

DYNAMICS OF AN EXPLOITED PREY-PREDATOR SYSTEM WITH NON-MONOTONIC FUNCTIONAL RESPONSE

T. K. KAR¹, S. K. CHATTOPADHYAY², AND R. P. AGARWAL³

¹Department of Mathematics, Bengal Engineering & Science University, Shibpu,
Howrah-711103, West Bengal, India
E-mail: t_k_karyahoo.com

²Department of Mathematics, Sree Chaityanya College Habra, 24 PGs (North)
West Bengal, India

³Department of Mathematics, Florida Institute of Technology
Melbourne, FL 32901 USA

ABSTRACT. A prey-predator model with non-monotonic functional response and harvesting of either species is considered. The purpose of the work is to offer mathematical analysis of the model and to discuss some significant qualitative results. At the end, some numerical simulations are carried out.

Key words: Prey-predator, global stability, bifurcation, limit-cycle.

AMS (MOS) Subject Classification: 34C05, 34D23, 92D25.

1. INTRODUCTION

Extinction of biological species is an important concern of the current age. Extinction is likely whenever a renewable resource is harvested persistently at a rate exceeding the level required to sustain its current stock. Depending on the nature of the applied harvesting strategy, the long run stationary density of the population may be significantly smaller than the long run stationary density of a population in the absence of harvesting. If a population is subjected to positive extinction rate then harvesting can drive the population density to a dangerously low level at which extinction becomes sure no matter how the harvester affects the population afterwards.

In particular predation is believed to play a major role in the community structure of marine fish; for example, in the north-west Atlantic the importance of predation by spiny dogfish in structuring the Georges Bank fish community is becoming increasingly recognized. Thus harvesting may affect entire communities via species interactions, although the models currently being used for management purposes are

predominantly single species approaches. Hannesson (1982), Clark (1990) and Strobele and Wacker (1995) analyze some economic aspects of a predator-prey system. Imeson et al. (2002) derived two symmetric Golden Rules from a prey-predator system and showed that, the cost decrease in prey harvesting when extra predators are fished. As the prey are less eaten so the prey stock size increases, which in turn makes fishing less costly. Conversely, fishing more prey causes predators to starve, resulting in a lower stock size and an increase in the cost of fishing. Kar (2005) considered a prey-predator model with stage-structure for predator and shown that, if the unharvested system is permanent, then a sufficiently small harvesting rate will not change drastically the qualitative behaviour of the system but region of coexistence shrinks as the harvesting rate increases. Recently, Kar and Matsuda (2006) considered a harvesting of mature predator species in a prey-predator model. They have also discussed the effects of bycatch of the immature species.

Schooling fish species like anchovy, sardine, herring, etc. move in groups forming closely packed, compact formations known as schools of fish. The advantages of schooling lie in navigation, food searching, mating, breeding, training of young mates and protection against predators. In the opinion of biologists, no advantage of schooling is as important as protection against predators. Because of this group defense, the first species develop as a dispensatory growth process which may lead to critical dispensation if it is heavily exploited. Thus heavy exploitation of schooling fish species sometimes leads to sudden population crashes that may not be followed by recoveries even if exploitation is severely reduced. This is actually what happened to many of the schooling fish species throughout the world.

The purpose of the work is to illustrate the use of harvesting efforts as control to obtain strategies for the control of a prey-predator system with non-monotonic functional response. Recent years have seen the overexploitation and collapse of several biological resources. This is due to unconventional and indiscrete harvesting of the resources. Consequently, there is much current concern to find principles for the control and management of multispecies fisheries. For a perfect model we would need to consider so many factors, namely growth rate, death rate, carrying capacity, stage structure, predation rate, stochasticity etc. But it is obvious that a perfect model cannot be achieved even if we could include all the above factors in a model, the model could never predict ecological catastrophes. So it is best to look for analyzable model that describes the reality.

An issue of particular importance is how the predators respond to changes in prey availability (functional response). It is necessary to mention that the types of functional response greatly affect model predictions (Gao et al. 2000; Steele and Hendesson, 1992). Holling (1965) described three types of functional response and some persons (Haldane, 1930; Crawley, 1992; Andrewk, 1968; and Yane, 1969) used

another type of functional response called Holling type-IV. A type-IV functional response introduced by Haldane (1930) in enzymology was

$$\Phi(n) = \frac{mn}{a + bn + cn^2} \quad (1.1)$$

which was later on used by Andrew (1968), Yane (1969) as substrate uptake function. Colling (1997) also used this functional response in a mite prey-predator interaction model and called it a Holling type-IV function.

In this paper we shall use this functional response (1.1) to model group defense. This response function (1.1) satisfies the following properties together with its non-monotonocity behaviour,

$$\Phi(0) = 0, \Phi(n) > 0 \quad \text{for all } n > 0$$

and

$$\begin{aligned} \Phi'(n) &= \frac{m(a - cn^2)}{(a + bn + cn^2)^2} > 0 \quad \text{for } 0 < n < \sqrt{a/c} \\ &< 0 \quad \text{for } n > \sqrt{a/c}. \end{aligned} \quad (1.2)$$

We shall introduce this functional response in Rosenzweing-Mac Arthur system in a prey-predator model together with independent harvest efforts. We first propose the following prey-predator model

$$\frac{dn}{dT} = rn \left(1 - \frac{n}{k}\right) - \frac{mnp}{a + bn + cn^2} \quad (1.3)$$

$$\frac{dp}{dT} = \mu \frac{mnp}{a + bn + cn^2} - lp \quad (1.4)$$

in which n, p are the numbers of prey, predators respectively in time T . We assume that in absence of predator the prey grows logistically with intrinsic growth rate r and carrying capacity k . The predator possesses a constant per capita mortality rate l , consumes the prey with functional response (1.1) and converts the consumed prey into new predators with efficiency μ . Here n, p are positive variables and r, k, μ, a, b, c, m, l are all positive constants. The constant 'm' represents a measure of maximum per capita predation rate, 'a' measure of half-saturation constant and 'c' is an inverse measure of predators immunity from the prey. As c increases predators foraging efficiency decreases.

