Potential effects of invasive *Pterois volitans* in coral reefs

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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).

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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 intraspecific 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 $P. \text{volitans}$ and the transformation rate from juvenile to adult $P. \text{volitans}$ are proportional to the existing juvenile population with proportionality constants $D_2$ and $\mu$, respectively.

(H4) The death rate of adult $P. \text{volitans}$ is proportional to the existing adult population with a proportionality constant $D_3$.

(H5) $$\frac{m_3y^2z}{a_3^2 + y^2}$$ represents the rate of cannibalism of adult $P. \text{volitans}$ ($z$) by consuming juvenile $P. \text{volitans}$ ($y$) leading to the growth of new juveniles. The growth rate of new juveniles is $$\frac{\alpha m_3y^2z}{a_3^2 + y^2}, \quad 0 < \alpha < 1.$$ Thus, $$\frac{(1 - \alpha)m_3y^2z}{a_3^2 + y^2}$$ represents the reduction in growth rate of juvenile $P. \text{volitans}$ due to cannibalism.

The basic equations with all the parameters are

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{K}\right) - \frac{m_1P^2x}{a_1^2 + P^2}$$

$$\frac{dx}{dt} = x\left(\frac{\alpha_1m_1P^2}{a_1^2 + P^2} - D_1 - \frac{m_2xz}{a_2^2 + x^2}\right)$$

$$\frac{dy}{dt} = \frac{\alpha_2m_2x^2z}{a_2^2 + x^2} - (\mu + D_2)y - \frac{(1 - \alpha)m_3y^2z}{a_3^2 + y^2}$$

$$\frac{dz}{dt} = \mu y - D_3z - \frac{hz}{c + z},$$

(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 $P. \text{volitans}$ in its juvenile stage, $h$ is the maximum harvesting rate of adult $P. \text{volitans}$, $c$ is the concentration of adult $P. \text{volitans}$ 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 $P. \text{volitans}$, $m_3$ is the maximal uptake rate of juvenile $P. \text{volitans}$ by the adult $P. \text{volitans}$ and $a_i$ are the corresponding half saturation constants ($i = 1, 2, 3$). The parameters $\alpha$ and $\alpha_i$ 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, m₁, aᵢ, Dᵢ, α and α₁ 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

\[ \tilde{P} = \frac{P}{K}, \quad \tilde{x} = \frac{x}{\alpha_1 K}, \quad \tilde{y} = \frac{y}{\alpha_1 \alpha_2 K}, \quad \tilde{z} = \frac{z}{\alpha_1 \alpha_2 K}, \quad \tilde{t} = rt, \]

and defining non-dimensional parameters

\[ \tilde{a}_1 = \frac{a_1}{K}, \quad \tilde{a}_2 = \frac{a_2}{\alpha_1 K}, \quad \tilde{a}_3 = \frac{a_3}{\alpha_1 \alpha_2 K}, \quad \tilde{m}_1 = \frac{\alpha_1 m_1}{r}, \quad \tilde{m}_2 = \frac{\alpha_2 m_2}{r}, \quad \tilde{m}_3 = \frac{(1 - \alpha)m_3}{r}, \]
\[ \tilde{D}_1 = \frac{D_1}{r}, \quad \tilde{D}_2 = \frac{D_2}{r}, \quad \tilde{D}_3 = \frac{D_3}{r}, \quad \tilde{\mu} = \frac{\mu}{r}, \quad \tilde{h} = \frac{h}{\alpha_1 \alpha_2 r K}, \quad \tilde{c} = \frac{c}{\alpha_1 \alpha_2 K}. \]

