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RESEARCH ARTICLE

Modelling and Analysis of Food Chain Dynamics with Diffusion

Chauhan HVS*, Agrawal AK, Gupta AK

Department of Mathematics, University of Delhi, Delhi, India.

*Corresponding Author: Email: ***harsh.chauhan111@gmail.com***

Abstract

The study of population dynamics with special emphasis on migration (i.e., diffusion) in a food chain ecosystem is an important area of research in the field of mathematical biology dealing with survival of different populations. Keeping in view of the above, we have formulated and analyzed a realistic food chain mathematical model in this paper.

Keywords: *Food chain model, Diffusion, Stability, Population growth.*

Introduction

It is one of the important issues in ecology to identify some general properties about the structure of food web. It has been theoretically studied by not a few researchers (for instance, see Jordan et al. ([1] and its references). The length of food chain is one of the important features interesting for such theoretical studies. One method to estimate the length of food chain is to deal with the energy. It represents how many times the energy (or a certain material) is transferred from a primary producer to a consumer. The average number of links from each producer to each top predator is regarded as the length of food chain. Although the network of energy in a food web is in general rather complex, it could be theoretically simplified to a linear chain of energy. Using the method discussed by Higashi et al. [2]. Along their theory, we could resolve and reconstruct the network of energy into a linear chain for a food web. Teramoto [3] analyzed a system of differential equations for a food chain, taking account of the energy reserve of each trophic level. He obtained the following results: (a) The equilibrium with every trophic level of positive energy reserve is globally stable; (b) The finite upper limit for the number of trophic levels exists; (c) It has a positive correlation for the efficiency of energy reservation and the intrinsic growth rate of the first trophic level; (d) In the chain consisting of trophic levels as many as possible, the distribution of energy reserves among trophic levels is always such that the lower trophic level has greater energy reserve than the higher has, in other words, it has a pyramid shape; (e) When the intra-trophic density effect is sufficiently large, at the equilibrium with a pyramid shape of energy distribution, the pyramid shape could be maintained even if the top tropic level is removed.

Preliminaries

Concepts of Growth Rates

Since population is changing entity. We are interested not only in its size and composition but also in nature of its change. As varying from place to place population density also varies in time. Population may remain constant they may fluctuate or they may steadily increases or decreases. Such changes are the main focus of population ecology. It is customary to abbreviate the change in something by writing the symbol $\Delta(Delta)$, if N represents the number of organisms and t the time then

ΔN = The change in number of organisms.

$\frac{\Delta N}{\Delta t}$ =The average rate of change in the number of organisms per unit time

$\frac{1}{N}\frac{\Delta N}{\Delta t}$ = The average rate of change in the number of organisms per unit time per Organisms (The is often called specific growth rate)

If specific growth rate multiplied by 100, i.e., $\frac{1}{N}\frac{\Delta N}{\Delta t}\times 100$, it becomes the percent growth rate.

The Fundamental Equation for Population Growth

The study of population dynamics is called demography. The basic aim of any demographic study is to quantify the changes, is a population by finding out the number of birth, deaths immigrants and emigrants. The changes in population size over a given time can be calculated by adding births and immigration to the original population number at time t(N_t) and subtracting the number of deaths and emigrants to give a new population size at time t+1, (N_{t+1}). The sum is often represented by the equation:

$$N_{t+1} = N_t + B + I - D - E \quad (1.1)$$

Where

N_t Is the original population at time t.

N_{t+1} Is a new population at time t+1.

B = Births
D = Deaths
I = Immigration
E = Emigration.

When immigration and emigration play no significant role, then equation (1.1) reduced to

$$N_{t+1} = N_t + B - D \quad (1.2)$$

Continuous Growth Model for Population

Fundamental equation (Murray, 1990) for the change in population:

$$\frac{\Delta N}{\Delta t} = B - D + I - E$$

Where

ΔN = change in population
Δt = time interval
I = Rate of immigration
E = Rate of emigration
B = Birth
D = Death

The Logistic Population Model

We know that by "simplest model"

$$\frac{dN}{dt} = B(N) - D(N) \quad (1.3)$$

Where

$$B(N) = bN$$
$$D(N) = dN$$

Hence, $\frac{dN}{dt} = bN - dN$

Where d, b are constant.

