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Working Paper

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Foreword

A bifurcation analysis of a periodically forced ecological model shows that seasonalities can give rise to quasi-periodic and chaotic behavior of predator-prey communities. The analysis, performed with a continuation method, focuses on codimension two and three bifurcations and the results are in agreement with the local theory of forced Hopf bifurcations.

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BIFURCATIONS AND CHAOS IN A PERIODIC PREDATOR-PREY MODEL

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The model most often used by ecologists to describe interactions between predator and prey populations is analyzed in this paper with reference to the case of periodically varying parameters. A complete bifurcation diagram for periodic solutions of period one and two is obtained by means of a continuation technique. The results perfectly agree with the local theory of periodically forced Hopf bifurcation. The two classical routes to chaos, *i.e.*, cascade of period doublings and torus destruction, are numerically detected.

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1. Introduction

The problem of determining what regulates natural populations and makes them viable has engaged ecologists over the past fifty years. The most credited approach (see [May & Seger, 1986] for a recent discussion) is to think of plant and animal species as interacting components of a dynamical system driven by exogenous forces. The interaction mechanisms are nonlinear because rates of harvest, birth, death, and migration depend strongly on population densities, while the driving forces are periodic because food, temperature, humidity, light and other environmental factors vary periodically (seasons, daily, moon, and tide cycles). This implies that the theory of periodically forced nonlinear dynamical systems is the relevant theory: all modes of behavior of an aggregate of species living in a periodic environment can be classified, at least in principle, by looking at the bifurcation diagram of a dynamical system. In particular, the classical results on periodically forced Duffing and Van der Pol equations [Guckenheimer & Holmes, 1986] and the more specific results on periodically forced Hopf bifurcation [Rosenblat & Cohen, 1981; Kath, 1981; Gambaudo, 1985; Bajaj, 1986; Namachchivaya & Ariaratnam, 1987] are of great interest, because ecosystems with oscillating populations are, by far, the most intriguing ones. Taking this literature into account, one should therefore a priori expect that multiple attractors, catastrophic transitions, subharmonics, phase-locking, quasi-periodic behavior, and chaos show up quite frequently in ecosystems which are strongly influenced by some kind of seasonality.

Indeed, the analysis of a number of recorded time series of seasonally perturbed plant, animal, and human populations seems to confirm the existence of the above phenomena. Subharmonics of period 2, 3, and 8 days, as well as phase-locking with the moon cycle, have been found by analyzing the abundance of reef fishes influenced by tides [Robertson *et al.*, 1990]. A low dimensional strange attractor has been ascertained in the Canadian lynx population by applying Takens method to the 200 yr. long time series of number of skins shipped by the Hudson's Bay Company [Schaffer, 1984], while higher dimensional strange attractors have been detected in plant populations through the analysis of tree-rings [Gutierrez & Almiral, 1989]. But the most convincing and detailed analysis showing evidence of chaos in a periodically perturbed population is, with no doubt, the study carried out by Schaffer and coauthors on a number of childhood diseases which are strongly influenced by the seasonality of the contact rates induced by the Summer and Christmas vacations in schools [Kot *et al.*, 1988; Olsen *et al.*, 1988]. Other examples can be found in the broad area of food chain and food web systems which comprises forest ecosystems with recursive insect-pest outbreaks and aquatic ecosystems with chaotic algae blooms seasonally triggered by light intensity.

Parallel to the studies based on field data and laboratory experiments we have a number of purely theoretical investigations of the bifurcations of simple models which pretend to capture the essence of ecological systems. Some of these models are constant parameter discrete-time systems (maps) in which the time step coincides with the period of the forcing function, while the others are continuous-time systems with periodically varying parameters. Models of the first class are much more easy to handle and can give rise to spectacular dynamics, in particular when the map is non-invertible as in the famous case of seasonally breeding organisms with nonoverlapping generations [May, 1974]. Examples from this class are a study on bivoltine populations [Kot & Schaffer, 1984] which proves that seasonality can give rise to multiple attractors and chaos, and a study on host-parasitoid models based on Hopf bifurcations [Lauwerier & Metz, 1986] which shows that periodic, quasi-periodic and chaotic solutions are possible. More interesting, both biologically and mathematically, are the investigations concerning continuous-time models. Subharmonics of period two, three, and four have been numerically detected in classical SEIR epidemic models with periodic contact rates [Schwartz & Smith, 1983; Aron & Schwartz, 1984]. Periodic solutions of general Lotka-Volterra competition models are discussed in [Cushing, 1980; De Mottoni & Schiaffino, 1981; Namba, 1986] where it is proved that seasonality can support coexistence, while studies on more specific models which mimic the dynamics of two species of algae competing for the same nutrient in a lake with seasonally varying inflow have been carried out in [Smith, 1981; Butler *et al.*, 1985]. Seasonal Lotka-Volterra predator-prey systems have also been analyzed, mainly with reference to periodic solutions [Cushing, 1977; Bardi, 1981; Cushing, 1982], while much more realistic predator-prey models have been discussed in [Inoue & Kamifukumoto, 1984; Toro & Aracil, 1988; Schaffer, 1988; Allen, 1989].

