INTERACTIONS BETWEEN DISPERSAL AND DYNAMICS: COUPLED RICKER'S EQUATIONS

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Eratostenes Flores Torres

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Interactions Between Dispersal and Dynamics: Coupled Ricker's equations

Eratóstenes Flores Torres
Universidad Nacional Autónoma de México
Facultad de Ciencias

Abstract

We study a one patch model using Ricker's equation, $x_{n+1} = x_n e^{r-x_n}$, $r \geq 0$. We reproduce some results that Hastings (1993) obtained by coupling two discrete time logistic equations. Multiple attractors could occur with dispersion where there is only one attractor without dispersion. The boundary of the basins of atraction of the attractors can be fractal in nature. This makes prediction of the asymptotic behavior of most initial conditions difficult to analyze. Furthermore, we study the same model using Ricker's equation. We show that the qualitative nature of the results for a system of difference equations with dispersion depends on the form of the local dynamics.

1 Introduction

Ricker's equation, $x_{n+1} = x_n e^{r-x_n}$, $r \geq 0$, is used to study the population dynamics of single-species populations that cannot grow without bounds. It means, the environment where this species live can sustain only a maximal population level $x_n = 1$. The term $\Delta(x_n) = e^{r-x_n}$ reflects density dependence in the reproductive rate r. Also, if $r \in (0, 2)$ then the basin of attraction of the positive fixed point is $(0, \infty)$, i.e in Ricker's model local stability implies global stability, Paul Cull (1981). We also give the bifurcation diagram for this equation and conclude that Ricker's equation is chaotic.

We will reproduce some results obtained by Hastings(1993), in his studies of a two-patch discrete-time single species model where local dynamics are coupled by dispersion and where there is density dependence dynamics. In each patch i, let $x_i(t)$ be the population size after the local dynamics, but before the dispersal phase. The equation for the local dynamics used by Hastings is the logistic equation:

$$\tilde{x}_i = rx_i(1 - x_i) \tag{1}$$

The two patches are coupled by a simple exchange of a fixed fraction of the population each year. Let D be the fraction of the population that is exchanged. Therefore, the following equations describe the dispersal phase:

$$x_1(t+1) = \tilde{x}_1(t) + D[\tilde{x}_2(t) - \tilde{x}_1(t)] \tag{2}$$
$$x_2(t+1) = \tilde{x}_2(t) + D[\tilde{x}_1(t) - \tilde{x}_2(t)]. \tag{3}$$

Plugging in $\tilde{x}_i = rx_i(1 - x_i)$ into the above equations, we have

$$x_1(t+1) = r_1x_1(t)(1 - x_1(t)) + D[r_2x_2(t)(1 - x_2(t)) - r_1x_1(t)(1 - x_1(t))] \tag{4}$$
$$x_2(t+1) = r_2x_2(t)(1 - x_2(t)) + D[r_1x_1(t)(1 - x_1(t)) - r_2x_2(t)(1 - x_2(t))] \tag{5}$$

where the parameter D is restricted to $0 \leq D \leq 1/2$. When there is no dispersion, $D = 0$, we have an uncoupled system, and the behavior of the system could be chaotic (since the logistic equation and the Ricker's equation are chaotic for some choice of the parameters). When there is a complete dispersion i.e, $D = \frac{1}{2}$, there is a balance in the population that disperses to the other patch and to the population that remains in the patch. In order to understand the dynamics, numerical approaches like bifurcation diagrams and simulations are used to see the basin's of attraction. We will analyze, the case of identical local dynamics for the two patches, where $r_1 = r_2$, and then we repeat the work of Hastings with the following system where the local dynamics is governed by the Ricker's equation.

$$x_1(t+1) = x_1(t)e^{r_1 - x_1(t)} + D[x_2(t)e^{r_2 - x_2(t)} - x_1(t)e^{r_1 - x_1(t)}] \tag{6}$$
$$x_2(t+1) = x_2(t)e^{r_2 - x_2(t)} + D[x_1(t)e^{r_1 - x_1(t)} - x_2(t)e^{r_2 - x_2(t)}] \tag{7}$$

If there is no dispersion, then local dynamics is given by $x_i(t+1) = x_i(t)e^{r - x_i(t)}$. We will prove that the line $\{(x_1, x_2) : x_1 = x_2\}$ is invariant in the system with dispersion if $r_1 = r_2$. In fact, the dynamical behavior of the system with dispersion on this line is equivalent to the behavior of the single patch Ricker's equation.

