

The dynamics of nutrient, toxic phytoplankton, nontoxic phytoplankton and zooplankton model

Hasnaa Fiesal Mohammed Hussien *, Raid Kamel Naji, Azhar Abbas Majeed

Department of Mathematic, College of Science, University of Baghdad, Baghdad- Iraq

*Corresponding author E-mail: hasnaafmh@gmail.com

Abstract

The objective of this paper is to study the dynamical behavior of an aquatic food web system. A mathematical model that includes nutrients, phytoplankton and zooplankton is proposed and analyzed. It is assumed that, the phytoplankton divided into two compartments namely toxic phytoplankton which produces a toxic substance as a defensive strategy against predation by zooplankton, and a nontoxic phytoplankton. All the feeding processes in this food web are formulating according to the Lotka-Volterra functional response. This model is represented mathematically by the set of nonlinear differential equations. The existence, uniqueness and boundedness of the solution of this model are investigated. The local and global stability conditions of all possible equilibrium points are established. The occurrence of local bifurcation and Hopf bifurcation are investigated. Finally, numerical simulation is used to study the global dynamics of this model.

Keywords: Aquatic Food Web; HOPF Bifurcation; Local Bifurcation; Stability Analysis.

1. Introduction

Nutrient-phytoplankton-zooplankton NPZ models have been used in oceanography for at least three decades, and are still a common research tool. The NPZ model incorporates one of the simplest sets of dynamics that usefully describe oceanic plankton dynamics [1]. Phytoplankton-zooplankton models have been studied by many authors [2-10]. Some type of phytoplankton produce toxin as a defensive strategy against the predation by zooplankton, these types are known as toxic phytoplankton. In [2], models of nutrient-plankton interaction with a toxic substance that inhibit either the growth rate of phytoplankton, zooplankton, or both trophic levels are proposed and studied. In [3], authors have dealt with a nutrient-plankton model in an aquatic environment in the context of phytoplankton bloom. Roy [4] has constructed a mathematical model for describing the interaction between a nontoxic and a toxic phytoplankton under a single nutrient. Saha and Bandyopadhyay [5] considered a toxin producing phytoplankton-zooplankton model. Since the phytoplankton is a base of all the aquatic food chain and food web systems and most of zooplankton organism depends directly on the phytoplankton in its feeding process. Therefore toxic substances released by toxic phytoplankton play an important role in this context see for example [11]. Phytoplankton organisms are the dominant primary producers in the pelagic environment. They convert inorganic materials into new organic compounds by the process of photosynthesis, starting there by most aquatic food webs [12]. Fan et al. [7] constructed a model to study a NPZ food chain ecosystem involving nontoxic phytoplankton. Rashid and Naji [13] proposed and analyzed NPZ food chain ecosystem model with a toxic phytoplankton. The objective of our model is to determine the interaction between (toxic, nontoxic) phytoplankton and zooplankton under single nutrient in food web ecosystem.

2. Formulation of a mathematical model

In this section, a food web system that contains nutrient, toxic phytoplankton, nontoxic phytoplankton and zooplankton is proposed and analyzed. It is assumed that the density of the nutrient at time T is denoted by $N(T)$, the density of toxic phytoplankton at time T represents by $P_1(T)$, while $P_2(T)$ represents the density of the nontoxic phytoplankton at time T . Finally the density of the zooplankton at time T denote by $P_3(T)$. Now, in order to formulate the interaction in the above system among these species mathematically the following assumptions are obtained:

- 1) There is a constant concentration of nutrient inter to the system $N_0 > 0$ with constant rate of dilution $D > 0$. The nutrient uptakes by toxic phytoplankton P_1 and nontoxic phytoplankton P_2 according to Lotka-Volterra type of functional response with consumption rates $\alpha_1 > 0$ and $\alpha_2 > 0$ respectively, and conversion rates $k_1 > 0$ and $k_2 > 0$ respectively. On the other hand a portion of the dead toxic phytoplankton P_1 , non-toxic phytoplankton P_2 and zooplankton P_3 return to the nutrient due to the decomposition operation with rates $0 < m_1 < 1$, $0 < m_2 < 1$ and $0 < m_3 < 1$ respectively.
- 2) In the absence of nutrient the toxic phytoplankton P_1 and the non-toxic phytoplankton P_2 decay exponentially due to dilution and natural death rates $\epsilon_1 > 0$ and $\epsilon_2 > 0$ respectively. Further decay facing the toxic phytoplankton P_1 and the non-phytoplankton P_2 due to the feeding process by zooplankton P_3 .
- 3) The zooplankton feeds on the toxic phytoplankton P_1 and the non-toxic phytoplankton P_2 according to Lotka-Volterra type of functional response with consumption rates $\beta_1 > 0$ and $\beta_2 > 0$ respectively, and conversion rates $k_3 > 0$ and $k_4 > 0$ respectively. Further it is assumed that the zooplankton affected by the toxin produced by the toxic phytoplank-

ton P_1 during the predation process, with θ which stand for the liberation rate of toxin substance, δ the maximum zooplankton in gestation rate for the toxic substance. Consequently, the dynamics of the above system can be formulated mathematically by the following set of equations: An easy way to comply with the paper formatting requirements is to use this document as a template and simply type your text into it.

$$\frac{dN}{dt} = D(N_0 - N) - \alpha_1 NP_1 - \alpha_2 NP_2 + m_1 \varepsilon_1 P_1 + m_2 \varepsilon_2 P_2 + m_3 \varepsilon_3 P_3$$

$$\frac{dP_1}{dt} = k_1 \alpha_1 NP_1 - (D + \varepsilon_1) P_1 - \beta_1 P_1 P_3 \quad (1)$$

$$\frac{dP_2}{dt} = k_2 \alpha_2 NP_2 - (D + \varepsilon_2) P_2 - \beta_2 P_2 P_3$$

$$\frac{dP_3}{dt} = k_3 \beta_1 P_1 P_3 + k_4 \beta_2 P_2 P_3 - (D + \varepsilon_3) P_3 - \theta \delta P_1 P_3$$

Note that the above proposed model has eighteen parameters in all, which make the analysis difficult. So, in order to simplify the system, the number of parameters is reduced by using the following dimensionless variables and parameters:

$$\begin{aligned} t &= DT, x = \frac{N}{N_0}, y = \frac{\alpha_1}{D} P_1, z = \frac{\alpha_2}{D} P_2, w = \frac{m_3 \varepsilon_3}{DN_0} P_3, \\ u_1 &= \frac{m_1 \varepsilon_1}{\alpha_1 N_0}, u_2 = \frac{m_2 \varepsilon_2}{\alpha_2 N_0}, u_3 = \frac{k_1 \alpha_1 N_0}{D}, u_4 = \frac{(D + \varepsilon_1)}{D}, \\ u_5 &= \frac{\beta_1 N_0}{m_3 \varepsilon_3}, u_6 = \frac{k_2 \alpha_2 N_0}{D}, u_7 = \frac{(D + \varepsilon_2)}{D}, u_8 = \frac{\beta_2 N_0}{m_3 \varepsilon_3}, \\ u_9 &= \frac{k_3 \beta_1}{\alpha_1}, u_{10} = \frac{k_4 \beta_2}{\alpha_2}, u_{11} = \frac{(D + \varepsilon_3)}{D}, u_{12} = \frac{\theta \delta}{\alpha_1} \end{aligned}$$

Then the non-dimensional form of system (1) can be written as:

$$\frac{dx}{dt} = 1 - x - xy - xz + u_1 y + u_2 z + w = F_1(x, y, z, w)$$

$$\frac{dy}{dt} = u_3 xy - u_4 y - u_5 yw = F_2(x, y, z, w) \quad (2)$$

$$\frac{dz}{dt} = u_6 xz - u_7 z - u_8 zw = F_3(x, y, z, w)$$

$$\frac{dw}{dt} = s_1 yw + u_{10} zw - u_{11} w = F_4(x, y, z, w)$$

Where $s_1 = u_9 - u_{12}$, with initial condition $x(0) \geq 0, y(0) \geq 0, z(0) \geq 0$ and $w(0) \geq 0$. It is observed that the number of parameters have been reduced from eighteen in the system (1) to twelve in the system (2). Obviously the interaction functions of the system (2) are continuous and have continuous partial derivatives on the four dimensional space

$$R_+^4 = \{(x, y, z, w) \in R^4: x(0) \geq 0, y(0) \geq 0, z(0) \geq 0, w(0) \geq 0\}$$

Therefore these functions are Lipschitzian on R_+^4 , and hence the solution of the system (2) exists and is unique. Moreover, the boundedness of the solution of the system (2) in R_+^4 is established in the following theorem.

Theorem 1: All the solutions of system (2) which initiate in R_+^4 are uniformly bounded as t goes to ∞ .

Proof: Let $(x(t), y(t), z(t), w(t))$ be any solution of the system (2) with non-negative initial condition $(x_0, y_0, z_0, w_0) \in R_+^4$. Define the function: $M(t) = x(t) + y(t) + z(t) + w(t)$, and then take the time derivative of $M(t)$ along the solution of the system (2) we get:

$$\frac{dM}{dt} \leq 1 - x - (u_4 - u_1)y - (u_7 - u_2)z - (u_{11} - 1)w$$

Then $\frac{dM}{dt} + sM \leq 1$, where $s = \min \{1, u_4 - u_1, u_7 - u_2, u_{11} - 1\}$.

Now, by using the comparison theorem on the differential inequality for the initial value $M(0) = M_0$, we get:

$$M(t) \leq \frac{1}{s} + (M_0 - \frac{1}{s}) e^{-st}$$

Thus, $\lim_{t \rightarrow \infty} M(t) \leq \frac{1}{s}$, and hence $0 \leq M(t) \leq \frac{1}{s}, \forall t > 0$. So, all the solutions of system (2) are uniformly bounded as $t \rightarrow \infty$. ■

3. Existence of equilibrium points

It is observed that, system (2) has at most seven biologically feasible equilibrium points, namely $E_i, i=0,1,2,3,4,5,6$. The existence conditions for each of these equilibrium points are discussed in the following:

- The single species equilibrium point $E_0 = (1, 0, 0, 0)$ always exists.
- The first planar equilibrium point $E_1 = (x_1, y_1, 0, 0)$, where:

$$x_1 = \frac{u_4}{u_3} \text{ and } y_1 = \frac{u_4 - u_3}{u_1 u_3 - u_4} \quad (3a)$$

Exists uniquely in $\text{Int. } R_+^2$ (interior of R_+^2) of xy -plane under the following necessary and sufficient condition:

$$u_1 u_3 < u_4 < u_3 \text{ or } u_1 u_3 > u_4 > u_3 \quad (3b)$$

- The second planar equilibrium point $E_2 = (x_2, 0, z_2, 0)$, where:

$$x_2 = \frac{u_7}{u_6} \text{ and } z_2 = \frac{u_7 - u_6}{u_2 u_6 - u_7} \quad (4a)$$

Exists uniquely in $\text{Int. } R_+^2$ of xz -plane under the following necessary and sufficient condition:

$$u_2 u_6 < u_7 < u_6 \text{ or } u_2 u_6 > u_7 > u_6 \quad (4b)$$

- The first 3D boundary equilibrium point $E_3 = (x_3, y_3, 0, w_3)$, where:

$$x_3 = \frac{u_4 s_1 - u_5(u_1 u_{11} + s_1)}{u_3 s_1 - u_5(u_{11} + s_1)}, y_3 = \frac{u_{11}}{s_1},$$

$$w_3 = \frac{u_4(u_{11} + s_1) - u_3(u_1 u_{11} + s_1)}{u_3 s_1 - u_5(u_{11} + s_1)} \quad (5a)$$

Exists uniquely in $\text{Int. } R_+^3$ of xyw -space under the following necessary and sufficient conditions:

$$s_1 > 0 \quad (5b)$$

With

$$\left. \begin{aligned} u_4(u_{11} + s_1) &> u_3(u_1 u_{11} + s_1) \\ u_4 s_1 &> u_5(u_1 u_{11} + s_1) \\ u_3 s_1 &> u_5(u_{11} + s_1) \end{aligned} \right\} \quad (5c)$$