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

\[ \frac{dX}{dt} = f(X), \] (2)

where \( X = [P \ x \ y \ z]^T \) and \( f(X) = [F^1 \ F^2 \ F^3 \ F^4]^T \) with

\[ F^1(P, x) = P(1 - P) - \frac{m_1 x P^2}{a_1^2 + P^2}, \]
\[ F^2(P, x, z) = x \left( \frac{m_1 P^2}{a_1^2 + P^2} - \frac{m_2 x z}{a_2^2 + x^2} - D_1 \right), \]
\[ F^3(x, y, z) = \frac{m_2 x z}{a_1^2 + x^2} - \frac{m_3 y^2 z}{a_2^2 + y^2} - (\mu + D_2) y, \]
\[ F^4(y, z) = \mu y - \frac{h z}{c + z} - D_3 z. \]

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 \( \Omega \) 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 $\varepsilon > 0$, there exists $t_\varepsilon > 0$ such that all the solutions of (2) with positive initial values fall into the set \( \{(P, x, y, z) \in \Omega : P(t) + x(t) + y(t) + z(t) < 1/D + \varepsilon, \varepsilon > 0\} \) whenever $t \geq t_\varepsilon$, 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 $\lambda$ 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 $\lambda$ 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 $u_i, M_i \in (0, \infty)$ such that
\[
u_i, \leq \lim u_i(t) \leq M_i
\]
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
\[
x_1 = \frac{m_2 M_3(a_1^2 + p_1^2)}{(m_1 - D_1)(p_1^2 - \lambda^2)}, \quad y_1 > 0, \quad \text{and} \quad z_1 > \frac{M_2(a_1^2 + x_1^2)(\mu + D_2)}{(m_2 - m_3)x_1^2 - m_3 a_2^2},
\]
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 $H = \text{diag}(\varepsilon_1, \ldots, \varepsilon_4)$ such that $HJ(X)H$ has non-positive off-diagonal elements,
where $J(X)$ is the Jacobian of the system (2) and $\epsilon_i$ 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

$$\frac{m_3y^2(t)}{a_3^2 + y^2(t)} < \frac{m_2x^2(t)}{a_2^2 + x^2(t)}$$

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

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

$$x(t) > x_1 > \sqrt{\frac{m_3a_2^2}{m_2 - m_3}}$$

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

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

with

$$\theta(P) = \frac{(1 - P)(a_1^2 + P^2)}{m_1P}, \quad \phi(P) = \frac{1}{\mu}\left(D_3 + \frac{h}{c + \psi(P)}\right)\psi(P), \quad \text{and}$$

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

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

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

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

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

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

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

where \( L \) is the minimum of the following six quantities:

(i) \( D_1 + 2P^* + \frac{2m_1P^*x^*a_1^2}{(a_1^2 + P^* z^*)^2} + \frac{2m_2x^*z^*a_2^2}{(a_2^2 + x^* z^*)^2} \),

(ii) \( 2P^* + \mu + D_2 + \frac{2m_3y^*z^*a_3^2}{(a_3^2 + y^* z^*)^2} + \frac{2m_4P^*x^*a_1^2}{(a_1^2 + P^2 z^*)^2} \),

(iii) \( 2P^* + D_3 + \frac{2m_1P^*x^*a_1^2}{(a_1^2 + P^* z^*)^2} + \frac{c}{(c + z^*)^2} \),

(iv) \( \mu + D_1 + D_2 + \frac{2m_2x^*z^*a_2^2}{(a_2^2 + x^* z^*)^2} + \frac{2m_3y^*z^*a_3^2}{(a_3^2 + y^* z^*)^2} \),

(v) \( D_1 + D_3 + \frac{2m_2x^*z^*a_2^2}{(a_2^2 + x^* z^*)^2} + \frac{c}{(c + z^*)^2} \),

(vi) \( \mu + D_1 + D_3 + \frac{c}{(c + z^*)^2} + \frac{2m_3y^*z^*a_3^2}{(a_3^2 + y^* z^*)^2} \).

