

Impact of invasive lionfish on macroalgae in coral reef system with intratrophic predation

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ABSTRACT

The excessive population of macroalgae along with invasion of lionfish (Pterois volitans) in the coral reefs poses a major challenge to their ecosystem. The community shape of coral reef approaches to macroalgae-dominated ecosystem due to aggressive nature of macroalgae. The herbivores fish like parrotfish act as a favourable character in controlling the abundance of macroalgae. The abundance of lionfish play negative impact on parrotfish and decline its population growth and disrupt the impact on control of macro-algae growth. In this present article, a macro-algae- parrotfish-lionfish prey-predator in reef system is developed and analyzed. A harvesting term is introduced to control the invasion of lionfish on parrotfish. The model go through a supercritical Hopf-bifurcation when intrinsic growth rate of macroalgae crosses a particular value. Increase in carrying capacity of macroalgae renders the system unstable while intensity of intratrophic predation play a vital role in its stabilization. Also, the system switches from stable coexistence to oscillation around coexistence and lionfish free equilibrium for lower and higher harvesting rate of lionfish. The optimal harvest policy is calculated by using Pontryagin's maximum principle. Numerical simulations are presented to confirm our analytical results.

Keywords: Macroalgae; Parrotfish, Pterois volitans, Intratrophic predation, Optimal Harvesting policy.

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1 Introduction

Tropical coral reefs are fundamental habitats for macroalgae in coral reef ecosystem. Macroalgae are an important part of the coral reef community and are vital to various environmental functions such as reef structure stability, conservation of nutrient and recycling and initial productivity. Coral bleaching may take place due to major change of environmental conditions

such as nutrients, light and temperature. As a result, the coral throw out the symbiotic algae living in its tissue. In such situation, they are more susceptible to disease due to loses its major food source. Some time macroalgae play negative role on coral via shading, abrasion, and overgrowth (McCook L, 2001), chemical mechanisms like allelopathy (Rasher DB, 2011; Vieira C, 2016) or suppression of coral settlement (Dixon DL, 2014). Macroalgae consumption by parrotfish (*Sparisoma* spp.) in the western Atlantic helps in stabilizing the coral ecosystem (Rotjan, 2006; Fishelson, 1997).

Rapid depletion of coral results from high consumption of herbivorous fish by predatory lionfish such as *Pterois volitans*. *P. volitans* have two stages of life cycle from juvenile to adult at a top level of ecosystem. Adult lion fish exhibits cannibalism by eating their own juvenile species (Morris, 2009). It minimizes the hunting on others (Rudolf, 2008). The effect of *P. volitans* on *Sparisoma* spp. is studied under a two-tier stage-structured model with Holling III functional response function (Bhattacharyya, 2014). The scientists in (Mumby, 2007) demonstrated a coral reef based model on the feeding of coral-macroalgal phase shifts. After that, the scientists in (Blackwood, 2012) introduced parrotfish into this system and examine the grazing dynamics of parrotfish. In recent past, the author in (CE, 2015) analyzed that invasiveness of *P. volitans* may drastic decrease the herbivores fish population. Recently, invasion of lionfish play a key factor to disorder the acute coral reef ecosystem in the western Atlantic (Fishelson, 1997; Kindinger TL, 2017). According to (Albins MA, 2008), the scientists suggest that lionfish predation on native fishes is 2.5 times faster than other similar native predator. Moreover, the author in (CE, 2015) examine the cooperative hunting behavior of lion fish at a high density. The author in (Bhattacharyya J, 2013) show that herbivorous predator play a vital role to stabilize the stage-structured predator-prey diffusive system by varying the intrinsic growth rate. Furthermore, under influence of harvesting, they study cannibalism and predation of a top most predator species (Bhattacharyya J, 2016). Recently, the scientists in (Maji, 2019) point out that the cannibalistic stage-structure predator-prey system exhibits chaotic dynamic under influence of time delay. In tropical coral reef ecosystem, parrotfish consume the excessive algae to develop the biodiversity of system (Fishelson, 1997; Rotjan, 2006). Various techniques of biological control are introduced such as harvesting of lionfish, pathogens, predators etc., to combat the lionfish invasion (Morris, 2009).

Here, we introduce a three species algae-parrotfish-lionfish model to analyze the bottom up and top down effects. In addition, we consider intratrophic predation on top predator and effect of cannibalism. It is a specific behavior of intratrophic predation. We study the various equilibrium point and their existence and stability criteria. Hopf bifurcation is also discussed. Our main target is to explore the impact of harvesting on top predator. The optimal tax policy is shown by applying Pontryagin's maximum principle. Our study indicates that intratrophic predation play a key parameters to stabilize the system. Intrinsic growth rate and carrying capacity of macro-algae also influence the system. Our numerical results justify the analytical findings by using specific parametric values. A brief conclusion is presented in the last section.

2 Formulation of mathematical model

Firstly, we consider some basic assumption:

(A₁) Let $x(t)$, $y(t)$ and $z(t)$ be the concentrations of Macroalgae, prey (Parrotfish), predator (Lionfish) respectively at time t .

(A₂) In the absence of parrotfish, macroalgae grows logistically at the rate r with carrying capacity k .

(A₃) The uptake of parrotfish is modeled by $\frac{m_1xy}{a_1+x}$ with half-saturation constant a_1 . Let m_1 and γ be the maximal uptake rate and death rate of parrotfish, respectively, with α the net parrotfish conversion rate.

(A₄) The resource of food for lionfish can be represented by $y + bz$ where b , $0 \leq b \leq 1$, stands for the intensity of intratrophic predation. Therefore, intratrophic predation does not occur if $b = 0$ which indicates that the predator only depends on prey (parrotfish) for food resource. If $b = 1$, the lionfish counts Parrotfish and predator having the same characteristics.

(A₅) The uptake of lionfish is modeled by $\frac{m_2yz}{a_2+y+bz}$, where a_2 and m_2 stand for half-saturation constant and maximal uptake rate of predator respectively. Let β represents the conversion rate of lionfish.

(A₆) The death rate of lionfish is δ .

(A₇) The constant harvesting rate on lionfish is h .

The basic equations are

$$\begin{aligned}\frac{dx}{dt} &= rx\left(1 - \frac{x}{k}\right) - \frac{m_1xy}{a_1+x} \\ \frac{dy}{dt} &= \frac{\alpha m_1xy}{a_1+x} - \frac{m_2yz}{a_2+y+bz} - \gamma y \\ \frac{dz}{dt} &= \frac{\beta m_2(y+bz)z}{a_2+y+bz} - \frac{m_2bz^2}{a_2+y+bz} - \delta z - hz.\end{aligned}\quad (2.1)$$

where $r, k, a_1, m_1, m_2, a_2, \gamma, \delta, h \geq 0$, $0 \leq \alpha, \beta \leq 1$, with initial conditions

$$x(0) \geq 0, y(0) \geq 0, z(0) \geq 0. \quad (2.2)$$

3 The Non-dimensional System

First, we non-dimensionalize system (2.1) by substituting $\bar{x} = \frac{x}{k}$, $\bar{y} = \frac{y}{\alpha k}$, $\bar{z} = \frac{z}{\alpha \beta k}$, $\bar{t} = rt$, $\bar{a}_1 = \frac{a_1}{k}$, $\bar{m}_1 = \frac{\alpha m_1}{r}$, $\bar{a}_2 = \frac{a_2}{\alpha k}$, $\bar{m}_2 = \frac{\beta m_2}{r}$, $\bar{\gamma} = \frac{\gamma}{r}$, $\bar{\delta} = \frac{\delta}{r}$, $\bar{h} = \frac{h}{r}$.

