Bifurcation Analysis for Metapopulation Models

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1. ABSTRACT

Two models with four components of chain populations are considered. In the model, a prey population X is predated by individuals of a specialist predator population Y, and another prey population Z is predated by individuals of a generalist predator population U. This model is governed by a system of four nonlinear first order ordinary differential equations. To study the dynamics of the food chain model, the mentioned system of ordinary differential equations solved numerically. One of the biological parameters varied in a sufficiently large range and its effects on the dynamics of the system are observed. Along the $w-$axis of the predating rate of the specialist predator Y, around four points $w_1 = 0.045,\ w_2 = 0.088,\ \ w_3 = 0.3000,\ and\ \ w_4 = 0.920$ we meet chaos. At each time chaos precedes period doublings.

Key words: Food chain models, Dynamical systems, Chaos, Specialist and Generalist Predators.

Mathematics Subject Classification 2000: 92B05, 92D25, 92D40

2. INTRODUCTION

If a very small change in initial conditions can produce drastic, even sometimes unpredictable results, the system is said to be sensitively dependent on the initial conditions. In general nonlinearity in the systems makes long-term predictions impossible. Henri Poincaré says that: “A small cause, that is not noticed, can produce an effect which will not take into consideration, and we say that this effect depends on chance…. Small difference in initial conditions causes big variation. Predictions become impossible…” This characteristic behavior of nonlinear systems is sometimes called as the butterfly effect. In theory, the flutter of a butterfly's wings in Australia could, for example, produce a snow storm in the Northeastern America, thousands of miles away.

We can not predict the behavior of a system simply looking at the governing equations. A slightly nonlinear term in an equation makes it difficult to answer simple practical questions about the evolution of the phenomena described. However, mathematical models of ecological systems, computer simulations of these models and comparison with real field data help to understand and predict the future of these ecosystems.

Life as an ecosystem is very complex. Ecological systems have all the elements to produce chaotic dynamics. Although chaos is commonly predicted by mathematical models, evidence of its existence in natural world is scarce and inconclusive.

Food chains are ecosystems with extremely simple structure. However they have a very complex dynamics. Modeling efforts of the dynamics of food chains initiated long ago confirm that food chains have a very rich dynamics.

First, V.Volterra [23] and A. Lotka [10] independently developed a simple model of interacting species that still bears their joint names.

$$\frac{dX}{dt} = \Phi(X) - g(X,Y)Y$$
$$\frac{dY}{dt} = \Psi(X,Y)Y - a_2 Y \tag{1}$$

In this model, $\Phi(X)$ is the pray growth rate in the absence of the predators, $g(X,Y)$ is the capture rate of prey by per predator, $\Psi(X,Y)$ is the rate at which each predator converts captured prey into predator births and a_2 is the constant rate at which die in the absence of pray. In the first predator-pray model of Lotka-Volterra, they have $\Phi(x) = a_1 X$ and a linear functional response $g(X,Y) = a_1 X$.

In general $\Psi(X,Y) = \lambda\, g(X,Y)$, where λ is called the ecological efficiency. They showed that ditrophic food chains (i.e. prey-predator systems) can permanently oscillate for any initial condition if the prey growth rate is constant and the predator functional response is linear.

Michael Rosenzweig [16], as a graduate student with Robert MacArthur in 1960s, added density dependence and predator behavior to the Lotka-Volterra equations that an ecological model capable of displaying true nonlinear limit cycle was developed.

In the early and mid 1970s, physicist Robert May [11, 12] demonstrated that the simplest ecological models could generate complex dynamics, including the logistic map. His extremely simple model of density-dependent population growth with discrete generations was of the form:

$$X_{t+1} = F(X_t) \tag{2}$$

Since the pioneering theoretical works by Lotka and Volterra early at that time, the study of realistic mathematical models in ecology, especially the study of relations between species and their environment, has became a very popular topic that interested mathematicians as well as biologists. Investigations on various population models reflect their use in helping to understand the dynamical processes involved in such areas as predator-prey, competition and ecological control of pests. The increasing use of mathematics in biology is inevitable as biology becomes more quantitative. In fact, most realistic biology problems could be solved on the fundament of constructing suitable mathematical models.

