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Persistence and Stability of a Food Chain Model with Mixed Selection of Functional Responses

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Abstract. One approach to the study of an ecological community begins with an important object: its food web. Theoretical studies of food web must contend with the question of how to couple the large number of interacting species. One line of investigation assumes that the "building blocks" are species interacting in a pairwise fashion. The model we analyze in this paper describes a tritrophic food chain composed of logistic prey, a classical Lotka-Volterra functional response for prey and predator, and a Holling type-II functional response for predator and superpredator. Dynamical behaviours such as boundedness, stability, persistence, bifurcation et cetera of the model are studied critically. Computer simulations are carried out to explain the analytical findings. Finally it is discussed how these ideas illuminate some of the observed properties of real populations in the field, and explores practical implications.

Keywords: food chain model, boundedness, persistence, stability, Hopf bifurcation.

AMS classification: 92D25.

1 Introduction

Ever since the pioneering work of Lotka [1] and Volterra [2], theoretical studies of food webs in ecology, for the most part, focused on the study of ditrophic food chains. However, it has long been recognized that the limited "caricature" of ecological systems by two interacting species can account for only a small number of the phenomena that are commonly exhibited in nature. Theoretical ecology remained silent about the astonishing array of dynamical behaviours of three-species models for a long time. Of course, the increasing number of differential equations and the increasing dimensionality raise considerable additional problems both for the experimenter and theoretician. Nonetheless, such models need to be analyzed because certain three-species communities have become the focus of considerable attention. For example, in waste treatment process, food chain of waste (or nutrient)-bacteria-ciliates has got the attention of scientists [3]. In many field situations, the plant-herbivore-parasitoid food chains have become extremely important and it has been shown that parasitoids may determine fitness of the plant by destroying herbivores (for experimental evidences see references [4–6]. Also to reduce the indiscriminate use of pesticides, recently tea scientists are using predators or pathogens to control the pests of tea [7, 8]. Thus three-species systems like plant-herbivore-parasitoid, plant-pest-predator et cetera are emerging in different branches of biology in their own right.

To the best of our knowledge, it was only in the late seventies that some interest in the mathematics of tritrophic food chain models (composed of prey predator and superpredator) emerged [9–11]. Almost each of these contributions dealt with the problem of persistence (except [11]). Subsequently, some researchers have investigated several dynamical behaviours of tritrophic food chains (for references see [12]), but the analysis of the dynamics of most of the cases are numerical, without any analytic guide. Not that we undervalue such works, far from it, but analytical results are important because they can show the dynamical behaviours of a class of models, rather than a particular model. This is particularly important in ecology, where confidence in exact form of any particular model is weak.

In this paper we shall study analytically the dynamical behaviours of a tritrophic food chain model. It is beyond doubt that the dynamics of tritrophic food chains are very complicated and constructing accurate mathematical model is even more complicated. This is so because to have a perfect model we would need to consider so many factors, namely, growth rate, death rate, carrying capacity, conversion factor et cetera. Nonetheless, it is obvious that a perfect model cannot be achieved because even if we could put all these factors in a model, the model could never predict ecological catastrophes or Mother Nature caprice. Therefore, the best we can do is to look for analyzable models that describe as well as possible the reality. Before we introduce the model and dip into the thick of the rigorous analysis, we would like to present a brief sketch of the construction of the model which may indicate the biological relevance of it.

1. We have three populations namely the prey, whose population density is denoted by X, the predator whose population density is denoted by Y and the superpredator(or top-predator), whose population density is denoted by Z.

2. Behaviour of the entire community is assumed to arise from the coupling of these interacting species, where Z prey on Y and only on Y and Y prey on X. This is an interesting practical assumption from both mathematical and biological point of view. In a waste treatment process, the bacteria lives on the waste (or nutrient) while other organisms as ciliates feed on the bacteria [3]. Also in tea plant-pest-predator interaction, the pest specializes on tea plants and predator destroys pests by feeding on them [7, 8]. A distinct feature of these food chains is the so called domino effect: if one species dies out, all the species at higher trophic level die out as well.

