Journal of Sustainability Science and Management ISSN: 1823-8556
Volume 6 *Number* 2, December 2011: 215-223

THE DYNAMICS OF A THREE-SPECIES FOOD CHAIN INTERACTION MODEL WITH MICHAELIS-MENTEN TYPE FUNCTIONAL RESPONSE

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Abstract: In this paper, we study an ecological model with a tritrophic food chain composed of a classical Lotka-Volterra functional response for prey and predator, and a Michaelis-Menten-type functional response for predator and top predator. There are two equilibrium points of the system. In the parameter space, there are passages from instability to stability, which are called Hopf bifurcation points. For the first equilibrium point, it is possible to find bifurcation points analytically and to prove that the system has periodic solutions around these points. Furthermore the dynamical behaviours of this model are investigated. The dynamical behaviour is found to be very sensitive to parameter values as well as the parameters of the practical life. Computer simulations are carried out to explain the analytical findings.

KEYWORDS: food-chain model, Hopf bifurcation, modified Lotka-Volterra model, modified Michaelis-Menten-type functional response

Introduction

The real interaction of prey-predator in nature is complex and comprises both interspecies and external environmental factors. Therefore, several simplifications are usually assumed so that a basic model can be constructed and then developed or modified to approach the real system.

One of the simplest dynamical models to describe the interaction between two interacting species, namely one prey and one predator, is the classical Lotka-Volterra equation (Chauvet *et al.*, 2002) which can be stated as

$$\left.\begin{aligned} \frac{dx}{dt} &= a_1 x - b_1 xy \\ \frac{dy}{dt} &= -a_2 y + b_2 xy \end{aligned}\right\} \qquad (1)$$

where x is a prey, y is a predator, the predator y preys on x, a_1 is the prey growth rate in the absence of the predators, b_1 is the capture rate of prey by per predator, b_2 is the rate at which each predator converts captured prey into predator births and a_2 is the constant rate at which death occurs in the absence of prey. They showed that ditrophic food chains (i.e. prey-predator systems) permanently oscillate for any initial condition if the prey growth rate is constant and the predator functional response is linear.

The term "ratio-dependent predation" is introduced in Arditi and Ginzburg, (1989) to describe situations in which the feeding rates of predators depend on the ratio of the number of preys to the number of predators rather than on prey density alone, as is the case in most classical models. One advantage of the ratio dependence is that they prevent paradoxes of enrichment and biological control predicted by classical models (Arditi and Saiah, 1992; Gakkar and Naji, 2003).

Experimental observations (Ginzburg and Akçakaya, 1992) suggest that prey-dependent models are appropriate in homogeneous situations and ratio-dependent models are good in heterogeneous cases. Many investigators (Ginzburg and Akçakaya, 1992; McCarthy *et al.*, 1995) have also concluded that natural systems

Received: 31 January 2011 / Accepted: 22 June 2011

are closer to the models with ratio dependence than to the ones with prey-density dependence (Jost *et al*., 1999).

Almost each of the food-chain models considered in ecological literature are constructed by invoking same type of functional responses for (x, y) and (y, z) populations (Mamat *et al*., 2011). But a different selection of functional response would be perhaps more realistic in this context. In 2011, a mathematical model of three species model by mixed Lotka-Volterra and Holling Type-II functional response was proposed (Mada Sanjaya *et al*., 2011). From this point of view, in this paper, a classical (nonlogistic) Lotka-Volterra functional response for the species x and y and a Michaelis-Menten type functional response for the species y and z is considered (Kara and Can, 2006; Hsu *et al*., 2001; Hsu *et al*., 2003; Abrams, 1994; Abrams and Ginzburg, 2000; Beretta and Kuang, 1998).

