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Physica D 15X (2001) 69–82

PHYSICA D

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On the structure of attractors for discrete, periodically forced systems with applications to population models

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Received 10 January 2001 ; received in revised form 27 May 2001 ; accepted 2 July 2001
Communicated by J.P. Keener

Abstract

This work discusses the effects of periodic forcing on attracting cycles and more complicated attractors for autonomous systems of nonlinear difference equations. Results indicate that an attractor for a periodically forced dynamical system may inherit structure from an attractor of the autonomous (unforced) system and also from the periodicity of the forcing. In particular, a method is presented which shows that if the amplitude of the k-periodic forcing is small enough then the attractor for the forced system is the union of k homeomorphic subsets. Examples from population biology and genetics indicate that each subset is also homeomorphic to the attractor of the original autonomous dynamical system. © 2001 Elsevier Science B.V. All rights reserved.

PACS: 89.60.+x; 02.40.Vh

Keywords: Periodic forcing; Attractors; Discrete population models

1. Introduction

The effects of periodic variations in system inputs and parameters on the behavior of both continuous and discrete dynamical systems have been widely studied since the work of Cartwright and Littlewood [1] in 1945 on the forced van der Pol equation. During the last 2.5 years, Cushing [2,3], Mackey and Glass [4], Inoue and Kamifukumoto [5], Schaffer [6], Kot et al. [7], Rinaldi et al. [8], Buchanan and Selgrade [9], Costantino et al. [10], King and Schaffer [11], Henson [12], Henson et al. [13] and others have investigated new behaviors that result when periodic forcing is introduced into biological models. Periodic fluctuations may occur in parameters intrinsic to an ecosystem such as intraspecific and interspecific interaction parameters or birth, growth and death rates. On the other hand, periodic variations may also appear in extrinsic parameters such as stocking and harvesting or migration effects. In both instances, these periodic changes may be due to environmental factors such as seasons, climate and food supply or due to the seasonal nature of stocking and harvesting.

Periodic forcing has been used to control chaotic behavior. Güémez and Matías [14] illustrated how a state-dependent stocking or harvesting may be used to produce stable periodic oscillation in population size for models

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Research supported by the USDA Forest Service, Southern Research Station, Southern Institute of Forest Genetics, Saucier, MS, USA

PII: S0167-2789(01)00324-4

with logistic and exponential maps, which produce chaotic regimes without forcing. In their examples, the period of the resulting attracting cycle was a multiple of the period of the forcing. Alternatively, Ott et al. [15] controlled chaos by periodically perturbing intrinsic system parameters. Both approaches were discussed in Solé et al. [16], who also considered the complication of noise in the system.

In laboratory experiments, Jillson [17] effectively forced a flour beetle (*Tribolium*) population by alternating food supply between high and low amounts in a 2-periodic fashion. He noticed that beetle population size cycled with period 2 and that the average population size was greater than the size attained by a population given a constant amount of food equal to the average of the 2-periodic food amounts. Henson and Cushing [18], Costantino et al. [10] and Henson et al. [19] explained this phenomenon both mathematically and biologically by showing that two different 2-cycles occurred in the population sizes. One cycle (referred to as *resonant*) had an average population size larger than the population given a constant food supply, corresponding to Jillson's observations, while the other cycle (called *attenuant*) had a smaller average population size. Both 2-cycles were observed in controlled laboratory experiments. Recently, Henson et al. [13] have illustrated the simultaneous occurrence of locally stable 4-cycles in beetle populations and investigated the dual role of determinism and stochasticity in asymptotic approach to these cycles. From a mathematical point of view, the 2-cycles and 4-cycles are attractors in a discrete, nonautonomous dynamical system.

Here, we study small amplitude periodic forcing of discrete dynamical systems. We show that the attractor for a periodically forced system inherits structure from the attractor of the original autonomous dynamical system and also from the periodicity of the forcing. Because the forcing is periodic, we view the nonautonomous system as a composition of a finite number of autonomous maps which allows us to study how attractors of the autonomous system are changed by small amplitude forcing. Using this approach, we extend the work of Henson [12] which described how small amplitude forcing affects attracting periodic orbits of the autonomous system. Henson [12] showed that if the forcing is k-periodic then a hyperbolic attracting fixed point of the autonomous system continues to an attracting k-cycle of the nonautonomous system and, furthermore, if m divides k then a hyperbolic attracting m-cycle for the autonomous system produces m attracting k-cycles for the nonautonomous system. If the attractor for the autonomous system is more complicated than a cycle, we conjecture that the nonautonomous attractor consists of k subsets each homeomorphic to the autonomous attractor. Although, we do not establish this rigorously, we do prove that sequences of k maps which define the nonautonomous system are locally conjugate if the autonomous map is a diffeomorphism in a neighborhood of the attractor of the autonomous system. Thus, we show that the attractor for the nonautonomous system is the union of k homeomorphic subsets. In the examples we present, these subsets are also all homeomorphic to the attractor of the autonomous system.

Section 2 introduces a model from population genetics which motivates our study. Section 3 discusses the general framework of our approach and examples of the continuation and bifurcation of attracting periodic orbits under k-periodic forcing. Section 4 presents a method for studying the continuation of more general attractors. This method is applied to a prey-predator system in Section 5, where the attractor for the autonomous system is an invariant loop. We prove that the autonomous map is a diffeomorphism in a neighborhood of this loop and show that its continuation under small amplitude 2-periodic forcing is the union of two homeomorphic loops which are mapped back and forth by the nonautonomous system. Section 6 discusses an example of 5-periodic forcing in a population interaction model, where the attractor is the union of five loops.

2. An example of 2-periodic forcing from population genetics

In order to motivate our discussion of how periodic forcing affects the structure of a nonperiodic attractor of an autonomous system, we introduce a model from ecological genetics that accounts for the effects of selection and migration on the allele frequency and the population density of a single population (see [20,21]). Let x denote population size or density of a diploid population with two alleles, A and a, at an autosomal locus and let p denote the frequency of the A allele prior to selection, where $0 \leq p \leq 1$. Hence, the population consists of individuals having one of the three genotypes, AA, Aa, or aa. The genotypes have nonnegative per capita growth rate functions (fitnesses), f_{AA}, f_{Aa}, and f_{aa}, which represent the pressures of natural selection and which are decreasing functions of x. Allele fitnesses f_A and f_a are defined by $f_A \equiv pf_{AA} + (1-p)f_{Aa}$ and $f_a \equiv pf_{Aa} + (1-p)f_{aa}$. Accordingly, the population mean fitness f is given by $f \equiv pf_A + (1-p)f_a$. Assuming random mating, the following system of difference equations describes the changes in allele frequency and population size that take place from generation $n-1$ to generation n for $n = 1, 2, \ldots$,

$$p_n = \frac{p_{n-1} f_A(p_{n-1}, x_{n-1})}{f(p_{n-1}, x_{n-1})}, \qquad x_n = x_{n-1} f(p_{n-1}, x_{n-1}). \tag{2.1}$$

This model is of "gene-pool" type (see [22]) and does not contain the details associated with specific, realistic populations. However, the value of such models has been aptly summarized by Crow [22], who states "The gene-pool model is a wonderful, simplifying convention. . . Often it is such a simplified view that provides the most useful insights into evolutionary processes."

