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Stability and Bifurcation Analysis of a Delayed Three Species Food Chain Model with Crowley-Martin Response Function

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Abstract

In this paper we have studied the dynamical behaviors of three species prey-predator system. The interaction between prey and middle-predator is Crowley-Martin type functional response. Positivity and boundedness of the system are discussed. Stability analysis of the equilibrium points is presented. Permanence and Hopf-bifurcation of the system are analyzed under some conditions. The effect of discrete time-delay is studied, where the delay may be regarded as the gestation period of the super-predator. The direction and the stability criteria of the bifurcating periodic solutions are determined with the help of the normal form theory and the center manifold theorem. Extensive numerical simulations are carried out to validate our analytical findings. Implications of our analytical and numerical findings are discussed critically.

Keywords: Food web; Prey-predator species; Stability; Permanence; Hopf-bifurcation; Time-delay

MSC 2010 No.: 34D20, 34C23, 34F10

1. Introduction

In the last few decades, the study of ecological modeling has become most interesting to theoretical biologists and mathematicians due to its rich dynamics, and it contributes important realizations into complex biological systems. Earlier, single species models (Ricker (1954), Vandermeer (2010)) and two species models such as predator-prey, plant-pest or plant-herbivore were studied extensively (Arditi et al. (1989), Berreta and Kuang (1998), Berrymem (1992), Hsu et al. (2001), Xiao and Ruan (2001)). Biomathematicians almost remained silent on the dynamical behaviors of three species systems for a long time. The explanation may be the lack of mathematical equipments to handle the increasing number of differential equations. However, urge for including more species had been noticed day by day and hence more emphasis should be made to review the complex behaviour presented by deterministic models consists of three or more tropic levels. In fact, different tritropic models have become issue of significant attention in their own right. Some mathematical models for tritropic food chains have been developed and analyzed in recent past but still theoretical studies on such systems are mostly inadequate. Some theoretical works on food chain models may be found in the works of many researchers (Freedman and Waltman (1977), Gard and hallam (1980), Freedman and Ruan (1992), Takeuchi et al. (1992), Ruan (1993), Boer et al. (1999), Kuznetsov et al. (2001), Hsu et al. (2001), Maiti et al. (2005, 2006), Pathak et al. (2009)).

The crucial element in prey-predator interaction is "predator functional response on prey population", which describes the number (biomass) of prey consumed per predator per unit time. Depending upon behavior of populations, more suitable functional responses have been developed as a quantification of the corresponding responsiveness of the predation rate to change in prey biomass at various population of prey. Functional response has a vital role on the stability and bifurcation dynamics of the underlying system. Several functional responses have been developed: Volterra functional response (Holling type-I), Michaelis- Menton type (Holling type-II), Holling type-III, Holling type-IV, Ratio dependent, Beddington - DeAngelis, Crowley-Martin (Berreta and Kuang (1998), Haiyin and Takeuchi (2011), Hsu et al. (2001), Liu et al. (2010), Oaten and Murdoch (1975), Ruan and Xiao (2001), Upadhyay and Naji (2009)). Holling I, II, III and IV type functional responses are prey dependent (i.e. functional response is a function of only prey's biomass) while Ratio dependent, Beddington - DeAngelis, Crowley-Martin response functions depend on prey and predator both (i.e. functional response is a function of both the prey's and predator's biomass). Mathematicians and ecologists have studied extensively on the dynamical behaviour of predator-prey models with Holling type-I, II, III and IV functional responses. Sklaski and Gillian (2001) explains in their work that predator- (and prey-) dependent functional responses can produce better description of predator feeding over a range of predator-prey abundance. It is observed through experiments that decrease in feeding rate of consumers (middle-predators) per unit consumer is due to mutual interference among predators (Hassell (1971), Tripathi et al. (2015)).

The prey-predator system with Beddington-DeAngelis functional response approve that handling and interference are complete activities (Dong et al. (2013), Haiyin and Takeuchi (2011), Tripathi et al. (2015)). According to Crowley and Martin (1989) when predator biomass is high, predator's predation rate decreases (interference among the predator individuals), in spite of prey biomass is high (in presence of handling or searching of the prey by predator individual). There are very few literatures available on prey-predator model with Crowley-Martin functional response (Dong et al. (2013), Crowley and Martin (1989), Sklaski and Gillian (2001), Upadhyay and Naji (2009), Upadhyay et al. (2010)). The Crowley-Martin (C-M) functional response is predator dependent. The instantaneous per capita feeding rate is given by

$$f(x,y) = \frac{ax}{(1+bx)(1+cy)}, \tag{1}$$

where the positive parameters a, b, c are considered as effects of capturing rate, handling time and magnitude of interference among predators respectively on the feeding rate. Compare to Beddington-DeAngelis functional response, C-M response has an additional term that models mutual interference among predators. Moreover, C-M type functional response allows for interference among predators nevertheless whether an individual predator is directly handling prey or searching for prey. Thus, the ecological model with C-M functional response gives momentum to Michaelis-Menton model and Beddington-DeAngelis model.

It is generally understood that the introduction of time delay into the population model is more realistic to model the interaction of the prey. In reality, time delays occur in almost every biological situation so that to ignore them is to ignore reality (Gopalsamy (1992), Hassard et al. (1981), Kuang (1993), Macdonald (1989)). It has been accepted that delay can have very complex impact on the dynamics of a system. Time delay due to gestation is a common example and it represents the time duration for conversion of prey biomass into predator biomass. The reproduction of predator after consuming prey in not instantaneous, but takes some discrete time (lag) required for gestation. The presence of gestation delay in predator growth affects the abundance of predator. Because the growth rate of predator species depends upon the amount of biomass added in predator population biomass as affect of prey killing. Thus, the main objective in studying delay differential equations is to assess the qualitative or quantitative differences that arise from including time-delays in an explicit way compare to the results with their non-delayed counterpart (Berreta and Kuang (1998), Celik (2008), Chen et al. (2007), May (1974), Qu and Wei (2007), Wangersky and Cunnigham (1957)).

In this work we have developed a mathematical model with a three-dimensional food-web system consisting a prey population (X), a middle-predator (Y) feeding on the prey and a super-predator (Z) feeding only on Y species. Here it is assumed that the interaction of the prey species (X) with the middle-predator (Y) is governed by Crowley-Martin functional response. A Holling type-II functional response is taken to represent the interaction between middle predator (Y) and super-predator (Z). It is assumed that there is no interaction between prey and super-predator. The construction of our model system is sketched in Section 2. The rest of the paper is organized as follows. In Section 3, positivity and boundedness of the basic deterministic model is discussed. Section 4 deals with the existence and stability of equilibria. Permanence of the system is studied in section 5. Hopf bifurcation around the interior equilibrium has been analyzed in Section 6. The effect of discrete time-delay is studied in Section 7. Direction and stability of the Hopf Bifurcation is discussed in Section 8. In Section 9, computer simulation of a variety of numerical solutions of the system is presented. Section 10 consists of the general discussions on the obtained analytical results and biological implications of our mathematical findings.

2. The Mathematical Model

Before introducing the mathematical model, let us perform brief sketch of the construction of the underlying model which indicates the biological relevance of the model.

1. Consider three species, namely the prey with population density (biomass) X at time T, the middle-predator with population density (biomass) Y at time T and the super-predator having population density (biomass) Z at time T.

2. Behavior of the entire community is assumed to arise from the coupling of the following interactions: Z preys only on Y and Y preys on X (see below). A distinctive feature of such a community is the so called 'domino effect': if one species dies out, all the species at the higher trophic level die out as well.

$$\begin{array}{c}\text{species } X\\ \downarrow\\ \text{species } Y\\ \downarrow\\ \text{species } Z\end{array}$$

The feeding relationship in the food chain

3. It is assumed that in the absence of predator the prey population biomass grows according to a logistic curve with carrying capacity K $(K > 0)$ and with an intrinsic growth rate constant r $(r > 0)$.

4. It is also assumed that the prey-predator interaction is governed by Crowley-Martin (simply written as C-M) response function of the form:

$$\frac{\beta xy}{(1 + Ax)(1 + By)}, \tag{2}$$

which was first proposed by Bazykin (1988). It is very important in theoretical ecology on its own right. Here β, A and B are positive parameters that describe the effects of capture rate, handling time, and the magnitude of interference among middle-predators on the feeding rate, respectively. This is a function of the biomass of both prey and predator due to predator interference. If the prey biomass is high, then also predator feeding rate can decrease by higher predator biomass. Therefore, the effects of predator interference on feeding rate remain important all the time whether an individual predator is handling or searching for a prey at a given instant of time (Zhou (2014)). This represents the per capita feeding rate of predator.

Depending on parameters A and B, the following cases arise:

(i) When $A = 0, B = 0$, the C-M functional response reduces to the Holling type-I (or Volterra) functional response.

(ii) When $A > 0, B = 0$, the C-M functional response reduces to the Holling type-II functional response.

(iii) When $A = 0, B > 0$, it expresses a saturation response of the middle-predator.

5. On the other hand, Holling type-II functional response is considered for the interaction of species (Y, Z).

These considerations lead to a food chain model under the framework of the following set of nonlinear ordinary differential equations:

$$\begin{aligned}
\frac{dX}{dT} &= rX\left(1-\frac{X}{K}\right) - \frac{\beta XY}{(1+AX)(1+BY)},\\
\frac{dY}{dT} &= \frac{\beta_1 XY}{(1+AX)(1+BY)} - D_1Y - \frac{\gamma YZ}{M+Y},\\
\frac{dZ}{dT} &= \frac{\gamma_1 YZ}{M+Y} - D_2 Z,
\end{aligned} \tag{3}$$

with

$$X(0) = X_0 > 0, Y(0) = Y_0 > 0, Z(0) = Z_0 > 0.$$

The model parameters $\beta,\ \gamma,\ \beta_1,\ \gamma_1,\ D_1,\ D_1$ and M are all assumed to be positive with following biological meanings:

β: Capturing rate (or predation coefficient) of middle-predator,

γ: Capturing rate (or predation coefficient) of super-predator,

β_1: Conversion rate of prey into middle-predator after predation,

γ_1: Conversion rate of middle predator into super-predator after predation,

D_1: Per capita death rate of middle-predator,

D_2: Per capita death rate of super-predator,

M: Half saturation constant for middle-predator.

To reduce the number of parameters, we use the following scaling (non-dimensionalization):

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

Then, the system (3) takes the form (after some simplifications):

$$\begin{aligned}
\frac{dx}{dt} &= x(1-x) - \frac{a_1xy}{(1+a_2x)(1+a_3y)},\\
\frac{dy}{dt} &= \frac{a_4xy}{(1+a_2x)(1+a_3y)} - d_1y - \frac{a_5yz}{1+a_6y},\\
\frac{dz}{dt} &= \frac{a_7yz}{1+a_6y} - d_2z,
\end{aligned} \tag{4}$$

with

$$x(0) = x_0 > 0, \quad y(0) = y_0 > 0, \quad z(0) = z_0 > 0,$$

where

$$a_1 = \frac{\beta K}{r}, a_2 = AK, a_3 = BK, a_4 = \frac{\beta_1 K}{r}, a_5 = \frac{\gamma K}{Mr}, a_6 = \frac{K}{M}, a_7 = \frac{\gamma_1 K}{Mr}, d_1 = \frac{D_1}{r}, d_2 = \frac{D_2}{r}.$$

3. Positivity and Boundedness

Positivity and boundedness of a model guarantee that the model is biologically well posed. For positivity of the system (4) , we have the following theorems.

Theorem 3.1.

All solutions of system (4) that start in $\mathbb{R}^3_+$ remain positive forever.

Proof:

From the first equation of system (4), we get

$$x(t) = x(0)\exp\left[\int_0^t \left\{1 - x(\theta) - \frac{a_1y(\theta)}{(1+a_2x(\theta))(1+a_3y(\theta))}\right\} d\theta\right] \Rightarrow x(t) > 0.$$

From the second equation of system (4), we get

$$y(t) = y(0)\exp\left[\int_0^t \left\{\frac{a_4x(\theta)}{(1+a_2x(\theta))(1+a_3y(\theta))} - d_1 - \frac{a_5z(\theta)}{1+a_6y(\theta)}\right\} d\theta\right] \Rightarrow y(t) > 0.$$

From the third equation of system (4), we get

$$z(t) = z(0)\exp\left[\int_0^t \left\{\frac{a_7y(\theta)}{1+a_6y(\theta)} - d_2\right\} d\theta\right] \Rightarrow z(t) > 0.$$

This proves the theorem. ■

Theorem 3.2.

All solutions of system (4) that start in $\mathbb{R}^3_+$ are uniformly bounded.

Proof:

Since

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

we have

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

Suppose

$$W_1 = x + \frac{a_1}{a_4}y + \frac{a_1 a_5}{a_4 a_7}z$$

$$\therefore \frac{dW_1}{dt} = x(1-x) - \frac{a_1 d_1 y}{a_4} - \frac{a_1 a_5 d_2 z}{a_4 a_7}$$

$$\Rightarrow \frac{dW_1}{dt} \leq x - \frac{a_1 d_1 y}{a_4} - \frac{a_1 a_5 d_2 z}{a_4 a_7}$$

$$\therefore \frac{dW_1}{dt} \leq 2x - RW_1, \text{ where } R = \min\{1, d_1, d_2\}.$$

$$\text{Hence, } \frac{dW_1}{dt} + RW_1 \leq 2x \leq 2, \text{ for large t, since } \lim_{t\to\infty} \sup x(t) \leq 1.$$

Applying a theorem on differential inequalities, we obtain

$$0 \leq W_1(x,y,z) \leq \frac{2}{R} + \frac{W_1(x(0),y(0),z(0))}{e^{Rt}} \Rightarrow 0 \leq W_1 \leq \frac{2}{R} \text{ as } t \to \infty.$$

Thus, all solutions of system (4) enter into the region:

$$B = \left\{(x,y,z) : 0 \leq W_1 < \frac{2}{R} + \epsilon, \text{ for any } \epsilon > 0\right\}.$$

This proves the theorem. ■

4. Equilibria and their Stability

System (4) may have the following equilibrium points.

(A) The trivial equilibrium point $E_0(0,0,0)$: It always exists.

(B) The axial equilibrium point $E_1(1,0,0)$: This predator free equilibrium exists unconditionally.

