Journal of Difference Equations and Applications, Vol. 11, No. 4–5, April 2005, 365–377

Multiple attractors via CUSP bifurcation in periodically varying environments

JOHN E. FRANKE†* and ABDUL-AZIZ YAKUBU‡

†Department of Mathematics, North Carolina State University, Raleigh, NC 27695, USA
‡Department of Mathematics, Howard University, Washington, DC 20059, USA

(Received 26 May 2004; in final form 3 November 2004)

Periodically forced (non-autonomous) single species population models support multiple attractors via tangent bifurcations, where the corresponding autonomous models support single attractors. Elaydi and Sacker obtained conditions for the existence of single attractors in periodically forced discrete-time models. In this paper, the Cusp Bifurcation Theorem is used to provide a general framework for the occurrence of multiple attractors in such periodic dynamical systems.

Keywords: Periodic dynamical systems; Semi-conjugacy; Tangent bifurcation; Multiple attractors

1. Introduction

Many population models support multiple attractors or alternative life history outcomes [1,2,4,10,15,16,19–21,38,39]. In a recent paper, Yakubu studied the mathematical and biological mechanisms that generate multiple attractors in discrete-time autonomous juvenile-adult population models [38]. Henson [19], Franke and Selgrade [10] have used periodicity as a mechanism for generating multiple attractors in discrete-time nonautonomous population models. The flour beetle, *Tribolium*, is an example of a natural population that supports multiple attractors [19–24].

This paper is on an explanation for multiple attractors in discrete-time nonautonomous single species population models. In particular, we use the Cusp Bifurcation Theorem to show that simple nonautonomous population models are capable of generating multiple attractors through a tangent bifurcation, where the corresponding autonomous models support single attractors (no multiple attractors) [26].

Others have studied discrete-time nonautonomous population models [4,5,7,8,14, 19–21,27,37]. In recent papers, Elaydi and Sacker [7,8] proved that for a *k-periodic* dynamical system, if a periodic orbit of period r is globally asymptotically stable (no multiple attractors) then r must be a divisor of k. This result is an extension of a result of Elaydi and Yakubu [9] on the characterization of global attractors for discrete-time autonomous models.

In Section 2, we introduce discrete-time autonomous and nonautonomous single-species population models. We use the response of a single species population to a *T-periodic* fluctuating environment to generate *T-periodic* dynamical systems. Such systems consist of

*Corresponding author. Email: john_franke@ncsu.edu

Journal of Difference Equations and Applications
ISSN 1023-6198 print/ISSN 1563-5120 online
http://www.tandf.co.uk/journals
DOI: 10.1080/10236190412331335436

T maps, and in Section 3 we prove that cyclic compositions of the T maps are semi-conjugate. In Section 4, we use the Cusp Bifurcation Theorem to show that *T-periodic* dynamical systems are capable of generating multiple attractors via tangent bifurcation. In Section 5, a specific 2-*periodic* dynamical system based on the classic Ricker model is used to display the creation of multiple attractors via the tangent bifurcation. The results of this manuscript are discussed in Section 6.

2. Population models in periodically varying environments

Single species, single patch, autonomous ecological models of the general form

$$x_{t+1} = x_t g(x_t) \tag{1}$$

have been used to study the long-term dynamics of discretely reproducing closed populations, where x_t is the population size at generation t and the map $g : [0, \infty) \rightarrow [0, \infty)$ is the per capita growth rate [3,6,9–13,17,18,25,28–34]. The Ricker model,

$$x_{t+1} = x_t \exp(r - x_t),$$

and the Beverton-Holt model,

$$x_{t+1} = \frac{\mu K x_t}{K + (\mu - 1)x_t},$$

are examples of Model (1); where $\mu > 1$, K and r are positive constants [28–34,36–39]. To account for a periodic fluctuating environment, the dynamics at generation t of the discretely reproducing population is *typically* modeled by the nonautonomous equation

$$x_{t+1} = x_t g(t, x_t), \tag{2}$$

where the per capita growth rate, $g : Z_+ \times [0, \infty) \rightarrow (0, \infty)$, is assumed to be positive and differentiable (C^∞ on $[0, \infty)$), and where there exists a *smallest positive integer T* satisfying $g(t + T, x) = g(t, x)$. That is, in this case g is periodic with period T. The nonautonomous Ricker model,

$$x_{t+1} = x_t \exp(r_t - x_t),$$

and the nonautonomous Beverton-Holt model,

$$x_{t+1} = \frac{\mu K_t x_t}{K_t + (\mu - 1)x_t},$$

are examples of Model (2); where $r_{t+T} = r_t$, $K_{t+T} = K_t$ for all $t \in Z_+$.

To study the population dynamics of Model (2), we consider a general smooth function

$$f : Z_+ \times [0, \infty) \rightarrow (0, \infty)$$

that generates the nonautonomous difference equation

$$x_{t+1} = f(t, x_t), \quad t \in Z_+$$

where $f(t + T, x) = f(t, x)$ for all $t > 0$. For a simpler notation, we denote $f(t, x_t)$ by $f_t(x_t)$.

Consequently,

$$x_{t+1} = f_t(x_t)$$

for all $t \in Z_+$. We use the following definitions and examples to explore the long-term behavior of initial conditions under *f−iterations*.

DEFINITION 1 *A T−periodic dynamical system is a finite sequence of T maps.*

For an example of a *T-periodic* dynamical system, define the one-dimensional function

$$f_t : [0, \infty) \rightarrow [0, \infty)$$

by

$$f_t(x) = xg(t, x),$$

for each $t \in \{0, 1, 2, \ldots, T-1\}$. For $t \geq T$, let $f_t(x) = f_{t\text{mod}(T)}(x)$. Then the sequence of single species maps $\{f_0, f_1, \ldots, f_t, \ldots\}$ from [0,∞) to [0,∞) is a *T-periodic* dynamical system. To model intraspecific competition, it is assumed that g is strictly decreasing in the second coordinate (that is, $g(t, x) > g(t, y)$ whenever $x < y$). In addition $g(t, 0) > 1$ and $\lim_{x\to\infty} g(t, x) < 1$ for each $t \in \{0, 1, \ldots, T-1\}$. Then $f_t(x) = xg(t, x)$ describes the population dynamics of a pioneer species in a periodically fluctuating environment [10–13].