In this paper we analyze the most commonly used predator-prey model, from now on called canonical, in which the prey has a per capita growth rate decreasing with density (intraspecific competition) and the predator has a saturating functional response due to its limited gut capacity (this is not so in Lotka-Volterra systems !). We analyze the effect that seasons can have by assuming that the time needed by a predator to find its prey varies periodically. We will show that this implies that only one parameter of the model must be varied periodically, and that this parameter directly affects the dynamics of both prey and predator. This is not so neither in [Schaffer, 1988] where the quality of the prey is periodically varied, nor in [Inoue & Kamifukumoto, 1984; Toro & Aracil, 1988; Allen, 1989] where the prey reproductive rate is the perturbed parameter (see next section for a criticism on the correctness of this assumption). The discussion in [Inoue & Kamifukumoto, 1984] is mainly focused on the influence of the frequency of the forcing function, which is classical in mechanics and electronics but has a very little sense in ecology, while in [Toro & Aracil, 1988; Allen, 1989] only the results of a few simulations are shown. On the contrary, the discussion in [Schaffer, 1988] is more systematic and points out that chaos can be obtained through torus destruction by increasing the magnitude of the seasonal variations. This is confirmed by our analysis which, nevertheless, shows that the period doubling route to chaos is also present.

The paper is organized as follows. In the next section we describe the periodically forced predator-prey model and in Sec.3 we recall its properties in the limit case of no environmental variability. In Sec.4 we briefly describe the continuation method and the corresponding interactive package we have used. The results of the analysis, comprising the proof of the existence of multiple attractors, phase-locking, torus destruction and strange attractors, are presented in Sec.5. They are mainly focused on resonances and codimension two and three bifurcations and they perfectly agree with the local theory of periodically forced Hopf bifurcation [Gambaudo, 1985; Bajaj, 1986]. The final section is devoted to the discussion of the results and to the comparison with related works.

As for the style of the paper, we have taken the liberty of being somehow naive in the presentation of the model and in the biological interpretation of the results, as well as in the description of the mathematical technicalities. We hope that this will make the paper accessible to a broader class of readers, ranging from theoretical biologists to applied mathematicians.

2. The Model

We now describe the canonical model [Gilpin, 1972; May, 1972; Shimazu *et al.*, 1972] that has been used in the last twenty years to interpret the behavior of many predator-prey communities and has been modified and extended to study more complex ecosystems, such as food chains and competition systems. The model accounts for the relationships between prey and predator populations in the case that the individuals are uniformly distributed in space and that age-structure and sex-ratio do not significantly affect the rate of growth of both populations. Under these assumptions, the dynamics of the two species is described by the following differential equations

$$\dot{x} = r\left(1 - \frac{x}{K}\right)x - p(x)y \tag{1}$$

$$\dot{y} = ep(x)y - dy \tag{2}$$

where x and y are the numbers of individuals of prey and predator populations or suitable (but equivalent) measures of density or biomass. In the absence of predators ($y = 0$) the rate of growth of prey per unit of biomass, namely $r(1 - x/K)$, decreases with x. This is the standard assumption of *logistic growth* of populations [Verhulst, 1845] which accounts for competition for food and space among individuals of the same species and for increased mortality at high density due, for example, to higher chances of epidemics at higher frequency of encounters among individuals. The *intrinsic growth rate* r describes the exponential growth of the prey population at low densities, while the *carrying capacity* K is the prey biomass at equilibrium in the absence of predators. The intrinsic growth rate and the carrying capacity increase with the amount of food available to the prey population and can therefore undergo synchronous periodic variations during the year. Realistic values of r and K for various kinds of aquatic and terrestrial populations living in different habitats can be found in the literature. The function $p(x)$ in Eqs. (1), (2) is the *functional response* of the predator [Holling, 1965], namely the prey biomass destroyed by each predator in one unit of time. The parameter e in Eq.(2) is a simple conversion factor, called *efficiency*, that specifies the number of newly born predators for each captured prey, while d is the predator *death rate* per capita.