To include immigration, let a number of individuals proportional to x migrate into this population from a nearby population or collection of populations in each generation. We study immigration of period 2 by taking this constant of proportionality to be given by $h(1+\alpha(-1)^n)$, where $h > 0$, $0 \leq \alpha < 1$, and n is a positive integer. When n is even, the immigration term is $h(1+\alpha)x$ and, when n is odd, the immigration term is $h(1-\alpha)x$. Thus αh measures the variation in migration from an average rate of h. Following immigration, random mating is assumed to take place yielding Hardy-Weinberg proportions in the population of zygotes that form the next generation. In the population of migrants, let the allele frequency for A be constant and given by q, where $0 < q < 1$. Then counting alleles and numbers of individuals, Roberds et al. [20,21] obtained the following system:

$$p_n = \frac{p_{n-1} f_A + qh(1+\alpha(-1)^n)}{f + h(1+\alpha(-1)^n)}, \qquad x_n = x_{n-1}[f + h(1+\alpha(-1)^n)]. \tag{2.2}$$

The dynamical behavior of (2.2) is determined by repeated composition of two maps corresponding to even and odd values of n.

Fix the allele frequency in the immigrating population at $q = 0.95$ and consider exponential allele fitnesses of the form

$$f_{AA}(x) = \mathrm{e}^{1-0.15x} \qquad f_{Aa}(x) = \mathrm{e}^{0.5-x} \qquad f_{aa}(x) = \mathrm{e}^{3-0.3x}. \tag{2.3}$$

The aa genotype's fitness is large when x is small and decreases rapidly as x increases. This produces unstable equilibria for small p and h and $\alpha = 0$, see [20]. In fact, without immigration ($h = 0$), the line $\{p = 0\}$ is invariant and the dynamical behavior of (2.1) on this line is given by iterating a one-hump map which is chaotic on an attracting interval. If immigration is introduced ($h > 0$), the line $\{p = 0\}$ loses its invariance, and the attractor bifurcates into the region where $p > 0$ and forms a fish-hook (see Fig. 1) by spreading apart the fold which occurs at the maximum of the one-hump map. This fish-hook is a chaotic attractor and is the unstable manifold of the saddle point $(p, x) \approx (0.029, 9.907)$, indicated by $\triangle$ in Fig. 1. The existence of the fish-hook indicates that immigration is a source of genetic variation, i.e., in this case dynamical behavior on an attractor where both alleles are present and where the allele frequency and population density vary in an apparently random fashion.

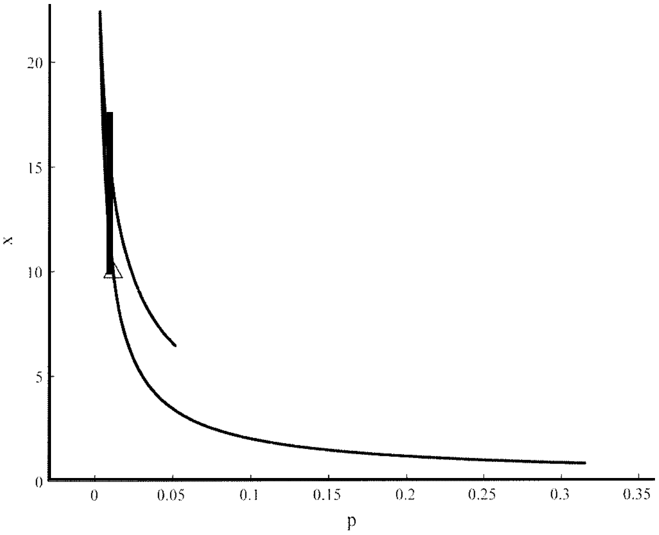

Fig. 1. Fish-hook attractor for (2.2) and (2.3) with $h = 0.012$ and $\alpha = 0$.

When $\alpha > 0$, the 2-periodic forcing results in an attractor which is the union of two fish-hooks, see Fig. 2, which are mapped back and forth sequentially. Even iterates map one fish-hook to itself and odd iterates map the other fish-hook to itself. Except for the tip of its spike, the fish-hook formed by odd iterates is narrower and lies inside the fish-hook formed by even iterates. The spike of the odd fish-hook extends above the spike of the even fish-hook. When $\alpha > 0$, the even and odd fish-hooks appear homeomorphic to each other and to the fish-hook attractor when $\alpha = 0$. Careful comparison of Figs. 1 and 2 indicates that the even fish-hook is a bit broader and the odd fish-hook a bit narrower than the fish-hook when $\alpha = 0$.

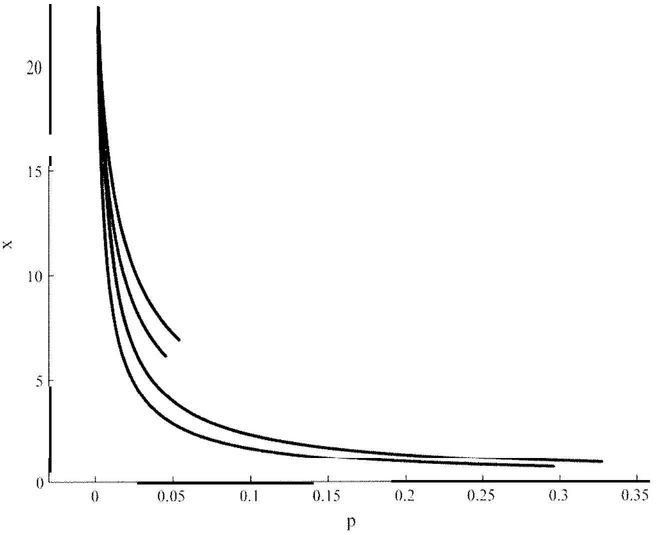

Fig. 2. Double fish-hook attractor for (2.2) with $h = 0.012$ and $\alpha = 0.2$.