The dynamic relationship between predators and their prey has long been and will continue to be one of the dominant themes in both ecological and mathematical ecology due to its universal existence and importance. These problems may appear to be simple mathematically at first sight, they are, in fact, often very challenging and complicated. There are a lot of predator-prey models in literature. Among these models, Rosenzweig-MacArthur [16] (Rosenzweig and MacArthur, 1963) model and Holling&Tanner model [8, 17] are took as basis in this study.

3. SPECIALIST AND GENERALIST PREDATORS, OUR MODEL

There are four basic interactions among species: Predator-prey, competition, interference and mutualism. Predator-prey interaction is the most common. There are two types of predators: (i) specialists and (ii) generalists [8-20]. A specialist predator feeds only one food. When its favorite food is absent or is in short supply, its population density decreases exponentially. Generalist predators have alternative food options. When their most preferred food is in short supply, they switch over alternative food options [7, 22]. The Rosenzweig-MacArthur model is the one, which describes the dynamics of a specialist predator and its prey. Commonly it used to define that predator-prey interaction between two biological species, for this reason it is a continuous time model of the following form:

$$\frac{dX}{dt} = a_1 X - b_1 X^2 - \frac{w\,X\,Y}{X+D}$$
$$\frac{dY}{dt} = -a_2 Y + \frac{w_1\,X\,Y}{X+D_1} \qquad (3)$$

This model consists of logistic prey and specialist predator with Holling II type functional response [17]. X and Y are population densities of prey and predator respectively. a_1 is the rate of self-reproduction for prey. The parameter a_2 measures how fast the predator Y will die when there is no prey to capture, kill and eat. b_1 measures the intensity of competition among individuals of species X for space, food etc. And *D* measures the efficiency of prey in evading a predator's attack. It depends on the protection afforded by the environment to the prey. D_1 has similar meaning as that of *D*.

A model given by Holling and Tanner [8, 17] describes the dynamics of a generalist predator and its prey:

$$\frac{dZ}{dt} = A\,Z\left(1-\frac{Z}{K}\right) - \frac{w_3\,U\,Z}{Z+D_3}$$
$$\frac{dU}{dt} = cU - \frac{w_4 U^2}{Z} \qquad (4)$$

where Z is the most favorite food for generalist predator U. In this model, prey and predator both grow logistically. A and K are respectively the rate of self-reproduction and carrying capacity for the prey Z. *c* is the growth rate of the generalist predator due to sexual reproduction. The last term in second line in Eq. (4) describes how loss in species *U* depends on per capita availability of its prey (*Z*). The other parameters have their usual meaning.

As linking specialist and generalist predator models showed above, we obtain meta population models, which we will investigate in this study. For our model, this link mechanism can be mathematically represented by adding a term $-w_2 Y^2 U \big/ \left(Y^2 + D_2^2\right)$ to the second equation of first subsystem:

$$\frac{dX}{dt} = a_1 X - b_1 X^2 - \frac{w\,Y\,X}{X+D}$$
$$\frac{dU}{dt} = -a_2 Y + \frac{w_1\,Y\,X}{X+D_1} - \frac{w_2 Y^2 U}{Y^2 + D_2{}^2}$$
$$\frac{dZ}{dt} = A\,Z\left(1-\frac{Z}{K}\right) - \frac{w_3\,U\,Z}{Z+D_3}$$
$$\frac{dU}{dt} = cU - \frac{w_4 U^2}{Y+Z} \qquad (5)$$

where Y is a specialist predator, i.e. X is the only food for it. Therefore, Y dies out exponentially in the absence of X. The last term in the second line in Eq. (5) represents functional response of the predator U, which is a generalist predator. It switches its prey whenever its favorite food option Z is in short supply. The last term in the last line in Eq. (5) describes how loss in species U depends on per capita availability of its preys (Z and Y).