3. We assume that in the absence of the predators the prey population density grows according to a logistic curve with carrying capacity $K(K > 0)$ and with an intrinsic growth rate constant $r(r > 0)$.

4. Almost each of the food chain models considered in ecological literature are constructed by invoking same type of functional responses for (X, Y) and (Y, Z) populations. But a different selection of functional response would be perhaps more realistic in this context. From this viewpoint we have considered a classical Lotka-Volterra functional response for the species X and Y and a Hooling type-II functional response for the species Y and Z.

The above considerations motivate us to introduce a tritrophic food chain model under the framework of the following set of nonlinear ordinary differential equations:

$$\begin{aligned}
\frac{dX}{d\tau} &= rX\Big(1 - \frac{X}{K}\Big) - b_1XY, \quad X(0) > 0,\\
\frac{dY}{d\tau} &= -d_1Y + c_1XY - \frac{b_2YZ}{a_1 + Y}, \quad Y(0) > 0,\\
\frac{dZ}{d\tau} &= -d_2Z + \frac{c_2YZ}{a_1 + Y}, \quad Z(0) > 0.
\end{aligned} \tag{1}$$

Here the positive constants b_1, d_1, c_1, b_2, a_1, d_2 and c_2 respectively denote the predation rate of the predator, the death rate of the predator, the conversion rate, the maximal growth rate of the predator, the half saturation constant, the death rate of the superpredator and the conversion factor.

The model we have just specified has nine parameters, which makes analysis difficult. To reduce the number of parameters and to determine which combinations of parameters control the behaviour of the system, we nondimensionalize the system (1) [13]. We choose

$$x = \frac{X}{K}, \quad y = \frac{Y}{K}, \quad z = \frac{Z}{K} \quad \text{and} \quad t = r\tau.$$

Then the system (1) takes the form (after some simplification)

$$\begin{aligned}
\frac{dx}{dt} &= x(1-x) - bxy = xF(x,y), \quad x(0) > 0,\\
\frac{dy}{dt} &= -dy + cxy - \frac{pyz}{1+ay} = yG(x,y,z), \quad y(0) > 0,\\
\frac{dz}{dt} &= -mz + \frac{qyz}{1+ay} = zH(y), \quad z(0) > 0,
\end{aligned} \tag{2}$$

where $b = \frac{b_1 K}{r}$, $d = \frac{d_1}{r}$, $c = \frac{c_1 K}{r}$, $a = \frac{K}{a_1}$, $p = \frac{b_2 K}{a_1 r}$, $m = \frac{d_2}{r}$, $q = \frac{c_2 K}{a_1 r}$.

The rest of the paper is organized as follows. In Section 2, we discuss the boundedness of the system (2) and study the stability of the boundary equilibrium points of it. Persistence of the system (2) is studied in Section 3. In Section 4, we find the necessary and sufficient condition for the existence of the interior equilibrium point $E^*(x^*, y^*, z^*)$ and study its local and global stability. A criterion for Hopf bifurcation is derived in Section 5. In Section 6, computer simulation of a variety of numerical solutions of the system (2) is presented. Section 7 contains the general discussions of the paper and biological implications of our mathematical findings.

2 Boundedness, boundary equilibria and stability

Boundedness of a model guarantees its validity. Further, it is necessary to determine persistence of the model. The following theorem establishes the uniform boundedness of the system (2).

Theorem 1. *All the solutions of the system* (2) *which start in* R^3_+ *are uniformly bounded.*

Proof. Let $(x(t), y(t), z(t))$ be any solution of the system with positive initial conditions.