(C) The boundary equilibrium point $E_2(\hat{x},\hat{y},0)$ of system (4) is given by

$$b_1\hat{x}^3 + b_2\hat{x}^2 + b_3\hat{x} + a_1 d_1 = 0,$$

and

$$\hat{y} = \frac{\hat{x}(a_4 - a_2 d_1) - d_1}{d_1(a_3 + a_2 a_3 \hat{x})},$$

where

$$b_1 = a_2 a_3 a_4, \quad b_2 = a_3 a_4(1 - a_2) \text{ and } b_3 = a_1 a_2 d_1 + a_4(a_1 - a_3).$$

(D) The interior equilibrium point $E^*(x^*, y^*, z^*)$ of system (4) is given by

$$x^* = \frac{a_2 - 1}{2a_2} + \sqrt{\left(\frac{a_2 - 1}{2a_2}\right)^2 + b_4},$$

$$y^* = \frac{d_2}{a_7 - d_2 a_6},$$

and

$$z^* = \frac{1 + a_6 y^*}{a_5} \left\{ \frac{a_4 x^*}{(1 + a_2 x^*)(1 + a_3 y^*)} - d_1 \right\},$$

where

$$b_4 = 1 - \frac{a_1 d_2}{a_7 + d_2(a_3 - a_6)}.$$

This interior equilibrium exists only when

$$(i)\ a_7 > d_2 a_6,\ (ii)\ a_3 > a_1 \text{ and } (iii)\ a_4 x^* > d_1(1 + a_2 x^*)(1 + a_3 y^*).$$

Now we study the local stability behaviour of the equilibrium points by computing corresponding variational matrix:

$$V(x, y, z) = \begin{bmatrix} v_{11} & v_{12} & 0 \\ v_{21} & v_{22} & v_{23} \\ 0 & v_{32} & v_{33} \end{bmatrix},$$

where

$$v_{11} = 1 - 2x - \frac{a_1 y}{(1 + a_2 x)^2 (1 + a_3 y)}, \qquad v_{12} = -\frac{a_1 x}{(1 + a_2 x)(1 + a_3 y)^2},$$

$$v_{21} = \frac{a_4 y}{(1 + a_2 x)^2 (1 + a_3 y)}, \qquad v_{22} = \frac{a_4 x}{(1 + a_2 x)(1 + a_3 y)^2} - d_1 - \frac{a_5 z}{(1 + a_3 y)^2}$$

$$v_{23} = -\frac{a_5 y}{(1 + a_6 y)}, \qquad v_{32} = \frac{a_7 z}{(1 + a_6 y)^2}, \qquad v_{33} = \frac{a_7 y}{(1 + a_6 y)} - d_2.$$

At E_0, the variational matrix $V(E_0)$ becomes

$$V(E_0) = \begin{bmatrix} 1 & 0 & 0 \\ 0 & -d_1 & 0 \\ 0 & 0 & -d_2 \end{bmatrix}.$$

The corresponding eigenvalues are $1, -d_1, -d_2$ and hence, we have the following theorem:

Theorem 4.1.

E_0 is unstable.

At E_1, the variational matrix $V(E_1)$ is given by

$$V(E_1) = \begin{bmatrix} -1 & -\frac{a_1}{a_2+1} & 0 \\ 0 & \frac{a_4}{a_2+1} - d_1 & 0 \\ 0 & 0 & -d_2 \end{bmatrix}.$$

The corresponding eigenvalues are $-1, \frac{a_4}{a_2+1} - d_1$and $-d_2$.

Theorem 4.2.

E_1 is locally asymptotically stable if

$$\frac{a_4}{a_2+1} < d_2.$$

At E_2, the variational matrix $V(E_2)$ is given by

$$V(E_2) = \begin{bmatrix} 1 - 2\hat{x} - \frac{a_1\hat{y}}{(1+a_2\hat{x})^2(1+a_3\hat{y})} & -\frac{a_1\hat{x}}{(1+a_2\hat{x})^2} & 0 \\ \frac{a_4\hat{y}}{(1+a_2\hat{x})^2(1+a_3\hat{y})} & \frac{a_4\hat{x}}{(1+a_2\hat{x})(1+a_3\hat{y})^2} - d_1 - \frac{a_5\hat{y}}{1+a_6\hat{y}} & \\ 0 & 0 & \frac{a_7\hat{y}}{1+a_6\hat{y}} - d_2 \end{bmatrix}.$$

If the corresponding eigenvalues are λ_1, λ_2 and λ_3, then λ_1 and λ_2 are roots of the quadratic equation

$$\lambda^2 + C_1\lambda + C_2 = 0,$$

and

$$\lambda_3 = \frac{a_7\hat{y}}{1+a_6\hat{y}} - d_2,$$

where

$$C_1 = \hat{x} - \frac{a_1a_2\hat{x}\hat{y}}{(1+a_2\hat{x})^2(1+a_3\hat{y})} + \frac{a_3a_4\hat{x}\hat{y}}{(1+a_2\hat{x})(1+a_3\hat{y})^2},$$

and

$$C_2 = \frac{a_3a_4\hat{x}\hat{y}}{(1+a_2\hat{x})(1+a_3\hat{y})^2} + \frac{a_1a_4\hat{x}\hat{y}}{(1+a_2\hat{x})^3(1+a_3\hat{y})^3}\{1 - a_2a_3\hat{x}\hat{y}\}.$$

If $a_3a_4(1 + a_2\hat{x}) > a_1a_2(1 + \hat{y})$ and $a_2a_3\hat{x}\hat{y} < 1$, then C_1 and C_2 are positive. Therefore, all roots of $\lambda^2 + C_1\lambda + C_2 = 0$ are negative or having negative real parts. Also, if $a_7\hat{y} < d_2(1 + a_6)\hat{y}$, then E_2 is locally asymptotically stable. Hence, we have the following theorem:

Theorem 4.3.

E_2 is locally asymptotically stable if

$$a_3a_4(1 + a_2\hat{x}) > a_1a_2(1 + \hat{y}), a_2a_3\hat{x}\hat{y} < 1 \text{ and } a_7\hat{y} < d_2(1 + a_6)\hat{y}.$$

At E^*, the variational matrix $V(E^*)$ is given by

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

where

$$m_{11} = -x^* + \frac{a_1a_2x^*y^*}{(1 + a_3y^*)(1 + a_2x^*)^2}, \quad m_{12} = -\frac{a_1x^*}{(1 + a_2x^*)(1 + a_3y^*)^2},$$

$$m_{21} = \frac{a_4y^*}{(1 + a_2x^*)^2(1 + a_3y^*)}, \quad m_{22} = -\frac{a_3a_4x^*y^*}{(1 + a_3y^*)^2(1 + a_2x^*)} + \frac{a_5a_6y^*z^*}{(1 + a_6y^*)^2},$$

$$m_{23} = -\frac{a_5y^*}{(1 + a_6y^*)}, \quad m_{32} = \frac{a_7z^*}{(1 + a_6y^*)^2}.$$

The corresponding characteristic equation is given by

$$\lambda^3 + D_1\lambda^2 + D_2\lambda + D_3 = 0,$$

where

$$D_1 = -(m_{11} + m_{22}), \quad D_2 = (m_{11}m_{22} + m_{23}m_{32} - m_{12}m_{21}) \text{ and } D_3 = m_{11}m_{23}m_{32}.$$

By Routh-Hurwitz's criterion, all eigenvalues of $V(E^*)$ have negative real parts if

$$(i)\ D_1 > 0,\ (ii)\ D_3 > 0, \text{ and } (iii)\ D_1D_2 - D_3 > 0.$$

Thus, we have the following theorem.

Theorem 4.4.

E^* is locally asymptotically stable if $D_1 > 0, D_3 > 0$ and $D_1D_2 - D_3 > 0$.

Theorem 4.5.

Let E^* exists and $D = \left\{(x, y, z) \in \mathbb{R}^3_+ : y > \frac{a_5a_6a_7d_2x^*y^* - a_3(a_5d_2z^* + a_7d_1y^*)}{a_3a_6a_7d_1x^*y^*}\right\}$, then the equilibrium point E^* is globally asymptotically stable in D.

Proof:

Let us consider the following positive definite function about E^*:

$$V(x,y,z) = M\left(x - x^* - x^* \ln \frac{x}{x^*}\right) + \left(y - y^* - y^* \ln \frac{y}{y^*}\right) + N\left(z - z^* - z^* \ln \frac{z}{z^*}\right),$$

where M and N are positive constants to be specified later on. Differentiating V with respect to t along the solution of (4), a little algebraic manipulation yields:

$$\begin{aligned}\frac{dV}{dt} =& - M\left\{1 - \frac{a_1 a_2 y^*}{(1+a_2x)(1+a_2x^*)(1+a_3y^*)}\right\}(x-x^*)^2 + \left\{\frac{a_7N - a_5(1+a_6y^*)}{(1+a_6y)(1+a_6y^*)}\right\}\times \\ &(y-y^*)(z-z^*) - \left\{\frac{a_3a_6a_7d_1x^*y^*y - a_5a_6a_7d_2x^*y^* + a_3(a_5d_2z^* + a_7d_1y^*)}{(1+a_3y)(1+a_2x^*)(1+a_3y^*)(1+a_6y)(1+a_6y^*)}\right\} \\ &+ \left\{\frac{a_4(1+a_3y^*) - Ma_1(1+a_2x^*)}{(1+a_2x)(1+a_2x^*)(1+a_3y)(1+a_3y^*)}\right\}(x-x^*)(y-y^*).\end{aligned}$$

Let us choose $M = \frac{a_4(1+a_3y^*)}{a_1(1+a_2^*)}$ and $N = \frac{a_5(1+a_6y^*)}{a_7}$. It is noted that the existence of E^* implies $1 - \frac{a_1a_2y^*}{(1+a_2x)(1+a_2x^*)(1+a_3y^*)} > \frac{a_2x^*}{1+a_2x} > 0$. Therefore, $\frac{dV}{dt}$ is negative definite in D. Consequently, by the LaSalle Theorem (Harrison (1979), LaSalle (1976)) is globally asymptotically stable in D. ■

5. Permanence of the System

To prove the permanence of the system (4), we shall use the Average Liapunov functions (Gard and Hallam (1979)).

Theorem 5.1.

Suppose that the system (4) satisfies the following conditions:

$$(i)\ \frac{a_4}{a_2+1} > d_1,$$
$$(ii)\ \frac{a_7\hat{y}}{1+a_6\hat{y}} > d_2.$$

Then the system (4) is permanent.

Proof:

Let us consider the average Lyapunov function in the form $V(x,y,z) = x^{\theta_1}y^{\theta_2}z^{\theta_3}$ where each θ_i $(i = 1,2,3)$ is assumed to be positive. In the interior of $\mathbb{R}^3_+$, we have

$$\frac{\dot{V}}{V} = \psi(x,y,z) = \theta_1\left[(1-x) - \frac{a_1y}{(1+a_2x)(1+a_3y)}\right]$$

$$+\theta_2\left[\frac{a_4x}{(1+a_2x)(1+a_3y)} - d_1 - \frac{a_5z}{1+a_6y}\right] + \theta_3\left[\frac{a_7y}{1+a_6y} - d_2\right].$$

To prove permanence of the system we shall have to show that $\psi(x,y,z) > 0$ for all boundary equilibria of the system. The values of $\psi(x,y,z)$ at the boundary equilibria E_0, E_1, and E_2 are the following:

$$E_0 : \theta_1 - \theta_2 d_1 - \theta_3 d_2,$$
$$E_1 : \theta_2(\tfrac{a_4}{a_2+1} - d_1) - \theta_3 d_2,$$
$$E_2 : \theta_3 \left\{ \tfrac{a_7 \hat{y}}{1+a_6\hat{y}} - d_2 \right\}.$$

Now, $\psi(0,0,0) > 0$ is automatically satisfied for some $\theta_i > 0$ $(i = 1,2,3)$. Also, if the inequalities (i)-(ii) hold, ψ is positive at E_1 and E_2. Therefore, the system (4) is permanent. Hence the theorem. ■

Remark.

The conditions

$$E_1 : \tfrac{a_4}{a_2+1} - d_1 > 0;$$
$$E_2 : \tfrac{a_7\hat{y}}{1+a_6\hat{y}} - d_2 > 0,$$

guarantee that the boundary equilibrium points E_1 and E_2 are unstable.

6. Hopf Bifurcation at $E^*(x^*, y^*, z^*)$

The characteristic equation of the system (4) at $E^*(x^*, y^*, z^*)$ is given by

$$\lambda^3 + D_1(a_4)\lambda^2 + D_2(a_4)\lambda + D_3(a_4) = 0, \tag{5}$$

where

$$D_1(a_4) = \frac{a_3a_4x^*y^*}{(1+a_3y^*)^2(1+a_2x^*)} - \frac{a_5a_6y^*z^*}{(1+a_6y^*)^2} + x^* - \frac{a_1a_2x^*y^*}{(1+a_3y^*)(1+a_2x^*)^2},$$

$$D_2(a_4) = \frac{a_5a_7y^*z^*}{(1+a_6y^*)^3} + \frac{a_3a_4x^{*2}y^*}{(1+a_3y^*)(1+a_2x^*)} + \frac{a_1a_2a_5a_6x^*y^{*2}z^*}{(1+a_3y^*)(1+a_2x^*)^2(1+a_6y^*)^2}$$
$$+\frac{a_1x^*y^*}{(1+a_3y^*)^3(1+a_2x^*)^3} - \frac{a_1a_2a_3a_4x^{*2}y^{*2}}{(1+a_3y^*)^3(1+a_2x^*)^3} - \frac{a_5a_6x^*y^*z^*}{(1+a_6y^*)^2},$$

and

$$D_3(a_4) = \frac{a_5a_7y^*z^*}{(1+a_6y^*)^3}\left(\frac{a_1a_2x^*y^*}{(1+a_3y^*)(1+a_2x^*)^2} - x^*\right).$$

In order to see the instability of system (4) let us consider a_4 as bifurcation parameter. For this purpose let us first state the following theorem.

Theorem 6.1 (Hopf Bifurcation Theorem (Murray (1989))).

If $D_i(a_4), i = 1,2,3$ are smooth functions of a_4 in an open interval about $a_4^* \in \mathbb{R}$ such that the characteristic equation (5) has

(i) a pair of complex eigenvalues $\lambda = \alpha(a_4) \pm i\beta a_4$ (with $\alpha(a_4), \beta(a_4) \in \mathbb{R}$) so that they become purely imaginary at $a_4 = a_4^*$ and $\frac{d\alpha}{da_4}|_{a_4=a_4^*} \neq 0$,

(ii) the other eigenvalue is negative at $a_4 = a_4^*$, then a Hopf bifurcation occurs around E^* at $a_4 = a_4^*$ (i.e., a stability change of E^* accompanied by the creation of a limit cycle at $a_4 = a_4^*$).

Theorem 6.2.

System (4) possesses a Hopf bifurcation around E^* when a_4 passes through a_4^* provided $D_1(a_4^*), D_2(a_4^*) > 0$ and $D_1(a_4^*)D_2(a_4^*) = D_3(a_4^*)$.

Proof:

For $a_4 = a_4^*$, the characteristic equation of system (4) at E^* becomes

$$(\lambda^2 + D_2)(\lambda + D_1) = 0,$$

providing roots $\lambda_1 = i\sqrt{D_2}, \lambda_2 = -i\sqrt{D_2}$ and $\lambda_3 = -D_1$. Thus, there exists a pair of purely imaginary eigenvalues and a strictly negative real eigenvalue. Also $D_i (i = 1, 2, 3)$ are smooth functions of a_4.

So, for a_4 in a neighbourhood of a_4^*, the roots have the form $\lambda_1(a_4) = p_1(a_4) + ip_2(a_4)$, $\lambda_2(a_4) = p_1(a_4) - ip_2(a_4), \lambda_3 = -p_3(a_4)$, where $p_i(a_4), i = 1, 2, 3$ are real.