Or

$$\left. \begin{aligned} u_4(u_{11} + s_1) &< u_3(u_1 u_{11} + s_1) \\ u_4 s_1 &< u_5(u_1 u_{11} + s_1) \\ u_3 s_1 &< u_5(u_{11} + s_1) \end{aligned} \right\} \quad (5d)$$

- The second 3D boundary equilibrium point $E_4 = (x_4, 0, z_4, w_4)$, where:

$$x_4 = \frac{u_7 u_{10} - u_8 (u_2 u_{11} + u_{10})}{u_6 u_{10} - u_8 (u_{10} + u_{11})}, z_4 = \frac{u_{11}}{u_{10}},$$

$$w_4 = \frac{u_7 (u_{10} + u_{11}) - u_6 (u_2 u_{11} + u_{10})}{u_6 u_{10} - u_8 (u_{10} + u_{11})} \quad (6a)$$

Exists uniquely in $\text{Int. } R_+^3$ of xzw -space under the following necessary and sufficient conditions:

$$\left. \begin{aligned} u_7 (u_{10} + u_{11}) &> u_6 (u_2 u_{11} + u_{10}) \\ u_7 u_{10} &> u_8 (u_2 u_{11} + u_{10}) \\ u_6 u_{10} &> u_8 (u_{10} + u_{11}) \end{aligned} \right\} \quad (6b)$$

Or

$$\left. \begin{aligned} u_7 (u_{10} + u_{11}) &< u_6 (u_2 u_{11} + u_{10}) \\ u_7 u_{10} &< u_8 (u_2 u_{11} + u_{10}) \\ u_6 u_{10} &< u_8 (u_{10} + u_{11}) \end{aligned} \right\} \quad (6c)$$

• The third 3D boundary equilibrium point $E_5 = (x_5, y_5, z_5, 0)$, where:

$$x_5 = \frac{u_4}{u_3}, y_5 = \frac{u_4 - u_3 + (u_4 - u_2 u_3) z_5}{u_1 u_3 - u_4}, \quad (7a)$$

$$z_5 = \frac{u_4 - u_3 + (u_4 - u_1 u_3) y_5}{u_2 u_3 - u_4}$$

Exists uniquely in $\text{Int. } R_+^3$ of xyz -space under the following necessary and sufficient conditions:

$$u_4 u_6 = u_3 u_7 \quad (7b)$$

With

$$\left. \begin{aligned} u_4 (1 + z_5) &> u_3 (1 + u_2 z_5), \text{ and } u_1 u_3 > u_4 \\ u_4 (1 + y_5) &> u_3 (1 + u_1 y_5), \text{ and } u_2 u_3 < u_4 \end{aligned} \right\} \quad (7c)$$

Or

$$\left. \begin{aligned} u_4 (1 + z_5) &< u_3 (1 + u_2 z_5), \text{ and } u_1 u_3 < u_4 \\ u_4 (1 + y_5) &< u_3 (1 + u_1 y_5), \text{ and } u_2 u_3 < u_4 \end{aligned} \right\} \quad (7d)$$

Finally,

• The positive (coexistence) equilibrium point $E_6 = (x_6, y_6, z_6, w_6)$, where:

$$x_6 = \frac{s_2}{s_4}, y_6 = \frac{s_4 (u_2 u_{11} + u_{10}) + u_{10} s_3 - s_2 (u_{10} + u_{11})}{u_2 s_1 s_4 + u_{10} s_2 - s_1 s_2 - u_1 u_{10} s_4} \quad (8a)$$

$$z_6 = \frac{s_2 (u_{11} + s_1) - u_1 u_{11} s_4 - s_1 (s_3 + s_4)}{u_2 s_1 s_4 + u_{10} s_2 - s_1 s_2 - u_1 u_{10} s_4}, w_6 = \frac{s_3}{s_4}$$

Here $s_2 = u_5 u_7 - u_4 u_8$, $s_3 = u_3 u_7 - u_4 u_6$, $s_4 = u_5 u_6 - u_3 u_8$ exists uniquely in $\text{Int. } R_+^4$ under the following necessary and sufficient conditions:

$$u_{11} > u_{10} z_6$$

With

$$\left. \begin{aligned} s_2 > 0, s_3 > 0 \text{ and } s_4 > 0 \\ \text{or} \\ s_2 < 0, s_3 < 0 \text{ and } s_4 < 0 \end{aligned} \right\}$$

With

$$\left. \begin{aligned} s_2 (u_{11} + s_1) &> u_1 u_{11} s_4 + s_1 (s_3 + s_4) \\ u_2 s_1 s_4 + u_{10} s_2 &> s_1 s_2 + u_1 u_{10} s_4 \end{aligned} \right\}$$

Or

$$\left. \begin{aligned} s_2 (u_{11} + s_1) &< u_1 u_{11} s_4 + s_1 (s_3 + s_4) \\ u_2 s_1 s_4 + u_{10} s_2 &< s_1 s_2 + u_1 u_{10} s_4 \end{aligned} \right\} \quad (8e)$$

4. Local stability analysis

In this section, the local stability analysis of system (2) around each of the above equilibrium points is discussed through computing the Jacobian matrix $J(x, y, z, w)$ of system (2) at each of them. The general Jacobian matrix of system (2) can be written as follows:

$$J = \begin{bmatrix} -(1+y+z) & u_1 - x & u_2 - x & 1 \\ u_3 y & u_3 x - u_4 - u_5 w & 0 & -u_5 y \\ u_6 z & 0 & u_6 x - u_7 - u_8 w & -u_8 z \\ 0 & s_1 w & u_{10} w & s_1 y - u_{10} z - u_{11} \end{bmatrix} \quad (9)$$

• The Jacobian matrix of system (2) at E_0 can be written as:

$$J_0 = \begin{bmatrix} -1 & u_1 - 1 & u_2 - 1 & 1 \\ 0 & u_3 - u_4 & 0 & 0 \\ 0 & 0 & u_6 - u_7 & 0 \\ 0 & 0 & 0 & -u_{11} \end{bmatrix} \quad (10a)$$

Clearly, J_0 has the following eigenvalues:

$$\lambda_{0x} = -1, \lambda_{0y} = u_3 - u_4, \lambda_{0z} = u_6 - u_7, \lambda_{0w} = -u_{11}$$

Therefore all the eigenvalues have negative real parts and hence the equilibrium point E_0 is locally asymptotically stable provided that

$$u_4 > u_3 \quad (10b)$$

$$u_7 > u_6 \quad (10c)$$

Otherwise it will be saddle point.

• The Jacobian matrix of system (2) at E_1 can be written as:

$$J_1 = \begin{bmatrix} \frac{u_3 - u_1 u_3}{u_1 u_3 - u_4} & \frac{u_1 u_3 - u_4}{u_3} & \frac{u_2 u_3 - u_4}{u_3} & 1 \\ \frac{u_3 (u_4 - u_3)}{u_1 u_3 - u_4} & 0 & 0 & \frac{u_5 (u_3 - u_4)}{u_1 u_3 - u_4} \\ 0 & 0 & \frac{u_4 u_6 - u_3 u_7}{u_3} & 0 \\ 0 & 0 & 0 & \frac{s_1 (u_4 - u_3)}{u_1 u_3 - u_4} - u_{11} \end{bmatrix} \quad (11a)$$

The characteristic equation of this Jacobian matrix is given by:

$$\left(\left(\frac{s_1 (u_4 - u_3)}{u_1 u_3 - u_4} - u_{11} - \lambda_{1w} \right) \left(\frac{u_4 u_6 - u_3 u_7}{u_3} - \lambda_{1z} \right) \right) \quad (8b)$$

$$\left[\lambda_1^2 - \frac{u_3 - u_1 u_3}{u_1 u_3 - u_4} \lambda_1 + (u_3 - u_4) \right] \Bigg\} = 0 \quad (8c)$$

Therefore,

$$\lambda_{1x}, \lambda_{1y} = \frac{u_3 - u_1 u_3}{2(u_1 u_3 - u_4)} \pm \frac{1}{2} \sqrt{\left(\frac{u_3 - u_1 u_3}{u_1 u_3 - u_4} \right)^2 - 4(u_3 - u_4)}, \quad (8d)$$

$$\lambda_{1z} = \frac{u_4 u_6 - u_3 u_7}{u_3}, \lambda_{1w} = \frac{s_1 (u_4 - u_3)}{u_1 u_3 - u_4} - u_{11} \quad (11b)$$

Then all the eigenvalues have negative real parts and hence the equilibrium point E_1 is locally asymptotically stable, if the existence condition (3b) along with the following conditions satisfies:

$$u_3 u_7 > u_4 u_6 \quad (11c)$$

$$u_{11} > \frac{s_1(u_4 - u_3)}{u_1 u_3 - u_4} \quad (11d)$$

- The Jacobian matrix of system (2) at E_2 can be written as:

$$J_2 = \begin{bmatrix} \frac{u_6 - u_2 u_6}{u_2 u_6 - u_7} & \frac{u_1 u_6 - u_7}{u_6} & \frac{u_2 u_6 - u_7}{u_6} & 1 \\ 0 & \frac{u_3 u_7 - u_4 u_6}{u_6} & 0 & 0 \\ \frac{u_6(u_7 - u_6)}{u_2 u_6 - u_7} & 0 & 0 & \frac{u_8(u_6 - u_7)}{u_2 u_6 - u_7} \\ 0 & 0 & 0 & \frac{u_{10}(u_7 - u_6)}{u_2 u_6 - u_7} - u_{11} \end{bmatrix} \quad (12a)$$

The characteristic equation of this Jacobian matrix is given by:

$$\left(\left(\frac{u_{10}(u_7 - u_6)}{u_2 u_6 - u_7} - u_{11} - \lambda_{2w} \right) \left(\frac{u_3 u_7 - u_4 u_6}{u_6} - \lambda_{2y} \right) \right. \\ \left. \left[\lambda_2^2 - \frac{u_6 - u_2 u_6}{u_2 u_6 - u_7} \lambda_2 + (u_6 - u_7) \right] \right) = 0$$

Therefore,

$$\lambda_{2x}, \lambda_{2z} = \frac{u_6 - u_2 u_6}{2(u_2 u_6 - u_7)} \pm \frac{1}{2} \sqrt{\left(\frac{u_6 - u_2 u_6}{u_2 u_6 - u_7} \right)^2 - 4(u_6 - u_7)},$$

$$\lambda_{2y} = \frac{u_3 u_7 - u_4 u_6}{u_6}, \lambda_{2w} = \frac{u_{10}(u_7 - u_6)}{u_2 u_6 - u_7} - u_{11} \quad (12b)$$

Then all the eigenvalues have negative real parts and hence the equilibrium point E_2 is locally asymptotically stable if the existence condition (4b) along with the following conditions satisfies:

$$u_4 u_6 > u_3 u_7 \quad (12c)$$

$$u_{11} > \frac{u_{10}(u_7 - u_6)}{u_2 u_6 - u_7} \quad (12d)$$

- The Jacobian matrix of system (2) at E_3 can be written as:

$$J_3 = \begin{bmatrix} -(1+y_3) & u_1 - x_3 & u_2 - x_3 & 1 \\ u_3 y_3 & 0 & 0 & -u_5 y_3 \\ 0 & 0 & u_6 x_3 - u_7 - u_8 w_3 & 0 \\ 0 & s_1 w_3 & u_{10} w_3 & 0 \end{bmatrix} = (a_{ij})_{4 \times 4} \quad (13a)$$

The characteristic equation of J_3 can be written as:

$$(a_{33} - \lambda_{3z}) \left[\lambda_3^3 + A_1 \lambda_3^2 + A_2 \lambda_3 + A_3 \right] = 0$$

Here

$$A_1 = -a_{11}, A_2 = -(a_{24} a_{42} + a_{12} a_{21}), A_3 = a_{42}(a_{11} a_{24} - a_{21} a_{14}) \quad (13b)$$

Now, it is easy to verify that:

$$\Delta = A_1 A_2 - A_3 = a_{21}(a_{11} a_{12} + a_{14} a_{42}).$$

Clearly, the eigenvalue λ_{3z} in z-direction has negative real part if and only if the following condition holds:

$$u_6 x_3 < u_7 + u_8 w_3 \quad (13c)$$

However, according to existence condition (5c), it is observed that $A_i > 0, \forall i = 1, 3$, further $\Delta > 0$ if and only if:

$$u_3 < u_5(1 + y_3) \quad (13d)$$

$$u_1 < x_3 \quad (13e)$$

So, according to Routh-Hurwitz criterion the roots of the third degree polynomial in the characteristic equation have negative real parts and hence the equilibrium point E_3 is locally asymptotically stable.