To define the model completely, we must specify the functional response $p(x)$. For this we select the *type 2* functional response proposed by Holling which is, by far, the most commonly used in this type of study. This functional response can be justified as follows (for a more detailed interpretation see [Metz & van Batenburg, 1985]). Let us assume that the *searching time*, namely the time the predator spends to find a unit of prey is inversely proportional to prey density, *i.e.*, s/x, where s is a suitable parameter. If the time needed by each predator to handle one unit of prey is h and all other activities of the predator occupy a fraction u of its time, we can write

$$\frac{s}{x} p(x) + hp(x) + u = 1$$

from which it follows that

$$p(x) = \frac{ax}{b + x} \tag{3}$$

with

$$a = \frac{1 - u}{h} \qquad b = \frac{s}{h} \tag{4}$$

Thus, $p(x)$ is a concave saturating function and a is the *maximum harvest rate* of each predator, while b is the *half saturation constant*, namely the density of prey at which the predation rate is half maximum. In conclusion, by taking Eqs.(1)-(4) into account, the canonical model turns out to be

$$\dot{x} = x\left[r\left(1 - \frac{x}{K}\right) - \frac{ay}{b + x} \right] \tag{5}$$

$$\dot{y} = y\left[e\frac{ax}{b + x} - d \right] \tag{6}$$

where the six parameters r, K, a, b, d, e are positive.

Of course, the parameters must be time varying if relevant environmental factors fluctuate in time. For example, seasonal variations in the caloric content of plants eaten by herbivores can be simply modelled by assuming that the efficiency e of the herbivores is periodic of period 1 year [Schaffer, 1988], while the periodic presence of a superpredator exploiting the predator population can be taken into account by periodically varying the death rate d in Eq.(6). In these cases the seasonality is taken into account by perturbing only one parameter appearing in one of the two equations. Physical and biological mechanisms giving rise to periodicities in the amount of food available to the prey population can be modelled by varying r and K in Eq.(5). Thus, results of analysis dealing with periodic variations of only one of these two parameters, like those presented in [Inoue & Kamifukumoto, 1984; Toro & Aracil, 1988; Allen, 1989] are difficult to be interpreted biologically. Finally, there are more complex seasonality mechanisms which can be modelled only varying parameters which directly affect both differential equations. This happens, for example, when the degree of mimicry of the prey is not constant during the year or when variations of the habitat facilate the escape or the capture of the prey in some specific season. In these cases the searching time of the predator is still inversely proportional to the prey density but the coefficient of proportionality (s in Eq.(4)) is periodically varying in time with period 1 year. Thus, from Eqs.(1)-(4) it follows that only one parameter of the model, namely b, is periodic, but this parameter appears in both equations. This is the case we analyze in this paper, because we believe that mechanisms involving periodicities in the parameters of the functional response are the most interesting ones from a biological point of view (the analysis we have carried out on the other seasonality mechanisms confirms this guess). Therefore, in the following, we analyze Eqs.(5)-(6) with r, K, a, d, e constant and b periodic of period 1 year. For simplicity we consider sinusoidal perturbations, *i.e.*,

$$b = b_0(1 + \varepsilon \sin 2\pi t) \tag{7}$$

where b_0 is the average value of b and εb_0 is the amplitude of the perturbation. Obviously, $0 \leq \varepsilon \leq 1$, because b cannot be negative: $\varepsilon = 0$ corresponds to absence of seasonality, while $\varepsilon = 1$ means that the searching time of the predator in its most unfavourable season is twice its average value.