Verhulst in 1836 proposed that a self limiting process when a population becomes too large.

Suppose

$$D(N) = dN + CN^2$$

Here, dN = Natural death

In that case by equation

$$\frac{dN}{dt} = bN - dN - CN^2$$
$$\frac{dN}{dt} = (b-d)N - CN^2$$
$$\frac{dN}{dt} = rN - CN^2$$

$Here \gamma = b - d$

Modify this model is given by

$$\frac{dN}{dt} = rN(1 - \frac{N}{k})$$

This model is called a logistic model.

Mathematical Preliminaries

Consider the mathematical model which is given by the following set of Non-autonomous differential equations.

$$\frac{dx}{dt} = F(x, t) \quad (1.4)$$

Where $X = (X_1, X_2, \ldots\ldots X_n)$

The function F(x, t) is a non-linear function of X_1, X_2, ……X_n, and takes into account various factors governing the system.

Equilibrium Point

The system (1.4) is said to have an equilibrium point at $X=X_0$, if

$$\frac{dt}{dx} = 0$$

at this point. This point is obtained by putting f(x) = 0 and is also called stationary point.

Stability and Instability

When a system governed by a mathematical equation such as (1.4) is disturbed from its equilibrium state or point by some mechanism and if it returns to it as time passes then the system is said to be stable. Under that kind of perturbation if the system is not stable then it is called unstable.

Mathematical Definitions of Stability

The mathematical models that describe physical phenomena are in most cases, ordinary differential equations of the form.

X'=F(x, t) (X'= $\frac{dx}{dt}$) (1.5)

with initial data x (t_0) =x_0.

Definition of Stability

We define the concepts of stability for the solution X (t, t_0, x_0) of (1.5) and by stability we mean stability over an interval (t_0, ∞).

Definition

The solution x (t) of (1.5) is said to be stable if for each $\varepsilon \succ 0$, there exist a $\delta = \delta(\varepsilon) > 0$, such that for any solution x (t) = x (t_0, x_0) of the inequality $\|\bar{X}_0 - X_0\| < \delta$ implies $\|\bar{X}(t) - X(t)\| < \varepsilon$ for all t > 0.

Definition

The solution x (t) of (1.5) is called asymptotically stable if it is stable and if there exist a $\delta_0 > 0$ such that $\|\bar{X}_0 - X_0\| < \delta_0$ implies that

$\|\bar{X}(t) - X(t)\| \to 0$ as $t \to \infty$

The Variational Equation

Consider an autonomous system of differential equation

X'= F(x) (x' = $\frac{dx}{dt}$) (1.6)

And let Θ (t) be a solution of this system i.e.

Θ' (t) =F (θ (t))

then variation equation of system (1.6) with respect to θ(t)

is the linear part of expansion of system (1.6). It is formally given by the linear system

$$Y' = F_x(\theta(t))Y \qquad (1.7)$$

Where the variational matrix F_x (θ(t)) is the matrix whose i-i th component is ($\frac{\partial F_i}{\partial X_i}$ at $\theta(t)$).

To decide about the negativity of the real part of the Eigen value the following theorem is used.

Theorem 1: If there exists a positive definite scalar function V(x) such that $V'(x) \le 0$, on S_ρ, then the zero solution of (1.9) is stable.

Theorem 2: If there exists a positive definite scalar function V(x) such that $V'(x)$ is negative definite on S_ρ, then the zero solution of (1.9) is asymptotically stable.

Theorem 3: If there exists a scalar function V(x) = 0, such that $V'(x)$ is positive definite on S_ρ and if in every neighbourhood N of the origin, $N \subset S_\rho$, there is point x_0, where $V(x_0) > 0$, then the zero solution of (1.9) is a unstable.

Now, let Ω be an open set in R^n containing the origin. Suppose V(x) is a scalar continuous function defined on Ω.

The scalar function or liapunov function V(x) can be classified as follows.

Positive Definite Function

A scalar function V(x) is said to be positive definite on the set Ω if and only if V (0) = 0 and V(x)>0 for x ≠ 0 and $x \in \Omega$.

Negative Definite Function

A scalar function V(x) is said to be negative definite on the set Ω if and only if –V(x) is positive definite in Ω.

Positive Semi-definite Function

A scalar function V(x) is called positive semi-definite on the set Ω when V is positive throughout Ω except at certain points or when it is zero.