In the following subsection, firstly sensitive dependence on the parameters and secondly sensitive dependence on initial populations will numerically be investigated.
Parameter values used for this model are around the ones in [15]:

$$\{A, a_1, a_2, b_1, c, D, D_1, D_2, D_3, K, w, w_1, w_2, w_3, w_4\}$$
$$=$$
$$\{1.5, 3, 0.7, 0.05, 0.2, 10, 10, 10, 20, 100, 1, 4, 0.05, 0.74, 0.1\}$$

4. HOPF POINT ANALYSIS IN *w*

To understand the sensitive dependence on the parameters, initial populations, and understand the situations that lead the system to chaos, one needs to make a Hopf point analysis. Since for a reach system like in (5), it is almost impossible to make an overall analysis, hence we confine ourselves to a sub manifold

$$\{X(0),\,Y(0),\,Z(0),\,U(0),A,a_1,a_2,b_1,c,D,D_1,D_2,D_3,K,w,w_1,w_2,w_3,w_4\}$$
$$\{0.1,0.1,0.1,0.1,1.5,3,0.7,0.05,0.2,10,10,10,20,100,\text{w},4,0.05,0.74,0.1\}$$
.

Equilibrium points are the zeros of the nonlinear system of algebraic equations

$$\begin{aligned}
&3X-0.05X^2-\frac{wYX}{X+10}=0\\
&-0.7\,Y+\frac{4YX}{X+10}-\frac{0.05\,Y^2U}{Y^2+100}=0\\
&1.5\,Z\left(1-\frac{Z}{100}\right)-\frac{0.74\,U\,Z}{Z+20}=0\\
&0.2\,U-\frac{0.1\,U^2}{Y+Z}=0
\end{aligned}$$

(6)

which is obtained simply equating the right hand sides in (5) to zero.

The dynamical system in (5) has some of its equilibrium points on the boundaries of the positive sub manifold. They are all unstable equilibriums:

	(X,Y,Z,U)	Eigenvectors
E0	{0, 0, 0, 0}	{3.,1.5, -0.7, 0.2}
E1	{60, 0, 0, 0}	{-3.,2.73,1.5,0.2}
E2	{0, 0, 100, 0}	{3.,-1.5,-0.7, 0.2}
E3	{60, 0, 100, 0}	{-3.,2.73,-1.5, 0.2}
E4	{0, 0, 36.35, 72.70}	{3.,-0.7, -0.06+0.42 □, -0.06-0.42 □}
E5	{70/33, 35.08/w, 0, 0}	{1.5, 0.20 +1.28 □, 0.20 -1.28 □, 0.2}
E6	{60, 0, 36.35, 72.70}	{-3., 2.7,-0.06+0.42 □,-0.06-0.42 □}
E7	{70/33, 35.08/w, 100, 0}	{-1.5, 0.20 +1.28 □,0.20 -1.28□, 0.2}
E8	{2.43,20.21,0.30,41.03}	{0.24 +1.34 □, 0.24 -1.34□,-0.13,-0.02}

Our investigation also revealed that, there is a unique additional unstable inner equilibrium point E8 for each $w > 1.76$. E8 in the table is obtained for $w = 1.77$

5. CHAOTIC REGIONS ON w AXIS

Numerical solutions with several initial data $\{X(0),\,Y(0),\,Z(0),\,U(0)\}$ investigated for several values of the parameter w.

w	Qualitative behavior
0.01	Two attractors with Z=0 and U=0.
0.0335	Period doubling
0.045	Chaos
0.05	Period doubling
0.088	Chaos
0.09	Period tripling
0.10	Period doubling
0.30	Chaos
0.50	Period tripling
0.92	Chaos
0.9351	Period doubling
0.97	Periodic solution
1.00	Period doubling
1.20	Periodic solution
1.77	Two attractors with T=27.8 and T=14.2

Table 1. Qualitative behavior of the solution for several values of the parameter w.

In the following, the dynamics of the system will be investigated for the values of w as in the above table. Starting from a smaller value $w = 0.01$, which is the predating rate of the specialist predator Y, for all initial states with $\mathrm{U0} = 0$, we have an attractor limit cycle with $\mathrm{U} = 0, \mathrm{Z} = 100$, with period $T = 17.38$ as shown in Fig. 1a. For all initial states with $U0 \neq 0$, we have an attractor limit cycle with $\mathrm{Z} = 0$, with period $T = 17.59$ as shown in Fig. 1b.