Applying these above substitution and drop the bar's symbol, the system (2.1) becomes

$$\frac{dX}{dt} = f(X) \quad (3.1)$$

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

$$\begin{aligned}H^1 &= x\left(1 - \frac{x}{k}\right) - \frac{m_1xy}{a_1+x} \\ H^2 &= \frac{m_1xy}{a_1+x} - \frac{m_2yz}{a_2+y+bz} - \gamma y \\ H^3 &= \frac{m_2(y+bz)z}{a_2+y+bz} - \frac{m_2bz^2}{a_2+y+bz} - \delta z - hz\end{aligned}$$

$$x(0) \geq 0, y(0) \geq 0, z(0) \geq 0.$$

4 Mathematical preliminaries

4.1 Existence and Boundedness of the System

The system (2.1) can be penned as $\frac{dX}{dt} = H(X)$, where $X = [x, y, z]^T$ and $H = [H^1, H^2, H^3]^T$. If $X(0) = X_0 = (x_0, y_0, z_0) \in R_+^3 = \{(x, y, z) : x > 0, y > 0, z > 0\}$, such that $F_i(X)|_{X_i=0} \geq 0$ can be smoothly checked. As per Nagumo's lemma (Nagumo, 1942) the system (3.1) has a solution $X(t) = X(t; X_0)$ (say) in which $X(0) = X_0 \in R_+^3$ and $X(t) \in R_+^3$, for all $t > 0$. So, it can be safely stated that the system (3.1) has all the solutions in the region R_+^3 and it remain non-negative for all $t > 0$.

Theorem 1: The solution of the system (3.1) is uniformly bounded in

$$\Omega = \left\{ (x, y, z) : 0 \leq x(t) + y(t) + z(t) \leq \frac{1}{\mu} + \epsilon, \text{ for all } \epsilon > 0 \right\}.$$

Proof: We assume the function $U(t) = x(t) + y(t) + z(t)$. Now using the equations (3.1), we have

$$\begin{aligned} \frac{dU}{dt} &= \frac{dx}{dt} + \frac{dy}{dt} + \frac{dz}{dt} \\ &= x(1-x) - \gamma y - (\delta + h)z \\ &\leq 2x - x^2 - \mu U, \text{ if } \mu = \min \{1, \gamma, \delta + h\}. \end{aligned}$$

Therefore,

$$\frac{dU}{dt} + \mu U \leq 1, \text{ if } \mu = \min \{1, \gamma, \delta + h\}. \quad (4.1)$$

We can choose μ in such a way that $\mu = \min \{1, \gamma, \delta + h\}$, which indicates that

$$\frac{dU}{dt} + \mu U \leq 1$$

Now we apply the theory of differential inequality property ((Birkhoff and Rota, n.d.)) and obtain

$$0 \leq U(t) \leq \frac{1}{\mu}.$$

As $t \rightarrow \infty$, then $0 \leq U(t) \leq \frac{1}{\mu}$. Therefore, the function $U(t)$ is a bounded.

Thus for any $\epsilon > 0$ all the solutions of the system (3.1) are uniformly bounded in the region

$$\Omega = \left\{ (x, y, z) : 0 \leq x(t) + y(t) + z(t) \leq \frac{1}{\mu} + \epsilon, \text{ for all } \epsilon > 0 \right\}.$$

Hence proves the theorem.

5 Analysis of existence equilibria and their stability

The equilibrium points of the system (3.1) are:

(B₁) The trivial equilibrium point is $E_0(0, 0, 0)$.

(B₂) The prey and predator free equilibrium point is $E_1(1, 0, 0)$.

(B₃) The only predator extinction equilibrium point is $E_2\left(\lambda, \frac{(1-\lambda)\lambda}{\gamma}, 0\right)$ where $\lambda = \frac{a_1\gamma}{m_1-\gamma}$ which exists if $m_1 > \gamma$.

(B₄) The coexistence equilibrium point is $E^*(x^*, y^*, z^*)$, where $y^* = \frac{(1-x^*)(a_1+x^*)}{m_1}$, $z^* = \frac{(m_2-\delta-h)y^*-(\delta+h)a_2}{(\delta+h)b}$ and $A_0x^{*2} + A_1x^* + A_2 = 0$, $A_0 = m_2 - \delta - h + b\gamma - bm_1$, $A_1 = bm_1 + (a_1 - 1)(m_2 - \delta - h + b\gamma)$, $A_2 = (\delta + h)a_2m_1 - (m_2 - \delta - h + b\gamma)a_1$.

5.1 Local stability Analysis

At $\bar{E} = (\bar{x}, \bar{y}, \bar{z})$, the Jacobian matrix is calculated as

$$\bar{V} = \begin{bmatrix} 1 - 2\bar{x} - \frac{m_1 a_1 \bar{y}}{(a_1 + \bar{x})^2} & -\frac{m_1 \bar{x}}{a_1 + \bar{x}} & 0 \\ \frac{m_1 a_1 \bar{y}}{(a_1 + \bar{x})^2} & \frac{m_1 \bar{x}}{a_1 + \bar{x}} - \frac{m_2 \bar{z}(a_2 + b\bar{z})}{(a_2 + \bar{y} + b\bar{z})^2} - \gamma & -\frac{m_2 \bar{y}(a_2 + \bar{y})}{(a_2 + \bar{y} + b\bar{z})^2} \\ 0 & \frac{m_2 \bar{z}(a_2 + b\bar{z})}{(a_2 + \bar{y} + b\bar{z})^2} & \frac{m_2 \bar{y}(a_2 + \bar{y})}{(a_2 + \bar{y} + b\bar{z})^2} - \delta - h \end{bmatrix}. \quad (5.1)$$

Trivial equilibrium E_0 : The eigenvalues of the trivial equilibrium at E_0 evaluate from (5.1) are $1, -\gamma$ and $-\delta - h$.

Result 1. The equilibrium point $E_0(0, 0, 0)$ is unstable as one eigenvalue of the Jacobian matrix is always positive.