3. General framework

The nonautonomous system of difference equations may be written as

$$z_n = f(\alpha, z_{n-1}, \mathrm{n}) \quad \text{for } n = 1, 2, \ldots , \tag{3.1}$$

where $z_n \in \mathbb{R}^l$, $f : \mathbb{R} \times \mathbb{R}^l \times \mathbb{Z} \to \mathbb{R}^l$, and α is a parameter which measures the amplitude of the periodic forcing. Since time-dependence occurs only in the forcing term, when $\alpha = 0$, we define the time-independent map from $\mathbb{R}^l$ to R’ by $F(z) = f(0, z, \mathrm{n})$. For example, inserting $\alpha = 0$ in (2.2), we obtain the autonomous system

$$p_n = \frac{p_{n-1} f_A + qh}{f + h}, \qquad x_n = x_{n-1}[f + \mathrm{hl}.$$

When the forcing has period 2, the iterations of system (3. 1) are the repeated compositions of precisely two maps, F_1 and F_2, applied in order. The map $F_1 : \mathbb{R}^l \to$ R’ is determined by odd values of n and the map $F_2 : \mathbb{R}^l \to \mathbb{R}^l$ is determined by even values of n. For the map in (2.2), the second component of F_1 is

$$x_{n-1}[f + h(1 - \alpha)],$$

and the second component of F_2 is

$$x_{n-1}[f + h(1 + \alpha)].$$

The forcing term oscillates with magnitude ***ah*** about an average of ***h*.** Each map depends on the parameter α which is indicated by the additional subscript α. Hence, $F_{1,\alpha}(z) \equiv f(\alpha, z, \mathbf{2n} - 1)$ and $F_{2,\alpha}(z) \equiv f$ (a, z, 2n) for all ***n*** and the even iterates of (3.1) are given by

$$z_{n+2} = F_{2,\alpha}(F_{1,\alpha}(z_n)) \quad \text{for } n = 0, 2, 4, \ldots$$

Notice that $F_{1,\alpha} = F_{2,\alpha} = \boldsymbol{F}$ if $\alpha = 0$.

In general, when the forcing has period ***k*,** the iterations of system (3.1) are the repeated compositions of precisely k maps, $F_{1,\alpha}, F_{2,\alpha}, \ldots, F_{k,\alpha}$, applied in order. Clearly, $F_{i,0} = \boldsymbol{F}$ for $i = 1, 2, \ldots, k$. The trajectory of a point z_0 under (3.1) is given by the n-fold composition of ***k*** maps, i.e.,

$$z_n = \underline{\cdots \circ F_{2,\alpha} \circ F_{1,\alpha} \circ F_{k,\alpha} \circ \ldots \circ F_{2,\alpha}} \circ F_{1,\alpha}(z_0).$$

Henson [12] investigated how a hyperbolic fixed point or m-cycle for the autonomous system perturbs under small amplitude, k-periodic forcing, using the implicit function theorem in a Hilbert space of periodic sequences. When $\alpha = 0$, the m-cycle $\{\bar{z}_0, \bar{z}_1, \ldots, \bar{z}_{m-1}\}$ being hyperbolic means that the derivative of the ***m*-*fold*** composition of $\boldsymbol{F}$ at $\bar{z}_0$ has no eigenvalue on the unit circle and, hence, the derivative of the m-fold composition of $\boldsymbol{F}$ at each $\bar{z}_i$, $i = 0, 1, \ldots, m-1$, has no eigenvalue on the unit circle. Henson [12] showed that if ***m*** divides ***k*** then a hyperbolic, attracting m-cycle for the autonomous system continues to ***m*** attracting k-cycles for the nonautonomous system. These k-cycles may or may not be distinct.

By considering families of compositions, we extend Henson’s analysis to other bifurcations and more general attractors. For instance, when the forcing is k-periodic, consider the composition $G_\alpha \equiv F_{k,\alpha} \circ \cdots \circ F_{2,\alpha} \circ F_{1,\alpha}$. A fixed point of G_α corresponds to a k-cycle of the nonautonomous system (3.1). When $\alpha = 0$ and ***m*** divides ***k*,** a hyperbolic m-cycle for the autonomous system produces m hyperbolic fixed points of G_0. Since G_α is a C^1 perturbation of G_0 for small $\alpha > 0$, each of these fixed points continues to a hyperbolic fixed point of G_α and hence produces a k-cycle of (3.1). If a more complicated attractor has a uniform hyperbolic structure (see [23, p. 241]) then it would be preserved by C^1 perturbation. However, uniform hyperbolicity is very difficult to verify for complicated attractors and often attractors appearing in biological systems do not have such structure. For example, the fish-hook in Section 2 is not a normally contracting submanifold (see [23, p. 444]) nor does it have a uniform hyperbolic structure because of the contraction within the attractor near the spike. In the next section, we study properties of the nonautonomous attractor without making such strong assumptions about the autonomous attractor.

For (3.1) under 2-periodic forcing, the bifurcation from 2-cycle to 4-cycle as α varies corresponds to a period-doubling (flip) bifurcation for G,. More generally, under k-periodic forcing, the bifurcation from k-cycle to $2k$-cycle corresponds to a period-doubling bifurcation for G,. Let $\{\bar{z}_{0,\alpha_0}, \bar{z}_{1,\alpha_0}, . \;, \bar{z}_{k-1,\alpha_0}\}$ be a k-cycle for (3.1) when $\alpha = \alpha_0$. Hence $F_{i+1,\alpha_0}(\bar{z}_{i,\alpha_0}) = \bar{z}_{i+1,\alpha_0}$ for $i = 0, 1, . \;, k-2$ and $F_{k,\alpha_0}(\bar{z}_{k-1,\alpha_0}) = \bar{z}_{0,\alpha_0}$. A period-doubling bifurcation occurs at $\alpha = \alpha_0$ and $z = \bar{z}_{0,\alpha_0}$ only if $DG_{\alpha_0}(\bar{z}_{0,\alpha_0})$ has an eigenvalue of 1. We compute that

$$DG_{\alpha_0}(\bar{z}_{0,\alpha_0}) = DF_{k,\alpha_0}(\bar{z}_{k-1,\alpha_0})DF_{k-1,\alpha_0}(\bar{z}_{k-2,\alpha_0}) \cdots DF_{1,\alpha_0}(\bar{z}_{0,\alpha_0}). \tag{3.2}$$

Typically, when a period-doubling bifurcation occurs, a stable k-cycle loses stability and is replaced by a stable $2k$-cycle.