Since g is a strictly decreasing continuous function (in the second coordinate), for each $t \in \{0, 1, 2, \ldots, T-1\}$, $f_t(x) = xg(t, x)$ has a unique positive fixed point denoted by $X_{t\infty}$. Furthermore, $f_t(x) > x$ whenever $0 < x < X_{t\infty}$ and $f_t(x) < x$ whenever $x > X_{t\infty}$. Consequently, $I_t \equiv f_t([0, X_{t\infty}])$ is a global attractor under f_t iterations.

DEFINITION 2 *The orbit of the point* $x_0 \in [0, \infty)$ *under the T−periodic dynamical system is* $\{x_0, f_0(x_0), f_1(x_1), \ldots, f_t(x_t), \ldots\}$ *or* $\{x_0, x_1, x_2, \ldots, x_t, \ldots\}$.

DEFINITION 3 *A point* x_0 *is a fixed point for the T-periodic dynamical system* $\{f_0, f_1, \ldots, f_t, \ldots\}$ *if its orbit is* $\{x_0, x_0, x_0, \ldots\}$.

LEMMA 1 *If for some* $i \neq j$, f_i *and* f_j *have no common fixed points, then the T-periodic dynamical system* $\{f_0, f_1, \ldots, f_t, \ldots\}$ *has no fixed points.*

Proof Suppose x is a fixed point for the *T-periodic* dynamic dynamical system $\{f_0, f_1, \ldots, f_{T-1}\}$. Then $f_k(x) = x$ for each k. That is, x is a fixed point of each f_k. This contradicts f_i and f_j not having a common fixed point. □

By Lemma 1, non-oscillatory equilibrium dynamics are rare in *T-periodic* dynamical systems.

DEFINITION 4 *An orbit* $\{x_0, x_1, \ldots x_t, \ldots\}$ *is a k-cycle of the T-periodic dynamical system* $\{f_0, f_1, \ldots, f_t, \ldots\}$ *if* $x_t = x_{t\text{mod}(k)}$ *for all* $t \in Z_+$ *and k is the smallest such integer.*

In Section 5, we use the nonautonomous Ricker model to illustrate stable *cycles* in a 2-*periodic* dynamical system (see figure 2).

3. Semi-conjugacy in periodic dynamical systems

A *T-periodic* dynamical system generates T maps $\{f_0, f_1, \ldots, f_{T-1}\}$. In this section, we show that cyclic compositions of these maps are *semi-conjugate* and have the same number of *k-cycles*. In Theorem 6 and Corollary 7, we display that *attracting cycles* of *T-periodic* dynamical systems are locally asymptotically stable.

Lemma 2 *The T cyclic compositions* $f_{T-1} \circ \ldots \circ f_1 \circ f_0, f_T \circ \ldots \circ f_2 \circ f_1, \ldots, f_{2T-2} \circ \ldots \circ f_T \circ f_{T-1}$ *are semi-conjugate to each other.*

Proof Since $(f_T \circ f_{T-1} \circ \ldots \circ f_1) \circ f_0 = f_T \circ (f_{T-1} \circ \ldots \circ f_1 \circ f_0)$ and $f_T = f_0$ we see that f_0 is a semi-conjugacy between $f_T \circ f_{T-1} \circ \ldots \circ f_1$ and $f_{T-1} \circ \ldots \circ f_1 \circ f_0$. Similar proofs show that the rest of the compositions are also semi-conjugate. □

Theorem 3 *Each of the T- cyclic compositions have the same number of periodic points of each period.*

Proof If x and y are two periodic points of $f_{T-1} \circ \ldots \circ f_1 \circ f_0$ with the same prime period $k > 1$, then $f_0(x)$ and $f_0(y)$ are fixed points of $(f_0 \circ f_{T-1} \circ \ldots \circ f_1)^k$. Since

$$x = (f_{T-1} \circ \ldots \circ f_1 \circ f_0)^{k-1} \circ f_{T-1} \circ \ldots f_1(f_0(x)) \tag{3}$$

$$y = (f_{T-1} \circ \ldots \circ f_1 \circ f_0)^{k-1} \circ f_{T-1} \circ \ldots f_1(f_0(y)) \tag{4}$$

then $f_0(x)$ and $f_0(y)$ are not equal. Composing both sides of equations (3) and (4) with f_0 gives

$$f_0(x) = (f_0 \circ f_{T-1} \circ \ldots \circ f_1)^k (f_0(x)) \tag{5}$$

and

$$f_0(y) = (f_0 \circ f_{T-1} \circ \ldots \circ f_1)^k (f_0(y)). \tag{6}$$

Therefore, $f_0(x)$ and $f_0(y)$ are fixed points of $f_0 \circ f_{T-1} \circ \ldots \circ f_1)^k$. That is, the number of fixed points of $(f_{T-1} \circ \ldots \circ f_1 \circ f_0)^k$ is not more than that of $(f_0 \circ f_{T-1} \circ \ldots \circ f_1)^k$. Repeating this process using equations (5) and (6) with f_1 shows the number of fixed points of $(f_0 \circ f_{T-1} \circ \ldots \circ f_1)^k$. is not more than that of $(f_1 \circ f_0 \circ f_{T-1} \circ \ldots \circ f_2)^k$. Continuing this process shows the number of fixed points of $(f_{i-1} \circ \ldots \circ f_{T-1} \circ \ldots \circ f_i)^k$ is not more than that of $(f_i \circ \ldots \circ f_0 \circ f_{T-1} \circ \ldots \circ f_{i+1})^k$. That is, since this process is periodic each cyclic composition raised to the k-th power has the same number of fixed points. □

Lemma 4 *If the orbit of x is k-cycle for the T-periodic dynamical system* $\{f_0, f_1, \ldots, f_t, \ldots\}$, *Then* $f_0(x)$ *is a k-cycle for the T-periodic dynamical system* $\{f_1, f_2, \ldots, f_{t+1}, \ldots\}$.

