DENSITY DEPENDENT MORTALITY OF INTERMEDIATE PREDATOR CONTROLS CHAOS-CONCLUSION DRAWN FROM A TRI-TROPHIC FOOD CHAIN

BINAYAK NATH[1] AND KRISHNA PADA DAS[2†]

[1] DEPARTMENT OF PHYSICS, MAHADEVANANDA MAHAVIDYALAYA, MONIRAMPORE, P.O. BARRACKPORE KOLKATA 700120, INDIA

[2] DEPARTMENT OF MATHEMATICS, MAHADEVANANDA MAHAVIDYALAYA, MONIRAMPORE, P.O. BARRACKPORE KOLKATA 700120, INDIA
E-mail address: krishnaisi@yahoo.co.in

ABSTRACT. The paper explores a tri-trophic food chain model with density dependent mortality of intermediate predator. To analyze this aspect, we have worked out the local stability of different equilibrium points. We have also derived the conditions for global stability of interior equilibrium point and conditions for persistence of model system. To observe the global behaviour of the system, we performed extensive numerical simulations. Our simulation results reveal that chaotic dynamics is produced for increasing value of half-saturation constant. We have also observed trajectory motions around different equilibrium points. It is noticed that chaotic dynamics has been controlled by increasing value of density dependent mortality parameter. So, we conclude that the density dependent mortality parameter can be used to control chaotic dynamics. We also applied basic tools of nonlinear dynamics such as Poincare section and Lyapunov exponent to investigate chaotic behaviour of the system.

1. INTRODUCTION

In ecology, energy is transferred from one trophic level to another trophic level through the food chain. Chaos in a food chain model reveals that due to irregular and aperiodic population abundance, sustainability of the food chain through predator-prey relation is not preserved. The density-dependent processes occur when population growth rates are regulated by the density of a population. Chaotic dynamics is a very common factor in tri-trophic food chain.

Hastings and Powell [14] produced a chaotic population system in a simple tri-trophic food chain model with type-II functional response. After HP model, many researchers analyzed chaotic dynamics in a food chain model and also studied how to control chaos with the help of different biological parameters. Rai and Sreenivasan [31] presented a new model for a food chain involving three species showing the presence of a period-doubling scenario leading to chaos and discussed the application of this study to aquacultural research.

Ruxton [33, 34] investigated that the system of linked populations or imposition of a population floor on HP model has a stabilizing effect on tri-trophic food chain model. Eisenberg and Maszle [11] revisited the HP model and observed that gradual addition of refugia provides a stabilizing influence for which the chaotic dynamics collapsed to stable limit cycles.

MaCann and Hastings [20] re-investigated the role of omnivory in food webs using a non-equilibrium perspective. Varriale and Gomes [42] studied HP model using two different approaches. Firstly, they observed the asymptotic states of the system resulting from numerical integration of the equations. Secondly, they applied the embedding procedure to extract the relevant dynamical exponents from a time series for only one scalar variable.

Xu and Li [43] investigated the role of intraspecific density dependence(IDD), another important ecological factor, in the dynamics of two versions (deterministic and stochastic) of a food chain. They showed that the addition of IDD to a deterministic three-species food chain model stabilizes the food chain system and the very famous teacup chaotic attractor disappears. They also showed that the addition of IDD to a stochastic one at most results in a reduction in amplitude and frequency of dynamical fluctuations and can never eliminate the stochastic behavior.

Chattopadhyay and Sarkar [7] included the effect of the toxin, produced by toxin producing phytoplankton, as extra mortality term in zooplankton population and observed that chaotic behavior is less likely to occur in a real food chain dynamics. Lonngren et al. [23] also investigated the HP model with different set of parameters by using techniques from modern control theory. They observed that the synchronization of two diverse food chain systems is possible.

Maionchi and Reis [25] proposed a spatial version of the HP model in which predators seek their preys only in a finite neighborhood of their home location. They showed that local predation leads to spontaneous pattern formation and to qualitative changes in the global dynamics of the system. They also observed that the chaotic strange attractor present in the original HP model can be replaced by a stable fixed point or by an attractor of simpler topology depending on the size of the predation neighborhoods.

Bairagi et al. [6] studied the role of harvesting in a predator-prey-parasite system. Using impulsive harvesting effort as control parameter, they showed that it is possible to control the cyclic behavior of the system populations leading to the persistence of all species and other desired stable equilibrium can be obtained.

Younghae Do et al. [10] investigated a three-species food chain system with two types of functional response, Holling type and Beddington-DeAngelis type. Upadhyay and Raw [40] investigated analytically as well as numerically the dynamical complexities of a three species food chain model with Holling type IV predator response.

Zhang et al. [44] studied the effect of feeding selectivity on transfer of methylmercury (MeHg) through the marine food chains. The varying concentration of Hg in the microalgae species as well as the selectivity of zooplankton to the algal diet resulted in varying Hg accumulation in three zooplankton species i.e., feeding selectivity plays a key role in the transfer of MeHg along marine food chains.

Sunaryo et al. [35] studied ecological model with a tri-trophic food chain composed of a classical Lotka-Volterra functional response for prey and predator, and a Holling type-III functional response for predator and superpredator. They found the dynamical behavior of this model is very sensitive to parameter values as well as the parameters of the practical life. Greenhalgh et al. [13] analyzed the features of a predator-prey model with disease amongst the prey and ratio-dependent functional response for both infected and susceptible prey.

The above reviews clearly indicate that a lot of research has already been performed on HP model. As far as our knowledge goes, none of the studies take into account the density dependent mortality of intermediate predator in the system. We like to see how density dependent mortality in intermediate predator influence the dynamics of tri-trophic food chain model proposed by Hastings and Powell [14]. The control of chaotic dynamics with various ecological factors, namely, migration, predation, refuge, omnivory, habitat-heterogeneity is the most challenging task in such studies and thus it receives a good deal of attention from various scientists [7, 23, 42, 43].

To the best of our knowledge, there are few literatures which have considered the inhibitory effect of intra specific density dependence, but it has the ability to regulate the population dynamics significantly [43]. The main objective of the paper is to extend the prey-predator-top predator model by incorporating density dependent death rate of intermediate predator. We have analyzed the local asymptotic stability behaviour of the coexisting equilibrium points. Then, we have obtained the global stability conditions for the system. Finally, extensive numerical simulations are performed to make a further in depth analysis of the system.

The paper is organized as follows. In the section 2, we outline the mathematical model with some basic assumption. We study the stability of the equilibrium points in section 3. We have studied the global stability as well as persistence of the system in section 4. We perform an extensive numerical simulations and discussion in section 5.

2. MODEL FORMULATION

Incorporating "type II" saturating functional responses in both of the consumer species, the HP model takes the form:

$$
\begin{aligned}
\frac{dX}{dT} &= R_0 X \left(1 - \frac{X}{K_0}\right) - C_1 A_1 \frac{YX}{B_1 + X} \\
\frac{dY}{dT} &= A_1 \frac{YX}{B_1 + X} - A_2 \frac{YZ}{B_2 + Y} - D_1 Y \\
\frac{dZ}{dT} &= C_2 A_2 \frac{YZ}{B_2 + Y} - D_2 Z.
\end{aligned}
\tag{2.1}
$$

Let X be the numbers of the species at the lowest level of the food chain, Y the numbers of the species that preys upon X, Z the numbers of the species that preys upon Y and T is time. The constant R_0 is the intrinsic growth rate, and the constant K_0 is the carrying capacity of species X. The constants C_1 and C_2 are conversion rates of prey to predator for species Y and Z respectively; D_1 and D_2 are constant death rates for species Y and Z respectively. The

constants A_i and B_i for $i = 1, 2$ are maximal predation rate and half saturation constants for Y and Z respectively. Now we introduce density dependent mortality in intermediate predator

$$
\begin{aligned}
\frac{dX}{dT} &= R_0 X \left(1 - \frac{X}{K_0}\right) - C_1 A_1 \frac{YX}{B_1 + X} \\
\frac{dY}{dT} &= A_1 \frac{YX}{B_1 + X} - A_2 \frac{YZ}{B_2 + Y} - D_1 Y - DY^2 \\
\frac{dZ}{dT} &= \frac{C_2 A_2 YZ}{B_2 + Y} - D_2 Z.
\end{aligned}
\tag{2.2}
$$