2 Ricker's equation

Some species of fish, like salmon, habitually cannibalize their eggs and young. Ricker (1954-1958) observed this phenomena and in order to understand the population dynamics of this phenomena, he assumed a per capita death rate proportional to the initial size of the young population and got the model,
$x_{n+1} = x_n e^{r-x_n}$, $r \geq 0$, now known as Ricker's equation.

2.1 Equilibria

We calculate the fixed points by solving

$$x = xe^{r-x}. \tag{8}$$

$$x(e^{r-x} - 1) = 0. \tag{9}$$

Thus, $x = 0$ and $x = r$ are the equilibrium points of the above model.

2.2 Stability

We use the derivative of the reproduction function

$$f'(x) = e^{r-x} - xe^{r-x} \tag{10}$$

to determine the stability of the fixed points. We have

$$f'(0) = e^r \geq 1. \tag{11}$$

Thus $x = 0$ is an unstable fixed point for all values of $r > 0$. For the second fixed point, we have

$$f'(r) = 1 - r. \tag{12}$$

Thus, the positive fixed point $x = r$ is locally stable $\Leftrightarrow -1 < 1-r < 1$, i.e $\Leftrightarrow 0 < r < 2$.

2.3 Further Result

The reproduction function reaches it's maximum when $x = 1$, i.e

$$f'(x) = e^{r-x} - xe^{r-x} = 0 \Leftrightarrow x = 1 \tag{13}$$

2.4 Density Dependence

To verify that the Ricker's model reflects a density dependence in the reproductive rate, we analyze the growth function,

$$\Delta(x_n) = e^{r-x_n}. \tag{14}$$

The reproduction function $\Delta(x)$ is strictly decreasing fuction wich takes the value 1 when $x = r$. $\Delta'(x) = -e^{r-x}$ is negative $\forall x \in \mathbf{R}$ so that the graph of $\Delta(x)$ is concave up every where. If $x_n < r$ then $e^{r-x_n} > 1$ and x_{n+1} is greater than x_n by the factor e^{r-x_n}. If $x_n > r$ then $e^{r-x_n} < 1$ and x_{n+1} is less than x_n by the factor e^{r-x_n}. Besides, $x = r$ is a fixed point of the Ricker's model and it is stable if $r \in (0, 2)$. Thus, the population continues to grow and reproduce only if $x_n < r$.

2.5 Global Stability

Theorem 2.5.1. *In the Ricker's equation let $r \in (0, 2)$. Then the basin of attraction of the positive fixed point, r, is $(0, \infty)$.*

Proof. We will consider two cases:

1. $x = r \leq 1$.
2. $x = r > 1$.

Recall that $x = 1$ is the value where the reproduction function reaches it's maximum. Case 1. We have

$$x_{n+1} = x_n e^{r-x_n} \tag{15}$$

$$x_{n+2} = x_{n+1} e^{r-x_{n+1}} = x_n e^{r-x_n} e^{r-x_n e^{r-x}} \tag{16}$$

If $x_{n+1} = x_{n+2}$, we have

$$x_n e^{r-x_n} = x_n e^{r-x_n} e^{r-x_n e^{r-x}} \tag{17}$$

$$\frac{r}{x} = e^{r-x} \tag{18}$$

where we have omitted the sub-index n. Let $g(x) = \frac{r}{x}$ and $h(x) = e^{r-x}$. Clearly $x = r$ satisfies the previous equation, $f(x)$ and $g(x)$ are C^∞ in $(0, \infty)$. By the Taylor series expansion, around $x = r$ we have

$$g(x) = 1 + \frac{1}{r}(r-x) + \frac{(r-x)^2}{r^2} + ... + \frac{(r-x)^n}{r^n} + ... \tag{19}$$

$$h(x) = 1 + (r-x) + \frac{(r-x)^2}{2!} + ... + \frac{(r-x)^n}{n!} + ... \tag{20}$$