Model System

The classical food-chain models with only two trophic levels are shown to be insufficient to produce realistic dynamics (Freedman and Waltman, 1977; Hastings and Powell, 1991; Hastings and Klebanoff, 1993; Dubey and Upadhyay, 2004; Mada Sanjaya *et al*., 2011). Therefore, in this paper, by modifying and composing the classical Lotka-Volterra and Michaelis-Menten type functional response model the dynamics of a three-species food-chain interaction are analysed and simulated. With non-dimensionalisation, the system of three-species food chain can be written as

$$\left.\begin{aligned} \frac{dx}{dt} &= (a_1 - b_1 y)x \\ \frac{dy}{dt} &= \left(-a_2 + b_2 x - \frac{c_1 z}{y+z}\right)y \\ \frac{dz}{dt} &= \left(-a_3 + \frac{c_2 y}{y+z}\right)z \end{aligned}\right\} \qquad (2)$$

where x, y, and z denoted the non-dimensional population density of the prey, predator, and top predator respectively. The predator y preys on x and the top predator z preys on y. Furthermore a_1, a_2, a_3, b_1 , b_2, c_1, and c_2 are prey intrinsic growth rate, predator's death rates, top predators death rates, predation rate of the predator, the conversion rate, the maximal growth rate of the predator, and conversion-factor constant respectively.

Equilibrium Point Analysis

According to Ginoux (2009), May (2001), Mada Sanjaya *et al.* (2011) and Mamat *et al*. (2011), the equilibrium points of (2) denoted by $E(\bar{x},\bar{y},\bar{z})$, are the zeros of its nonlinear algebraic system which can be written as

$$\left.\begin{aligned} &(a_1 - b_1 y)x = 0 \\ &\left(-a_2 + b_2 x - \frac{c_1 z}{y+z}\right)y = 0 \\ &\left(-a_3 + \frac{c_2 y}{y+z}\right)z = 0 \end{aligned}\right\} \qquad (3)$$

By considering the positivity of the parameters and the unknowns, there are two positive equilibrium given by E_1 (x_1, y_1,0) with

$$x_1 = a_2 / b_2, \text{ and } y_1 = a_1 / b_1 ,$$

and E_2 (x_2, y_2,z_2) with

$$x_2 = -\frac{a_3 c_1 - a_2 c_2 - c_1 c_2}{b_2 c_2},\ y_2 = a_1 / b_1, \text{ and } z_3 = -\frac{a_1(a_3 - c_2)}{a_3 b_1},$$

where

$$a_2 c_2 + c_1 c_2 > a_3 c_1 \text{ and } c_2 > a_3.$$

Stability of Equilibrium Points

The dynamical behaviour of equilibrium points is studied by computing the eigenvalues of the Jacobian matrix J of system (2) where

$$J(\bar{x},\bar{y},\bar{z}) = \begin{bmatrix} a_1 - b_1\bar{y} & -b_1\bar{x} & 0 \\ b_2\bar{y} & -a_2 + b_2\bar{x} - \frac{c_1\bar{z}^2}{(\bar{y}+\bar{z})^2} & -\frac{c_1\bar{y}^2}{(\bar{y}+\bar{z})^2} \\ 0 & \frac{c_2\bar{z}^2}{(\bar{y}+\bar{z})^2} & -a_3 + \frac{c_2\bar{y}^2}{(\bar{y}+\bar{z})^2} \end{bmatrix} \qquad (4)$$

At most, there exists two positive equilibrium points for system (2). The existence and local stability conditions of these equilibrium points are as follows.

1. The Jacobian matrix (4) at the equilibrium point E_1 $(x_1, y_1, 0)$, is

$$J(x_1, y_1, 0) = \begin{bmatrix} 0 & -\frac{b_1 a_2}{b_2} & 0 \\ \frac{b_2 a_1}{b_1} & 0 & -c_1 \\ 0 & 0 & -a_3 + c_2 \end{bmatrix} \quad (5)$$

The eigenvalues of the Jacobian matrix (5) are $\lambda_{1,2} = \pm\sqrt{-a_1 a_2}$, and $\lambda_3 = c_2 - a_3$. Hence, the equilibrium point E_1 is a locally-stable spiral sink if $c_2 < a_3$ and E_1 is a locally-unstable spiral source if $c_2 > a_3$.