To reduce the number of parameters and to determine which combinations of parameters control the behaviour of the system, we dimensionalize the system with the following scaling

$$
x = \frac{X}{K_0}, y = \frac{C_1 Y}{K_0}, z = \frac{C_1 Z}{C_2 K_0} \text{ and } t = R_0 T
$$

Then system (2.2) takes the form,

$$
\begin{aligned}
\frac{dx}{dt} &= x(1 - x) - \frac{a_1 xy}{1 + b_1 x} \\
\frac{dy}{dt} &= \frac{a_1 xy}{1 + b_1 x} - \frac{a_2 yz}{1 + b_2 y} - d_1 y - dy^2 \\
\frac{dz}{dt} &= \frac{a_2 yz}{1 + b_2 y} - d_2 z
\end{aligned}
\tag{2.3}
$$

where

$$
a_1 = \frac{A_1 K_0}{B_1 R_0}, b_1 = \frac{K_0}{B_1}, a_2 = \frac{A_2 C_2 K_0}{B_2 C_1 R_0}, b_2 = \frac{K_0}{B_2 C_1}, d = \frac{D K_0}{R_0 C_1}, d_1 = \frac{D_1}{R_0} \text{ and } d_2 = \frac{D_2}{R_0}
$$

TABLE 1. Table summarizing the symbol of parameters used in system (2.3).

Dimentionalised parameters	Biological significance of parameters
$a_1 = \frac{A_1 K_0}{R_0 B_1}$	Maximal predation rate of intermediate predator
$a_2 = \frac{C_2 A_2 K_0}{C_1 R_0 B_2}$	Maximal predation rate of top predator
$b_1 = \frac{K_0}{B_1}$	Half saturation constant in the functional response for intermediate predator
$b_2 = \frac{K_0}{C_1 B_2}$	Half saturation constant in the functional response for top predator
$d_1 = \frac{D_1}{R_0}$	Death rate of intermediate predator
$d_2 = \frac{D_2}{R_0}$	Death rate of top predator
$d = \frac{D K_0}{R_0 C_1}$	Density dependent mortality rate of the intermediate predator

System (2.3) has to be analyzed with the following initial conditions:

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

3. EXISTENCE AND LOCAL STABILITY OF EQUILIBRIUM POINTS

The system has four equilibrium points. The trivial equilibrium point $E_0(0, \ 0, \ 0)$ and the axial equilibrium point $E_1(1, \ 0, \ 0)$ exist for all parametric values. The top-predator free equilibrium point is $E_2(\bar{x}, \ \bar{y}, \ 0)$, where $\bar{x}$ is the positive root of the equation

$$x^3 + q_1 x^2 + q_2 x + q_3 = 0$$

where

$$q_1 = \frac{(2b_1 d - b_1^2 d)}{b_1^2 d}, q_2 = \frac{(d - 2b_1 d + a_1^2 - a_1 b_1 d_1)}{b_1^2 d}, q_3 = -\frac{(a_1 d_1 + d)}{b_1^2 d}$$

and

$$\bar{y} = -\frac{d_1}{d} + \frac{a_1 \bar{x}}{d(1 + b_1 \bar{x})} = \frac{(a_1 - b_1 d_1)\bar{x} - d_1}{d(1 + b_1 \bar{x})}$$

Here if $q_1 > 0$ and $q_2 > 0$ i.e., $(2b_1 d - b_1^2 d) > 0$ and $(d - 2b_1 d + a_1^2 - a_1 b_1 d_1) > 0$ then by Descartes' rule of sign, there is one sign change. Therefore the equation has at least one positive root. The positive condition for the existence of E_2 is $(a_1 - b_1 d_1)\bar{x} - d_1 > 0$ i.e. $(a_1 - b_1 d_1)\bar{x} > d_1$. The interior equilibrium point is given by $E^*(x^*, \ y^*, \ z^*)$, where x^* is the positive root of the equation

$$p_1 x^2 + p_2 x + p_3 = 0 \tag{3.1}$$

where

$$p_1 = (b_1 b_2 d_2 - a_2 b_1), p_2 = (b_2 d_2 + a_2 b_1 - a_2 - b_1 b_2 d_2), p_3 = (a_2 - a_1 d_2 - b_2 d_2)$$

If $p_1 > 0$, $p_2 > 0$ and $p_3 < 0$ or $p_1 > 0$, $p_2 < 0$ and $p_3 < 0$ or $p_1 < 0$, $p_2 < 0$ and $p_3 > 0$ then there is only one sign change. Thus the equation has at least one positive root.

$$y^* = \frac{d_2}{a_2 - b_2 d_2}$$

$$z^* = \frac{a_1 x^*}{(a_2 - b_2 d_2)(1 + b_1 x^*)} - \frac{d_1}{(a_2 - b_2 d_2)} - \frac{dd_2}{(a_2 - b_2 d_2)^2}$$

$$= \frac{(a_2 - b_2 d_2)[a_1 x^* - d_1(1 + b_1 x^*)] - dd_2(1 + b_1 x^*)}{(a_2 - b_2 d_2)^2(1 + b_1 x^*)}$$

The positive conditions for the existence of E^* are

(i) $\quad a_2 - b_2 d_2 > 0$

(ii) $\quad [a_1 x^* - d_1(1 + b_1 x^*)] - dd_2(1 + b_1 x^*) > 0$

i.e., $[a_1 x^* - (d_1 + dd_2)(1 + b_1 x^*)] > 0$.

The Jacobian matrix J of the system (2.3) at any arbitrary point (x, y, z) is given by

$$\begin{bmatrix} 1 - 2x - \frac{a_1 y}{(1+b_1 x)^2} & \frac{-a_1 x}{1+b_1 x} & 0 \\ \frac{a_1 y}{(1+b_1 x)^2} & \frac{a_1 x}{1+b_1 x} - \frac{a_2 z}{(1+b_2 y)^2} - d_1 - 2dy & -\frac{a_2 y}{1+b_2 y} \\ 0 & \frac{a_2 z}{(1+b_2 y)^2} & \frac{a_2 y}{(1+b_2 y)} - d_2 \end{bmatrix}. \qquad (3.2)$$

Theorem 1. The trivial equilibrium point E_0 is always unstable. The axial equilibrium point E_1 is locally stable if $R_{01} < 1$ where $R_{01} = \frac{1}{d_1}\left(\frac{a_1}{1+b_1}\right)$. The top-predator free equilibrium point E_2 is locally asymptotically stable if $(1 + b_1 \bar{x})^2 > a_1 b_1 \bar{y}$ and $R_{02} < 1$, where $R_{02} = \frac{1}{d_2}\left(\frac{a_2 \bar{y}}{1+b_2 \bar{y}}\right)$.

Proof. The Jacobian matrix at trivial equilibrium point E_0 is given by

$$J_0 = \begin{bmatrix} 1 & 0 & 0 \\ 0 & -d_1 & 0 \\ 0 & 0 & -d_2 \end{bmatrix}$$

The characteristic roots of the Jacobian matrix J_0 are $1, -d_1$ and $-d_2$.

Since one of the eigenvalues associated with the Jacobian matrix computed around E_0 is $1 > 0$, so the equilibrium point E_0 is always unstable.

The Jacobian matrix at axial equilibrium point E_1 is given by

$$J_1 = \begin{bmatrix} -1 & \frac{-a_1}{1+b_1} & 0 \\ 0 & \frac{a_1}{1+b_1} - d_1 & 0 \\ 0 & 0 & -d_2 \end{bmatrix}$$

The characteristic roots of the Jacobian matrix J_1 are -1, $-d_2$ and $\frac{a_1}{1+b_1} - d_1$

Hence E_1 is stable if $\frac{a_1}{1+b_1} - d_1 < 0$ which implies $R_{01} < 1$ where $R_{01} = \frac{1}{d_1}\left(\frac{a_1}{1+b_1}\right)$.