For simplicity we reduce the number of parameters by introducing the dimensionless variables, as

$$x = \frac{bn}{a}, \quad y = \frac{mp}{ar}, \quad t = rT \quad (1.5)$$

so that the equations (1.3) and (1.4) reduce to

$$\frac{dx}{dt} = x \left(1 - \frac{x}{bk/a}\right) - \frac{xy}{1 + x + x^2/\frac{b^2}{ac}}, \quad (1.6)$$

$$\frac{dy}{dt} = \frac{m\mu}{rb} \frac{xy}{1 + x + \frac{x^2}{\frac{b^2}{ac}}} - \frac{l}{r}y. \quad (1.7)$$

Again we introduce the following transformation of parameters,

$$\alpha = \frac{b^2}{ac}, \quad \beta = \frac{m\mu}{bl}, \quad \delta = \frac{l}{r}, \quad \gamma = \frac{bk}{a}, \quad (1.8)$$

so that the equation (1.6) and (1.7) become

$$\frac{dx}{dt} = x(1 - x/\gamma) - \frac{xy}{1 + x + \frac{x^2}{\alpha}} \quad (1.9)$$

$$\frac{dy}{dt} = \frac{\beta\delta xy}{1 + x + \frac{x^2}{\alpha}} - \delta y. \quad (1.10)$$

We notice that the parameter α is directly proportional to the predators immunity and γ is proportional to the carrying capacity. Now, we introduce scaled harvesting efforts E_1 and E_2 for prey and predator species respectively so that the dynamics of our model is governed by the equations

$$\frac{dx}{dt} = x(1 - x/\gamma) - \frac{xy}{\frac{x^2}{\alpha} + x + 1} - E_1x, \quad (1.11)$$

$$\frac{dy}{dt} = \frac{\beta\delta xy}{\frac{x^2}{\alpha} + x + 1} - \delta y - E_2y. \quad (1.12)$$

In the present paper we discuss the equilibrium analysis, stability and instability analysis of the system in the sense of local and global considering the harvesting efforts E_1, E_2 as our control parameters. Other natural parameters of the system will be kept fixed for structural qualitative analysis. Kot (2001) discussed the model without the harvesting efforts and considered the predators immunity and carrying capacity as control parameters.

This paper is organized as follows. Equilibrium of the system is analyzed in section 2. We study the local stability analysis in section 3. The global stability analysis is considered in the section 4. Bifurcation analysis with numerical examples are considered in section 5. The paper ends with a brief conclusion in section 6.

2. EQUILIBRIA OF THE SYSTEM

If we take

$$f(x) = \frac{x}{\frac{x^2}{\alpha} + x + 1}, \quad g(x) = \left(\frac{x^2}{\alpha} + x + 1 \right) \left(1 - E_1 - \frac{x}{\gamma} \right),$$

$$h(x) = \beta f(x) - (1 + E_2/\delta) \quad (2.1)$$

then the equations (1.11) and (1.12) governing our model become

$$\frac{dx}{dt} = f(x)[g(x) - y], \quad (2.2)$$

$$\frac{dy}{dt} = \delta h(x)y. \quad (2.3)$$

The prey-zero growth lines are obtained from $\frac{dx}{dt} = 0$ and are $f(x) = 0$, $y = g(x)$ that is $x = 0$ (y -axis) and the curve $y = g(x)$. The curve $y = g(x)$ passes through the points $(0, 1 - E_1)$ and $((1 - E_1)\gamma, 0)$. We see that $g'(x) = \left(\frac{2x}{\alpha} + 1\right) \left(1 - E_1 - \frac{x}{\gamma}\right) - \frac{1}{\gamma} \left(\frac{x^2}{\alpha} + x + 1\right)$. $\therefore g'(0) = 1 - E_1 - \frac{1}{\gamma}$ and

$$g'((1 - E_1)\gamma) = -\frac{1}{\gamma} \left[\frac{(1 - E_1)^2 \gamma^2}{\alpha} + (1 - E_1)\gamma + 1 \right].$$

Thus, if $(1 - E_1)\gamma > 1$, then $g'(0) > 0$ and $g'((1 - E_1)\gamma) < 0$, so $g(x)$ has a local maximum between $x = 0$ and $x = (1 - E_1)\gamma$. The predators zero growth lines are obtained from $\frac{dy}{dt} = 0$ that is $\delta y h(x) = 0$ and so they are $y = 0$ (x -axis) and $h(x) = 0$. Thus the isoclines other than x -axis are the zeros of $h(x)$ or at the points where $f(x) = (\delta + E_2)/\beta\delta$. That is at the points where

$$\frac{\beta\delta}{\delta + E_2} x = \frac{x^2}{\alpha} + x + 1$$

or,

$$\frac{x^2}{\alpha} + \left(1 - \frac{\beta\delta}{\delta + E_2}\right)x + 1 = 0. \quad (2.4)$$

Thus if, $\left(1 - \frac{\beta\delta}{\delta + E_2}\right)^2 > \frac{4}{\alpha}$ or if,

$$\frac{\beta\delta}{\delta + E_2} < \left(1 - \frac{2}{\sqrt{\alpha}}\right) \text{ or } > \left(1 + \frac{2}{\sqrt{\alpha}}\right) \quad (2.5)$$

$h(x)$ has real zeros. But for positive zeros of $h(x)$ we need

$$\frac{\beta\delta}{\delta + E_2} > 1 \quad (2.6)$$

Thus (2.5) and (2.6), in combination, show that $h(x) = 0$ has two positive real roots if

$$\frac{\beta\delta}{\delta + E_2} > \left(1 + \frac{2}{\sqrt{\alpha}}\right)$$

i.e.,

$$E_2 < \delta \left[\frac{\beta}{1 + 2/\sqrt{\alpha}} - 1 \right] \quad (2.7)$$

and then the roots of $h(x) = 0$ are

$$x_1, x_2 = \frac{\alpha}{2} \left[\left(\frac{\beta\delta}{\delta + E_2} - 1 \right) \mp \sqrt{\left(\frac{\beta\delta}{\delta + E_2} - 1 \right)^2 - \frac{4}{\alpha}} \right]. \quad (2.8)$$