Prey (parrotfish) and predator (lionfish) free equilibrium E_1 : By factorizing jacobian (5.1) at E_1 gives three eigenvalues which are $-1, \frac{m_1}{a_1+1} - \gamma$ and $-\delta - h$. So, we come to the following result:

Result 2. The prey and predator free equilibrium point $E_1(1, 0, 0)$ is stable if $\lambda = \frac{a_1\gamma}{m_1-\gamma} > 1$.

Predator (lionfish) extinction equilibrium E_2 : The Jacobian matrix at $E_2(\lambda, \frac{(1-\lambda)\lambda}{\gamma}, 0)$ is represented by

$$J(E_2) = \begin{bmatrix} 1 - 2x_1 - \frac{m_1 a_1 y_1}{(a_1 + x_1)^2} & -\frac{m_1 x_1}{a_1 + x_1} & 0 \\ \frac{m_1 a_1 y_1}{(a_1 + x_1)^2} & \frac{m_1 x_1}{a_1 + x_1} - \gamma & -\frac{m_2 y_1}{(a_2 + y_1)} \\ 0 & 0 & \frac{m_2 y_1}{(a_2 + y_1)} - \delta - h \end{bmatrix},$$

where $x_1 = \lambda$ and $y_1 = \frac{\lambda(1-\lambda)}{\gamma}$. The eigenvalues are $\frac{m_2\lambda(1-\lambda)}{a_2\gamma+\lambda(1-\lambda)} - \delta - h$ and the two roots of the equation $t^2 + M_1t + M_2 = 0$, where $M_1 = -\frac{(1-2\lambda)\gamma(a_1+\lambda)^2 - m_1a_1\lambda(1-\lambda) + m_1\lambda(a_1+\lambda)\gamma}{\gamma(a_1+\lambda)^2}$ and $M_2 = \frac{m_1\lambda}{a_1+\lambda}(1-2\lambda)$.

For stability, the conditions are $\frac{m_2\lambda(1-\lambda)}{a_2\gamma+\lambda(1-\lambda)} - \delta - h < 0$ i.e. $\frac{m_2\lambda(1-\lambda)}{a_2\gamma+\lambda(1-\lambda)} < \delta + h$ and $M_1 > 0$, $M_2 > 0$ which is possible if $\lambda < \frac{1}{2}$.

Result 3. The predator extinction equilibrium point $E_2(\lambda, \frac{(1-\lambda)\lambda}{\gamma}, 0)$ stable if $\frac{m_2\lambda(1-\lambda)}{a_2\gamma+\lambda(1-\lambda)} < \delta + h$ and $\lambda < \frac{1}{2}$.

Coexistence equilibrium E^* :

Theorem 2: The coexistence equilibrium $E^*(x^*, y^*, z^*)$ of the system (3.1) is locally asymptotically stable if $\Omega_i > 0, i = 1, 2, 3$ $\Omega_1\Omega_2 - \Omega_3 > 0$, where $\Omega_1, \Omega_2, \Omega_3$ are given in the proof of the theorem.

Proof: At $E^*(x^*, y^*, z^*)$, the Jacobian matrix is calculated for the system (3.1) as

$$J(E^*) = \begin{bmatrix} v_{11} & v_{12} & 0 \\ v_{21} & v_{22} & v_{23} \\ 0 & v_{32} & v_{33} \end{bmatrix}$$

where

$$\begin{aligned} v_{11} &= 1 - 2x^* - \frac{m_1 a_1 y^*}{(a_1 + x^*)^2}, \quad v_{12} = -\frac{m_1 x^*}{a_1 + x^*} < 0, \quad v_{21} = \frac{m_1 a_1 y^*}{(a_1 + x^*)^2} > 0, \quad v_{22} = \frac{m_2 y^* z^*}{(a_2 + y^* + bz^*)^2} > 0, \\ v_{23} &= -\frac{m_2 y^* (a_2 + y^*)}{(a_2 + y^* + bz^*)^2} < 0, \quad v_{32} = \frac{m_2 z^* (a_2 + bz^*)}{(a_2 + y^* + bz^*)^2} > 0, \quad v_{33} = -\frac{m_2 by^* z^*}{(a_2 + y^* + bz^*)^2} < 0. \end{aligned}$$

The characteristic equation at $E^*(x^*, y^*, z^*)$ is defined by

$$\rho^3 + \Omega_1 \rho^2 + \Omega_2 \rho + \Omega_3 = 0, \quad (5.2)$$

where

$$\begin{aligned} \Omega_1 &= -(v_{11} + v_{22} + v_{33}), \\ \Omega_2 &= v_{11}v_{22} + v_{22}v_{33} + v_{33}v_{11} - v_{12}v_{21} - v_{23}v_{32}, \\ \Omega_3 &= v_{11}v_{23}v_{32} + v_{12}v_{21}v_{33} - v_{11}v_{22}v_{33}. \end{aligned}$$

According to Routh-Hurwitz criteria, each roots of the characteristic equation have negative real parts iff $\Omega_i > 0$, $i = 1, 2, 3$ and $\Omega_1\Omega_2 - \Omega_3 > 0$. Now $\Omega_1 > 0$ if $2x^* + \frac{m_1 a_1 y^*}{(a_1 + x^*)^2} + \frac{m_2 by^* z^*}{(a_2 + y^* + bz^*)^2} > 1 + \frac{m_2 y^* z^*}{(a_2 + y^* + bz^*)^2}$.

We already determine the sign of each v_{ij} , where $i, j=1, 2, 3$ except v_{11} . Therefore we have to analyze two cases for sign of v_{11} :

Case 1: If $v_{11} > 0$ then $\Omega_2 > 0$ if $(v_{11}v_{22} - v_{12}v_{21} - v_{23}v_{32}) > -(v_{11}v_{33} + v_{22}v_{33})$

and $\Omega_3 > 0$ if $v_{12}v_{21}v_{33} - v_{11}v_{22}v_{33} > -v_{11}v_{23}v_{32}$.

Case 2: If $v_{11} < 0$ then $\Omega_2 > 0$ if $(v_{11}v_{33} - v_{12}v_{21} - v_{23}v_{32}) > -(v_{11}v_{22} + v_{22}v_{33})$

and $\Omega_3 > 0$ if $v_{11}v_{23}v_{32} + v_{12}v_{21}v_{33} > v_{11}v_{22}v_{33}$.

Now,

$$\begin{aligned} \Omega_1\Omega_2 - \Omega_3 &= -(v_{11} + v_{22} + v_{33})(v_{11}v_{22} + v_{22}v_{33} + v_{33}v_{11} - v_{12}v_{21} - v_{23}v_{32}) \\ &\quad - (v_{11}v_{23}v_{32} + v_{12}v_{21}v_{33} - v_{11}v_{22}v_{33}) > 0, \end{aligned}$$

if $-(v_{11} + v_{22} + v_{33})(v_{11}v_{22} + v_{22}v_{33} + v_{33}v_{11} - v_{12}v_{21} - v_{23}v_{32}) > (v_{11}v_{23}v_{32} + v_{12}v_{21}v_{33} - v_{11}v_{22}v_{33})$.