Model (5)-(7) is of the form

$$\dot{x} = xf(x,y,t)$$

$$\dot{y} = yg(x,y,t)$$

with f and g periodic with respect to t and $f(0,y,t)$ *and* $g(x,0,t)$ bounded for all $t,x,y \geq 0$. It is therefore a positive dynamical system, since $x(0)$, $y(0) \geq 0$ implies $x(t)$, $y(t) \geq 0$ for all $t \geq 0$. Autonomous systems of this kind have been studied by Kolmogorov in a celebrated paper [Kolmogorov, 1936] and by many other authors since then [Cushing, 1982]. In the autonomous case and under suitable (but biologically sound) conditions, Kolmogorov systems have a single attractor (equilibrium or limit cycle) in the first quadrant [Wrzosek, 1990]. We will see in the next sections that the canonical model (5)-(7)

satisfies this property in the absence of seasonality ($\varepsilon = 0$), but has multiple attractors when there is a sufficiently high degree of seasonality.

3. The Constant Parameter Case

For $\varepsilon = 0$ system (5)-(7) becomes the autonomous second order system

$$\dot{x} = x\left[r\left(1 - \frac{x}{K}\right) - \frac{ay}{b_0 + x} \right] \tag{8}$$

$$\dot{y} = y\left[e\frac{ax}{b_0 + x} - d \right] \tag{9}$$

where all parameters and state variables are nonnegative. The analysis of the local stability of its equilibria shows that there is a *Hopf* bifurcation at

$$b_0 = \frac{K(ea - d)}{ea + d} \tag{10}$$

and a *self-crossing* bifurcation at

$$b_0 = \frac{K(ea - d)}{d} \tag{11}$$

The Hopf bifurcation is always supercritical[1], *i.e.*, the corresponding appearing limit cycle is always stable, and the asymptotic period of this cycle is

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[1] The computation of the Liapunov number is relatively easy if one considers the orbitally equivalent system obtained by multiplying Eqs.(8),(9) by (b_0+x).

$$T_H = 2\pi \left(\frac{K}{r b_0 d} \right)^{1/2}$$

Moreover, the limit cycle is unique [Cheng, 1981; Wrzosek, 1990] and its period T is a decreasing function of b_0.

Thus, the parameter space is partitioned into three regions, characterized by low, intermediate and high values of b_0 (see Eqs.(10),(11) for the critical values of b_0 identifying the three cases). For all combinations of the parameters there is a single attractor which is globally stable in the first quadrant as indicated in **Fig.1**. More precisely, for b_0 sufficiently small the attractor is a stable limit cycle. For increasing values of b_0 this cycle shrinks and disappears through a Hopf bifurcation. Then the attractor is a stable equilibrium which is positive for intermediate values of b_0 and trivial (absence of predator population) for high values of b_0.

4. Bifurcation Curves and Method of Investigation

For $\varepsilon > 0$ system (5)-(7), adding the equation $\dot{t} = 1$ $(t \bmod 1)$, can be transformed into an autonomous three- dimensional system for which Poincaré section and first return map $(x(0),y(0)) \longmapsto (x(1),y(1))$ can be defined [Arnold, 1982; Guckenheimer & Holmes, 1986]. Fixed points of the k-th iterate of the map correspond to periodic solutions of Eqs.(5)-(7) with period k. We will refer to these points as *period* k *fixed points.* It should be noted that a periodic solution with period k corresponds to a k-ple of period k fixed points of the Poincaré map. Moreover, closed and regular invariant curves of the Poincaré map correspond to quasi-periodic solutions (*invariant tori*) of the three-dimensional system, while irregular invariant sets correspond to chaotic solutions (*strange attractors*).

Fixed points, regular invariant curves and all other orbits of the Poincaré map form its *phase portrait*. In our figures (see the bottom part of **Figs.2, 4**) we always have an odd number of fixed points: the central one is a period one fixed point while the others are period two fixed points (fixed points of period three or higher are not shown in the portraits). We will use schematic phase portraits of the Poincaré map to illustrate the behavior of system (5)-(7). The stability of the fixed points and of the closed invariant curves is clearly detectable from these portraits. It is important to remark that in some subregions of the parameter space the phase portraits are not so regular as shown in our figures. In particular, the closed and regular invariant curves might be substituted by strange attractors like the one shown in **Fig.3**.

Fixed points of the Poincaré map of system (5)-(7) can bifurcate at some parameter values. We use the following notation for fixed point codimension one bifurcation curves.

$h^{(k)}$ - *Hopf (Neimark-Sacker) bifurcation curve.* For parameter values on this curve the map has a period k fixed point with a pair of multipliers on the unit circle: $\mu^{(k)}_{1,2} = e^{\pm i\omega}$, $\omega > 0$.

$f^{(k)}$ - *flip (period doubling) bifurcation curve.* For parameter values on this curve the map has a period k fixed point with a multiplier $\mu^{(k)}_{1} = -1$.

