Mathematical Modelling of Three Species Food Web with Lotka-Volterra Interaction and Intraspecific Competition

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Abstract

Food chain is the transformation of energy from autotrophs to heterotrophs in an ecological zone. Food web is a system of interconnected food chains. In this study, three species food web with intraspecific competition for limited environmental resources and Lotka-Volterra interaction of one species on the other was considered. There were five equilibrium points obtained from the assumptions of no prey exists, no predator exists, no intermediate predator exists, no top predator exists, and coexistence of the species in the environment. Taking these assumptions in to account the dynamics of the model is investigated qualitatively and the result showed that all the species settle down to their corresponding existence equilibrium points provided that $\alpha_{21} < d_1$, $\alpha_{31} < d_2$ in the absence of any predators, $\alpha_{21}x_2 < d_1 + \alpha_{23}z_2$ in the absence of the intermediate predator and $\alpha_{31}x_3 + \alpha_{32}y_3 < d_2$ in the absence of the top predator. Scaling, Stability analysis and numerical simulation of the model were also considered.

Keywords: Food web, Lotka-Volterra interaction, Stability analysis, Numerical simulation.

1. Introduction

To grow, maintain their bodies, develop, and reproduce, all organisms need energy. Food chain is the linear (non-cyclic) transformation of energy from autotrophs to heterotrophs in an ecological zone. Food webs in nature have multiple connections among a diversity of consumers and resources. Three species food web consists of Prey (basal resource), an intermediate consumer (predator) or intraguild prey, and top consumer (predator) or intraguild predator. Existence of complex food web increases the stability of an ecosystem. The classical idea of food chain arises from the two species Lotka-Volterra model and three species food chain is a modification of the two species food chain model [1, 3, 6, 7, 8, 10].

The interaction of natural communities such as predators and preys is complex and it may lead to various outcomes. Studying how predators affect the prey populations and vice versa and what stabilizes prey-predator interactions and what prevents their extinction is an important and interesting biological phenomena as food web is special case of prey–predator interaction [9, 12].

Ecologists and other researchers use mathematical models to study the interactions of species, dynamics of species, to manage wildlife resource and to predict the long term size of species in their habitat. The interaction and dynamics of population in an environment can be modeled by autonomous differential equation or system (linear or nonlinear) of autonomous differential equations [1,3,6-10]. Many of the mathematical models (differential equations), especially nonlinear differential equations have no analytic solution, but using qualitative approach with numerical method insights the behaviors of its solution [2, 4, 5, 12].

The objective of this study was to investigate the dynamics of three species food web with intra-specific competition for limited environmental resources and Lotka-Volterra interaction for one species to the other using qualitative study.

2. Mathematical Model

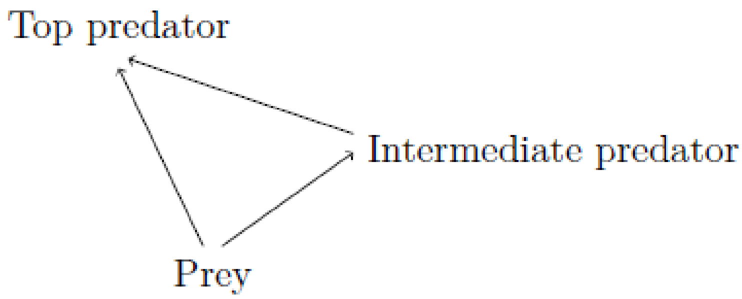


Figure 1: Three species food web with one predator. The arrows indicate flow of energy from one species to the other.