Since

$$\frac{dx}{dt} \leq x(1-x),$$

by a standard comparison theorem, we have

$$\limsup_{t\to\infty} x(t) \leq 1.$$

Let

$$W = \frac{c}{b}x + y + \frac{p}{q}z.$$

Then

$$\frac{dW}{dt} = \frac{c}{b}x(1-x) - dy - \frac{mp}{q}z \leq \frac{2c}{b} - \kappa W, \quad \text{where} \quad \kappa = \min\{1, d, m\}.$$

Therefore

$$\frac{dW}{dt} + \kappa W \leq \frac{2c}{b}.$$

Applying a theorem on differential inequalities [14], we obtain

$$0 \leq W(x,y,z) \leq \frac{2c}{b\kappa} + \frac{W\big(x(0), y(0), z(0)\big)}{e^{\kappa t}}.$$

and for $t \to \infty$,

$$0 \leq W \leq \frac{2c}{b\kappa}.$$

Thus, all the solutions of the system (2) enter into the region

$$B = \Big\{(x,y,z)\colon 0 \leq W \leq \frac{2c}{b\kappa} + \epsilon, \quad \text{for any} \quad \epsilon > 0\Big\}$$

This proves the theorem. ☐

Computations of the boundary equilibria and their stability provide the information needed to determine the persistence of the system (2). In the following lemma we have mentioned the boundary equilibria of the system (2) and the condition of existence of them.

Lemma 1. *System* (2) *always have two boundary equilibrium points* $E_0(0,0,0)$ *and* $E_1(1,0,0)$*. The third boundary equilibrium point* $E_2(\hat{x},\hat{y},0)$ *exists if and only if* $c > d$*. When this condition is satisfied,* $\hat{x}$*,* $\hat{y}$ *are given by* $\hat{x} = \frac{d}{c}$*,* $\hat{y} = \frac{c-d}{bc}$*.*

The simplest equilibrium point is E_0. The variational matrix $V(E_0)$ at E_0 is given by

$$V(E_0) = \begin{bmatrix} 1 & 0 & 0 \\ 0 & -d & 0 \\ 0 & 0 & -m \end{bmatrix}.$$

for which two of the eigen values are negative and one is positive, giving a point at the origin with non-empty stable manifolds and an unstable manifold.

The equilibrium point $V_1(1,0,0)$ has the variational matrix

$$V(E_1) = \begin{bmatrix} -1 & -b & 0 \\ 0 & c-d & 0 \\ 0 & 0 & -m \end{bmatrix},$$

which has two negative and one positive eigen values whenever $c > d$ and again has non-empty stable and unstable manifolds.

The variational matrix $V(E_2)$ at the equilibrium point $E_2(\hat{x},\hat{y},0)$ is given by

$$V(E_2) = \begin{bmatrix} -\frac{d}{c} & -\frac{bd}{c} & 0 \\ \frac{c-d}{b} & 0 & -\frac{p\hat{y}}{1+a\hat{y}} \\ 0 & 0 & -m + \frac{q\hat{y}}{1+a\hat{y}} \end{bmatrix}.$$

The characteristic equation of $V(E_2)$ is

$$\left\{c\lambda^2 + d\lambda + d(c-d)\right\}\left\{\lambda + m - \frac{q\hat{y}}{1+a\hat{y}}\right\} = 0.$$

The eigen values are $\lambda_{1,2} = \frac{-d \pm \sqrt{d^2 - 4cd(c-d)}}{2c}$ and $\lambda_3 = -m + \frac{q\hat{y}}{1+a\hat{y}}$.

Since $c > d$, therefore the signs of the real parts of λ_1 and λ_2 are negative. This implies that E_2 is locally asymptotically stable in xy-plane. Now E_2 is asymptotically stable in z-direction if and only if $m\{bc + a(c-d)\} > q(c-d)$.