The Jacobian matrix at top-predator free equilibrium point E_2 is given by

$$J_2 = \begin{bmatrix} -\bar{x} + \frac{a_1 b_1 \bar{x}\bar{y}}{(1+b_1 \bar{x})^2} & \frac{-a_1 \bar{x}}{1+b_1 \bar{x}} & 0 \\ \frac{a_1 \bar{y}}{(1+b_1 \bar{x})^2} & -d\bar{y} & -\frac{a_2 \bar{y}}{1+b_2 \bar{y}} \\ 0 & 0 & \frac{a_2 \bar{y}}{1+b_2 \bar{y}} - d_2 \end{bmatrix}$$

The characteristic roots of the Jacobian matrix J_2 are $\left(\frac{a_2 \bar{y}}{1+b_2 \bar{y}} - d_2\right)$ and the roots of the equation

$$\lambda^2 + \lambda\left(\bar{x} - \frac{a_1 b_1 \bar{x}\bar{y}}{(1 + b_1 \bar{x})^2} + d\bar{y}\right) + d\bar{y}\left(\bar{x} - \frac{a_1 b_1 \bar{x}\bar{y}}{(1 + b_1 \bar{x})^2}\right) + \frac{a_1^2 \bar{x}\bar{y}}{(1 + b_1 \bar{x})^3} = 0$$

It is clear that E_2 is stable if $\left(1 - \frac{a_1 b_1 \bar{y}}{(1+b_1 \bar{x})^2}\right) > 0$ i.e. $(1+b\bar{x})^2 > a_1 b_1 \bar{y}$ and $\frac{a_2 \bar{y}}{1+b_2 \bar{y}} - d_2 < 0$ i.e. $R_{02} < 1$ where $R_{02} = \frac{1}{d_2}\left(\frac{a_2 \bar{y}}{1+b_2 \bar{y}}\right)$.

Hence the theorem.

Theorem 2. The interior equilibrium point $E^*(x^*,\ y^*,\ z^*)$ of the system (2.3) is locally asymptotically stable if the following conditions hold:

$$\frac{a_1 b_1 y^*}{(1 + b_1 x^*)^2} < 1 \text{ and } \frac{1}{d}\left(\frac{a_2 b_2 z^*}{1 + b_2 y^*}\right) < 1$$

Proof. The Jacobian matrix at the interior point $E^*(x^*,\ y^*,\ z^*)$ is

$$V = \left[\begin{array}{ccc} A_{11} & A_{12} & A_{13} \\ A_{21} & A_{22} & A_{23} \\ A_{31} & A_{32} & A_{33} \end{array}\right]$$

Where

$$A_{11} = -x^* + \frac{a_1 b_1 x^* y^*}{(1 + b_1 x^*)^2},\ A_{12} = \frac{-a_1 x^*}{1 + b_1 x^*},\ A_{13} = 0$$

$$A_{21} = \frac{a_1 y^*}{(1 + b_1 x^*)^2},\ A_{22} = \frac{a_2 b_2 y^* z^*}{1 + b_2 y^*} - dy^*,\ A_{23} = -d_2$$

$$A_{31} = 0,\ A_{32} = \frac{a_2 z^*}{(1 + b_2 y^*)^2},\ A_{33} = 0$$

The characteristic equation of Jacobian matrix is given by

$$\lambda^3 + \sigma_1 \lambda^2 + \sigma_2 \lambda + \sigma_3 = 0$$

where

$$\begin{aligned} \sigma_1 &= -(A_{11} + A_{22}), \\ \sigma_2 &= A_{11} A_{22} - A_{23} A_{32} - A_{12} A_{21}, \\ \sigma_3 &= A_{11} A_{23} A_{32} \end{aligned}$$

$$\sigma_1 \sigma_2 - \sigma_3 = -A_{11}^2 A_{22} + A_{11} A_{12} A_{21} - A_{11} A_{22}^2 + A_{22} A_{23} A_{32} + A_{22} A_{12} A_{21}$$

The sufficient conditions for $\sigma_1 > 0$, $\sigma_3 > 0$ and $\sigma_1 \sigma_2 - \sigma_3 > 0$ are as follows:

$$A_{11} < 0 \text{ and } A_{22} < 0$$

which implies the conditions

$$\frac{a_1 b_1 y^*}{(1 + b_1 x^*)^2} < 1 \text{ and } \frac{1}{d}\left(\frac{a_2 b_2 z^*}{1 + b_2 y^*}\right) < 1$$

Thus, if the condition stated in the theorem holds, then all the Routh-Hurwitz criteria (i) $\sigma_1 > 0$ (ii)$\sigma_1 \sigma_2 - \sigma_3 > 0$ (iii) $\sigma_3 > 0$ are satisfied, and the system (2.3) is locally asymptotically stable around the positive equilibrium point.

4. GLOBAL STABILITY AND PERSISTENCE

Theorem 3. The interior equilibrium E_3 is globally asymptotically stable if the conditions

$$\text{(i)} \left(1 - \frac{a_1 b_1 y^*}{M}\right) > 0,$$

$$\text{(ii)} \left(1 - \frac{a_1 b_1 y^*}{M}\right)\left(d - \frac{a_2 b_2 z^*}{M'}\right) - \left(\frac{a_1 b_1 x^*}{2M}\right)^2 > 0$$

hold.

Proof:
We consider the following Lyapunov function

$$V = A(x - x^* - x^* \ln \frac{x}{x^*}) + B(y - y^* - y^* \ln \frac{y}{y^*}) + C(z - z^* - z^* \ln \frac{z}{z^*})$$

Taking the time derivative along the solution of (3) and after some simplification we get,

$$\frac{dV}{dt} = -A\left(1 - \frac{a_1 b_1 y^*}{M}\right)(x - x^*)^2 - B\left(d - \frac{a_2 b_2 z^*}{M'}\right)(y - y^*)^2 - (\frac{Aa_1}{M} - \frac{Ba_1}{M}$$

$$+ \frac{Aa_1 b_1 x^*}{M})(x - x^*)(y - y^*) - \left(\frac{Ba_2}{M'} - \frac{Ca_2}{M'} + \frac{Ba_2 b_2 y^*}{M'}\right)(y - y^*)(z - z^*)$$

where $M = (1 + b_1 x)(1 + b_1 x^*) \ and \ M' = (1 + b_2 y)(1 + b_2 y^*)$

Considering A=B=C=1 the right hand side of the above equation can be written as $-L^T QL$, where $L = (x - x^*)(y - y^*)(z - z^*)$ and the symmetric matrix Q is given by

$$Q = \begin{bmatrix} 1 - \frac{a_1 b_1 y^*}{M} & \frac{a_1 b_1 x^*}{2M} & 0 \\ \frac{a_1 b_1 x^*}{2M} & d - \frac{a_2 b_2 z^*}{M'} & \frac{a_2 b_2 y^*}{2M'} \\ 0 & \frac{a_2 b_2 y^*}{2M'} & 0 \end{bmatrix}$$

If the symmetric matrix Q is positive definite, it can be concluded that $\frac{dV}{dt} < 0$. Q is positive definite if

$$\text{(i)} \left(1 - \frac{a_1 b_1 y^*}{M}\right) > 0$$

$$\text{(ii)} \left(1 - \frac{a_1 b_1 y^*}{M}\right)\left(d - \frac{a_2 b_2 z^*}{M'}\right) - \left(\frac{a_1 b_1 x^*}{2M}\right)^2 > 0$$

Hence the system around the interior equilibrium point is globally asymptotically stable.

From biological aspect, permanence of a system reveals information about the survival of all populations of the system in a future time. In Mathematics, permanence of a system means that strictly positive solutions do not have omega limit points on the boundary of the non negative cone.

Theorem 4. System (2.3) is permanent around the interior equilibrium point if the conditions

$$\text{(i) } R_{01} > 1$$
$$\text{(ii) } R_{02} < 1$$

hold.