2. Suppose that the Jacobian matrix (4) is denoted by $J = (a_{ij})_{3x3}$, By substitution E_2 (x_2, y_2, z_2) into (4), we have

$$a_{11} = 0,$$

$$a_{12} = \frac{b_1(c_1 a_3 - a_2 c_2 - c_1 c_2)}{b_2 c_2},$$

$$a_{12} = 0,$$

$$a_{21} = \frac{a_1 b_2}{b_1},$$

$$a_{22} = -a_2 - \frac{c_1 a_3 - a_2 c_2 - c_1 c_2}{c_2} - \frac{c_1 a_1^2 (a_3 - c_2)^2}{a_3^2 b_1^2 \left(\frac{a_1}{b_1} - \frac{a_1(a_3 - c_2)}{a_3 b_1}\right)^2},$$

$$a_{23} = -\frac{c_1 a_1^2}{b_1^2 \left(\frac{a_1}{b_1} - \frac{a_1(a_3 - c_2)}{a_3 b_1}\right)^2},$$

$$a_{31} = 0,$$

$$a_{32} = \frac{c_2 a_1^2 (a_3 - c_2)^2}{a_3^2 b_1^2 \left(\frac{a_1}{b_1} - \frac{a_1(a_3 - c_2)}{a_3 b_1}\right)^2},$$

and

$$a_{33} = -a_3 + \frac{c_2 a_1^2}{b_1^2 \left(\frac{a_1}{b_1} - \frac{a_1(a_3 - c_2)}{a_3 b_1}\right)^2}.$$

The characteristic equation of the Jacobian matrix (4) of E_2 (x_2, y_2, z_2) is $\lambda^3 + \sigma_1\lambda^2 + \sigma_2\lambda + \sigma_3 = 0$ where

$$\left.\begin{aligned} \sigma_1 &= -\frac{a_3(c_2 - a_3)(c_1 - c_2)}{c_2^2} \\ \sigma_2 &= \frac{a_1(a_2 c_2 + c_1 c_2 - c_1 a_3)}{c_2} \\ \sigma_3 &= \frac{(c_2 - a_3)(a_2 c_2 + c_1 c_2 - c_1 a_3)a_1 a_3}{c_2^2} \end{aligned}\right\} \quad (6)$$

According to the Routh–Hurwitz criterion (Ginoux, 2009; May, 2001; Mada Sanjaya *et al.*, 2011; Mamat *et al.*, 2011), E_2 (x_2, y_2, z_2) is locally and asymptotically stable if one sets

$$\sigma_1 > 0, \sigma_3 > 0, \text{ and } \sigma_1 \sigma_2 > \sigma_3, \quad (7)$$

then

$$c_2 > a_3, c_2 > c_1, \text{ and } c_2 c_2 + c_1 c_2 > a_3 c_1. \quad (8)$$

Hopf Bifurcation Point

When attempting to study periodic or quasi-periodic behaviour of a dynamical system, the Hopf bifurcation point needs to be considered. The dynamical system generally (Ginoux, 2009; May, 2001; Kara and Can, 2006; Mada Sanjaya *et al.*, 2011) can be written as

$$\dot{v} = F(v, \mu) \quad (9)$$

where

$$v = (x, y, z), = (a_1, a_2, a_3, b_1, b_2, c_1, c_2) \quad (10)$$

According to Ginoux (2009), May (2001), and Kara and Can (2006) for the system (2) which can be written in the form (9-10), if an ordered pair (v_0, μ_0) satisfied the conditions

(1) $F(v_0, \mu_0) = 0$,

(2) $J(v,\mu)$ has two complex conjugate eigenvalues $\lambda_{1,2} = a(v,\mu) \pm ib(v,\mu)$, around (v_0, μ_0),

(3) $a(v_0, \mu_0) = 0$, $\nabla a(v_0, \mu_0) \neq 0$, $b(v_0, \mu_0) \neq 0$, and

(4) The third eigenvalues $\lambda_3(v_0, \mu_0) \neq 0$,

then (v_0, μ_0) is called a Hopf bifurcation point.

For the system (2), two equilibrium points E_1 $(x_1, y_1, 0)$ and E_2 (x_2, y_2, z_2), satisfy the condition , and for the equilibrium point E_1 $(x_1, y_1, 0)$, there are two complex conjugate eigenvalues for which the real part of the eigenvalues are zero.