Thus the three predators zero growth lines are $y = 0$, $x = x_1$, $x = x_2$. Now,

$$\begin{aligned} h(x) &= \beta f(x) - \left(1 + \frac{E_2}{\delta}\right) \\ &= -\frac{(E_2 + \delta)}{\delta \left(\frac{x^2}{\alpha} + x + 1\right)} \left[\frac{x^2}{\alpha} + \left(1 - \frac{\beta\delta}{\delta + E_2}\right)x + 1 \right] \end{aligned} \quad (2.9)$$

Thus if, $E_2 < \delta \left[\frac{\beta}{1+2/\sqrt{\alpha}} - 1 \right]$ then $h(x) > 0$ between its roots and if $\left(1 - \frac{\beta\delta}{\delta+E_2}\right)^2 < \frac{4}{\alpha}$ or if,

$$\delta \left(\frac{\beta}{1+2/\sqrt{\alpha}} - 1 \right) < E_2 < \delta \left(\frac{\beta}{1-2/\sqrt{\alpha}} - 1 \right) \quad (2.10)$$

then $h(x) < 0 \forall x \geq 0$.

Thus for $E_2 < \delta \left(\frac{\beta}{1+2/\sqrt{\alpha}} - 1 \right)$ we see that

$$h(x) = \begin{cases} > 0 & \text{for } x_1 < x < x_2 \\ < 0 & \text{for } 0 < x_1, \quad x > x_2. \end{cases}$$

That is,

$$h(x_1) > 0 \text{ and } h(x_2) < 0 \quad (2.11)$$

The equilibria of the system are the points of intersection of prey and predators zero growth isoclines. The equalitaria of the system are listed below:

Equilibria	Coordinates	Condition for existence
P_0	(0,0)	–
P_1	$((1 - E_1)\gamma, 0)$	$E_1 < 1$
P_2	(x_1, y_1)	$E_2 < \delta \left(\frac{\beta}{1+2/\sqrt{\alpha}} - 1 \right)$ $E_1 < (1 - x_1/\gamma)$
P_3	(x_2, y_2)	$E_2 < \delta \left(\frac{\beta}{1+2/\sqrt{\alpha}} - 1 \right)$ $E_1 < (1 - x_2/\gamma)$

Table 2.1

We see that at P_0 both the species are extinct, at P_1 the predator is extinct and at P_2, P_3 both the species co-exist. Moreover we see that the existence of P_3 implies the existence of all equilibrium points.

3. STABILITY ANALYSIS

The Jacobian for the system of equations (2.2) and (2.3) is given by

$$J(x, y) = \begin{bmatrix} f'(x)(g(x) - y) + f(x)g'(x) & -f(x) \\ \delta h'(x)y & \delta h(x) \end{bmatrix} \quad (3.1)$$

At $P_0(0, 0)$ the corresponding community matrix is

$$J(0, 0) = \begin{bmatrix} 1 - E_1 & 0 \\ 0 & -(\delta + E_2)/\delta \end{bmatrix} \quad (3.2)$$

where eigenvalues are $\lambda_1^0 = 1 - E_1$, $\lambda_2^0 = -(\delta + E_2)/\delta$. Thus $P_0(0, 0)$ is a stable equilibrium if $E_1 > 1$ and an unstable equilibrium if $E_1 < 1$. At $P_1((1 - E_1)\delta, 0)$ the

matrix in (3.1) becomes

$$J((1 - E_1)\gamma, 0) = \begin{bmatrix} -(1 - E_1) & f((1 - E_1)\gamma) \\ 0 & \delta h((1 - E_1)\gamma) \end{bmatrix} \quad (3.3)$$

This matrix has the eigenvalues $\lambda_1^1 = -(1 - E_1)$ and $\lambda_2^1 = \delta h((1 - E_1)\gamma)$. Now, $\lambda_2^1 < 0$ if $\delta \left(\frac{\beta}{1+2/\sqrt{\alpha}} - 1 \right) < E_2 < \delta \left(\frac{\beta}{1-2/\sqrt{\alpha}} - 1 \right)$ and so P_1 is stable node if this condition holds good and $E_1 < 1$. Again P_1 becomes an unstable node if $E_2 < \delta \left(\frac{\beta}{1+2/\sqrt{\alpha}} - 1 \right)$ and $x_1 < (1 - E_1)\gamma < x_2$, P_1 returns to being a stable node for $E_2 < \delta \left(\frac{\beta}{1+2/\sqrt{\alpha}} - 1 \right)$ and either $0 < (1 - E_1)\gamma < x_1$ or $(1 - E_1)\gamma > x_2$.

At the point P_2 the community matrix becomes

$$J(x_1, g(x_1)) = \begin{bmatrix} \frac{\delta + E_2}{\beta\delta} g'(x_1) & -(\delta + E_2)/\beta\delta \\ \delta h'(x_1)g(x_1) & 0 \end{bmatrix} \quad (3.4)$$

The characteristic equation is

$$\lambda^2 - \frac{\delta + E_2}{\beta\delta} g'(x_1)\lambda + \frac{\delta + E_2}{\beta} h'(x_1)g(x_1) = 0. \quad (3.5)$$

Now $h'(x_1) > 0$ and $g(x_1) > 0$ for $(1 - E_1)\lambda > x_1$, which we assume for existence of P_2 . Thus by Descartes' rule of signs P_2 is a node or a focus or a centre. By Routh-Hurwitz condition the equilibrium P_2 is asymptotically stable if $g'(x_1) < 0$ and is unstable if $g'(x_1) > 0$. A limit cycle is expected close to the curve $h'(x_1) = 0$. Here we introduced two remarks.