Negative Semi-definite Function

The Basic Mathematical Model

Let us consider a simple food chain by taking one prey and two classes of predator population. We assume that in absence of first class predator, prey population grows logistically with constant growth rate and fixed carrying capacity. Further the first class predator and second class predator wholly dependent upon prey and first class predator respectively. Keeping in view of the above, we propose a mathematical model of the food chain model by the system of differential equations A scalar function V(x) is called negative semi-definite on the set Ω if –V(x) is positive sign throughout Ω expect at certain points or where it is zero.

$$\frac{dP}{dt} = rP\left(1-\frac{P}{k}\right) - \alpha_1 PN_1 \qquad \text{----------(2.1)}$$

$$\frac{dN_1}{dt} = \beta_1 PN_1 - \gamma_1 N_1 - \alpha_2 N_1 N_2 \qquad \text{----------(2.2)}$$

$$\frac{dN_2}{dt} = \beta_2 N_1 N_2 - \gamma_2 N_2 \qquad \text{----------(2.3)}$$

Where,

N_1 = First predator population density at time *t*
N_2 = Second predator population density at time t
r = Intrinsic growth rate prey
P = Prey density at time t.
K = Caring capacity rate.
α_1 = Depletion of prey population due to first predator
α_2 = Depletion rate of first predator in the presence of second predator
β_1 = Conversion rate of first predator due to prey
β_2 = Conversion rate of second predator in the presence of first predator
γ_1 = Natural death rate of first predator
γ_2 = Natural death rate of second predator

All the constants r, P, k, α_1, α_2, β_1, β_2, γ_1, γ_2, N_1, N_2, are positive. With initial conditions: $P(0) = P_0 > 0$, $N_1(0) = N_{10} > 0$ and $N2(0) = N_{20} > 0$.

Equilibrium Points and Stability Analysis

The model has three possible equilibrium points, which are given by,

E_0: ($P^*=0$, $N_1^*=0$, $N_2^*=0$)

E_1: ($P^*=K$, $N_1^*=0$, $N_2^*=0$)

$$E_2 = (P^* = \frac{k}{r}\left[r - \frac{\alpha_1\gamma_2}{\beta_2}\right], N_1^* = \frac{\gamma_2}{\beta_2}, N_2^* = \frac{1}{\alpha_2}\left[\frac{\beta_1 k}{r}\left(r - \frac{\alpha_1\gamma_2}{\beta_2}\right) - \gamma_1\right]$$

The general community matrix of the model is

$$A = \begin{bmatrix} r - \frac{2rp}{k} - \alpha_1 N_1 & -\alpha_1 p & 0 \\ \beta_1 N_1 & \beta_1 P - \gamma_1 - \alpha_2 N_2 & -\alpha_2 N_2 \\ 0 & \beta_2 N_2 & \beta_2 N_1 - \gamma_2 \end{bmatrix}$$

The variation matrices about the equilibrium E_0, E_1, and E_2 which be denoted by A_0, A_1 and A_2, respectively are given by

$$A_0 = \begin{bmatrix} r & 0 & 0 \\ 0 & -\gamma_1 & 0 \\ 0 & 0 & -\gamma_2 \end{bmatrix}$$

$$A_1 = \begin{bmatrix} -r & -\alpha_1 k & 0 \\ 0 & \beta_1 k - \gamma_1 & 0 \\ 0 & 0 & -\gamma_2 \end{bmatrix}$$

$$A_2 = \begin{bmatrix} r - \frac{2rP^*}{k} - \frac{\alpha_1\gamma_1}{\beta_2} & -\alpha_1 P^* & 0 \\ \frac{\beta_1\gamma_2}{\beta_2} & 0 & \frac{-\alpha_2\gamma_2}{\beta_2} \\ 0 & \frac{\beta_2}{\alpha_2}(\beta_1 P^* - \gamma_1) & 0 \end{bmatrix}$$

The characteristic equation corresponding to A_0, A_1 and A_2 are respectively

$(r-\lambda)(-\gamma_1-\lambda)(-\gamma_2-\lambda) = 0$ --------- (2.4)