- The Jacobian matrix of system (2) at E_4 can be written as:

$$J_4 = \begin{bmatrix} -(1+z_4) & u_1 - x_4 & u_2 - x_4 & 1 \\ 0 & u_3 x_4 - u_4 - u_5 w_4 & 0 & 0 \\ u_6 z_4 & 0 & 0 & -u_8 z_4 \\ 0 & s_1 w_4 & u_{10} w_4 & u_{10} z_4 - u_{11} \end{bmatrix} = (b_{ij})_{4 \times 4} \quad (14a)$$

The characteristic equation of J_4 can be written as:

$$(b_{22} - \lambda_{4y}) \left[\lambda_4^3 + B_1 \lambda_4^2 + B_2 \lambda_4 + B_3 \right] = 0$$

Here

$$B_1 = -b_{11}, B_2 = -(b_{43} b_{34} + b_{13} b_{31}), B_3 = b_{43}(b_{11} b_{34} - b_{31} b_{14}) \quad (14b)$$

Further, it is easy to verify that:

$$\Delta = B_1 B_2 - B_3 = b_{31}(b_{11} b_{13} + b_{14} b_{43}).$$

Clearly, the eigenvalue λ_{4y} in y-direction has negative real part if and only if the following condition holds:

$$u_3 x_4 < u_4 + u_5 w_4 \quad (14c)$$

However, according to existence condition (6b), we obtain that $B_i > 0, \forall i = 1, 3$, further $\Delta > 0$ if and only if:

$$u_6 < u_8(1 + z_4) \quad (14d)$$

$$u_2 < x_4 \quad (14e)$$

So, according to Routh-Hurwitz criterion the roots of the third degree polynomial in the characteristic equation have negative real parts and hence the equilibrium point E_4 is locally asymptotically stable.

- The Jacobian matrix of system (2) at E_5 can be written as:

$$J_5 = \begin{bmatrix} -(1+y_5+z_5) & u_1 - x_5 & u_2 - x_5 & 1 \\ u_3 y_5 & 0 & 0 & -u_5 y_5 \\ u_6 z_5 & 0 & 0 & -u_8 z_5 \\ 0 & 0 & 0 & s_1 y_5 - u_{10} z_5 - u_{11} \end{bmatrix} = (c_{ij})_{4 \times 4} \quad (15)$$

The characteristic equation of J_5 can be written as:

$$(c_{44} - \lambda_{5w}) (\lambda_5^2 - c_{11} \lambda_5 - (c_{13} c_{31} + c_{21} c_{12})) = 0$$

Clearly, the equilibrium point E_5 has a zero eigenvalue that's mean its non-hyperbolic point. So, the linearization failed and we will study the stability of E_5 by Lyapunov method in the next section.

• The Jacobian matrix of system (2) at E_6 can be written as:

$$J_6 = \begin{bmatrix} -(1+y_6+z_6) & u_1-x_6 & u_2-x_6 & 1 \\ u_3y_6 & 0 & 0 & -u_5y_6 \\ u_6z_6 & 0 & 0 & -u_8z_6 \\ 0 & s_1w_6 & u_{10}w_6 & s_1y_6-u_{10}z_6-u_{11} \end{bmatrix} = (d_{ij})_{4 \times 4} \quad (16a)$$

The characteristic equation of J_6 can be written as:

$$\lambda_6^4 + D_1\lambda_6^3 + D_2\lambda_6^2 + D_3\lambda_6 + D_4 = 0 \quad (16b)$$

Here

$$D_1 = -(d_{11} + d_{44})$$

$$D_2 = -(d_{11}d_{44} + d_{12}d_{21} + d_{13}d_{31} + d_{24}d_{42} + d_{34}d_{43})$$

$$D_3 = d_{43}(d_{11}d_{34} - d_{31}) + d_{42}(d_{11}d_{24} - d_{21}) + d_{44}(d_{12}d_{21} - d_{13}d_{31})$$

$$D_4 = d_{12}d_{21}d_{34}d_{43} + d_{13}d_{31}d_{42}d_{24} - d_{12}d_{31}d_{24}d_{43} - d_{13}d_{21}d_{42}d_{34}$$

Consequently,

$$\Lambda_1 = D_1D_2 - D_3 = d_{11}\Gamma_2 + d_{44}\Gamma_3 - d_{11}d_{44}\Gamma_1 + \Gamma_4$$

And

$$\Lambda_2 = D_3(D_1D_2 - D_3) - D_1^2D_4 = F_1 + F_2 + F_3 + F_4$$

Where

$$F_1 = (d_{11}\Gamma_3 + d_{44}\Gamma_2)(d_{11}\Gamma_2 + d_{44}\Gamma_3 + \Gamma_4)$$

$$F_2 = -(d_{11}\Gamma_3 + d_{44}\Gamma_2)(d_{11}d_{44}\Gamma_1)$$

$$F_3 = -\Gamma_4(d_{11}d_{44}\Gamma_1)(\Gamma_2 + d_{44}\Gamma_3 + \Gamma_4)$$

$$F_4 = \Gamma_1^2\Gamma_5(d_{13}d_{42} - d_{12}d_{43})$$

With

$$\Gamma_1 = d_{11} + d_{44}$$

$$\Gamma_2 = d_{12}d_{21} + d_{13}d_{31}$$

$$\Gamma_3 = d_{24}d_{42} + d_{34}d_{43}$$

$$\Gamma_4 = d_{21}d_{42} + d_{31}d_{43}$$

$$\Gamma_5 = d_{21}d_{34} - d_{31}d_{24}$$

$$\Gamma_6 = d_{13}d_{42} - d_{12}d_{43}$$

Now, according to existence condition (8c) it is observed that $D_i > 0$, $i = 1, 3, 4$, further $\Delta_2 > 0$ if and only if the following conditions hold:

$$u_{11} > s_1y_6 + u_{10}z_6 \quad (16c)$$

$$u_2 > x_6 > \max \left\{ \frac{u_1u_{10} - u_2s_1}{u_{10} - s_1}, u_1 \right\} \quad (16d)$$

$$y_6 > \max \left\{ \frac{u_6}{u_8} - z_6 - 1, \frac{u_3}{u_5} - z_6 - 1, \frac{(u_2 - x_6)u_6z_6}{(u_1 - x_6)u_3} \right\} \quad (16e)$$

So, according to Routh-Hurwitz criterion the roots of the third degree polynomial in the characteristic equation have negative real parts and hence the equilibrium point E_6 is locally asymptotically stable.

5. Global stability analysis

In this section the global stability for the equilibrium points of system (2) is studied analytically by using the Lyapunov method as shown in the following theorems:

Theorem 2: Assume that, the equilibrium point E_0 of system (2) is locally asymptotically stable and the following conditions hold:

$$u_3 < \min \left\{ \frac{u_4}{1+u_1}, \frac{u_5u_{11}}{s_1} \right\} \quad (17a)$$

$$u_6 < \min \left\{ \frac{u_7}{1+u_2}, \frac{u_8u_{11}}{u_{10}} \right\} \quad (17b)$$

Then E_0 is globally asymptotically stable in the R_+^4 .

Proof: Consider the following function:

$$V_0 = c_1(x - 1 - \ln(x)) + c_2y + c_3z + c_4w$$

Where c_i , $i = 1, 2, 3, 4$ are positive constants to be determine. Clearly $V_0: R_+^4 \rightarrow R$ is C^1 positive definite function. Now by differentiating V_0 with respect to time t , we get:

$$\begin{aligned} \frac{dV_0}{dt} = & -\frac{c_1}{x}(x-1)^2 + (c_1(1+u_1) - c_2u_4)y + (c_1(1+u_2) - c_3u_7)z \\ & + (c_1 - c_4u_{11})w + (c_2u_3 - c_1)xy + (c_3u_6 - c_1)xz \\ & + (c_4s_1 - c_2u_5)yw + (c_4u_{10} - c_3u_8)zw - \frac{c_1}{x}(u_1y + u_2z + w) \end{aligned}$$

So by choosing the positive constants as below:

$$c_1 = 1, \quad c_2 = \frac{1}{u_3}, \quad c_3 = \frac{1}{u_6}, \quad c_4 = \frac{1}{u_{11}}$$

We obtain that:

$$\begin{aligned} \frac{dV_0}{dt} \leq & -\frac{(x-1)^2}{x} + \left(1+u_1 - \frac{u_4}{u_3}\right)y + \left(1+u_2 - \frac{u_7}{u_6}\right)z \\ & + \left(\frac{s_1}{u_{11}} - \frac{u_5}{u_3}\right)yw + \left(\frac{u_{10}}{u_{11}} - \frac{u_8}{u_6}\right)zw \end{aligned}$$

According to conditions (17)(a,b) we have $\frac{dV_0}{dt} < 0$. Therefore E_0 is globally asymptotically stable in the R_+^4 , and hence the proof is complete.

Theorem 3: Assume that, the equilibrium point E_1 of system (2) is locally asymptotically stable. Then the basin of attraction of E_1 , say $B(E_1) \subset R_+^4$, satisfy the following conditions:

$$(u_1 - x_1 + u_3y)^2 \leq 4(1+y)(u_4 - u_3x_1) \quad (18a)$$

$$x_1 + u_2 + \frac{u_6}{u_8} < x < x_1 + \frac{u_{11}}{u_{10}} \quad (18b)$$

$$y > y_1 + \frac{s_1}{u_5 u_{10}} \quad (18c)$$

Proof: Consider the following function:

$$V_1 = c_1 \frac{(x - x_1)^2}{2} + c_2 \frac{(y - y_1)^2}{2} + c_3 z + c_4 w$$

Where $c_i, i = 1, 2, 3, 4$ are positive constant to be determine. Clearly $V_1 : R_+^4 \rightarrow R$ is C^1 positive definite function. Now by differentiating V_1 with respect to time t , we get:

$$\frac{dV_1}{dt} = -c_1(1+y)(x - x_1)^2 + (c_1(u_1 - x_1) + c_2 u_3 y)(x - x_1)(y - y_1)$$

$$-c_2(u_4 - u_3 x_1)(y - y_1)^2 - (c_1 u_2 x_1 + c_3 u_7 z)$$

$$+ (c_1(x - x_1) - c_4 u_{11})w + (c_1(x_1 + u_2 - x) + c_3 u_6)xz$$

$$+ (c_4 s_1 - c_2 u_5(y - y_1))yw + (c_4 u_{10} - c_3 u_8)zw$$

So by choosing the positive constants as below:

$$c_1 = 1, c_2 = 1, c_3 = \frac{1}{u_8}, c_4 = \frac{1}{u_{10}}$$

And according to condition (18a) we obtain that:

$$\frac{dV_1}{dt} \leq -\left[\sqrt{(1+y)}(x - x_1) - \sqrt{(u_4 - u_3 x_1)}(y - y_1)\right]^2$$

$$+ \left(x - x_1 - \frac{u_{11}}{u_{10}}\right)w + \left(x_1 + u_2 - x + \frac{u_6}{u_8}\right)xz$$

$$+ \left(\frac{s_1}{u_{10}} - u_5(y - y_1)\right)yw$$

Obviously $\frac{dV_1}{dt} < 0$ for every initial point satisfying conditions (18)(b,c) and then V_1 is a Lyapunov function provided that conditions (18)(a-c) hold. Thus E_1 is globally asymptotically stable in the interior of $B(E_1)$, which means that $B(E_1)$ is the basin of attraction and this completes the proof.