Proof. We consider the average Lyapunov function of the form

$$V(x, y, z) = x^{\alpha_1} y^{\alpha_2} z^{\alpha_3}$$

where α_1 and α_2 are assumed positive and α_3 is negative. We have

$$\frac{\dot{V}}{V} = \frac{\alpha_1}{x}\frac{dx}{dt} + \frac{\alpha_2}{y}\frac{dy}{dt} + \frac{\alpha_3}{z}\frac{dz}{dt}$$

$$= \alpha_1[1 - x - \frac{a_1 y}{1 + b_1 x}] + \alpha_2[\frac{a_1 x}{1 + b_1 x} - \frac{a_2 z}{1 + b_2 y} - d_1 - dy] + \alpha_3[\frac{a_2 y}{1 + b_2 y} - d_2]$$

For equilibrium the following conditions should be satisfied

$$\frac{\dot{V}}{V}(E_1) = \alpha_2[\frac{a_1}{1 + b_1} - d_1] + \alpha_3[-d_2] > 0$$

$$\frac{\dot{V}}{V}(E_2) = \alpha_3[\frac{a_2 \bar{y}}{1 + b_2 \bar{y}} - d_2] > 0$$

if the conditions

$$\text{(i) } R_{01} > 1$$
$$\text{(ii) } R_{02} < 1$$

hold.

Under these conditions system is permanent around the interior equilibrium point.

5. NUMERICAL RESULTS AND DISCUSSION

In this section we perform extensive numerical experiments to observe the role density dependent mortality of intermediate predator on the dynamics of tri-trophic food chain. For this we have taken a set of parameter values $a_1 = 5.0$, $a_2 = 0.1$, $b_1 = 3.0$, $b_2 = 2.0$, $d_1 = 0.4$, $d_2 = 0.01$, $d = 0.002$ and for this set of parameter values we observe the time series chaotic aperiodic solution (Figure(1)).

Hastings and Powell [14] already observed stable focus, limit cycle, period-doubling and chaotic dynamics of the system by changing half saturation constant b_1. Our aim is first to observe the exchange of states (stability-limit cycle-period doubling-chaos) as shown in HP model for different values of b_1 and subsequently to observe the system under the variation of density dependent mortality in intermediate predator d. Thus we will first revisit the dynamics of the system for variation half saturation constant b_1.

From Figure(2) we observe that system shows chaotic dynamics for $b_1 = 2.9$ and we also observe the trajectory of this chaotic dynamics in phase plane. This chaotic dynamics in phase
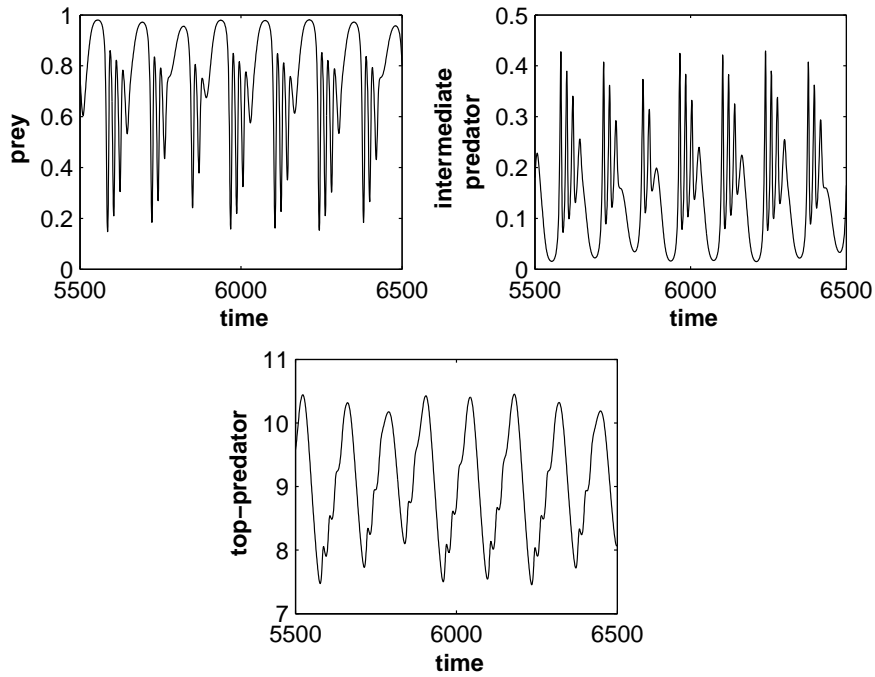
FIGURE 1. Figure depicts the chaotic dynamics of the system(2.3) for $a_1 = 5.0$, $a_2 = 0.1$, $b_1 = 3.0$, $b_2 = 2.0$, $d_1 = 0.4$, $d_2 = 0.01$, $d = 0.002$.
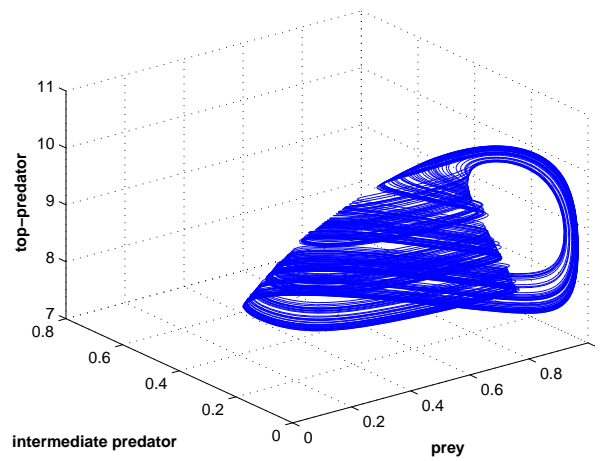

FIGURE 2. Figure shows the tea-cup chaotic attractor in phase plane for $b_1 = 2.9$ and other parameter values given in the Figure 1.

plane takes a shape of teacup attractor. To observe the trajectory behaviour of our system around the different equilibrium points for different values of different key parameters, we draw phase diagram of trajectory.
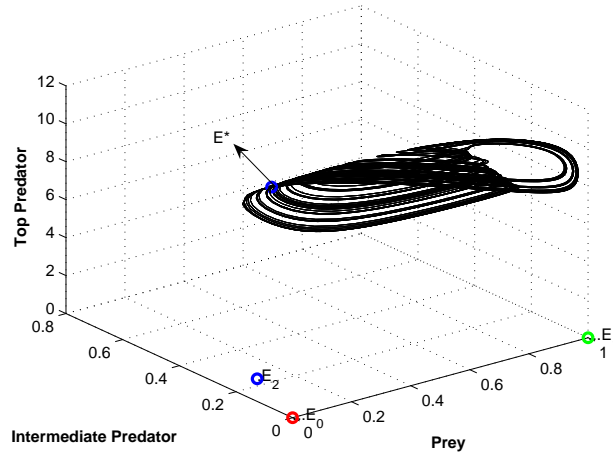

FIGURE 3. Figure indicates the motion of trajectory of the system(2.3) around the different equilibrium points corresponding to Figure 1.

From Figure (3), we have observed chaotic trajectory around the interior equilibrium point and the motion of trajectories around the other equilibrium points.

To observe a clear picture we draw a bifurcation diagram for b_1 (Figure(4)) and from this diagram we observe that system enters into chaotic dynamics from stable focus. We observe that for $b_1 < 2.1$ the system is stable around the positive steady state and for $2.1 \leq b_1 < 2.3$ it shows limit cycle oscillations. The period doubling is observed at $b_1 = 2.3$. Finally chaotic dynamics is observed for $2.3 < b_1 \leq 3.0$. The dynamics within the attractor is given roughly as follows. Starting in the "handle" of the "teacup", the system moves to the wide part of the teacup and then spirals along the teacup to the narrow end, entering the handle again. In terms of the species behavior, the top predator Z crashes, allowing wide swings in the population levels of X and Y. As Z increases in numbers, the swings in X and Y become damped, until Z causes the levels of Y to crash. This leads to a crash in Z and an outbreak in X, starting the process again. The sequence of events in terms of species numbers, always follows the same general pattern. What is unpredictable is the timing. One way to express this is that the time between crashes of species Z varies in an erratic fashion. Also, the number of peaks in species Y between major crashes varies and the population size at the peaks varies. Trajectory behaviour around the equilibrium points will be changed for variation of parameter b_1. These variations are observed in Figure(5).
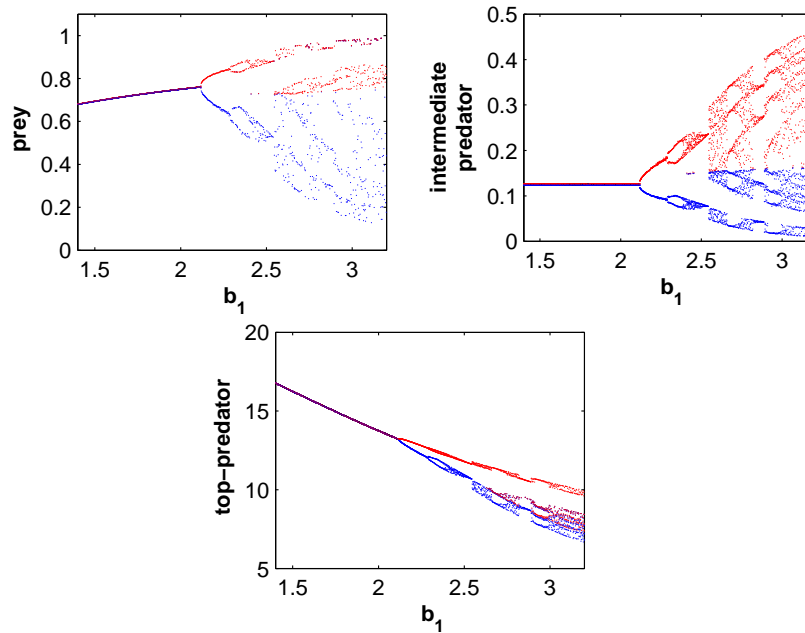
FIGURE 4. Figure indicates the bifurcation diagram for $b_1 \in [1.4, 3.5]$ and also indicates that the system(2.3) ultimately settles down into chaotic dynamics after passing through different dynamics like stable, limit cycle and period-doubling for variation of b_1 and other parameter values given in the Figure1.