Next we shall verify the transversality conditions:

$$\frac{d}{da_4}(Re(\lambda_i(a_4)))|_{a_4=a_4^*} \neq 0,\ i = 1, 2.$$

Substituting $\lambda = p_i(a_4) + ip_i(a_4)$ into the characteristic equation (5), we get

$$(p_1 + ip_2)^3 + D_1(p_1 + ip_2)^2 + D_2(p_1 + ip_2) + D_3 = 0. \tag{6}$$

Now, let us take derivative of both sides of (6) with respect to a_4:

$$3(p_1+ip_2)^2(\dot{p_1}+i\dot{p_2})+2D_1(p_1+ip_2)(\dot{p_1}+i\dot{p_2})+\dot{D}_1(\dot{p_1}+i\dot{p_2})^2+D_2(\dot{p_1}+i\dot{p_2})+\dot{D}_2(\dot{p_1}+i\dot{p_2})+D_3 = 0. \tag{7}$$

Equating real and imaginary parts from the both sides of (7), we get

$$B_1\dot{p_1} - B_2\dot{p_2} + B_3 = 0, \tag{8}$$

and

$$B_2\dot{p_1} + B_1\dot{p_2} + B_4 = 0, \tag{9}$$

where

$$B_1 = 3(p_1^2 - p_2^2) + 2D_1p_1 + D_2, B_2 = 6p_1p_2 + 2D_1p_2,$$

$$B_3 = \dot{D}_1(p_1^2 - p_2^2) + \dot{D}_2p_1 + \dot{D}_3 \text{ and } B_4 = 2\dot{D}_1p_1p_2 + \dot{D}_2p_2.$$

From (8) and (9), we get

$$\dot{p_1} = -\frac{B_2 B_4 + B_1 B_3}{B_1^2 + B_2^2}. \tag{10}$$

Now,

$$B_3 = \dot{D}_1(p_1^2 - p_2^2) + \dot{D}_2 p_1 + \dot{D}_3 \neq \dot{D}_1(p_1^2 - p_2^2) + \dot{D}_2 p_1 + \dot{D}_1 D_2 + \dot{D}_2 D_1.$$

At $a_4 = a_4^*$:

Case I:

$$p_1 = 0, p_2 = \sqrt{D_2},$$

$$B_1 = -2D_2, B_2 = 2D_1\sqrt{D_2}, B_3 \neq \dot{D}_2 D_1, B_4 = \dot{D}_2\sqrt{D_2}.$$

Therefore,

$$B_2 B_4 + B_1 B_3 \neq 2D_1 D_2 \dot{D}_2 - 2D_1 D_2 \dot{D}_2 = 0.$$

So, $B_2 B_4 + B_1 B_3 \neq 0$ at $a_4 = a_4^*$, when $p_1 = 0, p_2 = \sqrt{D_2}$.

Case II:

$$p_1 = 0, p_2 = -\sqrt{D_2},$$

$$B_1 = -2D_2, B_2 = -2D_1\sqrt{D_2}, B_3 \neq \dot{D}_1 \dot{D}_2, B_4 = -\dot{D}_2\sqrt{D_2}.$$

Therefore,

$$B_2 B_4 + B_1 B_3 \neq 2D_1 D_2 \dot{D}_2 - 2D_1 D_2 \dot{D}_2 = 0.$$

So, $B_2 B_4 + B_1 B_3 \neq 0$ at $a_4 = a_4^*$, when $p_1 = 0, p_2 = -\sqrt{D_2}$.

Therefore,

$$\frac{d}{da_4}(Re(\lambda_i(a_4)))|_{a_4 = a_4^*} = -\frac{B_2 B_4 + B_1 B_3}{B_1^2 + B_2^2}|_{a_4 = a_4^*} \neq 0,$$

and

$$-p_3(a_4^*) = -D_1(a_4^*) < 0.$$

Hence, by theorem (5), the result follows. ∎

7. Effect of time-delay

In recent years, it is well understood that many of the processes, both natural and manmade, in biology, medicine, etc., involve some of the past histories which lead to introduce time-delays in the underlying model system. Time-delays occur so often, in almost every circumstances, that to ignore them is to ignore reality. The time-delay or lag can represent gestation time, incubation period, transport delay, or can simply lump complicated biological processes together, accounting only for the time required for these processes to occur. Kuang (1993) clearly mentioned that animals must take time to digest their food before further activities and responses. Hence, any model of species dynamics without time delay is an approximation at the best. In the last few decades, mathematical models based on delay differential equations (DDEs) have become more popular, appearing in many areas of mathematical biology. In general, delay differential equations (DDEs) exhibit much more complicated dynamics compare to ordinary differential equations (ODEs). A time-delay could cause a stable equilibrium to become unstable and cause the population to fluctuate. Detailed explanation on importance and usefulness of time-delay in realistic models may be found in the classical books of Macdonald (1989), Gopalsamy (1992), and Kuang (1993). Let us consider the model (4) with a discrete time-delay as follows:

$$\begin{aligned} \frac{dx}{dt} &= x(1-x) - \frac{a_1 xy}{(1+a_2x)(1+a_3y)}, \\ \frac{dy}{dt} &= \frac{a_4 xy}{(1+a_2x)(1+a_3y)} - d_1 y - \frac{a_5 yz}{1+a_6 y}, \\ \frac{dz}{dt} &= \frac{a_7 y(t-\tau) z}{1+a_6 y(t-\tau)} - d_2 z, \end{aligned} \tag{11}$$

with

$$x(0) = x_0 > 0, y(0) = y_0 > 0, z(0) = z_0 > 0.$$

System (11) has same equilibrium points as in system (4) mentioned in section 4. The eigenvalues corresponding to the variational matrix of the boundary equilibrium points $E_0(0,0,0), E_1(1,0,0), E_2(\hat{x},\hat{y},0)$ are same as in the case without delay. Consequently, the boundary equilibrium points of (4) and (11) behave alike with respect to local stability.

We now study the stability behavior of $E^*(x^*,y^*,z^*)$ in presence of delay ($\tau \neq 0$). Let us linearize system (11) using the following transformations:

$$x = x^* + u, y = y^* + v, z = z^* + w.$$

Then, the linear system is given by

$$\frac{dV}{dt} = A_1 V(t) + B_1 V(t-\tau), \tag{12}$$

with

$$V = [u, v, w]^T,$$

$$A_1 = \begin{bmatrix} c_{11} & c_{12} & 0 \\ c_{21} & c_{22} & c_{23} \\ 0 & 0 & 0 \end{bmatrix}, \quad B_1 = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & d_{32}e^{-\lambda\tau} & 0 \end{bmatrix},$$

where

$$c_{11} = -x^* + \frac{a_1a_2x^*y^*}{(1+a_3y^*)(1+a_2x^*)^2}, \;\; c_{12} = -\frac{a_1x^*}{(1+a_2x^*)(1+a_3y^*)^2},$$

$$c_{21} = \frac{a_4y^*}{(1+a_2x^*)^2(1+a_3y^*)}, \;\; c_{22} = -\frac{a_3a_4x^*y^*}{(1+a_3y^*)^2(1+a_2x^*)} + \frac{a_5a_6y^*z^*}{(1+a_6y^*)^2},$$

$$c_{23} = -\frac{a_5y^*}{(1+a_6y^*)}, \;\; d_{32} = \frac{a_7z^*}{(1+a_6y^*)^2}.$$

Let us choose solution of (11) in the form: $V(t) = \rho e^{\lambda t},\ 0 \neq \rho \in R^3$. Then, the characteristic equation is

$$\lambda^3 + P_1\lambda^2 + P_2\lambda + P_3(\lambda + P_4)e^{-\lambda\tau} = 0, \tag{13}$$

where

$$P_1 = -(c_{11} + c_{22}), P_2 = c_{11}c_{22} - c_{12}c_{21}, P_3 = -c_{23}d_{32} \text{ and } P_4 = c_{11}c_{23}d_{32}.$$

The system (11) is asymptotically stable in presence of delay if (i) equation (13) has no purely imaginary roots and (ii) it is asymptotically stable for $\tau = 0$. Otherwise, there exists $\tau = \tau_0$, where change of stability occurs. For $\tau = 0$, E^* is asymptotically stable if conditions of Theorem 4.4. are satisfied. Now we want to determine if the real part of some roots increases to reach zero and eventually becomes positive as τ varies or vice versa (that is, real parts of all roots decrease and become negative). For this we substitute $\lambda = \eta + i\omega$ in (13) and separating real and imaginary parts, we get

$$\eta^3 - 3\eta\omega^2 + P_1\left(\eta^2 - \omega^2\right) + P_2\eta + P_3\left\{(\eta + P_4)\, cos\ \omega\tau + \omega\ sin\ \omega\tau\right\} e^{-\eta\tau} = 0, \tag{14}$$

and

$$3\eta^2\omega - \omega^3 + 2\eta\omega P_1 + P_2\omega + P_3\left\{\omega\ cos\ \omega\tau - (\eta + P_4)\ sin\ \omega\tau\right\} e^{-\eta\tau} = 0. \tag{15}$$

Now, we check whether equation (13) have purely imaginary roots or not. So, we set $\eta = 0$. Then, (14) and (15) become

$$-P_1\omega^2 + P_3\left\{P_4 \cos\ \omega\tau + \omega \sin\ \omega\tau\right\} = 0, \tag{16}$$

and

$$-\omega^3 + P_2\omega + P_3\left\{\omega \cos\ \omega\tau - P_4 \sin\ \omega\tau\right\} = 0. \tag{17}$$

Eliminating τ from (16) and (17), we get the equation for determining ω as

$$\omega^6 + (p_1^2 - 2P_2)\omega^4 + (P_2^2 - P_3^2)\omega^2 - P_4^2P_3^2 = 0. \tag{18}$$

Substituting $\omega^2 = \alpha$ in (18), we get a cubic equation given by

$$\alpha^3 + R_1\alpha^2 + R_2\alpha + R_3 = 0, \tag{19}$$

where

$$R_1 = (P_1^2 - 2P_2), R_2 = (P_2^2 - P_3^2), R_3 = -P_4^2 P_3^2.$$

Since $R_3 < 0$, so equation (19) has at least one positive root.

Theorem 7.1.

Equation $\alpha^3 + R_1\alpha^2 + R_2\alpha + R_3 = 0$ has exactly three positive roots if $\beta_1^2 - 4\beta_0^3 \leq 0, R_1 < 0$ and $R_2 > 0$, otherwise it has only one positive real root, where $\beta_0 = R_1^2 - 3R_2,$ and $\beta_1 = 3R_1\beta_0 - R_1^3 + 27R_3$.

Proof:

Since $\beta_1^2 - 4\beta_0^3 \leq 0$, so the equation (19) has three real roots. Now $R_3 < 0$ implies that it has at least one positive root. Other two roots are real and positive or real and negative. Let α_0 be a positive real root of equation (19). Then, other two roots of the equation (19) are obtained from

$$\alpha^2 + (R_1 + \alpha_0)\alpha + R_2 + R_1\alpha_0 + \alpha_0^2 = 0. \tag{20}$$

Now we prove that equation (20) have two positive roots if $R_1 < 0$. If possible, let $R_1 > 0$. Then, sum of two positive roots is equal to $-(R_1 + \alpha_0) < 0$, which is impossible. Hence, $R_1 < 0$. So by Decartes' rule of sign equation (20) has three positive real roots if $R_2 > 0$. Hence, the theorem. ■

Theorem 7.2.

Let α_0 be a positive real root of equation (19). Then, (19) has

(i) exactly one real positive root, two imaginary roots if $\gamma(\alpha_0) > R_1^2 - 3R_2$,

(ii) one positive, two negative real roots if $\gamma(\alpha_0) < R_1^2 - 3R_2,\ R_2 + R_1\alpha_0 + \alpha_0^2 > 0$ and $R_1 + \alpha_0 > 0$,

(iii) three positive real roots if $\gamma(\alpha_0) < R_1^2 - 3R_2,\ R_2 + R_1\alpha_0 + \alpha_0^2 > 0$ and $R_1 + \alpha_0 < 0$, where $\gamma(\alpha) = 3\alpha^2 + 2\alpha R_1 + R_2$.

Proof:

Since $R_3 < 0$, so it has at least one positive real root α_0 (say).

Other two roots of (19) are obtained from

$$\alpha^2 + (R_1 + \alpha_0)\alpha + R_2 + R_1\alpha_0 + \alpha_0^2 = 0.$$

Then,

$$\alpha = \frac{-(R_1 + \alpha_0) \pm \sqrt{R_1^2 - 3R_2 - \gamma(\alpha_0)}}{2}.$$

Thus, if (i) holds, then equation (19) have one real positive root, two imaginary roots. If (ii) holds, then it has one positive, two negative roots. Finally, if (iii) holds, then (19) has three positive real roots. ■

Now we state a lemma which was proved by R Ruan and Wei (2003).

Theorem 7.3.

Consider the exponential polynomial:

$$\begin{aligned} Q(\lambda, e^{-\lambda\tau_1}, ..., e^{-\lambda\tau_m}) = {} & \lambda^n + Q_1^{(0)}\lambda^{n-1} + ... + Q_{n-1}^{(0)}\lambda + Q_n^{(0)} \\ & + \left[Q_1^{(1)}\lambda^{n-1} + ... + Q_{n-1}^{(1)}\lambda + Q_n^{(1)}\right] e^{-\lambda\tau_1} \\ & + ... + \left[Q_1^{(m)}\lambda^{n-1} + ... + Q_{n-1}^{(m)}\lambda + Q_n^{(m)}\right] e^{-\lambda\tau_m}, \end{aligned}$$

where $\tau_i \geq 0$ $(i = 1, 2, .., m)$ and $Q_j^{(i)}$ $(i = 0, 1, ..., m;\ j = 1, 2, ..., n)$ are constants. As $(\tau_1, \tau_2, .., \tau_m)$ vary, the sum of the orders of the zeros of $Q(\lambda, e^{-\lambda\tau_1}, ..., e^{-\lambda\tau_m})$ on the open half plane can change only if a zero appears on or crosses the imaginary axis.

Then, we show the existence of Hopf bifurcation near E^* by taking τ as bifurcation parameter.

Theorem 7.4.

Let E^* exists and the equation (19) has exactly one positive root, say $\alpha_0 = \omega_0^2$. Then, there exists a $\tau = \tau^*$ such that E^* is asymptotically stable when $\tau \in [0, \tau^*)$ and unstable when $\tau > \tau^*$, where

$$\tau_j^* = \frac{1}{\omega_0} \arccos \frac{\omega_0^2(\omega_0^2 + P_1P_4 - P_2)}{P_3(\omega_0^2 + P_4^2)} + \frac{2j\pi}{\omega_0}, j = 0, 1, 2 \cdots \tag{21}$$

and $\tau^* = \min_{j\geq 0} \tau_0^*$. In other words, system (11) exhibits a supercritical Hopf bifurcation near E^* for $\tau = \tau^*$.

Proof:

For $\tau = 0$, the real parts of all the roots of the characteristic equation (13) are negative. Now, the equation (13) has exactly one pair of purely imaginary roots when $\tau = \tau_j^*$.

It is easy to see that when $\tau \neq \tau_j^*,\ j = 0, 1, 2, \cdots$, equation (13) has no root with zero real part, and it has exactly one pair of purely imaginary roots when $\tau = \tau_j^*$. Now, τ^* is the minimum value of τ_j^* for $j = 0, 1, 2, \cdots$ and so, by Lemma 7.3., we conclude that all roots of (13) have negative real parts when $\tau \in [0, \tau^*)$. That is, E^* is stable for $\tau < \tau^*$.