Consider the three species food web system whose interaction is Lotka-Volterra interaction among species (inter-specific competition) including intra-specific competition for limited environmental resources.

$$\begin{cases} \frac{dx_1}{dt} = rx_1 - a_{11}x_1^2 - a_{12}x_1x_2 - a_{13}x_1x_3 \\ \frac{dx_2}{dt} = -r_1x_2 + a_{21}x_1x_2 - a_{22}x_2^2 - a_{23}x_2x_3 \\ \frac{dx_3}{dt} = -r_2x_3 + a_{31}x_1x_3 + a_{32}x_2x_3 - a_{33}x_3^2 \end{cases} \quad (1)$$

where x_1, x_2, and x_3 denote the densities of prey population, an intermediate consumer (intraguild prey) population, and top consumer (intraguild predator) population at time t, respectively. All the parameters are positive where r, r_1, and r_2 denote intrinsic growth rate of x_1, death rate of x_2 in the absence of x_1, and death rate of x_3 in the absence of x_1 and x_2, respectively. The parameter a_{ij} denoted intra-specific competition of x_i species for $i = j$, rate of consumption of species x_i by species x_j for $i < j$ and measures the contribution of the victim x_i to the growth of the consumer x_j for $i > j$ where $i = 1, 2, 3$ and $j = 1, 2, 3$. For the nonexistence of predator species, the prey species x_1 follows the logistic growth model with carrying capacity of $K = r/a_{11}$. The visible region is: $R = \{(x_1, x_2, x_3) \in \mathbb{R}^3 | x\ x_1, x_2, x_3 \in \mathbb{R}^+\}$ because there is no negative population.

To make the model in equation (1) more convenient, it can be simplified using scaling method as follows:

Let $x_1 = \frac{r}{a_{11}}x$, $x_2 = \frac{r}{a_{12}}y$, $x_3 = \frac{r}{a_{13}}z$ and $t = \frac{\tau}{r}$ where x, y, z and τ are dimensionless. Then the scaled model looks like the following:

$$\begin{cases} \frac{dx}{d\tau} = x(1 - x - y - z) \\ \frac{dy}{d\tau} = y(-d_1 + \alpha_{21}x - \alpha_{22}y - \alpha_{23}z) \\ \frac{dz}{d\tau} = z(-d_2 + \alpha_{31}x + \alpha_{32}y - \alpha_{33}z) \end{cases} \quad (2)$$

where $d_i = \frac{r_i}{r}$, for $i = 1, 2$, $\alpha_{2j} = \frac{a_{2j}}{a_{1j}}$ and $\alpha_{3j} = \frac{a_{3j}}{a_{1j}}$, for $j = 1, 2, 3$.

3. Stability analysis of the equilibrium point

In application it is interesting to look what happens to the trajectories (solution curves) of autonomous system of ordinary differential equations (ODE) towards the equilibrium point, because the idea of stability analysis is investigated by the behavior of the trajectories towards the equilibrium point. Generally, the equilibrium point is stable if any trajectory whose initial value starts close to the equilibrium point stay close to it for all future time unless unstable.

The solution curve of autonomous (linear or linearized) system $\frac{dX}{dt} = J(X^*)X$where $X^t \in \mathbb{R}^n$and X^* is an equilibrium point of the system and$J(X^*)$is the Jacobian matrix of the system at $X^*$and is given by $X(t) = \sum_{i=1}^{n} c_i V_i e^{\lambda_i t}$where $c_i$is arbitrary constant, $\lambda_i$and $V_i$are eigenvalues and eigenvector of $J(X^*)$. The consequence is the solution curve of the system for increasing time is the equilibrium point whenever the eigenvalues have negative real values. Therefore, investigating the dynamics of interactions of species is simply determining the sign of eigenvalues of linear (linearized) system (Jacobian matrix at the equilibrium point).

The equilibrium point of the system in equation (2) is the solution of the system and is solved by equating to zero:

$$\begin{aligned} \boldsymbol{x(1-x-y-z)=0} \\ \boldsymbol{y(-d_1+\alpha_{21}x-\alpha_{22}y-\alpha_{23}z)=0} \\ \boldsymbol{z(-d_2+\alpha_{31}x+\alpha_{32}y-\alpha_{33}z)=0} \end{aligned} \qquad (3)$$