The last conditionis $\lambda_3(v_0, \mu_0) \neq 0$ satisfied if

$$c_2 \neq a_3. \quad (11)$$

The equation (7), (8) and (11), are satisfied if a_3 is chosen not as

$$a_{30} = c_2. \quad (12)$$

Hence, E_2 is stable spiral and E_1 is unstable spiral for $a_3 < a_{30}$, E_1 and E_2 is centre point for $a_3 = a_{30}$, and E_1 is stable spiral and E_2 is unstable spiral for $a_3 > a_{30}$. The point (v_0, μ_0) which corresponds to $a_3 = a_{30}$, is a Hopf bifurcation point. This Hopf bifurcation states sufficient condition for the existence of periodic solutions. As one parameter is varied, the dynamics of the system change from a stable spiral to a centre to an unstable spiral (Table 1).

Numerical Simulation

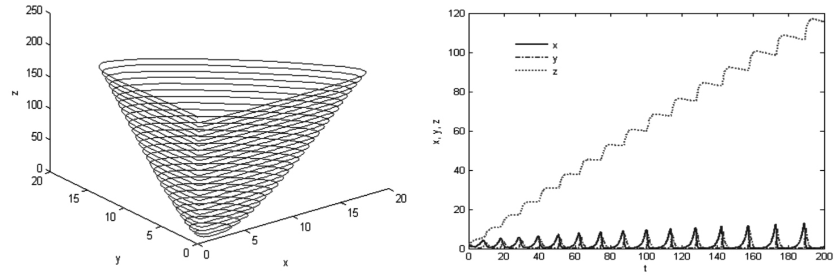
Analytical studies always remain incomplete without numerical verification of the results. In this section a numerical simulation to illustrate the results obtained in previous sections are presented. The numerical simulation was implemented in MATLAB R2010a. The numerical experiments are designed to show the dynamical behaviour of the system in four main different sets of parameters: I. The case $a_3 < a_{30}$. II. The case $a_3 = a_{30}$. III. The case $a_3 > a_{30}$. IV. The chaotic attractor in equilibrium. The coordinates of equilibrium points and the corresponding eigenvalues can be found in Table1. For showing the dynamics of the system (2) change, the parameter set $\{a_1, a_2, b_1, b_2, c_1, c_2\} = \{0.5, 0.5, 0.5, 0.5, 0.6, 0.75\}$ given as a fixed parameters, and a_3 as a varied parameters. The calculation for the parameter set given Hopf bifurcation point $a_{30} = c_2 = 0.75$ as a control parameter, is equal to analysis result (12).

I. The case $a_3 < a_{30}$

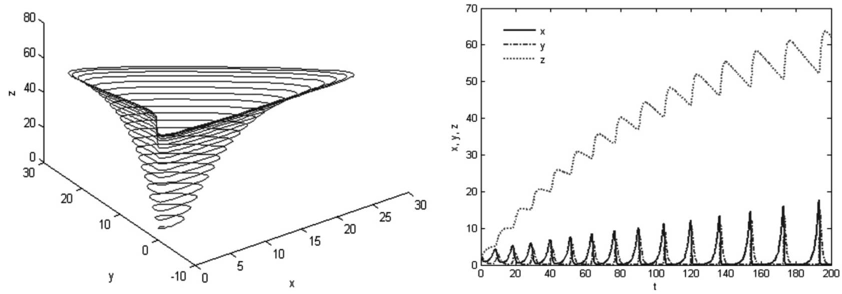
For the case $a_3 < a_{30}$ E_2 is stable, E_1 is unstable as in previous sections. For the case $a_3 < a_{30}$ (Table 1) of the two eigenvalues, E_1 is pure imaginary with initially-spiral stability corresponding with centre manifold in *xy* plane and one positive real eigenvalue corresponding with unstable one-dimensional invariant curve in z axes and different condition in E_2 that has two eigenvalues with complex-conjugate initially-spiral stability and one negative real eigenvalue corresponding with stable one-dimensional invariant curve. Hence the equilibrium point E_2 is a locally-stable spiral sink and E_1 is a locally-unstable spiral source.