Therefore E^* is locally asymptotically stable.

Theorem 3. The system (3.1) experiences a Hopf bifurcation at $r = r_c$ iff

(i) $G(r_c) = \Omega_1(r_c)\Omega_2(r_c) - \Omega_3(r_c) = 0$,

(ii) $\left[\frac{d}{dr}(\Omega_1\Omega_2 - \Omega_3)\right]_{r=r_c} \neq 0$.

Proof: Let us consider a value $r = r_c$ such that $\Omega_1(r_c)\Omega_2(r_c) - \Omega_3(r_c) = 0$. Then at $r = r_c$ the characteristic equation (5.2) becomes $(\rho + \Omega_1)(\rho^2 + \Omega_2) = 0$. Clearly the equation has three roots which are $-\Omega_1$ and $\pm\sqrt{\Omega_2}i$ i.e. one root is negative along with a pair of complex conjugate roots. To satisfy the transversality condition, let us choose any point r of ϵ -neighborhood

of r_c where $\rho_{1,2} = a(r) \pm ib(r)$. Putting this in (5.2) and separate the real and imaginary parts which show the following results:

$$a^3 - 3ab^2 + \Omega_1(a^2 - b^2) + \Omega_2a + \Omega_3 = 0 \quad (5.3)$$

$$(3a^2b - b^3) + 2\Omega_1ab + \Omega_2 = 0 \quad (5.4)$$

Since $b(r) \neq 0$, then from (5.4) we have $b^2 = 3a^2 + 2\Omega_1a + \Omega_2$.

Putting the value of b^2 in (5.2) we have

$$8a^3 + 8\Omega_1a^2 + 2a(\Omega_1^2 + \Omega_2) + \Omega_1\Omega_2 - \Omega_3 = 0. \quad (5.5)$$

Now differentiating w.r.t r at $r = r_c$ we get the following results

$$\left[\frac{da}{dr}\right]_{r=r_c} = - \left[\frac{1}{2(\Omega_1^2 + \Omega_2)} \frac{d}{dr} (\Omega_1\Omega_2 - \Omega_3) \right]_{r=r_c} \neq 0 \text{ provided } \left[\frac{d}{dr} (\Omega_1\Omega_2 - \Omega_3)\right]_{r=r_c} \neq 0.$$

5.2 Stability of bifurcating periodic solution

Next, we apply Poore's sufficient condition (Poore, 1976) to scrutinize the existence of periodic solution. We investigate the nature of Hopf bifurcation periodic solution (subcritical / supercritical) for which we calculate the sign (negative/ positive) of the real part of ϕ , where

$\phi = -a_l H_{u_j u_m u_s}^l b_j b_m \bar{b}_s + 2a_l H_{u_j u_m}^l b_j (J_{E^*}^{-1})_{mg} H_{u_p u_q}^g b_p \bar{b}_q + a_l H_{u_j u_k}^l \bar{b}_j [(J_{E^*} - 2i\omega_0)^{-1}] H_{u_p u_q}^g b_p b_q$ where the repeated indices in between each term signify a addition from 1 to 3 and each derivatives of H^l are estimated at E^* with $u_1 = x, u_2 = y, u_3 = z$. Here $[(J_{E^*})^{-1}]_{mg}$ represents the elements of $(J_{E^*})^{-1}$ with row m and g column. Here $\mathbf{a} = (a_1, a_2, a_3)$ and $\mathbf{b} = (b_1, b_2, b_3)^T$ denote the left and right normalized eigenvectors at J_{E^*} for eigenvalues $\pm i\omega_0$ at $r = r_c$ in which $\mathbf{a}\mathbf{b} = 1$. Here $\mathbf{a}$ and $\mathbf{b}$ of Jacobian matrix J_{E^*} is given by

$\mathbf{a} = \frac{\zeta_1}{H_u^2 H_v^3} (H_u^2 H_v^3, H_v^3 (i\omega_0 - H_u^1), (H_u^1 H_v^2 - \omega_0^2 - H_v^1 H_u^2) - i\omega_0 (H_u^1 + H_v^2))$ and

$\mathbf{b} = \frac{\zeta_2}{H_v^1 H_w^2} (H_v^1 H_w^2, (i\omega_0 - H_u^1) H_w^2, (H_u^1 H_v^2 - \omega_0^2 - H_v^1 H_u^2) - i\omega_0 (H_u^1 + H_v^2))^T$ where ζ_1 and ζ_2 are complex numbers. Now we determine the value $\zeta_1 \zeta_2$ by applying $\mathbf{a}\mathbf{b} = 1$. Next we determine $(J_{E^*} - 2i\omega_0)^{-1} = (Q_{\omega_0}^{ij})_{3 \times 3}$ where

$Q_{\omega_0}^{11} \Delta = (H_v^2 H_w^3 - 4\omega_0^2 - H_v^3 H_w^2) - 2i\omega_0 (H_w^3 + H_v^2)$, $Q_{\omega_0}^{12} \Delta = H_v^1 (2i\omega_0 - H_w^3)$, $Q_{\omega_0}^{13} \Delta = H_v^1 H_w^2$, $Q_{\omega_0}^{21} \Delta = H_v^2 (2i\omega_0 - H_w^3)$, $Q_{\omega_0}^{22} \Delta = (H_v^1 H_w^3 - 4\omega_0^2) - 2i\omega_0 (H_v^1 + H_w^3)$, $Q_{\omega_0}^{23} \Delta = H_w^2 (2i\omega_0 - H_v^1)$, $Q_{\omega_0}^{31} \Delta = H_u^2 H_v^3$, $Q_{\omega_0}^{32} \Delta = H_v^3 (2i\omega_0 - H_u^1)$, $Q_{\omega_0}^{33} \Delta = (H_u^1 H_v^2 - 4\omega_0^2 - H_u^2 H_v^1) - 2i\omega_0 (H_u^1 + H_v^2)$ and

$$\Delta = [H_u^1 (H_v^2 H_w^3 - H_v^3 H_w^2 - 4\omega_0^2) - 4\omega_0^2 (H_v^2 + H_w^3) - H_v^1 H_u^2 H_w^3] - 2i\omega_0 [H_u^1 (H_v^2 + H_w^3) + (H_v^2 H_w^3 - 4\omega_0^2 - H_v^3 H_w^2 - H_v^1 H_w^2 \kappa_u)].$$

Putting $\omega_0 = 0$, in the above expressions, we get the components of $(J_{E^*})^{-1} = Q_{3 \times 3}^{ij}$. Next we calculate all the second and third order derivatives of H^l , ($l = 1, 2, 3$). Finally, we estimate the value $(\phi)_{r=r_c}$. If $(\phi)_{r=r_c} > 0$, then the system (3.1) experiences supercritical Hopf-bifurcation as r increases through r_c so that a family of stable periodic solutions exist.