There are five equilibrium points which are obtained from assumptions of no prey exists $(x=0)$ $E_0 = (0,0,0)$, no predator exists $(x \neq 0, y = z = 0)$ $E_1 = (1,0,0)$, no intermediate predator exists$(x \neq 0, y = 0, z \neq 0)$ $E_2 = (x_2, 0, z_2) = \left(\frac{\alpha_{33}+d_2}{\alpha_{31}+\alpha_{33}}, 0, \frac{\alpha_{31}-d_2}{\alpha_{31}+\alpha_{33}}\right)$, no top predator exists$(x \neq 0, y \neq 0, z = 0)$ $E_3 = (x_3, z_3, 0) = \left(\frac{\alpha_{22}+d_1}{\alpha_{21}+\alpha_{22}}, \frac{\alpha_{21}-d_1}{\alpha_{21}+\alpha_{22}}, 0\right)$, and coexistence of species $(x \neq 0, y \neq 0, z \neq 0)$$E_* = (x_*, y_*, z_*)$ where

$$x_* = \frac{\alpha_{22}\alpha_{33} + \alpha_{23}\alpha_{32} + (\alpha_{32}+\alpha_{33})d_1 + (\alpha_{22}-\alpha_{23})d_2}{\alpha_{22}\alpha_{33} + \alpha_{23}\alpha_{32} + \alpha_{21}\alpha_{33} - \alpha_{23}\alpha_{31} + \alpha_{21}\alpha_{32} + \alpha_{22}\alpha_{31}}$$
$$y_* = \frac{\alpha_{21}\alpha_{33} - \alpha_{23}\alpha_{31} - (\alpha_{21}+\alpha_{33})d_1 + (\alpha_{21}+\alpha_{23})d_2}{\alpha_{22}\alpha_{33} + \alpha_{23}\alpha_{32} + \alpha_{21}\alpha_{33} - \alpha_{23}\alpha_{31} + \alpha_{21}\alpha_{32} + \alpha_{22}\alpha_{31}}$$
$$z_* = \frac{\alpha_{21}\alpha_{32} + \alpha_{22}\alpha_{31} + (\alpha_{31}-\alpha_{32})d_1 - (\alpha_{21}+\alpha_{22})d_2}{\alpha_{22}\alpha_{33} + \alpha_{23}\alpha_{32} + \alpha_{21}\alpha_{33} - \alpha_{23}\alpha_{31} + \alpha_{21}\alpha_{32} + \alpha_{22}\alpha_{31}}$$

in the environment provided that all the equilibrium points are positive.

The Jacobian matrix of the system in equation (2), at any point $J(x,y,z)$ is given by

$$J(x,y,z) = \begin{pmatrix} 1-2x-y-z & -x & -x \\ \alpha_{21}y & -d_1+\alpha_{21}x-2\alpha_{22}y-\alpha_{23}z & -\alpha_{23}y \\ \alpha_{31}z & \alpha_{32}z & -d_2+\alpha_{31}x+\alpha_{32}y-2\alpha_{33}z \end{pmatrix}.$$

The Jacobian matrix at the trivial equilibrium point E_0 is

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

The eigenvalues are the $\lambda_1 = 1, \lambda_2 = -d_1$and $\lambda_3 = -d_2$. Hence all of the parameters are non-negative indicating that one of the eigenvalue is positive implying the trivial equilibrium point is unstable (saddle).The Jacobian matrix at the equilibrium point $E_1 = (1,0,0)$ is

$$J(E_1) = \begin{pmatrix} -1 & -1 & -1 \\ 0 & -d_1+\alpha_{21} & 0 \\ 0 & 0 & -d_2+\alpha_{31} \end{pmatrix}$$

and the eigenvalues are the elements of the main diagonal. The equilibrium point $E_1 = (1,0,0)$ is stable whenever $d_1 > \alpha_{21}$and $d_2 > \alpha_{31}$. The Jacobian matrix at $E_2 = (x_2, 0, z_2)$ is

$$J(E_2) = \begin{pmatrix} -x_2 & -x_2 & -x_2 \\ 0 & -d_1+\alpha_{21}x_2-\alpha_{23}z_2 & 0 \\ \alpha_{31}z_2 & \alpha_{32}z_2 & -\alpha_{33}z_2 \end{pmatrix}.$$