For the "gene-pool" model introduced in Section 2, we illustrate a cascade of period-doubling bifurcations as the 2-periodic forcing amplitude increases. When $\alpha = 0$ and $h = 0.09$, system (2.2) exhibits a hyperbolic saddle point at $\bar{z} = (0.0907, 9.6995)$ denoted by A in Fig. 3(a) and an attracting 2-cycle given by

$$\{\bar{z}_0 = (0.23235, 5.155), \bar{z}_1 = (0.0578, 13.826)\},$$

and denoted by + in Fig. 3(a).

As α increases from 0, the hyperbolic saddle $\bar{z}$ is replaced by a saddle 2-cycle consisting of the points ((0.11176, 9.0176), (0.08811, 10.5254)) for $\alpha = 0.1$ and depicted by △ in Fig. 3(b). The attracting 2-cycle $\{\bar{z}_0, \bar{z}_1\}$ is replaced by two attracting 2-cycles. For $\alpha = 0.1$, one 2-cycle is the set

$$\{\bar{z}_{0,0.1}, F_{1,0.1}(\bar{z}_{0,0.1})\} = \{(0.23686, 4.6977), (0.05667, 14.2699)\},$$

and represented by + in Fig. 3(b) and the other 2-cycle is the set

$$\{\bar{z}_{1,0.1}, F_{1,0.1}(\bar{z}_{1,0.1})\} = ((0.05785, 13.312), (0.2222, 5.7092)\},$$

denoted by x Note that the order of the points in these 2-cycles is important. For instance, the orbit of the second point in the 2-cycle denoted by ×, i.e., the orbit

$$((0.2222, 5.7092), F_{1,0.1}(0.2222, 5.7092), F_{2,0.1}(F_{1,0.1}(0.2222, 5.7092)), . \;. \},$$

approaches the 2-cycle denoted by +.

At $\alpha \approx 0.15$, the 2-cycle represented by + undergoes a period-doubling bifurcation resulting in an attracting 4-cycle. This attracting it-cycle is denoted by + in Fig. 3(c) when $\alpha = 0.2$. The attracting 2-cycle denoted by x in Fig. 3(b) continues as an attractor when $\alpha = 0.2$ and is denoted by x in Fig. 3(c). Also, the saddle 2-cycle persists as △ in Fig. 3(c), but notice that the two points on its orbit have spread apart. In fact, when a ≈ 0.228, the saddle 2-cycle (△) and the attracting 2-cycle (x) annihilate each other in a saddle-node bifurcation. When $\alpha \approx 0.333$, the attracting 4-cycle (+) undergoes period-doubling resulting in an attracting 8-cycle (+) pictured in Fig. 3(d). As α continues to increase, a period-doubling cascade ensues resulting in an attractor when $\alpha = 0.5$ consisting of two connected components pictured in Fig. 4.

This sequence of bifurcations illustrates how changes in the amplitude of the periodic immigration change the character of the genetic variation exhibited by the model. As the amplitude increases, the bistable periodic behavior in Fig. 3(b) is replaced by one attractor of higher period in Fig. 3(d) and finally by a chaotic attractor in Fig. 4. This

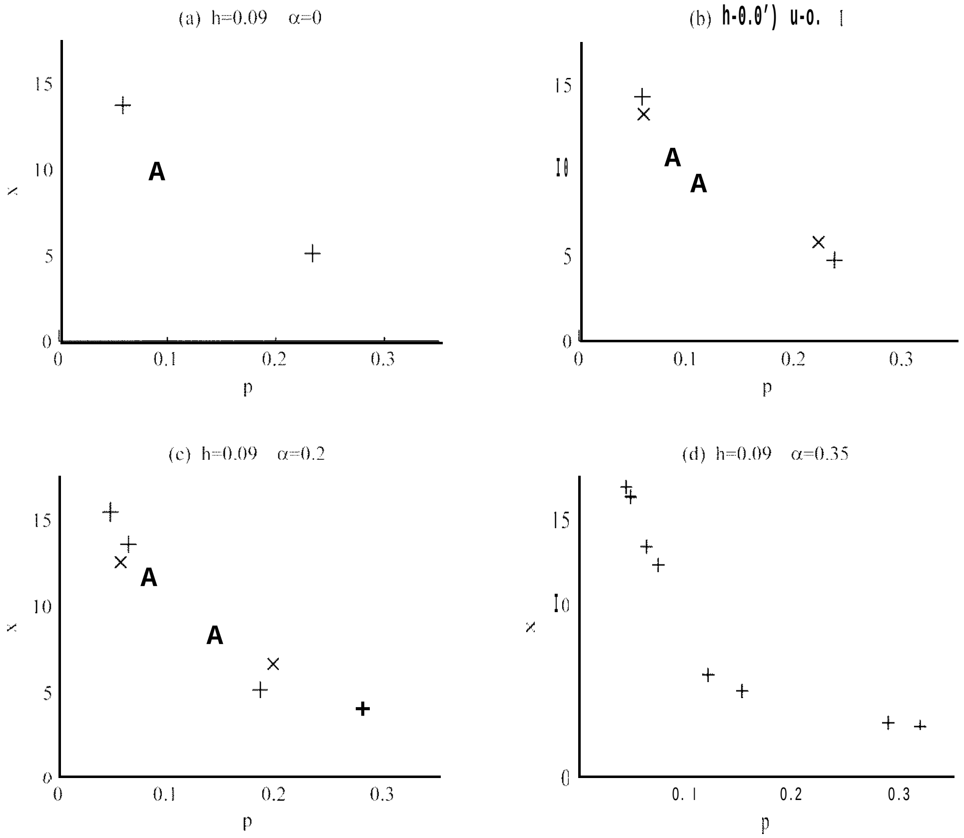

Fig. 3. Sequence of attractors as α increases: (+) a point on a stable 2-, 4-, or 8-cycle; (△) a saddle point or saddle 2-cycle; (×) a point on a stable 2-cycle.