Remark 1. It is easy to check that $g'(x_1) = 0$ implies $E_1 = \Phi(E_2)$, $g'(x_1) > 0$ implies $E_1 < \Phi(E_2)$ and $g'(x_1) < 0$ implies $E_1 > \Phi(E_2)$ where

$$\Phi(E_2) = \frac{(2 + \gamma) - \left[\frac{\beta\delta}{\delta + E_2} - 1 - \sqrt{\left(\frac{\beta\delta}{\delta + E_2} - 1 \right)^2 - \frac{4}{\alpha}} \right] \left[\frac{3\alpha}{2} \left(\frac{\beta\delta}{\delta + E_2} - 1 \right) - (\gamma - \alpha) \right]}{\gamma \left[\frac{\beta\delta}{\delta + E_2} - \sqrt{\left(\frac{\beta\delta}{\delta + E_2} - 1 \right)^2 - \frac{4}{\alpha}} \right]} \quad (3.6)$$

Remark 2. It is clear that if $E_1 > \Phi(E_2)$ then P_2 is locally asymptotically stable. Now if the value of E_1 be such that $E_1 > \Phi(E_2)$ then P_2 is unstable in the positive quadrant of x_1x_2 -plane. For $E_1 = \Phi(E_2)$, $g'(x_1) = 0$ and hence the roots of the characteristic equation (3.5) becomes purely imaginary and they are conjugate to each other. Also we have

$$\frac{d}{dE_1} [\text{trace } J]_{E_1 = \Phi(E_2)} = - \left(\frac{2x_1}{\alpha} + 1 \right) \frac{\delta + E_2}{\beta\delta} \neq 0.$$

Hence by Hopf bifurcation theorem [Hassard *et. al.*, 1981] the system (2.2), (2.3) enters into a Hopf type small amplitude periodic oscillation at the parametric value

$E_1 = \Phi(E_2)$, near the positive interior equilibrium point P_2 . Taking back our attention to the discussion about stability analysis, we see that the characteristic equation at the point P_3 of the community matrix of our system is

$$\lambda^2 - \frac{\delta + E_2}{\beta\delta} g'(x_2)\lambda + \frac{\delta + E_2}{\beta} h'(x_2)g(x_2) = 0 \quad (3.7)$$

As we have discussed earlier that $h'(x_2) < 0$ and $g(x_2) > 0$ for existence of P_3 . Thus by Descartes' rule of signs the roots of (3.7) are both real and of opposite signs. Hence P_3 is an unstable saddle point whatever the signs of $g'(x_1)$ may be. The following table shows the condition for stability and unstability of the system at different points of equilibrium.

Points Equilibrium	Conditions	Nature
$P_0(0, 0)$	$E_1 > 1$	Stable
	$E_1 > 1$	Unstable
$P_1((1 - E_1)\gamma, 0)$	$\delta \left(\frac{\beta}{1+2/\sqrt{\alpha}} - 1 \right) < E_2 < \delta \left(\frac{\beta}{1-2/\sqrt{\alpha}} - 1 \right)$ and $E_1 < 1$	Stable
	$E_2 < \delta \left(\frac{\beta}{1+2/\sqrt{\alpha}} - 1 \right)$, $x_1 < (1 - E_1)\gamma < x_2$	Unstable
	$E_2 < \delta \left(\frac{\beta}{1+2/\sqrt{\alpha}} - 1 \right)$ and $0 < (1 - E_1)\gamma < x_1$ or $(1 - E_1)\gamma > x_2$, $E_1 < 1$	Stable
$P_2(x_1, y_1)$	$E_2 < \delta \left(\frac{\beta}{1+2/\sqrt{\alpha}} - 1 \right)$, $(1 - E_1)\gamma > x_1$, $E_1 < 1$, $E_1 > \Phi(E_2)$	Asymptotically stable
	$E_2 < \delta \left(\frac{\beta}{1+2/\sqrt{\alpha}} - 1 \right)$, $E_1 < 1$, $(1 - E_1)\gamma > x_1$, $E_1 < \Phi(E_2)$	Unstable
$P_3(x_2, y_2)$	$E_2 < \delta \left(\frac{\beta}{1+2/\sqrt{\alpha}} - 1 \right)$, $(1 - E_1)\gamma > x_2$, $E_1 < 1$	Unstable

Table 3.1

From (2.8) we get,

$$\frac{dx_1}{dE_2} = \frac{\beta\delta}{(\delta + E_2)^2} \frac{x_1}{\sqrt{\left(\frac{\beta\delta}{\delta+E_2} - 1\right)^2 - \frac{4}{\alpha}}} \quad (3.8)$$

and

$$\frac{dx_2}{dE_2} = \frac{-\beta\delta}{(\delta + E_2)^2} \frac{x_2}{\sqrt{\left(\frac{\beta\delta}{\delta+E_2} - 1\right)^2 - \frac{4}{\alpha}}} \quad (3.9)$$

From (3.8) we see that when the existence of P_2 is assumed, $dx_1/dE_2 > 0$. Thus x_1 increases as E_2 , the harvesting effort for predators increases. Under the existence condition of P_3 we see that $dx_2/dE_2 < 0$ That is the number of prey at the unstable critical point P_3 decreases as E_2 increases. Moreover we see that under the stability

condition, when E_2 increases and $E_2 \rightarrow \delta \left(\frac{\beta}{1+2/\sqrt{\alpha}} - 1 \right)$ from left x_1 increases up to $1\sqrt{\alpha}$ and x_2 decreases to $1\sqrt{\alpha}$ and if $E_2 \rightarrow \delta \left(\frac{\beta}{1+2/\sqrt{\alpha}} - 1 \right)$ from right x_1, x_2 do not exist.

4. GLOBAL STABILITY

The question of global stability in population biology is a very interesting mathematical problem. Usually the biologist believes that a unique positive, locally asymptotically stable equilibrium in an ecological system is globally stable. However, this is not always the case. It is generally agreed that analysis of global stability of the equilibrium points is essential for a better understanding of stability of ecological systems.