Remark 1. *It is to be noted that the existence of E_2 destabilizes E_1.*

3 Persistence

From biological point of view, persistence of a system means the survival of all populations of the system in future time. Mathematically, persistence of a system means that strictly positive solutions do not have omega limit points on the boundary of the non-negative cone. Butler *et al.* [15], Freedman and Waltman [16, 17] developed the following definition of persistence:

Definition. *If a population $N(t)$ is such that $N(t) > 0$, we say that $N(t)$ persists if $\liminf_{t\to\infty} N(t) > 0$. Further, if $N(t) \in \ell$, where ℓ is a certain class of function, and there exists $\delta > 0$ such that $\liminf_{t\to\infty} N(t) > \delta$ for all $N(t) \in \ell$, then $N(t)$ is said to be uniformly persistent (also known as permanence). A system is said to (uniformly) persist if each component (uniformly) persists.*

The following result guarantees the uniform persistence of the system (2) whenever there is a finite number of limit cycles in the xy-plane..

Theorem 2. *If $m\{bc + a(c-d)\} > q(c-d) > 0$ and there exists a finite number (say, n) of periodic solutions $x = \phi_i(t)$, $y = \psi_i(t)$, $i = 1, 2, \ldots, n$ in the xy-plane. Then the system* (2) *is uniformly persistent, provided for each periodic solution of period T,*

$$-m + \frac{1}{T}\int_0^T \frac{q\psi_i(t)}{1 + a\psi_i(t)}dt > 0, \quad i = 1, 2, \ldots, n.$$

Proof. Let $\theta(X)$ be the orbit through the point $X = (x, y, z)$ and $\Omega(X)$ be the omega-limit set of the orbit through X. Note that $\Omega(X)$ is bounded.

We claim that E_0 does not belong to $\Omega(X)$. If $E_0 \in \Omega(X)$, by Butler-McGehee lemma [16], there exists a point P in $\Omega(X) \cap W^S(E_0)$, where $W^S(E_0)$ denotes the stable manifold of E_0. Since $\theta(P)$ lies in $\Omega(X)$ and $W^S(E_0)$ is the yz-plane, we conclude that $\theta(P)$ is unbounded, which is a contradiction.

Next E_1 does not belong to $\Omega(X)$, for otherwise, since E_1 is a saddle point, which follows from the condition $c > d$, by Butler McGehee lemma, there exists a point P in $\Omega(X) \cap W^S(E_1)$. Now $W^S(E_1)$ is the x-axis implies that an unbounded orbit lies in $\Omega(X)$, which is contrary to the boundedness of the system.

Lastly we show that no periodic orbit in the xy-plane or E_2 belongs to $\Omega(X)$. The condition $m\{bc + a(c-d)\} > q(c-d) > 0$ implies that the eigenvalues λ_1 and λ_2 of $V(E_2)$ have negative real parts. Let $\gamma_i (i = 1, 2, \ldots, n)$ denotes the closed orbit of the periodic solution $(\phi_i(t), \psi_i(t))$ in xy-plane such that γ_i lies inside γ_{i-1}. The variational matrix $V_i(\phi_i(t), \psi_i(t), 0)$ corresponding to γ_i is given by

$$V_i = \begin{bmatrix} F(\phi_i(t), \psi_i(t)) & \phi_i(t)F_y(\phi_i(t), \psi_i(t)) & 0 \\ \psi_i(t)G_x(\phi_i(t), 0) & G(\phi_i(t), 0) & \psi_i(t)G_z(\phi_i(t), 0) \\ 0 & 0 & H(\psi_i(t)) \end{bmatrix}.$$

Here $H(\psi_i(t)) = -m + \frac{q\psi_i(t)}{1+a\psi_i(t)}$. Computing the fundamental matrix of the linear periodic system

$$M' = V_i(t)M, \quad M(0) = I,$$

we find that its Floquet multiplier in the z-direction is $e^{\eta_i(t)}$. Then proceeding in an analogous manner like Kumar and Freedman [18], we conclude that no γ_i lies in $\Omega(X)$. Thus $\Omega(X)$ lies in the positive octant and system (2) is persistent. Finally, since only the closed orbits and the equilibria form the omega limit set of the solutions on the boundary of R^3_+ and system (2) is dissipative, by the main theorem in [15], the system (2) is uniformly persistent. ☐

Corollary 1. *Let* $m\{bc + a(c-d)\} > q(c-d) > 0$ *and* $-m + \frac{q\hat{y}}{1+a\hat{y}} > 0$. *If there is no limit cycle in the* xy*-plane, system* (2) *is uniformly persistent.*

Proof is obvious.