Now, if $x \in (0, r)$ then we have the next inequality $n! > r^n$ Thus,

$$\frac{1}{n!} < \frac{1}{r^n} \tag{21}$$

and

$$\frac{(r-x)^n}{n!} > \frac{(r-x)^n}{r^n} \tag{22}$$

We got an inequality for the general terms of the Taylor series expansions, so that

$$g(x) = \frac{r}{x} > e^{r-x} = h(x) \tag{23}$$

$$0 < r - xe^{r-x} \tag{24}$$

$$e^0 < e^{r-xe^{r-x}} \tag{25}$$

$$xe^{r-x} < xe^{r-x}e^{r-xe^{r-x}} \tag{26}$$

Therefore,

$$x_{n+2} > x_{n+1} \tag{27}$$

And as there are no fixed points between $x = 0$ and $x = r \leq 1$ where the reproduction function reaches it's maximum, in this case $x_n \to r$ as $n \to \infty$. If the positive fixed point r is such that $r < 1$, there is an interval $(r, 1)$ such that given any initial condition here, the sequence x_n is strictly decrasing (see section 3), Therefore in Case 1. Any initial condition $x_n \in (0, 1]$ is such that $x_n \to r$ as $n \to \infty$

Case 2. The following lemma will we helpfull in this case.

Lemma 2.5.1. *If $r \in (0, 2)$ then $f(x) = x\exp(r - x)$ has no period-2 points.*

Proof. Since period-2 points satisfy

$$f^2(x) = f(f(x)) = x \tag{28}$$

In our case we have that period-2 points satisfy

$$x = x\exp(2r - x - x\exp(r - x)) \tag{29}$$

$x = 0$ is a fixed point of f so that we can assume $x \neq 0$ and get the next equation for the 2-period points

$$\frac{2r}{x} = 1 + \exp(r - x) \tag{30}$$

Let us call the left hand side of the previous equation $g_1(x)$ and the rigth hand side $h_1(x)$. It is easy to see that $x = r$ satisfy $g_1(x) = h_1(x)$ so that we just have to prove that $x = r$ is the only point where $g_1(x)$ and $h_1(x)$ intersect each other. We can see that $g_1(x) \to 0$ as $x \to \infty$ and that $h_1(x) \to 1$ as $x \to \infty$ besides both functions are strictly decreasing so that for $x \geq 2r$, $g(x)$ and $h(x)$ do not have points in common and so there are no period-2 points in this interval. Now, clearly $x = r$ satisfy the previous equation so that if we take the Taylor Series around r of each function we have

$$\begin{aligned} g(x) &= 2 + \frac{2}{r}(r-x) + \frac{2}{r^2}(r-x)^2 + ... + \frac{2}{r^n}(r-x)^n \quad (31) \\ h(x) &= 2 + (r-x) + \frac{(r-x)^2}{2!} + ... + \frac{(r-x)^n}{n!} \quad (32) \end{aligned}$$

and the next inequality follows for the general terms

$$\frac{2}{r^n}(r-x)^n > \frac{(r-x)^n}{n!} \quad (33)$$

if $0 < r < 2$ and $x \in (0, r)$ then $2n! > r^n \to \frac{2}{r^n} > \frac{1}{n!} \to \frac{2}{r^n}(r-x)^n > \frac{1}{n!}(r-x)^n$ so that if we take an initial condition in this interval we have no period-2 points. Now we just have to check what happens for $x \in (r, 2r)$. The next lemma will be helpfull.