Proof Since $\{x_0, x_1, \ldots x_t, \ldots\}$ is a *k-cycle* of the *T-Periodic* dynamical system $\{f_0, f_1, \ldots, f_t, \ldots\}$, then $x_t = x_{t \bmod (k)}$ for all $t \in Z_+$ and k is the smallest such integer. The orbit of $f_0(x_0)$ under the *T-periodic* dynamical system $\{f_1, f_2, \ldots f_{t+1}, \ldots\}$ is $\{x_1, x_2, \ldots, x_t, \ldots\}$, where $x_t = x_{t \bmod (k)}$ for all $t \in Z_+$ If k is the smallest such integer we are done. Otherwise, there is a smaller integer l such that $x_t = x_{t \bmod (l)}$ for all $t \in \{1, 2, 3, \ldots\}$. Note that $x_0 = x_k = x_{k+l} = x_l$. Therefore, $x_t = x_{t \bmod (l)}$for all $t \in Z_+$. This is a contradiction to k being the smallest such integer. □

By Lemma 4, *k-cycles* are mapped to *k-cycles.* Consequently, the following result is immediate.

Corollary 5 *Each of the T-cyclic compositions have the same number of periodic points of each prime period. Furthermore, each of the T-periodic dynamical systems obtained by permuting the f_i have the same number of k-cycles.*

If $\{x_0, x_1, \ldots, x_i, \ldots\}$ *is a k-cycle of the T-periodic dynamical system* $\{f_0, f_1, \ldots, f_t, \ldots\}$ *then* x_0 *is a fixed point of the map* $F(x) = f_{Tk-1}(\ldots(f_1(f_0(x)))\ldots)$.

Definition 5 *If the spectral radius of D_xF, the Jacobian matrix of F, is less than one, then x_0 is attracting and we say that the k-cycle is attracting.*

Theorem 6 *Let* $\{x_0, x_1, \ldots, x_i, \ldots\}$ *be an attracting k-cycle of the T-periodic dynamical system* $\{f_0, f_1, \ldots, f_t, \ldots\}$, *then there is a neighborhood U of* x_0 *such that if* $y_0 \in U$ *its orbit limits on the orbit of* x_0 *That is,* $\lim_{n\to\infty} y_{kn+i} = x_i$ *for each* $i \in Z_+$.

Proof Let $\epsilon > 0$. By the continuity of each f_i, there exists a $\delta > 0$ such that if

$$\|y - x_0\| < \delta$$

then

$$\|f_{i-1}(\ldots(f_1(f_0(y))) - f_{i-1}(\ldots(f_1(f_0(x_0)))\| < \epsilon$$

for all i between 0 and Tk. Since x_0 is an attracting *k-cycle*, the spectral radius of $D_xF(x_0) =$ spectral radius of $D_x f_{Tk-1}(\ldots(f_1(f_0(x_0)))\ldots) < 1$. This is equivalent to x_0 is an attracting fixed point of the autonomous differentiable map F. Thus, there is neighborhood U of x_0 such that if $y \in U$ then $\lim_{t\to\infty} F^t(y) = x_0$. Therefore, there exists N such that if $n \geq N$ then $\|F^n(y) - x_0\| < \delta$. This implies $\|f_{i-1}(\ldots(f_1(f_0(F^n(y)))) - f_{i-1}(\ldots(f_1(f_0(x_0)))\| < \epsilon$. By the Reminder Theorem, $i = jk + l$ where $0 \leq l < k$. Note that $f_{i-1}(\ldots(f_1(f_0(x_0))) = x_i = x_{jk+l} = x_l$ and $f_{i-1}(\ldots(f_1(f_0(F^n(y)))) = y_{nTk+i} = y_{(nT+j)k+l}$. Hence, if $n \geq N$ then $\|y_{(nT+j)k+l} - x_l\| < \epsilon$. Thus, if $m \geq (N+1)T$, then $\|y_{mk+l} - x_l\| < \varepsilon$ and we are done. □

The following corollary follows directly from the proof of Theorem 6.

Corollary 7 *Attracting k-cycles of T-periodic dynamical systems are locally asymptotically stable.*

4. Multiple attractors VIA Cusp bifurcation

In this section, we illustrate that periodic dynamical systems are capable of generating multiple attractors through a tangent bifurcation in the presence of another attracting cycle. Thus, periodicity is a mechanism for generating alternative life-history of evolution (multiple attractors). The following bifurcation result, Lemma 9.1 of [26] (Cusp Bifurcation Theorem), will be used to illustrate this bifurcation in periodic dynamical systems.

Theorem 8 (*Cusp bifurcation*) *Suppose that a one-dimensional system*

$$x \to f(x, \alpha), \quad x \in R^1, \quad \alpha \in R^2,$$

with f smooth, has at $\alpha = 0$ *the fixed point* $x = 0$ *for which the cusp bifurcation conditions hold:*

$$\mu = f_x(0,0) = 1, \quad a = \frac{1}{2} f_{xx}(0,0) = 0.$$

Assume that the following genericity conditions are satisfied:

$$f_{xxx}(0,0) \neq 0; \quad (f_{\alpha_1} f_{x\alpha_2} - f_{\alpha_2}, f_{x\alpha_1})(0,0) \neq 0$$

Then there are smooth invertible coordinate and parameter changes transforming the system into

$$\eta \to \eta + \beta_1 + \beta_2 \eta + s\eta^3 + \mathcal{O}(\eta^4),$$

where $s = \text{sign } f_{xxx}(0,0) = \pm 1$.