$(-r-\lambda)(\beta_1 k - \gamma_1 - \lambda)(-\gamma_2-\lambda) = 0$ --------- (2.5)

$$\lambda^3 - \lambda^2\left(r - \frac{2rP^*}{K} - \frac{\alpha_1\gamma_1}{\beta_2}\right) + \lambda\left[\gamma_2(\beta_1 P^* - \gamma_1) + \frac{\beta_1\alpha_1\gamma_2 P^*}{\beta_2}\right]$$

$$+\left[\frac{r\gamma_1\gamma_2}{\beta_2} + 2rP^{*2}\frac{\gamma_2\beta_1}{K} + \alpha_1\gamma_2^2\frac{\beta_1 P^*}{\beta_2} - r\gamma_2\beta_1 P^* - \frac{2rP^*\gamma_1\gamma_2}{K\beta_2} - \frac{\alpha_1\gamma_2^2\gamma_1}{\beta_2^2}\right] = 0$$

(2.6)

From characteristic equation (2.4), we get two negative roots and one positive root given by

$\lambda = r$, $\lambda = -\gamma_1$, $\lambda = -\gamma_2$

Thus E_0 is stable in 2-dimensional and 1-dimensional unstable equilibrium point.

From characteristic equation (2.5), we get two roots are negative one root is positive, given by

$\lambda = -r$, $\lambda = -\gamma_2$, $\lambda = (\beta_1 k - \gamma_1)$

Thus E1 is a 2-dimensional stable and 1-dimensional unstable if

$\beta_1 k > \gamma_1$ *and stable* if $\beta_1 k < \gamma_1$.

From characteristic equation (2.6), we get roots are given by now the equation (2.6):

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0$$

Where,

$$a_1 = -(r - \frac{2rP^*}{k} - \frac{\alpha_1\gamma_1}{\beta_2})$$

$$a_2 = \left[\gamma_2(\beta_1 P^* - \gamma_1) + \frac{\beta_1\alpha_1\gamma_2 P^*}{\beta_2}\right]$$

$$a_3 = -(\beta_1 P^* - \gamma_1)\left(r\gamma_2 - \frac{2rP^*\gamma_2}{\beta_2} - \frac{\alpha_1\gamma_1\gamma_2}{\beta_2}\right)$$

From the existence of interior equilibrium point now from the Routh-Hurwitz criterion, the necessary and sufficient condition for the above system to be stable around the interior equilibrium point is that

1. $a_1 > 0$
2. $a_2 > 0$
3. $a_3 > 0$
4. $a_1 a_2 - a_3 > 0$

Now $a_1 a_2 - a_3$

$$= \frac{\alpha_1\gamma_2\beta_1}{\beta_2} P^* \left[\frac{2rP^*}{K} + \frac{\alpha_1\gamma_2}{\beta_2} - r\right]$$

The system is locally stable around E_2 if

$$a_1 \cong \frac{2rP^*}{K} + \frac{\alpha_1\gamma_2}{\beta_2} - r > 0 \Rightarrow r > \frac{\alpha_1\gamma_2}{\beta_2}$$

Again if $a_1 > 0$, then $a_1 a_2 - a_3$ is always strictly positive Hence condition (4) is automatically satisfied.

Again $a_3 > 0$ only when $r > \dfrac{\alpha_1\gamma_2 K\beta_1\beta_2}{K\beta_1\beta_2 - \gamma_1}$ and if $a_3 > 0$ then a_2 is always strictly positive.

Hence the system is stable around only when

$$r > \max\left\{\frac{\alpha_1\gamma_2}{\beta_2}, \frac{\alpha_1\gamma_2 K\beta_1\beta_2}{K\beta_1\beta_2 - \gamma_1}\right\}.$$

The Proposed Mathematical Model

Now introducing the movement in both the predator populations with constant diffusion rate. Let D_1 and D_2 are diffusion coefficients respectively for first and second class predator. Then the model equations become:

$$\frac{\partial P}{\partial t} = rP\left(1 - \frac{P}{k}\right) - \alpha_1 P N_1 \qquad (2.7)$$

$$\frac{\partial N_1}{\partial t} = \beta_1 P N_1 - \gamma_1 N_1 - \alpha_2 N_1 N_2 + D_1 \frac{\partial^2 N_1}{\partial x^2} \qquad (2.8)$$

$$\frac{\partial N_2}{\partial t} = \beta_2 N_1 N_2 - \gamma_2 N_2 + D_2 \frac{\partial^2 N_2}{\partial x^2} \qquad (2.9)$$

