u_{1_i} \leq \lim u_i(t) \leq M_i$$

for each organism $u_i(t)$ in the system ($i = 1, \ldots, 4$). Permanence represents convergence on an interior attractor from any positive initial conditions, and hence, can be regarded as a strong form of coexistence. From a biological point of view, the permanence of a system ensures the survival of all the organisms in the long run. Without any loss of generality, we assume that $m_1 > D_1$ and $m_2 > D_2$. The condition given in the following Lemma rules out the possibility of extinction of any organism in the system.

Lemma 4.3: *If there exists $p_1, 0 < p_1 < \lambda$, then for large t, there exists*

$$x_1 = \frac{m_2 M_3 (a_1^2 + p_1^2)}{(m_1 - D_1)(p_1^2 - \lambda^2)}, \quad y_1 > 0, \quad \text{and} \quad z_1 > \frac{M_2 (a_2^2 + x_1^2)(\mu + D_2)}{(m_2 - m_3)x_1^2 - m_3 a_2^2},$$

such that each solution of the system (2) with positive initial values falls into the compact set

$$\{(P, x, y, z) : p_1 \leq P(t) \leq 1/D, \ x_1 \leq x(t) \leq M_1, \ y_1 \leq y(t) \leq M_2, \ z_1 \leq z(t) \leq M_3\},$$

and stays there.

System (2) is called competitive (Smith, 1995) if there exists a diagonal matrix $H = \text{diag}(\epsilon_1, \ldots, \epsilon_4)$ such that $HJ(X)H$ has non-positive off-diagonal elements,

where $J(X)$ is the Jacobian of the system (2) and ϵ_i is either 1 or –1 ($i = 1, \ldots, 4$). By choosing $H = \text{diag}(1, -1, -1, 1)$, we see that the off-diagonal elements of $HJ(X)H$ are non-positive if

$$\frac{m_3 y^2(t)}{a_3^2 + y^2(t)} < \frac{m_2 x^2(t)}{a_2^2 + x^2(t)}$$

for all $t > 0$. This leads to the following result:

Lemma 4.4: *The system* (2) *is competitive if*

$$x(t) > x_1 > \sqrt{\frac{m_3 a_2^2}{m_2 - m_3}}$$

for large t, where $m_2 > m_3$.

5. Equilibria and their stability

The system (2) possesses the following feasible equilibria:

(i) Organism-free equilibrium $E_0 = (0, 0, 0, 0)$;
(ii) Parrotfish- and *P. volitans*-free equilibrium $E_1 = (1, 0, 0, 0)$;
(iii) *P. volitans*-free equilibrium $E_2 = \left(\lambda, \frac{\lambda(1-\lambda)}{D_1}, 0, 0\right)$;
(iv) The equilibrium of coexistence $E^* = (P^*, x^*, y^*, z^*)$, where P^* is a positive root of the equation

$$\frac{m_2 \theta^2(P)\psi(P)}{a_2^2 + \theta^2(P)} - \frac{m_3 \phi^2(P)\psi(P)}{a_3^2 + \phi^2(P)} = (\mu + D_2)\phi(P)$$

with

$$\theta(P) = \frac{(1-P)(a_1^2 + P^2)}{m_1 P}, \quad \phi(P) = \frac{1}{\mu}\left(D_3 + \frac{h}{c + \psi(P)}\right)\psi(P), \quad \text{and}$$

$$\psi(P) = \frac{(m_1 - D_1)(P^2 - \lambda^2)(a_2^2 + \theta^2(P))}{m_2(a_1^2 + P^2)\theta(P)}; \quad x^* = \theta(P^*), \ y^* = \psi(P^*), \ z^* = \phi(P^*).$$

We see that E_0 and E_1 always exist, E_2 exists if $\lambda < 1$, and E^* exists if $P^* > \lambda$.

We analyse the local stability of system (2) using eigenvalue analysis of the Jacobian matrix, $J(X)$, evaluated at the appropriate equilibrium. The eigenvalues of $J(X)$ at E_0 are $1, -D_1, -\mu - D_2$ and $-D_3 - h/c$. This gives the following result:

Lemma 5.1: *The organism-free equilibrium* E_0 *of the system* (2) *is always a saddle point.*

Therefore, the system (2) is very unlikely to collapse.

Lemma 5.2: *The critical point* E_1 *of the system* (2) *is locally asymptotically stable if* $D_1 > m_1/(a_1^2 + 1)$.

Therefore, with a high mortality rate of Parrotfish, the system (2) stabilizes at the Parrotfish- and *P. volitans*-free equilibrium E_1. The decrease in the mortality rate of Parrotfish changes the stability of the system (2) from an algae-dominated state in the absence of Parrotfish to an algae-Parrotfish coexistence state. The following Lemma gives

the condition for which coexistence of Parrotfish and algae is possible in the absence of *P. volitans*.

Lemma 5.3: *The critical point* $E_2 = \left(\lambda, \frac{\lambda(1-\lambda)}{D_1}, 0, 0\right)$ *of the system* (2) *is locally asymptotically stable if*

$$\lambda < 1 \ and \ \frac{\lambda(1-\lambda)}{a_2} \sqrt{\frac{c\mu m_2}{(\mu + D_2)(cD_3 + h)} - 1} < D_1 < \frac{m_1}{2(1-\lambda)}.$$

The system is persistent at E^* if all the boundary equilibria repel interior trajectories (Ruan, 1993). The following Lemma gives the condition of persistence of the system (2) at E^*:

Lemma 5.4: *All the organisms will persist if* $\lambda < 1$ *and*

$$D_1 \leq \min\left\{\frac{m_1}{a_1^2 + 1}, \frac{\lambda(1-\lambda)}{a_2} \sqrt{\frac{c\mu m_2}{(\mu + D_2)(cD_3 + h)} - 1}\right\}.$$

Therefore, with a low mortality rate of Parrotfish, all the organisms in the system (2) coexist.

Lemma 5.5: *The system* (2) *has no periodic solution around the positive equilibrium* E^* *if*

$$1 + \mu + m_1\left(1 + \frac{2x^*}{P^*}\right) + m_2\left(1 + \frac{2z^*}{x^*}\right) + m_3 < L,$$

where L is the minimum of the following six quantities:

(i) $D_1 + 2P^* + \frac{2m_1 P^* x^* a_1^2}{(a_1^2 + P^{*2})^2} + \frac{2m_2 x^* z^* a_2^2}{(a_2^2 + x^{*2})^2}$,

(ii) $2P^* + \mu + D_2 + \frac{2m_3 y^* z^* a_3^2}{(a_3^2 + y^{*2})^2} + \frac{2m_1 P^* x^* a_1^2}{(a_1^2 + P^{*2})^2}$,

(iii) $2P^* + D_3 + \frac{2m_1 P^* x^* a_1^2}{(a_1^2 + P^{*2})^2} + \frac{ch}{(c+z^*)^2}$,

(iv) $\mu + D_1 + D_2 + \frac{2m_2 x^* z^* a_2^2}{(a_2^2 + x^{*2})^2} + \frac{2m_3 y^* z^* a_3^2}{(a_3^2 + y^{*2})^2}$,

(v) $D_1 + D_3 + \frac{2m_2 x^* z^* a_2^2}{(a_2^2 + x^{*2})^2} + \frac{ch}{(c+z^*)^2}$,

(vi) $\mu + D_1 + D_3 + \frac{ch}{(c+z^*)^2} + \frac{2m_3 y^* z^* a_3^2}{(a_3^2 + y^{*2})^2}$.

Corollary 5.1: *If the conditions stated in Lemmas 5.4 and 5.5 both hold, then the positive equilibrium is locally asymptotically stable.*

Now we use the Routh–Hurwitz criterion to find the necessary and sufficient conditions for stability of the system (2) at E^*.