The characteristic equation of this matrix is

$$\big(\lambda - (-d_1+\alpha_{21}x_2-\alpha_{23}z_2)\big)(\lambda^2 + (x_2+\alpha_{33}z_2)\lambda + (\alpha_{31}+\alpha_{33})x_2z_2) = 0$$
$$\Rightarrow \lambda = -d_1+\alpha_{21}x_2-\alpha_{23}z_2 \,\&\, \lambda^2 + (x_2+\alpha_{33}z_2)\lambda + (\alpha_{31}+\alpha_{33})x_2z_2 = 0.$$

Since $x_2 + \alpha_{33}z_2$ and $(\alpha_{31} + \alpha_{33})x_2z_2$ are positive non-zero values, all roots of the polynomial $\lambda^2 + (x_2 + \alpha_{33}z_2)\lambda + (\alpha_{31} + \alpha_{33})x_2z_2 = 0$ have negative value using Routh's condition. Thus, the given equilibrium point E_2 is stable whenever $d_1 + \alpha_{23}z_2 > \alpha_{21}x_2$. The Jacobian matrix at $E_3 = (x_3, y_3, 0)$ is

$$J(E_3) = \begin{pmatrix} -x_3 & -x_3 & -x_3 \\ \alpha_{21}y_3 & -\alpha_{22}y_3 & -\alpha_{23}y_3 \\ 0 & 0 & -d_2 + \alpha_{31}x_3 + \alpha_{32}y_3 \end{pmatrix}.$$

The characteristic equation of this matrix is

$$\big(\lambda - (-d_2 + \alpha_{31}x_3 + \alpha_{32}y_3)\big)(\lambda^2 + (x_3 + \alpha_{22}y_3)\lambda + (\alpha_{21} + \alpha_{22})x_3y_3) = 0$$
$$\Rightarrow \lambda = -d_2 + \alpha_{31}x_3 + \alpha_{32}y_3 \,\&\, \lambda^2 + (x_3 + \alpha_{22}y_3)\lambda + (\alpha_{21} + \alpha_{22})x_3y_3 = 0.$$

Since $x_3 + \alpha_{22}y_3$ and $(\alpha_{21} + \alpha_{22})x_3y_3$ are positive non-zero values, all roots of the polynomial $\lambda^2 + (x_3 + \alpha_{22}y_3)\lambda + (\alpha_{21} + \alpha_{22})x_3y_3 = 0$ have negative real part using Routh's condition. Therefore, the equilibrium point E_2 is stable if $d_2 > \alpha_{31}x_3 + \alpha_{32}y_3$. The Jacobian matrix at the coexistence equilibrium point is

$$J(E_*) = J(x_*, y_*, z_*) = \begin{pmatrix} -x_* & -x_* & -x_* \\ \alpha_{21}y_* & -\alpha_{22}y_* & -\alpha_{23}y_* \\ \alpha_{31}z_* & \alpha_{32}z_* & -\alpha_{33}z_* \end{pmatrix}$$

and its characteristics equation is given by

$$\lambda^3 + p_1\lambda^2 + p_2\lambda + p_3 = 0, \text{ where}$$
$$p_1 = x_* + \alpha_{22}y_* + \alpha_{33}z_*$$
$$p_2 = (\alpha_{21} + \alpha_{22})x_*y_* + (p_3 = (\alpha_{22}\alpha_{33} + \alpha_{23}\alpha_{32})y_*z_* + (\alpha_{31} + \alpha_{33})x_*z_*$$
$$p_3 = (\alpha_{22}\alpha_{33} + \alpha_{23}\alpha_{32} + \alpha_{21}\alpha_{33} - \alpha_{23}\alpha_{31} + \alpha_{21}\alpha_{32} + \alpha_{22}\alpha_{31})x_*y_*z_*$$

Since both $p_1, p_1p_2 - p_3$and p_3 are positive, using Routh's stability criterion the coexistence equilibrium point is stable without any condition.