4 The interior equilibrium point: its existence and stability

Lemma 2. *The interior equilibrium point* $E^*(x^*, y^*, z^*)$ *of the system* (2) *exists if* $q > m(a+b)$ *and* $m\{bc + a(c-d)\} < q(c-d)$. *When these condition are satisfied, then* x^*, y^*, z^* *are given by*

$$x^* = \frac{q - m(a+b)}{q - am}, \; y^* = \frac{m}{q - am} \text{ and } z^* = \frac{q\big[q(c-d) - m\big\{bc + a(c-d)\big\}\big]}{p(q-am)^2}.$$

The variational matrix of the system (2) at E^* is given by

$$V(E^*) = \begin{bmatrix} a_{11} & a_{12} & 0 \\ a_{21} & a_{22} & a_{23} \\ 0 & a_{32} & 0 \end{bmatrix},$$

where $a_{11} = -x^*,\ a_{12} = -bx^*,\ a_{21} = cy^*,\ a_{22} = \frac{am(cx^*-d)}{q},\ a_{23} = -\frac{py^*}{1+ay^*}$ and $a_{32} = \frac{qz^*}{(1+ay^*)^2}$.

The characteristic equation is

$$\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3 = 0,$$

where $A_1 = -a_{11} - a_{22} = \frac{qx^*-am(cx^*-d)}{q},\ A_2 = a_{11}a_{22} - a_{23}a_{32} - a_{12}a_{21}$ and $A_3 = a_{11}a_{23}a_{32} = \frac{pqx^*y^*z^*}{(1+ay^*)^3} > 0$.

We have

$$\Delta = A_1A_2 - A_3 = \frac{Dc^2 + Ec + F}{q^2y^*},$$

where

$$\begin{aligned} D &= amx^{*2}\{amx^*y^* - (bqy^{*2} + m^2)\}, \\ E &= q^2bx^{*2}y^{*2} + amqx^*y^*(bdy^* - x^{*2}) + 2am^2dx^*(m - ax^*y^*), \\ F &= a^2m^2d^2x^*y^* + amd(qx^{*2}y^* - m^2d). \end{aligned}$$

Now we have the following theorem guaranteeing the local stability of E^*.

Theorem 3. *If E^* exists with $qx^* - am(cx^* - d) > 0$ and $Dc^2 + Ec + F > 0$, then E^* is locally asymptotically stable.*

Proof. The condition $qx^* - am(cx^* - d) > 0$ implies that $A_1 > 0$. A_3 is always positive. Finally $Dc^2 + Ec + F > 0$ implies that $\Delta = A_1A_2 - A_3 > 0$. Hence, by Routh Hurwitz criterion, the theorem follows. ☐

Let Υ be the region in the xy-plane given by $\Upsilon = \{(x, y)\colon y^* < y < \frac{y^*z}{z^*}$ or $\frac{y^*z}{z^*} < y < y^*\}$. Then a criterion for the global stability of E^* in Υ is the following.

Theorem 4. *If E^* is locally asymptotically stable, then it is globally asymptotically stable in Υ.*

Proof. In Υ, let us consider the following positive definite function about E^*:

$$J(x,y,z) = M\Big(x-x^*-x^*\ln\frac{x}{x^*}\Big)+\Big(y-y^*-y^*\ln\frac{y}{y^*}\Big)+N\Big(z-z^*-z^*\ln\frac{z}{z^*}\Big),$$

where M, N are positive constants to be specified later on.