Lemma 5.6: *The positive equilibrium* E^* *of the system* (2) *is locally asymptotically stable if*
$$Q_1 > 0, \quad Q_1 Q_2 > Q_3, \quad and \quad Q_1 Q_2 Q_3 > Q_3^2 + Q_1^2 Q_4,$$

where

$$Q_1 = -\left(F_P^1|_{E^*} + F_x^2|_{E^*} + F_y^3|_{E^*} + F_z^4|_{E^*}\right),$$

$$Q_2 = \left(F_S^1|_{E^*} + F_x^2|_{E^*}\right)\left(F_y^3|_{E^*} + F_z^4|_{E^*}\right) + F_P^1|_{E^*} F_x^2|_{E^*} + F_y^3|_{E^*} F_z^4|_{E^*}$$
$$- \mu F_z^3|_{E^*} - F_x^1|_{E^*} F_P^2|_{E^*},$$

$$Q_3 = \left(\mu F_z^3|_{E^*} - F_y^3|_{E^*} F_z^4|_{E^*}\right)(F_P^1|_{E^*} + F_x^2|_{E^*})$$
$$+ \left(F_x^1|_{E^*} F_P^2|_{E^*} - F_P^1|_{E^*} F_x^2|_{E^*}\right)\left(F_y^3|_{E^*} + F_x^4|_{E^*}\right) - \mu F_x^3|_{E^*} F_z^2|_{E^*},$$
$$Q_4 = \left(F_y^3|_{E^*} F_z^4|_{E^*} - \mu F_z^3|_{E^*}\right)\left(F_P^1|_{E^*} F_x^2|_{E^*} - F_x^1|_{E^*} F_P^2|_{E^*}\right) + \mu F_P^1|_{E^*} F_z^2|_{E^*} F_x^3|_{E^*}.$$

Due to the complexity in the algebraic expressions involved, it is difficult to interpret the results in ecological terms; however, numerical simulations are used to illustrate the dynamical behaviour of the system about E^*.

6. Hopf bifurcation

We will study the Hopf bifurcation of the system (2) at E^*, taking m_2 as a bifurcation parameter.

The characteristic equation of the Jacobian matrix at E^* is $G(\lambda) = u^4 + Q_1 u^3 + Q_2 u^2 + Q_3 u + Q_4 = 0$. Solving $Q_1 Q_2 Q_3 - Q_3^2 - Q_1^2 Q_4 = 0$, the critical value of m_2 can be obtained, say, $m_2 = m_{2_{cr}}$.

Lemma 6.1: *The system undergoes a Hopf bifurcation at $m_2 = m_{2_{cr}}$ if and only if*

(i) $f_1(m_{2_{cr}}) = f_2(m_{2_{cr}})$,
(ii) $\left[M(m_2)K(m_2) - N(m_2)L(m_2)\right]_{m_2 = m_{2_{cr}}} \neq 0$,

where

$$f_1(m_2) = Q_1(m_2)Q_2(m_2)Q_3(m_2), \ f_2(m_2) = Q_3^2(m_2) + Q_1^2(m_2)Q_4(m_2),$$
$$K(m_2) = 4\beta_1^3(m_2) - 12\beta_1(m_2)\beta_2^2(m_2) + 3\left(\beta_1^2(m_2) - \beta_2^2(m_2)\right)Q_1(m_2)$$
$$+ 2\beta_1(m_2)Q_2(m_2) + Q_3(m_2),$$
$$L(m_2) = 12\beta_1^2(m_2)\beta_2(m_2) - 4\beta_2^3(m_2) + 6\beta_1(m_2)\beta_2(m_2)Q_1(m_2) + 2\beta_2(m_2)Q_2(m_2),$$
$$M(m_2) = \beta_1^3(m_2)Q_1'(m_2) - 3\beta_1(m_2)\beta_2^2(m_2)Q_1'(m_2) + \left(\beta_1^2(m_2) - \beta_2^2(m_2)\right)Q_2'(m_2)$$
$$+ \beta_1(m_2)Q_3'(m_2),$$
$$N(m_2) = 3\beta_1^2(m_2)\beta_2(m_2)Q_1'(m_2) - \beta_2^3 Q_1'(m_2) + 2\beta_1(m_2)\beta_2(m_2)Q_2'(m_2)$$
$$+ \beta_2(m_2)Q_3'(m_2);$$

$\beta_1(m_2)$ and $\beta_2(m_2)$ are real and imaginary parts, respectively, of a pair of eigenvalues for all $m_2 \in (m_{2_{cr}} - \epsilon, m_{2_{cr}} + \epsilon)$.

The condition (ii) is equivalent to $dg(m_2)/dm_2|_{(m_2 = m_{2_{cr}})} \neq 0$. Thus, using numerical methods, condition (i) can be verified by showing that the curves $y = f_1(m_2)$ and $y = f_2(m_2)$ intersect at $m_2 = m_{2_{cr}}$, whereas the condition (ii) can be verified by showing that the tangent to the curve $y = g(m_2)$ at $m_2 = m_{2_{cr}}$ is not parallel to the m_2 axis (Siekmann, Malchow, & Venturino, 2008).

Corollary 6.1: *The period τ of the bifurcating periodic orbits close to $m_2 = m_{2_{cr}}$ is given by*

$$\tau(m_{2_{cr}}) = 2\pi\sqrt{\frac{Q_1(m_{2_{cr}})}{Q_3(m_{2_{cr}})}}.$$

6.1. Stability of bifurcating periodic solution

We investigate the orbital stability of the Hopf-bifurcating periodic solution using Poore's sufficient condition (Poore, 1976). The supercritical/subcritical nature of Hopf-bifurcating periodic solution is determined by the positive/negative sign of the real part of Φ, respectively, where

$$
\begin{aligned}
\Phi = &-a_l F^l_{u_j u_m u_s} b_j b_m \bar{b}_s + 2a_l F^l_{u_j u_m} b_j (J^{-1}_{E^*})_{mr} F^r_{u_p u_q} b_p \bar{b}_q \\
&+ a_l F^l_{u_j u_k} \bar{b}_j \left[(J_{E^*} - 2i\omega_0)^{-1} \right]_{kr} F^r_{u_p u_q} b_p b_q,
\end{aligned}
$$

the repeated indices within each term imply a sum from 1 to 4, all the derivatives of F^l are evaluated at the equilibrium E^* with $u_1 = P$, $u_2 = x$, $u_3 = y$, $u_4 = z$, and J_{E^*} is the Jacobian matrix of (2) calculated at E^*. $\left[(J_{E^*})^{-1} \right]_{mr}$ denotes the element in row m, column r of $(J_{E^*})^{-1}$.

The left and right normalized eigenvectors of J_{E^*} with respect to the eigenvalues $\pm i\omega_0$ at $m_2 = m_{2_{cr}}$ are given by

$$
\mathbf{a} = \frac{\xi_1}{F^2_P F^3_x F^4_y} \left(F^2_P F^3_x F^4_y, a_2 F^3_x F^4_y, a_3 F^4_y, a_4 \right) \quad \text{and}
$$

$$
\mathbf{b} = \frac{\xi_2}{F^1_x F^2_z F^4_y} \left(F^1_x F^2_z F^4_y, b_2 F^2_z F^4_y, b_3, b_4 F^4_y \right)^T,
$$

where ξ_1 and ξ_2 are complex numbers,

$a_2 = i\omega_0 - F^1_P$,

$a_3 = F^4_y [(F^1_P F^2_x - F^1_x F^2_P - \omega^2_0) - i\omega_0 (F^1_P + F^2_x)]$,

$a_4 = \omega^2_0 (F^1_P + F^2_x) - F^3_y (F^1_P F^2_x - F^1_x F^2_P - \omega^2_0) + i\omega_0 \{F^1_P F^2_x - F^1_x F^2_P - \omega^2_0 + F^3_P (F^1_P + F^2_x)\}$,

$b_2 = i\omega_0 - F^1_P$,

$b_3 = \omega^2_0 (F^1_P + F^2_x) - F^4_z (F^1_P F^2_x - F^1_x F^2_P - \omega^2_0) + i\omega_0 \{F^1_P F^2_x - F^1_x F^2_P - \omega^2_0 + F^4_z (F^1_P + F^2_x)\}$,

$b_4 = [\omega^2_0 (F^1_P + F^2_x) - F^4_z (F^1_P F^2_x - F^1_x F^2_P - \omega^2_0) + i\omega_0 \{F^1_P F^2_x - F^1_x F^2_P - \omega^2_0 + F^4_z (F^1_P + F^2_x)\}]$.

Using $\mathbf{a}.\mathbf{b} = 1$, we obtain $\xi_1 \xi_2$.