Therefore, it is very important to find conditions, which may guarantee the global stability of the unique positive interior equilibrium. In this section we consider the global stability behaviour of the model system (2.2) and (2.3) whose original forms are in (1.11) and (1.12), without any help of Lyapunov function. Our global stability analysis is based on purely algebraic criterion provided by Cheng *et. al.* (1981) which is an application of Floquet theory and the Poincare-Bendixon theorem. For this global stability analysis we recall our model system (1.11) , (1.12) in the following form slightly different from (2.2) and (2.3).

$$\begin{aligned} \frac{dx}{dt} &= xr(x) - yf(x) \\ \frac{dy}{dt} &= y[\beta\delta f(x) - (E_2 + \delta)] \end{aligned} \quad (4.1)$$

where $r(x) = \left(1 - \frac{x}{\gamma} - E_1\right)$ and $f(x) = \frac{x}{1+x+x^2/\alpha}$. Already we have shown that for

$$E_1 < \left(1 - \frac{x_1}{\gamma}\right), \quad E_2 < \delta \left(\frac{\beta}{1 + 2/\sqrt{\alpha}} - 1\right)$$

and $E_1 > \Phi(E_2)$, the equilibrium point $P_2(x_1, y_1)$ is asymptotically stable. Cheng *et. al.* (1981) proved that the model system of the form (4.1) will be globally stable around the locally asymptotically stable positive interior equilibrium point P_2 if and only if the following condition holds.

$$\frac{d}{dx} \left[\frac{Q(x) - Q(x_1)}{f(x) - f(x_1)} \right] \leq 0$$

where $Q(x) = \frac{d}{dx}[xr(x)] - \frac{xr(x)}{f(x)}$, $\frac{d}{dx}[f(x)]$. By the help of above results and using some mathematical calculation, we can conclude that the positive interior equilibrium $P_2(x_1, y_1)$ is globally asymptotically stable provided it is locally asymptotically stable.

5. BIFURCATION ANALYSIS IN THE PARAMETRIC SPACE (E_1, E_2)

In this section we discuss the bifurcations taking place when the boundary lines of the existence and stability regions of the equilibrium states in the (E_1, E_2) -plane are crossed. First of all, in figure 1 we report the curves in (E_1, E_2) -plane relevant to the existence condition and to changes in the stability properties of the equilibrium states. These curves divide the plane in five regions. All curves are obtained analytically.

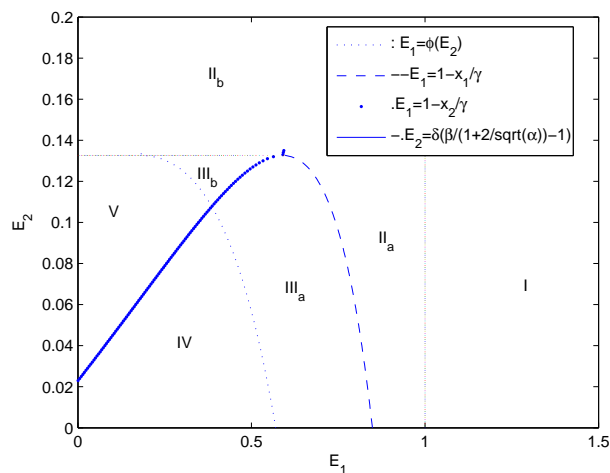


Figure 1. Existence and stability regions of the equilibrium states in the parameter space (E_1, E_2) . Values of dimensionless biological parameters used in simulation are $\alpha = 4.2$, $\beta = 2.5$, $\gamma = 5$, $\delta = 0.5$.

We now describe in detail the mathematical structure of the equilibria in different regions of the figure 1 and discuss the bifurcations across the boundaries.

Region - I = $\{(E_1, E_2) \in R_+^2 : E_1 > 1\}$. In this region the trivial equilibrium state $P_0(0, 0)$ is stable. From biological point of view, the stability of P_0 , representing the total extinction of both prey and predators. No other positive equilibrium state exist in this region. Therefore, persistent of the system cannot be reached here. For $E_1 > 1$, the prey resource goes to zero asymptotically, and hence the predator also gets extinct due to non-availability of prey. Taking the point $(1.1, 0.02)$ in the region 1 we describe this in the figure 2.

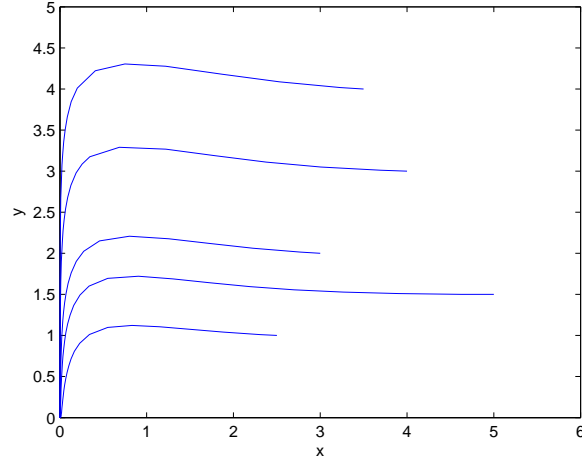


Figure 2. Phase diagram for $(E_1, E_2) = (1.1, 0.02)$.

Through $E_1 = 1$ to region II. One real eigenvalue of P_0 becomes positive and the equilibrium state changes from stable to unstable. Along $E_1 = 1$, equilibrium states P_1, P_2 and P_3 do not exist.

Region - II = $\{(E_1, E_2) \in R_+^2 := \text{II}_a + \text{II}_b \text{ where } \text{II}_a : 1 - \frac{x_1}{\gamma} < E_1 < 1, \text{II}_b : E_1 < 1 - \frac{x_1}{\gamma}, E_2 > \delta \left(\frac{\beta}{1+2/\sqrt{\alpha}} - 1 \right)\}$.

The equilibria P_0 is unstable, while P_1 is locally stable in the whole region. Co-existence equilibrium do not exist in this region.

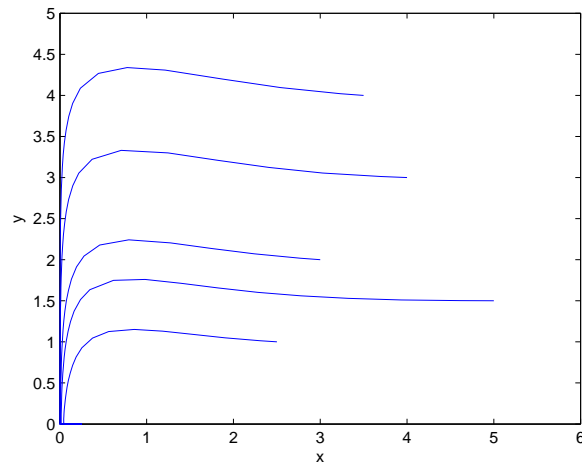


Figure 3. Phase diagram for $(E_1, E_2) = (0.95, 0.02)$.