Differentiating J with respect to t along the solution of (2), a little algebraic manipulation yields

$$\begin{aligned}\frac{dJ}{dt} =& - M(x-x^*)^2 + (c-Mb)(x-x^*)(y-y^*)\\ &+ \frac{(Nq-p)(y-y^*)(z-z^*)}{(1+ay)(1+ay^*)} - \frac{ap(y^*z-yz^*)(y-y^*)}{(1+ay)(1+ay^*)}.\end{aligned}$$

Choosing $M = \frac{c}{b}$ and $N = \frac{p}{q}$, we see that $\frac{dJ}{dt}$ is negative definite in Υ and consequently J is a Lyapunov function with respect to all solutions in Υ, proving the theorem. ☐

5 Bifurcation analysis

In this section we provide conditions for the occurrence of a simple Hopf bifurcation near E^*. First we give, the definition of a simple Hopf bifurcation for a general three-species population model. Assume that the interior equilibrium depends smoothly on some parameter μ in an open interval I of R. If there exists a $\mu \in I$ such that (i) a simple pair of complex eigenvalues of the variational matrix of the interior equilibrium point exists, say, $\alpha(\mu) \pm i\beta(\mu)$ such that they becomes purely imaginary at $\mu = \mu^*$, whereas the other eigenvalue remain real and negative; and (ii) $\left(\frac{d\alpha}{d\mu}\right)_{\mu=\mu^*} \neq 0$, then at μ^* we have a simple Hopf bifurcation. Liu [19] derived a criterion of Hopf bifurcation without using the eigenvalues of the variational matrix of the interior equilibrium point. We specify below those results for the current case.

Liu's Criterion. *If the characteristic equation of the interior equilibrium point is given by* $\lambda^3 + a_1(\mu)\lambda^2 + a_2(\mu)\lambda + a_3(\mu) = 0$, *where* $a_1(\mu), a_3(\mu)$, $\Delta(\mu) = a_1(\mu)a_2(\mu) - a_3(\mu)$ *are smooth functions of* μ *in an open interval about* $\mu^* \in R$ *such that*

(i) $a_1(\mu^*) > 0,\ \ \Delta(\mu^*) = 0,\ \ a_3(\mu^*) > 0,$

(ii) $(\frac{d\Delta}{d\mu})_{\mu=\mu^*} \neq 0$,

then a simple Hopf bifurcation occurs at $\mu = \mu^*$.

Now, owing to the above criterion we have the following theorem.

Theorem 5. *If* E^* *exists with* $D < 0$, $E > 0$, $F < 0$ *and* $E^2 > 4DF$, *then a simple Hopf bifurcation occurs at the unique value* $c = c^* = \frac{1}{2D}(-E - \sqrt{E^2 - 4DF})$, *provided* $qx^* - am(c^*x^* - d) > 0$.

Proof. The characteristic equation of E^* is given by

$$\lambda^3 + A_1(c)\lambda^2 + A_2(c)\lambda + A_3(c) = 0.$$

We notice that $A_3 > 0$ for all positive values of c. Now $\Delta(c) = A_1(c)A_2(c) - A_3(c) = \frac{Dc^2+Ec+F}{q^2y^*}$ and it is easy to see that $\Delta(c^*) = 0$. Now, the condition $qx^* - am(c^*x^* - d) > 0$ implies that $A_1(c^*) > 0$. Furthermore, $(\frac{d\Delta}{dc})_{c=c^*} = -\frac{\sqrt{E^2-4DF}}{q^2y^*} < 0$. Hence, by Liu's criterion, the theorem follows. ☐