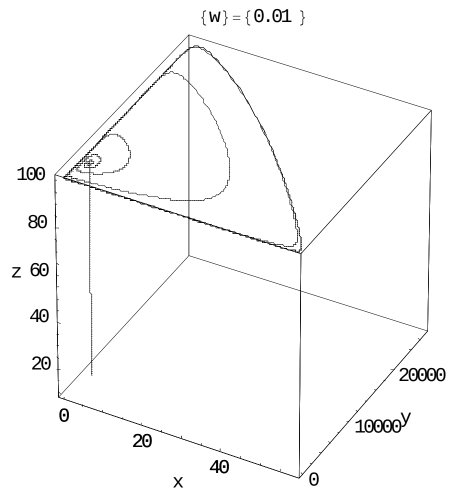

Fig. 2a. Trajectories projected on 3-dimensional XYZ phase space when w=0.01 , $\mathrm{U} = 0, \mathrm{Z} = 100$ on the limit cycle with the period $T = 17.38$, initvec ={70/33, 3508, 10, 0.}.

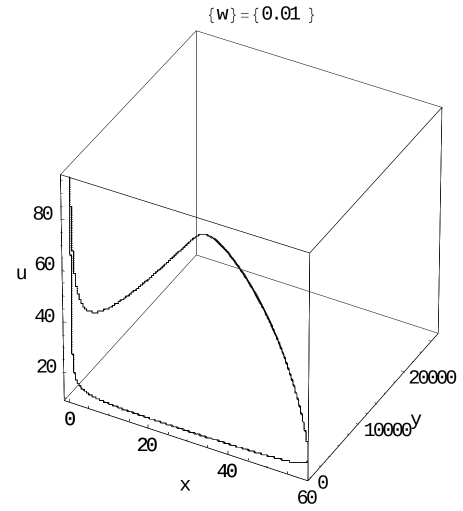

Fig. 2b. Trajectories projected on 3-dimensional *XYU* phase space when *w*=0.01 . $Z = 0$ on the limit cycle with the period $T = 17.59$, initvec ={70/33, 3508.`, 100., .001}.

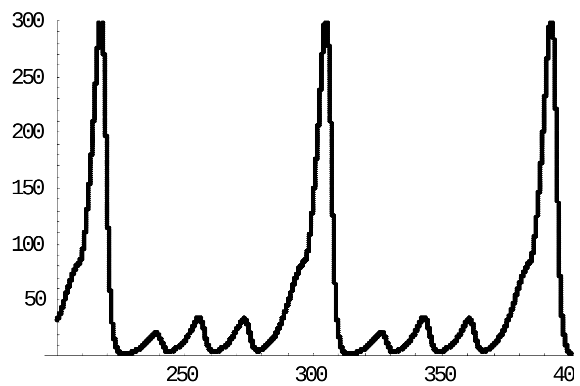

Fig. 2. Time plot of $U(t)$. While the other three components are simple periodic functions, $U(t)$ undergoes a period multiplication when *w*=0.0335. The period is $T = 87.69$. The attractor is not sensitive to the initial conditions.

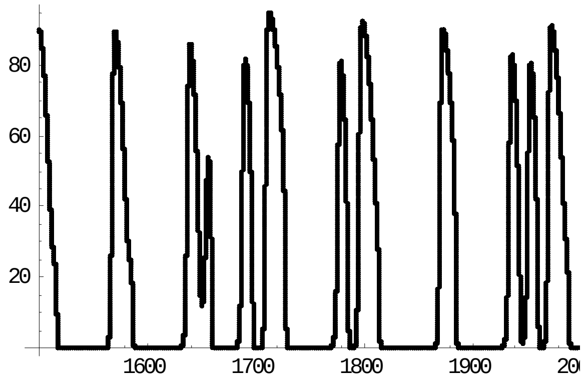

Fig. 3. (a) Time plot for $Z(t)$.