We take the points $(0.95, 0.02)$ in the region II_a and $(0.6, 0.18)$ in the region II_b to describe this in the figures 3 and 4 respectively.

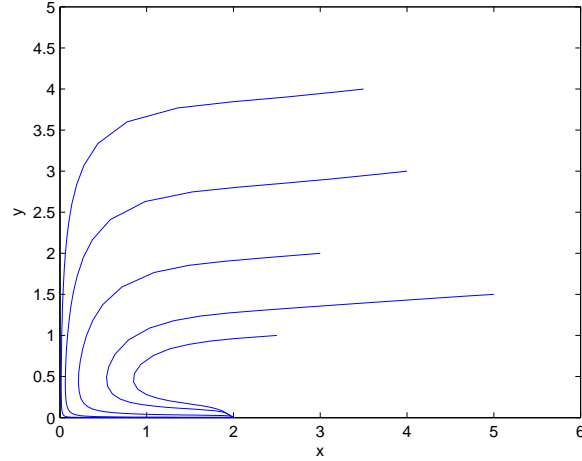


Figure 4. Phase diagram for $(E_1, E_2) = (0.06, 0.18)$.

As the trajectories tend to the boundary equilibrium P_1 , then it means that the predator population will ultimately tend to extinction, and the prey population with different initial conditions goes to the equilibrium level.

Region - III = $III_a + III_b = \{(E_1, E_2) \in R_+^2 : E_2 < \delta \left(\frac{\beta}{1+2/\sqrt{\alpha}} - 1 \right), E_1 < 1 - \frac{x_1}{\gamma}, E_1 > \varphi(E_2)\}$.

In this region the nonexistence equilibrium states P_0 and P_1 are unstable in the whole region as well as $P_3(E_1, E_2)$, which exists only for $E_2 < \delta \left(\frac{\beta}{1+2/\sqrt{\alpha}-1} \right)$, $E_1 < 1 - \frac{x_2}{\gamma}$.

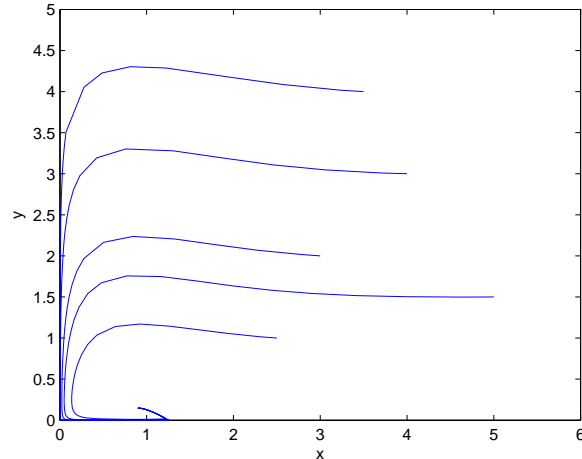


Figure 5. Phase diagram for $(E_1, E_2) = (0.75, 0.04)$.

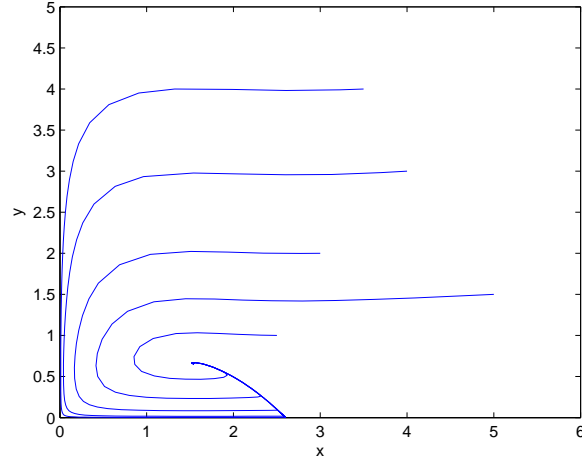


Figure 6. Phase diagram for $(E_1, E_2) = (0.48, 0.12)$.

As the trajectories tend to the stable equilibrium P_2 , then it means that the predator-prey interactions will ultimately tend to the balance behavior. Co-existence equilibrium P_2 exists and stable in this region.

Region - IV $-\{(E_1, E_2) \in R_+^2 : E_1 < 1 - \frac{x_2}{\gamma}, E_1 < \Phi(E_2)\}$. The equilibrium state P_2 changes from stable to unstable. In the (E_1, E_2) plane a locally stable limit cycle arises around P_2 . This is shown by the phase diagram in the figure 7 by taking the point $(0.25, 0.02)$ in the region iv. In fact, it is possible to prove the existence of a super critical Hopf bifurcation for the equilibrium P_2 .

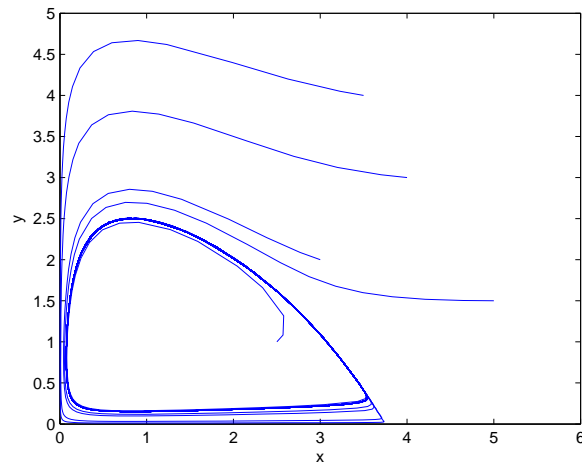


Figure 7. Phase diagram for $(E_1, E_2) = (0.25, 0.02)$.