6 Optimal harvesting policy

Here, an optimal harvesting policy is examined in unreserved zone. We replace $h = qE$ of system (3.1). Here q represents catchability coefficient of lionfish. E be the harvesting effort

applied on lionfish. Let c and p are the cost per unit effort due to harvesting and price per unit biomass for the lionfish. We impose the Pontryagin's maximum principle and explore the optimal harvesting policy. We count the continuous time-stream function J (S. Toaha and Bahri, 2014).

$$J = \int_0^\infty \mathbf{L}(x, y, z, E, t) e^{-\delta_1 t} dt, \quad (6.1)$$

where $\mathbf{L}$ performs the net revenue which is interpreted as

$$\mathbf{L}(x, y, z, E, t) = (pqz - c)E, \quad (6.2)$$

δ_1 stands for the instantaneous annual rate of discount. Now our main aim is to maximize J subjected to the system (3.1).

Firstly, we construct the following Hamiltonian function

$$H = e^{-\delta_1 t} [(pqz - c)E] + \lambda_1 \left[x(1 - x) - \frac{m_1 xy}{a_1 + x} \right] + \lambda_2 \left[\frac{m_1 xy}{a_1 + x} - \frac{m_2 yz}{a_2 + y + bz} - \gamma y \right] + \lambda_3 \left[\frac{m_2 (y + bz)z}{a_2 + y + bz} - \frac{m_2 bz^2}{a_2 + y + bz} - \delta z - qEz \right],$$

where the three additional unknown functions λ_1 , λ_2 and λ_3 are performed as adjoint variables. Here, E acts as control variable satisfying the constraint $0 \leq E \leq (E)_{max}$ and the expression $\phi_1(t) = e^{-\delta t}(pqZ - c) - \lambda_3 qz$ is represented the switching function. Our prior aim is to demonstrated an optimal equilibrium $((x)_\delta, (y)_\delta, (z)_\delta, (E)_\delta)$ to maximize Hamiltonian H .

Since H is linear in E , i.e., the control variable. Therefore, the optimal control can be represent as the singular control. Thus we have

$E = (E)_{max}$, when $\phi_1(t) > 0$ i.e., when $\lambda_3(t)e^{\delta t} < p - \frac{c}{qz}$; $E = 0$, when $\phi_1(t) < 0$ i.e., when $\lambda_3(t)e^{\delta t} > p - \frac{c}{qz}$;
when $\phi_1(t) = 0$, $\lambda_3(t)e^{\delta t} = p - \frac{c}{qz}$ or

$$\frac{\partial H}{\partial E_1} = 0, \quad (6.3)$$

In this scenario, the optimal control can be referred as the singular control, and maximization of Hamiltonian H occurs when it fulfills the necessary conditions (6.3). As per Pontryagin's maximal principle, the equation stands as

$$\frac{d\lambda_1}{dt} = -\frac{\partial H}{\partial x} = -\left[\lambda_1 \left\{ (1 - 2x) - \frac{m_1 a_1 y}{(a_1 + x)^2} \right\} + \lambda_2 \frac{m_1 a_1 y}{(a_1 + x)^2} \right], \quad (6.4)$$

$$\frac{d\lambda_2}{dt} = -\frac{\partial H}{\partial y} = -\left[-\lambda_1 \frac{m_1 x}{a_1 + x} + \lambda_2 \left(\frac{m_1 x}{a_1 + x} - \frac{m_2 z(a_2 + bz)}{(a_2 + y + bz)^2} - \gamma \right) + \lambda_3 \frac{m_2 z(a_2 + y)}{(a_2 + y + bz)^2} \right], \quad (6.5)$$

$$\frac{d\lambda_3}{dt} = -\frac{\partial H}{\partial Z} = -[e^{-\delta_1 t} pqE + \lambda_2 \frac{m_2 (a_2 + y)y}{(a_2 + y + bz)^2} + \lambda_3 \{ \frac{m_2 (a_2 + y)y}{(a_2 + y + bz)^2} - \delta - qE \}]. \quad (6.6)$$

Based on coexistence equilibrium $E^*(x^*, y^*, z^*)$ and substituting λ_3 from (6.3) in (6.6) we get

$$\lambda_2 = \frac{e^{-\delta_1 t} [\delta_1 (p - \frac{c}{qz^*}) - pqE - (p - \frac{c}{qz^*}) \frac{m_2 by^* z^*}{(a_2 + y^* + bz^*)^2}]}{\frac{m_2 (a_2 + y^*) y^*}{(a_2 + y^* + bz^*)^2}} = e^{-\delta_1 t} A_1, \quad (6.7)$$

Here A_1 is defined by $A_1 = [\delta_1 (p - \frac{c}{qz^*}) - pqE - (p - \frac{c}{qz^*}) \frac{m_2 by^* z^*}{(a_2 + y^* + bz^*)^2}] \frac{m_2 (a_2 + y^*) y^*}{(a_2 + y^* + bz^*)^2}$,

Now using (6.3), (6.7) in (6.4) we get

$$\frac{d\lambda_1}{dt} - \lambda_1 A_2 = -A_3 e^{-\delta_1 t}$$

where $A_2 = \frac{m_1 a_1 y^*}{(a_1 + x^*)^2} - (1 - 2x^*)$, $A_3 = \frac{m_1 a_1 y^* A_1}{(a_1 + x^*)^2}$.

We figure out that

$$\lambda_1 = \frac{A_3}{A_2 + \delta_1} e^{-\delta_1 t}. \quad (6.8)$$

Similarly, based on coexistence equilibrium $E^*(x^*, y^*, z^*)$ and substituting λ_1 and λ_2 from (6.7), (6.8) in (6.6) we get

$$\frac{d\lambda_3}{dt} - A_5 \lambda_3 = -A_6 e^{-\delta_1 t}$$

where $A_5 = \frac{m_2 by^* z^*}{(a_2 + y^* + bz^*)^2}$ and $A_6 = pqE - A_1 \frac{m_2 (a_2 + y^*) y^*}{(a_2 + y^* + bz^*)^2}$. We figure out that

$$\lambda_3 = \frac{A_6}{A_5 + \delta_1} e^{-\delta_1 t}. \quad (6.9)$$

It is obviously that $\lambda_1(t)$, $\lambda_2(t)$ and $\lambda_3(t)$ are bounded as $t \rightarrow \infty$.