From the stability analysis study it was concluded that the existence equilibrium point is stable provided that $d_1 > \alpha_{21}$, $d_2 > \alpha_{31}$in the absence of any predators, $d_1 + \alpha_{23}z_2 > \alpha_{21}x_2$ in the absence of the intermediate predator and $d_2 > \alpha_{31}x_3 + \alpha_{32}y_3$ in the absence of the top predator. Mathematically, this can be interpreted that all solution curve whose initial value starts near the equilibrium point attracts towards the equilibrium point. Biologically, it can be interpreted that the long term population size of the species is the existence equilibrium point.

4. Numerical simulation

Analytical methods are usually more suitable whenever accurate in for mationis available, but most of mathematical models, especially the non-linear models have no analytic solution. However, the qualitative approach with the aid of computer (numerical method) gives approximate solutions.

In this study the numerical simulation was based on the assumptions of no prey exist, no predator exists, no intermediate predator exists, no top predator exists, and coexistence of species in the environment. The nonexistence equilibrium point is unstable because the trajectories whose initial values approached the equilibrium point go away from it see figure (3-6). When this is biologically interpreted it means that, if the ecological zone is has no species initially and a few species are introduced, then the species grow due to sufficient resource availability in the environment. However, for the non-existence of prey population permanently, the trivial equilibrium point is stable (i.e. all trajectories will be attracted towards the equilibrium point). Biologically, this means that in the absence of prey population the intraguild prey population decays and extinct, similarly the intraguild predator population decays and extinct due to insufficient resources see figure (2).

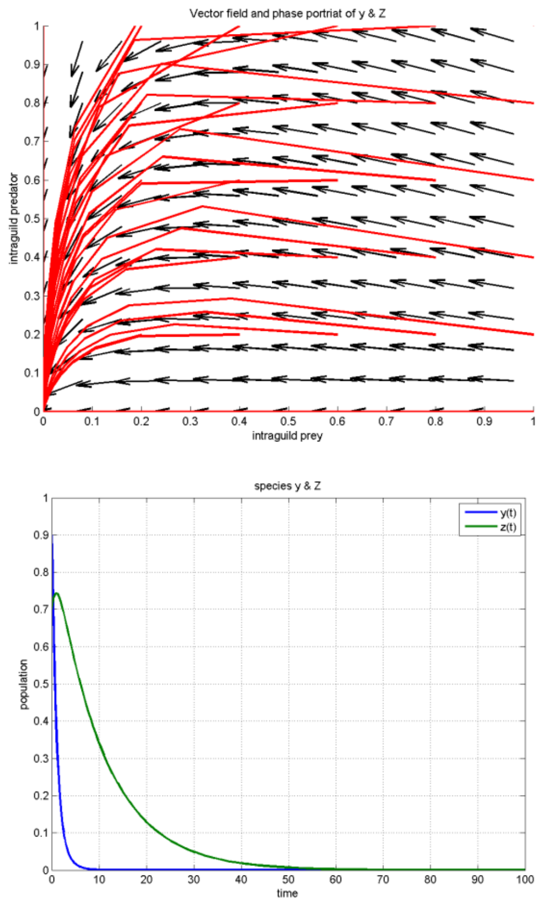


Figure 2:Vector field, phase portrait and time series solution of predators without living of prey.

In the absence of any predator population the existing equilibrium point is $E_1 = (1, 0, 0)$ and it is stable or the trajectories are attracted towards the equilibrium point whenever $d_1 > \alpha_{21}$ and $d_2 > \alpha_{31}$see figure (3). Biologically, this means that in the absence of predator population the prey population grows towards its carrying capacity (long term size of prey population in the absence of predator) and the predator population decays and extincts regardless of the initial population size.