**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

\[
Q_1 > 0, \quad Q_1Q_2 > Q_3, \quad \text{and} \quad Q_1Q_2Q_3 > Q_3^2 + Q_1^2Q_4,
\]

where

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

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

\[
Q_3 = \left( F_p^1|_{E^*} + F_x^2|_{E^*} \right) \left( F_y^3|_{E^*} + F_z^4|_{E^*} \right) + F_p^1|_{E^*}F_x^2|_{E^*} + F_y^3|_{E^*}F_z^4|_{E^*}
- \mu F_z^2|_{E^*} - F_p^1|_{E^*}F_z^2|_{E^*},
\]

\[
Q_4 = \left( F_p^1|_{E^*} + F_x^2|_{E^*} \right) \left( F_y^3|_{E^*} + F_z^4|_{E^*} \right) + F_p^1|_{E^*}F_x^2|_{E^*} + F_y^3|_{E^*}F_z^4|_{E^*}
- \mu F_z^2|_{E^*} - F_p^1|_{E^*}F_z^2|_{E^*}.
\]
\[ Q_3 = (\mu F'_z|E^* - F'_y|E^*F'_z|E^*) (F'_1|E^* + F'_2|E^*) + (F'_1|E^*F'_2|E^* - F'_1|E^*F'_2|E^*) (F'_3|E^* + F'_4|E^*) - \mu F'_1|E^*F'_2|E^*. \]

\[ Q_4 = (F'_1|E^*F'_3|E^* - \mu F'_1|E^*) (F'_1|E^*F'_2|E^* - F'_1|E^*F'_2|E^*) + \mu F'_1|E^*F'_2|E^*F'_3|E^*. \]

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 \( G(\lambda) = u^4 + Q_1u^3 + Q_2u^2 + Q_3u + Q_4 = 0 \). Solving \( Q_1Q_2Q_3 - Q^2_1Q^2_4 = 0 \), the critical value of \( m_2 \) can be obtained, say, \( m_2 = m_{2\text{cr}} \).

**Lemma 6.1:** The system undergoes a Hopf bifurcation at \( m_2 = m_{2\text{cr}} \) if and only if

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

where

\[
\begin{align*}
 f_1(m_2) &= Q_1(m_2)Q_2(m_2)Q_3(m_2), \quad f_2(m_2) = Q^3_3(m_2) + Q^2_1(m_2)Q_4(m_2),
 K(m_2) &= 4\beta_1^3(m_2) - 12\beta_1(m_2)\beta_2^2(m_2) + 3(\beta_1^2(m_2) - \beta_2^2(m_2))Q_1(m_2) + 2\beta_1(m_2)Q_2(m_2) + Q_3(m_2),
 L(m_2) &= 12\beta_1^2(m_2)\beta_3(m_2) - 4\beta_2^3(m_2) + 6\beta_1(m_2)\beta_2(m_2)Q_1(m_2) + 2\beta_2(m_2)Q_2(m_2),
 M(m_2) &= \beta_1^3(m_2)Q'_1(m_2) - 3\beta_1(m_2)\beta_2^2(m_2)Q'_1(m_2) + (\beta_1^2(m_2) - \beta_2^2(m_2))Q'_2(m_2) + \beta_1(m_2)Q'_3(m_2),
 N(m_2) &= 3\beta_1^2(m_2)\beta_2(m_2)Q'_1(m_2) - \beta_2^3Q'_1(m_2) + 2\beta_1(m_2)\beta_2(m_2)Q'_2(m_2) + \beta_2(m_2)Q'_3(m_2);
\end{align*}
\]

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

The condition (ii) is equivalent to \( dg(m_2)/dm_2|_{m_2 = m_{2\text{cr}}} \neq 0 \). 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 \( m_2 = m_{2\text{cr}} \), whereas the condition (ii) can be verified by showing that the tangent to the curve \( y = g(m_2) \) at \( m_2 = m_{2\text{cr}} \) is not parallel to the \( m_2 \) axis (Siekmann, Malchow, & Venturino, 2008).