Lemma 2.5.2. *Let f:$R \to R$ be a continous function and assume that $\exists\ p < q \in R$ such that $f(p) = q$ and $f^2(p) = p$. Then $\exists\ s \in R$ with $p < s < q$ such that $f(s) = s$.*

Proof. Construct $G(x) = f(x) - x$ its easy to see that $G(x)$ is a continuous function, now

$$\begin{aligned} &G(p) = f(p) - p = q - p > 0 \\ &\text{and } G(q) = f(q) - q = p - q < 0. \end{aligned} \quad (34)$$

By the intermediate value theorem we know that there exists $s \in R$, such that $G(s) = 0$, then $g(s) = f(s) - s = 0 \to f(s) = s$. □

The proof of the previous Lemma let us say that we do not have period-2 points before $x = r$ and between $(r, 2r)$. Therefore, the Ricker's equation has no period-2 points if $r \in (0, 2)$ □

Using the Sharkovski's theorem for f we do not have period-n points for $n \geq 2$, and as there are no other fixed points except $x_\infty = r$ and $x_\infty = 0$. Since $x_\infty = 0$ is unstable, we can say now that every initial condition x_0 is such that $x_n \to r$ as $n \to \infty$ which finishes the proof of the theorem. Theorem 2.5.1 could be proved by applying the results of Cull (1981). $\square$

2.6 Numerics

In this section we give the bifurcation diagram for the Ricker's model. To obtain it we use Mathematica 3.0. It seems that for $r \in (0, 2)$

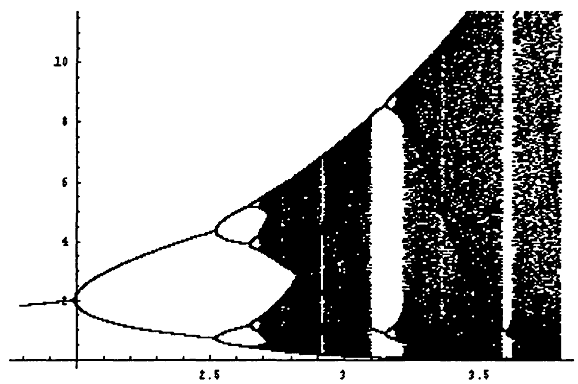

Figure 1: Bifurcation diagram for the Ricker's equation

we just have a stable fixed point. We will prove, in the next section, that if r is in this interval, local stability implies global stability. Also by looking at the bifurcation diagram, we can see that for values of $r \in (3.10, 3.20)$, we have a stable period-3 orbit.

To state Sarkovskii's theorem, we first recall the Sarkovskii's ordering of the positive integers:

$$
\begin{aligned}
3 \triangle 5 \triangle 7 \triangle 9 \triangle ... \\
2 \cdot 3 \triangle 2 \cdot 5 \triangle 2 \cdot 7 \triangle 2 \cdot 9 \triangle ... \\
2^2 \cdot 3 \triangle 2^2 \cdot 5 \triangle 2^2 \cdot 7 \triangle 2^2 \cdot 9 ... \\
2^n \cdot 3 \triangle 2^n \cdot 5 \triangle 2^n \cdot 7 \triangle 2^n \cdot 9 ... \\
2^n \triangle 2^{n-1} \triangle 2^{n-2} \triangle 2^{n-3} ... \\
2^3 \triangle 2^2 \triangle 2 \triangle 1
\end{aligned}
$$

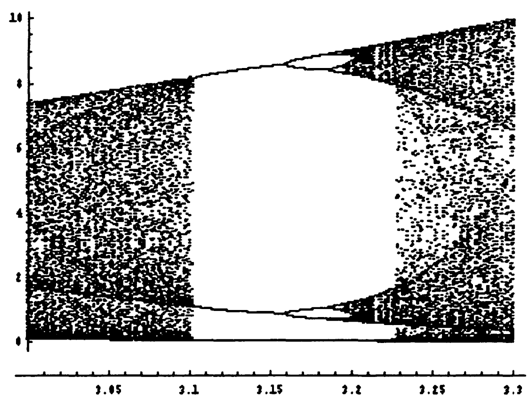

Figure 2: Interval of period-3 points

Theorem 2.6.1. *Let $f : I -> I$ be a continuous function. If f has a period-k point and $k \triangle r$ in the Sarkovskii's ordering, then f has a period r point.*

By the Sakovskii's thorem, if f has a period-3 point, then f has a point of every period. Using this consequence of Sarkovskii's theorem, also proved by Yorke in 1976, we conclude that Ricker's equation is chaotic.