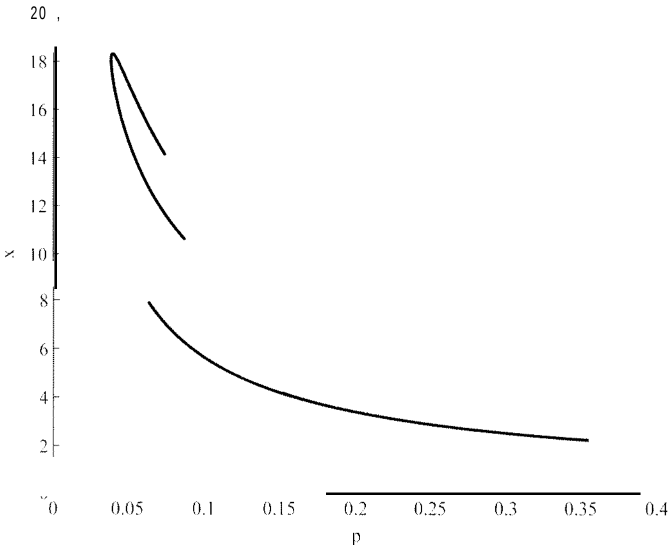

Fig. 3. Two component attractor for system (2.2) when $\alpha = 0.5$

chaotic attractor inherits its two component nature from the period of the immigration but it is not homeomorphic to the pair of fish-hooks in Fig. 2 which occurs at smaller immigration levels.

4. Continuation for more complicated attractors

Fig. 2 illustrates the continuation of a fish-hook, which is an attractor when $\alpha = 0$, under small amplitude forcing of period 2. The resulting attractor is the union of two fish-hooks and the dynamical system maps one fish-hook to the other sequentially. The fish-hooks appear homeomorphic to one another and homeomorphic to the original attracting fish-hook when $\alpha = 0$. Below, we demonstrate a method which shows that if the amplitude of the k-periodic forcing is small enough then the attractor is the union of ***k*** homeomorphic subsets.

For instance, when the forcing has period 2, orbits may be decomposed into odd and even iterates, see Fig. 2. This is accomplished by defining the two maps $G_{1,\alpha} \equiv F_{2,\alpha} \circ F_{1,\alpha}$ and $G_{2,\alpha} \equiv F_{1,\alpha} \circ F_{2,\alpha}$. For $n \geq 1$, the points $G^n_{1,\alpha}(z_0)$ are the even iterates of the orbit of z_0 under (3.1) and the points $G^n_{2,\alpha}(F_{1,\alpha}(z_0))$ are the odd iterates of the orbit of z_0. Clearly, $F_{1,\alpha} \circ G_{1,\alpha} = G_{2,\alpha} \circ F_{1,\alpha}$ and $F_{1,\alpha} \circ G^n_{1,\alpha} = G^n_{2,\alpha} \circ F_{1,\alpha}$ for all $n \geq 1$. $F_{1,\alpha}$ is called a semiconjugacy and it takes orbits of $G_{1,\alpha}$ to orbits of $G_{2,\alpha}$. Similarly, $F_{2,\alpha} \circ G_{2,\alpha} = G_{1,\alpha} \circ F_{2,\alpha}$ and $F_{2,\alpha}$ ***o*** $G^n_{2,\alpha} = G^n_{1,\alpha} \circ F_{2,\alpha}$, ***so*** $F_{2,\alpha}$ is also a semiconjugacy. Since $G_{1,\alpha}$ and $G_{2,\alpha}$ are autonomous dynamical systems, the semiconjugacies $F_{1,\alpha}$ and $F_{2,\alpha}$ indicate that the dynamical behavior of each system is quite similar. For example, periodic orbits of $G_{1,\alpha}$ correspond to periodic orbits of $G_{2,\alpha}$ and convergent orbits of $G_{1,\alpha}$ correspond to convergent orbits of $G_{2,\alpha}$. If $F_{1,\alpha}$ has an inverse then $G^n_{2,\alpha} = F_{1,\alpha} \circ G^n_{1,\alpha} \circ F^{-1}_{1,\alpha}$ and, hence, $G_{1,\alpha}$ and $G_{2,\alpha}$ are conjugate dynamical systems, i.e., their dynamical behavior is essentially’ the same (see [23, p. 40]). For instance, if ***A,*** is an attractor for $G_{1,\alpha}$ then $F_{1,\alpha}$ ***(A,)*** is an attractor for $G_{2,\alpha}$ which is homeomorphic to ***A,.***

If α is small then $F_{1,\alpha}$ is a C^1 perturbation of ***F,*** the autonomous dynamical system for $\alpha = 0$. If ***F*** is a diffeomorphism in a neighborhood of the attractor A_0 then $F_{1,\alpha}$ is a diffeomorphism in a neighborhood of ***A,*** because of the openness of the set of C^1 diffeomorphisms, e.g., see [24, p. 38]. Hence, $G_{1,\alpha}$ and $G_{2,\alpha}$ are conjugate locally. $F_{1,\alpha}(A_\alpha)$ is an attractor for $G_{2,\alpha}$ homeomorphic to ***A,*** and ***A,*** ∪ $F_{1,\alpha}$ ***(A,)*** is an attractor for the nonautonomous system (3.1). Notice that this process does not prove that ***A,*** is homeomorphic to A_0 because there is no conjugacy for ***F.*** However, in our examples these attractors appear to be homeomorphic. For (2.2) when $\alpha = 0$, the attractor for the autonomous system is the fish-hook in Fig. 1. In Fig. 2, where $\alpha = 0.2$, one fish-hook is an attractor for $G_{1,\alpha}$, i.e., the even iterates of (2.2), and the other fish-hook is its image under $F_{1,\alpha}$ and is an attractor for $G_{2,\alpha}$, the odd iterates of (2.2). The union of these two fish-hooks is the attractor for the nonautonomous system.

An example due to Henson [12] shows that the sets ***A,*** and $F_{1,\alpha}(A_\alpha)$ may not be distinct. Consider the scalar equation $x_n = 0.5(1 + a(-1)^n)x_{n-1}$ for $n \geq 1$. The map ***F(x)*** $= 0.5x$ has an attracting fixed point at the origin and is a diffeomorphism. Since $G_{1,\alpha} = G_{2,\alpha} = 0.25(1 - \alpha^2)x$, the origin is the only attractor for the nonautonomous map, i.e., ***A,*** $= F_{1,\alpha}(A_\alpha) = \{0\}$.