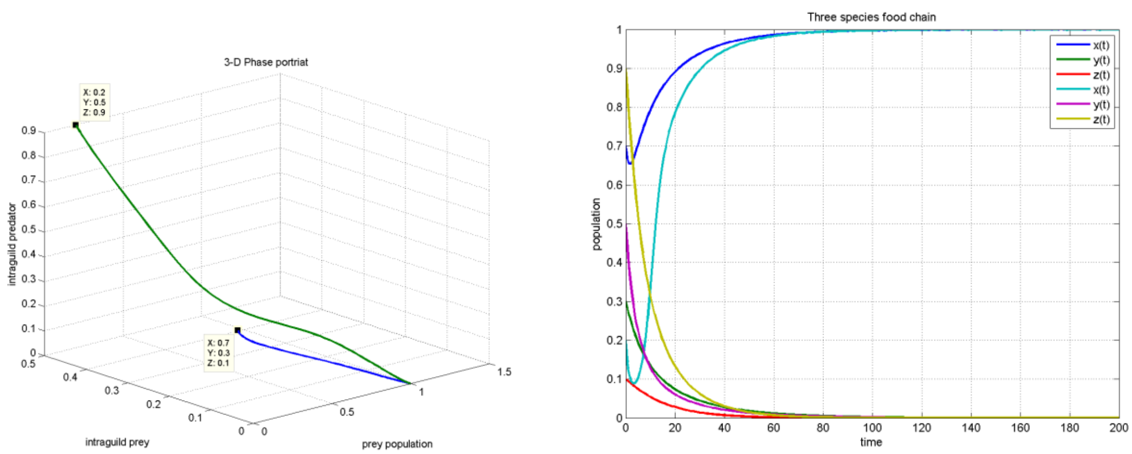


Figure 3: Phase portrait and time series solution of prey-predator with initial value $(0.7, 0.3, 0.1)$ and $(0.2, 0.5, 0.9)$ and parameters$d_1 = 0.05 > \alpha_{21} = 0.01$, $d_2 = 0.09 > \alpha_{31} = 0.02$, $\alpha_{22} = 0.15, \alpha_{23} = 0.09$, $\alpha_{32} = 0.1$, $\alpha_{33} = 0.08$.

In the absence of the intermediate predator population the existing equilibrium point is E_2 and it is stable whenever $d_1 + \alpha_{23}z_2 > \alpha_{21}x_2$ because the trajectories attracts towards the equilibrium point see figure (4). In this case it is indicated that, even if the intermediate predator does not exit the top predator does not extinct as the prey population exists.