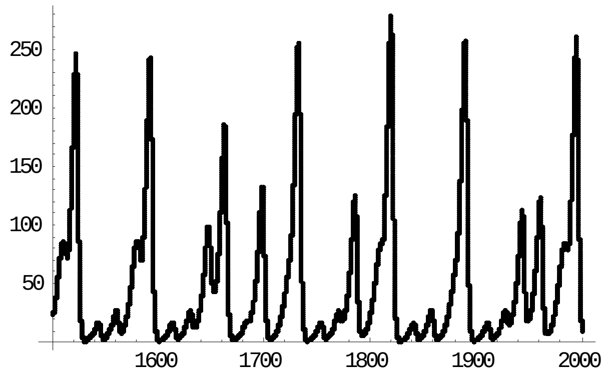

Fig. 3. (b) Time plot of $U(t)$. They are not periodic while $X(t), Y(t)$ are periodic functions. For *w*=0.045 dynamical system undergoes a chaotic state.

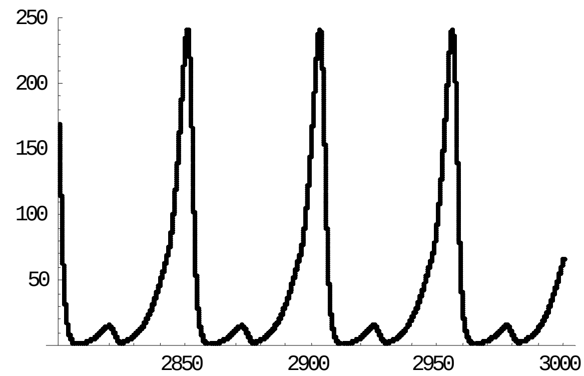

Fig. 4. Time plot of $U(t)$. While the other three components are simple periodic functions, $U(t)$ undergoes a period multiplication when *w*=0.0335. The period is $T = 52.49$. The attractor is not sensitive to the initial conditions.

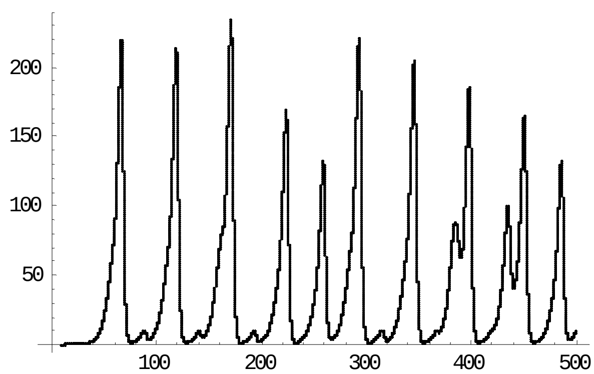

Fig. 5. Time plot of $U(t)$. $Z(t)$, $U(t)$ are not periodic while $X(t)$, $Y(t)$ are simple periodic functions. For w=0.088 dynamical system undergoes a chaotic state.

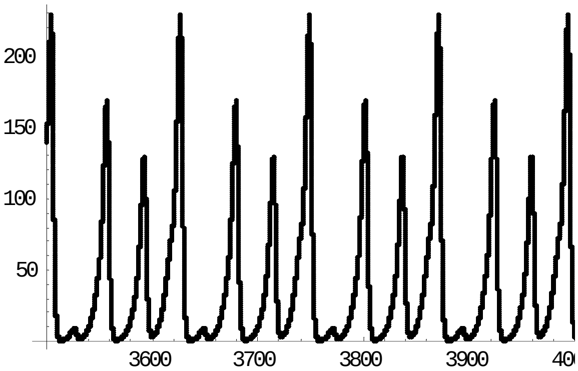

Fig. 6. Time plot of $U(t)$. While the other three components are simple periodic functions, $Z(t)$, $U(t)$ undergoes a period multiplication while $X(t)$, $Y(t)$ are simple periodic functions when w=0.09. The period is $T = 122.13$. The attractor is not sensitive to the initial conditions.