Where $0 \le x \le L$,

With the initial conditions

$$P(0,x) = \overline{P}(x), \quad N_1(0,x) = \overline{N}_1(x), \quad N_2(0,x) = \overline{N}_2(x) \qquad (2.10)$$

and no-flux boundary conditions

$$\frac{\partial P(0,t)}{\partial x} = \frac{\partial P(L,t)}{\partial x} = 0, \qquad \mathbf{(2.11)}$$

$$\frac{\partial N_1(0,t)}{\partial x} = \frac{\partial N_1(L,t)}{\partial x} = 0 \qquad (2.12)$$

$$\frac{\partial N_2(0,t)}{\partial x} = \frac{\partial N_2(L,t)}{\partial x} = 0. \qquad \mathbf{(2.13)}$$

Where,

N_1 = First predator population density at time t and at the location x

N_2 = Second predator population density at time t and at the location x

P = Prey density at time t and at the location x

r = Intrinsic growth rate

k = Carrying capacity rate

α_1 = Depletion of prey population due to first predator

α_2 = Depletion rate of first predator in presence of second predator

β_1 = Conversion rate of first predator due to prey

β_2 = Conversion rate of second predator in presence of first predator

γ_1 = Natural death rate of first predator

γ_2 = Natural death rate of second predator

D_1 = Diffusion coefficient of first predator

D_2 = Diffusion coefficient of second predator

All the constants $r, P, k, \alpha_1, \alpha_2, \beta_1, \beta_2, \gamma_1, \gamma_2, N_1, N_2, D_1, D_2$ are positive.

Stability Analysis of the Intrisic Equilibrium

The above system has an interior equilibrium, namely,

$$E\left(P^* = \frac{k}{r}\left[r - \frac{\alpha_1\gamma_2}{\beta_2}\right], N_1^* = \frac{\gamma_2}{\beta_2}, N_2^* = \frac{1}{\alpha_2}\left(\frac{\beta_1 k}{r}\left[r - \frac{\alpha_1\gamma_2}{\beta_2}\right] - \gamma_1\right)\right)$$

Now using the perturbations

$$P = P^* + P_t$$
$$N_1 = N_1^* + N_t$$
$$N_2 = N_2^* + N_s$$

Where P_t, N_t, N_s are very small.

Using the perturbation in above equation and neglecting higher power terms we get

$$\frac{\partial(P^* + P_t)}{\partial t} = r(P^* + P_t)\left(1 - \frac{P^* + P_t}{k}\right) - \alpha_1(P^* + P_t)(N_1^* + N_t)$$

$$\Rightarrow \frac{\partial P_t}{\partial t} = -\frac{rP^* P_t}{k} - \alpha_1 P^* N_t$$

$$\frac{\partial(N_1^* + N_t)}{\partial t} = \beta_1(P^* + P_t)(N_1^* + N_t) - \gamma_1(N_1^* + N_t) - \alpha_2(N_1^* + N_t)(N_2^* + N_s) + D_1\frac{\partial^2(N_1^* + N_t)}{\partial x^2}$$

$$\frac{\partial N_t}{\partial t} = \beta_1 P_t N_1^* - \alpha_2 N_1^* N_s + D_1\frac{\partial^2 N_t}{\partial x^2}$$

$$\frac{\partial(N_2^* + N_s)}{\partial t} = \beta_2(N_1^* + N_t)(N_2^* + N_s) - \gamma_2(N_2^* + N_s) + D_2\frac{\partial^2(N_2^* + N_s)}{\partial x^2}$$

$$\frac{\partial N_s}{\partial t} = \beta_2 N_t N_2^* + D_2\frac{\partial^2 N_s}{\partial x^2}$$

Now taking positive definite function

$$G(t) = \int_0^L \frac{1}{2}(P_t^2 + N_t^2 + N_s^2)dx$$

$$\frac{\partial G}{\partial t} = \int_0^L\left(P_t\frac{\partial P_t}{\partial t} + N_t\frac{\partial N_t}{\partial t} + N_s\frac{\partial N_s}{\partial t}\right)dx$$

$$= \int_0^l\left[P_t\left(-\gamma\frac{P^* P_t}{K} - \alpha_1 P^* N_t\right) + N_t\left(\beta_1 P_t N_t^* - \alpha_2 N_1^* N_s + D_1\frac{\partial^2 N_t}{\partial x^2}\right) + \mathrm{N}_s\left(\beta_2 N_t N_2^* + D_2\frac{\partial^2 N_s}{\partial x^2}\right)\right]dx$$