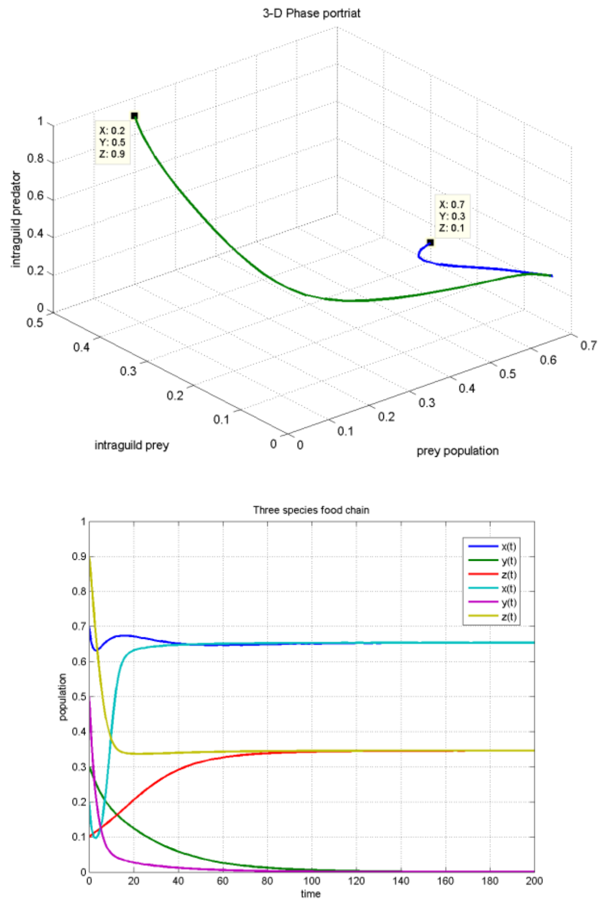


Figure 4: Phase portrait and time series solution of prey-predator with initial value $(0.7, 0.3, 0.1)$ and $(0.2, 0.5, 0.9)$ and parameters $d_2 = 0.09$, $\alpha_{21} = 0.3$, $\alpha_{22} = 0.15$, $\alpha_{23} = 0.09$, $\alpha_{31} = 0.18$, $\alpha_{32} = 0.1$, $\alpha_{33} = 0.08$, $\alpha_{21}x_2 - \alpha_{23}z_2 < d_1 = 0.2$

In the absence of the top predator the existence equilibrium point $E_3$is stable whenever $d_2 > \alpha_{31}x_3 + \alpha_{32}y_3$ because both the prey-predator population size settle down to their corresponding existence equilibrium point see figure (5).

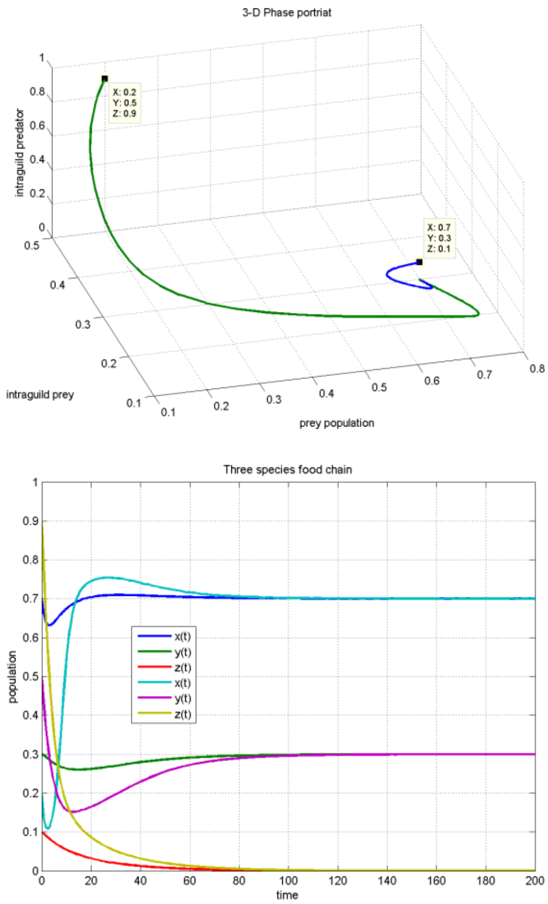
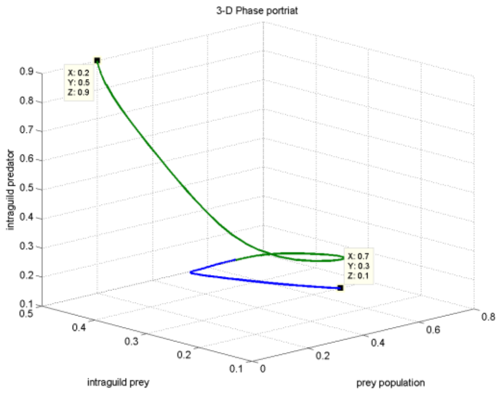


Figure 5: Phase portrait and time series solution of prey-predator with initial value $(0.7, 0.3, 0.1)$ and $(0.2, 0.5, 0.9)$ and parameters $d_1 = 0.09$, $\alpha_{21} = 0.18$, $\alpha_{22} = 0.12$, $\alpha_{23} = 0.09$, $\alpha_{31} = 0.18$, $\alpha_{32} = 0.1$, $\alpha_{33} = 0.08$, $\alpha_{31}x_3 + \alpha_{32}y_3 < d_2 = 0.2$

The coexistence equilibrium point is stable because both the prey-predator population size settle down to their corresponding coexistence equilibrium point without any condition see figure (6).