3 Logistic v_s Ricker's equations

We analyze the case when the growth rate is equal in both patches i.e, $r_1 = r_2$. It is possible to find an analytical expresion for the period-2 solutions with local dynamics governed by the logistic equation. Hastings(1993) analyzed the stability of these solutions. In the case of the Ricker's equations it is not possible to find explicit formulas for the periodic points. We use numerical tools like bifurcation diagrams to understand the dynamics. The bifurcation diagrams were obtained using matlab 5. If the local dynamics is governed by either the logistic or the Ricker's equation, then there are no coexisting multiple attractors without dispersion. However, coexisting multiple attractors could occur in the system with dispersion. For $r = 3.8$ and $D = 0.15$

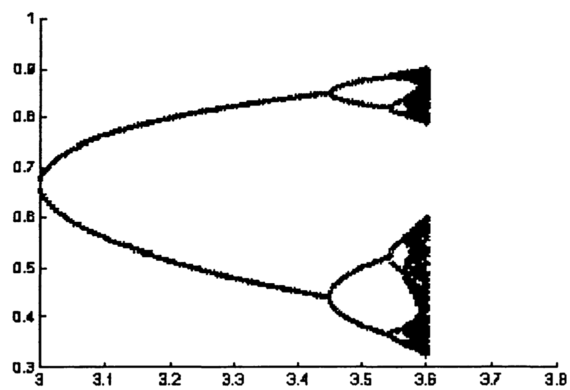

Figure 3: Bifurcation diagram for the coupled logistic model with $r_1 = r_2$ and $x_1 = x_2$. The total population v_s r

there are 3 different attractors. Initial conditions are either attracted to a period-2 solution or to a period-4 solution or to a chaotic attractor. When $r_1 = r_2$ and $x_1 = x_2$, the dynamics of the total population reduces to the one dimensional logistic model in each patch. In the next section, we will give a general proof of this fact.

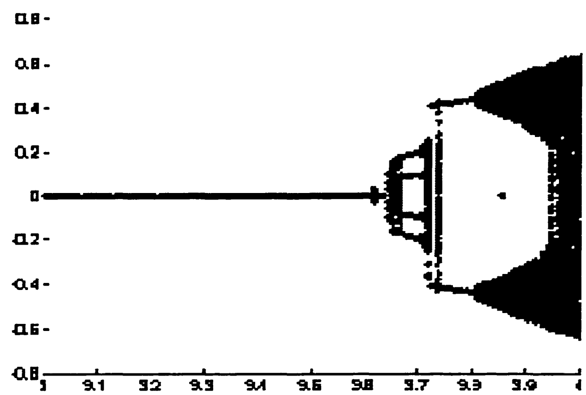

Figure 4: Bifurcation diagram for the coupled logistic model with $r_1 = r_2$ and $x_1 \neq x_2$. The difference in population sizes v_s r

In the case $r_1 = r_2$ and $x_1 \neq x_2$ we plotted the difference in population sizes against r. These are the so called out of phase solutions. In this case, the population in each patch alternates between high and low population sizes.

4 Invariant Line

Theorem 4.0.2. *If* $r_1 = r_2$ *in system (2)(3) , then the line* $\{(x_1, x_2) : x_1 = x_2\}$ *is invariant.*

Before the proof of the theorem we define pioneer species. These are species that thrive at a very low densities when they are in isolation, like pine trees. Asociated with every pioneer species we have a pioneer growth function, $g : [0, \infty) \to (0, \infty)$ such that :

g is positive
g is strictly decreasing
$g(0) > 1$, and
$lim_{x \to \infty} g(x) = 0$

Notice that when $r > 1$ either e^{r-x} and $r(1-x)$ are pioneer growth functions each of them asociated to the Ricker's equation and to the logistic equation respectively.