If $(\Phi)_{m_2 = m_{2_{cr}}} > 0$, then the system (2) undergoes a supercritical Hopf bifurcation as m_2 is increased through $m_{2_{cr}}$, so that the bifurcating periodic orbit is asymptotically orbitally stable.

7. Numerical simulations

In this section, we investigate the effects of various parameters on the qualitative behaviour of our system using the numerical approach of Bhattacharyya and Pal (2013) using MATLAB. The default set of parameter values, mostly taken from Bhattacharyya and Pal (2013), is given in Table 1. Under this set of parameter values, it is observed that the system becomes locally asymptotically stable at E^* (cf. Figure 1).

We will now verify the feasibility of the criteria of stability in Section 5.

Table 1. Default parameter values used in the numerical analysis.

| Parameters	Description of parameters	Default value	Dimension
r	Intrinsic growth rate of Algae	4	1/time
K	Carrying capacity of the system	5	mass/volume
m_1	Maximal uptake rate of Parrotfish on Algae	3	1/time
m_2	Maximal uptake rate of adult *Pterois volitans* on Parrotfish	5	1/time
m_3	Maximal uptake rate of adult *Pterois volitans* on juvenile *Pterois volitans*	5	1/time
a_1	Half saturation const. for uptake of Algae by Parrotfish	2	mass/volume
a_2	Half saturation const. for uptake of Parrotfish by adult *Pterois volitans*	2	mass/volume
a_3	Half saturation const. for uptake of juvenile Pterois volitans by adult *Pterois volitans*	3	mass/volume
α_1	Growth efficiency of Parrotfish on Algae	0.3	–
α_2	Growth efficiency of adult *Pterois volitans* on Parrotfish	0.6	–
α	Growth efficiency of adult *Pterois volitans* growth on juvenile *Pterois volitans*	0.4	–
D_1	Death rate of Parrotfish	0.3	1/time
D_2	Death rate of juvenile *Pterois volitans*	0.2	1/time
D_3	Death rate of adult *Pterois volitans*	0.1	1/time
$\frac{1}{\mu}$	Total time spent by *Pterois volitans* in its juvenile stage	0.2	time
h	Maximal harvesting rate of adult *Pterois volitans*	2	1/time
c	Half saturation constant for harvesting of adult *Pterois volitans*	1	1/time
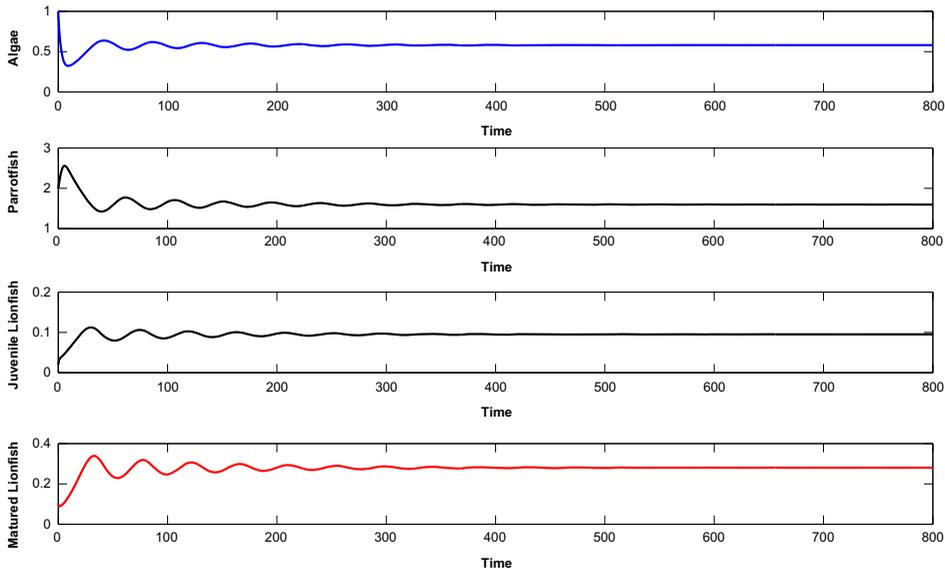
Figure 1. Time series analysis of the system for the parameters given in Table 1, the system has a stable focus at E^*.

Example 1: If the maximal harvesting rate of adult *P. volitans* is increased (viz. $h = 2.5$), and all other parameters are as given in Table 1, then we obtain

$$\lambda < 1 \text{ and } 0.0503 = \frac{\lambda(1-\lambda)}{a_2}\sqrt{\frac{c\mu m_2}{(\mu + D_2)(cD_3 + h)} - 1} < D_1 < \frac{m_1}{2(1-\lambda)} = 0.1569,$$

satisfying the condition of stability at $E_2 = (0.2828, 2.7046, 0, 0)$ as given in Lemma 5.3. E_2 is a stable focus with eigenvalues -0.0477, -1.9023 and $-0.1195 \pm i0.2396$ (cf. Figure 2).
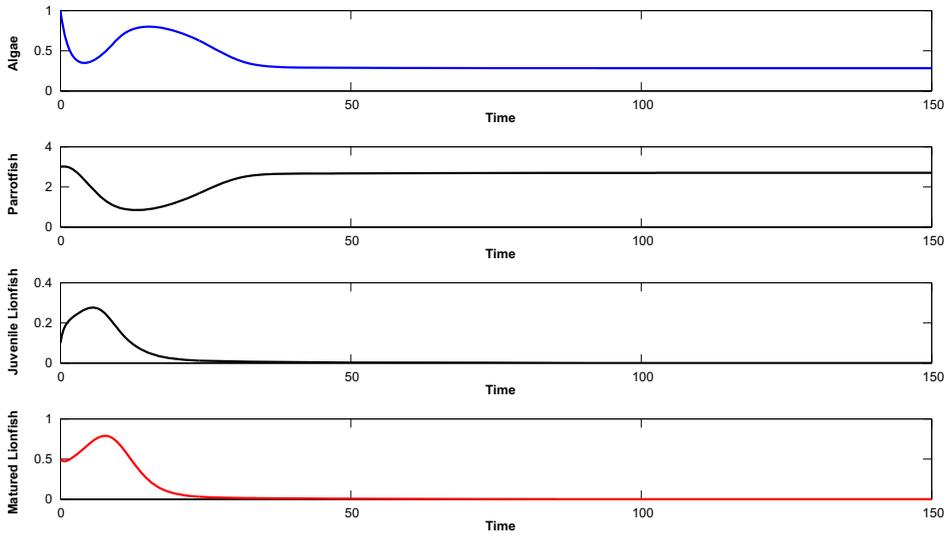
Figure 2. Time series analysis of the system for $h = 2.5$ and other parameter values as given in Table 1, the system has a stable focus at E_2.
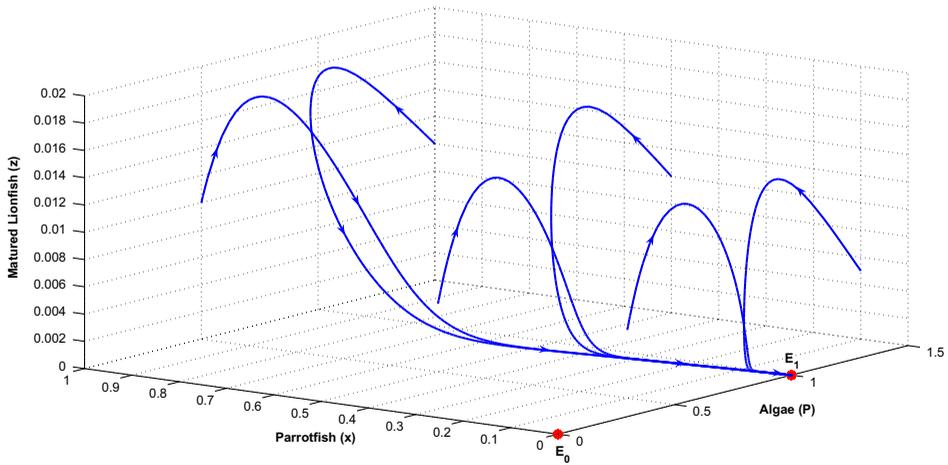

Figure 3. Phase plane diagram of the system projected on Pxz-space for $D_1 = 0.85$ and other parameter values as given in Table 1, the system has a stable node at E_1.