$t^{(k)}$ - *tangent (fold) bifurcation curve.* For parameter values on this curve the map has a period k fixed point with a multiplier $\mu^{(k)}_{1} = 1$.

Phase portraits of the Poincaré map for parameter values near these curves are described in [Arnold, 1982; Guckenheimer & Holmes, 1986].

The bifurcation curves presented in the following section have been computed by means of a continuation method interactively supported by the program LOCBIF developed by the first author and by A. Khibnik, V. Levitin and

E. Nikolaev at the Research Computing Centre of the USSR Academy of Sciences at Pushchino.

The method can be briefly described as follows (see [Khibnik, 1990a,b]). Each bifurcation curve is computed by projecting a one-dimensional manifold located in the four dimensional space (x,y,p_1,p_2) on the (p_1,p_2)- plane, where p_1 and p_2 are two parameters of (5)-(7). The manifold is determined by the two fixed point equations and by a bifurcation condition imposed on the multipliers of the fixed point. This condition is written using the characteristic polynomial $det\ (A - \mu I)$, where A is the Jacobian matrix of the Poincaré map at point (x,y) and I is the unit matrix. More precisely, the bifurcation conditions are the following

$$R\ [det\ (A - \mu I),\ det\ (\mu A - I)] = 0 \qquad \text{(for } Hopf \text{ bifurcation}^{2}\text{)},$$

$$det\ (A + I) = 0 \qquad \text{(for } flip \text{ bifurcation)},$$

$$det\ (A - I) = 0 \qquad \text{(for } tangent \text{ bifurcation)},$$

where $R\ [\cdot,\cdot]$ stands for the *resultant* of two polynomials [Lancaster & Tismenetsky, 1985]. In the program LOCBIF the bifurcation curves are computed by means of an adaptive prediction-correction continuation procedure with tangent prediction and Newton correction. All relevant derivatives, as well as the Poincaré map, are evaluated numerically. Codimension two bifurcation points are detected automatically. The program LOCBIF also produces phase

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[2] Actually, this condition implies that $\mu_1\mu_2 = 1$ and, therefore, corresponds also to a nonbifurcating *neutral saddle* fixed point with $\mu_1 = 1/\mu_2$ with real $\mu_{1,2}$.

portraits of the Poincaré map, continues fixed points in any (x,y,p_1)-space and detects codimension one bifurcations.

5. Analysis of the Results

In this section we present bifurcation diagrams of system (5)-(7) in the (ε,b_0)-plane for fixed values of the remaining parameters. Parameter values for which the period T_H of the appearing limit cycle is integer will play an important role since in these cases the ratio between the period T_H and the period of the forcing function (see Eq.(7)) is integer. Parameters e, a and d will be fixed during the analysis ($e = 1$, $a = 2\cdot 2\pi$, $d = 2\pi$), while r will vary and cross 'resonant' values r_1 and r_2 corresponding to $T_H = 1$ and $T_H = 2$ respectively. Note that $r_1 > r_2$; for example, for our values of e, a and d we have $r_1 = 3\cdot 2\pi$ and $r_2 = 0.75\cdot 2\pi$.

5.1. Case $r < r_2$ (see Fig.2)

On the b_0-axis there is a point H corresponding to the Hopf bifurcation of the nontrivial equilibrium in the constant parameter system. Since $r < r_2$ the period T_H of the limit cycle appearing through the Hopf bifurcation is greater than 2 and increases while b_0 decreases. In what follows we assume that r is fixed at some generic value ($r = 0.73\cdot 2\pi$) and present bifurcation curves in the (ε,b_0)-plane (Fig.2).

Hopf bifurcation of period one fixed points $[h^{(1)}]$

Point H is a root of the Hopf bifurcation curve $h^{(1)}$ of system (5)-(7). The curve $h^{(1)}$ shown in **Fig.2** has been obtained by continuation starting from point H. When curve $h^{(1)}$ is crossed from above (*i.e.*, from region 0 to region

1 in **Fig.2**) a small stable closed invariant curve of the Poincaré map appears: in other words, the forced stable cycle of period 1 of system (5)-(7) bifurcates into a stable torus.