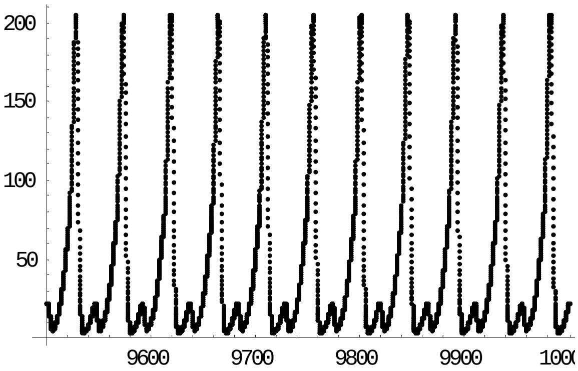

Fig. 7 Time plot of $U(t)$. While the other three components are simple periodic functions, $U(t)$ undergoes a period multiplication when w=0.10. The period is $T = 45.4$. The attractor is not sensitive to the initial conditions.

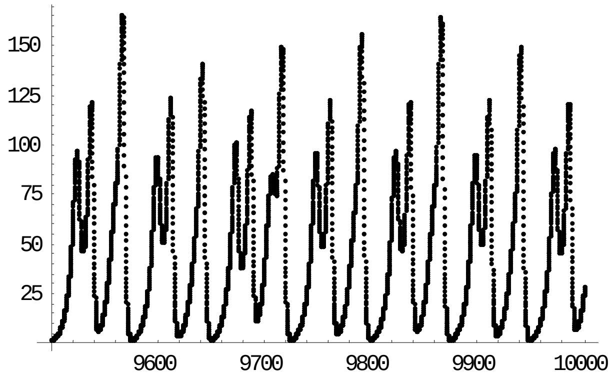

Fig. 8. Time plot of $U(t)$. $Z(t)$, $U(t)$ are not periodic while $X(t)$, $Y(t)$ are simple periodic functions. For w=0.30 dynamical system undergoes a chaotic state.

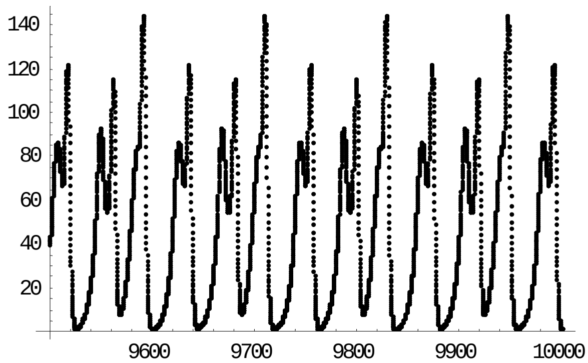

Fig. 9. Time plot of $U(t)$. While the other two components are simple periodic functions, $Z(t)$, $U(t)$ undergoes a period multiplication when w=0.50. The period is $T = 29.5$ The attractor is not sensitive to the initial conditions.

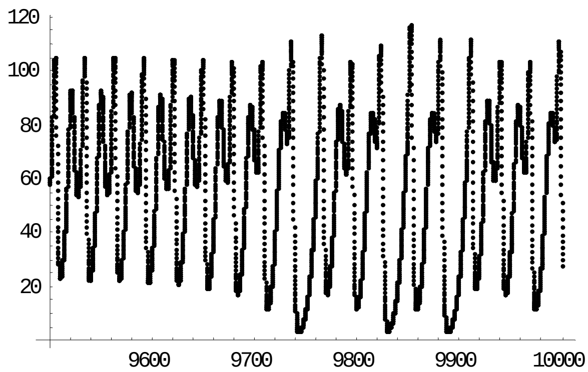

Fig. 10. Time plot of $U(t)$. $Z(t)$, $U(t)$ are not periodic while $X(t)$, $Y(t)$ are simple periodic functions. For w=0.92 dynamical system undergoes a chaotic state.