Example 2: If the death rate of Parrotfish is increased (viz. $D_1 = 0.85$), leaving all other parameters unaltered, then the system approaches a stable node at $E_1 = (1, 0, 0, 0)$, with eigenvalues -1, -0.0185, -0.525 and -1.3. In this case, we obtain $D_1 > m_1/(a_1^2 + 1) = 0.194$, satisfying Lemma 5.2 (cf. Figure 3).

Example 3: Under the set of parameter values are as given in Table 1, the system is locally asymptotically stable at $E^* = (0.5803, 1.5968, 0.095, 0.2801)$, with eigenvalues -1.7192,
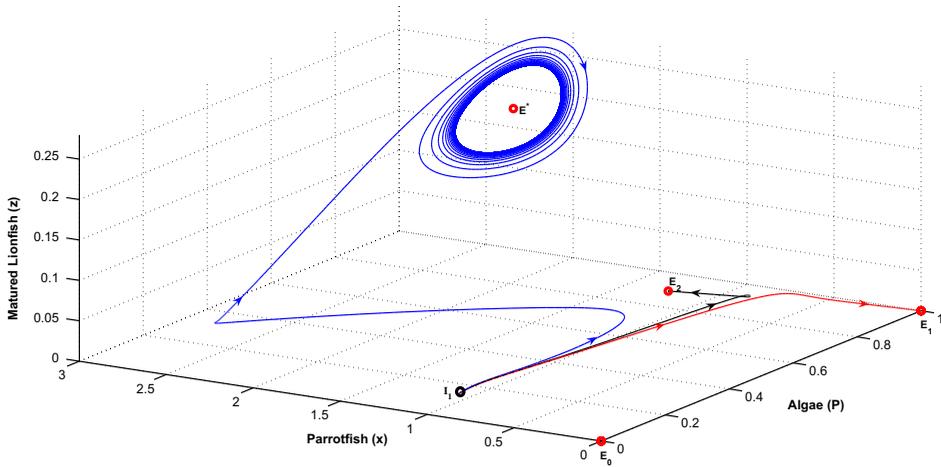
Figure 4. Phase plane diagram of the system projected on Pxz-space for $m_1 = 2.5$ and other parameters as given in Table 1 with initial value I_1. The system is oscillatory around E^* (in black). For $m_1 = 1.2$ and other parameters as given in Table 1, the system is locally asymptotically stable at E_2 (in blue). For $m_1 = 0.5$ and other parameters as given in Table 1, the system is locally asymptotically stable at E_1 (in red).
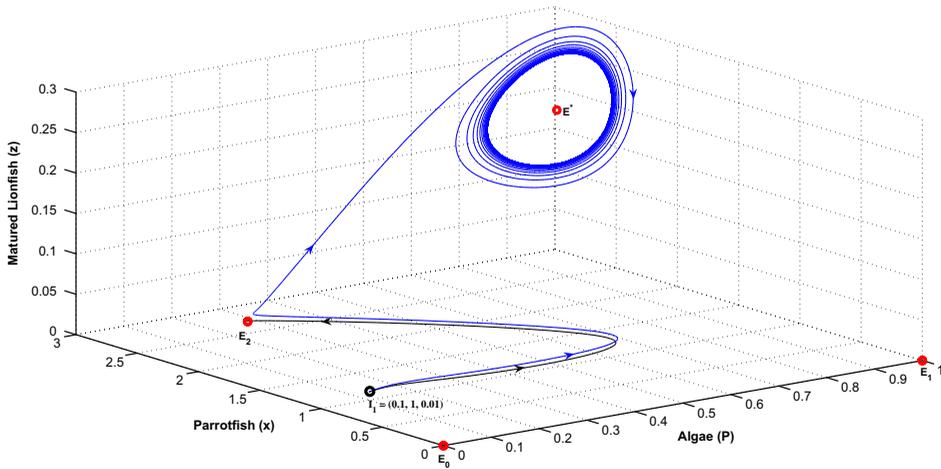

Figure 5. Phase plane diagram of the system projected on Pxz-space for $m_2 = 7$ and other parameters as given in Table 1 with initial value $I_1 = (0.1, 1, 0.01)$. The system is oscillatory around E^* (in blue). For $m_2 = 7$ and $h = 3.2$, other parameters as given in Table 1, the system is locally asymptotically stable at E_2 (in black).

-0.3302 and $-1.0076 \pm i0.1422$. In this case we obtain

$$\lambda < 1 \quad \text{and} \quad D_1 \leq \frac{\lambda(1-\lambda)}{a_2} \sqrt{\frac{c\mu m_2}{(\mu + D_2)(cD_3 + h)} - 1} = 0.093,$$

satisfying the analytical conditions of persistence as given in Lemma 5.4. We also obtain

$$Q_1 = 1.2282, \quad Q_1 Q_2 - Q_3 = 1.2282, \quad \text{and} \quad Q_1 Q_2 Q_3 - Q_3^2 - Q_1^2 Q_4 = 0.0126,$$
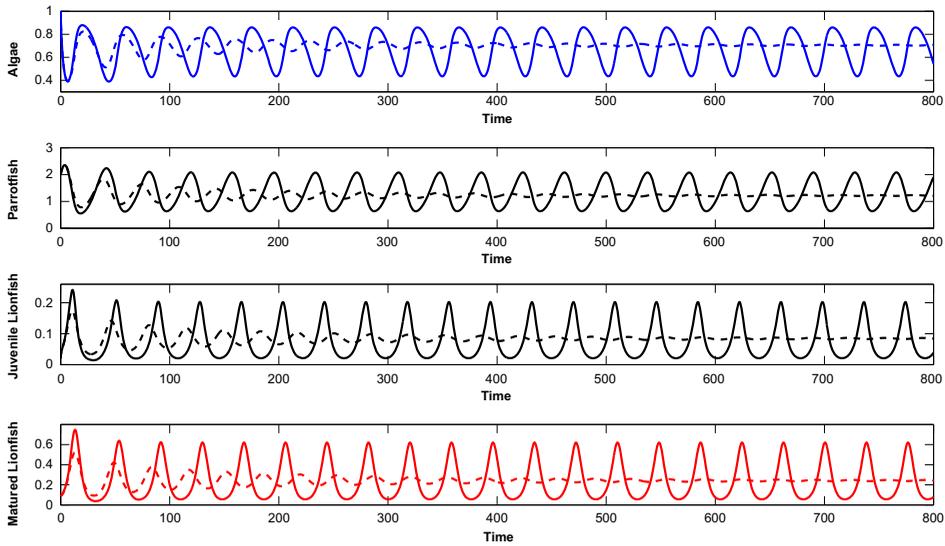
Figure 6. Time series analysis of the system for $m_2 = 7$ and other parameter values as given in Table 1, the system is oscillatory around E^* (solid). For $m_2 = 7$, $a_3 = 0.5$ and other parameter values as given in Table 1, the system is LAS at E^* (dotted).
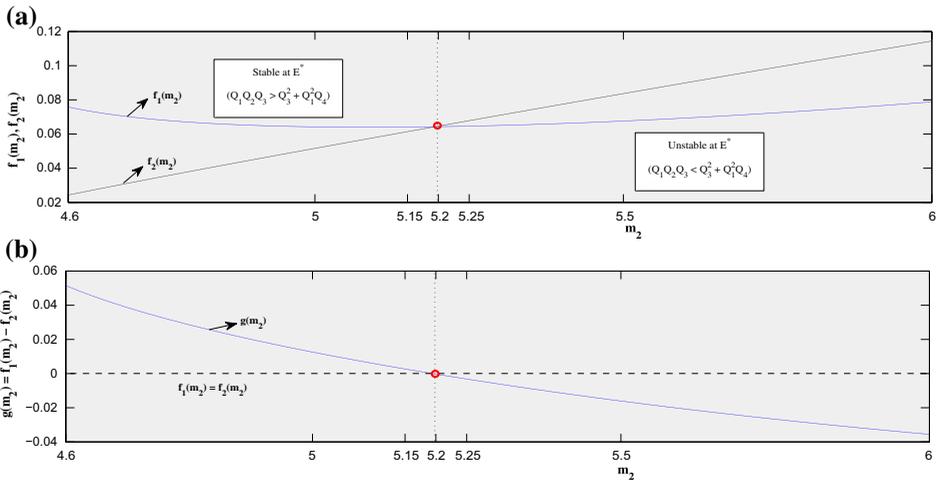

Figure 7. The relative position of $f_1(m_2)$, $f_2(m_2)$ and $g(m_2)$ showing that a Hopf bifurcation occurs when the two curves intersect at $m_{2cr} = 5.2$.

satisfying the analytical conditions of stability at E^* as given in Lemma 5.6 (cf. Figure 1).