Table 1. Numerical Analysis of Stability Equilibrium Point

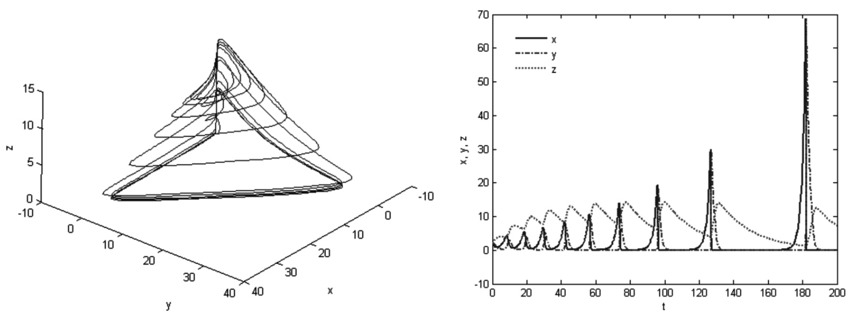
The Case	Parameter	Equilibrium point E_1	Equilibrium point E_2	Eigenvalues E_1	Eigenvalues E_2	Stability E_1	Stability E_2
$a_3 < a_{30}$	$a_3 = 0.002$	1, 1, 0	2.196, 1.000, 374.000	± 0.500 i, 0.748	0.00079 ± 0.74108 i, -0.00199	Unstable spiral	Stable spiral
	$a_3 = 0.01$	1, 1, 0	2.184, 1.000, 74.000	± 0.500 i, 0.740	0.00394 ± 0.73896 i, -0.00986	Unstable spiral	Stable spiral
	$a_3 = 0.05$	1, 1, 0	2.120, 1.000, 14.000	± 0.500 i, 0.700	0.01859 ± 0.72896 i, -0.04651	Unstable spiral	Stable spiral
Chaos	$a_3 = 0.05$, $c_2 = 2.5$	1, 1, 0	2.176, 1.000, 49.000	± 0.500 i, 2.450	0.00585 ± 0.73792 i, -0.04894	Unstable spiral	Stable spiral
$a_3 = a_{30}$	$a_3 = 0.75$	1, 1, 0	1.000,1.000, 0	± 0.500 i, 0	± 0.50000 i, 0	Limit cycle	Limit cycle
$a_3 > a_{30}$	$a_3 = 1$	1, 1, 0	0.600, 1.000, -0.250	± 0.500 i, -0.250	-0.09336 ± 0.43428 i, 0.25339	Stable spiral	Unstable spiral



(a) Phase space and population time series for $a_3 = 0.002$

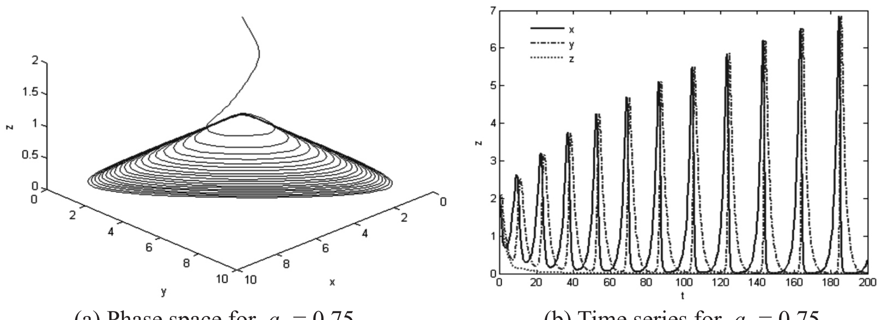


(b) Phase space and population time series for $a_3 = 0.01$



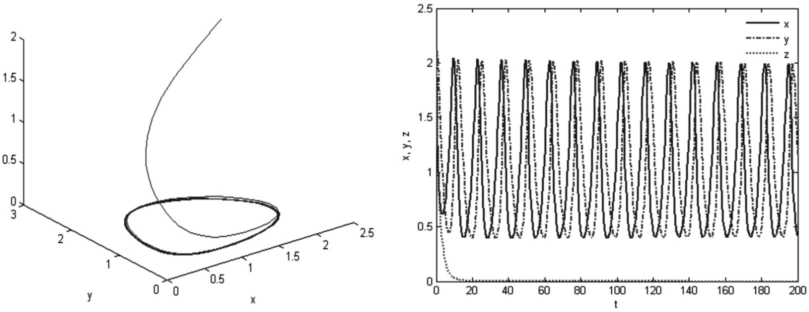
(c) Phase space and population time series for $a_3 = 0.05$

Figure 1: The solution for $a_3 < a_{30}$.