From Figure(5a) we have observed limit cycle trajectory around interior equilibrium point and all trajectories around other equilibrium points will settle down into the limit cycle oscillations. From Figure(5b), it is noticed that if we increase the value of b_1, limit cycle trajectory behaviour goes into period-doubling trajectory around the interior equilibrium point and other trajectories around the other equilibrium points will converge to period-doubling trajectory. From Figure(5c) we have noticed that the position of different equilibrium points and behaviour of trajectories for further increment of the value of b_1. From this figure we have observed chaotic trajectory around interior equilibrium point and other trajectories around the other equilibrium points will flow into chaotic trajectory.

From Figure(6a), it is observed the time series dynamics of Lyapunov exponents and a positive Lyapunov exponent. This positive Lyapunov exponent indicates chaos. Figure(6b) exhibits Poincare map of typical chaotic region on the plane x=0.5. The scattered distribution of the sampling points implies the chaotic behaviour of the system.

In our present study we observe that system shows chaotic dynamics in absence of density dependent mortality in intermediate predator. The terms chaos, strange attractor and fractal are becoming familiar to many, if not all, ecologists [36]. The key feature of chaotic dynamics is
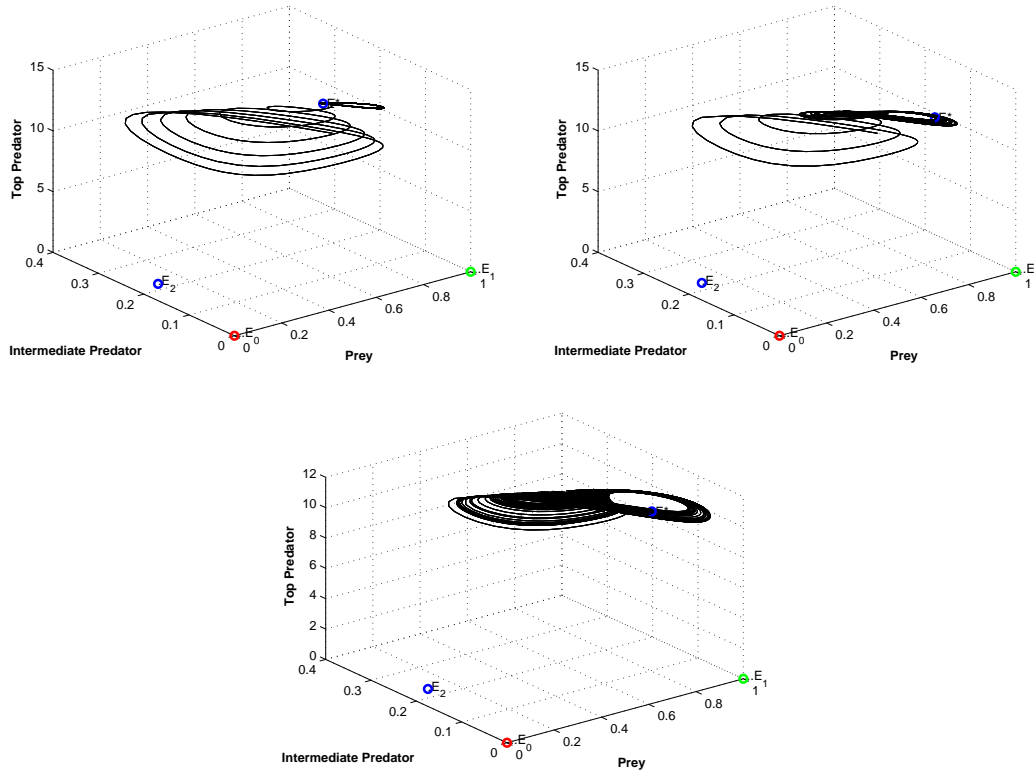
FIGURE 5. (a) Figure indicates the motion of trajectory of the system(2.3)around the different equilibrium points for $b_1 = 2.2$, (b) Figure shows the positions of different equilibrium points for $b_1 = 2.4$, (c) Figure depicts the dynamics of the system(2.3)around the different equilibrium points for $b_1 = 2.6$ and other parameter values given in the Figure1.

the sensitive dependence on initial conditions. Even a very small change in initial conditions can lead to different results. Indeed, the divergence between results grows exponentially in time for virtually all pairs of starting conditions. Several early mathematical investigations of chaos were of ecological models [27]. An investigation by Gilpin [12] showed that a system of one predator and two competing prey can exhibit chaotic behavior. A number of simple ecological and epidemiological systems with seasonality in contact rates unequivocally demonstrate chaos [37]. Schaffer and Kot [38] and Olsen et al. [29] show that measles in New York, Baltimore and Denmark may be a specific example of this behavior. Tri-trophic food chain model suggests that chaotic behaviour may be much more common in natural systems with interacting producers and consumers (Predators and prey) than Hassel et al. [16] predicted on the basis of
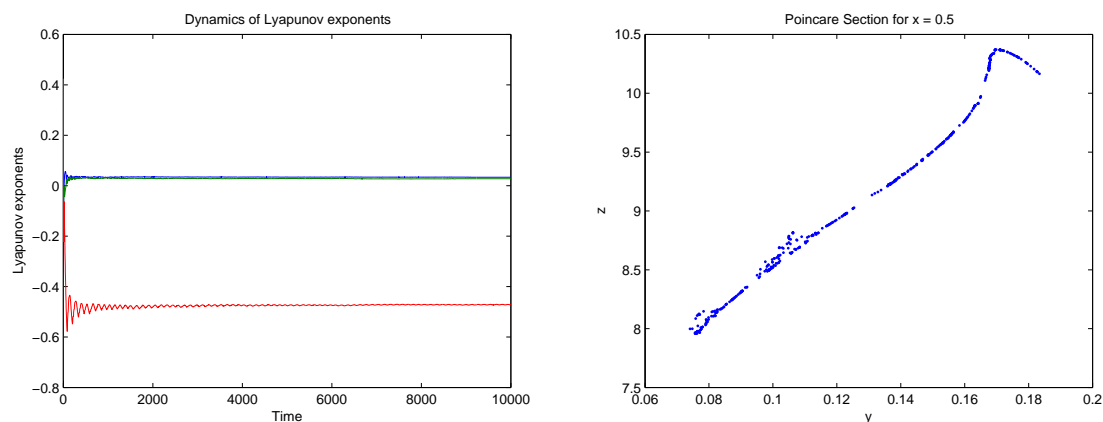
FIGURE 6. (a) Figure indicates the time series dynamics of Lyapunov exponents for $b_1 = 3.0$, (b) Figure shows the phase plane poincare section in y-z plane for $b_1 = 3.0$ and other parameter values given in the Figure1.