Substitute (6.3) and (6.9) we subsist a singular path

$$p - \frac{c}{qz^*} = \frac{A_6}{A_5 + \delta_1}. \quad (6.10)$$

Using x^* , y^* and z^* , the value of A_1 , A_2 , A_3 , A_4 , A_5 and A_6 can be determined. Thus from (6.10), it express as

$$G_1(z^*) = \left(p - \frac{c}{qz^*} \right) - \frac{A_6}{A_5 + \delta_1}.$$

There exists a unique positive root $z^* = (z^*)_\delta$ of $G_1(z^*) = 0$ in the interval $0 < z^* < \theta$ if the following hold $G_1(0) < 0$, $G_1(\theta) > 0$, $G_1'(z^*) > 0$ for $z^* > 0$. Thus, we get $x^* = (x^*)_\delta$, $y^* = (y^*)_\delta$, $z^* = (z^*)_\delta$,

$$(E)_\delta = \frac{1}{q} \left[\frac{m_2 y^*}{a_2 + y^* + bz^*} - \delta \right].$$

The optimal harvesting effort $(E)_\delta$ is computed after computing the optimal equilibrium, $((x)_\delta, (y)_\delta, (z)_\delta)$. Hence if the optimal equilibrium, $((x)_\delta, (y)_\delta, (z)_\delta)$ is determined, then the optimal harvesting effort $(E)_\delta$, can also be determined. As per (6.3), (6.7), (6.8) and (6.9), we get $\lambda_i(t)$ where $i = 1, 2, 3$ which are constant with time at optimal equilibrium. Therefore, they still remain bounded when $t \rightarrow \infty$.

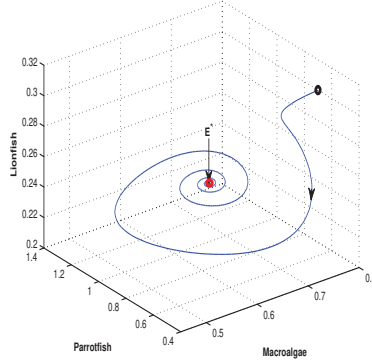


Figure 1: Phase plane diagrams depicting local stability at E^* .

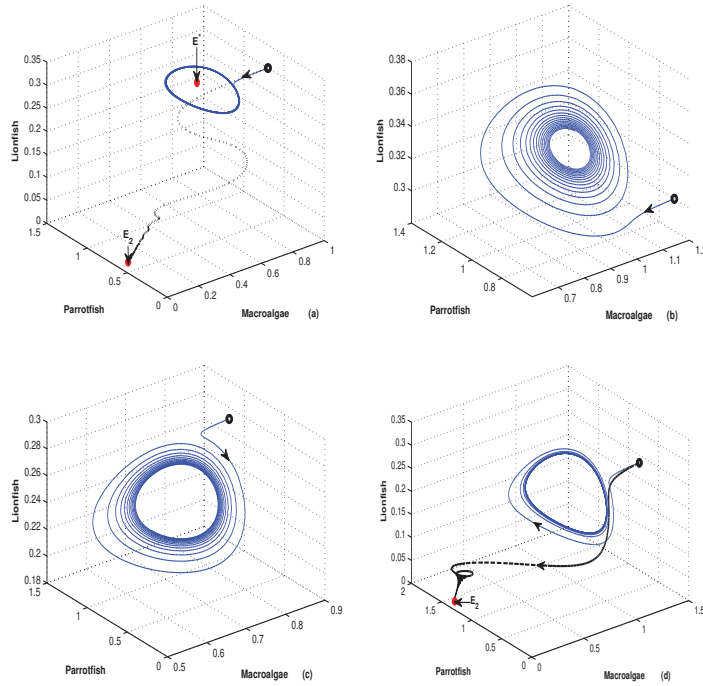
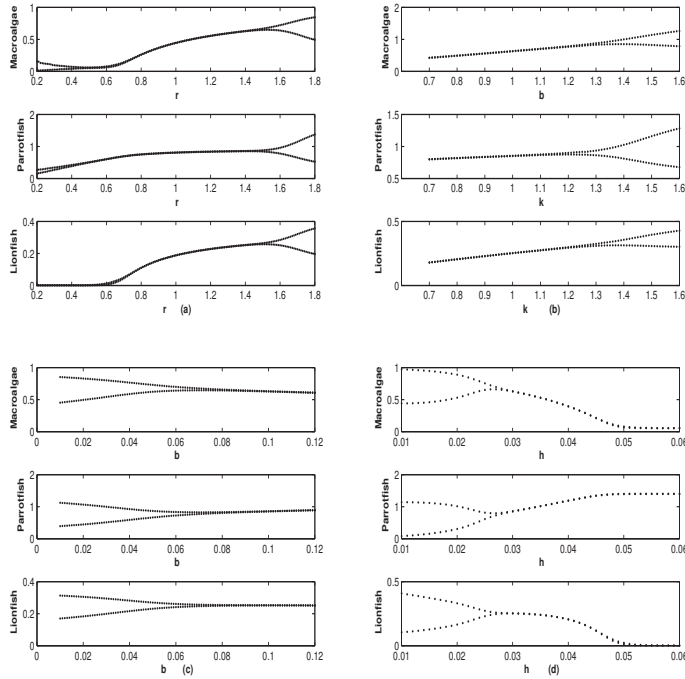


Figure 2: **(a)** Solution of system (2.1) for $r = 1.7$ (blue line) and 0.6 (black dot). **(b)** Solution of system (2.1) for $k = 1.4$. **(c)** Solution of system (2.1) for $b = 0.04$. **(d)** Solution of system (2.1) for $h = 0.03$.

7 Numerical simulations

We illustrate some numerical simulation to explore the dynamic nature of the system (2.1). We fix a set of parametric values (Jang, 2002)

$$\begin{aligned} r &= 1.4, \quad k = 1, \quad a_1 = 1, \quad a_2 = 1, \quad \delta = 0.01, \quad m_1 = 1, \\ m_2 &= 0.5, \quad b = 0.1, \quad \alpha = 0.2, \quad \beta = 0.2, \quad \gamma = 0.01, \quad h = 0.03. \end{aligned} \quad (7.1)$$


 Figure 3: (a-d) Bifurcation diagram for r , k , b and h respectively.

and note that $E^* = (0.63, 0.85, 0.25)$ is persist and asymptotically stable (cf. Fig. 1). Now we vary the different parametric values to demonstrate the dynamic behavior of the system. Taking $r = 1.7$, we see that each species start oscillate around $E^* = (0.75, 0.74, 0.30)$. But in case of $r = 0.6$, the coexistence equilibrium switches to predator free equilibrium $E_2 = (0.06, 0.60, 0)$ (cf. Fig. 2(a)). From Fig. 2(b) illustrate that the system (2.1) shifts to oscillatory behaviour around $E^* = (0.97, 0.84, 0.34)$ for high value of carrying capacity of macro-algae ($k = 1.4$). Similar situation arises due to low value of intensity of intratrophic predation of predator, $b = 0.04$ (cf. Fig. 2(c)). Further from Fig. 2(d), it follows that low harvesting rate of predator (viz. $h = .02$) for which the (2.1) switches to oscillatory behavior around $E^* = (0.59, 0.94, 0.20)$. To continue further, when $h = 0.05$ it is pointed out that the system again shifts to $E_2 = (0.06, 1.39, 0)$ (cf. Fig. 2(d)). Now taking r as free parameter, then we see the different steady state behavior of each species (cf. Fig. 4(a-c)). Here we have a Hopf point (H) at $r = 1.648780$ with first Lyapunov coefficient $-5.126493e^{-02}$ indicating stable limit cycle bifurcate from Hopf point. It's indicate that a super critical bifurcation generate at that point. Here a branch point is located at $r = 0.668519$ which connects to transcritical bifurcation. To continue further, a family stable limit cycle generate from H point (cf. Fig. 4(d)). From Fig. 5(a-c) it follows different stability behavior for free parameter k . At $k = 1.416971$, the Hopf point indicates the super critical bifurcation with first Lyapunov coefficient $-7.782603e^{-02}$ and predator becomes extinct at $k = 0.096110$. Fig. 5(d) depicts a family of stable limit cycles and generates period-doubling bifurcation (PD) at $k = 2.223950$ with period $1.221487e^{+02}$. When