When $\tau = \tau^*$, the characteristic equation (13) has a pair of purely imaginary roots and the underlying system loses its stability. It is noted that

$$\left[\frac{d\eta}{d\tau}\right]_{\tau=\tau^*} = \frac{\alpha_0\gamma(\alpha_0)}{A_3^2 + B_3^2} = \frac{\omega_0^2\gamma(\omega_0^2)}{A_3^2 + B_3^2},$$

where

$$A_3 = -3\omega_0^2 + P_2 + P_3(1 - P_4\tau^*)\cos\omega_0\tau^* - P_3\omega_0\tau^*\sin\omega_0\tau^*,$$

$$B_3 = -2P_1\omega_0 + P_3(1 - P_4\tau^*)\sin\omega_0\tau^* + P_3\omega_0\tau^*\cos\omega_0\tau^*.$$

Since equation (19) has only one positive root α_0, therefore, other two roots of the equation are either negative or complex conjugates. Now we prove that, in both cases, $\gamma(\omega_0^2) > 0$.

First we assume that other two roots of (13) are negative, say $-\alpha_3, -\alpha_4$ (so that $\alpha_3 > 0, \alpha_4 > 0$).

Then,

$$f(\alpha) \equiv \alpha^3 + R_1\alpha^2 + R_2\alpha + R_3 = (\alpha - \alpha_0)(\alpha + \alpha_3)(\alpha + \alpha_4),$$

$$\gamma(\omega_0^2) = f'(\alpha_0) = 3\alpha_0^2 + 2R_1\alpha_0 + R_2 = (\alpha_0 + \alpha_3)(\alpha_0 + \alpha_4) > 0. \tag{22}$$

Next we assume that other two roots of (13) are complex conjugates, say $\alpha_5 \pm i\alpha_6$. Then,

$$f(\alpha) = \alpha^3 + R_1\alpha^2 + R_2\alpha + R_3 = (\alpha - \alpha_0)\{(\alpha - \alpha_5)^2 + \alpha_6^2\},$$

$$\gamma(\omega_0^2) = f^{/}(\alpha_0) = 3\alpha_0^2 + 2R_1\alpha_0 + R_2 = (\alpha_0 - \alpha_5)^2 + \alpha_6^2 > 0.$$

So by Rouche's Theorem, when $\tau > \tau^*$, the characteristic equation (13) will have at least one root with positive real part, then the underlying system becomes unstable. That is, system (11) exhibits a Hopf-bifurcation near E^* for $\tau = \tau^*$. ■

Theorem 7.5.

Let E^* exists with $D_1 > 0, D_3 > 0$ and $D_1D_2 - D_3 > 0$. Let the equation (19) has three positive real roots $\alpha_0 = \omega_0^2, \alpha_1 = \omega_1^2, \alpha_2 = \omega_2^2$ such that ω_1^2 is lying between ω_0^2 and ω_2^2. Also let

$$\tau_j^{(i)} = \frac{1}{\omega_i} \arccos \frac{\omega_i^2(\omega_i^2 + P_1P_4 - P_2)}{P_3(\omega_i^2 + P_4^2)} + \frac{2j\pi}{\omega_i},\ i = 0, 1, 2; j = 0, 1, 2, \cdots,$$

$$\tau_k^+ = \min\{\tau_k^{(i)} : \ i = 0, 1, 2\},\ \tau_k^- = \tau_k^{(1)},\ \tau_k^* = \max\{\tau_k^{(i)} : \ i = 0, 1, 2\},\ k = 0, 1, 2, ...$$

(i) If $\tau_0^+ < \tau_0^- < \tau_1^+ < \tau_1^- < \cdots < \tau_k^+ < \tau_0^* < \tau_k^-$, then E^* is asymptotically stable when $\tau \in [0, \tau_0^+), (\tau_0^-, \tau_1^+), \cdots, (\tau_{k-1}^-, \tau_k^+)$ and unstable when $\tau \in [\tau_0^+, \tau_0^-), [\tau_1^+, \tau_1^-), \cdots, [\tau_{k-1}^+, \tau_{k-1}^-)$, $\tau \geq \tau_k^+$.

(ii) If $\tau_0^+ < \tau_0^- < \tau_1^+ < \tau_1^- < \cdots < \tau_k^+ < \tau_k^- < \tau_0^* < \tau_{k+1}^+$, then E^* is asymptotically stable when $\tau \in [0, \tau_0^+), (\tau_0^-, \tau_1^+), \cdots, (\tau_{k-1}^-, \tau_k^+), (\tau_k^-, \tau_0^*)$ and unstable when $\tau \in [\tau_0^+, \tau_0^-), [\tau_1^+, \tau_1^-), \cdots,$ $[\tau_k^+, \tau_k^-), \tau \geq \tau_0^*$.

(iii) If $\tau_0^+ < \tau_0^- < \tau_1^+ < \tau_1^- < \cdots < \tau_k^+ < \tau_{k+1}^+ < \tau_k^-$, then E^* is asymptotically stable when $\tau \in [0, \tau_0^+), (\tau_0^-, \tau_1^+), \cdots, (\tau_{k-1}^-, \tau_k^+)$, and unstable when $\tau \in [\tau_0^+, \tau_0^-), [\tau_1^+, \tau_1^-), \cdots, [\tau_{k-1}^+, \tau_{k-1}^-)$, $\tau \geq \tau_k^+$.

Proof:

For $\tau = 0$, real parts of all roots of the characteristic equation (13) are negative (see Theorem 4.4.).

Now the equation (19) has exactly three positive roots. In other words, equation (13) has purely imaginary roots when $\tau = \tau_k^+, \tau = \tau_k^-, \tau = \tau_k^*, k = 0, 1, 2, \cdots$. Since $\tau_k^+ < \tau_k^- < \tau_k^*$, by Lemma , we conclude that real parts of all roots of the characteristic equation (13) still remain negative when $\tau < \tau_0^+$. That is, E^* is stable in $[0, \tau_0^+)$. When τ takes any one of the values among $\tau_k^+, \tau_k^-, \tau_k^*$, the system loses its stability.

Now, we have the following two possible cases:

$a)$ $\left[\frac{d\eta}{d\tau}\right]_{\tau=\tau_k^+} = \frac{\alpha_0\gamma(\alpha_0)}{A_0^2(\tau_k^+)+B_0^2(\tau_k^+)} = \frac{\omega_0^2\gamma(\omega_0^2)}{A_0^2(\tau_k^+)+B_0^2(\tau_k^+)}$, $\left[\frac{d\eta}{d\tau}\right]_{\tau=\tau_k^*} = \frac{\alpha_2\gamma(\alpha_2)}{A_2^2(\tau_k^*)+B_2^2(\tau_k^*)} = \frac{\omega_2^2\gamma(\omega_2^2)}{A_2^2(\tau_k^*)+B_2^2(\tau_k^*)}$,

or

$b)$ $\left[\frac{d\eta}{d\tau}\right]_{\tau=\tau_k^+} = \frac{\alpha_2\gamma(\alpha_2)}{A_2^2(\tau_k^+)+B_2^2(\tau_k^+)} = \frac{\omega_2^2\gamma(\omega_2^2)}{A_2^2(\tau_k^+)+B_2^2(\tau_k^+)}$, $\left[\frac{d\eta}{d\tau}\right]_{\tau=\tau_k^*} = \frac{\alpha_0\gamma(\alpha_0)}{A_0^2(\tau_k^*)+B_0^2(\tau_k^*)} = \frac{\omega_0^2\gamma(\omega_0^2)}{A_0^2(\tau_k^*)+B_0^2(\tau_k^*)}$.

Also

$$\left[\frac{d\eta}{d\tau}\right]_{\tau=\tau_k^-} = \frac{\alpha_1\gamma(\alpha_1)}{A_1^2(\tau_k^-)+B_1^2(\tau_k^-)} = \frac{\omega_1^2\gamma(\omega_1^2)}{A_1^2(\tau_k^-)+B_1^2(\tau_k^-)}.$$

Here,

$$A_i(\tau) = -3\omega_i^2 + P_2 + P_3(1-P_4\tau)\cos\omega_i\tau - P_3\omega_i\tau\sin\omega_i\tau, i = 0,1,2,$$

and

$$B_i(\tau) = -2P_1\omega_i + P_3(1-P_4\tau)\sin\omega_i\tau + P_3\omega_i\tau\cos\omega_i\tau, i = 0,1,2.$$

Since, ω^2 $(i = 0,1,2)$ are roots of (19), so we rewrite the left side of equation (19) as

$$f(\alpha) = \alpha^3 + R_1\alpha^2 + R_2\alpha + R_3 = \prod_{i=0}^{2}(\alpha - \omega_i^2).$$

Then,

$$\gamma(\alpha) = \frac{df}{d\alpha} = 3\alpha^2 + 2R_1\alpha + R_2 = (\alpha-\omega_0^2)(\alpha-\omega_1^2) + (\alpha-\omega_0^2)(\alpha-\omega_2^2) + (\alpha-\omega_1^2)(\alpha-\omega_2^2).$$

So,

$$\gamma(\omega_0^2) > 0,\ \gamma(\omega_1^2) < 0,\ \gamma(\omega_2^2) > 0.$$

Hence, real part of at least one root of equation (13) becomes positive when $\tau > \tau_k^+$ and $\tau < \tau_k^-$ and all roots of (13) have negative real part when $\tau \in (\tau_{k-1}^-, \tau_k^+)$. Hence, if the conditions of (i) hold, then system is stable when $\tau \in (\tau_0^-, \tau_1^+), \cdots, (\tau_{k-1}^-, \tau_k^+)$ and unstable when $\tau \in [\tau_0^+, \tau_0^-), [\tau_1^+, \tau_1^-), \cdots, [\tau_{k-1}^+, \tau_{k-1}^-)$.

It is easy to see that, $\left[\frac{d\eta}{d\tau}\right]_{\tau=\tau_k^+}$ is positive. Also $\left[\frac{d\eta}{d\tau}\right]_{\tau=\tau_0^*}$ is positive. So the system is unstable when $\tau \geq \tau_k^+$.

Hence, (i) is proved.

In an analogous manner, (ii) and (iii) can be proved. ■

8. Direction and Stability of the Hopf Bifurcation

In the previous section, we obtained the conditions under which the Hopf bifurcation occurs. In this section, we shall derive the direction of the Hopf bifurcation and sufficient conditions of the stability of bifurcating periodic solution from the positive equilibrium E^* of the system (4) at the critical value $\tau = \tau^*$. We will utilize the approach of the normal form method and center manifold theorem introduced by Hassard et al. (1981).

Let $x_1 = x - x^*, x_2 = y - y^*, x_3 = z - z^*, \tau = \tau^* + \mu$, where τ^* is defined by (21) and $\mu \in \mathbb{R}$. Dropping the bars for simplification of notation, system (11) can be written as functional differential equation (FDE) in $C = C([-1, 0], \mathbb{R}^3)$ as

$$\dot{x(t)} = L_\mu(x_t) + f(\mu, x_t), \tag{23}$$

where $x(t) = (x_1, x_2, x_3)^T \in \mathbb{R}^3,$ and $L_\mu : C \to \mathbb{R}, f : \mathbb{R} \times C \to \mathbb{R}$ are given, respectively, by

$$L_\mu(\psi) = (\tau^* + \mu) \begin{bmatrix} c_{11} & c_{12} & 0 \\ c_{21} & c_{22} & c_{23} \\ 0 & 0 & 0 \end{bmatrix} \begin{bmatrix} \psi_1(0) \\ \psi_2(0) \\ \psi_3(0) \end{bmatrix} + (\tau^* + \mu) \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & d_{32} & 0 \end{bmatrix} \begin{bmatrix} \psi_1(-1) \\ \psi_2(-1) \\ \psi_3(-1) \end{bmatrix}, \tag{24}$$

$$f(\mu, \psi) = (\tau^* + \mu) \begin{bmatrix} -\psi_1^2(0) - \frac{a_1\psi_1(0)\psi_2(0)}{(1+a_2\psi_1(0))(1+a_3(0)\psi_2(0))} \\ \frac{a_4\psi_1(0)\psi_2(0)}{(1+a_2\psi_1(0))(1+a_3(0)\psi_2(0))} - \frac{a_5\psi_2(0)\psi_3(0)}{(1+a_6\psi_2(0))} \\ \frac{a_7\psi_2(-1)\psi_3(0)}{(1+a_6\psi_2(-1))} \end{bmatrix}. \tag{25}$$

By the Riesz representation theorem, there exists a (3×3) matrix, $\eta(\theta, \mu)(-1 \le \theta \le 0)$, where elements are bounded variation function such that

$$L_\mu\psi = \int_{-1}^{0} d\eta(\theta, \mu)\psi(\theta), \text{ for } \psi \in C. \tag{26}$$

In fact, we can choose

$$\eta(\theta, \mu) = (\tau^* + \mu) \begin{bmatrix} c_{11} & c_{12} & 0 \\ c_{21} & c_{22} & c_{23} \\ 0 & 0 & 0 \end{bmatrix} \delta(\theta) - (\tau^* + \mu) \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & d_{32} & 0 \end{bmatrix} \delta(\theta + 1), \tag{27}$$

where δ is the Direc delta function defined by

$$\delta(\theta) = \begin{cases} 0, & \theta \ne 0, \\ 1, & \theta = 0. \end{cases} \tag{28}$$

For $\psi \in C^1([-1, 0], \mathbb{R}^3)$, define the operator $A(\mu)$ as

$$A(\mu)\psi(\theta) = \begin{cases} \frac{d\psi(\theta)}{d\theta}, & \theta \in [-1, 0), \\ \int_{-1}^{0} d\eta(\mu, s)\psi(s), & \theta = 0, \end{cases} \tag{29}$$

$$R(\mu)\psi(\theta) = \begin{cases} 0, & \theta \in [-1, 0), \\ f(\mu, \psi), & \theta = 0. \end{cases}$$

Then, the system (23) is equivalent to

$$\dot{x}(t) = A(\mu)x_t + R(\mu)x_t, \tag{30}$$

where $x_t(\theta) = x(t+\theta)$ for $\theta \in [-1, 0]$. For $\phi \in C^1([0,1], (\mathbb{R}^3)^*)$, define

$$A^*\phi(s) = \begin{cases} \frac{-d\phi(s)}{ds}, & s \in [-1, 0), \\ \int_{-1}^{0} d\eta^T(t, 0)\phi(-t), & s = 0, \end{cases} \tag{31}$$

and a bilinear inner product

$$< \phi(s), \psi(\theta) >= \bar{\phi}(0)\psi(0) - \int_{-1}^{0}\int_{\xi=0}^{\theta} \bar{\phi}(\xi - \theta)d\eta(\theta)\psi(\xi)d\xi, \tag{32}$$

where $\eta(\theta) = \eta(\theta, 0)$. Then $A(0)$ and A^* are adjoint operators. we know that $\pm i\tau^*$ are eigenvalues of $A(0)$. Thus, they are also eigenvalues of A^*. We first need to compute the eigenvalues of $A(0)$ and A^* corresponding to $+i\tau^*\omega_0$ and $-i\tau^*\omega_0$ respectively.