Proof. In the general model (2)(3) suppose

$$\tilde{x}_1(t) = x_1(t) g_1(x_1(t)) \tag{35}$$

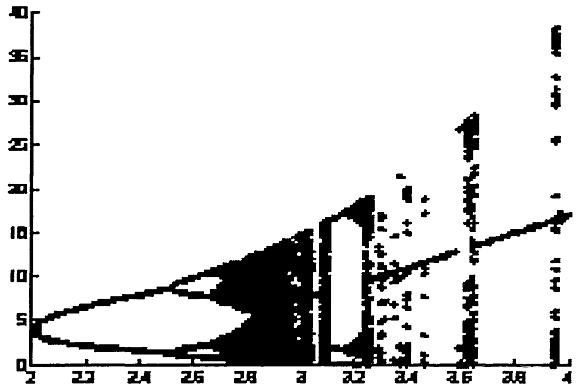

Figure 5: Bifurcation diagram for the coupled Ricker model with $r_1 = r_2$ and $x_1 = x_2$. The total population v_s r

$$\tilde{x}_2(t) = x_2(t)g_2(x_2(t)) \tag{36}$$

Where $g(x_i(t))$ is a pionner growth fuction. Let

$$F(x_1, x_2) = (x_1, x_2) = (x_1 g_1(x_1) + D[x_2 g_2(x_2) - x_1 g_1(x_1)] \\ , x_2 g_2(x_2) + D[x_1 g_1(x_1) - x_2 g_2(x_2)]).$$

Let $r_1 = r_2$. If $(x_1 = x_2) \in \{(x_1, x_2) : x_1 = x_2\}$, then $g_1 = g_2$ and

$$F(x_1, x_2) = (x_1 g_1(x_1), x_2 g_2(x_2)).$$

That is,

$$\tilde{x}_1 = \tilde{x}_2$$

Thus,

$$F_1(x_1, x_2) = F_2(x_1, x_2)$$

So that the line $x_1 = x_2$ is F-invariant. $\square$

Notice that under the assumptions of the above theorem, (35) and (36) become

$$x_1(t+1) = \tilde{x}_1(t)$$

So that the dynamics on the line $x_1 = x_2$ is equivalent to the dynamics of the single patch Ricker's equation studied in the first section.

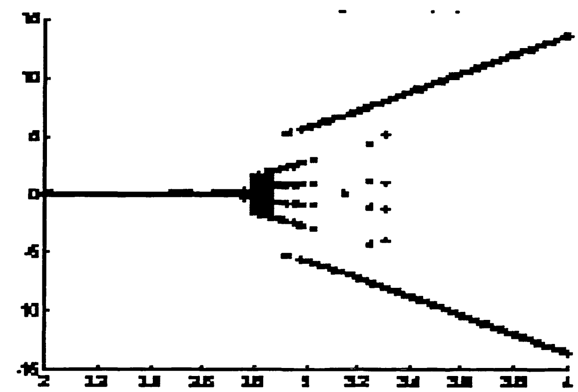

Figure 6: Bifurcation diagram for the coupled Ricker model with $r_1 = r_2$ and $x_1 \neq x_2$. The difference in population sizes v_s r

If $D = 0$, the system has only one chaotic attractor. From zero as we increase D past .0148 a stable period two emerges. The presence of the chaotic atractor coexisting with the period two divide the set of initial conditions in to two sets, those that converge to the chaotic attractor and the ones that converge to the period two cycle. We will see in figures that the boundary between the two sets is a fractal. A period double behavior lead the system to a four period solution

as when $D = .015$ and so on until $D \approx .01952967$, when there is a discrete hopf bifurcation, leading to a two "closed" curves, then if we continue increasing D this "closed" two curves begin to loose points leading to a period two attractor like when $D = .06$, but if we continue increasing D the attractor obtained when $D = .0148$ becomes chaotic and the set of initial conditions that tends to this attractor is smaller every time as when $D = .157$. For values of $D = .158$ or greater, we just have again one chaotic attractor. It is interesting to notice that inside the chaotic attractor present for any choice of D, the invariant set $x_1 = x_2$ behaves chaotically as well.