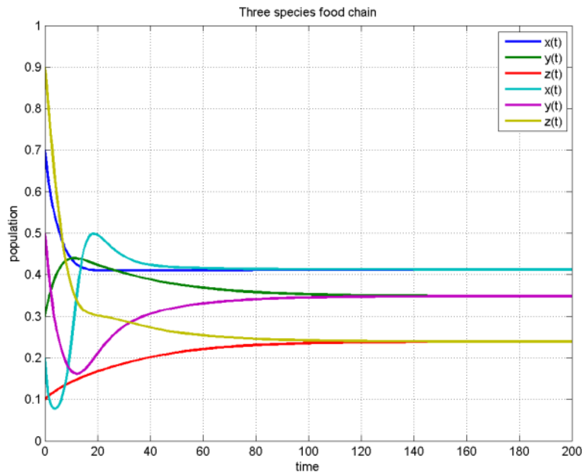


Figure 6: Phase portrait and time series solution of prey-predator with initial value $(\mathbf{0.7}, \mathbf{0.3}, \mathbf{0.1})$ and $(\mathbf{0.2}, \mathbf{0.5}, \mathbf{0.9})$ and parameters $\boldsymbol{d_1 = 0.05}$,$\boldsymbol{d_2 = 0.09}$,$\boldsymbol{\alpha_{21} = 0.3}$, $\boldsymbol{\alpha_{22} = 0.15}$, $\boldsymbol{\alpha_{23} = 0.09}$, $\boldsymbol{\alpha_{31} = 0.18}$, $\boldsymbol{\alpha_{32} = 0.1}$, $\boldsymbol{\alpha_{33} = 0.08}$.

From the numerical simulation study it was observed that the trajectories (solution curves) of the system settle down to their corresponding existence equilibrium point regardless the initial value provided that $d_1 > \alpha_{21}$, $d_2 > \alpha_{31}$ in the absence of any predators, $d_1 + \alpha_{23}z_2 > \alpha_{21}x_2$in the absence of intermediate predator and $d_2 > \alpha_{31}x_3 + \alpha_{32}y_3$in the absence of top predator. Biologically, this means that the long term population size is its existence equilibrium point in the environment provided that$d_1 > \alpha_{21}$, $d_2 > \alpha_{31}$in the absence of any predators, $d_1 + \alpha_{23}z_2 > \alpha_{21}x_2$ in the absence of intermediate predator and $d_2 > \alpha_{31}x_3 + \alpha_{32}y_3$ in the absence of top predator.

5. Conclusion

In this study, system of autonomous nonlinear ODE of three species food web with intraspecific competition for limited environmental resources and Lotka-Volterra interaction for one species to the other was considered using qualitative study. There were five equilibrium points which were obtained from the assumptions that is no prey species, there is only prey species, there are prey and top predator species, there are prey and intermediate predator, and the coexistence of the three species in the environment. The dynamics of the system was investigated and its result showed that the trajectories (solution curves) of the system settle down to their corresponding existence equilibrium point regardless of the initial value provided that $d_1 > \alpha_{21}$, $d_2 > \alpha_{31}$in the absence of any predators, $d_1 + \alpha_{23}z_2 > \alpha_{21}x_2$ in the absence of intermediate predators and $d_2 > \alpha_{31}x_3 + \alpha_{32}y_3$ in the absence of top predators. Biologically, this means that the long term population size is its existence equilibrium point in the environment provided that$d_1 > \alpha_{21}$, $d_2 > \alpha_{31}$in the absence of any predators, $d_1 + \alpha_{23}z_2 > \alpha_{21}x_2$in the absence of intermediate predator and $d_2 > \alpha_{31}x_3 + \alpha_{32}y_3$ in the absence of top predator.

In general, the qualitative study has revealed some insights to the three species food web model considered in this paper so that it can be applied to the real-world situations to keep balanced the prey-predator relationship in the environment.

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