Suppose that $q(\theta) = (1, q_1, q_2)^T e^{i\theta\omega_0\tau^*}$, is the eigenvector of $A(0)$ corresponding to $i\tau^*\omega_0$. Then, $A(0)q(\theta) = i\tau^*\omega_0 q(\theta)$. It follows from the definition of $A(0)$ and (24),(26) and (27) that

$$\tau^* \begin{bmatrix} i\omega_0 + c_{11} & c_{12} & 0 \\ c_{21} & i\omega_0 + c_{22} & c_{23} \\ 0 & d_{32}e^{-i\omega_0\tau^*} & i\omega_0 \end{bmatrix} q(0) = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}. \tag{33}$$

Thus, we can easily obtain

$$q(0) = (1, q_1, q_2)^T, \tag{34}$$

where

$$q_1 = \frac{i\omega_0 + c_{11}}{c_{12}} \text{ and } q_2 = \frac{d_{32}}{c_{12}}(i\omega_0 + c_{11})e^{-i\omega_0\tau^*}.$$

Similarly, let $q^*(s) = D(1, q_1^*, q_2^*)^T e^{is\omega_0\tau^*}$ be the eigenvector of A^* corresponding to $-i\omega_0\tau^*$. By the definition of A^*, we can compute

$$q^*(s) = D(1, q_1^*, q_2^*)^T e^{is\omega_0\tau^*} = D\left(1, \frac{(-i\omega_0 + c_{11})}{c_{12}}, \frac{d_{32}}{c_{12}}(-i\omega_0 + c_{11})e^{-i\omega_0\tau^*}\right). \tag{35}$$

In order to assure $< q^*(s), q(\theta) >= 1$, we need to determine the value of D. From (32), we have

$$\begin{aligned} < q^*(s), q(\theta) > &= \bar{D}(1, \bar{q}_1^*, \bar{q}_2^*)(1, q_1, q_2)^T - \textstyle\int_{-1}^0 \int_{\xi=0}^\theta \bar{D}(1, \bar{q}_1^*, \bar{q}_2^*)e^{i\omega_0\tau^*(\xi-\theta)}d\eta(\theta)(1, q_1, q_2)^T e^{i\omega_0\xi\tau^*}d\xi \\ &= \bar{D}\{1 + q_1\bar{q}_1^* + q_2\bar{q}_2^* - \textstyle\int_{-1}^0 (1, \bar{q}_1^*, \bar{q}_2^*)\theta e^{i\omega_0\theta\tau^*}d\eta(\theta)(1, q_1, q_2)^T\} \\ &= \bar{D}\{1 + q_1\bar{q}_1^* + q_2\bar{q}_2^* + \tau^* q_2^* q_1 d_{32} e^{-i\omega_0\tau^*}\}. \end{aligned} \tag{36}$$

Thus, we can choose $\bar{D}$ as

$$\begin{aligned} \bar{D} &= \frac{1}{\{1+q_1\bar{q}_1^*+q_2\bar{q}_2^*+\tau^* q_2^* q_1 d_{32} e^{-i\omega_0\tau^*}\}} \\ D &= \frac{1}{\{1+\bar{q}_1 q^*+\bar{q}_2 q^*+\tau^* q_2^* q_1 d_{32} e^{i\omega_0\tau^*}\}}. \end{aligned} \tag{37}$$

In the remainder of this section, we use the theory of Hassard et al. (1981) to compute the conditions describing center manifold C_0 at $\mu = 0$. Let x_t be the solution of (30) when $\mu = 0$.

Define

$$z(t) =< q^*, x_t >, W(t, \theta) = x_t(\theta) - 2Re\{z(t)q(\theta)\}. \tag{38}$$

On the center manifold C_0, we have

$$W(t, \theta) = W(z(t), \bar{z}(t), \theta), \tag{39}$$

where

$$W(z, \bar{z}, \theta) = W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta)z\bar{z} + W_{02}(\theta)\frac{\bar{z}^2}{2} + W_{30}(\theta)\frac{z^3}{6} + ... \tag{40}$$

z and $\bar{z}$ are local coordinates for center manifold C_0 in the direction of q^* and $\bar{q}^*$. Note that W is real if x_t is real. We only consider real solutions. For solution $x_t C_0$ of (30). Since $\mu = 0$, we have,

$$\dot{z}(t) = i\omega_0\tau^* z + \bar{q}^*(0)f(0, W(z, \bar{z}, \theta)) + 2Rezq(\theta) =^{def} i\omega_0\tau^* z + \bar{q}^*(0)f(z, \bar{z}). \tag{41}$$

We rewrite this equation as

$$\dot{z}(t) = i\omega_0\tau^* z(t) + g(z, \bar{z}), \tag{42}$$

where

$$g(z,\bar{z}) = \bar{q}^*(0) f_0(z,\bar{z}) \\ = g_{20}\frac{z^2}{2} + g_{11} z\bar{z} + g_{02}\frac{\bar{z}^2}{2} + g_{21}\frac{z^2\bar{z}}{2} + ... \tag{43}$$

We have $x_t(\theta) = (x_{1t}(\theta), x_{2t}(\theta), x_{3t}(\theta))$ and $q(\theta) = (1, q_1, q_2)^T e^{i\theta\omega_0\tau^*}$ so from (38) and (40) it follows that

$$x_t(\theta) = W(t,\theta) + 2Re z(t) q(t) \\ = W_{20}\frac{z^2}{2} + W_{11} z\bar{z} + W_{02}\frac{\bar{z}^2}{2} + (1, q_1, q_2)^T e^{i\omega_0\tau^*} z + (1, \bar{q}_1, \bar{q}_2)^T e^{-i\omega_0\tau^*}\bar{z} + ...$$

and then, we have

$$x_{1t}(0) = z + \bar{z} + W_{20}^{(1)}\frac{z^2}{2} + W_{11}^{(1)} z\bar{z} + W_{02}^{(1)}\frac{\bar{z}^2}{2} + \dots\ , \\ x_{2t}(0) = q_1 z + \bar{q}_1\bar{z} + W_{20}^{(2)}\frac{z^2}{2} + W_{11}^{(2)} z\bar{z} + W_{02}^{(2)}\frac{\bar{z}^2}{2} + \dots\ , \\ x_{3t}(0) = q_2 z + \bar{q}_2\bar{z} + W_{20}^{(3)}\frac{z^2}{2} + W_{11}^{(3)} z\bar{z} + W_{02}^{(3)}\frac{\bar{z}^2}{2} + \dots\ , \tag{44}$$

$$x_{1t}(-1) = z e^{-i\omega_0\tau^*} + \bar{z} e^{i\omega_0\tau^*} + W_{20}^{(1)}\frac{z^2}{2} + W_{11}^{(1)} z\bar{z} + W_{02}^{(1)}\frac{\bar{z}^2}{2} + \dots\ , \\ x_{2t}(-1) = q_1 z e^{-i\omega_0\tau^*} + \bar{q}_1\bar{z} e^{i\omega_0\tau^*} + W_{20}^{(2)}\frac{z^2}{2} + W_{11}^{(2)} z\bar{z} + W_{02}^{(2)}\frac{\bar{z}^2}{2} + \dots\ , \\ x_{3t}(-1) = q_2 z e^{-i\omega_0\tau^*} + \bar{q}_2\bar{z} e^{i\omega_0\tau^*} + W_{20}^{(3)}\frac{z^2}{2} + W_{11}^{(3)} z\bar{z} + W_{02}^{(3)}\frac{\bar{z}^2}{2} + \dots\ .$$

It follows from together with (25) that

$$g(z,\bar{z}) = \bar{q}^*(0) f_0(z,\bar{z}) = \bar{q}^*(0) f(0, x_t)$$

$$= \tau^*\bar{D}(1, \bar{q_1}^*, \bar{q_2}^*) \begin{pmatrix} x_{1t^2}(0) - \frac{a_1 x_{1t}(0) x_{2t}(0)}{(1+a_2 x_{1t}(0))(1+a_3 x_{2t}(0))} \\ \frac{a_4 x_{1t}(0) x_{2t}(0)}{(1+a_2 x_{1t}(0))(1+a_3 x_{2t}(0))} - \frac{a_5 x_{2t}(0) x_{3t}(0)}{(1+a_6 x_{2t}(0))} \\ \frac{a_7 x_{2t}(-1) x_{3t}(0)}{(1+a_6 x_{2t}(-1))} \end{pmatrix}$$

$$= \tau^*\bar{D}[(1 - a_1 q_1 + a_4 q_1^* q_1 - a_5 q_1^* q_1 q_2) + a_7 q_2^* q_1 q_2 e^{-i\omega_0\tau^*} z^2$$

$$+(2 - 2a_1 Re(q_1) + 2a_4 q_1^* Re(q_1) - 2a_5 q_1^* Re(q_1\bar{q_2})) + 2a_4 q_2^* Re(q_2\bar{q_1}) z\bar{z}$$

$$+(1 - a_1\bar{q_1} + a_4 q_1^* q_1 - a_5 q_1^*\bar{q_1}\bar{q_2}) + a_7 q_2^*\bar{q_1}\bar{q_2} e^{-i\omega_0\tau^*}\bar{z}^2 + \{(W_{20}^{(1)}(0) + 2W_{11}^{(1)}(0)$$

$$-\frac{a_1}{2}\bar{q_1} W_{20}^{(1)}(0) - \frac{a_1}{2} W_{20}^{(1)}(0) - a_1 q_1 W_{11}^{(1)}(0) - a_1 W_{11}^{(2)}(0) + a_1 a_2 q_1 + 2a_1 a_3 \mid q_1 \mid^2$$

$$+2a_1 a_2 Re(q_1) a_1 a_3 q_1^2) + q_1^*(\frac{a_4}{2} W_{20}^{(1)}(0) + \frac{a_4}{2} W_{20}^{(2)}(0) + a_4 W_{11}^{(1)}(0) q_1 + a_4 W_{11}^{(2)}(0)$$

$$-a_2 a_4 q_1 - a_3 a_4\bar{q_1} - 2a_2 a_4 Re(q_1) - 2a_3 a_4 q_1 Re(q_1) - \frac{a_5}{2}\bar{q_2} W_{20}^{(2)}(0) - \frac{a_5}{2}\bar{q_1} W_{20}^{(3)}(0)$$

$$-a_5 q_2 W_{11}^{(2)}(0) - a_5 q_1 W_{11}^{(3)}(0) + a_5 a_6 \mid q_1 \mid^2 q_2 + 2a_5 a_6 q_1 Re(q_1\bar{q_2}))$$

$$+\bar{q_2}^*(\frac{a_7}{2} W_{20}^{(3)}(0)\bar{q_1} e^{i\omega_0\tau^*}\frac{a_7}{2} W_{20}^{(2)}(-1)\bar{q_2} + a_7 W_{11}^{(3)}(0) q_1 e^{-i\omega_0\tau^*} + a_7 W_{11}^{(2)}(-1) q_2$$

$$-a_6a_7 \mid q_1 \mid^2 q_2e^{-i\omega_0\tau^*} - 2a_6a_7q_1Re(q_2\bar{q_1}))\}z^2\bar{z}]. \tag{45}$$

Comparing the coefficients with (43) that, we get

$$\begin{aligned}
g_{20} &= 2\tau^*\bar{D}[(1-a_1q_1) + \bar{q_1}^*(a_4q_1 - a_5q_1q_2) + \bar{q_2}^*a_7q_1q_2e^{-i\omega_0\tau^*}]\\
g_{11} &= 2\tau^*\bar{D}[(1-a_1Re(q_1)) + \bar{q_1}^*(a_4Re(q_1) - a_5Re(q_1\bar{q_2})) + \bar{q_2}^*a_7Re(\bar{q_1}q_2)]]\\
g_{02} &= 2\tau^*\bar{D}[(1-a_1\bar{q_1}) + \bar{q_1}^*(a_4\bar{q_1} - a_5\bar{q_1}\bar{q_2}) + \bar{q_2}^*a_7\bar{q_1}\bar{q_2}e^{i\omega_0\tau^*}
\end{aligned}$$

$$\begin{aligned}
g_{21} =&\tau^*\bar{D}[\{(2-a_1\bar{q_1})W_{20}^{(1)}(0) + 2(1-a_4q_1)W_0^{(1)}(0) - a_1(W_{20}^{(1)}(0) + 2W_{11}^{(1)}(0))\\
&+ 2a_1a_2(q_1 + 2Re(q_1)) + 2a_1a_3(q_1^2 + 2 \mid q_1 \mid^2)\} + \bar{q_1}^*\{a_4(2W_{11}^{(1)}(0)q_1 + W_{20}^{(1)}(0)\bar{q_1} + W_{20}^{(2)}(0)\\
&+ 2W_{11}^{(2)}(0)) - a_5(W_{20}^{(2)}(0)\bar{q_2} + 2W_{11}^{(2)}(0)q_2 + W_{20}^{(3)}(0)\bar{q_1} + 2W_{11}^{(2)}(0)\bar{q_1})\\
&- 2a_2a_4(q_1 + 2Re(q_1)) - 2a_3a_4(\bar{q_1} + 2q_1Re(q_1)) + 2a_5a_6(\mid q_1 \mid^2 q_2 + 2q_1Re(q_1\bar{q_2}))\}\\
&+ \bar{q_2}^*a_7(W_{20}^{(1)}(-1)\bar{q_1} + 2W_{11}^{(2)}(-1)q_2 + W_{20}^{(2)}(0)\bar{q_1}e^{i\omega_0\tau^*})\\
&- 2a_6a_7(\mid q_1 \mid^2 e^{-i\omega_0\tau^*} + 2q_1Re(q_2\bar{q_1}))].
\end{aligned} \tag{46}$$

Since these are $W_{20}(\theta)$ and $W_{11}(\theta)$ in g_{21}, we still need to compute them. From (30) and (38), we have

$$\dot{W} = \dot{x_t} - \dot{z}q - \dot{\bar{z}}\bar{q} = \begin{cases} AW - 2Re\bar{q}^*f_0q(\theta), & \theta \in [-1, 0) \\ AW - 2Re\bar{q}^*f_0q(\theta) + f_0, & \text{if } \theta = 0. \end{cases} \tag{47}$$

By definition $= AW + H(z, \bar{z}, \theta)$, where

$$H(z, \bar{z}, \theta) = H_{10}(\theta)\frac{z^2}{2} + H_{11}(\theta)z\bar{z} + H_{02}\frac{\bar{z}}{2} + ... \ . \tag{48}$$

Substituting the corresponding series into (47) and comparing the coefficients, we obtain

$$(A - 2i\omega_0\tau^*)W_{20} = -H_{20}(\theta), \ \ AW_{11}(\theta) = -H_{11}(\theta). \tag{49}$$

From (47), we know that for $\theta \in [-1, \theta)$,

$$H(z, \bar{z}, \theta) = -\bar{q}^*(0)f_0q(\theta) - q^*(0)\bar{f_0}\bar{q}(\theta) = -g(z, \bar{z})q(\theta) - \bar{g}(z, \bar{z})\bar{q}(\theta). \tag{50}$$

Comparing the coefficients with (48) ,we get

$$H_{20}(\theta) = -g_{20}(\theta)q(\theta) - \bar{g_{02}}(\theta)\bar{q}(\theta), \tag{51}$$

$$\dot{H_{11}}(\theta) = -g_{11}(\theta)q(\theta) - \bar{g_{11}}(\theta)\bar{q}(\theta). \tag{52}$$

From (49) and (51) and the definition of A, it follows that

$$\dot{H_{20}}(\theta) = 2i\omega_0\tau^*W_{20}(\theta) + g_{20}(\theta)q(\theta) + \bar{g_{02}}(\theta)\bar{q}(\theta). \tag{53}$$

Notice that $q(\theta) = (1, \beta, \gamma)^Te^{i\omega_0\tau^*\theta}$, hence

$$W_{20}(\theta) = \frac{ig_{20}}{\omega_0\tau^*}q(0)e^{i\omega_0\tau^*\theta} + \frac{i\bar{g_{20}}}{3\omega_0tau^*}\bar{q_0}e^{-i\omega_0\tau^*\theta} + E_1e^{2i\omega_0\tau^*\theta}, \tag{54}$$

where $E_1 = (E_1^1, E_1^2, E_1^3) \in \mathbb{R}^3$ is a constant vector.