We get

$$\int_0^L D_1 N_t\frac{\partial^2 N_t}{\partial x^2}dx = -D_1\int_0^l\left(\frac{\partial N_t}{\partial x}\right)^2 dx$$

By Poin-caire inequality, we have

$$-\int_0^L\left(\frac{\partial N_s}{\partial x}\right)^2 dx \le -\frac{\pi^2}{L^2}\int_0^L N_t^2 dx$$

$$-\int_0^L\left(\frac{\partial N_s}{\partial x}\right)^2 dx \le -\frac{\pi^2}{L^2}\int_0^L N_s^2 dx$$

$$\int_0^L D_2 N_s\frac{\partial^2 N_s}{\partial x^2}dx = -D_2\int_0^L\left(\frac{\partial N_s}{\partial x}\right)^2 dx$$

$$\frac{\partial G}{\partial t} \le -\int_0^L\left[\frac{r}{k}P^* P_t^2 + (\alpha_1 P^* - \beta_1 N_1^*)P_t N_t + (\alpha_2 N_1^* - \beta_2 N_2^*)N_s N_t + D_1\frac{\pi^2}{L^2}N_s^2 + D_2\frac{\pi^2}{L^2}N_s^2\right]dx$$

$$= -\int_0^L\left[\begin{array}{l}[\frac{1}{2}\left(\frac{r}{k}P^*\right)P_t^2 + (\alpha_1 P^* - \beta_1 N_1^*)P_t N_t + \frac{1}{2}\left(D_1\frac{\pi^2}{L^2}\right)N_t^2] \\ + \left[\frac{1}{2}\left(D_1\frac{\pi^2}{L^2}\right)N_t^2 + (\alpha_2 N_1^* - \beta_2 N_2^*)N_t N_s + \frac{1}{2}\left(D_2\frac{\pi^2}{L^2}\right)N_s^2\right] \\ s + \left[\frac{1}{2}\left(D_2\frac{\pi^2}{L^2}\right)N_s^2 + 0.N_s P_t + \frac{1}{2}\left(\frac{r}{k}P^*\right)P_t^2\right]\end{array}\right]$$

dx By using Sylvester's criterion, we get, $\frac{\partial G}{\partial t}$ is negative definite if

B^2-4AC<0$\Rightarrow$

$$(\alpha_1 P^* - \beta_1 N_1^*)^2 - \left(\frac{r}{k}P^*\right)\left(D_1\frac{\pi^2}{L^2}\right) < 0 \quad \text{------- (2.14)}$$

$$(\alpha_1 N_1^* - \beta_2 N_2^*)^2 - \left(D_1\frac{\pi^2}{L^2}\right)\left(D_2\frac{\pi^2}{L^2}\right) < 0 \quad \text{------ (2.15)}$$

$$\left(D_2\frac{\pi^2}{L^2}\right)\left(\frac{r}{k}P^*\right) > 0 \quad \text{------- (2.16)}$$

The (2.16) condition is automatic.

Hence the system is stable around E if the condition (2.14) & (2.15) are satisfied .further it is clear from the condition (2.14) & (2.15) that in presence of the diffusion (i.e. the diffusion coefficient D_1 & D_2) the system become more stable. Therefore diffusion process increases stability of the system.

Numerical Solutions

In this section the numerical solutions of the system (2.1)-(2.3) shown in figure-1(a)-(b), Figure-2 and Figure-3 with different set of parameters, using Mat Lab software. From the figure it was observed that the conversion rate of the second class predator is very sensitive [4-16].