The Cusp Bifurcation Theorem implies that if a one-parameter family of maps is "generically" close to another one-parameter family of maps which supports a pitchfork bifurcation, then the generic one-parameter family will not support a pitchfork bifurcation. However, it will support a tangent bifurcation. When the tangent bifurcation occurs, two new fixed points appear, one stable and the other unstable. The total number of fixed points increases from 1 to 3 with the two new ones occurring some distance away from the original stable fixed point.

THEOREM 9 *Suppose that a one-dimensional system*

$$x \to f(x, \alpha_1, \alpha_2), \quad x \in R^1, \quad (\alpha_1, \alpha_2) \in R^2,$$

with f smooth, has at $(\alpha_1, \alpha_2) = (0,0)$ *the fixed point* $x = 0$ *for which the following conditions hold:*

$$\begin{aligned} &f_x(0,0,0) = -1, \\ &\qquad f_{a_1}(0,0,0) \neq 0, \\ &\qquad f_{a_2}(0,0,0) \neq 0, \quad 2f_{xxx}(0,0,0) + 3(f_{xx}(0,0,0))^2 \neq 0, \\ &\qquad f_{xx}(0,0,0) f_{\alpha_1}(0,0,0) + 2f_{x\alpha_1}(0,0,0) \neq 0. \end{aligned}$$

Then $f(f(x, \alpha_1, \alpha_2), \alpha_1, 0)$ *satisfies the hypotheses of the Cusp Bifurcation Theorem.*

Proof First, we show that

$$\mu = \frac{\partial}{\partial x} f(f(x, \alpha_1, \alpha_2), \alpha_1, 0)|_{(0,0,0)} = 1.$$

$\frac{\partial}{\partial x} f(f(x, \alpha_1, \alpha_2), \alpha_1, 0) = f_x(f(x, \alpha_1, \alpha_2), \alpha_1, 0) f_x(x, \alpha_1, \alpha_2)$. Since $f_x(0,0,0) = -1$, we have that $\frac{\partial}{\partial x} f(0,0,0) = (-1)^2 = 1$.

Next, we show that

$$a = \frac{1}{2} \frac{\partial^2}{\partial x^2} f(f(x, \alpha_1, \alpha_2), \alpha_1, 0)|_{(0,0,0)} = 0.$$

$$\begin{aligned} \frac{\partial^2}{\partial x^2} f(f(x, \alpha_1, \alpha_2), \alpha_1, 0) = {} & f_{xx}(f(x, \alpha_1, \alpha_2), \alpha_1, 0)(f_x(x, \alpha_1, \alpha_2))^2 \\ & + f_x(f(x, \alpha_1, \alpha_2), \alpha_1, 0) f_{xx}(x, \alpha_1, \alpha_2) \end{aligned}$$

and

$$\begin{aligned} \frac{\partial^2}{\partial x^2} f(f(0,0,0), 0, 0)) = {} & f_{xx}(f(0,0,0), 0, 0)(f_x(0,0,0))^2 \\ & + f_x(f(0,0,0), 0, 0) f_{xx}(0,0,0) = (-1)^2 f_{xx}(0,0,0) \\ & + (-1) f_{xx}(0,0,0) = 0. \end{aligned}$$

Now, we show that

$$\frac{\partial^3}{\partial x^3} f(f(x,\alpha_1,\alpha_2),\alpha_1,0)|_{(0,0,0)} \neq 0.$$

$$\begin{aligned}
\frac{\partial^3}{\partial x^3} f(f(x,\alpha_1,\alpha_2),\alpha_1,0) &= \frac{\partial}{\partial x}(f_{xx}(f(x,\alpha_1,\alpha_2),\alpha_1,0)(f_x(x,\alpha_1,\alpha_2))^2 \\
&\quad + f_x(f(x,\alpha_1,\alpha_2),\alpha_1,0)(f_{xx}(x,\alpha_1,\alpha_2)) \\
&= f_{xxx}(f(x,\alpha_1,\alpha_2),\alpha_1,0)(f_x(x,\alpha_1,\alpha_2))^3 \\
&\quad + 2f_{xx}(f(x,\alpha_1,\alpha_2),\alpha_1,0)f_{xx}(x,\alpha_1,\alpha_2)f_x(x,\alpha_1,\alpha_2) \\
&\quad + f_{xx}(f(x,\alpha_1,\alpha_2),\alpha_1,0)f_x(x,\alpha_1,\alpha_2)f_{xx}(x,\alpha_1,\alpha_2) \\
&\quad + f_x(f(x,\alpha_1,\alpha_2),\alpha_1,0)f_{xxx}(x,\alpha_1,\alpha_2).
\end{aligned}$$

Hence,

$$\begin{aligned}
\frac{\partial^3}{\partial x^3} f(0,0,0) &= (-1)^3 f_{xxx}(0,0,0) + (-1)f_{xxx}(0,0,0) + 3(f_{xx}(0,0,0))^2(-1) \\
&= -2f_{xxx}(0,0,0) - 3(f_{xx}(0,0,0))^2 \neq 0.
\end{aligned}$$