Example 4: For $m_1 = 2.5$, the system is oscillatory around E^* (cf. Figure 4). When we decrease the value of m_1 (viz. $m_1 = 1.2$), the system becomes stable at E_2. On further lowering the value of m_1 (viz. $m_1 = 0.5$), we find that the system stabilizes at E_1.
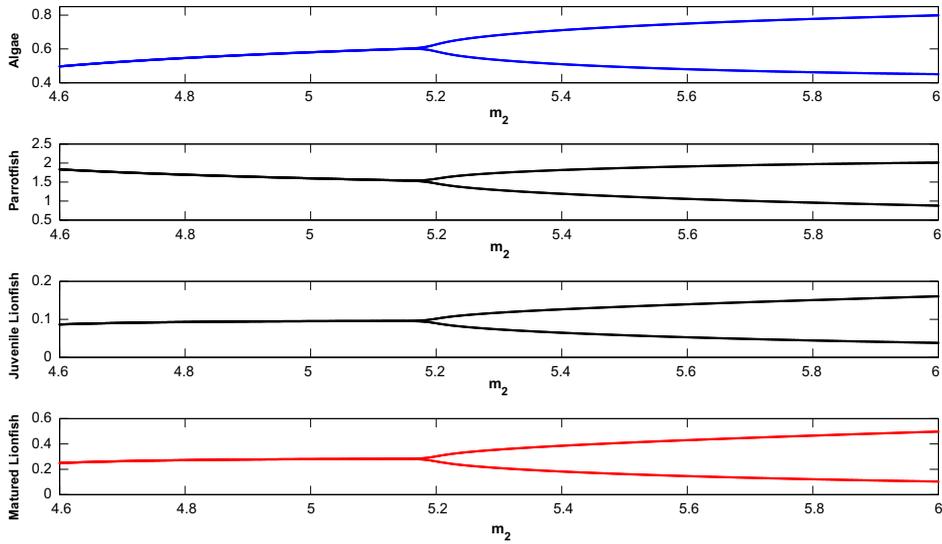
Figure 8. The system undergoes a supercritical Hopf bifurcation as m_2 is increased through $m_{2_{cr}} = 5.2$ with other parameter values as given in Table 1.

Example 5: We observe that the system is oscillatory around E^* for $m_2 = 7$ (cf. Figure 5). In this case by increasing the maximal harvesting rate of adult *P. volitans* (viz. $h = 3.2$), the system becomes locally asymptotically stable at E_2.

Example 6: For high invasiveness of adult *P. volitans*, the system becomes oscillatory around E^* (cf. Figure 5). When the value of a_3 is lowered (viz. $a_3 = 0.5$), the system stabilizes at E^* (cf. Figure 6).

7.1. Hopf bifurcation

We observe that the system becomes oscillatory when the maximal uptake rate of adult *P. volitans* is high. We therefore consider m_2 as a bifurcation parameter. For $m_2 < 5.2$ we see that $f_1(m_2) > f_2(m_2)$, satisfying the Routh–Hurwitz condition, so that the system is locally asymptotically stable at E^*. For $m_2 > 5.2$ we see that $f_1(m_2) < f_2(m_2)$ and so the system is unstable at E^* (cf. Figure 7(a)). Moreover, we observe that the tangent to the graph of $g(m_2)$ at $m_2 = 5.2$ is not parallel to the m_2 axis (cf. Figure 7(b)), satisfying the condition $(dg/dm_2)\,|_{(m_2=5.2)} \neq 0$. In Figure 8, we observe that a supercritical Hopf bifurcation occurs when the parameter m_2 is increased through the critical value $m_{2_{cr}} = 5.2$.

8. Discussion

We have considered a tri-trophic food chain model consisting of algae and Parrotfish in the first two trophic levels, respectively, while juvenile and adult *P. volitans* reside in the third trophic level. We analyse the effect of predation with stage-structured cannibalism and study the effect of harvesting of the adult *P. volitans* on the dynamics of the system. The threshold values for the existence and stability of various steady states of the system

are worked out. In order to keep sustainable development of the coral reef ecosystem, it is desirable to have a positive equilibrium which is asymptotically stable. Keeping this view in mind, we have established some strong criteria for existence of the positive equilibrium. We studied bifurcation with respect to the parameter representing the invasiveness of adult *P. volitans* in the system. The critical parameter value at which bifurcation occurs is determined to preserve the system under consideration in its natural state. We observe that when the maximal uptake rate of adult *P. volitans* on Parrotfish crosses a certain critical value, the system enters into Hopf bifurcation that induces oscillation around the positive equilibrium. The stability as well as the direction of Hopf bifurcation near the interior equilibrium is obtained by applying the algorithm due to Poore (1976). We have also provided numerical simulations to substantiate our analytic results. From analytical and numerical observations we obtain the following conclusions:

(i) If the growth rate of Parrotfish is low, then the Parrotfish would become extinct.
(ii) Higher mortality rate of Parrotfish can lead to the extinction of both Parrotfish and *P. volitans* from the system. This represents the fact that rapid elimination of herbivorous fish can be fatal for the coral reef ecosystem.
(iii) High rate of predation of adult *P. volitans* on Parrotfish induces oscillation around the positive equilibrium leading to dynamic instability, representing the phenomenon of ecological imbalance due to high invasiveness of *P. volitans* in the coral reef ecosystem. This dynamic instability can be controlled by increasing the rate of harvesting of adult *P. volitans*. Moreover, a high harvesting rate of adult *P. volitans* can eliminate *P. volitans* from the system.
(iv) The increase of cannibalism of *P. volitans* stabilizes the system even with high invasiveness of adult *P. volitans*.

Throughout the article we focus on searching for a suitable way to control the growth of algae, Parrotfish and *P. volitans*, and maintain a stable coexistence of all the species. Our numerical simulations suggest that the maximal harvesting rate of adult *P. volitans* can be used as a control parameter to maintain the stability of the system at the coexistence steady state.

Our results are based on a model that has no growth equation for the corals. It would be interesting to incorporate corals in our system to study the dynamics of coral reefs in the presence of invasive *P. volitans*.

ORCID

Samares Pal http://orcid.org/0000-0002-8792-0031

References

Albins, M. A., & Hixon, M. A. (2008). Invasive Indo-Pacific lionfish (*Pterois volitans*) reduce recruitment of Atlantic coral-reef fishes. *Marine Ecology Progress Series, 367*, 233–238. doi:10.3354/meps07620

Benkwitt, C. E. (2015). Non-linear effects of invasive lionfish density on native coral-reef fish communities. *Biological Invasions, 17*, 1383–1395. doi:10.1007/s10530-014-0801-3

Bhattacharyya, J., & Pal, S. (2013). Stage-structured cannibalism with delay in maturation and harvesting of an matured predator. *Journal of Biological Physics, 39*, 37–65. doi:10.1007/s10867-012-9284-6

Bhattacharyya, J., & Pal, S. (2014). Dynamics of a stage-structured system with harvesting and discrete time delays. *Systems Science & Control Engineering: An Open Access Journal, 2*, 192–215. doi:10.1080/21642583.2014.886973

Bhattacharyya, J., & Pal, S. (2015). Hysteresis in coral reefs under macroalgal toxicity and overfishing. *Journal of Biological Physics, 41*, 151–172. doi:10.1007/s10867-014-9371-y

Edwards, A. M., & Brindley, J. (1999). Zooplankton mortality and the dynamical behaviour of plankton population models. *Bulletin of Mathematical Biology, 61*, 303–339.

Fishelson, L. (1997). Experiments and observations on food consumption growth and starvation in dendrochirus brachypterus and Pterois volitans (Pteroinae, Scorpaenidae). *Environmental Biology of Fishes, 50*, 391–403.

Goreau, T. J., & Hayes, R. (1994). Coral bleaching and ocean "hot spots". *Ambio, 23*, 176–180.