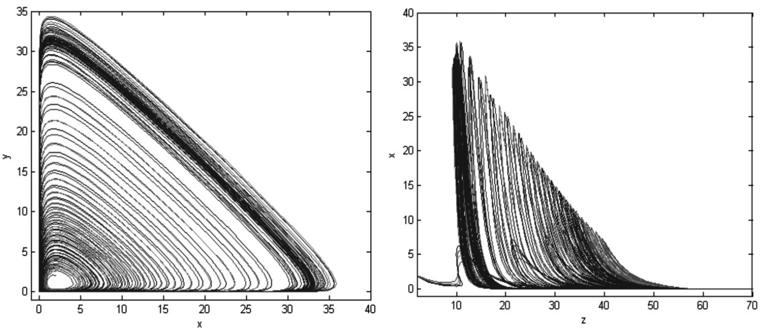
(a) Phase space for $a_3 = 0.75$ (b) Time series for $a_3 = 0.75$

Figure 2: The solution for $a_3 = a_{30}$.

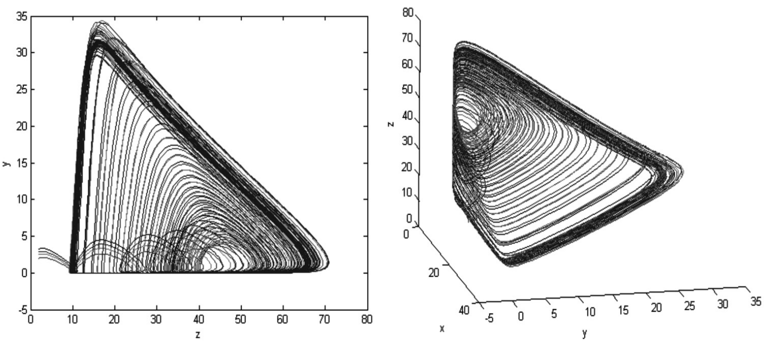


(a) Phase space for $a_3 = 1$ (b) Time series for $a_3 = 1$

Figure 3: The solution for $a_3 > a_{30}$.



(a) *x*-*y* phase plane (b) *x*-*z* phase plane



(c) *y*-*z* phase plane (d) *x*-*y*-*z* phase plane

Figure 4: The chaotic solution for $c_2 > a_3$ and $c_2 > c_1$, different colour for different initial condition.

As shown in Figure 1, the top predator z can survive, growing periodically unstable. On the other hand, prey *x* and predator *y* persist and have populations that vary periodically over time with a common period.

II. The case $a_3 = a_{30}$

For the case $a_3 = a_{30}$ the system just has one E_1 equilibrium point and E_2 disappears. The equilibrium E_1 has three eigenvalues with zero real-part corresponding with stable centre point in *xy* plane (see Table 1). In this case, top predators die. On the other hand, prey and predator growth increase over time as shown in Figure 2.

III. The case $a_3 > a_{30}$

For the case $a_3 > a_{30}$ equilibrium point E_1 is stable, E_2 is unstable as in previous sections. For the case (Table 1) of the two eigenvalues, E_1 is pure imaginary with initially-spiral stability corresponding with centre manifold in *xy* plane and one negative real-part eigenvalue corresponding with stable one-dimensional invariant curve in z axes and in different condition in E_2 that has two eigenvalues, with complex conjugate initially-spiral stability and one positive real-part eigenvalue corresponding with unstable one-dimensional invariant curve. Hence the equilibrium point E_1 is a locally-stable spiral sink and E_2 is a locally-unstable spiral source.