Finally, we show that,

$$\begin{aligned}
&\left(\frac{\partial}{\partial \alpha_1} f(f(x,\alpha_1,\alpha_2),\alpha_1,0)\frac{\partial}{\partial x\alpha_2} f(f(x,\alpha_1,\alpha_2),\alpha_1,0)\right. \\
&\qquad \left. - \frac{\partial}{\partial \alpha_2} f(f(x,\alpha_1,\alpha_2),\alpha_1,0)\frac{\partial}{\partial x\alpha_1} f(f(x,\alpha_1,\alpha_2),\alpha_1,0)\right)|_{(0,0,0)} \neq 0.
\end{aligned}$$

$$\frac{\partial}{\partial \alpha_1} f(f(x,\alpha_1,\alpha_2),\alpha_1,0) = f_x(f(x,\alpha_1,\alpha_2),\alpha_1,0)f_{\alpha_1}(x,\alpha_1,\alpha_2) + f_{\alpha_1}(f(x,\alpha_1,\alpha_2),\alpha_1,0),$$

and $$\frac{\partial}{\partial \alpha_1} f(f(0,0,0),0,0) = f_x(f(0,0,0),0,0)f_{\alpha_1}(0,0,0) + f_{\alpha_1}(f(0,0,0),0,0) = 0.$$

$$\frac{\partial}{\partial \alpha_2} f(f(x,\alpha_1,\alpha_2),\alpha_1,0) = f_x(f(x,\alpha_1,\alpha_2),\alpha_1,0)f_{\alpha 2}(x,\alpha_1,\alpha_2),$$

and $$\frac{\partial}{\partial \alpha_2} f(f(0,0,0),0,0) = f_x(f(0,0,0),0,0)f_{\alpha_2}(0,0,0) = -f_{\alpha_2}(f(0,0,0),0,0)$$

$$\begin{aligned}
\frac{\partial^2}{\partial x \partial \alpha_1} f(f(x,\alpha_1,\alpha_2),\alpha_1,0) &= \frac{\partial}{\partial x}(f_x(f(x,\alpha_1,\alpha_2),\alpha_1,0)f_{\alpha_1}(x,\alpha_1,\alpha_2) \\
&\quad + f_{\alpha_1}(f(x,\alpha_1,\alpha_2),\alpha_1,0)) \\
&= f_{xx}(f(x,\alpha_1,\alpha_2),\alpha_1,0)(f_x(x,\alpha_1,\alpha_2)f_{\alpha_1}(x,\alpha_1,\alpha_2) \\
&\quad + f_x(f(x,\alpha_1,\alpha_2),\alpha_1,0)f_{x\alpha_1}(x,\alpha_1,\alpha_2) \\
&\quad + f_{x\alpha_1}(f(x,\alpha_1,\alpha_2),\alpha_1,0)f_x(x,\alpha_1,\alpha_2).
\end{aligned}$$

$$\frac{\partial^2}{\partial x \partial \alpha_1} f(f(0,0,0),0,0) = -f_{xx}(f(0,0,0),0,0) f_{\alpha_1}(0,0,0) - 2f_{x\alpha_1}(0,0,0).$$

$$\text{At } (0,0,0), f_{\alpha_1} f_{x\alpha_2} - f_{\alpha_3}, f_{x\alpha_1} = (f_{xx}(f(0,0,0),0,0) f_{\alpha_1}(f(0,0,0),0,0) + 2f_{x\alpha_1}(f(0,0,0),0,0)) f_{\alpha_2}(f(0,0,0),0,0)) \neq 0.$$

Thus, all of the conditions for the Cusp Bifurcation are satisfied.

Theorem 9 and the Cusp Bifurcation Theorem establish that $f(f(x,\alpha_1,\alpha_2),\alpha_1,0)$ contains a one parameter family of maps going through $f^2(x,0,0)$ that undergoes a pitchfork bifurcation. This observation leads to the following result.

THEOREM 10 *Let* $f(\alpha,x)$ *be a one-parameter family of maps on R which undergoes a period-doubling bifurcation at* (α_0,x_0). *Let* $\{f_0,f_1,\ldots,f_{T-1}\}$ *be a collection of one-parameter family of maps on R close f. Then each of the T cyclic compostions,* $\{f_{T-1}\circ\ldots\circ f_1\circ f_0, f_0\circ f_{T-1}\circ\ldots\circ f_2\circ f_1,\ldots, f_{T-2}\circ\ldots\circ f_0\circ f_{T-1}\}$, *are generic perturbations of* f^T. *When T is even, each of the T cyclic compositions undergo tangent bifurcations* (see figure 1).

By Corollary 5, each of the *T* cyclic compositions have the same number of periodic points. Hence, the tangent bifurcations of the *T cyclic* compositions, predicted by Theorem 10, occur at the same bifurcation parameter. For the *T-periodic* dynamical system this means that after the bifurcation, we have two stable coexisting cycles (multiple attractors). In the next section, we use a specific example to illustrate this bifurcation in a 2-*periodic* dynamical system.

5. Multiple attractors: 2-*Periodic* Ricker's Model

Single species autonomous parametric models such as the classic Ricker and Beverton-Holt models do not support multiple attractors. However, *T-periodic* dynamical systems such as

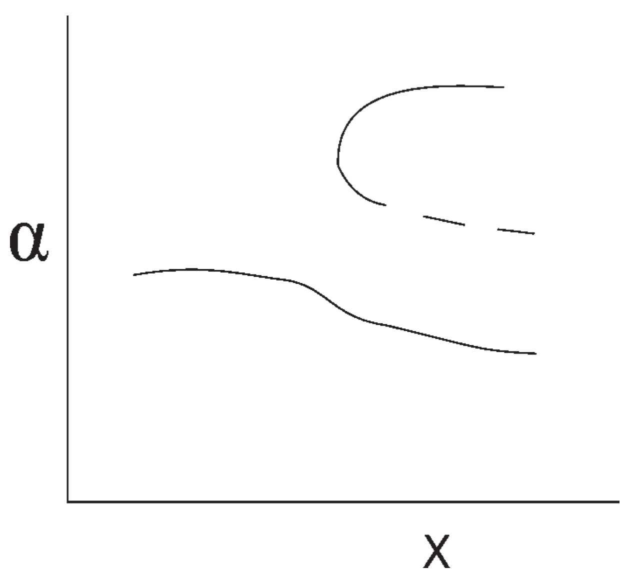

Figure 1. Tangent bifurcation in a perturbation of a pitchfork bifurcation.