As the stable limit cycle around the equilibrium P_2 arises, then this indicates that the predator coexists with the prey with oscillatory balance behavior.

Theorem 1. For $E_1 = \Phi(E_2)$, a super critical Hopf bifurcation takes place for the equilibrium P_2 .

Proof. Let us consider the Jacobian matrix (3.4). By direct calculation it follows that the eigenvalues are given by

$$\lambda_{1,2} = \frac{T(E_1, E_2) \pm \sqrt{T^2 - 4D(E_1, E_2)}}{2}.$$

Now $T = 0$, $D > 0$ and in correspondence of the value $E_1 = \phi(E_2)$ the matrix has two purely imaginary eigenvalues $\lambda_{1,2} = \pm i\sqrt{D}$.

Moreover, $\frac{d}{dE_1}(\text{Re}(\lambda_{1,2}))_{E_1} = \Phi(E_2)$. Then all the condition of Hopf theorem are satisfied and a stable limit cycle for $E_1 < \Phi(E_2)$ can be found. All these conditions together prove the existence of a super critical Hopf bifurcation for the equilibrium P_2 .

Region - V = $\left\{ (E_1, E_2) \in R_+^2 : E_1 < 1 - \frac{x_1}{\gamma}, E_2 < \delta \left(\frac{\beta}{1+2/\sqrt{\alpha}} - 1 \right) \right\}$

In this region both the co-existence equilibria exist but either is stable. We have shown the phase diagram by the figure 8 taking $(0.125, 0.1)$ in this region of (E_1, E_2) plane.

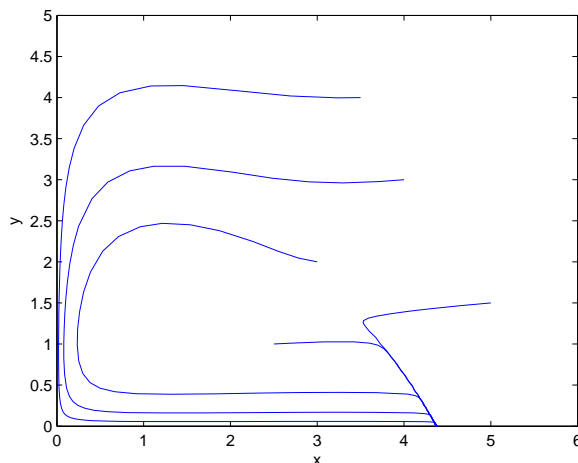


Figure 8. Phase diagram for $(E_1, E_2) = (0.125, 0.1)$.

In our formulation, the harvesting efforts E_1 and E_2 play the role of main bifurcation parameters, since we are interested in discussing the consequence of their variation. It is interesting to find conditions under which we can prevent cycle in the system considered. If the system parameters are such that the system admits a limit cycle, then it is possible to control the system in such a way that all solutions of the system approach an equilibrium point instead of a limit cycle. This will be possible only if the required limiting value of the solution can be made an asymptotically stable equilibrium of the system. Let the harvesting efforts \bar{E}_1, \bar{E}_2 satisfy the following conditions:

$$\bar{E}_2 < \delta \left(\frac{\beta}{1 + 2/\sqrt{\alpha}} - 1 \right), \quad \bar{E}_1 < 1 - \frac{x_1}{\gamma}, \bar{E}_1 < \Phi(\bar{E}_2),$$

then the system admits a limit cycle. Again let the harvesting efforts $\bar{\bar{E}}_1, \bar{\bar{E}}_2$ are such that $(x^*(\bar{\bar{E}}_1, \bar{\bar{E}}_2), y^*(\bar{\bar{E}}_1, \bar{\bar{E}}_2)) = (\bar{x}, \bar{y})$, where (\bar{x}, \bar{y}) is the required limit value for the solution of the system. For (\bar{x}, \bar{y}) to be asymptotically stable, $(\bar{\bar{E}}_1, \bar{\bar{E}}_2)$ must satisfy the following conditions:

$$\bar{\bar{E}}_1 < \delta \left(\frac{\beta}{1 + 2/\sqrt{\alpha}} \right), \quad \bar{\bar{E}}_1 < 1 - \frac{x_1}{\gamma}, \quad \text{and} \quad \bar{\bar{E}}_1 > \Phi(\bar{\bar{E}}_2),$$

Thus by choosing the effort function $(E_1(t), E_2(t))$ in such a way that $(E_1(0), E_2(0)) = (\bar{E}_1, \bar{E}_2)$ and $(E_1(\infty), E_2(\infty)) = (\bar{\bar{E}}_1, \bar{\bar{E}}_2)$, it is possible to drive the system to the state (\bar{x}, \bar{y}) . In this way it is possible to prevent cycles and drive the state of the consider system to a stable state by choosing harvesting function appropriately.

As an example let us take $(\bar{E}_1, \bar{E}_2) = (0.48, 0.12)$, which lies in the region-IV (in figure 1), as the initial value of the system, and $(\bar{\bar{E}}_1, \bar{\bar{E}}_2) = (0.3, 0.06)$, which lies in the region-III_a, as the limiting value of the system. We aim to move from the limit cycle to the limiting value.

The control that we have considered as follows:

$$S_1 : (E_1(t), E_2(t)) = (0.25, 0.02), \quad \text{for } t \geq 0,$$

$$S_2 : (E_1(t), E_2(t)) = \left\{ \begin{array}{ll} (0.3, 0.06), & \text{for } 0 < t < 50, \\ (0.5, 0.02), & \text{for } 50 \leq t < 100 \\ (0.48, 0.12), & \text{for } t \geq 100. \end{array} \right\}$$

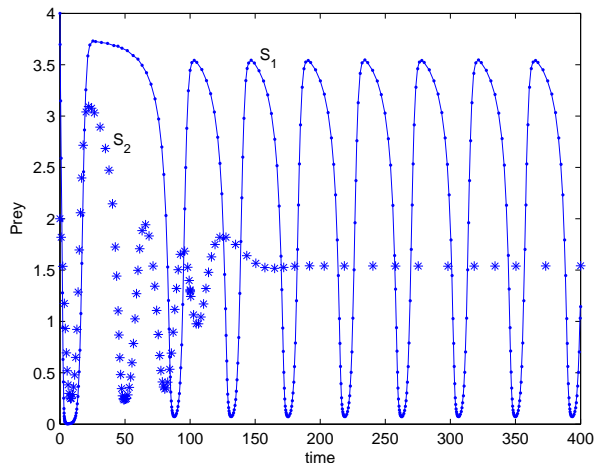


Figure 9. Paths of prey species.