one species discrete time models. It is our interpretation that chaos ultimately arises in this food chain model because of the tendency for predator-prey systems to oscillate. One predator-prey subsystem, for concreteness say X and Y oscillates at one frequency, while another, Y and Z oscillates at a different frequency; the frequencies are determined by the model parameters. In particular, the interaction at the higher trophic levels has a longer natural period because the average lifetime of the top predators is longer than the average lifetime of the consumers at the lower trophic levels. The two systems are coupled through species Y because the predator in one is the prey in the other. We conjecture that when the period of one oscillation is not some multiple of the other frequency (i.e., the frequencies are incommensurate) chaos arises in a manner similar to the occurrence of chaos in periodically forced oscillations. Food webs depict a complex net coupled producer-consumer interactions; accordingly one should not be surprised to find many subsystems within a food web going through the oscillations that are a common feature of all predator-prey systems. It seems unlikely that the frequencies of all the linked subsystems will be commensurate. Accordingly, one expects that at least some, perhaps most of the linked predator-prey subsystems may be simultaneously undergoing chaotic oscillations. It is instructive to compare this view with the three species study (a predator consuming two competing prey) of Gilpin [12], in which chaotic behavior was identified. Typically, one does not associate oscillations with competition models based on results from two species Lotka-Volterra competition [26]. However, once three or more species are allowed, oscillations can occur [28, 30]. We conjecture that food webs containing a number of competing species can also go chaotic in the same way as our consumer-producer food chain does.

To observe the effect of density dependent mortality in intermediate predator, we increase the density dependent mortality parameter d keeping the half-saturation constant b_1 fixed at $b_1 = 2.9$. For $d = 0.05$ the system shows chaotic dynamics (Figure(7a)). For $d = 0.08$
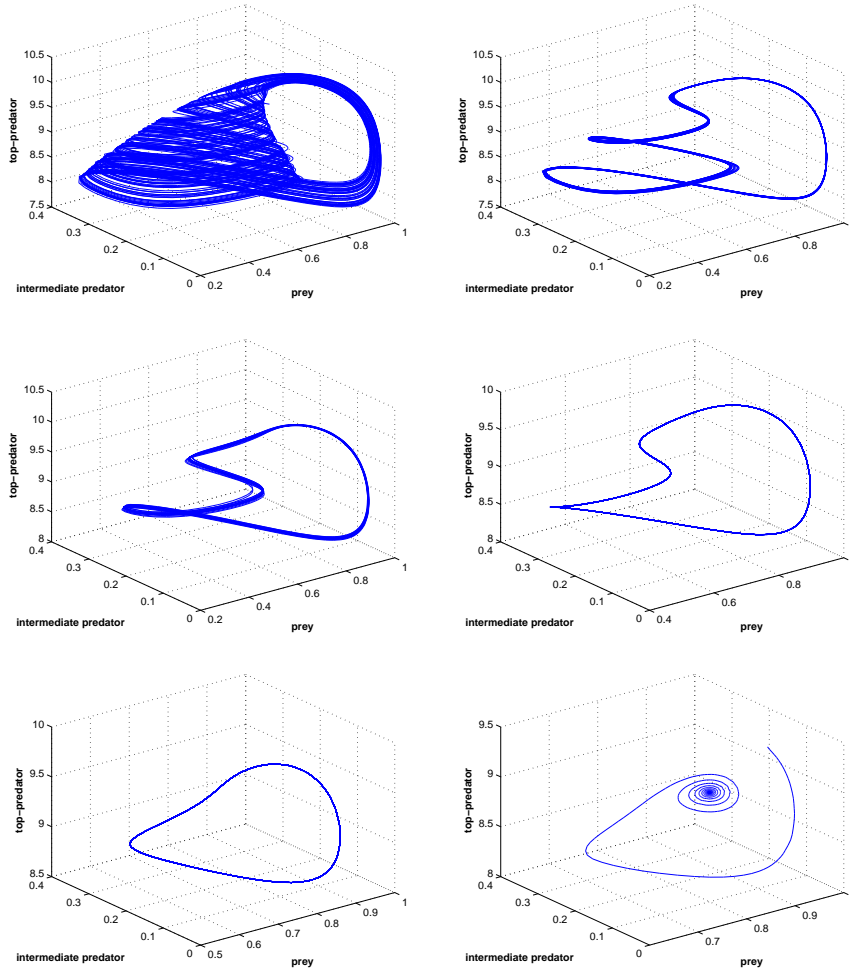
FIGURE 7. (a) depicts the chaotic dynamics for $d = 0.05$, (b) depicts periodic solution with period four for $d = 0.08$, (c) depicts periodic solution with period three for $d = 0.1$, (d) depicts period-doubling for $d = 0.17$, (e) depicts the limit cycle oscillations for $d = 0.24$. Finally, (f) depicts the stable focus for $d = 0.5$ and other parameter values given in Figure 1.

the system shows periodic solutions with period four (Figure(7b)) and for $d = 0.1$ the system shows periodic solutions with period three (Figure(7c)). For $d = 0.17$ the system enters into period doubling position from periodic solutions of period three and very famous teacup chaotic attractor is disappeared (Figure(7d)). This shows that the presence of density dependent mortality in intermediate predator prevents the system from entering into chaotic region. The

system goes into the limit cycle oscillation from period-doubling for $d = 0.24$ (Figure(7e)). The system goes into the steady stable position from limit cycle for $d = 0.5$ (Figure(7f)).
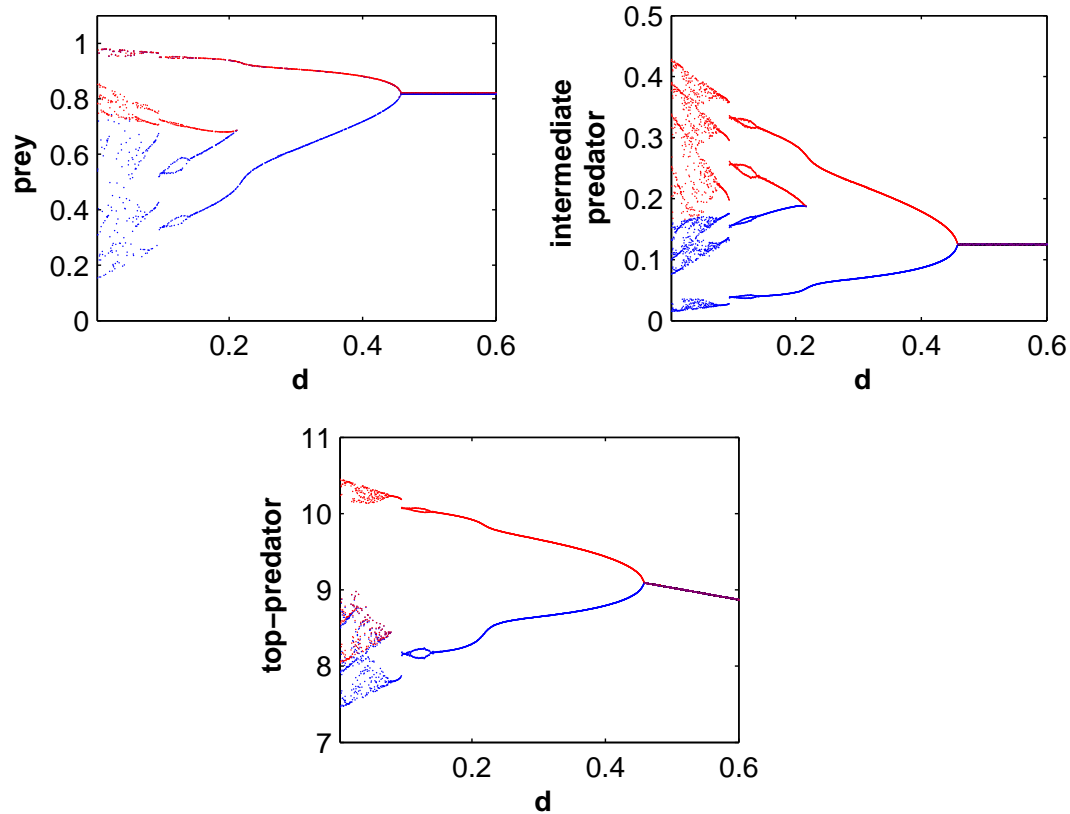

FIGURE 8. Figure indicates the bifurcation diagram for $d \in [0.002, 0.6]$ and also indicates that the system(2.3) ultimately settles down into chaotic dynamics after passing through different dynamics like stable, limit cycle and period-doubling for variation of d and other parameter values given in Figure1.