the nonautonomous Ricker model are capable of supporting multiple attractors. To construct a 2-*periodic* dynamical system based on the classic Ricker model we let

$$g(t, x_t) = \exp(r + \alpha(-1)^t - x_t)$$

where r, $\alpha > 0$ and $r - \alpha > 0$. Then Model (2) becomes

$$x_{t+1} = x_t \exp(r + \alpha(-1)^t - x_t). \tag{7}$$

Since $g(t+2, x_t) = g(t, x_t)$ and $g(t+1, x_t) \neq g(t, x_t)$, Equation (7) is a 2-*periodic* single species model with corresponding 2-*periodic* dynamical system $\{f_0, f_1, \ldots, f_t, \ldots\}$ where $f_0(x) = x \exp(r + \alpha - x)$ and $f_1(x) = x \exp(r - \alpha - x)$. The maps f_0 and f_1 are the Ricker models, where $X_{0\infty} = r + \alpha$ and $X_{1\infty} = r - \alpha$. When $\alpha = 0, f_0 = f_1$ and Equation (7) is the classic Ricker equation (see figure 2(a)). However, when $\alpha > 0$ then f_0 and f_1 have unique positive fixed points that are not equal, and the 2-*periodic* dynamical system $\{f_0, f_1, \ldots, f_t, \ldots\}$ has no positive fixed points (Lemma 1). In this case, Equation (7) is Ricker's model with a cyclically varying intrinsic growth rate. figure 2(b) shows that, as in the autonomous Ricker equation, increasing values of r force period doubling bifurcations route to chaos in Equation (7), where α is kept fixed at $\alpha = 0.01$.

Figure 2(b) starts with a stable 2-*cycle* rather than a fixed point. At $r = 2$, the fixed point of the autonomous Ricker model undergoes a period doubling bifurcation and a stable 2-*cycle* is born.

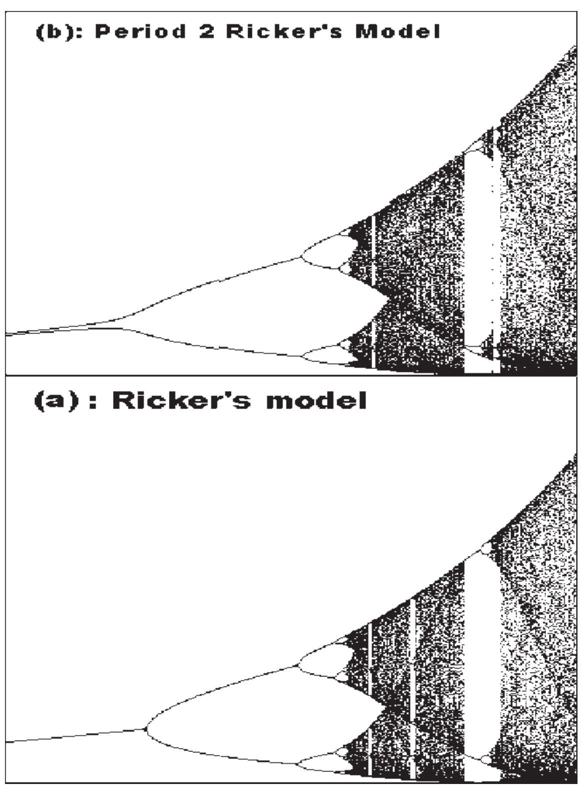

Figure 2. Period Doubling Bifurcations. In (a), $\alpha = 0.01$. On the horizontal axis, $1.5 < r < 3.5$ and on the vertical axis, $0 < y < 15$.

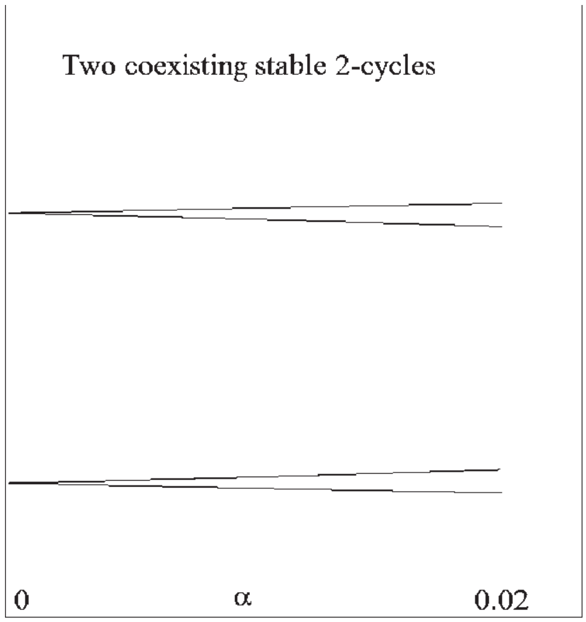

Figure 3. The inner two curves form one 2-cycle and the outer two curves form the other 2-cycle. On the horizontal axis, $0 < \alpha < 0.2$ where $r = 2.2$.

If $r > 2$, as α is increased from *zero* the stable 2-*cycle* generates two coexisting stable 2-*cycles*. Figure 3 displays the coexisting two stable 2-*cycles* when $r = 2.2$ (multiple attractors). These two 2-*cycles* are predicted in perturbation theorems of Henson [19], Franke and Selgrade [10].