Theorem 4: Assume that, the equilibrium point E_2 of system (2) is locally asymptotically stable. Then the basin of attraction of E_2 , say $B(E_2) \subset R_+^4$, satisfy the following conditions:

$$(u_2 - x_2 + u_6 z)^2 \leq 4(1+z)(u_7 - u_6 x_2) \quad (19a)$$

$$x_2 + u_1 + \frac{u_3}{u_5} < x < x_2 + \frac{u_{11}}{s_1} \quad (19b)$$

$$z > z_2 + \frac{u_{10}}{s_1 u_8} \quad (19c)$$

Proof: Consider the following function:

$$V_2 = c_1 \frac{(x - x_2)^2}{2} + c_2 y + c_3 \frac{(z - z_2)^2}{2} + c_4 w$$

Where $c_i, i = 1, 2, 3, 4$ are positive constants to be determine. Clearly $V_2 : R_+^4 \rightarrow R$ is C^1 positive definite function. Now by differentiating V_2 with respect to time t , we get:

$$\frac{dV_2}{dt} = -c_1(1+z)(x - x_2)^2 + (c_1(u_2 - x_2) + c_3 u_6 z)(x - x_2)(z - z_2)$$

$$-c_3(u_7 - u_6 x_2)(z - z_2)^2 - (c_1 u_1 x_2 + c_2 u_4)y$$

$$+ (c_1(x - x_2) - c_4 u_{11})w + (c_1(x_2 + u_1 - x) + c_2 u_3)xy$$

$$+ (c_4 s_1 - c_2 u_5)yw + (c_4 u_{10} - c_3 u_8(z - z_2))zw$$

So by choosing the positive constants as below:

$$c_1 = 1, c_2 = \frac{1}{u_5}, c_3 = 1, c_4 = \frac{1}{s_1}$$

And according to condition (19a) we obtain that:

$$\frac{dV_2}{dt} \leq -\left[\sqrt{(1+z)}(x - x_2) - \sqrt{(u_7 - u_6 x_2)}(z - z_2)\right]^2$$

$$+ \left(x - x_2 - \frac{u_{11}}{s_1}\right)w + \left(x_2 + u_1 - x + \frac{u_3}{u_5}\right)xy$$

$$+ \left(\frac{u_{10}}{s_1} - u_8(z - z_2)\right)zw$$

Obviously $\frac{dV_2}{dt} < 0$ for every initial point satisfying conditions (19)(b,c) and then V_2 is a Lyapunov function provided that conditions (19)(a-c) hold. Thus E_2 is globally asymptotically stable in the interior of $B(E_2)$, which means that $B(E_2)$ is the basin of attraction and this completes the proof.

Theorem 5: Assume that, the equilibrium point E_3 of system (2) is locally asymptotically stable. Then the basin of attraction of E_3 , say $B(E_3) \subset R_+^4$, satisfy the following conditions:

$$(u_1 - x_3 + u_3 y)^2 \leq (1+y)(u_4 + u_5 w - u_3 x_3) \quad (20a)$$

$$(s_1 w - u_5 y_3)^2 \leq (u_4 + u_5 w - u_3 x_3)(u_{11} - s_1 y_3) \quad (20b)$$

$$(1+y)(u_{11} - s_1 y_3) \geq 1 \quad (20c)$$

$$x > x_3 + u_2 + u_6 \quad (20d)$$

$$w < w_3 \quad (20e)$$

Proof: Consider the following function:

$$V_3 = \frac{(x-x_3)^2}{2} + \frac{(y-y_3)^2}{2} + z + \frac{(w-w_3)^2}{2}$$

Clearly $V_3 : R_+^4 \rightarrow R$ is C^1 positive definite function. Now by differentiating V_3 with respect to time t , and according to conditions (20)(a-c) we obtain that:

$$\begin{aligned} \frac{dV_3}{dt} \leq & - \left[\sqrt{\frac{(1+y)}{2}}(x-x_3) - \sqrt{\frac{(u_4+u_5w-u_3x_3)}{2}}(y-y_3) \right]^2 \\ & - \left[\sqrt{\frac{(1+y)}{2}}(x-x_3) - \sqrt{\frac{(u_{11}-s_1y_3)}{2}}(w-w_3) \right]^2 \\ & - \left[\sqrt{\frac{(u_4+u_5w-u_3x_3)}{2}}(y-y_3) - \sqrt{\frac{(u_{11}-s_1y_3)}{2}}(w-w_3) \right]^2 \\ & + (x_3+u_2-x+u_6)xz + u_{10}(w-w_3)zw \end{aligned}$$

Obviously $\frac{dV_3}{dt} < 0$, and then V_3 is a Lyapunov function provided that the given conditions hold. Therefore E_3 is globally asymptotically stable in the interior of $B(E_3)$, which means that $B(E_3)$ is the basin of attraction of E_3 and the proof is complete.

Theorem 6: Assume that, the equilibrium point E_4 of system (2) is locally asymptotically stable. Then the basin of attraction of E_4 , say $B(E_4) \subset R_+^4$, satisfy the following conditions:

$$(u_2-x_4+u_6z)^2 \leq (1+z) (u_7+u_8w-u_6x_4) \quad (21a)$$

$$(u_{10}w-u_8z_4)^2 \leq (u_7+u_8w-u_6x_4) (u_{11}-u_{10}z_4) \quad (21b)$$

$$(1+z) (u_{11}-u_{10}z_4) \geq 1 \quad (21c)$$

$$x > x_4 + u_1 + u_3 \quad (21d)$$

$$w < w_4 \quad (21e)$$

Proof: Consider the following function:

$$V_4 = \frac{(x-x_4)^2}{2} + y + \frac{(z-z_4)^2}{2} + \frac{(w-w_4)^2}{2}$$

Clearly $V_4 : R_+^4 \rightarrow R$ is C^1 positive definite function. Now by differentiating V_4 with respect to time t , and according to conditions (21)(a-c) we obtain that:

$$\begin{aligned} \frac{dV_4}{dt} \leq & - \left[\sqrt{\frac{(1+z)}{2}}(x-x_4) - \sqrt{\frac{(u_7+u_8w-u_6x_4)}{2}}(z-z_4) \right]^2 \\ & - \left[\sqrt{\frac{(1+z)}{2}}(x-x_4) - \sqrt{\frac{(u_{11}-u_{10}z_4)}{2}}(w-w_4) \right]^2 \end{aligned}$$

$$\begin{aligned} & - \left[\sqrt{\frac{(u_7+u_8w-u_6x_4)}{2}}(z-z_4) - \sqrt{\frac{(u_{11}-u_{10}z_4)}{2}}(w-w_4) \right]^2 \\ & + (x_4+u_1-x+u_3)xy + s_1(w-w_4)yw \end{aligned}$$

Obviously $\frac{dV_4}{dt} < 0$, and then V_4 is a Lyapunov function provided that the given conditions hold. Therefore E_4 is globally asymptotically stable in the interior of $B(E_4)$, which means that $B(E_4)$ is the basin of attraction of E_4 and the proof is complete.

Theorem 7: Assume that, the equilibrium point E_5 of system (2) is locally asymptotically stable. Then the basin of attraction of E_5 , say $B(E_5) \subset R_+^4$, satisfy the following conditions:

$$(u_1-x_5+u_3y)^2 \leq 2(1+y+z) (u_4-u_3x_5) \quad (22a)$$

$$(u_2-x_5+u_6z)^2 \leq 2(1+y+z) (u_7-u_6x_5) \quad (22b)$$

$$u_{11} > x + (u_5y_5 + s_1)y + (u_8z_5 + u_{10})z \quad (22c)$$

Proof: Consider the following function:

$$V_5 = \frac{(x-x_5)^2}{2} + \frac{(y-y_5)^2}{2} + \frac{(z-z_5)^2}{2} + w$$

Clearly $V_5 : R_+^4 \rightarrow R$ is C^1 positive definite function. Now by differentiating V_5 with respect to time t , and according to conditions (22)(a,b) we obtain that:

$$\begin{aligned} \frac{dV_5}{dt} \leq & - \left[\sqrt{\frac{(1+y+z)}{2}}(x-x_5) - \sqrt{(u_4-u_3x_5)}(y-y_5) \right]^2 \\ & - \left[\sqrt{\frac{(1+y+z)}{2}}(x-x_5) - \sqrt{(u_7-u_6x_5)}(z-z_5) \right]^2 \\ & + [x-u_{11}+(s_1+y_5)y+(u_{10}-z_5)z]w \end{aligned}$$

Obviously $\frac{dV_5}{dt} < 0$, and then V_5 is a Lyapunov function provided that the given conditions hold. Therefore E_5 is globally asymptotically stable in the interior of $B(E_5)$, which means that $B(E_5)$ is the basin of attraction of E_5 and the proof is complete.

Theorem 8: Assume that, the equilibrium point E_6 of system (2) is locally asymptotically stable. Then the basin of attraction of E_6 , say $B(E_6) \subset R_+^4$, satisfy the following conditions:

$$(u_1-x_6+u_3y)^2 \leq \frac{2}{3}(1+y+z) (u_4-u_3x_6+u_5w) \quad (23a)$$

$$(u_2-x_6+u_6z)^2 \leq \frac{2}{3}(1+y+z) (u_7-u_6x_6+u_8w) \quad (23b)$$

$$\frac{4}{9}(1+y+z) (u_{11}-s_1y_6-u_{10}z_4) \geq 1 \quad (23c)$$

$$(s_1w-u_5y_6)^2 \leq \frac{2}{3}(u_4-u_3x_6+u_5w) (u_{11}-s_1y_6-u_{10}z) \quad (23d)$$

$$(u_{10}w - u_8z_6)^2 \leq \frac{2}{3}(u_7 - u_6x_6 + u_8w)(u_{11} - s_1y_6 - u_{10}z) \quad (23e)$$

Proof: Consider the following function:

$$V_6 = \frac{(x - x_6)^2}{2} + \frac{(y - y_6)^2}{2} + \frac{(z - z_6)^2}{2} + \frac{(w - w_6)^2}{2}$$

Clearly $V_6: \mathbb{R}_+^4 \rightarrow \mathbb{R}$ is C^1 positive definite function. Now by differentiating V_6 with respect to time t , and according to conditions (23)(a-e) we obtain that:

$$\begin{aligned} \frac{dV_6}{dt} \leq & - \left[\sqrt{\frac{(1+y+z)}{3}}(x - x_6) - \sqrt{\frac{(u_4 - u_3x_6 + u_5w)}{2}}(y - y_6) \right]^2 \\ & - \left[\sqrt{\frac{(1+y+z)}{3}}(x - x_6) - \sqrt{\frac{(u_7 - u_6x_6 + u_8w)}{2}}(z - z_6) \right]^2 \\ & - \left[\sqrt{\frac{(1+y+z)}{3}}(x - x_6) - \sqrt{\frac{(u_{11} - s_1y_6 - u_{10}z)}{3}}(w - w_6) \right]^2 \\ & - \left[\sqrt{\frac{(u_4 - u_3x_6 + u_5w)}{2}}(y - y_6) - \sqrt{\frac{(u_{11} - s_1y_6 - u_{10}z)}{3}}(w - w_6) \right]^2 \\ & - \left[\sqrt{\frac{(u_7 - u_6x_6 + u_8w)}{2}}(z - z_6) - \sqrt{\frac{(u_{11} - s_1y_6 - u_{10}z)}{3}}(w - w_6) \right]^2 \end{aligned}$$

Obviously $\frac{dV_6}{dt} < 0$, and then V_6 is a Lyapunov function provided that the given conditions hold.

Therefore E_6 is globally asymptotically stable in the interior of $B(E_6)$, which means that $B(E_6)$ is the basin of attraction of E_6 and the proof is complete.