To make it more clear we plot the bifurcation diagram for all the populations with d as the bifurcating parameter (Figure 8). We observe that the system shows chaotic dynamics in the range $0 < d < 0.08$, periodic solutions of period four in the range $0.08 \leq d < 0.1$, periodic solutions of period three in the range $0.1 \leq d < 0.17$, period-doubling in the range $0.17 \leq d < 0.24$, limit cycle in $0.24 \leq d < 0.5$ and finally system settles down to steady solutions, a stable situation for $d \geq 0.5$ keeping other parameters fixed. So it is clear that increasing the strength of density dependent mortality up to a certain level reduce the prevalence of chaos, period-doubling and limit cycle oscillations. This observations indicate that the density dependent mortality factor in intermediate predator could be used as a biological control parameter for persistence of the species. To observe the motion of trajectory around the

different equilibrium points for variation of density dependent mortality parameter, we draw
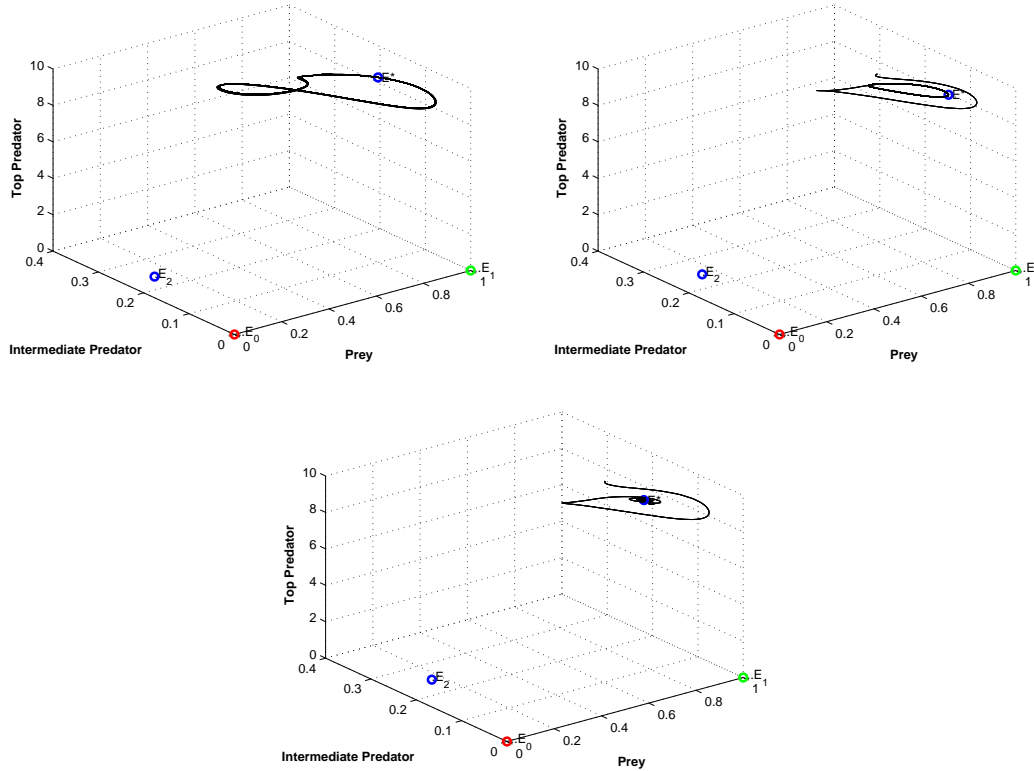phase diagram of trajectory.

FIGURE 9. (a) Figure indicates the motion of trajectory of the system(2.3)
around the different equilibrium points for $d = 0.2$, (b) Figure shows the
positions of different equilibrium points for $d = 0.4$, (c) Figure depicts the
dynamics of the system(2.3) around the different equilibrium points for $d = 0.55$ and other parameter values given in the Figure1.

From Figure(9a) we have noticed period-doubling trajectories around the interior equilib-
rium point and all trajectories around the other equilibrium points go into period-doubling. If
we increase the value of density dependent mortality parameter, we have found period-doubling
trajectory settles down into limit cycle oscillation around the interior equilibrium point and the
position and motion of trajectories around the other equilibrium points (Figure(9b)). If we
further increase the value of density dependent mortality parameter,the trajectory shows stable
focus around the interior equilibrium point and all trajectories around the other equilibrium
points converge to stable focus (Figure(9c)).

In this paper we have studied the dynamics of HP model by including density dependent mortality in intermediate predator. We first observe the dynamics of original HP model and then we observe the role of density dependent mortality in intermediate predator in controlling chaotic dynamics. In original HP model we observe the chaotic dynamics. Chaotic oscillations is common in food chain models. Oscillating resident communities are particularly worthwhile to study, because prey-predator (or host-parasitoid, plant-herbivore, consumer-resource) systems are well known examples of inherently fluctuating populations [39]. They represent interesting and relevant scenarios in biological control and resource management, because recurrent outbreaks in both terrestrial and aquatic ecosystems pose central problems in ecology (Insect outbreaks and algal blooms, see [1, 8, 17, 19]). Oscillations are also a concern of biological conservation, because populations could reach such small abundances that they are likely to go extinct [32]. However we observe that chaotic oscillations in tri-trophic food chain model is common and control of such oscillations is utmost important from ecological point of view. Our analysis shows that food chain model shows chaotic dynamics in absence of density dependent mortality in intermediate predator. The chaotic oscillatory behavior due to enhancement of half saturation constant can be prevented by increasing the density dependent mortality in intermediate predator. Now we explain the biological reasons of stabilization of chaos for increasing the density dependent mortality. When we increase the density dependent mortality in intermediate predator, the prey species increases due to decrease in intermediate predator and top predator decreases due to low level of food availability. Such type population pressure stabilizes the chaotic dynamics. Thus we may conclude that density dependent mortality in intermediate predator may be used as a biological control for the persistence of the system.

Now we compare our model and results with most of earlier studies. Kooi et al. [21] considered a tri-trophic food chain model consisting of a prey consuming a nutrient, a predator consuming a prey and an omnivore which preys on the predator and the prey. There were two limiting cases where the omnivore is a specialist; a food chain where the omnivore does not consume the prey and competition where the omnivore does not prey on the predator. They used bifurcation analysis to study the long-term dynamic behavior for various degrees of omnivory and observed that attractor can be equilibria, limit cycles or chaotic behavior depending on the control parameters of the chemostat. They also analyzed how the trophic structure of the food web evolves following invasion where a new invader is introduced one at the time. Generally, with an invasion, the invader settles itself and persists with all other species, however, the invader may also replace another species. They observed that the food web model has a global bifurcation, being a heteroclinic connection from a saddle equilibrium to a limit cycle of saddle type. This global bifurcation separates regions in the bifurcation diagram with different attractors to which the system evolves after invasion. Vandermeer [41] considered a tri-trophic food chain model and introduced the concept of omnivory. They observed that omnivory may be either stabilizing or destabilizing depending in part, on the conditions of the parent systems from which it derives. It was further conjectured that the tri-trophic to competition gradient can not be entirely stable that there must be an instability at some level of intermediate omnivory. In the present study we consider HP model and introduce density dependent mortality in intermediate predator. We observe chaotic dynamic in absence of density dependent mortality

and we also observe that density dependent mortality reduces the chaotic dynamics. In recent time Aziz-Alaoui [3] considered a tri-trophic food-chain model with modified Leslie-Gower type growth rate for top-predator population and established the chaotic dynamics exhibited by the model system for a certain choice of parameter values. Bandyopadhyay et al. [5] had modified the said model by incorporating density dependent death rate for predator population. Their findings revealed the fact that there were two coexisting equilibrium points one of which was a source and the other one was a sink. The positive equilibrium point which was sink is actually globally asymptotically stable under certain parametric conditions. They showed that the model system were capable to produce chaotic dynamics when the rate of intra specific completion was very low and chaotic dynamics disappeared for a certain value of the rate of intra specific completion for predator species. Their results suggested that the consideration of density dependent death rate for predator species had the ability to control the chaotic dynamics.