When α is fixed at 0.01 while r is increased from 1.8 to 2.3 an interesting bifurcation occurs not at $r = 2$ but near $r = 2.077$. Both $f_1 \circ f_0(x) = x \exp(2r - x - x \exp(r + \alpha - x))$ and $f_0 \circ f_1(x) = x \exp(2r - x - x \exp(r - \alpha - x))$ undergo a tangent bifurcation as predicted by Theorem 10 and figure 4. A new stable fixed point and an unstable fixed point are produced for a total of three fixed points. These give the 2-*periodic* dynamical system two new 2-*cycles* (one stable and one unstable) coexisting with the original stable 2-*cycle*. The creation of the unstable 2-*cycle* through tangent bifurcation has not been predicted

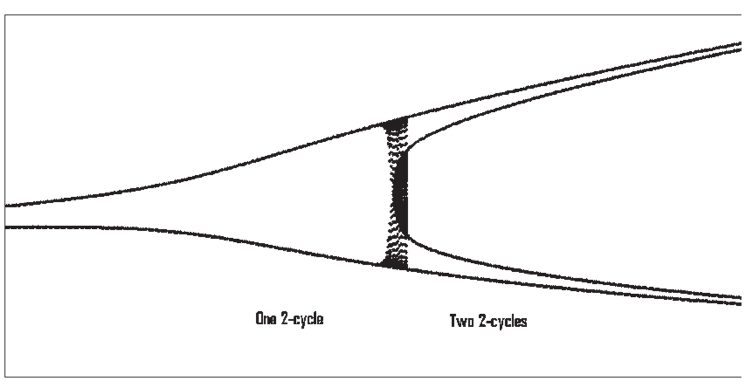

Figure 4. Two 2-cycle attractors in Equation 2 (Multiple attractors), where on the horizontal axis $1.8 \leq r \leq 2.3$ and on the vertical axis $0 \leq y \leq 4$.

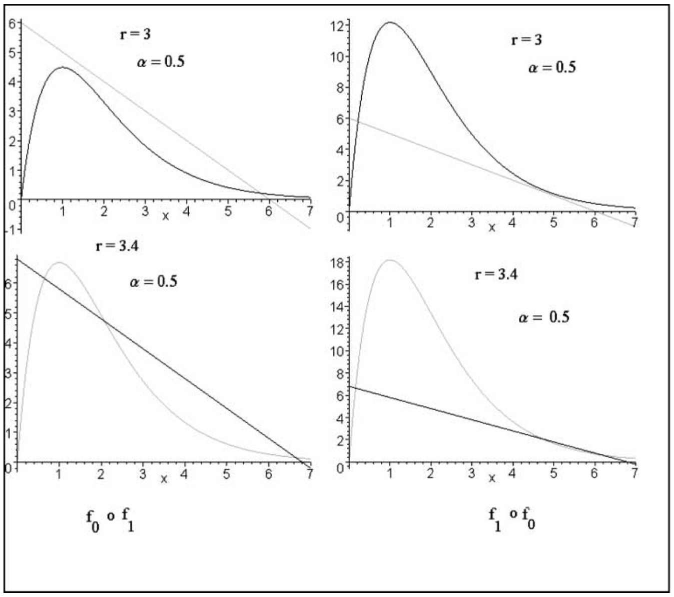

Figure 5. Tangent bifurcation in both $f_1 \circ f_0$ and $f_0 \circ f_1$.

by the results of Henson [19], Franke and Selgrade [10]. It is also interesting to note that f_0 and f_1 by themselves go through period doubling bifurcations before the 2-*periodic* dynamical system goes through the tangent bifurcation.

LEMMA 11 *With r and α positive $f_1 \circ f_0$ and $f_0 \circ f_1$ have the same number of positive fixed points which is either* 1,2*, or* 3.

Proof By Theorem 2, $f_1 \circ f_0$ and $f_0 \circ f_1$ have the same number of fixed points.

The positive fixed points of $f_1 \circ f_0$ and $f_0 \circ f_1$ are the points of intersection of the straight line $y = 2r - x$ and the Ricker curves $y = x\exp(r + \alpha - x)$ and $y = x\exp(r - \alpha - x)$, respectively. It is easy to see that the number of intersections is either 1,2 or 3 (see figure 5).

6. Conclusion

This paper focuses on the mathematical and biological mechanisms for generating multiple attractors in periodically forced (nonautonomous) single species population models. Henson [19], Franke and Selgrade [10] have shown that nonautonomous discrete-time models are capable of supporting multiple attractors where the corresponding autonomous models support single attractors. We prove that in periodically forced environments, it is possible to generate multiple attractors via tangent bifurcation.

In [7,8], Elaydi and Sacker showed that periodically forced discrete-time models support single attractors via globally stable periodic solutions. We demonstrate that, when conditions for the Cusp Bifurcation Theorem are satisfied such nonautonomous population models generate multiple attractors; and the ultimate life-history outcome depends on initial population densities.

Asymptotic dynamics of systems that support multiple attractors are usually extremely complicated. The degree of complexity is a function of the structure of the coexisting attractors and the topology of the basins of attraction. Rigorous studies of the basins of attraction of multiple attractors and basin boundaries in periodically forced discrete-time systems is an open question [1,35].

References

[1] Alexander, J.C., Yorke, J.A., You, Z. and Kan, I., 1992, Riddled Basins, *International Journal of Bifurcation and Chaos*, **2**(4), 795–813.

[2] Begon, M., Harper, J.L. and Townsend, C.R., 1996, *Ecology: Individuals, Populations and Communities* (Blackwell Science Ltd).

[3] Brauer, F. and Castillo-Chavez, C., 2001, Mathematical models in population biology and epidemiology. *Texts in Applied Mathematics*, Vol. 40 (New York: Springer Verlag).

[4] Costantino, R.F., Cushing, J.M., Dennis, B. and Desharnais, R.A., 1998, Resonant popopulation cycles in temporarily fluctuating habitats, *Bulletin of Mathematical Biology*, **60**, 247–273.