6. The local bifurcation analysis

In this section, the local bifurcation near the equilibrium points of the system (2) is investigated by using the Sotomayor's theorem [14] for local bifurcation. It is well known that the existence of nonhyperbolic equilibrium point is a necessary but not sufficient condition for bifurcation to occur. Now, according to Jacobian matrix of system (2) given in equation (9), it is clear to verify that for any non-zero vector $V = (v_1, v_2, v_3, v_4)^T$ we have:

$$D^2F(V, V) = \begin{pmatrix} -2v_1(v_2 + v_3) \\ 2v_2(u_3v_1 - u_5v_4) \\ 2v_3(u_6v_1 - u_8v_4) \\ 2v_4(s_1v_2 + u_{10}v_3) \end{pmatrix} \quad (24)$$

Here D^2 represent the derivative of Jacobian matrix of system (2), and $F = (F_1, F_2, F_3, F_4)^T$ with $F_i, i = 1, 2, 3, 4$ given in system (2). Therefore, $D^3F(V, V, V) = (0, 0, 0, 0)^T$.

So, according to Sotomayor's theorem the pitchfork bifurcation does not occur at each point $E_i, i = 0, 1, 2, 3, 4, 5, 6$.

Theorem 9: Assume that the local stability condition (10b) holds, and let the parameter value u_6 passing through the value $u_6^* = u_7$ then the system (2) at the equilibrium point E_0 has:

1) No saddle-node bifurcation.

2) Transcritical bifurcation.

Proof: According to the Jacobian matrix J_0 given by Eq. (10a) the system (2) at the equilibrium point E_0 has zero eigenvalue (say $\lambda_{0z} = 0$) at $u_6 = u_6^*$, and the Jacobian matrix J_0 with $u_6 = u_6^*$ becomes:

$$J_0^* = J(u_6 = u_6^*) = \begin{pmatrix} -1 & u_1 - 1 & u_2 - 1 & 1 \\ 0 & u_3 - u_4 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -u_{11} \end{pmatrix}$$

Now, let $V^{[0]} = (v_1^{[0]}, v_2^{[0]}, v_3^{[0]}, v_4^{[0]})^T$ be the eigenvector corresponding to the eigenvalue $\lambda_{0z} = 0$. Thus $J_0^* V^{[0]} = 0$, gives $V^{[0]} = ((u_2 - 1)v_3^{[0]}, 0, v_3^{[0]}, 0)^T$, where $v_3^{[0]}$ any nonzero real number. Let $\Psi^{[0]} = (\psi_1^{[0]}, \psi_2^{[0]}, \psi_3^{[0]}, \psi_4^{[0]})^T$ be the eigenvector corresponding to the eigenvalue $\lambda_{0z} = 0$ of the matrix J_0^{*T} . Then $J_0^{*T} \Psi^{[0]} = 0$, by solving this equation for $\Psi^{[0]}$ we get $\Psi^{[0]} = (0, 0, \psi_3^{[0]}, 0)^T$, where $\psi_3^{[0]}$ any nonzero real number. Now, consider:

$$\frac{\partial f}{\partial u_6} = f_{u_6}(X, u_6) = \left(\frac{\partial f_1}{\partial u_6}, \frac{\partial f_2}{\partial u_6}, \frac{\partial f_3}{\partial u_6}, \frac{\partial f_4}{\partial u_6} \right)^T = (0, 0, xz, 0)^T$$

Thus, $f_{u_6}(E_0, u_6^*) = (0, 0, 0, 0)^T$ and hence $(\Psi^{[0]})^T f_{u_6}(E_0, u_6^*) = 0$. So, according to Sotomayor's theorem the saddle-node bifurcation cannot occur, while the first condition of transcritical bifurcation is satisfied. Now, since

$$Df_{u_6}(X, u_6) = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ z & 0 & x & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}$$

Where $Df_{u_6}(X, u_6)$ represents the derivative of $f_{u_6}(X, u_6)$ with respect to $X = (x, y, z, w)^T$. Further, it is observed

$$Df_{u_6}(E_0, u_6^*)V^{[0]} = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} (u_2 - 1)v_3^{[0]} \\ 0 \\ v_3^{[0]} \\ 0 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ v_3^{[0]} \\ 0 \end{pmatrix}$$

$$\begin{aligned} (\Psi^{[0]})^T [Df_{u_6}(E_0, u_6^*)V^{[0]}] &= (0, 0, \psi_3^{[0]}, 0) (0, 0, v_3^{[0]}, 0)^T \\ &= v_3^{[0]} \psi_3^{[0]} \neq 0 \end{aligned}$$

Now, by substituting $V^{[0]}$ in (24) we get

$$D^2f(E_0, u_6^*)(V^{[0]}, V^{[0]}) = (0, 0, 2u_6^*(u_2 - 1)v_3^{[0]2}, 0)^T$$

Hence, it is obtain that:

$$\begin{aligned} (\Psi^{[0]})^T [D^2f(E_0, u_6^*)(V^{[0]}, V^{[0]})] &= (0, 0, \psi_3^{[0]}, 0) (0, 0, 2u_6^*(u_2 - 1)v_3^{[0]2}, 0)^T \\ &= 2u_6^*(u_2 - 1)v_3^{[0]2} \psi_3^{[0]} \neq 0 \end{aligned}$$

Since u_2 represent a consumption rate then $u_2 - 1 \neq 0$. Thus, according to Sotomayor's theorem system (2) has transcritical bifurcation at E_0 with the parameter $u_6 = u_6^*$. ■

Theorem 10: Assume that the local stability condition (11c) hold and suppose that the condition

$$u_1 u_5 + u_4 \neq u_1 u_3 + u_5 \quad (25)$$

Is satisfied. Then when the parameter value u_{11} passing through

$$u_{11}^* = \frac{s_1(u_4 - u_3)}{u_1 u_3 - u_4} \text{ system (2) at the equilibrium point } E_1 \text{ has:}$$

- 1) No saddle-node bifurcation.
- 2) Transcritical bifurcation.

Proof: According to the Jacobian matrix J_1 given by Eq. (11a) the system (2) at the equilibrium point E_1 has zero eigenvalue (say $\lambda_{1w} = 0$) at $u_{11} = u_{11}^*$, and the Jacobian matrix J_1 with $u_{11} = u_{11}^*$ becomes:

$$J_1^* = J(u_{11} = u_{11}^*)$$

$$= \begin{pmatrix} \frac{u_3 - u_1 u_3}{u_1 u_3 - u_4} & \frac{u_1 u_3 - u_4}{u_3} & \frac{u_2 u_3 - u_4}{u_3} & 1 \\ \frac{u_3(u_4 - u_3)}{u_1 u_3 - u_4} & 0 & 0 & \frac{u_5(u_3 - u_4)}{u_1 u_3 - u_4} \\ 0 & 0 & \frac{u_4 u_6 - u_3 u_7}{u_3} & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}$$

Now, let $V^{[1]} = (v_1^{[1]}, v_2^{[1]}, v_3^{[1]}, v_4^{[1]})^T$ be the eigenvector corresponding to the eigenvalue $\lambda_{1w} = 0$. Thus $J_1^* V^{[1]} = 0$, gives:

$$V^{[1]} = \left(v_1^{[1]}, \frac{L_1}{L_2} v_1^{[1]}, 0, \frac{u_3}{u_5} v_1^{[1]} \right)^T$$

Where, $L_1 = u_3^2(u_1(u_3 - u_5) - u_4 + u_5)$, $L_2 = u_5(u_1 u_3 - u_4)^2$ and $v_1^{[1]}$ any nonzero real number. Clearly, $u_1 u_3 \neq u_4$ due to the existence condition (3b). Let $\Psi^{[1]} = (\psi_1^{[1]}, \psi_2^{[1]}, \psi_3^{[1]}, \psi_4^{[1]})^T$ be the eigenvector associated with the eigenvalue $\lambda_{1w} = 0$ of the matrix J_1^{*T} . Then $J_1^{*T} \Psi^{[1]} = 0$, by solving this equation for $\Psi^{[1]}$ we get $\Psi^{[1]} = (0, 0, 0, \psi_4^{[1]})^T$, where $\psi_4^{[1]}$ any nonzero real number. Now, consider:

$$\frac{\partial f}{\partial u_{11}} = f_{u_{11}}(X, u_{11}) = (0, 0, 0, -w)^T$$

Thus, $f_{u_{11}}(E_1, u_{11}^*) = (0, 0, 0, 0)^T$ and hence

$$(\Psi^{[1]})^T f_{u_{11}}(E_1, u_{11}^*) = 0$$

So, according to Sotomayor's theorem the saddle-node bifurcation cannot occur, while the first condition of transcritical bifurcation is satisfied. Now, since:

$$Df_{u_{11}}(X, u_{11}) = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -1 \end{pmatrix}$$

Further, it is observed

$$Df_{u_{11}}(E_1, u_{11}^*) V^{[1]} = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -1 \end{pmatrix} \begin{pmatrix} v_1^{[1]} \\ v_2^{[1]} \\ v_3^{[1]} \\ v_4^{[1]} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \\ -v_4^{[1]} \end{pmatrix}$$

$$\begin{aligned} (\Psi^{[1]})^T [Df_{u_{11}}(E_1, u_{11}^*) V^{[1]}] &= (0, 0, 0, \psi_4^{[1]}) (0, 0, 0, -v_4^{[1]})^T \\ &= -v_4^{[1]} \psi_4^{[1]} \neq 0 \end{aligned}$$

Now, by substituting $V^{[1]}$ in (24) we get

$$\begin{aligned} D^2 f(E_1, u_{11}^*) (V^{[1]}, V^{[1]}) &= \left(-2 \frac{L_1}{L_2} (v_1^{[1]})^2, 0, 0, 2 \frac{s_1 u_3 L_1}{u_5 L_2} (v_1^{[1]})^2 \right)^T \end{aligned}$$

Hence, it is obtained that:

$$\begin{aligned} (\Psi^{[1]})^T [D^2 f(E_1, u_{11}^*) (V^{[1]}, V^{[1]})] &= 2 \frac{s_1 u_3 L_1}{u_5 L_2} (v_1^{[1]})^2 \psi_4^{[1]} \\ &\neq 0 \end{aligned}$$

Thus, according to Sotomayor's theorem system (2) has transcritical bifurcation at E_1 with the parameter $u_{11} = u_{11}^*$. Note that if the condition (25) does not satisfied then the system (2) does not have a bifurcation. ■

Theorem 11: Assume that the local stability condition (12c) hold and suppose that the condition

$$u_2 u_8 + u_7 \neq u_2 u_6 + u_8 \quad (26)$$

Is satisfied. Then when the parameter value u_{11} passing through

$$u_{11}^* = \frac{u_{10}(u_7 - u_6)}{u_2 u_6 - u_7} \text{ system (2) at the equilibrium point } E_2 \text{ has:}$$

- 1) No saddle-node bifurcation.
- 2) Transcritical bifurcation.