**Corollary 6.1:** The period \( \tau \) of the bifurcating periodic orbits close to \( m_2 = m_{2\text{cr}} \) is given by

\[
\tau(m_{2\text{cr}}) = 2\pi \sqrt{\frac{Q_1(m_{2\text{cr}})}{Q_3(m_{2\text{cr}})}}.
\]
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 \( \Phi \), respectively, where

\[
\Phi = -a_i F_{i, u_m u_k} b_j b_m b_k + 2a_i F_{i, u_m u_k} b_j (J_{E^*})_{mr} F_{r, u_q} b_p b_q + a_i F_{i, u_k} b_j [(J_{E^*} - 2i \omega_0)^{-1}]_{kr} F_{r, u_q} b_p b_q,
\]

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 \( E^* \). \([J_{E^*}]^{-1}\) 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 \( m_2 = m_{2r} \) are given by

\[
a = \frac{\xi_1}{F^2_x F^2_y F^2_z} \begin{pmatrix} F^2_x F^2_y, a_2 F^3_x F^2_y, a_3 F^4_x, a_4 \end{pmatrix}^T \quad \text{and} \quad b = \frac{\xi_2}{F^1_x F^2_y F^2_z} \begin{pmatrix} F^1_x F^2_x F^4, b_2 F^2_x F^4, b_3, b_4 F^4 \end{pmatrix}^T,
\]

where \( \xi_1 \) and \( \xi_2 \) are complex numbers,

\[
a_2 = i \omega_0 - F^1_x,
\]

\[
a_3 = F^1_y [(F^1_x F^2_x - F^1_x F^2_y - \omega_0^2) - i \omega_0 (F^1_x + F^2_x)],
\]

\[
a_4 = \omega_0^2 (F^1_x + F^2_x) - F^3_y (F^1_x F^2_x - F^1_x F^2_y - \omega_0^2) + i \omega_0 (F^1_x F^2_y - F^1_x F^2_y - \omega_0^2 + F^1_x F^2_x),
\]

\[
b_2 = i \omega_0 - F^1_y,
\]

\[
b_3 = \omega_0^2 (F^1_y + F^2_y) - F^4_x (F^1_x F^2_x - F^1_x F^2_x - \omega_0^2) + i \omega_0 (F^1_x F^2_x - F^1_x F^2_x - \omega_0^2 + F^1_x F^2_x),
\]

\[
b_4 = [\omega_0^2 (F^1_x + F^2_x) - F^4_y (F^1_y F^2_y - F^1_y F^2_y - \omega_0^2) + i \omega_0 (F^1_y F^2_y - F^1_y F^2_y - \omega_0^2 + F^1_y F^2_y)].
\]

Using \( a \cdot b = 1 \), we obtain \( \xi_1 \xi_2 \).

If \( (\Phi)_{m_2 = m_{2r}} > 0 \), then the system (2) undergoes a supercritical Hopf bifurcation as \( m_2 \) is increased through \( m_{2r} \), 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 |
| $\alpha_1$ | Growth efficiency of Parrotfish on Algae | 0.3           | –           |
| $\alpha_2$ | Growth efficiency of adult *Pterois volitans* on Parrotfish | 0.6           | –           |
| $\alpha$   | 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      |
| $\mu$      | 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 $-0.1195 \pm 0.2396$ (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 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 \( \mathbf{i}_1 \). 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 \( \mathbf{i}_1 = (0.1, 1, 0.01) \). 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 \(-1.0076 \pm i 0.1422 \). 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

\[
Q_1 = 1.2282, \quad Q_1Q_2 - Q_3 = 1.2282, \quad \text{and} \quad Q_1Q_2Q_3 - Q_2^2 - Q_1^2Q_4 = 0.0126,
\]
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 $m_2^{cr} = 5.2$.

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*.

**Disclosure statement**

No potential conflict of interest was reported by the authors.