Similarly, from (49) and (52), we obtain

$$W_{11}(\theta) = -\frac{ig_{11}}{\omega_0\tau^*}q(0)e^{i\omega_0\tau^*\theta} + \frac{i\bar{g_{11}}}{3\omega_0 tau^*}\bar{q_0}e^{-i\omega_0\tau^*\theta} + E_2, \tag{55}$$

where $E_2 = (E_2^1, E_2^2, E_2^3) \in \mathbb{R}^3$ is also a constant vector.

In what follows, are will seek appropriate E_1 and E_2 .From the definition of a A and (49), we obtain

$$\int_{-1}^{0} d\eta(\theta)W_{20}(\theta) = 2i\omega_0\tau^*W_{20}(0) - H_{20}(0), \tag{56}$$

$$\int_{-1}^{0} d\eta(\theta)W_{11}(\theta) = -H_{11}(0), \tag{57}$$

where $\eta(\theta) = \eta(0, \theta)$. By (47), we have

$$H_{20}(0) = -g_{20}q(0) - \bar{g_{02}}\bar{q_0} + 2\tau^* \begin{bmatrix} -1 + \frac{a_1q_1}{(1+a_3)(1+a_2)} \\ \frac{a_4q_1}{(1+a_2)(1+a_3)} - \frac{a_5q_1q_2}{1+a_6} \\ \frac{a_7q_1q_2}{(1+a_6)}e^{-2i\omega_0\tau^*} \end{bmatrix}, \tag{58}$$

$$H_{11}(0) = -g_{11}q(0) - \bar{g_{11}}\bar{q_0} + 2\tau^* \begin{bmatrix} -1 + \frac{a_1Re(q_1)}{(1+a_3)(1+a_2)} \\ \frac{a_4Re(q_1)}{(1+a_2)(1+a_3)} - \frac{a_5Re(q_1\bar{q_2})}{1+a_6} \\ \frac{a_7Re(q_1\bar{q_2})}{(1+a_6)} \end{bmatrix}. \tag{59}$$

Substituting (54) and (58) into (56) and noting that

$$(i\omega_0\tau^*I - \int_{-1}^{0} e^{i\omega_0\tau^*\theta}d\eta(0))q(0) = 0, \tag{60}$$

$$(-i\omega_0\tau^*I - \int_{-1}^{0} e^{-i\omega_0\tau^*\theta}d\eta(0))q(\bar{0}) = 0,$$

we obtain

$$\left(i\omega_0\tau^*I - \int_{-1}^{0} e^{i\omega_0\tau^*\theta}d\eta(0)\right)E_1 = 2\tau^* \begin{pmatrix} B_1^{(1)} \\ B_1^{(2)} \\ B_1^{(3)} \end{pmatrix}, \tag{61}$$

where

$$B_1^{(1)} = -1 + \frac{a_1 q_1}{(1+a_3)(1+a_2)}, B_1^{(2)} = \frac{a_4 q_1}{(1+a_2)(1+a_3)} - \frac{a_5 q_1 q_2}{1+a_6}, B_1^{(3)} = \frac{a_7 q_1 q_2}{(1+a_6)} e^{-2i\omega_0 \tau^*}.$$

This leads to

$$\begin{bmatrix} 2i\omega_0 - c_{12} & -c_{12} & 0 \\ c_{21} & 2i\omega_0 - c_{22} & -c_{23} \\ 0 & -d_{32}e^{i\omega_0\tau^*} & 2i\omega_0 \end{bmatrix} E_1 = 2 \begin{pmatrix} B_1^{(1)} \\ B_1^{(2)} \\ B_1^{(3)} \end{pmatrix}. \tag{62}$$

$$E_1^1 = \frac{2}{A} \begin{vmatrix} B_1^{(1)} & -c_{12} & 0 \\ B_1^{(2)} & 2i\omega_0 - c_{22} & -c_{23} \\ B_1^{(3)} & -d_{32}e^{2i\omega_0\tau^*} & 2i\omega_0 \end{vmatrix},$$

$$E_1^2 = \frac{2}{A} \begin{vmatrix} 2i\omega_0 - c_{11} & B_1^{(1)} & 0 \\ -c_{21} & B_1^{(2)} & -c_{23} \\ 0 & B_1^{(3)} & 2i\omega_0 \end{vmatrix},$$

$$E_1^3 = \frac{2}{A} \begin{vmatrix} 2i\omega_0 - c_{11} & -c_{12} & B_1^{(1)} \\ -c_{21} & 2i\omega_0 - c_{22} & B_1^{(2)} \\ 0 & -d_{32}e^{2i\omega_0\tau^*} & B_1^{(3)} \end{vmatrix}, \tag{63}$$

where

$$A = \begin{vmatrix} 2i\omega_0 - c_{12} & -c_{12} & 0 \\ c_{21} & 2i\omega_0 - c_{22} & -c_{23} \\ 0 & -d_{32}e^{i\omega_0\tau^*} & 2i\omega_0 \end{vmatrix}. \tag{64}$$

Similarly, substituting (53) and (59) into (57), we get

$$\begin{pmatrix} 2i\omega_0 - c_{12} & -c_{12} & 0 \\ c_{21} & 2i\omega_0 - c_{22} & -c_{23} \\ 0 & -d_{32}e^{i\omega_0\tau^*} & 2i\omega_0 \end{pmatrix} E_2 = 2 \begin{pmatrix} B_2^{(1)} \\ B_2^{(2)} \\ B_2^{(3)} \end{pmatrix}, \tag{65}$$

where

$$B_2^{(1)} = -1 + \frac{a_1 Re(q_1)}{(1+a_3)(1+a_2)}, \qquad B_1^{(2)} = \frac{a_4 Re(q_1)}{(1+a_2)(1+a_3)} - \frac{a_5 Re(q_1 q_2)}{1+a_6},$$
$$B_1^{(3)} = \frac{a_7 Re(q_1 q_2)}{(1+a_6)} e^{-2i\omega_0\tau^*}.$$

$$E_2^1 = \frac{2}{B} \begin{vmatrix} B_2^{(1)} & -c_{12} & 0 \\ B_2^{(2)} & 2i\omega_0 - c_{22} & -c_{23} \\ B_2^{(3)} & -d_{32} & 0 \end{vmatrix},$$

$$E_2^2 = \frac{2}{B} \begin{vmatrix} 2i\omega_0 - c_{11} & B_2^{(1)} & 0 \\ -c_{21} & B_2^{(2)} & -c_{23} \\ 0 & B_1^{(3)} & 0 \end{vmatrix},$$

$$E_2^3 = \frac{2}{B} \begin{vmatrix} 2i\omega_0 - c_{11} & -c_{12} & B_2^{(1)} \\ -c_{21} & 2i\omega_0 - c_{22} & B_2^{(2)} \\ 0 & -d_{32} & B_2^{(3)} \end{vmatrix}, \tag{66}$$

where

$$B = \begin{vmatrix} 2i\omega_0 - c_{11} & -c_{12} & 0 \\ c_{21} & 2i\omega_0 - c_{22} & -c_{23} \\ 0 & -d_{32} & 2i\omega_0 \end{vmatrix}. \tag{67}$$

Thus, we determine $W_{20}(\theta)$ and $W_{11}(\theta)$ from (54) and (59) into (58). Furthermore, g_{21} in (46) can be expressed by the parameters and delay. Thus, we can compute the following values:

$$\begin{aligned} c_1(0) &= \tfrac{i}{2\omega_0\tau^*}(g_{20}g_{11} - 2 \mid g_{11} \mid^2 - \tfrac{2|g_{12}|^2}{3}) + \tfrac{g_{11}}{2}, \\ \gamma_2 &= -\tfrac{Re\{c_1(0)\}}{Re\{\acute{\xi}(\tau^*)\}}, \\ \beta_2 &= 2Re\{c_1(0)\}, T_2 = -\tfrac{I_m c_1(0) + \gamma_2 I_m \acute{\xi}(\tau^*)}{\omega_0 \tau^*}. \end{aligned} \tag{68}$$

which determines the qualities of bifurcating periodic solution in the centre manifold at the critical value τ^*.

9. Numerical Simulation

Analytical studies can never be justified without numerical verification of the derived results. In this section, we present computer simulation of different solutions of system (4) using MATLAB.

First let us take the value of the parameters of system (4) as $a_1 = 0.2, a_2 = 0.3, a_3 = 0.17, a_4 = 0.4, d_1 = 0.38, a_5 = 1.9, a_6 = 1.5, a_7 = 0.09, d_2 = 0.3$. Then, the conditions of Theorem 4.2. are satisfied and consequently $E_1(1, 0, 0)$ is locally asymptotically stable (see Figure 1). Also we take the parameters of the system as $a_1 = 0.2, a_2 = 0.3, a_3 = 0.17, a_4 = 0.4, d_1 = 0.25, a_5 = 0.2, a_6 = 0.2, a_7 = 0.3, d_2 = 0.2$. Then, the conditions of Theorem 4.3. are satisfied and consequently $E_2(\hat{x}, \hat{y}, 0)$ is locally asymptotically stable (see Figure 2). Next, we take the parameters as $a_1 = 0.2, a_2 = 0.1, a_3 = 0.05, a_4 = 0.45, d_1 = 0.25, a_5 = 0.2, a_6 = 0.2, a_7 = 0.3, d_2 = 0.2$. Then, conditions are satisfied, and hence $E^*(0.8791, 0.7692, 0.5778)$ exists. Also the conditions of Theorem

4.4. are satisfied. Consequently, E^* is locally asymptotically stable. The phase portrait is shown Figure 3. The stable behaviour of x, y, z with t is presented in Figure 4.

It is noted that the conversion rate (a_4) of the prey populations has a great influence in the dynamic of system (4). It undergoes a Hopf-bifurcation around E^* at $a_4^* = 1.9890$. Figures 5 and 6 show stable phase portrait and stable behaviour of x, y, z in time of system (4) respectively when the value of the parameter a_4 is less than its critical value a_4^*, i.e. when $a_4 = 1.2 < a_4^* = 1.9890$. Figures 7 and 8 depict the unstable phase portrait and unstable behaviour of x, y, z in time respectively of system (4) when $a_4 = 3.5 > a_4^* = 1.9890$, values of other parameters remain same. Conditions of Theorem 6.2. are fulfilled.

It has already been mentioned that the stability criteria in absence of delay $(\tau = 0)$ will not necessarily guarantee the stability of system (11) in presence of delay $(\tau \neq 0)$. If we choose the value of the parameters of system (11) as $a_1 = 0.15, a_2 = 0.1, a_3 = 0.05, a_4 = 0.45, d_1 = 0.25, a_5 = 0.2, a_6 = 0.2, a_7 = 0.3, d_2 = 0.2$, then equation (19) has one positive and two imaginary roots, and Hopf-bifurcation occurs at $\tau = \tau_0^* = 1.79$. For $\tau = 1.6 < \tau_0^*$, we see that $E^*(0.8791, 0.7692, 0.5778)$ is asymptotically stable (Figures 9 and 10). Clearly the phase portrait is a stable spiral converging to E^*. If we gradually increase the value of τ (keeping other parameter fixed), it is observed that E^* loses its stability at $\tau = \tau_0^* = 1.8998$. For $\tau = 2.1 > \tau_0^*, E^*$ is unstable and there is a bifurcating periodic solution near E^*, which is shown in Figure 11. The oscillations of x, y, z with t is shown in Figure 12.

If we choose the value of the parameters of system (11) as $a_1 = 2.5; a_2 = 1; a_3 = 1.0; a_4 = 2; d_1 = 0.2; a_5 = 2; a_6 = 0.2; a_7 = 1.5; d_2 = 0.2$, then equation (19) has three positive real roots: 0.8821, 0.6183, 0.0084. The equilibrium point E^* is (0.8359, 0.1370,0.3020) and $\tau_0^+ = 0.4070, \tau_0^- = 2.5542, \tau_0^* = 13.8021, \tau_1^+ = 7.1046, \tau_1^- = 10.5448$, $\tau_2^+ = 18.5334$. It is noted that the equilibrium E^* is stable for $\tau \in [0, 0.4070)$, $(2.5542, 7.1046)$, $(10.5448, 13.8021)$ and unstable for $\tau \in [0.4070, 2.542)$, $[7.1046, 10.5448)$ and $\tau \geq 13.802$. Figure 13 depicts the stable phase portrait of the system when $\tau = 0.39$. Stable behavior of x, y, z with time is shown in Figure 14, when $\tau = 0.3$. Also Figure 15 depicts the unstable phase portrait of the system when $\tau = 1.4$. Unstable behavior of x, y, z with time is shown in Figures 16 when $\tau = 1.55$.

10. Conclusion

In this work, we have formulated a mathematical model with a three-dimensional food-web system consisting of a prey population (X), a middle-predator (Y) feeding on the prey and super-predator (Z) feeding on only Y species. Here it is assumed that the interaction of the prey species (X) with the middle-predators (Y) according to Crowley-Martin response function. Also middle predator (Y) is predated by the super-predator (Z) according to Holling Type-II response function. The details of the construction of the model is presented in section 2. Positivity and boundedness of the system are shown in section 3. In deterministic situation, theoretical ecologists are usually guided by an implicit assumption that most food chains observed in nature correspond to stable equilibria of the models. From this viewpoint, we have presented the stability analysis of the coexistence equilibrium point $E^*(x^*, y^*, z^*)$. The stability criteria provided in Theorem 4.4. are the conditions for stable coexistence of the prey, the middle-predator and the super-predator. The conditions for permanence and Hopf-bifurcation around interior equilibrium of the system are analyzed under some conditions. In this context it is mentioned that if fur seals are assumed as super-predator (Z) and commercial fishes as middle-predator (Y), then numerical simulations Figure 1, Figure 2 and Figure 4 are in good agreement with the experiments (using field data) performed by Yodzis (1998).

We have also investigated the effect of discrete time delay on the underlying model, where the delay can be regarded as a gestation period or reaction time of the super-predator. We have presented a rigorous analysis of the stability and bifurcation of the coexistence (interior) equilibrium point. Our analysis shows that the value of delay in certain specified range could guarantee the stable coexistence of the species. On the other hand, the delay could drive the system to an unstable state. Thus, the time-delay has a regulatory impact on the whole system. The normal form theory and center manifold reduction have been used and we have derived the explicit formulae which determine the stability, direction and other properties of bifurcating periodic solutions. The theoretical investigation which have been carried out in this work will definitely help the experimental ecologists to do some experimental studies and as a result the theoretical ecology may be developed to some extent.

Our model is not a case study and so it is difficult to choose parameter values from quantitative estimation. The hypothetical sets of parameter values are used to verify the analytical findings obtained in this work. In future work, it would be interesting to expand on simulations by using realistic data to estimate the parameters.