Hare, J. A., & Whitfield, P. E. (2003). An integrated assessment of the introduction of lionfish (*Pterois volitans/miles complex*) to the western Atlantic Ocean. *NOAA Technical Memorandum, NOS NCCOS, 2*, 1–21.

Leard, B., Lewis, C., & Rebaza, J. (2008). Dynamics of ratio-dependent predator-prey models with nonconstant harvesting. *Discrete and Continuous Dynamical Systems – Series S, 1*, 303–315.

Lenzini, P., & Rebaza, J. (2010). Nonconstant predator harvesting on ratio-dependent predator-prey models. *Applied Mathematical Sciences, 4*, 791–803.

Li, Y., & Muldowney, S. (1993). On Bendixson criteria. *Journal of Differential Equations, 106*, 27–39.

Luwig, D., Jones, D. D., & Holling, C. S. (1978). Qualitative analysis of insect outbreak systems: The spruce budworm and forest. *The Journal of Animal Ecology, 47*, 315–332.

Morris, J. A., Akins, J. L., Barse, A., Cerino, D., Freshwater, D. W., Green, S. J., ... Whitefield, P. E. (2009). Biology and ecology of invasive lionfishes, Pterois miles and Pterois volitans. *Gulf and Caribbean Fisheries Institute, 61*, 1–6.

Morris, Jr., J. A., & Whitfield, P. E. (2009). Biology, ecology, control and management of the invasive Indo-Pacific lionfish: An updated integrated assessment. *NOAA Technical Memorandum NOS-NCCOS, 99*, 1–65.

Poore, A. B. (1976). On the theory and applications of Hopf-Friedrichs bifurcation theory. *The Archive for Rational Mechanics and Analysis, 60*, 371–393.

Rotjan, R. D., & Lewis, S. M. (2006). Parrotfish abundance and selective corallivory on a Belizean coral reef. *Journal of Experimental Marine Biology and Ecology, 335*, 292–301.

Ruan, S. (1993). Persistence and coexistence in zooplanktonphytoplankton-nutrient models with instantaneous nutrient recycling. *Journal of Mathematical Biology, 31*, 633–654. doi:10.1007/bf00161202

Rudolf, V. H. W. (2007). The interaction of cannibalism and omnivory: Consequences for community dynamics. *Ecology, 88*, 2697–2705. doi:10.1890/06-1266.1

Rudolf, V. H. W. (2008). The impact of cannibalism in the prey on predator-prey dynamics. *Ecology, 89*, 3116–3127. doi:10.1890/07-0709.1

Siekmann, I., Malchow, H., & Venturino, E. (2008). An extension of the Beretta–Kuang model of viral diseases. *Mathematical Biosciences and Engineering, 5*, 549–565. doi:10.3934/mbe.2008.5.549

Smith, H. L. (1995). *Monotone dynamical systems: An introduction to the theory of competitive and cooperative systems.* Mathematical surveys and monographs. Providence, RI: American Mathematical Society.

Wang, W., & Chen, L. (1997). A predator-prey system with stage structure for predator. *Computers & Mathematics with Applications, 33*, 83–91. doi:10.1016/S0898-1221(97)00056-4

Zhang, X., Chen, L., & Neumann, A. U. (2000). The stage-structured predator-prey model and optimal harvesting policy. *Mathematical Biosciences, 168*, 201–210. doi:10.1016/s0025-5564(00)00033-x

Appendix 1.

A.1. Proof of Lemma 3.1

Proof: From the first two equations of the system (2) we have,

$$P(t) = P(0)e^{\int_0^t \left(1-P-\frac{m_1 xP}{a_1^2+P^2}\right)d\tau} \quad \text{and} \quad x(t) = x(0)e^{\int_0^t \left(\frac{\alpha_1 m_1 P^2}{a_1^2+P^2} - \frac{m_2 xz}{a_2^2+x^2} - D_1\right)d\tau}.$$

This implies, if $P(0) > 0$ and $x(0) > 0$, then $P(t) > 0$ and $x(t) > 0$ for all $t > 0$. Hence, if $y(t) > 0$ and $z(t) > 0$ for all t, it may be concluded that all the solutions of the system (2) are always positive. □

A.2. Proof of Lemma 4.1

Proof: Since $dP/dt \leq P(1-P)$, it follows that for $\epsilon > 0$, there exists $t_\epsilon > 0$ such that $P(t) \leq 1+\epsilon$ for all $t \geq t_\epsilon$. We have $d\Sigma(t)/dt < 1+\epsilon - D\Sigma(t)$ for all $t \geq t_\epsilon$, where $\Sigma(t) = P(t)+x(t)+y(t)+z(t)$ and $D = \min\{1, D_1, D_2, D_3\}$. Let $u(t)$ be the solution of $du/dt + uD = 1$, satisfying $u(0) = \Sigma(0)$. Then $u(t) = 1/D + (\Sigma(0) - 1/D) e^{-tD} \to 1/D$ as $t \to \infty$. By comparison, it follows that $P(t) + x(t) + y(t) + z(t) < 1/D + \epsilon$, for all $t \geq t_\epsilon$, proving the Lemma. □

A.3. Proof of Lemma 4.2

Proof: If possible, let $\lim_{t\to\infty} P(t) = 0$. Then if $P(t)$ decreases monotonically to zero, there exists $T_1 > 0$ such that $P(t)+m_1 x(t)P(t)/(a_1^2 + P^2(t)) < 1$ for all $t > T_1$. This gives $dP/dt > 0$ for all $t > T_1$, contradicting to our assumption. Therefore, there exists $0 < p_1 \leq 1/D$ such that $p_1 \leq P(t) \leq 1/D$ for all $t > T_1$, where $D = \min\{1, D_1, D_2, D_3\}$. Since $\lim_{t\to\infty} \sup[x(t) + y(t) + z(t)] < 1/D$, it follows that there exists $T_2 > 0$ such that $x(t) \leq M_1$, $y(t) \leq M_2$, and $z(t) \leq M_3$, where M_1, M_2, M_3 are finite positive constants satisfying $M_1 + M_2 + M_3 < 1/D$. For $t > \max\{T_1, T_2\}$, we have $dx/dt \geq x \left(m_1 p_1^2/(a_1^2 + p_1^2) - D_1 - m_2 M_3/x\right)$. This implies $(dx/dt)\mid_{x=x_1} \geq 0$ for $t > \max\{T_1, T_2\}$, where $x_1 = m_2 M_3(a_1^2 + p_1^2)/\{(m_1 - D_1)(p_1^2 - \lambda^2)\}$. It is also seen that, $x_1 > 0$ if $p_1 > \lambda$. This implies that if $p_1 > \lambda$ is satisfied, then there exists $T_3 > 0$ such that $x_1 \leq x(t) \leq M_1$ for all $t > T_3$. For $t > T_3$, we have $dy/dt \geq m_2 x_1^2 z/(a_2^2 + x_1^2) - (\mu + D_2)M_2 - m_3 z$, and so if $z(t) > M_2(a_2^2 + x_1^2)(\mu + D_2)/\{(m_2 - m_3)x_1^2 - m_3 a_2^2\}$ holds, then $dy/dt > 0$ for all $t > T_3$. Let there exist $z_1 > 0$ such that $M_2(a_2^2 + x_1^2)(\mu + D_2)/\{(m_2 - m_3)x_1^2 - m_3 a_2^2\} < z_1 < M_3$. If $z(t) \geq z_1 > 0$, we have $dy/dt > 0$ for all $t \geq T_3$, and so in this case, there exists $T_4 > 0$ and $0 < y_1 < M_2$ such that $y(t) \geq y_1$ for all $t \geq T_4$. Therefore, for all $t \geq T_4$, if $z(t) \geq z_1$ holds, then $y_1 \leq y(t) \leq M_2$ and $z_1 \leq z(t) \leq M_3$. Let $T = \max\{T_1, T_2, T_3, T_4\}$. Then for $t > T$, there exists finite positive real numbers $p_1, x_1, y_1, z_1, M_1, M_2, M_3$ with

$$M_1 + M_2 + M_3 < \frac{1}{D}, \quad p_1 > \lambda, \quad x_1 = \frac{m_2 M_3(a_1^2 + p_1^2)}{(m_1 - D_1)(p_1^2 - \lambda^2)} \quad \text{and} \quad z_1 > \frac{M_2(a_2^2 + x_1^2)(\mu + D_2)}{(m_2 - m_3)x_1^2 - m_3 a_2^2},$$

such that $p_1 \leq P(t) \leq 1/D$, $x_1 \leq x(t) \leq M_1$, $y_1 \leq y(t) \leq M_2$, and $z_1 \leq z(t) \leq M_3$. □