**Funding**

This work was supported by Science and Engineering Research Board [grant number SR/S4/MS:863/13].

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Appendix 1.

A.1. Proof of Lemma 3.1

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

$$P(t) = P(0)e^{\int_0^t \left(1 - \frac{m_1 P_t}{a_1^2 + z_1^2}\right) dt} \quad \text{and} \quad x(t) = x(0)e^{\int_0^t \left(\frac{a_1 M_1 z_1^2}{a_1^2 + P_t^2} - \frac{m_2 z_1^2}{a_2^2 + z_1^2} - D_1\right) dt}.$$ 

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 $u(t) = 1/D(\Sigma(0) - 1/D) e^{-D} \to 1/D$ 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 $dx/dt \geq x(m_1 p_2^2/(a_1^2 + p_1^2) - D_1 - m_2 M_3/x)$. This implies $(dx/dt)|_{x=x_1} = 0$ for $x > \max\{T_1, T_2\}$, 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 $x(t) \leq M_1$ for all $t > T_3$. For $t > T_3$, we have $dy/dt \geq m_2 z_1^2/(a_2^2 + x_1^2) - (\mu + D_2)M_2 - m_2 z_1$, 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 $y(t) \leq M_2$ and $z(t) \leq M_3$. 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

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

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 $dx/dt < -a_2^2 XD_1/(a_1^2 + P^2) < 0$. 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

$$x(t) \leq x(t_\epsilon)e^{-\frac{\mu_1^2}{a_1^2(t_\epsilon)}(t-t_\epsilon)} \rightarrow 0 \text{ as } t \rightarrow \infty,$$

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

(ii) Since $\lim_{t \rightarrow \infty} \sup \{P(t) + x(t) + y(t) + z(t)\} \leq 1/D$, 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 $dx/dt \leq x(m_1 - D_1) \{1/(1/D + \epsilon)^2 - \lambda^2\}/a_1^2$. Therefore, if $\lambda > 1/D + \epsilon$, then $dx/dt < 0$ for all $t \geq t_\epsilon$. This implies $\lim_{t \rightarrow \infty} x(t) = 0$, and consequently $\lim_{t \rightarrow \infty} y(t) = 0 = \lim_{t \rightarrow \infty} z(t)$. \hfill $\square$

### A.5. Proof of Lemma 4.4

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

$$J = \begin{bmatrix}
1 - 2P - \frac{2m_1Pxa_1^2}{(a_1^2 + P^2)^2} & -\frac{m_1P^2}{a_1^2 + P^2} & 0 & 0 \\
\frac{2m_1Pxa_1^2}{(a_1^2 + P^2)^2} & \frac{m_1P^2}{a_1^2 + P^2} - D_1 - \frac{2m_2xza_1^2}{(a_1^2 + x^2)^2} & 0 & -\frac{m_2x^2}{(a_1^2 + x^2)^2} + \mu \\
0 & \frac{2m_2xza_1^2}{(a_1^2 + x^2)^2} & -\mu - D_2 & \frac{2m_3zyza_1^2}{(a_1^2 + y^2)^2} - \frac{m_2y^2}{(a_1^2 + y^2)^2} \\
0 & 0 & \frac{m_3y^2}{(a_1^2 + y^2)^2} - \frac{m_3z^2}{a_1^2 + z^2} & -D_3 - \frac{m_3z^2}{(a_1^2 + z^2)^2}
\end{bmatrix}.$$