In general, if the forcing has period ***k,*** for each $i = 1, . . ,$ ***k,*** define the map $G_{i,\alpha} : \mathbb{R}^l \to$ R’ as the composition of ***k*** maps in the appropriate order starting with $F_{i,\alpha}$ which defines a solution orbit of (3.1), i.e.,

$$G_{i,\alpha} \equiv F_{i-1,\alpha} \circ \ldots \circ F_{k,\alpha} \circ \ldots \circ F_{i,\alpha},$$

where the term $F_{i-1,\alpha}$ is taken to be $F_{k,\alpha}$ when $i = 1$. Clearly, $F_{i,\alpha} \circ G_{i,\alpha} = G_{i+1,\alpha} \circ F_{i,\alpha}$ and $F_{i,\alpha} \circ G^n_{i,\alpha} = G^n_{i+1,\alpha} \circ F_{i,\alpha}$ for all $n \geq 1$. If $F_{i,\alpha}$ has an inverse then $G^n_{i+1,\alpha} = F_{i,\alpha} \circ G^n_{i,\alpha} \circ F^{-1}_{i,\alpha}$, i.e., $G_{i,\alpha}$ and $G_{i+1,\alpha}$ are conjugate dynamical systems. As in the case when ***k = 2,*** $F_{i,\alpha}$ will have a local inverse when α is small and when the autonomous map ***F*** is a diffeomorphism in a neighborhood of an attractor A_0. In this case, the attractor for (3.1) is the union of ***k*** homeomorphic subsets and has the form

$$\boldsymbol{A,} \cup F_{1,\alpha}(A_\alpha) \cup F_{2,\alpha}(F_{1,\alpha}(A_\alpha)) \cup \cdots \cup F_{k-1,\alpha}(\cdots F_{1,\alpha}(A_\alpha) \cdots).$$

This argument does not show **that** A, is homeomorphic to A_0. It is more difficult to determine conditions under which an attractor continues to a homeomorphic attractor under C^1 perturbation. An assumption of uniform hyperbolicity on A_0 would guarantee that A_0 continues to a homeomorphic attractor of $G_{i,\alpha}$. Hence, each subset of the attractor for (3.1) would be homeomorphic to A_0 and this would be a direct extension of Henson's results [12]. However, our assumption that F is a local diffeomorphism is different and weaker than hyperbolicity and, hence, our result is weaker.

5. A prey-predator example

In this section, we discuss a two-dimensional prey-predator system where the attractor for the autonomous system is an invariant loop which arises via Hopf bifurcation. We prove that the autonomous map F is a diffeomorphism in a neighborhood of this loop and, hence prove that for small amplitude period 2 forcing the attractor is the union of two homeomorphic subsets which are also loops.

Let x denote the prey population density and y, the predator density. In order to simplify the transition map, we assume that the per capita transition functions are linear functions of the population densities. Our model for the interaction of these two populations has the form

$$x_n = x_{n-1}(2 - x_{n-1} - 0.5y_{n-1}), \qquad y_n = y_{n-1}(0.8 + rx_{n-1}), \tag{5.1}$$

where the parameter r denotes the conversion rate from prey to predator. Here the prey has logistic growth in the absence of the predator with a stable equilibrium at $x = 1$. In the absence of prey, the predator population decreases exponentially. If $y > 4$, then the model is unrealistic because the prey population becomes negative, so we restrict our attention to small values for the population densities. The equilibrium $(x, y) = (0, 0)$ is always a saddle point. The equilibrium $(x, y) = (1, 0)$ is stable for small r, but undergoes a transcritical bifurcation as r increases through 0.2 which results in a stable interior equilibrium $(x, y) = (0.2/r, (2r - 0.4)/r)$ for $r > 0.2$. The interior equilibrium loses stability via Hopf bifurcation as r increases through 1.2 and the resulting stable invariant curve (see Fig. 5) persists until r becomes larger than 1.5.

The prey-predator system may experience periodic fluctuations in the parameter r or in any of the constants of (5.1) due to environmental variations such as weather or seasonal changes. We incorporate variation of period 2 with amplitude 0.8α in the intrinsic predator growth rate and consider the nonautonomous system:

$$x_n = x_{n-1}(2 - x_{n-1} - 0.5y_{n-1}), \qquad y_n = y_{n-1}(0.8(1 + \alpha(-1)^n) + 1.3x_{n-1}), \tag{5.2}$$

where $n = 1, 2, \ldots,$ and $\alpha > 0$. Hence, the growth rate alternates between $0.8(1+\alpha)$ and $0.8(1-\alpha)$ and averages to 0.8 over two generations. For small α, the attractor for (5.2) will be a set consisting of two subsets homeomorphic to each other (see Fig. 6) if the map of system (5.1) with $r = 1.3$ is a diffeomorphism in a neighborhood of the attracting invariant curve depicted in Fig. 5.

Let $F = (F_1, F_2)$ denote the map of system (5.1), i.e.,

$$F_1(x, y) = x(2 - x - 0.5y), \qquad F_2(x, y) = y(0.8 + 1.3x). \tag{5.3}$$

In this section, we show that F is a diffeomorphism in a neighborhood of the invariant curve in Fig. 5 by studying F defined on the open rectangle $R \equiv \{(x, y) : 0 < x < 0.5, 0 < y < 3\}$. The derivative of F is given by the matrix

$$DF(x, y) = \begin{bmatrix} 2 - 2x - 0.5y & -0.5x \\ 1.3y & 0.8 + 1.3x \end{bmatrix} \tag{5.4}$$