A.4. Proof of Lemma 4.3

Proof: (i) If $m_1 \leq D_1$, then $dx/dt < -a_1^2 x D_1/(a_1^2 + P^2) < 0$. This implies $\lim_{t\to\infty} x(t)$ exists and is non-negative. If possible, let $\lim_{t\to\infty} x(t) = \eta > 0$. Since $dP/dt \leq P(1 - P)$, it follows that for

$\epsilon > 0$, there exists $t_\epsilon > 0$ such that $P(t) \leq 1 + \epsilon$, for all $t \geq t_\epsilon$. Thus for all $t \geq t_\epsilon$, we get

$$x(t) \leq x(t_\epsilon) e^{-\frac{a_1^2 D_1 (t - t_\epsilon)}{a_1^2 + (1+\epsilon)^2}} \to 0 \quad \text{as} \quad t \to \infty,$$

this leads to a contradiction. Therefore, for $m_1 \leq D_1$, we must have $\lim_{t \to \infty} x(t) = 0$, and so $\lim_{t \to \infty} y(t) = 0 = \lim_{t \to \infty} z(t)$.

(ii) Since $\lim_{t \to \infty} \sup[P(t) + x(t) + y(t) + z(t)] \leq 1/D$, it follows that for all $\epsilon > 0$, there exists $t_\epsilon > 0$ such that $P(t) \leq 1/D + \epsilon$ for all $t \geq t_\epsilon$. If $m_1 > D_2$, then for all $t \geq t_\epsilon$ we have $dx/dt \leq x(m_1 - D_1) \left\{ (1/D + \epsilon)^2 - \lambda^2 \right\} / a_1^2$. Therefore, if $\lambda > 1/D + \epsilon$, then $dx/dt < 0$ for all $t \geq t_\epsilon$. This implies $\lim_{t \to \infty} x(t) = 0$, and consequently $\lim_{t \to \infty} y(t) = 0 = \lim_{t \to \infty} z(t)$. □

A.5. Proof of Lemma 4.4

Proof: The Jacobian of the system (2) at (P, x, y, z) is given by

$$J = \begin{bmatrix} 1 - 2P - \frac{2m_1 P x a_1^2}{(a_1^2 + P^2)^2} & -\frac{m_1 P^2}{a_1^2 + P^2} & 0 & 0 \\ \frac{2m_1 P x a_1^2}{(a_1^2 + P^2)^2} & \frac{m_1 P^2}{a_1^2 + P^2} - D_1 - \frac{2m_2 x z a_2^2}{(a_2^2 + x^2)^2} & 0 & -\frac{m_2 x^2}{a_2^2 + x^2} \\ 0 & \frac{2m_2 x z a_2^2}{(a_2^2 + x^2)^2} & -\mu - D_2 - \frac{2m_3 y z a_3^2}{(a_3^2 + y^2)^2} \frac{m_2 x^2}{a_2^2 + x^2} - \frac{m_3 y^2}{a_3^2 + y^2} & 0 \\ 0 & 0 & \mu & -D_3 - \frac{ch}{(c+z)^2} \end{bmatrix}.$$

Let us consider

$$H = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & -1 & 0 & 0 \\ 0 & 0 & -1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix}.$$

Then we have

$$HJH = \begin{bmatrix} 1 - 2P - \frac{2m_1 P x a_1^2}{(a_1^2 + P^2)^2} & -\frac{m_1 P^2}{a_1^2 + P^2} & 0 & 0 \\ -\frac{2m_1 P x a_1^2}{(a_1^2 + P^2)^2} & -\frac{m_1 P^2}{a_1^2 + P^2} + D_1 + \frac{2m_2 x z a_2^2}{(a_2^2 + x^2)^2} & 0 & -\frac{m_2 x^2}{a_2^2 + x^2} \\ 0 & -\frac{2m_2 x z a_2^2}{(a_2^2 + x^2)^2} & -\mu - D_2 - \frac{2m_3 y z a_3^2}{(a_3^2 + y^2)^2} \frac{m_3 y^2}{a_3^2 + y^2} - \frac{m_2 x^2}{a_2^2 + x^2} & 0 \\ 0 & 0 & -\mu & -D_3 - \frac{ch}{(c+z)^2} \end{bmatrix}.$$

All the off-diagonal elements of the matrix HJH are negative if $m_3 y^2 / (a_3^2 + y^2) < m_2 x^2 / (a_2^2 + x^2)$. Therefore, if $m_2 > m_3$ and

$$x(t) > x_1 > \sqrt{\frac{m_3 a_2^2}{m_2 - m_3}} \quad \text{for large } t,$$

all the off-diagonal elements of HJH are negative, and consequently, the system (2) is competitive. □

A.6. Proof of Lemma 5.1

Proof: The Jacobian matrix at E_0 is

$$V(E_0) = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & -D_1 & 0 & 0 \\ 0 & 0 & -\mu - D_2 & 0 \\ 0 & 0 & \mu & -D_3 - \frac{h}{c} \end{bmatrix}.$$

At E_0, the eigenvalues of the Jacobian matrix are $1, -D_1, -\mu - D_2$ and $-D_3 - h/c$. Therefore, the system (2) is always unstable at E_0. $\qquad\square$

A.7. Proof of Lemma 5.2

Proof: The Jacobian matrix at E_1 is

$$
V(E_1) = \begin{bmatrix}
-1 & -\frac{m_1}{a_1^2+1} & 0 & 0 \\
0 & \frac{m_1}{a_1^2+1} - D_1 & 0 & 0 \\
0 & 0 & -\mu - D_2 & 0 \\
0 & 0 & \mu & -D_3 - \frac{h}{c}
\end{bmatrix}.
$$

The eigenvalues of the Jacobian matrix evaluated at E_1 are $-1, -\mu - D_2, -D_2 - h/c$ and $m_1/(a_1^2 + 1) - D_1$. Therefore, the system (2) is locally asymptotically stable at E_1 if and only if $D_1 > m_1/(a_1^2+1)$. $\qquad\square$

A.8. Proof of Lemma 5.3

Proof: The Jacobian matrix at E_2 is

$$
V(E_2) = \begin{bmatrix}
\frac{(1-\lambda)(2D_1-m_1)}{m_1} & -D_1 & 0 & 0 \\
\frac{2D_1(1-\lambda)a_1^2}{m_1\lambda^2} & 0 & 0 & -\frac{m_2\lambda^2(1-\lambda)^2}{a_2^2 D_1^2 + \lambda^2(1-\lambda)^2} \\
0 & 0 & -\mu - D_2 & \frac{m_2\lambda^2(1-\lambda)^2}{a_2^2 D_1^2 + \lambda^2(1-\lambda)^2} \\
0 & 0 & \mu & -D_3 - \frac{h}{c}
\end{bmatrix}.
$$

The eigenvalues are obtained from the two quadratic equations:

$$
\eta^2 - \eta\frac{(1-\lambda)(2D_1 - m_1)}{m_1} + \frac{2D_1^2(1-\lambda)a_1^2}{m_1\lambda^2} = 0 \tag{A1}
$$

and

$$
\eta^2 + \eta\left(\mu + D_2 + D_3 + \frac{h}{c}\right) + (\mu + D_2)\left(D_3 + \frac{h}{c}\right) - \frac{\mu m_2\lambda^2(1-\lambda)^2}{a_2^2 D_1^2 + \lambda^2(1-\lambda)^2} = 0. \tag{A2}
$$

All the roots of Equation (A1) and Equation (A2) have negative real parts if

$$
\frac{\lambda(1-\lambda)}{a_2}\sqrt{\frac{c\mu m_2}{(\mu + D_2)(cD_3 + h)} - 1} < D_1 < \frac{m_1}{2(1-\lambda)}.
$$

Therefore, under the aforesaid conditions, the system (2) is locally asymptotically stable at E_2. $\qquad\square$