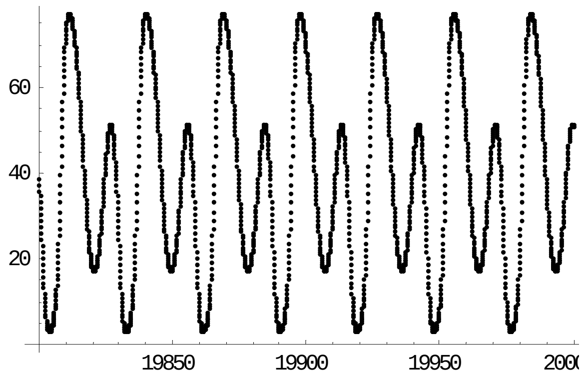

Fig. 11. Time plot of $U(t)$. While the other two components are simple periodic functions, $Z(t)$, $U(t)$ undergoes a period multiplication when w=0.97. The period is $T = 28.8$. The attractor is not sensitive to the initial conditions.

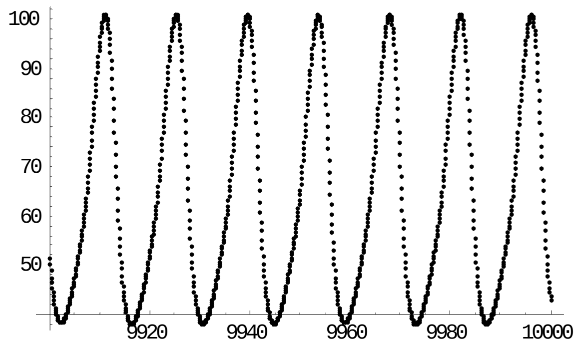

Fig. 12. Time plot of $U(t)$. While the other three components are also simple periodic functions when w=1.20. The period is $T = 14.2$. The attractor is not sensitive to the initial conditions.

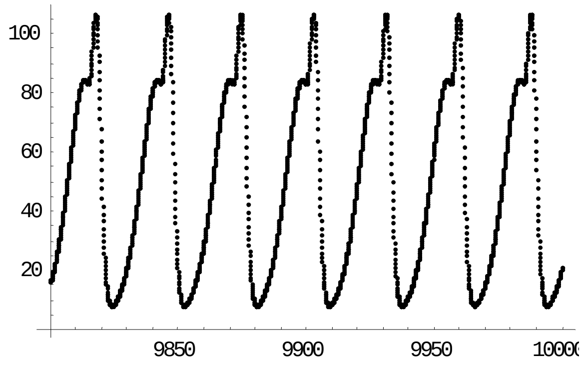

Fig. 13. $T = 14.2$.. For w=1.77 (a) Time plot for $U(t)$ when initvec = E8.. $U(t)$ lives a period doubling . The period is $T = 27.8$.

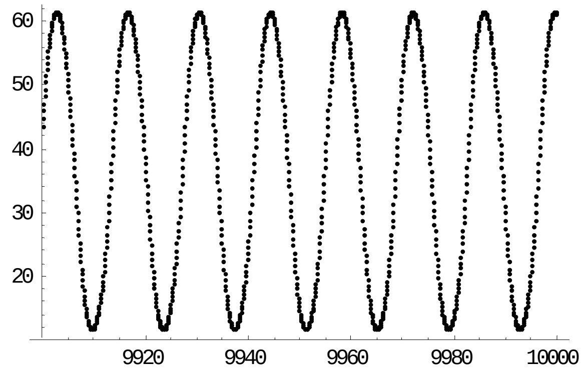

Fig. 13. $T = 14.2$.. For w=1.77 (b) Time plot of $U(t)$ when initvec near E7. All components are simple periodic functions with period $T = 14.2$. The attractor is sensitive to the initial conditions.

6. DISCUSSION

In this paper the chaos is searched in a sub manifold of the parameter space. Along the $w-$axis of the predating rate of the specialist predator Y, around four points
$w_1 = 0.045,\ w_2 = 0.088,\ w_3 = 0.3000,\ and\ \ w_4 = 0.920$
we meet chaos. At each time chaos precedes period doublings.

It is an interesting feature of the system that in all cases of chaos, the populations of pray $X(t)$ and the specialist predator $Y(t)$ remains periodic, and the population of the generalist predator $U(t)$ undergoes a chaotic regime, while only in two cases $Z(t)$ undergoes a chaotic regime too.

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