Proof: According to the Jacobian matrix J_2 given by Eq. (12a) the system (2) at the equilibrium point E_2 has zero eigenvalue (say $\lambda_{2w} = 0$) at $u_{11} = u_{11}^*$, and the Jacobian matrix J_2 with $u_{11} = u_{11}^*$ becomes:

$$J_2^* = J(u_{11} = u_{11}^*)$$

$$= \begin{pmatrix} \frac{u_6 - u_2 u_6}{u_2 u_6 - u_7} & \frac{u_1 u_6 - u_7}{u_6} & \frac{u_2 u_6 - u_7}{u_6} & 1 \\ 0 & \frac{u_3 u_7 - u_4 u_6}{u_6} & 0 & 0 \\ \frac{u_6(u_7 - u_6)}{u_2 u_6 - u_7} & 0 & 0 & \frac{u_8(u_6 - u_7)}{u_2 u_6 - u_7} \\ 0 & 0 & 0 & 0 \end{pmatrix}$$

Now, let $V^{[2]} = (v_1^{[2]}, v_2^{[2]}, v_3^{[2]}, v_4^{[2]})^T$ be the eigenvector corresponding to the eigenvalue $\lambda_{2w} = 0$. Thus $J_2^* V^{[2]} = 0$, gives:

$$V^{[2]} = \left(v_1^{[2]}, 0, \frac{L_3}{L_4} v_1^{[2]}, \frac{u_6}{u_8} v_1^{[2]} \right)^T$$

Where $L_3 = u_6^2(u_2(u_8 - u_6) + u_7 - u_8)$, $L_4 = u_8(u_2 u_6 - u_7)^2$ and $v_1^{[2]}$ any nonzero real number. Clearly, $u_2 u_6 \neq u_7$ due to the ex-

istence condition (4b). Let $\Psi^{[2]} = (\psi_1^{[2]}, \psi_2^{[2]}, \psi_3^{[2]}, \psi_4^{[2]})^T$ be the eigenvector associated with the eigenvalue $\lambda_{2w} = 0$ of the matrix J_2^{*T} . Then $J_2^{*T} \Psi^{[2]} = 0$, by solving this equation for $\Psi^{[2]}$ we get $\Psi^{[2]} = (0, 0, 0, \psi_4^{[2]})^T$, where $\psi_4^{[2]}$ any nonzero real number. Now, consider:

$$\frac{\partial f}{\partial u_{11}} = f_{u_{11}}(X, u_{11}) = (0, 0, 0, -w)^T$$

Thus, $f_{u_{11}}(E_2, u_{11}^*) = (0, 0, 0, 0)^T$ and hence

$$(\Psi^{[2]})^T f_{u_{11}}(E_2, u_{11}^*) = 0$$

So, according to Sotomayor's theorem the saddle-node bifurcation cannot occur, while the first condition of transcritical bifurcation is satisfied. Now, since:

$$Df_{u_{11}}(X, u_{11}) = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -1 \end{pmatrix}$$

Therefore,

$$Df_{u_{11}}(E_2, u_{11}^*)V^{[2]} = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -1 \end{pmatrix} \begin{pmatrix} \psi_1^{[2]} \\ \psi_2^{[2]} \\ \psi_3^{[2]} \\ \psi_4^{[2]} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \\ -\psi_4^{[2]} \end{pmatrix}$$

$$\begin{aligned} (\Psi^{[2]})^T [Df_{u_{11}}(E_2, u_{11}^*)V^{[2]}] &= (0, 0, 0, \psi_4^{[2]}) (0, 0, 0, -\psi_4^{[2]})^T \\ &= -\psi_4^{[2]} \psi_4^{[2]} \neq 0 \end{aligned}$$

Now, by substituting $V^{[2]}$ in (24) we get

$$\begin{aligned} D^2f(E_2, u_{11}^*)(V^{[2]}, V^{[2]}) \\ = \left(-2 \frac{L_3}{L_4} (v_1^{[2]})^2, 0, 0, 2 \frac{u_6 u_{10} L_3}{u_8 L_4} (v_1^{[2]})^2 \right)^T \end{aligned}$$

Hence, it is obtained that:

$$\begin{aligned} (\Psi^{[2]})^T [D^2f(E_2, u_{11}^*)(V^{[2]}, V^{[2]})] \\ = 2 \frac{u_6 u_{10} L_3}{u_8 L_4} (v_1^{[2]})^2 \psi_4^{[2]} \neq 0 \end{aligned}$$

Thus, according to Sotomayor's theorem system (2) has transcritical bifurcation at E_2 with the parameter $u_{11} = u_{11}^*$. ■

Theorem 12: Assume that the following conditions

$$u_7 - u_6 x_3 > w_3 \quad (27a)$$

$$u_3 u_8 \neq u_5 u_6 \quad (27b)$$

$$e_{13} e_{42} \neq e_{12} e_{43} \quad (27c)$$

Are satisfied. Then when the parameter value u_8 passing through

$$u_8^* = \frac{u_7 - u_6 x_3}{w_3} \text{ system (2) at the equilibrium point } E_3 \text{ has:}$$

1) No saddle-node bifurcation.

2) Transcritical bifurcation.

Proof: According to the Jacobian matrix J_3 given by Eq. (13a) the system (2) at the equilibrium point E_3 has zero eigenvalue (say $\lambda_{3z} = 0$) at $u_8 = u_8^*$, and the Jacobian matrix J_3 with $u_8 = u_8^*$ becomes:

$$J_3^* = J(u_8 = u_8^*) = (e_{ij})_{4 \times 4}$$

Where $e_{ij} = a_{ij}$ for all $i, j = 1, 2, 3, 4$ with $e_{33} = 0$.

Let $V^{[3]} = (v_1^{[3]}, v_2^{[3]}, v_3^{[3]}, v_4^{[3]})^T$ be the eigenvector corresponding to the eigenvalue $\lambda_{3z} = 0$. Thus $J_3^* V^{[3]} = 0$, which gives:

$$V^{[3]} = \left(-\frac{e_{24} L_5}{L_6} v_3^{[3]}, -\frac{u_{10}}{s_1} v_3^{[3]}, v_3^{[3]}, \frac{e_{21} L_5}{L_6} v_3^{[3]} \right)^T$$

Where $L_5 = e_{13} e_{42} - e_{12} e_{43}$, $L_6 = e_{42} (e_{11} e_{24} - e_{21})$ and $v_3^{[3]}$ any nonzero real number. Let $\Psi^{[3]} = (\psi_1^{[3]}, \psi_2^{[3]}, \psi_3^{[3]}, \psi_4^{[3]})^T$ be the eigenvector corresponding to the eigenvalue $\lambda_{3z} = 0$ of the matrix J_3^{*T} . Then we have $J_3^{*T} \Psi^{[3]} = 0$, by solving this equation for $\Psi^{[3]}$ we get $\Psi^{[3]} = (0, 0, \psi_3^{[3]}, 0)^T$, where $\psi_3^{[3]}$ any nonzero real number. Now, consider:

$$\frac{\partial f}{\partial u_8} = f_{u_8}(X, u_8) = (0, 0, -zw, 0)^T$$

Thus, $f_{u_8}(E_3, u_8^*) = (0, 0, 0, 0)^T$ and hence $(\Psi^{[3]})^T f_{u_8}(E_3, u_8^*) = 0$

So, according to Sotomayor's theorem the saddle-node bifurcation cannot occur, while the first condition of transcritical bifurcation is satisfied. Now, since

$$Df_{u_8}(X, u_8) = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & -w & -z \\ 0 & 0 & 0 & 0 \end{pmatrix}$$

Further, it is observed

$$Df_{u_8}(E_3, u_8^*)V^{[3]} = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & -w & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} -\frac{e_{24} L_5}{L_6} v_3^{[3]} \\ -\frac{u_{10}}{s_1} v_3^{[3]} \\ v_3^{[3]} \\ \frac{e_{21} L_5}{L_6} v_3^{[3]} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ -w v_3^{[3]} \\ 0 \end{pmatrix}$$

$$\begin{aligned} (\Psi^{[3]})^T [Df_{u_8}(E_3, u_8^*)V^{[3]}] &= (0, 0, \psi_3^{[3]}, 0) (0, 0, -w v_3^{[3]}, 0)^T \\ &= -w \psi_3^{[3]} v_3^{[3]} \neq 0 \end{aligned}$$

Now, by substituting $V^{[3]}$ in (24) we get

$$D^2f(E_3, u_8^*)(V^{[3]}, V^{[3]}) = (U_1, 0, U_2, 0)^T$$

Where

$$U_1 = 2 \frac{e_{42} L_5 (s_1 - u_{10})}{s_1 L_6} (v_3^{[3]})^2$$

$$U_2 = -2 \frac{u_{11}L_5(u_3u_8 - u_5u_6)}{s_1L_6} \left(v_3^{[3]} \right)^2$$

Hence, it is obtain that:

$$(\Psi^{[3]})^T [D^2f(E_3, u_8^*)(V^{[3]}, V^{[3]})] = U_2 \Psi_3^{[3]} \neq 0$$

Thus, according to Sotomayor's theorem system (2) has transcritical bifurcation at E_3 with the parameter $u_8 = u_8^*$. ■

Theorem 13: Assume that the following conditions

$$u_3x_4 > u_5w_4 \quad (28a)$$

$$u_3u_8 \neq u_5u_6 \quad (28b)$$

$$q_{13}q_{42} \neq q_{12}q_{43} \quad (28c)$$

Are satisfied. Then when the parameter value u_4 passing through $u_4^* = u_3x_4 - u_5w_4$ system (2) at the equilibrium point E_4 has:

- 1) No saddle-node bifurcation.
- 2) Transcritical bifurcation.

Proof: According to the Jacobian matrix J_4 given by Eq. (14a) the system (2) at the equilibrium E_4 has zero eigenvalue (say $\lambda_{4y} = 0$) at $u_4 = u_4^*$, and the Jacobian matrix J_4 with $u_4 = u_4^*$ becomes:

$$J_4^* = J(u_4 = u_4^*) = (q_{ij})_{4 \times 4}$$

Where $q_{ij} = b_{ij}$ for all $i, j = 1, 2, 3, 4$ with $q_{22} = 0$.

Let $V^{[4]} = (v_1^{[4]}, v_2^{[4]}, v_3^{[4]}, v_4^{[4]})^T$ be the eigenvector corresponding to the eigenvalue $\lambda_{4y} = 0$. Thus $J_4^* V^{[4]} = 0$, which gives:

$$V^{[4]} = \left(-\frac{q_{34}L_7}{L_8} v_2^{[4]}, v_2^{[4]}, -\frac{u_{10}}{s_1} v_2^{[4]}, \frac{q_{31}L_7}{L_8} v_2^{[4]} \right)^T$$

Where $L_7 = q_{12}q_{43} - q_{13}q_{42}$, $L_8 = q_{43}(q_{11}q_{34} - q_{31})$ and $v_2^{[4]}$ any nonzero real number. Let $\Psi^{[4]} = (\psi_1^{[4]}, \psi_2^{[4]}, \psi_3^{[4]}, \psi_4^{[4]})^T$ be the eigenvector corresponding to the eigenvalue $\lambda_{4y} = 0$ of the matrix J_4^{*T} . Then we have $J_4^{*T} \Psi^{[4]} = 0$, by solving this equation for $\Psi^{[4]}$ we get $\Psi^{[4]} = (0, \psi_2^{[4]}, 0, 0)^T$, where $\psi_2^{[4]}$ any nonzero real number. Now, consider:

$$\frac{\partial f}{\partial u_4} = f_{u_4}(X, u_4) = (0, -y, 0, 0)^T$$

Thus, $f_{u_4}(E_4, u_4^*) = (0, 0, 0, 0)^T$ and hence $(\Psi^{[4]})^T f_{u_4}(E_4, u_4^*) = 0$. So, according to Sotomayor's theorem the saddle-node bifurcation cannot occur, while the first condition of transcritical bifurcation is satisfied. Now, since

$$Df_{u_4}(X, u_4) = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & -1 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}$$

Further, it is observed

$$Df_{u_4}(E_4, u_4^*)V^{[4]} = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & -1 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} -\frac{q_{34}L_7}{L_8} v_2^{[4]} \\ v_2^{[4]} \\ -\frac{u_{10}}{s_1} v_2^{[4]} \\ \frac{q_{31}L_7}{L_8} v_2^{[4]} \end{pmatrix} = \begin{pmatrix} 0 \\ -v_2^{[4]} \\ 0 \\ 0 \end{pmatrix}$$

$$(\Psi^{[4]})^T [Df_{u_4}(E_4, u_4^*)V^{[4]}] = (0, \psi_2^{[4]}, 0, 0) \begin{pmatrix} 0 \\ -v_2^{[4]} \\ 0 \\ 0 \end{pmatrix}^T = -v_2^{[4]} \psi_2^{[4]} \neq 0$$

Now, by substituting $V^{[4]}$ in (24) we get

$$D^2f(E_4, u_4^*)(V^{[4]}, V^{[4]}) = (U_3, U_4, 0, U_5)^T$$

Where

$$U_3 = 2 \frac{q_{34}L_7(1-u_{10})}{s_1L_8} \left(v_2^{[4]} \right)^2$$

$$U_4 = -2 \frac{u_{11}L_7(u_5u_6 - u_3u_8)}{u_{10}L_8} \left(v_2^{[4]} \right)^2$$

$$U_5 = 2 \frac{q_{31}L_7(s_1^2 - u_{10}^2)}{s_1L_8} \left(v_2^{[4]} \right)^2$$

Hence, it is obtain that:

$$(\Psi^{[4]})^T [D^2f(E_4, u_4^*)(V^{[4]}, V^{[4]})] = U_4 \psi_2^{[4]} \neq 0$$

Thus, according to Sotomayor's theorem system (2) has transcritical bifurcation at E_4 with the parameter $u_4 = u_4^*$. ■

Remark: According to Sotomayor's theorem system (2) has no bifurcation at the nonhyperbolic equilibrium point E_5 for different parameter values, and that ensure the nonhyperbolic is a necessary but not sufficient condition for bifurcation to occur.