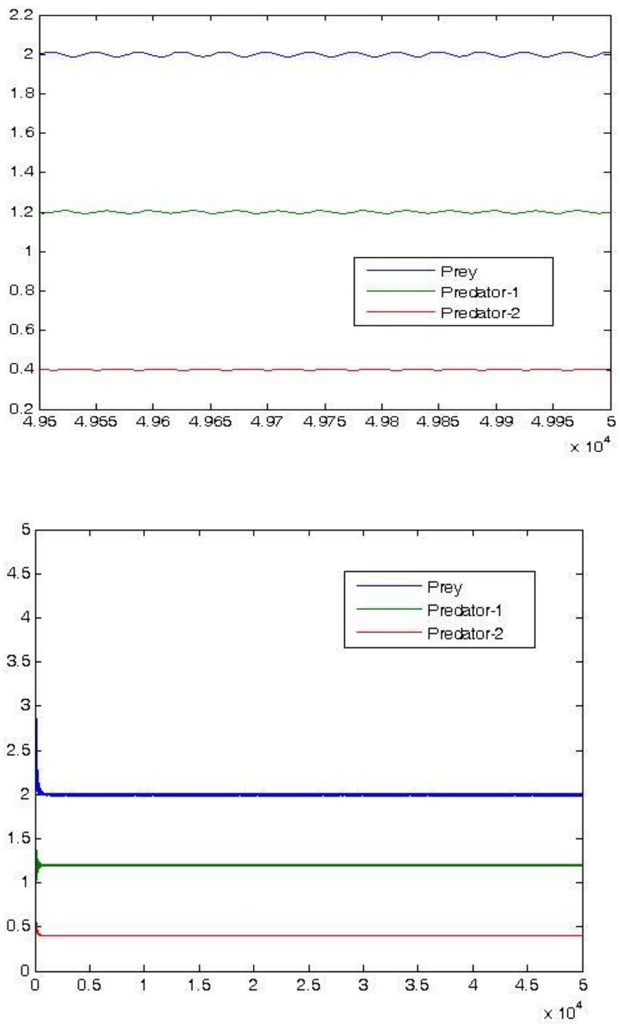

Fig. 1(a)-(b): The population trajectories, when $r = 0.2, K = 20, \alpha_1 = 0.15, \beta_1 = 0.05,$ $\gamma_1 = 0.02, \alpha_2 = 0.2, \beta_2 = 0.1, \gamma_2 = \mathbf{0.12}$

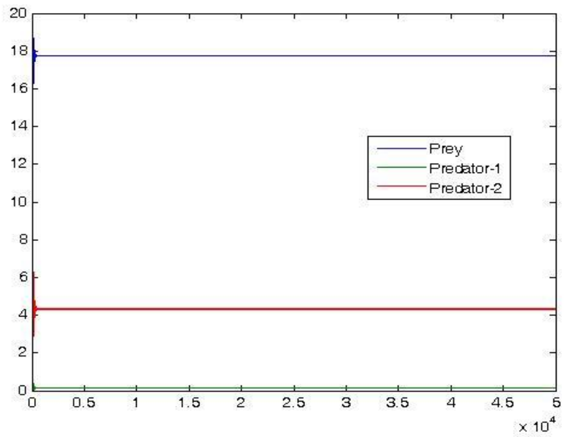

Fig. 2:The population trajectories, when $r = 0.2, K = 20, \alpha_1 = 0.15, \beta_1 = 0.05,$ $\gamma_1 = 0.02, \alpha_2 = 0.2, \beta_2 = 0.8, \gamma_2 = \mathbf{0.12}$

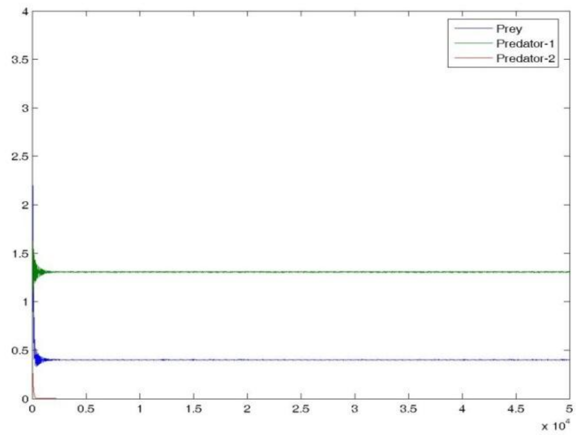

Fig. 3:The population trajectories, when $r = 0.2, K = 20, \alpha_1 = 0.15, \beta_1 = 0.05,$ $\gamma_1 = 0.02, \alpha_2 = 0.2, \beta_2 = 0.08, \gamma_2 = \mathbf{0.12}$

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