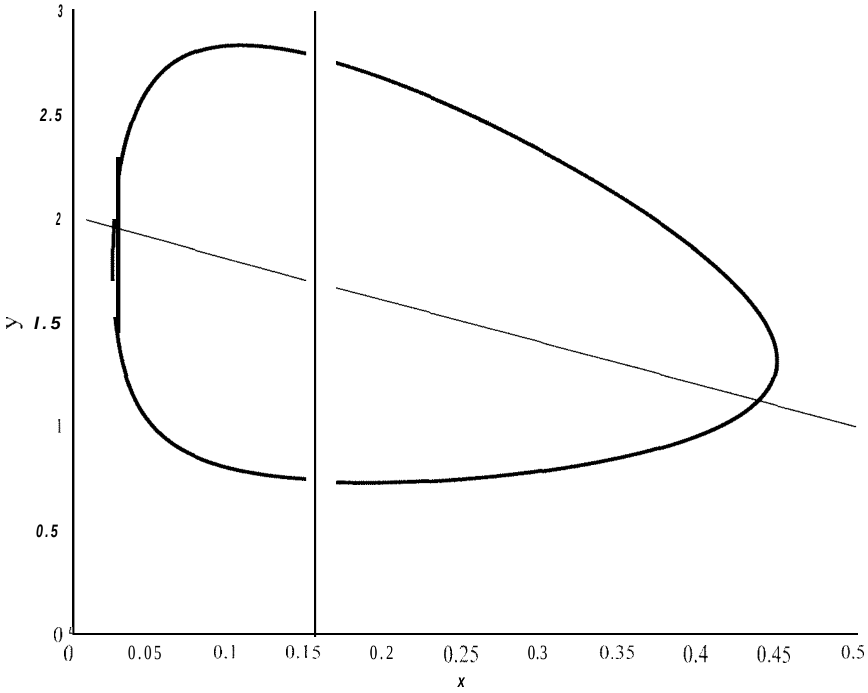

Fig. 5. Stable invariant curve and linear isoclines for (5.1) with $r = 1.3$

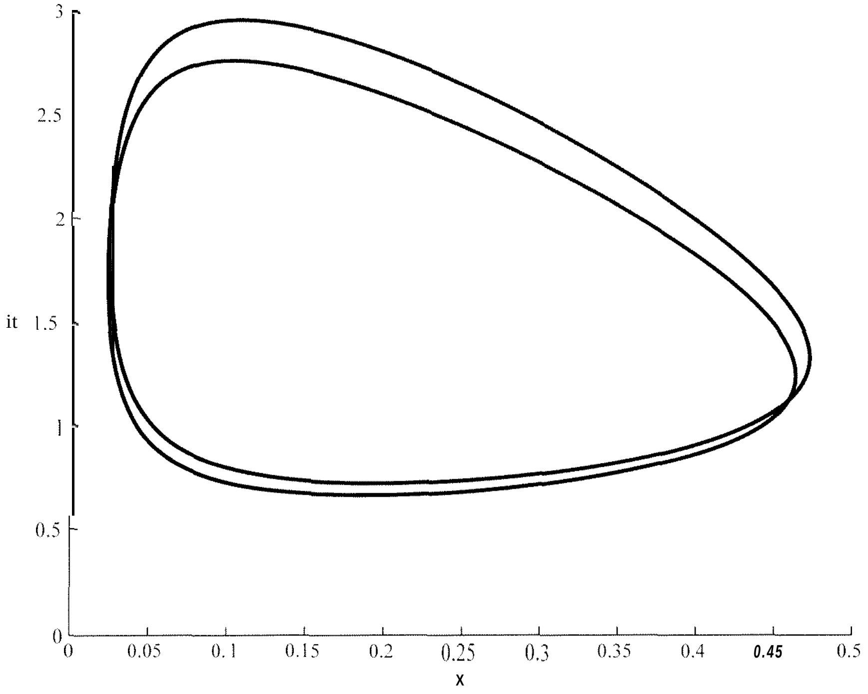

Fig. 6. Attractor for system (5.2) with $\alpha = 0.1$

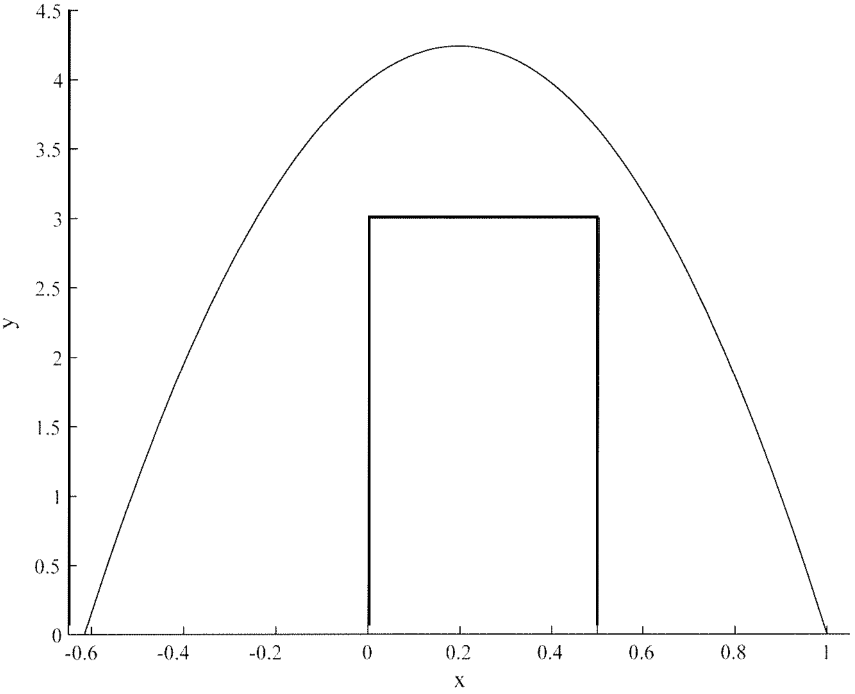

Fig. 7. Rectangle R and parabola where F may not be locally “l-l”.

By finding where the determinant of (5.4) is zero, we see that F may fail to be locally “l-l” only on the parabola given by

$$y = 4 + 2.5x - 6.5x^2. \tag{5.5}$$

As seen in Fig. 7, this parabola does not intersect the rectangle R.

By studying the component functions in (5.3), it is easy to see that F takes the rectangle R into the rectangle $S \equiv \{(x, y) : 0 \leq x \leq 0.75, 0 \leq y \leq 4.35)$. Here, we show that for each point (a, $b) \in S$ there is at most one point $(x, y) \in R$, so that $F(x, y) = (a$, b). Hence, F will be a “l-l” map on R. By setting $F_2(x, y) = b$ and solving for y in terms ofx and b, we see that

$$y = \frac{b}{0.8 + 1.3.X} \tag{5.6}$$

Inserting the right-hand side of (5.6) into the expression $F_1(x, y) =$ a, we obtain the following cubic equation for x with coefficients depending on a and b:

$$13x^3 - 18s' + (13a + 5b - 16)x + 8a = 0. \tag{5.7}$$

A straightforward but tedious analysis of the cubic function on the left-hand side of (5.7) shows that Eq. (5.7) has at most one solution x, so that $0 < x < 0.5$. Hence, each point (a, b) in the rectangle S has at most one preimage (x, y) in the rectangle R under F. R is a neighborhood of the attracting curve in Fig. 5. The map F from R onto $F(R)$ is “l-l” with a smooth inverse. Thus for α small enough, the attractor for system (5.2) is the union of two homeomorphic subsets as depicted in Fig. 6.