A.9. Proof of Lemma 5.4

Proof: In order to prove the persistence of the system, we shall show that all the boundary equilibria of the system are repellers. It is observed that the system is always unstable at E_0. If $D_1 \le m_1/(a_1^2+1)$, then the system is unstable at E_1. The system is unstable at E_2 if

$$
D_1 \le \frac{\lambda(1-\lambda)}{a_2}\sqrt{\frac{c\mu m_2}{(\mu + D_2)(cD_3 + h)} - 1} \quad \text{or} \quad D_1 \ge \frac{m_1}{2(1-\lambda)}.
$$

Since $m_1/(a_1^2 + 1) < m_1/\{2(1 - \lambda)\}$, it follows that all the boundary equilibria are repellers if

$$D_1 \leq \frac{\lambda(1 - \lambda)}{a_2} \sqrt{\frac{c\mu m_2}{(\mu + D_2)(cD_3 + h)} - 1}.$$

We have also proved that the system is bounded. Therefore, the system is persistent under the aforesaid conditions. □

A.10. Proof of Lemma 5.5

Proof: The second additive compound matrix of the Jacobian of the system (2) is

$$J^{(2)} = \begin{bmatrix} F_P + G_x & 0 & G_z & 0 & 0 & 0 \\ H_x & F_P + H_y & H_z & F_x & 0 & 0 \\ 0 & \mu & F_P + I_z & 0 & F_x & 0 \\ 0 & G_P & 0 & G_x + H_y & H_z & -G_z \\ 0 & 0 & G_P & \mu & G_x + I_z & 0 \\ 0 & 0 & 0 & 0 & H_x & H_y + I_z \end{bmatrix}.$$

Let $|X|_\infty = \sup_i |X_i|$. The logarithmic norm $\mu_\infty(J^{(2)})$ of $J^{(2)}$ endowed by the vector norm $|X|_\infty$ is the supremum of the following:

$$F_P + G_x + |G_z|, \quad F_P + H_y + |F_x| + |H_x| + |H_z|, \quad F_P + I_z + \mu + |F_x|,$$
$$G_x + H_y + |G_P| + |G_z| + |H_z|, \quad G_x + I_z + \mu + |G_P|, \quad \text{and} \quad H_y + I_z + |H_x|.$$

Now, $(F_P + G_x + |G_z|)_{E^*} < 0$ if

$$1 + m_1 + m_2 < D_1 + 2P^* + \frac{2m_1 P^* x^* a_1^2}{(a_1^2 + P^{*2})^2} + \frac{2m_2 x^* z^* a_2^2}{(a_2^2 + x^{*2})^2} = L_1,$$

$(F_P + H_y + |F_x| + |H_x| + |H_z|)_{E^*} < 0$ if

$$1 + m_1 + m_2 \left(1 + \frac{2z^*}{x^*}\right) + m_3 < 2P^* + \mu + D_2 + \frac{2m_3 y^* z^* a_3^2}{(a_3^2 + y^{*2})^2} + \frac{2m_1 P^* x^* a_1^2}{(a_1^2 + P^{*2})^2} = L_2,$$

$(F_P + I_z + \mu + |F_x|)_{E^*} < 0$ if

$$1 + \mu + m_1 < 2P^* + D_3 + \frac{2m_1 P^* x^* a_1^2}{(a_1^2 + P^{*2})^2} + \frac{ch}{(c + z^*)^2} = L_3,$$

$(G_x + H_y + |G_P| + |G_z| + |H_z|)_{E^*} < 0$ if

$$m_1 \left(1 + \frac{2x^*}{P^*}\right) + 2m_2 + m_3 < \mu + D_1 + D_2 + \frac{2m_2 x^* z^* a_2^2}{(a_2^2 + x^{*2})^2} + \frac{2m_3 y^* z^* a_3^2}{(a_3^2 + y^{*2})^2} = L_4,$$

$(G_x + I_z + \mu + |G_P|)_{E^*} < 0$ if

$$m_1 \left(1 + \frac{2x^*}{P^*}\right) + \mu < D_1 + D_3 + \frac{2m_2 x^* z^* a_2^2}{(a_2^2 + x^{*2})^2} + \frac{ch}{(c + z^*)^2} = L_5,$$

and $(H_y + I_z + |H_x|)_{E^*} < 0$ if

$$\frac{2m_2 z^*}{x^*} < \mu + D_1 + D_3 + \frac{ch}{(c + z^*)^2} + \frac{2m_3 y^* z^* a_3^2}{(a_3^2 + y^{*2})^2} = L_6.$$

Therefore, if $1 + \mu + m_1 \left(1 + 2x^*/P^*\right) + m_2 \left(1 + 2z^*/x^*\right) + m_3 < L$, then $\mu_\infty(J^{(2)}(E^*)) < 0$, where $L = \min\{L_1, \ldots, L_6\}$. As a direct application of the method adopted by Li and Muldowney (1993), we can say that under the aforesaid conditions, the system (2) has no periodic solutions around E^*. □

A.11. Proof of Lemma 6.1

Proof: The necessary and sufficient conditions for a Hopf bifurcation to occur at $m_2 = m_{2_{cr}}$ are

(i) $f_1(m_{2_{cr}}) = f_2(m_{2_{cr}})$,
(ii) $Re\left[\frac{d\lambda_j}{dm_2}\right]_{m_2 = m_{2_{cr}}} \neq 0$,

where $\lambda_j (j = 1, \ldots, 4)$ are the roots of $G(\lambda) = 0$. Let $g: (0, \infty) \to \mathbf{R}$ be a continuously differentiable function of m_2 defined by $g(m_2) = f_1(m_2) - f_2(m_2)$. The existence of $m_{2_{cr}}$ is ensured by solving the equation $g(m_{2_{cr}}) = 0$. At $m_2 = m_{2_{cr}}$, the characteristic equation $G(\lambda) = 0$ can be expressed as

$$\left(\lambda^2 + \frac{Q_3(m_{2_{cr}})}{Q_1(m_{2_{cr}})}\right)\left(\lambda^2 + \lambda Q_1(m_{2_{cr}}) + \frac{Q_1(m_{2_{cr}})Q_4(m_{2_{cr}})}{Q_3(m_{2_{cr}})}\right) = 0. \tag{A3}$$

Equation (A3) has the pair of purely imaginary roots $\lambda_1 = i\omega_0$ and $\lambda_2 = \bar{\lambda}_1$, where $\omega_0 = \sqrt{Q_3(m_{2_{cr}})/Q_1(m_{2_{cr}})}$. If λ_3 and λ_4 are not real, then $Re\lambda_3 = -Q_1(m_{2_{cr}})/2 < 0$. If λ_3 and λ_4 are real, then $\lambda_3 + \lambda_4 < 0$ and $\lambda_3\lambda_4 = Q_4(m_{2_{cr}})/\omega_0^2 > 0$. This implies $\lambda_3, \lambda_4 < 0$. Since g is a continuously differentiable function of m_2, there exists an open interval $(m_{2_{cr}} - \epsilon, m_{2_{cr}} + \epsilon)$, such that $\lambda_1(m_2) = \beta_1(m_2) + i\beta_2(m_2)$ and $\lambda_2(m_2) = \beta_1(m_2) - i\beta_2(m_2)$ for all $m_2 \in (m_{2_{cr}} - \epsilon, m_{2_{cr}} + \epsilon)$. Therefore, for all $m_2 \in (m_{2_{cr}} - \epsilon, m_{2_{cr}} + \epsilon)$, $dG(\lambda)/dm_2 = 0$ gives

$$\frac{d\lambda}{dm_2} = -\frac{\{M(m_2)K(m_2) - N(m_2)L(m_2)\} + i\{N(m_2)K(m_2) - M(m_2)L(m_2)\}}{K^2(m_2) + L^2(m_2)}.$$

Hence, if $\left[M(m_2)K(m_2) - N(m_2)L(m_2)\right]_{m_2 = m_{2_{cr}}} \neq 0$ holds, then $Re\left(d\lambda_j/dm_2\right)_{m_2 = m_{2_{cr}}} \neq 0$, and consequently, the system (2) undergoes a non-degenerate Hopf bifurcation at $m_2 = m_{2_{cr}}$. □