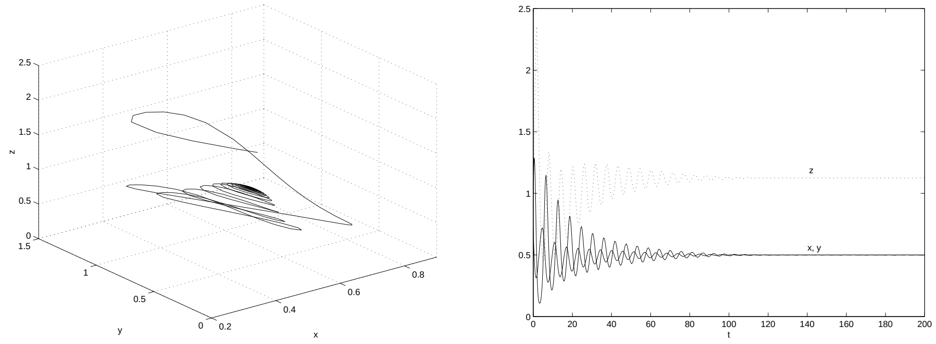
6 Numerical simulation

Analytical studies always remain incomplete without numerical verification of the results. Here we present computer simulation of some solutions of the system (2).

We take the parameters of the system as $b = 1,\ d = 1,\ c = 3,\ p = 1,\ a = 1,\ m = 1,\ q = 3$ and $(x(0), y(0), z(0)) = (0.7, 1, 1)$. Then $E^*(x^*, y^*, z^*) = (0.5, 0.5, 0.75)$ and $qx^* - am(cx^* - d) = 1 > 0$, $Dc^2 + Ec + F = 0.75 > 0$. Therefore, by Theorem 3, E^* is locally asymptotically stable. The corresponding phase portrait is shown in Fig. 1(a). Clearly the solution is a stable spiral converging to E^*. Fig. 1(b) shows that x, y and z populations approach to their steady-state values x^*, y^* and z^* respectively in finite time.

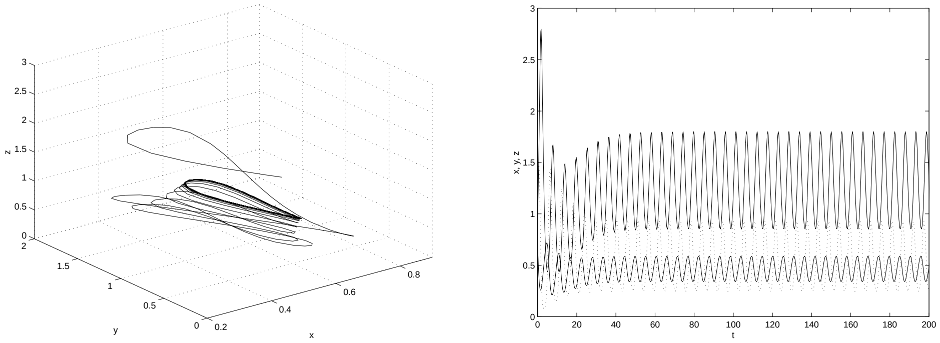
We notice that for the above choices of parameters, $D = -0.375 < 0$, $E = 1.5 > 0$, $F = -0.375 < 0$ and $E^2 - 4DF = 2.109375 > 0$. Now, if we gradually increase the value of c, keeping other parameters fixed, then following Theorem 5, we have a critical value $c^* = 3.7321$ such that E^* loses its stability as c passes through c^*. For $c = 4 > c^*$, we see that $E^* = (0.5, 0.5, 1.5)$ is unstable and there is a periodic orbit near E^*(see Fig. 2(a)). Oscillations of x, y, z in finite time are shown in Fig. 2(b).

The numerical study presented here shows that, using the parameter c as control, it is possible to break the stable behaviour of the system (2) and drive it to an unstable state. Also it is possible to keep the population levels at a required state using the above control.



(a) (b)

Fig. 1. Here $x(0) = 0.7,\ y(0) = 1,\ z(0) = 1$ and $b = 1,\ d = 1,\ c = 3,\ p = 1,$ $a = 1,\ m = 1,\ q = 3$. Phase portrait of the system (2) showing that E^* is locally asymptotically stable (a). $x,\ y,\ z$ approach to their equilibrium values in finite time (b).