ACKNOWLEDGMENT

REFERENCES

[1] Anderson R. M. & May R. M. (1980). Infectious diseases and population cycles of forest insects. Science 210, 658-61

[2] Anderson, R.M. & May, R.M., Infectious Diseases of Humans: Dynamics and Control. *Oxford University Press*, New York,(1991).

[3] Aziz-Alaoui MA. Study of a Leslieower-type tritrophic population model. Chaos Solitons Fractals 2002;14:1275-93.

[4] Butler, G. J., Freedman, H., Waltman, P., Uniformly persistent systems. *in: Proc. Am. Math. Soc.*, 96, 425-429, (1986).

[5] M. Bandyopadhyay, S. Chatterjee, S. Chakraborty, J. Chattopadhyay; Density Dependent Predator Death Prevalence Chaos In A Tri-Trophic Food Chain Model. Nonlinear Analysis: Modelling and Control, 2008, Vol. 13, No. 3, 305-324

[6] Bairagi,N., Chaudhuri,S., Chattopadhyay,J.,2009. Harvesting as a disease control measure in an eco-epidemiological system - A theoretical study. Mathematical Biosciences 217 (2009) 134-144

[7] Chattopadhyay, J.,Sarkar,R.R.,2003. Chaos to order: Preliminary experiments with a population dynamics models of three trophic levels. Ecological Modelling 163:45-50

[8] Dwyer, G., Dushoff, Yess, S.H., Generalist predators, specialist pathogens and insect outbreaks. *Nature*, 43, 341-345, (2004).

[9] Diekmann, O.,Heesterbeek, J.A.P., Metz, J.A.J., On the definition and the computation of the basic reproductive ratio R_0 in models for infectious diseases in heterogeneous populations.*J.Math.Biol.*, 28,365-382, (1990).

[10] Younghae Do, Hunki Baek, Yongdo Lim,Dongkyu Lim,2011. A Three-Species Food Chain System with Two Types of Functional Responses. Abstract and Applied Analysis Volume 2011 (2011), Article ID 934569

[11] Eisenberg, J.N., Maszle, D.R., 1995. The structural stability of a three-species food chain model. J. Theo. Biol. 176, 501-510.

[12] Gilpin, M. E. (1979). Spiral chaos in a predator-prey model. Am. Natural. 113, 306-308. doi: 10.1086/283389

[13] Greenhalgh,D.,Khan,Q.J.A.,Pettigrew,J.S.,2016. An eco-epidemiological predator‡rey model where predators distinguish between susceptible and infected prey. Mathematical methods in the applied sciences.Vol 40 ,Issue 1

[14] Hastings, A., Powell, T., 1991. Chaos in three-species food chain. Ecology 72 (3), 896-903.

[15] Hadeler, K.P., Freedman, H.I., 1989. Predator-prey populations with parasitic infection. J. Math. Biol. 27, 609-631.

[16] Hassell, M., J. Lawton and R. M. May, 1976. Pattern of dynamical behavior in single-species populations. Journal of Animal Ecology 45: 471-486

[17] Hallegraeff, G.M., A review of harmful algae blooms and the apparent global increase. *Phycologia*, 32, 79-99, (1993).

[18] Han L, Ma Z, Hethcote HW, Four predator prey models with infectious diseases, Math Comp Model 34:849-858, 2001.

[19] Hilker,F.M.,Malchow,H.,2006. Strange periodic attractors in a prey-predator system with infected prey. Math.Popul.Stud.13,119-134.

[20] Kevin McCann, Alan Hastings 1997. Re evaluating the omnivorytability relationship in food webs. Proceedings of the Royal Society B Biological Sciences

[21] Kooi, B. W., L. D. J. Kuijper, M. P. Boer and S. A. L. M. Kooijman (2002a). Numerical bifurcation analysis of a tri-trophic food web with omnivory. Mathematical Biosciences 177: 201-228.

[22] Kumar, R., Freedman, H., A mathematical model of facultative mutualism with populations interacting in a food chain. *Math. Biosci.*, 97, 235-261, (1989).

[23] Lonngren, K.E., Bai, E.W., Ucar, A., 2004. Dynamics and synchronization of the Hastingsowell model of the food chain. Chaos Solitons Fract. 20, 387-393

[24] Lotka, A. (1925), n the True Rate of Natural Increase? Journal of the American Statistical Association, 20(151):305-339.

[25] Maionchi, D.O., Reis, S.F.d., Aguiar, M.A.M.d., 2005. Chaos and pattern formation in a spatial tritrophic food chain. Ecol. Model., doi:10.1016/j. ecol.model. 2005.04.028.

[26] MAY, R. M. 1973. ltability and Complexity in Model Ecosystems,?Princeton Univ. Press, Princeton, N. J.

[27] May R.M.,Biological populations with nonoverlapping generations: stable points, stable cycles, and chaos. Science. 1974 Nov 15;186(4164):645-7

[28] May,M.R., Leonard J.W. 1975. Nonlinear Aspects of Competition Between Three Species. SIAM Journal on Applied Mathematics,Vol 29,Issue-2 243-253

[29] Olsen, L.F., Truty G.L. and Schaffer W.M., Oscillations and chaos in epidemics: a non-linear dynamic study of six childhood diseases in Copenhagen, Denmark. *Theoretical Population Biology*, 33, 344-370, (1988).

[30] Thomas Powell,Peter J Richerson, 1985. Temporal Variation, Spatial Heterogeneity, and Competition for Resources in Plankton Systems: A Theoretical Model. The American Naturalist 125(3) ?

[31] Rai, V., Sreenivasan, R., 1993. Period-doubling bifurcations leading to chaos in a model food chain. Ecol. Model. 69 (1-2), 63-77.

[32] Rosenzweig, M.L., Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science*, 171, 385-387,(1971).

[33] Ruxton, G.D., 1994. Low levels of immigration between chaotic populations can reduce system extinctions by inducing asynchronous cycles Proc. R. Soc. Lond. B 256, 189-193.

[34] Ruxton, G.D., 1996. Chaos in a three-species food chain with a l ower bound on the bottom population. Ecology 77 (1), 317-319.

[35] Mada Sanjaya Waryano Sunaryo,Zabidin Salleh,Mustafa Mamat,2013.Mathematical model of three species food chain with Holling Type-III functional response. International Journal of Pure and Applied Mathematics Volume 89 No. 5 2013, 647-657

[36] Schaffer, W. M., and M. Kot. 1986a. Chaos in ecological systems: the coals that Newcastle forgot. Trends in Ecology and Evolution 1:58-63.

[37] Schaffer, W. M., and M. Kot. 1986b. Differential systems in ecology and epidemiology. Pages 158-178 in A. V. Holden, editor. Chaos: an introduction. University of Manchester Press, Manchester, England.

[38] Schaffer, W. M., and M. Kot. 1985a. Nearly one dimensional dynamics in an epidemic. Journal of Theoretical Biology 112:403-427.

[39] Turchin,P., Complex Population Dynamics .A Theoretical / empirical Synthesis. *Princeton University Press, Princeton, NJ,* (2003).

[40] Upadhyay,R.K.,Raw, S.N.,2011. Complex dynamics of a three species food-chain model with Holling type IV functional response. Nonlinear Analysis: Modelling and Control, 2011, Vol. 16, No. 3, 353-374

[41] Vandermeer, J. 2006. Omnivory and the stability of food webs. Journal of Theoretical Biology 238: 497-504.

[42] Varriale,M.C., Gomes, A.A. 1998. A Study of a three species food chain, Ecol. Model.110, 119-133

[43] Xu, C., Li, Z., 2002. Influence of intraspecific density dependence on a three-species food chain with and without external stochastic disturbances. Ecol. Model. 155, 71-83

[44] Zhang P, Sun J, Chen J, Wei J, Zhao W, Liu Q, Sun H.2013. Effect of feeding selectivity on the transfer of methylmercury through experimental marine food chains. Mar Environ Res 89:39-44