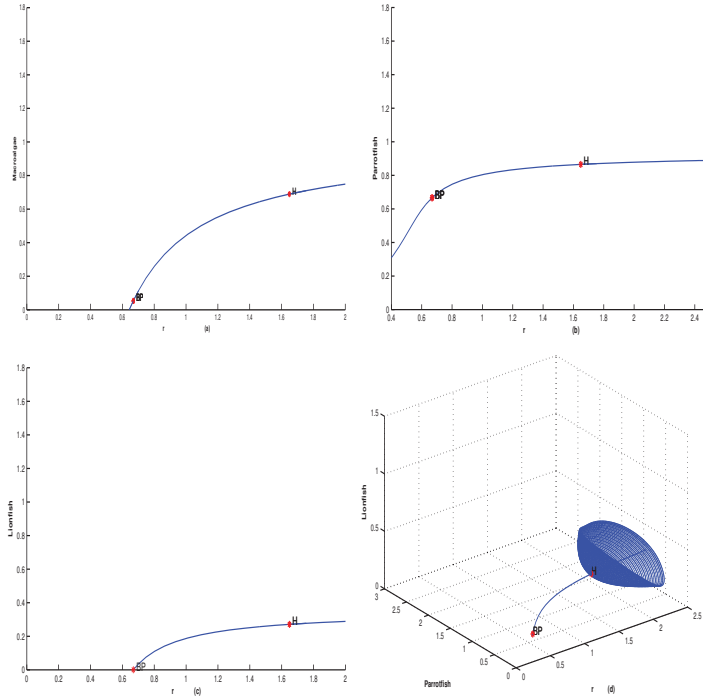


Figure 4: **(a-c)** Various steady state behavior of macro-algae, parrotfish and lionfish population respectively for the impact of r . **(d)** The family of limit cycles bifurcating from the Hopf point H for r .

we vary b as a free parameter, Fig. 6(a-c) shows system (2.1) experiences a hopf bifurcation at $b = 0.044293$ and produce a stable limit cycle (Fig. 6(d)). Next, we consider h as a free parameter. In such case, we have a Hopf point at $h = 0.024163$, a Branch point at $h = 0.048266$ (cf. Fig. 7(a-c)) and the stable limit cycle (cf. Fig. 7(d)).

In order to clear picture of dynamical change, we plot four bifurcation diagrams for r , k , b and h respectively (cf. Fig. 3(a-d)). Finally we plot two parameters bifurcation diagrams for $r - k$, $r - h$, $k - b$, and $k - h$ (cf. Fig. 8(a-d)). Here we see Generalized Hopf (GH), Zero Hopf (ZH) and Branch Point (BP). Summarizing the evaluations, we display the natures of equilibrium points in Table 1.

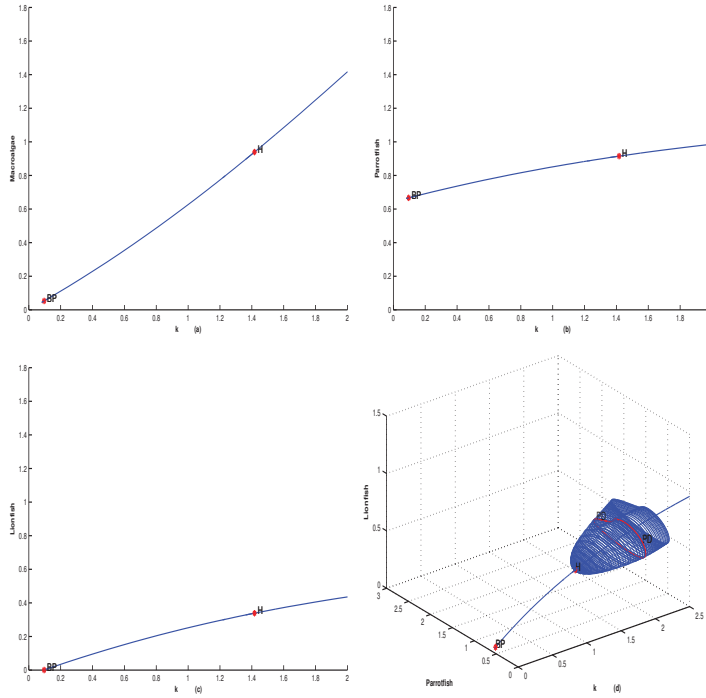


Figure 5: **(a-c)** Various steady state behavior of macro-algae, parrotfish and lionfish population under the influence of k respectively. **(d)** The family of limit cycles bifurcating from the Hopf point H for k .

8 Conclusion

In this paper, a macro algae-parrotfish-lionfish interaction model is developed. It is assume that several lionfish species combine into a single population and some time they feed other lionfish species. Here we fit in a linear harvesting form for lionfish species. Our model system indicates that when intensity of intratrophic predation is zero then no interspecies competition involve and it look likes a simple prey predator system with Holling II response function. Therefore intensity of intratrophic predation and rate of harvesting play significant role to maintain the ecological balance. Firstly, we derive some analytical conditions for existence and stability of various steady state. Further we analyze the optimal harvesting policy for lionfish by implementing Pontryagin's maximum principle. We note the following observations by numerical simulation:

- (i) The system becomes oscillatory around coexistence equilibrium E^* due to high intrinsic growth rate (r). But if r is low then the lionfish will not sustain in the system. Numerically we check that if $0.668519 < r < 1.648780$, then each species will persist in the system.
- (ii) The system becomes lionfish free equilibrium if the carrying capacity (k) of macroalgae is very low. But all the species become oscillate for high values of k . Numerically prove that the system may coexists during the range $0.096110 < k < 1.416971$.

Table 1: Natures of equilibrium points.