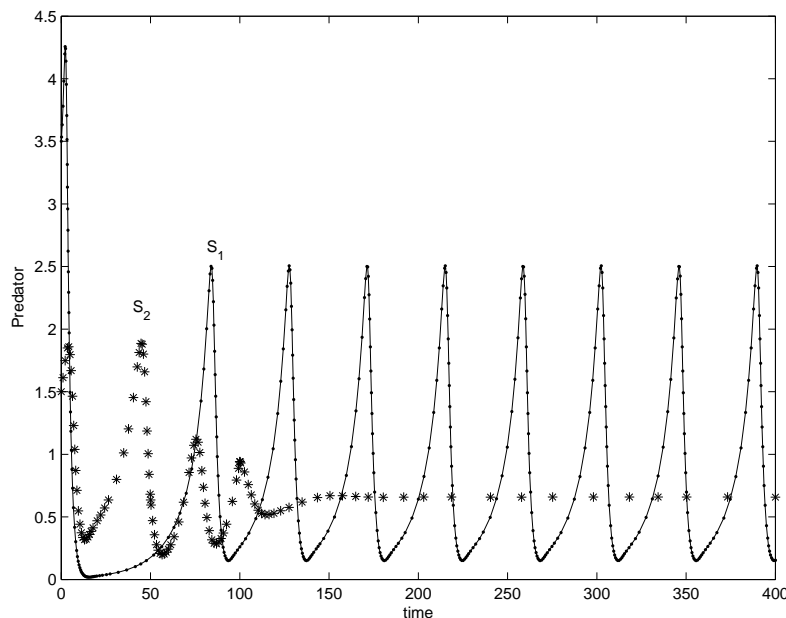


Figure 10. Paths of predator species.

6. CONCLUSION

Over exploitation and collapse of several biological resources is a major concern in recent times. This is due to unconventional and indiscrete harvesting of resources. So the current concern is to find principles for the control and management of multispecies system. The present work describes the use of harvesting efforts as control to obtain strategies for the control of a prey-predator system with non-monotonic functional response. This study shows a method of how to control a prey-predator system and drive the state either to the equilibrium point or to a limit cycle.

The system that we have considered admits four equilibrium points and out of which two interior equilibrium points are P_2 and P_3 are boundary equilibrium points represented by $P(x(E_2), y(E_1, E_2))$ and $P(x(E_2), y(E_1, E_2))$. It is observed that when P_2 exists, it is stable for $E_1 < 1$ and $E_1 > \Phi(E_2)$ and on the other hand it is unstable for $E_1 < \Phi(E_2)$. But P_3 is always unstable if it exists. It is proved that when the interior equilibrium point P_2 is locally asymptotically stable then it is also globally stable. It is also shown that the system can be controlled to the required steady state by adjusting the efforts E_1 and E_2 .

Acknowledgement

Research of T. K. Kar was supported by the Council of Scientific and Industrial Research (CSIR), India (Grant No. 25 (0160) /08 / EMR-II dated: 17.01.08).

REFERENCES

- [1] J. F. Andrew. A mathematical model for the continuous culture of micro-organisms utilizing inhibitory substances, *Biotechnology and Bioengineering*, **10**: 707–723, 1968.
- [2] K. S. Cheng, S. B. Hsu. and S. S. Lin. Some results on global stability of a predator prey system. *J. Math. Biol.* **12**:115–126, 1981.
- [3] C. W. Clark. *Mathematical Bioeconomics : The Optimal Management of Renewable Resources*. 2nd Edn. John Wiley & Sons, New York, 1990.
- [4] J. B. Collings. The effects of functional response on the bifurcation behaviour of a mite predator-prey interaction model. *Journal of Mathematical Biology*, **36**:149–168, 1997.
- [5] M. J. Crawley. *Natural Enemies. The population Biology of predators, Parasites and Disease*. Blackwell Scientific Publication, Oxford, 1992.
- [6] H. Gao, H. Wei, W. Sun and X. Zhai. Functions used in biological models and their influence on simulations. *Indian Journal of Marine Science* **29**: 230–237, 2000.
- [7] J. B. S. Haldane. *Enzymes*, Longmans, London, 1930.
- [8] R. Hannesson. Optimal harvesting of ecologically independent fish species, *J. Environ. Econ. Manage.* **10**: 329–345, 1982.
- [9] B. D. Hassard, N. D. Kazarinoff and Y. H. Wan. *Theory and Application of Hopf bifurcation*, Cambridge University Press, Cambridge, 1981.
- [10] C. S. Holling. The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the entomological society of Canada*. 45: -60, 1965.
- [11] R. J. Imeson, J. Van Den Bergh and J. Hoekstra. Integrated models of fisheries management and policy, *Environmental Modeling Assessment*, 7: 259–271, 2002.
- [12] T. K. Kar. Stability and optimal harvesting of a prey-predator model with stage-structure for predator, *Appli. Math.* **32**: 279–291, 2005.
- [13] T. K. Kar. and H. Matsuda. Controllability of a harvested prey-predator system with time delay, *J. Biol. Sys.* **14**: 1–12, 2006.
- [14] M. Kot. *Elements of Mathematical Ecology*. Cambridge Univ. Press, 2001.
- [15] J. H. Steele and E. W. Henderson. The role of predation in plankton models. *Journal of Plankton Research* 14: 157–172, 1992.
- [16] W. J. Strobele and H. Wacker. The economics of harvesting predator-prey systems. *J. Econ.* **61**: 65–81, 1995.
- [17] T. Yana. Dynamic behaviour of the Chemostat subject to substrate inhibitions. *Biotechnology and Bioengineering*, **11**: 139–153, 1969.