Theorem 14: system (2) has no bifurcation at equilibrium point E_6 .

Proof: According to the Jacobian matrix J_6 given by Eq. (16.a) the system (2) at the equilibrium point E_4 has zero eigenvalue (say $\lambda_6 = 0$) at $u_6 = u_6^*$ and the Jacobian matrix J_6 with $u_6 = u_6^*$ becomes:

$$J_6^* = J(u_6 = u_6^*) = (h_{ij})_{4 \times 4}$$

Where $h_{ij} = d_{ij}$ for all $i, j = 1, 2, 3, 4$ with $h_{31} = u_6^*z$.

Let $V^{[6]} = (v_1^{[6]}, v_2^{[6]}, v_3^{[6]}, v_4^{[6]})^T$ be the eigenvector corresponding to the eigenvalue $\lambda_6 = 0$. Thus $J_6^* V^{[6]} = 0$, which gives:

$$V^{[6]} = \left(\frac{u_5}{u_3} v_4^{[6]}, -\frac{(h_{43}L_9 + L_{10})}{L_{11}} v_4^{[6]}, -\frac{(h_{42}L_9 + L_{10})}{L_{11}} v_4^{[6]}, v_4^{[6]} \right)^T$$

Where $L_9 = h_{24}h_{11} - h_{21}$, $L_{10} = h_{44}h_{12}h_{21}$, $L_{11} = h_{21}(h_{12}h_{43} - h_{13}h_{42})$ and $v_4^{[6]}$ any nonzero real number.

Let $\Psi^{[6]} = (\psi_1^{[6]}, \psi_2^{[6]}, \psi_3^{[6]}, \psi_4^{[6]})^T$ be the eigenvector corresponding to the eigenvalue $\lambda_6 = 0$ of the matrix J_6^{*T} . Then we have $J_6^{*T} \Psi^{[6]} = 0$, by solving this equation for $\Psi^{[6]}$ we get :

$$\Psi^{[6]} = \begin{pmatrix} 0, -\frac{h_{34}}{h_{24}} \psi_3^{[6]}, \psi_3^{[6]}, 0 \end{pmatrix}^T$$

Where $\psi_3^{[6]}$ any nonzero real number. Now, consider:

$$\frac{\partial f}{\partial u_6} = f_{u_6}(X, u_6) = (0, 0, xz, 0)^T$$

Thus, $f_{u_6}(E_6, u_6^*) = (0, 0, xz, 0)^T$ and hence

$$(\Psi^{[6]})^T f_{u_6}(E_6, u_6^*) = xz \psi_3^{[6]}.$$

Now, by substituting $V^{[6]}$ in (24) we get

$$D^2 f(E_6, u_6^*)(V^{[6]}, V^{[6]}) = (U_6, 0, 0, U_7)^T$$

Where

$$U_6 = -2 \frac{u_5(2L_{10} + (h_{42} + h_{43})L_9)}{u_3 L_{11}} (v_4^{[6]})^2$$

$$U_7 = -2 \frac{s_1(h_{43}L_9 + L_{10}) + u_{10}(h_{42}L_9 + L_{10})}{L_{11}} (v_4^{[6]})^2$$

Hence, it is obtain that:

$$(\Psi^{[6]})^T [D^2 f(E_6, u_6^*)(V^{[6]}, V^{[6]})] = 0$$

Thus, according to Sotomayor's theorem system (2) has no bifurcation at E_6 with the parameter $u_6 = u_6^*$. ■

7. The Hopf bifurcation analysis

In this section, the occurrence of Hopf bifurcation of system (2) near the positive equilibrium point E_6 is studied below.

Theorem 15: Assume that the following conditions are hold:

$$\Gamma_1 > \frac{d_{11}^2 d_{44} d_{43}}{d_{21} \Gamma_6} \quad (29a)$$

$$\Gamma_2 > d_{11}(d_{11} d_{34} d_{43} + d_{44} \Gamma_2) + d_{44}(d_{44} d_{34} - d_{11} \Gamma_1 + \Gamma_4) \quad (29b)$$

Then system (2) possesses a Hopf bifurcation around the equilibrium point E_6 when the parameter u_5 passes through $u_5 = u_5^*$, where

$$u_5^* = \frac{1}{2y_6 R_1} (-R_2 + \sqrt{R_2^2 - 4R_1 R_3})$$

With

$$R_1 = d_{11} d_{44} d_{42}$$

$$R_2 = d_{31} \Gamma_1^2 \Gamma_6 + d_{11} d_{44} d_{42} \Gamma_1 (d_{11} + d_{44} \Gamma_4) - 2d_{11} d_{44} d_{42} d_{34} d_{43} - d_{42} (d_{11} \Gamma_4 + d_{44} \Gamma_2)$$

$$R_3 = \Gamma_2 [d_{11} (d_{11} d_{34} d_{43} + d_{44} \Gamma_2) + d_{44} (d_{44} d_{34} d_{43} - d_{11} \Gamma_1 + \Gamma_4)] - \Gamma_1 \Gamma_4 [d_{11} d_{44} (\Gamma_2 + d_{44} d_{34} d_{43} + \Gamma_4)] + \Gamma_1 [d_{34} (d_{21} \Gamma_1 \Gamma_6 - d_{11} d_{44} d_{43})]$$

Proof: According to the Hopf bifurcation theorem, the Hopf bifurcation can occur provided that: $D_i(u_5^*) > 0$, $i = 1, 3$; $\Delta_1 > 0$,

$D_1^3 - 4\Delta_1 > 0$ and $\Delta_2(u_5^*) = 0$. Therefore we obtain that $\Delta_2 = 0$ gives

$$u_5^2 y_6^2 R_1 + u_5 y_6 R_2 + R_3 = 0 \quad (29c)$$

Then Eq. (29c) has a unique positive root

$$u_5^* = \frac{1}{2y_6 R_1} (-R_2 + \sqrt{R_2^2 - 4R_1 R_3})$$

Provided that the conditions (29)(a,b) hold. Now, at $u_5 = u_5^*$ the characteristic equation can be written as:

$$\left(\lambda_6^2 + \frac{D_3}{D_1} \right) \left(\lambda_6^2 + D_1 \lambda_6 + \frac{\Delta_1}{D_1} \right) = 0$$

Which has four roots

$$\lambda_{6,1,2} = \pm i \sqrt{\frac{D_3}{D_1}}, \quad \lambda_{6,3,4} = \frac{1}{2} \left(-D_1 \pm \sqrt{D_1^2 - 4 \frac{\Delta_1}{D_1}} \right)$$

Clearly, at $u_5 = u_5^*$ there are two pure imaginary eigenvalues ($\lambda_{6,1,2}$ and $\lambda_{6,3,4}$) and two eigenvalues which are real and negative.

Now, for all values of u_5 in the neighborhood of u_5^* , the roots in general of the following form:

$$\lambda_{6,1} = \alpha_1 + i\alpha_2; \quad \lambda_{6,2} = \alpha_1 - i\alpha_2; \quad \lambda_{6,3,4} = \frac{1}{2} \left(-D_1 \pm \sqrt{D_1^2 - 4 \frac{\Delta_1}{D_1}} \right)$$

Clearly, $\text{Re}(\lambda_{6k}(u_5))|_{u_5=u_5^*} = \alpha_1(u_5^*) = 0, k = 1, 2$

That means the first condition of necessary and sufficient conditions for Hopf bifurcation is satisfied at $u_5 = u_5^*$. Now, to verify the transversality condition we must prove that $\bar{\Theta}(u_5^*) \bar{\Psi}(u_5^*) + \bar{\Gamma}(u_5^*) \bar{\Phi}(u_5^*) \neq 0$. Note that for $u_5 = u_5^*$ we have:

$$\alpha_1 = 0, \quad \alpha_2 = \sqrt{\frac{D_3}{D_1}},$$

Then

$$\begin{aligned} \bar{\Psi}(u_5^*) &= -2D_3(u_5^*) \\ \bar{\Phi}(u_5^*) &= 2 \frac{\alpha_2(u_5^*)}{D_1} (D_1 D_2 - 2D_3) \\ \bar{\Theta}(u_5^*) &= D_4'(u_5^*) - \frac{D_3(u_5^*)}{D_1(u_5^*)} D_2'(u_5^*) \\ \bar{\Gamma}(u_5^*) &= \alpha_2(u_5^*) \left(D_3'(u_5^*) - \frac{D_3(u_5^*)}{D_1(u_5^*)} D_1'(u_5^*) \right) \end{aligned}$$

Where:

$$D_1' = \frac{dD_1}{du_5} \Big|_{u_5=u_5^*} = 0$$

$$D_2' = \frac{dD_2}{du_5} \Big|_{u_5=u_5^*} = -y_6 d_{42}$$

$$D_3' = \frac{dD_3}{du_5} \Big|_{u_5=u_5^*} = y_6 d_{11} d_{42}$$

$$D_4' = \frac{dD_4}{du_5} \Big|_{u_5=u_5^*} = y_6 d_{31} \Gamma_6$$

Then we have

$$\bar{\Theta}(u_5^*)\bar{\Psi}(u_5^*) + \bar{\Gamma}(u_5^*)\bar{\Phi}(u_5^*) =$$

$$2y_6 D_1 D_3 \left[d_{42} \left(d_{11} \left(D_2 - 2 \frac{D_3}{D_1} \right) - D_1 D_3 \right) - d_{31} \Gamma_6 \right] \neq 0$$

So, we obtain that the Hopf bifurcation occurs around the equilibrium point E_6 at the parameter $u_5 = u_5^*$.

■

8. Numerical analysis

In this section the dynamical behavior of system (2) is studied numerically starting at different sets of initial points with different sets of parameters values. The objectives of this study are: first specify the control parameters on the dynamical behavior of system (2) and second ensure our obtained analytical results. It is observed that, for the following set of hypothetical parameters:

$$\begin{aligned} u_1 &= 0.1, u_3 = 0.5, u_4 = 0.1, u_5 = 0.4, u_6 = 0.5, \\ u_7 &= 0.1, u_8 = 0.4, u_{10} = 0.2, u_{11} = 0.2, s_1 = 0.2 \end{aligned} \quad (29)$$

The solution of system (2) approaches asymptotically to the positive equilibrium point $E_6 = (1.13, 0.46, 0.53, 1.16)$ and this is confirming our obtained analytical results as shown in Fig. (1).