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

$$HJH = \begin{bmatrix}
1 - 2P - \frac{2m_1Pxa_1^2}{(a_1^2 + P^2)^2} & -\frac{m_1P^2}{a_1^2 + P^2} & 0 & 0 \\
-\frac{2m_1Pxa_1^2}{(a_1^2 + P^2)^2} - \frac{m_1P^2}{a_1^2 + P^2} + D_1 + \frac{2m_2xza_1^2}{(a_1^2 + x^2)^2} & 0 & -\mu - D_2 & \frac{2m_3zyza_1^2}{(a_1^2 + y^2)^2} - \frac{m_2y^2}{(a_1^2 + y^2)^2} \\
0 & \frac{2m_2xza_1^2}{(a_1^2 + x^2)^2} & -\mu - D_2 & \frac{m_3y^2}{(a_1^2 + y^2)^2} - \frac{m_3z^2}{a_1^2 + z^2} \\
0 & 0 & \frac{m_3y^2}{(a_1^2 + y^2)^2} - \frac{m_3z^2}{a_1^2 + z^2} & -D_3 - \frac{m_3z^2}{(a_1^2 + z^2)^2}
\end{bmatrix}.$$

All the off-diagonal elements of the matrix $HJH$ are negative if $m_2 > m_3$ and

$$m_3y^2/(a_1^2 + y^2) < m_2x^2/(a_1^2 + x^2).$$

Therefore, if $m_2 > m_3$ and

$$x(t) > x_1 > \sqrt{\frac{m_3a_1^2}{m_2 - m_3}} \text{ for large } t,$$

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

### A.6. Proof of Lemma 5.1

**Proof:** The Jacobian matrix at $E_0$ is

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

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 \( D_1 > m_1/(a_1^2 + 1) \).

A.8. Proof of Lemma 5.3

**Proof:** The Jacobian matrix at \( E_2 \) is
\[
V(E_2) = \begin{bmatrix}
\frac{(1-\lambda)(2D_1 - m_1)}{m_1} & -D_1 & 0 & 0 \\
\frac{2D_1(1-\lambda)a_1^2}{m_1\lambda^2} & 0 & 0 & -\frac{m_2\lambda^2(1-\lambda)^2}{a_1^2D_1^2 + \lambda^2(1-\lambda)^2} \\
0 & 0 & -\mu - D_2 & 0 \\
0 & 0 & \mu & -D_3 - \frac{h}{c}
\end{bmatrix}.
\]
The eigenvalues are obtained from the two quadratic equations:
\[
\eta^2 - \eta \left( \frac{(1-\lambda)(2D_1 - m_1)}{m_1} \right) + \frac{2D_1^2(1-\lambda)a_1^2}{m_1\lambda^2} = 0 \tag{A1}
\]
and
\[
\eta^2 + \eta \left( \mu + D_2 + D_3 + \frac{h}{c} \right) + (\mu + D_2) \left( D_3 + \frac{h}{c} \right) - \frac{\mu m_2\lambda^2(1-\lambda)^2}{a_1^2D_1^2 + \lambda^2(1-\lambda)^2} = 0. \tag{A2}
\]
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 \( E_2 \).

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 \( D_1 \leq m_1/(a_1^2 + 1) \), then the system is unstable at \( E_1 \). The system is unstable at \( E_2 \) if
\[
D_1 \leq \frac{\lambda(1-\lambda)}{a_2} \sqrt{\frac{c\mu m_2}{(\mu + D_2)(cD_3 + h)}} - 1 \quad \text{or} \quad D_1 \geq \frac{m_1}{2(1-\lambda)}.
\]
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. 

\[\square\]

## 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:

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

$$1 + m_1 + m_2 < D_1 + 2P^* + \frac{2m_1P^*x^*a_1^2}{(a_1^2 + P^*)^2} + \frac{2m_2x^*z^*a_2^2}{(a_2^2 + x^2)^2} = L_1,$$ 

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

$$1 + m_1 + m_2 \left(1 + \frac{2z^*}{x^*}\right) + m_3 < 2P^* + \mu + D_2 + \frac{2m_3y^*z^*a_3^2}{(a_3^2 + y^2z^2)^2} + \frac{2m_1P^*x^*a_1^2}{(a_1^2 + P^*)^2} = L_2,$$ 