Parameters	Values	Eigenvalues	Equilibrium points
r	1.648780	$(-0.900996, \pm 0.442049i)$	Hopf (H)
	0.668519	$(0, -0.00175926 \pm 0.0775472i)$	Branch Point (BP)
k	1.416971	$(-0.666554, \pm 0.049673i)$	Hopf (H)
	0.096110	$(0, -0.726721, -0.0082792)$	Branch Point(BP)
b	0.044293	$(-0.747651, \pm 0.0431506i)$	Hopf (H)
h	0.024163	$((-0.811597, \pm 0.0438123i)$	Hopf (H)
	0.048266	$(0, -0.00368421 \pm 0.112189)$	Branch Point (BP)
(r, k)	(0.648093, 4.945421)	$(-0.075863, \pm 0.0863778i)$	Generalized Hopf (GH)
	(0.727356, 1.376905)	$(-0.0030537, \pm 0.140218i)$	Generalized Hopf (GH)
(k, b)	(7.493496, 0.257077)	$(-0.134019, \pm 0.094447i)$	Generalized Hopf (GH)
(k, h)	(6.955313, 0.051803)	$(-0.0891279, \pm 0.935177i)$	Generalized Hopf (GH)
	(1.468028, 0.046055)	$(-0.00349156, \pm 0.198258i)$	Generalized Hopf (GH)
	(1.105261, 0.048394)	$(0, \pm 0.11254i)$	Zero Hopf (ZH)

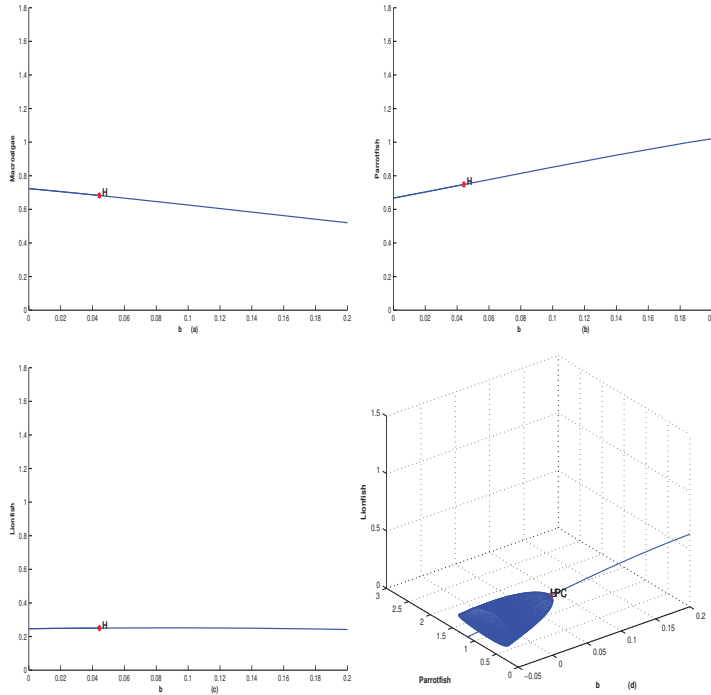


Figure 6: **(a-c)** Various steady state behavior of macro-algae, parrotfish and lionfish population under the influence of b respectively. **(d)** The family of limit cycles bifurcating from the Hopf point H for b .

(iii) All the species become oscillate for low intensity of intratrophic predation rate which indicates that intraspecies competition play a major role to stabilize the system.

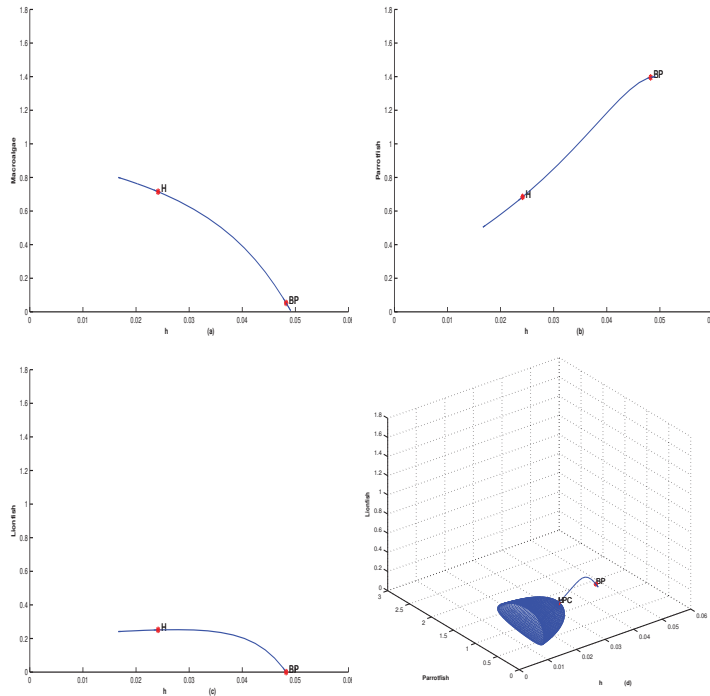


Figure 7: **(a-c)** Various steady state behavior of macro-algae, parrotfish and lionfish population under influence of h respectively. **(d)** The family of limit cycles bifurcating from the Hopf point H for h .

(iv) All species undergo oscillate for high harvesting rate of lionfish. Further if we increase the harvesting rate, the system stabilizes at lionfish free equilibrium. Clearly harvesting play a major role to maintain the ecosystem. Entire the analytical and numerical investigation, a challenge is taken to find for a suitable process to maintain stability of each species.

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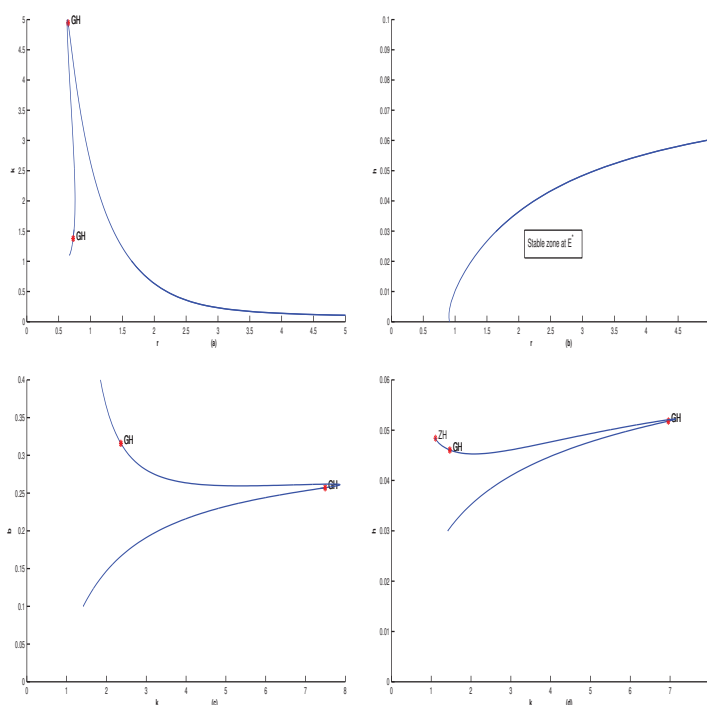


Figure 8: (a-d) The two parameters bifurcation diagram under the influence of $r - k$, $r - h$, $k - b$ and $k - h$ respectively.

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