5 Sensitive dependence

The next graphics where we take $r_1 = r_2 = 3.8$ and $D = .15$, reveals that the long-term behavior of the initial conditions could be essentially difficult to analyze. Hastings obtained a fractal structure separating qualitatively different outcomes using the logistic equation,

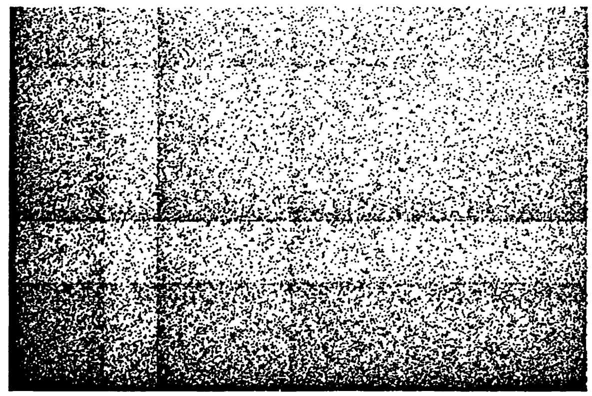

Figure 7: Chaotic attractor's shape when $D = 0$

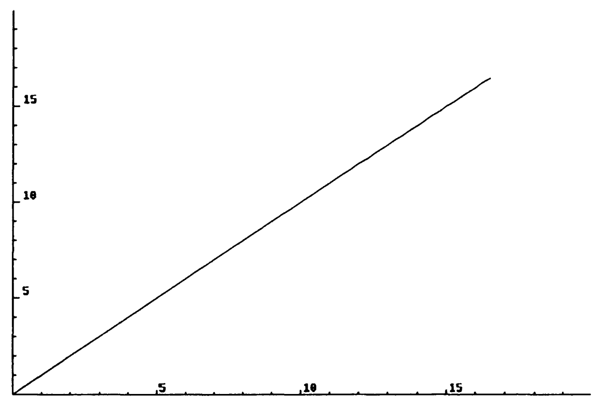

Figure 8: Invariant chaotic set $x_1 = x_2$

figure (9). For the Ricker's equation, I get a very different fractal structure wich reveals that the qualitatively nature of the results for a system of difference equations with dispersion definitely depends on the form of the local dynamics.

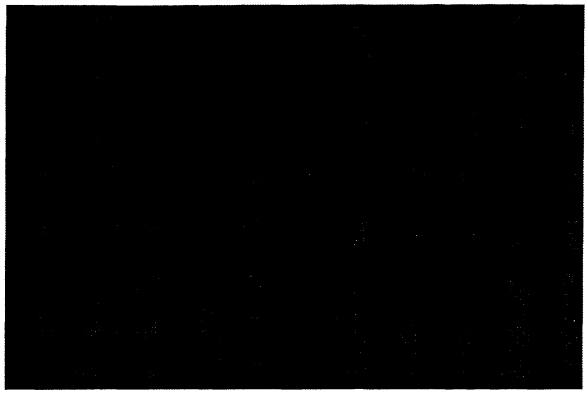

Figure 9: Fractal basin boundary using logistic equation

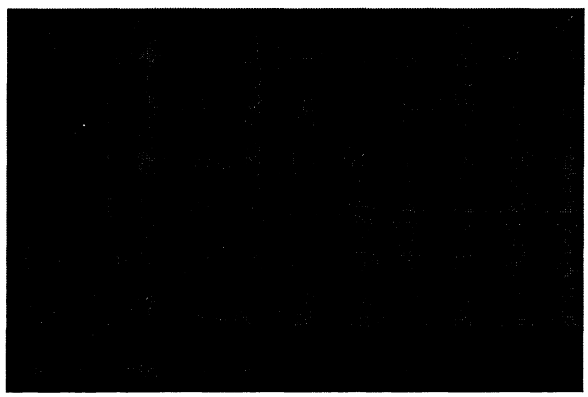

Figure 10: Fractal basin boundary using Ricker's equation

Changes of the fractal structure for Ricker's equation as the dispersion parameter is varied.