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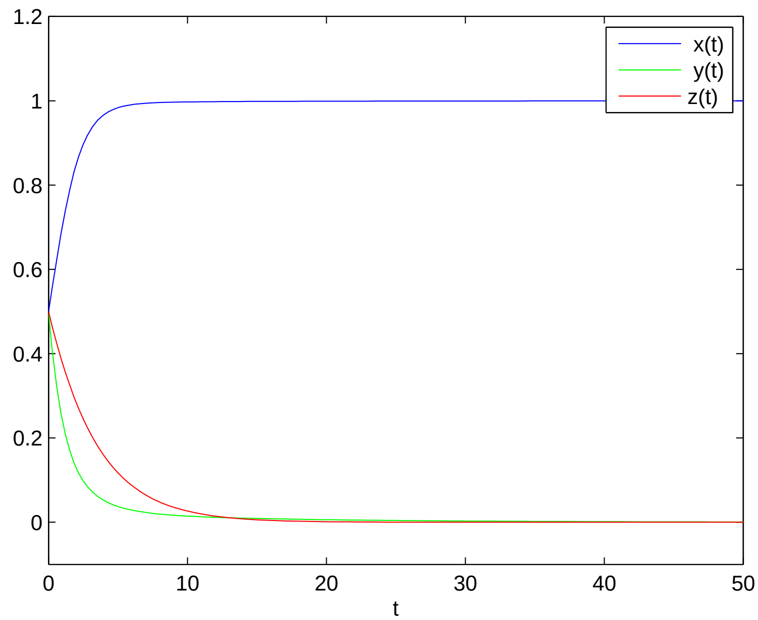

Figure 1. Here $a_1 = 0.2, a_2 = 0.3, a_3 = 0.17, a_4 = 0.4, d_1 = 0.38, a_5 = 1.9, a_6 = 1.5, a_7 = 0.09, d_2 = 0.3$ and $(x(0), y(0), z(0)) = (0.5, 0.5, 0.5)$, $E_1(1, 0, 0)$ is locally asymptotically stable.

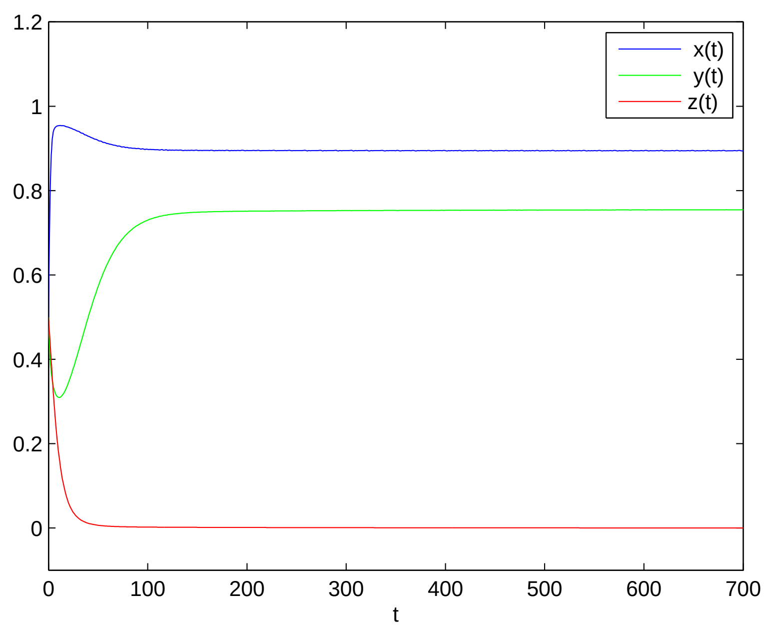

Figure 2. Here $a_1 = 0.2, a_2 = 0.3, a_3 = 0.17, a_4 = 0.4, d_1 = 0.25, a_5 = 0.2, a_6 = 0.2, a_7 = 0.3, d_2 = 0.2$ and $(x(0), y(0), z(0)) = (0.5, 0.5, 0.5)$, E_2 is locally asymptotically stable.

Figures 3 and 4. Here $a_1 = 0.2, a_2 = 0.1, a_3 = 0.05, a_4 = 0.45, d_1 = 0.25, a_5 = 0.2, a_6 = 0.2, a_7 = 0.3, d_2 = 0.2$. It shows that $E^*(x^*, y^*, z^*)$ is locally asymptotically stable, where $x^* = 0.8791, y^* = 0.7692, z^* = 0.5778$.

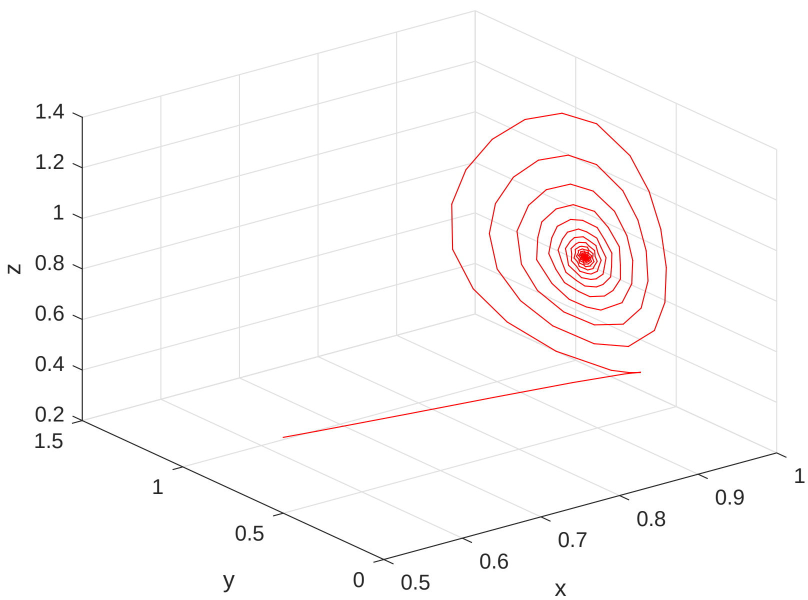

Figure 3. Here $a_1 = 0.2, a_2 = 0.1, a_3 = 0.05, a_4 = 0.45, d_1 = 0.25, a_5 = 0.2, a_6 = 0.2, a_7 = 0.3, d_2 = 0.2$. It shows that $E^*(x^*, y^*, z^*)$ is locally asymptotically stable, where $x^* = 0.8791, y^* = 0.7692, z^* = 0.5778$.

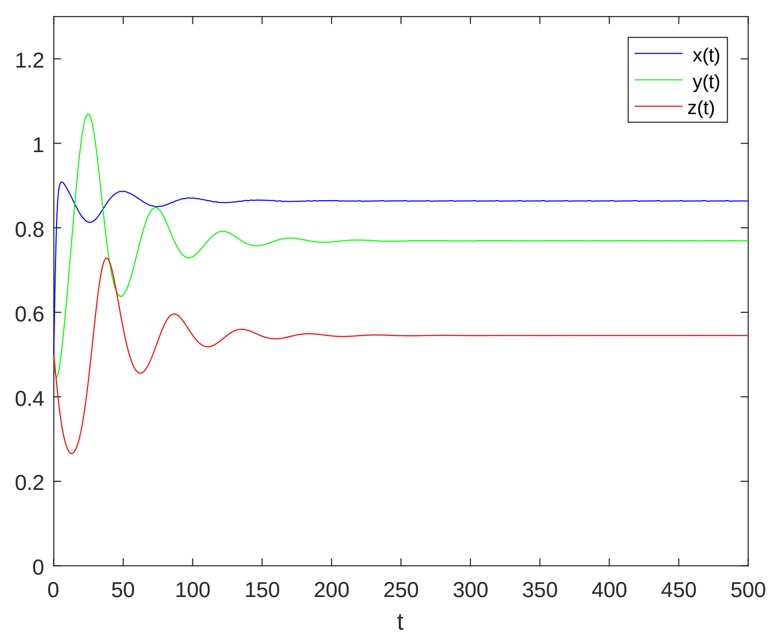

Figure 4. Here $a_1 = 0.2, a_2 = 0.1, a_3 = 0.05, a_4 = 0.45, d_1 = 0.25, a_5 = 0.2, a_6 = 0.2, a_7 = 0.3, d_2 = 0.2$. It shows that $E^*(x^*, y^*, z^*)$ is locally asymptotically stable, where $x^* = 0.8791, y^* = 0.7692, z^* = 0.5778$.

Figures 5 and 6. Here $a_1 = 0.2, a_2 = 0.1, a_3 = 0.05, d_1 = 0.25, a_5 = 0.2, a_6 = 0.2, a_7 = 0.3, d_2 = 0.2$ and $a_4 = 1.2 < a_4^* = 1.9890$ depicts the phase portrait stable behavior and also stable behavior of x, y, z with time t respectively.

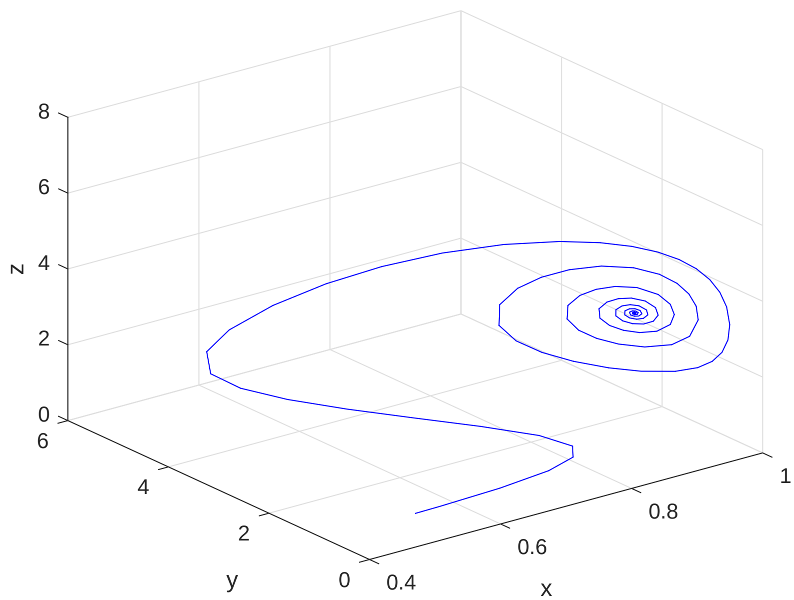

Figure 5

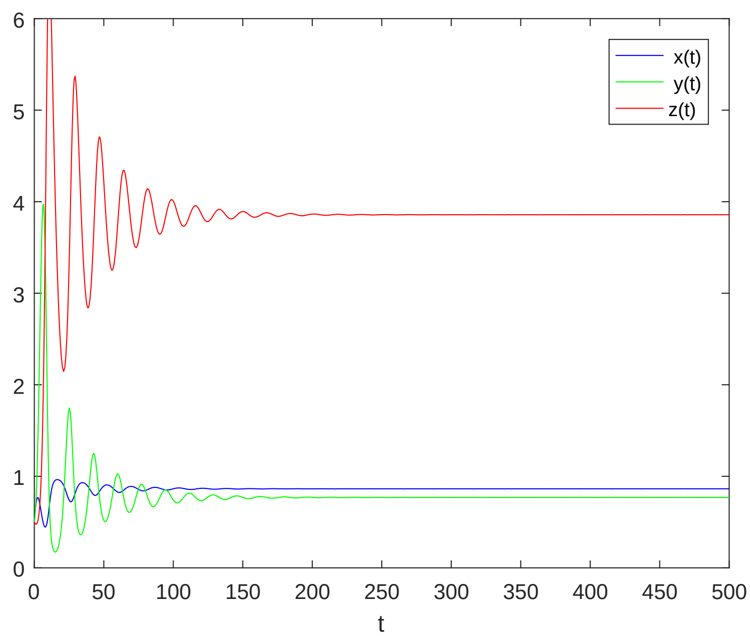

Figure 6

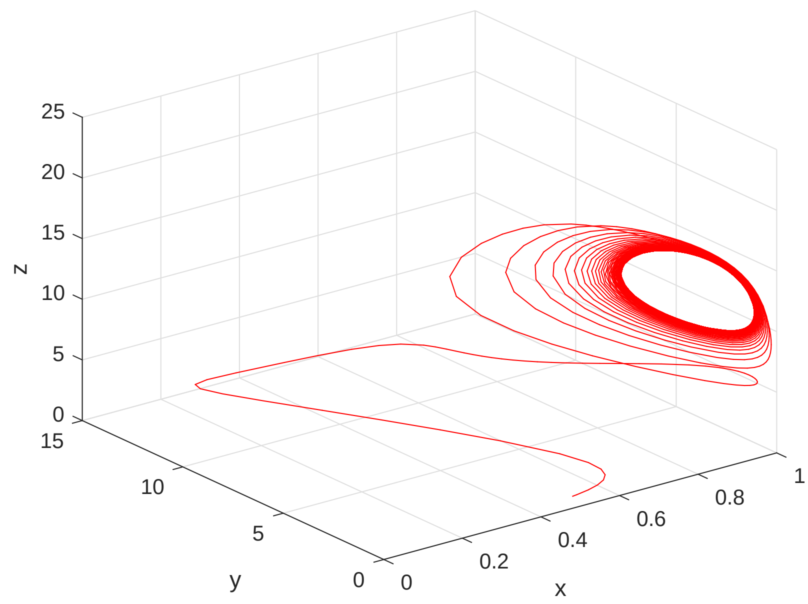

Figure 7

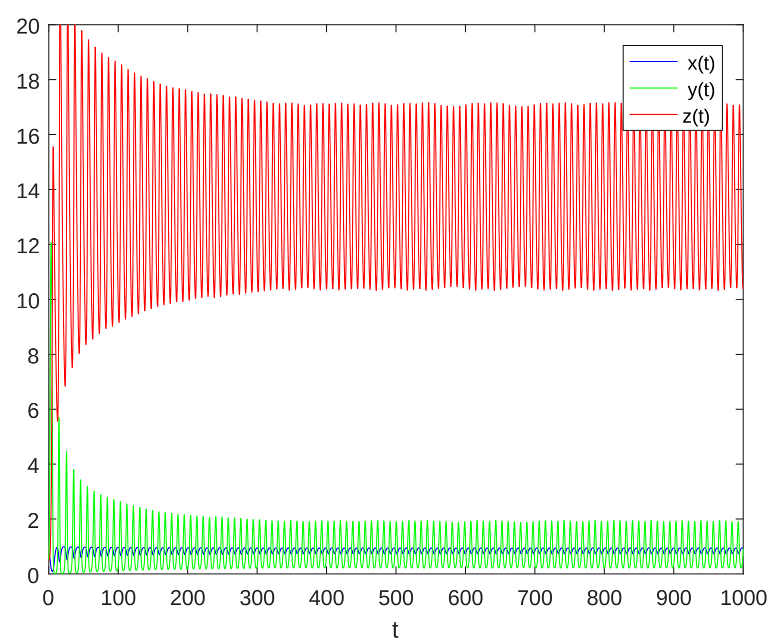

Figure 8

Figures 7 and 8. Here $a_1 = 0.2, a_2 = 0.1, a_3 = 0.05, a_4 = 3.5, d_1 = 0.25, a_5 = 0.2, a_6 = 0.2, a_7 = 0.3, d_2 = 0.2$ and $a_4 = 3.5 > a_4^* = 1.9890$ depicts the Phase portrait of the system showing a limit cycle which grows out of E^* and Oscillations of x, y, z in time t respectively.