(a) (b)

Fig. 2. Here all the parameter values are same as in Fig. 1 except $c = 4 > c^*$. Phase portrait of the system (2) showing periodic orbit near E^* (a). Oscillations of $x,\ y,\ z$ populations respectively in finite time. The top (solid) curve depicts $z(t)$, the bottom (solid) curve depicts $x(t)$ and the dotted one depicts $y(t)$ (b).

7 Concluding remarks

In this paper we have studied the dynamical behaviours of a tritrophic food chain model. As usual, a Lotka-Volterra functional response is taken to represent the interaction between prey and predator. The interaction between predator and superpredator is assumed to be governed by a Holling type-II functional response. Such different choices of functional responses may be particularly useful for plant-herbivore-parasitoid interactions or for plant-pest-predator interactions. It is shown (in Theorem 1) that the non-dimensionalized system (2) is uniformly bounded, which, in turn, implies that the system is biologically well behaved. Criteria for long time survival (persistence) of the populations of the system is presented in Section 3. It has long been recognized that most of the studies of continuous time deterministic models reveal two basic patterns: approach to an equilibrium or to a limit cycle. The basic rationale behind such type of analysis was the implicit assumption that most food chains we observe in nature correspond to stable equilibria of the model. From this viewpoint, we have presented the stability and bifurcation analysis of the most important equilibrium point E^*. The stability criteria given in Theorem 3 and 4 are the conditions for stable co-existence of the prey, the predator and the superpredator. Criteria for Hopf bifurcation (Theorem 5) provide the conditions for the existence of small amplitude periodic solution near E^*.

The nonlinear differential equations (2) may be looked upon as the mathematical model for tea plant (*Camellia sinensis L.*)-pest (e.g. Looper Caterpiller)-beneficial predator (natural enemy of the pest) (e.g. *Sarcophaga sp.*) [8]. Then we observe that the size of the tea plant (x) in the absence and presence of beneficial predator (z) are $\hat{x} = \frac{d}{c}$ and $x^* = \frac{q-m(a+b)}{q-am}$, respectively so that $x^* - \hat{x} = [c\{(q-am-bm) - d(q-am)\}/\{c(q-am)\}] > 0$. Also $\hat{y} - y^* = [\{c(q-am-bm) - d(q-am)\}/\{bc(q-am)\}] < 0$, where $\hat{y}$ and y^* are respectively the size of the pest population in absence and presence of predators. This implies that predator attack of pests enhance fitness of tea plants and cause depression for the pests. This gives a strong theoretical support to the approach of 'Bio-control of pests' which is suggested by several researchers to reduce the hazards of chemical pesticides [7, 8]. By similar arguments with the maize (*Zea mays*)-armyworm (*Spodoptera sp.*)-parasitoid (*Cotesa marginiventris*) system, we may arrive at the same conclusion with Turlings and Fritzsche [20] and

Fritzsche Hoballah and Turlings [4] that endoparasitic wasp or parasitoid may act as bodyguard for maize plant by attacking caterpillars. Also this result is in good agreement with the experimental findings of Gomez and Zamora [5] and Van Loon *et al.* [6] on plant-herbivore-parasitoid interactions.

All our important mathematical findings are numerically verified in section 6 and graphical representation of a variety of solutions of the systems (2) are depicted using MATLAB. Our numerical study shows that, using the parameter c as control, it is possible to break the stable (spiral) behaviour of the system and drive it to an unstable (cyclic) state. Also it is possible to keep the levels of the populations at a stable state using the above control.

It is well known that natural populations of plants and animals neither increase indefinitely to blanket the world nor become extinct (except in some rare cases and due to some rare reasons). Hence, in practice, we often want to reduce the predator y to an acceptable level in finite time. In order to accomplish this the parameters of the system should be regulated in such a way that $q > m(a + b)$, $m\{bc + a(c - d)\} < q(c - d)$, $qx^* - am(cx^* - d) > 0$ and $Dc^2 + Ec + F > 0$.

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