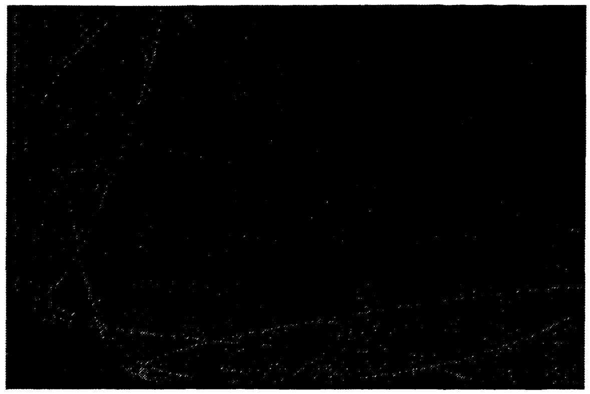

Figure 11: Shape of the chaotic attractor when $D = .014$

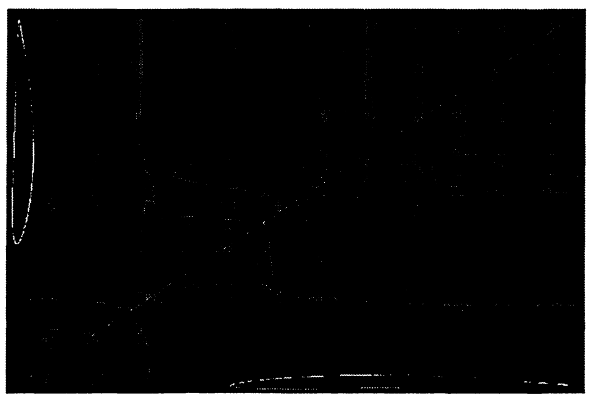

Figure 12: Fractal basin boundary for $D = .01952967$ the white "closed" curves give evidence of a discrete hopf bifurcation

6 Conclusions

The qualitative nature of the results depend on the exact form of the local dynamics. Multiple stable periodic orbits could coexist with a chaotic attractor in a two patch system where there is only a chaotic attractor without dispersion. Complex basins of attraction with fractal boundaries occur in systems with dispersion. Complex chaotic attractors occur in systems with dispersion. Dispersion could be used to control a chaotic one patch system. Hopf bifurcation occurs in two patch systems where none existed without dispersion.

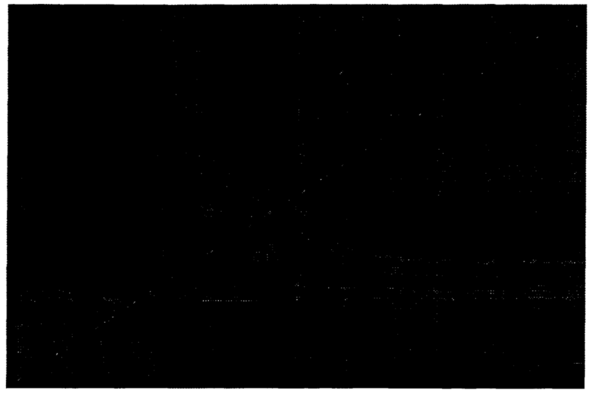

Figure 13: The white "closed" curves begin to loose points $D = .06$

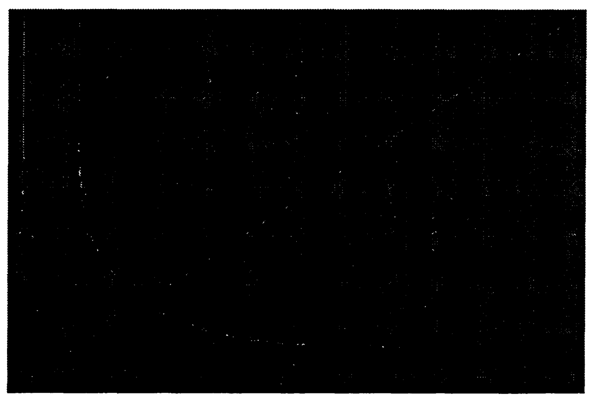

Figure 14: The set of points converging to the attractor that becomes chaotic is smaller the greater the value of D increases, $D = .06$

7 Acknowledgements

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