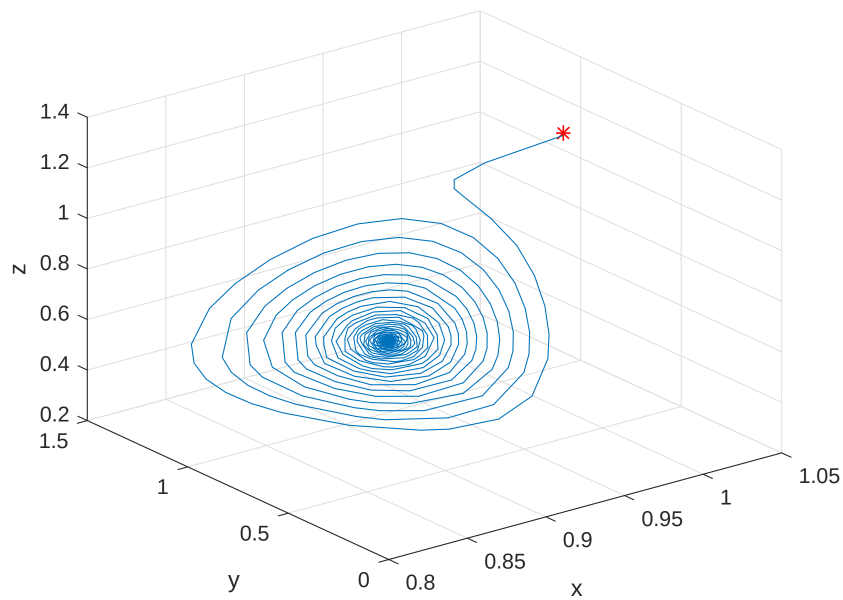

Figure 9. Here $a_1 = 0.15, a_2 = 0.1, a_3 = 0.05, a_4 = 0.45, d_1 = 0.25, a_5 = 0.2, a_6 = 0.2, a_7 = 0.3, d_2 = 0.2, \tau = 1.6 < \tau_0^*$ and $x(0) = 1.01, y(0) = 0.77, z(0) = 1.25$. It shows that $E^*(x^*, y^*, z^*)$ is locally asymptotically stable, where $x^* = 1.0101, y^* = 0.7692, z^* = 1.2432$.

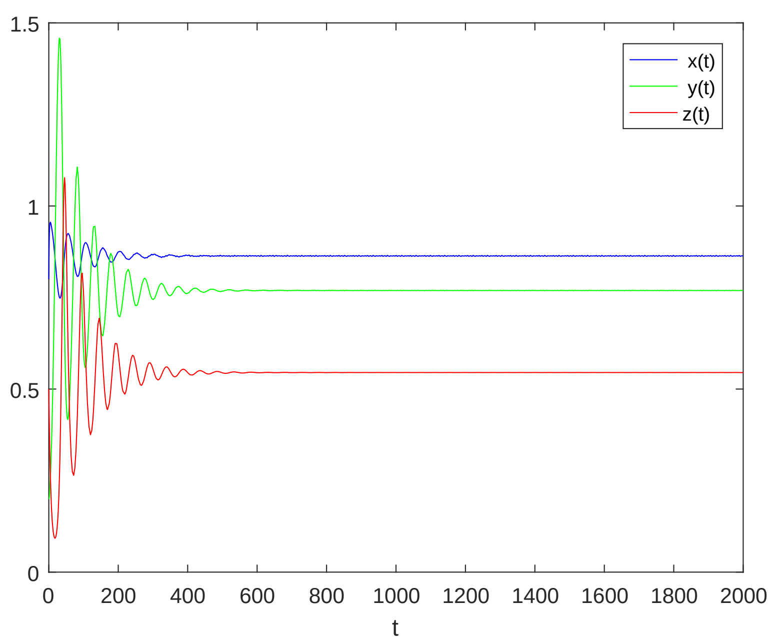

Figure 10. Here the parameters are same as in Figure 5.

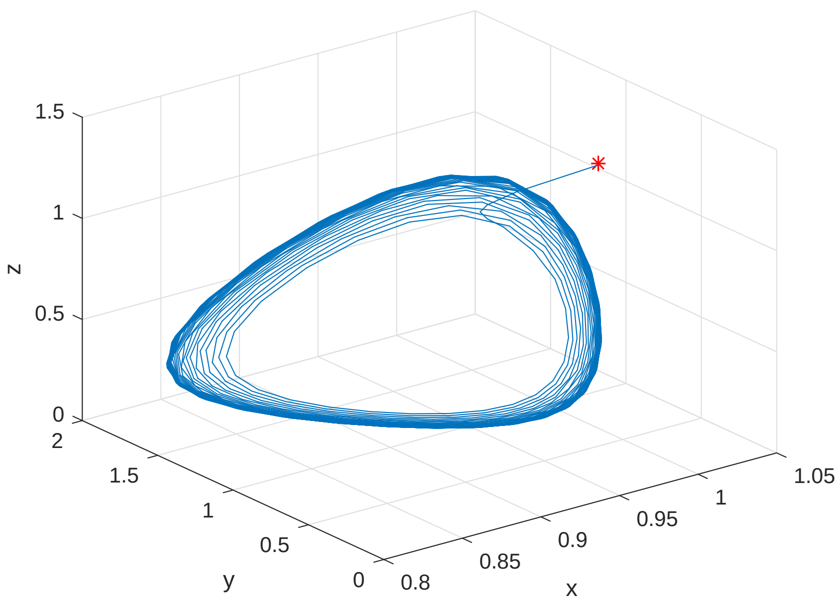

Figure 11. Here the parameters are same as in Fig. 9 and 10 except $\tau = 2.1 > \tau_0^*$. It is a limit cycle which grows out of E^*.

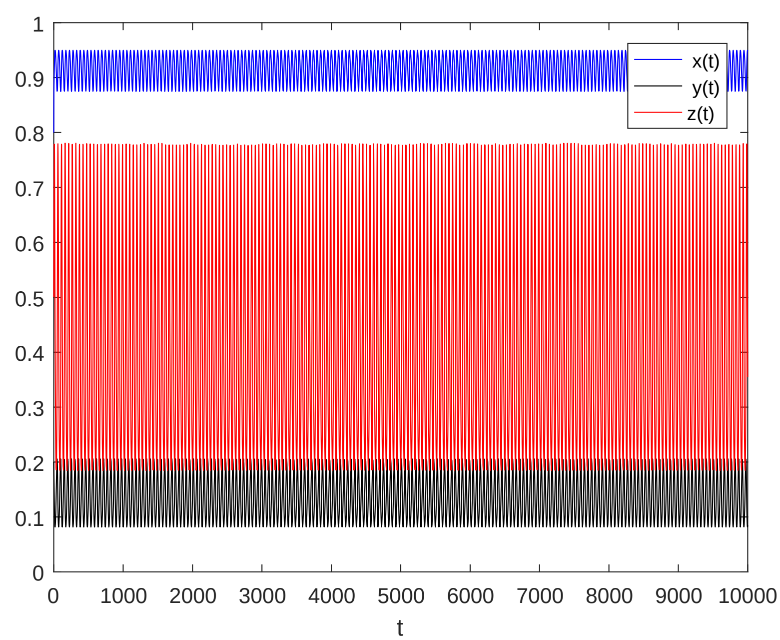

Figure 12. For the choices of parameters as in Figure 9 and 10, the oscillation of x, y, z with t.

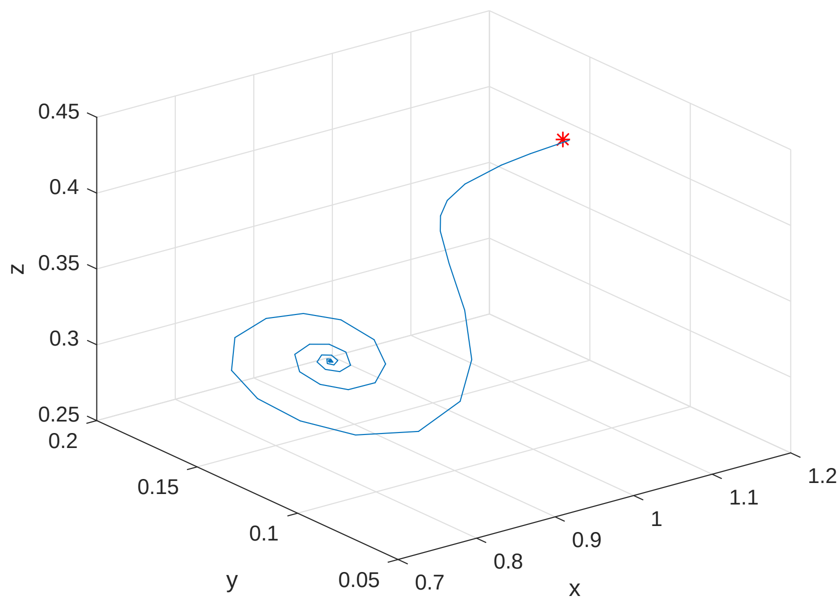

Figure 13. Here $a_1 = 2.5; a_2 = 1; a_3 = 1.0; a_4 = 2; d_1 = 0.2; a_5 = 2; a_6 = 0.2; a_7 = 1.5; d_2 = 0.2, \tau = 0.39 < \tau_0^+ = 0.4071$ and $x(0) = 1.14, y(0) = 0.14, z(0) = 0.41$ the equilibrium E^* for the system is stable.

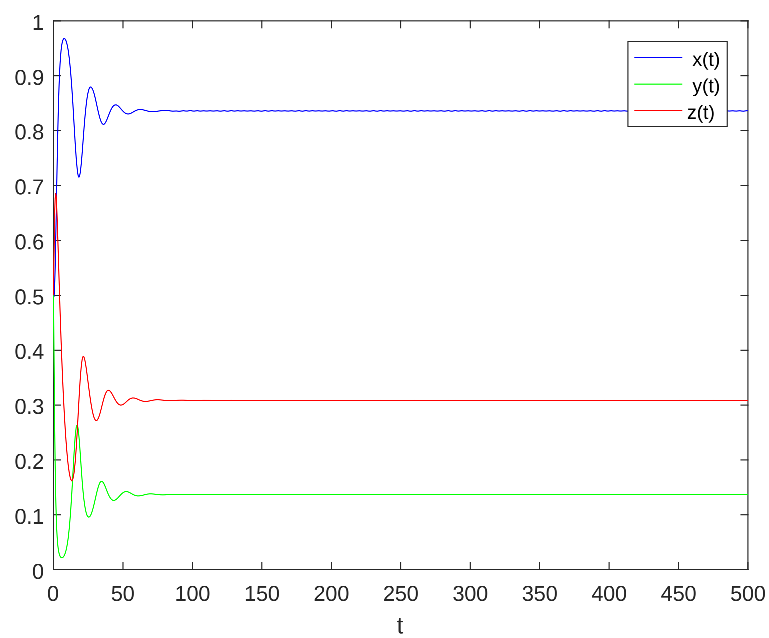

Figure 14. For the choices of parameters as in Fig. 13 and $\tau = 0.3 < \tau_0^+ = 0.4071$, the equilibrium E^* for the system is locally asymptotically stable.

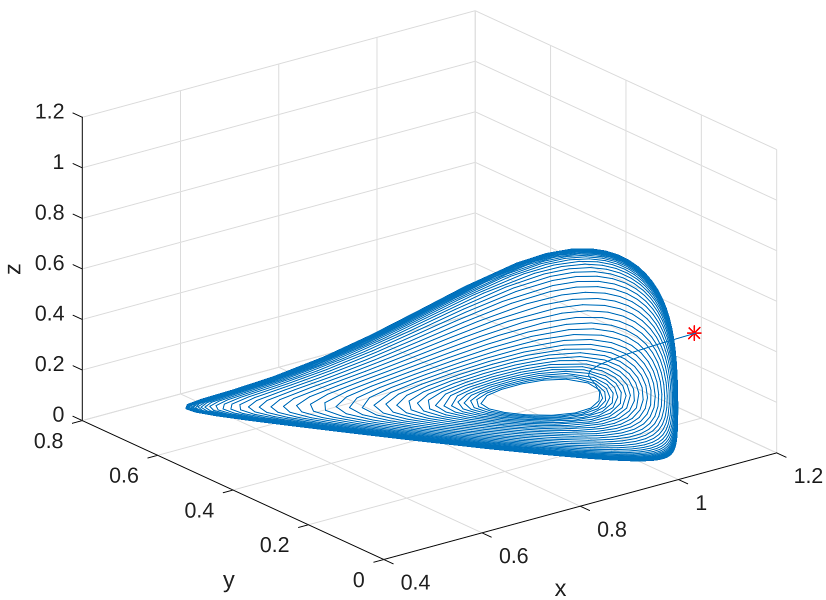

Figure 15. Here $a_1 = 2.5; a_2 = 1; a_3 = 1.0; a_4 = 2; d_1 = 0.2; a_5 = 2; a_6 = 0.2; a_7 = 1.5; d_2 = 0.2, \tau_0^+ < \tau = 1.4 < \tau_0^- = 2.5542$ and $x(0) = 1.14, y(0) = 0.14, z(0) = 0.41$, the equilibrium E^* for the system is a limit cycle.

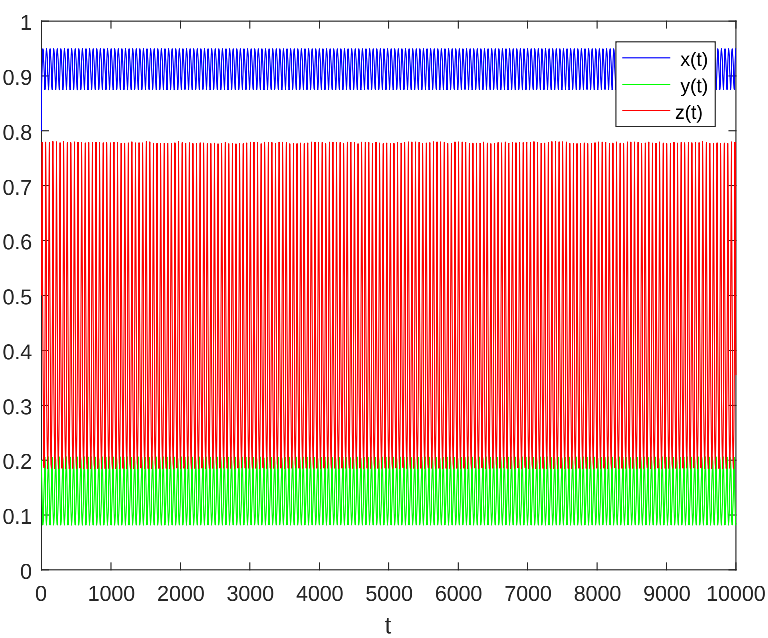

Figure 16. Here $a_1 = 2.5; a_2 = 1; a_3 = 1.0; a_4 = 2; d_1 = 0.2; a_5 = 2; a_6 = 0.2; a_7 = 1.5; d_2 = 0.2.\tau_0^+ < \tau = 1.55 < \tau_0^- = 2.5542$ the oscillation of x, y, z with t.