In this case, top predators die. On the other hand, prey x and predator y persist and has populations that vary periodically over time with a common period. The plot of the solution in Figure 3 exhibits this behaviour.

IV. Chaotic attractor in equilibrium point

For the parameter set: $\{a_1, a_2, a_3, b_1, b_2, c_1, c_2\}$= { 0.5, 0.5, 0.05, 0.5, 0.5, 0.6, 2.5} chaotic attractors occur if $a_3 < a_{30}$ for this parameters, with $a_{30} = c_2 = 2.5$ (12). The coordinates of equilibrium points and the corresponding eigenvalues can be found in Table1. The chaotics behaviour is sensitive to the changes in the parameter set and in the initial conditions as shown in Figure 4.

Now it shall be proven that the strange attractor shown in Figure 4, is actually chaotic in nature. For this all the Lyapunov exponents (Wolf *et al.*, 1985) associated with the strange attractor shown in Figure 4 shall first be calculated. The spectrum of Lyapunov exponent is shown in Figure 5. One can see that the largest Lyapunov exponent thus calculated is positive, showing that the strange attractor is chaotic in nature.

The dynamics of this model system depend on values of system parameters. Beyond a critical value of a crucial parameter, the system displays a peculiar behaviour, whose sensitively depends on initial condition. This is known as "deterministic chaos". The system trajectories meander aimlessly on a bounded phase space. The characteristic feature of this meandering is that initially close trajectories diverge exponentially from each other as time progresses.

Persistence of top species *z* in (2) depends on the parameters a_2, a_3, c_1 and c_2. In particular,

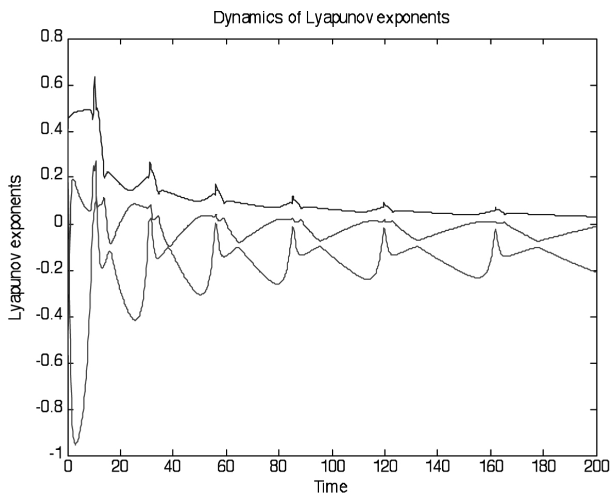


Figure 5. The spectrum of Lyapunov exponent calculated for the strange attractor shown in Figure 4.

if , then species z dies out, while if , then species z survives. On the other hand, species prey x and middle predator y can persist for all conditions.

Conclusions

In this paper, the dynamical behaviours of a three-species food-chain model have been studied. As usual, a Lotka-Volterra functional response is taken to represent the interaction between prey and predator. The interaction between predator and top predator is assumed to be governed by a Michaelis-Menten functional response. Such different choices of functional responses may be particularly useful for plant-pest-predator interactions. Mathematical models of food chains are analysed and possible dynamical behaviour of this system is investigated at equilibrium points. In the parameter space, there are passages from instability to stability, which are called Hopf bifurcation points. Models for biologically-reasonable parameter values, exhibits stable, limit cycles, unstable periodic and chaos. The dynamical behaviour is found to be very sensitive to parameter values and initial conditions as well as the parameters of the practical life. That is, a very small change in these values, produces unpredictable results known as chaos. Another property of the nonlinear systems also experienced during the calculations is long-term predictions are impossible. In this paper, all important mathematical findings are numerically verified and graphical representation of a variety of solutions of the systems (2) are depicted using MATLAB R2010a. Numerical study shows that, using the parameter a as control (12), it is possible to break the stable behaviour of the system and drive it to an unstable state. Also it is possible to keep the levels of the populations at a stable state using the above control.

Acknowledgement

The authors gratefully acknowledge the financial support from the Ministry of Higher Education, Malaysia under the FRGS Vot 59200.

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