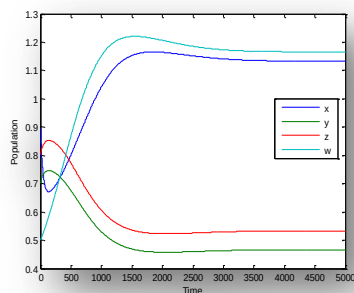


Fig. 1: Time series of the solution of system (2) that approaches asymptotically to the stable positive equilibrium point (1.13, 0.46, 0.53, 1.16)

Now, in order to specify the control parameters values of system (2), the system is solved numerically for the data given in (29) with varying one parameter each time. It is observed that, for the data given in (29) with varying one of the parameter values u_1 , u_2 , u_{10} and u_{11} , there is no change in the dynamical behavior of system (2) and the system still approaches to the positive equilibrium point and hence these parameters are not control parameters. It is observed that for the data as given in (29) with $u_3 < 0.5$, the solution of system (2) approaches asymptotically to E_4 as shown in Fig. (2a), however for $u_3 > 0.5$, the solution of system (2) approaches asymptotically to E_3 as shown in Fig. (2b). The solution of system (2) has similar behavior as that of varying u_3 when u_8 passing through 0.4.

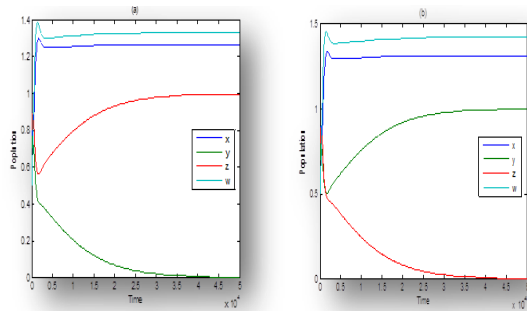


Fig. 2: Time series of the solution of system (2) for the data given by (29) with (a) $u_3 = 0.49$, which approaches to (1.26, 0, 0.99, 1.33) in the interior of positive octant of xzw -space, (b) $u_3 = 0.51$, which approaches to (1.31, 0.99, 0, 1.42) in the interior of positive octant of xyw -space

For the data given in (29) with $u_5 < 0.4$, the solution of system (2) approaches asymptotically to E_3 as shown in Fig. (3a), however for $u_5 > 0.4$, the solution of system (2) approaches asymptotically to E_4 as shown in Fig. (3b). the solution of system (2) has similar behavior as that of varying u_5 when u_6 passing through 0.5.

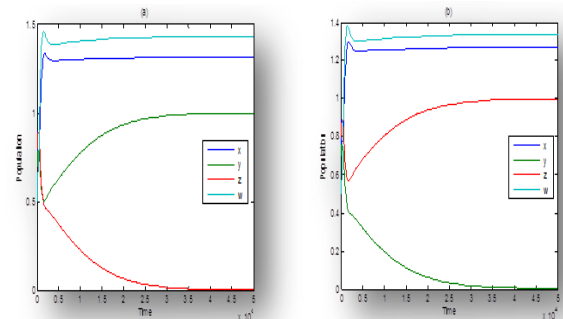


Fig. 3: Time series of the solution of system (2) for the data given by (29) with (a) $u_5 = 0.39$, which approaches to (1.31, 0.99, 0, 1.42) in the interior of positive octant of xyw -space, (b) $u_5 = 0.41$, which approaches to (1.26, 0, 0.99, 1.33) in the interior of positive octant of xzw -space

For the data given in (29) with $u_4 > 0.1$, the solution of system (2) approaches asymptotically to E_4 as shown in Fig. (4a). However, for $u_7 > 0.1$ with the rest of parameters as given in (29), the solution of system (2) approaches asymptotically to E_3 as shown in Fig. (4b).

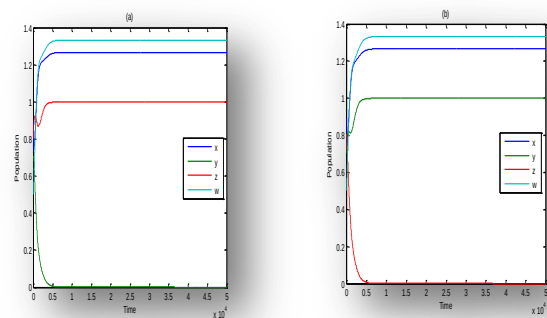


Fig. 4: Time series of the solution of system (2) for the data given by (29) with (a) $u_4 = 0.2$, which approaches to (1.26, 0, 1, 1.33) in the interior of positive octant of xzw -space, (b) $u_7 = 0.2$, which approaches to (1.26, 1, 0, 1.33) in the interior of positive octant of xyw -space

For the data give n in (29) with $s_1 \leq -0.22$, the solution of system (2) approaches asymptotically to E_5 as shown in Fig. (5).

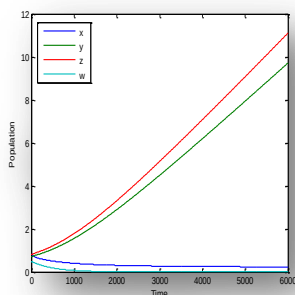


Fig. 5: Time series of the solution of system (2) for the data given by (29) with $s_1 = -0.22$, which approaches to $(0.23, 9.7, 11.09, 0)$

Now by varying the parameters u_4 , u_7 and s_1 keeping the rest of parameters values as in (29), it is observed that for $u_4 > 0.5$, $u_7 > 0.5$ and $s_1 \leq -0.22$, the solution of system (2) approaches asymptotically to E_0 as shown in Fig. (6a). However for $u_4 < 0.5$, $u_7 < 0.5$ and $s_1 \leq -0.22$, the solution of system (2) approaches asymptotically to E_1 as shown in Fig.(6b). Moreover for $u_4 > 0.5$, $u_7 < 0.5$ and $s_1 \leq -0.22$, the solution of system (2) approaches asymptotically to E_2 as shown in Fig. (6c).

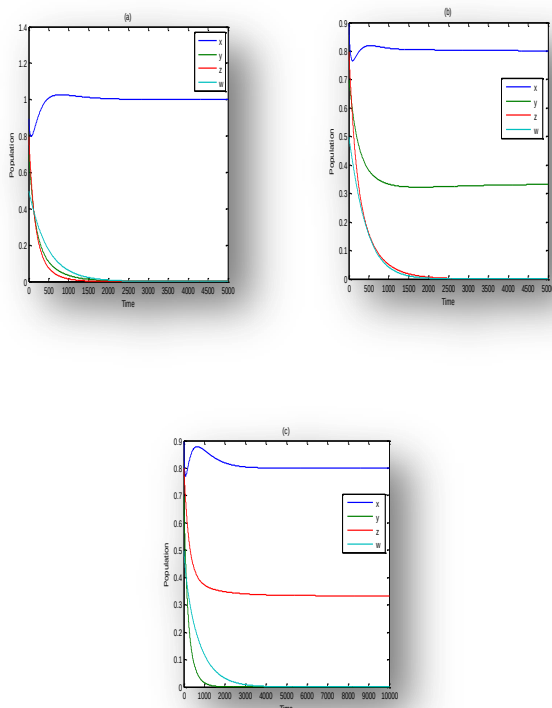


Fig. 6: Time series of the solution of system (2) for the data given by (29) with (a) $u_4 = 0.7$, $u_7 = 0.8$ and $s_1 = -0.23$, which approaches to $(1, 0, 0, 0)$ on the x -axis, (b) $u_4 = 0.4$, $u_7 = 0.6$ and $s_1 = -0.22$, which approaches to $(0.8, 0.3, 0, 0)$ in $\text{Int. } R_+^2$ of xy -plane, (c) $u_4 = 0.7$, $u_7 = 0.4$ and $s_1 = -0.23$, which approaches to $(0.7, 0, 0.3, 0)$ in $\text{Int. } R_+^2$ of xz -plane

9. Conclusion

In the previous section, we proposed and analyzed an ecological model that described the dynamical behavior of food web model with Lotka-Volterra type of functional response. It is assumed that: The phytoplankton divided into two compartments namely toxin producing phytoplankton which produces a toxic substance as a defensive strategy against predation by zooplankton, and a non-toxic phytoplankton. However the portion of the dead species of phytoplankton and zooplankton is returned to nutrient due to the decomposition operation. The boundedness of the proposed sys-

tem (2) has been discussed. The dynamical behavior of system (2) has been investigated locally as well as globally. To understand the effect of varying each parameter on the dynamics of system (2) and to confirm our obtained analytical results, system (2) has been solved numerically for a biological feasible set of hypothetical parameters values and the following results are obtained:

- 1) For the set of hypothetical parameters values given by (29) system (2) approaches asymptotically to stable positive equilibrium point, and hence the food web system coexists (persist).
- 2) It is observed that varying the parameters: u_1 , u_2 which stand for conversion rate from death (toxic, nontoxic) phytoplankton to nutrient, the consumption rate from nontoxic phytoplankton to zooplankton u_{10} and the zooplankton natural death rate u_{11} , do not have any effect on the dynamical behavior of system (2) and the system still approaches to a positive equilibrium point.
- 3) As the consumption rates from nutrient to toxic phytoplankton u_3 decreases from a critical value (0.5) keeping other parameters fixed as in (29) then the toxic phytoplankton faces extinction and the solution of system (2) approaches asymptotically to equilibrium point E_4 in the $\text{Int. } R_+^3$ of xzw -space. While increasing u_3 from that critical value will causes extinction in the nontoxic phytoplankton species and the solution of system (2) approaches asymptotically to equilibrium point E_3 in the $\text{Int. } R_+^3$ of xyw -space. It is observed that the consumption rate u_8 has the same effect as u_3 with different critical value. Clearly, these critical values are bifurcation points.
- 4) As the consumption rate from toxic phytoplankton to zooplankton u_5 decreases from a critical value (0.4) keeping other parameters fixed as in (29) then the nontoxic phytoplankton faces extinction and the solution of system (2) approaches asymptotically to equilibrium point E_3 in the $\text{Int. } R_+^3$ of xyw -space. While increasing u_5 from that critical value will causes extinction in the toxic phytoplankton species and the solution of system (2) approaches asymptotically to equilibrium point E_4 in the $\text{Int. } R_+^3$ of xzw -space. It is observed that the consumption rate u_6 has the same effect as u_5 with different critical value. Clearly, these critical values are bifurcation points.
- 5) As the toxic phytoplankton natural death rate u_4 increases from acritical value (0.1) keeping other parameters fixed as in (29) then again the toxic phytoplankton faces extinction and the solution of system (2) approaches asymptotically to equilibrium point E_4 , that means the system losses the persistence. Otherwise the solution still approaches to the positive equilibrium point. However, increasing nontoxic phytoplankton natural death rate u_7 from the same critical value with the other parameters as given in (29) has extinction effect in the nontoxic phytoplankton and the system approaches asymptotically to E_3 again that means the system losses the persistence. Otherwise the solution still approaches to the positive equilibrium point. Finally, these critical values represent bifurcation points.
- 6) Gradually decreasing the parameter s_1 from the critical value (-0.23) which stand for the difference between the consumption rate from toxic phytoplankton and the liberation rate of toxin substance, causes extinction in the zooplankton species and the system approaches to E_5 in the $\text{Int. } R_+^3$ of xyz -space. Hence, the system (2) bifurcate at that critical point.
- 7) As increasing the parameters u_4 , u_7 with $s_1 \leq -0.22$ causes extinction effect in phytoplankton (toxic, nontoxic) and zooplankton and the system approaches to E_0 on the x - axis. However decreasing the value of u_4 and increasing u_7 with $s_1 \leq -0.22$ causes extinction effect in the nontoxic phytoplankton and zooplankton and the system approaches to E_1 on xy - plane. While increasing the value of u_4 and decreasing u_7 with $s_1 \leq -0.22$ causes extinction effect in the

toxic phytoplankton and zooplankton and the system approaches to E_2 on xz – plane.

Acknowledgement

All thanks to Professor Dr. Raid Kamel Naji for very helpful suggestions, who gave me a lot of his time, and effort, guidance, and his sound opinions. I also wish to thank Dr. Azhar Abbas Majeed, for her guidance and encouragement during the supervision of my work, who I stand her all the respect and Allah bless her and extension in life and grant health and safety to be an asset to the science. Also I express my deep gratitude to college of science and colleagues who provided help me to accomplish this paper wishing to be modest effort can benefit from the service of science.

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