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

$$1 + \mu + m_1 < 2P^* + D_3 + \frac{2m_1P^*x^*a_1^2}{(a_1^2 + P^*)^2} + \frac{ch}{(c + z*)^2} = L_3,$$ 

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

$$m_1 \left(1 + \frac{2x^*}{P^*}\right) + 2m_2 + m_3 < \mu + D_1 + D_2 + \frac{2m_2x^*z^*a_2^2}{(a_2^2 + x^2)^2} + \frac{2m_3y^*z^*a_3^2}{(a_3^2 + y^2z^2)^2} = L_4,$$ 

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

$$m_1 \left(1 + \frac{2x^*}{P^*}\right) + \mu < D_1 + D_3 + \frac{2m_2x^*z^*a_2^2}{(a_2^2 + x^2)^2} + \frac{ch}{(c + z*)^2} = L_5,$$ 

$$m_1 \left(1 + \frac{2x^*}{P^*}\right) + \mu < D_1 + D_3 + \frac{2m_2x^*z^*a_2^2}{(a_2^2 + x^2)^2} + \frac{ch}{(c + z*)^2} = L_5,$$ 

$$m_1 \left(1 + \frac{2x^*}{P^*}\right) + \mu < D_1 + D_3 + \frac{2m_2x^*z^*a_2^2}{(a_2^2 + x^2)^2} + \frac{ch}{(c + z*)^2} = L_5,$$ 

$$m_1 \left(1 + \frac{2x^*}{P^*}\right) + \mu < D_1 + D_3 + \frac{2m_2x^*z^*a_2^2}{(a_2^2 + x^2)^2} + \frac{ch}{(c + z*)^2} = L_5,$$
and \((H_y + I_z + |H_x|)_{E^*} < 0\) if

\[
\frac{2m_2z^*}{x^*} < \mu + D_1 + D_3 + \frac{ch}{(c + z^*)^2} + \frac{2m_3y^*z^*a_3^2}{(a_3^2 + y^*)^2} = L_6.
\]

Therefore, if \(1 + \mu + m_1(1 + 2x^*/P^*) + m_2(1 + 2z^*/x^*) + m_3 < L\), then \(\mu_{\infty}(f^{(2)}(E^*)) < 0\), 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 \(E^*\).

\[\Box\]

**A.11. Proof of Lemma 6.1**

**Proof:** The necessary and sufficient conditions for a Hopf bifurcation to occur at \(m_2 = m_{2,\epsilon}\) are

\[\begin{enumerate}
\item (i) \(f_1(m_{2,\epsilon}) = f_2(m_{2,\epsilon})\),
\item (ii) \(\text{Re} \left\{ \frac{d\varphi}{dm_{2,\epsilon}} \right\}_{m_{2,\epsilon} = m_{2,\epsilon}} \neq 0\),
\end{enumerate}\]

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

\[
\left( \lambda^2 + \frac{Q_3(m_{2,\epsilon})}{Q_1(m_{2,\epsilon})} \right) \left( \lambda^2 + \lambda Q_1(m_{2,\epsilon}) + \frac{Q_1(m_{2,\epsilon})Q_4(m_{2,\epsilon})}{Q_3(m_{2,\epsilon})} \right) = 0. \tag{A3}
\]

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

Therefore, for all \(m_2 \in (m_{2,\epsilon} - \epsilon, m_{2,\epsilon} + \epsilon)\), \(dG(\lambda)/dm_2 = 0\) 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 \([M(m_2)K(m_2) - N(m_2)L(m_2)]_{m_2 = m_{2,\epsilon}} \neq 0\) holds, then \(\text{Re} \left\{ \frac{d\lambda_j}{dm_2} \right\}_{m_2 = m_{2,\epsilon}} \neq 0\), and consequently, the system (2) undergoes a non-degenerate Hopf bifurcation at \(m_2 = m_{2,\epsilon}\). \(\Box\)