[5] Cushing, J.M., 1977, Periodic time-dependent predator-prey systems, *SIAM Journal of Applied Mathematics*, **32**, 82–95.

[6] Elaydi, S.N., 2000, *Discrete Chaos* (Boca Raton, FL: Chapman & Hall/CRC).

[7] Elaydi, S.N. and Sacker, R.J., Global stability of periodic orbits of nonautonomous difference equations and population biology, *Journal of Differential Equations* (in press).

[8] Elaydi, S.N. and Sacker, R.J., Global stability of periodic orbits of nonautonomous difference equations in population biology and Cushing-Henson conjectures, *Journal of Differential Equations* (in press).

[9] Elaydi, S.N. and Yakubu, A.-A., 2002, Global stability of cycles: Lotka-Volterra competition model with stocking, *Journal of Difference Equations and Applications*, **8**(6), 537–549.

[10] Franke, J.E. and Selgrade, J.F., 2003, Attractor for Periodic Dynamical Systems, *Journal of Mathematical Analysis and Applications*, **286**, 64–79.

[11] Franke, J.E. and Yakubu, A.-A., 1996, Extinction and persistence of species in discrete competitive systems with a safe refuge, *Journal of Mathematical Analysis and Applications*, **23**, 746–761.

[12] Franke, J.E. and Yakubu, A.-A., 1992, Geometry of exclusion principles in discrete systems, *Journal of Mathematical Analysis and Applications*, **168**, 385–400.

[13] Franke, J.E. and Yakubu, A.-A., 1991, Mutual exclusion versus coexistence for discrete competitive systems, *Journal of Mathematical Biology*, **30**, 161–168.

[14] Guémez, J. and Matías, M.A., 1993, Control of chaos in unidimensional maps, *Physics Letters A*, **181**, 29–32.

[15] Hanski, I., 1991, Single-species metapopulation dynamics-concepts, models and observations, *Biological Journal of Linnean Society*, **42**, 17–38.

[16] Hanski, I.A. and Gilpin, M.E., 1997, *Metapopulation Biology: Ecology, Genetics, and Evolution* (San Diego, California: Academic Press Ltd).

[17] Hassell, M.P., 1976, The dynamics of competition and predation. *Studies in Biol*, Vol. 72 (The Camelot Press Ltd).

[18] Hassell, M.P., Lawton, J.H. and May, R.M., 1976, Patterns of dynamical behavior in single species populations, *Journal of Animal Ecology*, **45**, 471–486.

[19] Henson, S.M., 2000, Multiple attractors and resonance in periodically forced population models, *Physica D*, **140**, 33–49.

[20] Henson, S.M., Costantino, R.F., Cushing, J.M., Dennis, B. and Desharnais, R.A., 1999, Multiple attractors, saddles, and population dynamics in periodic habitats, *Bulletin of Mathematical Biology*, **61**, 1121–1149.

[21] S.M. Henson, R.F. Costantino, R.A. Desharnais, J.M. Cushing, B. Dennis, Basins of attraction: population dynamics with two stable 4-cycles (Preprint)

[22] Henson, S.M. and Cushing, J.M., 1996, Hierarchical models of intraspecific competition: scramble versus contest, *Journal of Mathematical Biology*, **34**, 755–772.

[23] Henson, S.M. and Cushing, J.M., 1997, The effect of periodic habitat fluctuations on a nonlinear insect population model, *Journal of Mathematical Biology*, **36**, 201–226.

[24] Jillson, D., 1980, Insect populations respond to fluctuating environments, *Nature*, **288**, 699–700.

[25] Kocic, V.L. and Ladas, G., 1993, *Global Behavior of Nonlinear Difference Equations of Higher Order with Applications* (Boston: Kluwer Academic).

[26] Kuznetsov, Y.A., 1995, *Elements of Applied Bifurcation Theory* (Springer-Verlag).

[27] Li, J., 1992, Periodic solutions of population models in a periodically fluctuating environment, *Mathematical Biosciences*, **110**, 17–25.

[28] May, R.M. and Oster, G.F., 1976, Bifurcations and dynamic complexity in simple ecological models, *American Naturalist*, **110**, 573–579.

[29] May, R.M., 1977, Simple mathematical models with very complicated dynamics, *Nature*, **261**, 459–469.

[30] May, R.M., 1974, *Stability and Complexity in Model Ecosystems* (Princeton University Press).

[31] May, R.M., Hassell, M.P., Anderson, R.M. and Tonkyn, D.W., 1981, Density dependence in host-parasitoid models, *Journal of Animal Ecology*, **50**, 855–865.

[32] Maynard Smith, J. and Slatkin, M., 1973, The stability of predator-prey systems, *Ecology*, **54**, 384–391.

[33] Milton, J.G. and Bélair, J., 1990, Chaos, noise, and extinction in models of population growth, *Theoretical Population Biology*, **37**, 273–290.
[34] Nicholson, A.J., 1954, Compensatory reactions of populations to stresses, and their evolutionary significance, *Australian Journal of Zoology*, **2**, 1–65.
[35] Nusse, H.E. and Yorke, J.A., 1997, *Dynamics: Numerical Explorations* (New York: Springer-Verlag).
[36] Ricker, W.E., 1954, Stock and recruitment, *Journal of Fisheries Research Board of Canada*, **II**(5), 559–623.
[37] Selgrade, J.F. and Roberds, H.D., 2001, On the structure of attractors for discrete, periodically forced systems with applications to population models, *Physica D*, **158**, 69–82.
[38] Yakubu, A.-A., 2003, Multiple attractors in juvenile-adult single species models, *Journal of Difference Equations and Appllications*, **9**(12), 1083–1093.
[39] Yodzis, P., 1989, *Introduction to Theoretical Ecology* (New York: Harper & Row, Publishers).