6. A population model with period forcing

Consider a two-dimensional system of difference equations that models the interaction between a population of a *pioneer* species with density x and a population of a *climax* species of density y. For ecological interactions of this type, competitive or cooperative effects impinging on each population can be modeled as functions of total density variables expressed as linear combinations of the individual population densities, see [25]. Total density variables of this form, u for pioneer populations and v for climax populations, may be defined as

$$u = c_{11}x + c_{12}y, \qquad v = c_{21}x + c_{22}y,$$

where the c_{ij} are positive constants that reflect competitive effects for a population of type j on a population of type i. If the per capita growth rates or fitnesses for the populations are assumed to be smooth functions of total density, changes in population densities between generations can be represented by the following system of equations for $n \geq 1$:

$$x_n = x_{n-1} f(u), \qquad y_n = y_{n-1} g(v).$$

The function f indicates the fitness function for the pioneer population and g, the fitness for the climax population. In keeping with characteristic fitness profiles for pioneer and climax species (see [25] or [26]), we may assume that f is a monotone decreasing function of u, whereas g is a one-humped function of v.

Fitness functions of various forms, including linear functions for pioneer populations and quadratic functions for climax populations, have been used to study the dynamics of these systems (see [26]). In this example, we illustrate the behavior produced by 5-periodic forcing on the pioneer population when pioneer fitness is linear (i.e., $f(u) = 2 - u$) and climax fitness is quadratic (i.e., $g(v) = 4v - v^2 - 2$). The system of difference equations that represents changes in population densities over time with stocking or harvesting of period k (not necessarily minimal period k) may be written as

$$\begin{aligned} x_n &= x_{n-1}\left[2 - (c_{11}x_{n-1} + c_{12}y_{n-1}) + h\left(1 + \alpha \sin\left(\frac{2\pi n}{k}\right)\right)\right], \\ y_n &= y_{n-1}[4(c_{21}x_{n-1} + c_{22}y_{n-1}) \quad (c_{21}x_{n-1} + c_{22}y_{n-1})^2 - 2], \end{aligned} \tag{6.1}$$

where $c_{11} = 0.78$, $c_{12} = c_{21} = 1$, $c_{22} = 0.5$, and $n \geq 1$. When $\alpha = 0$ and $h = 0.03$, the attractor for the autonomous system is an invariant loop. If $k = 5$ in (6.1) and α is increased through zero then the invariant loop for the autonomous system ($\alpha = 0$) splits into an attractor consisting of five loops (Fig. 8). The nonautonomous dynamical system maps these loops sequentially, one to the next, in a period 5 fashion. It is not difficult to show that when $\alpha = 0$ the autonomous map F has a nonsingular derivative matrix in a neighborhood of the attracting invariant loop. Hence, F has a local inverse at each point along the loop, but we have not been able to prove that F is a diffeomorphism in a neighborhood of this loop.

7. Summary

Here, we discuss the effects of small amplitude periodic forcing on an attractor for a discrete, autonomous system. The resulting attractor for the nonautonomous system inherits structure from the original attractor and from the period of the forcing. If the forcing is k-periodic then we extend the work of Henson [12] for attracting cycles of the autonomous system to more complicated attractors. Henson [12] showed that if m divides k then a hyperbolic attracting m-cycle for the autonomous system produces m attracting k-cycles for the nonautonomous system. From the dynamical behavior of various population models, we observe that a more complicated attractor of the

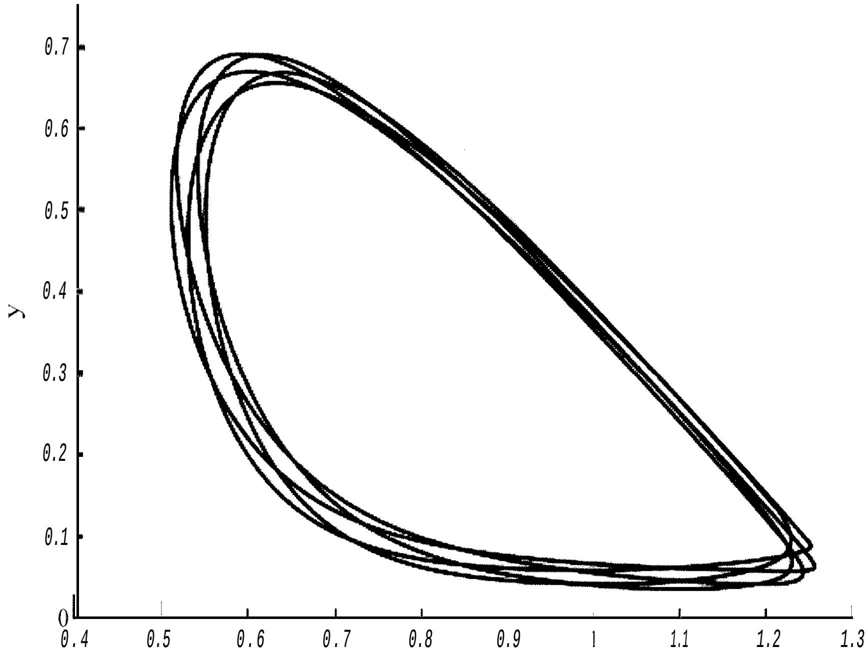

Fig. 8. Attractor with five loops for (6.1) with $k=5$, $\alpha=0.35$, and $h=0.03$

autonomous system continues to be a nonautonomous attractor which is the union of k subsets each homeomorphic to the autonomous attractor. Although, we do not establish this rigorously, we describe a method which may be used to prove that the attractor for the nonautonomous system is the union of k homeomorphic subsets. Our approach is to view the nonautonomous system as a composition of a finite number of autonomous maps. If the original autonomous map is a diffeomorphism in a neighborhood of the autonomous attractor then we show that sequences of k maps which define the nonautonomous system are locally conjugate. The conjugacies provide the homeomorphisms between attractor subsets. In Section 5, details needed to prove that the autonomous map is a diffeomorphism are carried out for a prey-predator model.

If the attractor for the autonomous system has additional structure which persists under C^1 perturbation then it may be possible to prove that each subset of the nonautonomous attractor is homeomorphic to the autonomous attractor. For example, the autonomous attractor may be a normally contracting submanifold (see [23, p. 444]). However, such properties are quite restrictive and are usually difficult to verify.

Acknowledgements

The authors would like to thank three anonymous referees for many helpful suggestions.

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