Flip bifurcation of period one fixed points $[f^{(1)}]$

While continuing curve $h^{(1)}$ from the left to the right the multipliers $\mu^{(1)}_{1,2}$ vary smoothly and become equal to -1 when the terminal point A_1 is reached. This is a codimension two bifurcation point called *strong resonance 1:2* which is studied in [Arnold, 1982] by means of the normal form approach. In the present case the two coefficients of the corresponding normal form are negative. A flip bifurcation curve $f^{(1)}$ passes through point A_1. The two branches of curve $f^{(1)}$ have been obtained by continuation starting from A_1 in the two possible directions.

Since the coefficients of the normal form are negative one can conclude [Arnold, 1982] that when curve $f^{(1)}$ is crossed from region 0 to region 2 the period one fixed point loses stability and a pair of period two fixed points appears. If curve $f^{(1)}$ is crossed from region 1 to region 3 (just below point A_1) a pair of repelling period two fixed points appears while the unstable period one fixed point becomes a saddle.

Tangent bifurcation of period two fixed points $[t^{(2)}]$

The analysis of the flip bifurcation on $f^{(1)}$ by means of the method developed in [Kuznetsov & Rinaldi, 1991] shows that there are two other codimension two bifurcation points (D_1 and D_2) on the flip bifurcation curve $f^{(1)}$ at which the coefficient of the cubic term in the normal form vanishes. These points are two terminal points of the tangent bifurcation curve $t^{(2)}$ [Arnold *et al.*, 1986]. When curve $t^{(2)}$ is crossed from region 1 to region 4 two pairs of period two fixed points appears: two are repelling points and two are saddle points. The two saddle points are the same points which disappear through the flip bifurcation on the segment D_1D_2 of curve $f^{(1)}$.

Hopf bifurcation of period two fixed points $[h^{(2)}]$

Point A_1 is also the origin of the Hopf bifurcation curve $h^{(2)}$ of period two fixed points [Arnold, 1982]. If $h^{(2)}$ is crossed from region 3 to region 2 then two small unstable invariant curves around the period two fixed points appear while the corresponding fixed points become stable.

Bifurcations of period three fixed points $[t^{(3)}$ *and* $f^{(3)}]$

If $r > r_3$ then there is a point on the b_0-axis at which the period T of the limit cycle of the unperturbed system is equal to 3. From this point two branches (not shown in **Fig.2**) of a tangent bifurcation curve $t^{(3)}$ originate. When curve $t^{(3)}$ is crossed two triplets of period three fixed points (one stable and one of saddle type) appear. Then, the stable fixed points of period three undergo a period doubling bifurcation on a curve $f^{(3)}$ (not shown in **Fig.2**).

Global bifurcations of closed invariant curves

As predicted by the normal form analysis of point A_1 [Arnold, 1982], the closed invariant curves of the Poincaré map shown on the phase portrait for region **2″** undergo global bifurcations of homoclinic type in region 2 and, finally, disappear. The same holds for the closed invariant curve appearing on curve $h^{(1)}$ which first loses smoothness and then disappears on some bifurcation set in regions 1, 3 and 4 thus giving rise to strange attractors like the one shown in **Fig.3**.

5.2. Case $r_2 < r < r_1$ (see Fig.4)

If r approaches r_2 the points A_1 and D_1 of **Fig.2** tend toward point H on the b_0-axis. In the limit, when $r = r_2$, curve $h^{(1)}$ does not exist and curves $f^{(1)}$, $h^{(2)}$ and $t^{(2)}$ originate from the same root (namely, from point H).

If $r_2 < r < r_1$ then the period T_H of the limit cycle appearing through the Hopf bifurcation in the unperturbed system is between 1 and 2. In the following section we assume that r is fixed at some generic value ($r = 1\cdot 2\pi$) and present bifurcation curves on the (ε, b_0)-plane (**Fig.4**).

Hopf and flip bifurcations of period one fixed points [$h^{(1)}$ *and* $f^{(1)}$]

For $r_2 < r < r_1$ the Hopf bifurcation curve $h^{(1)}$ is rooted at point H on the b_0-axis and terminates at point A_2 which is a codimension two bifurcation corresponding to $\mu^{(1)}_{1,2} = -1$. This strong resonance is different than in the preceding case because the coefficients of the corresponding normal form (see [Arnold, 1982]) are of opposite sign. This implies that no Hopf bifurcation curve $h^{(2)}$ originates at point A_2.

The flip bifurcation curve $f^{(1)}$ still goes through point A_2, but the character of the flip bifurcation in the neighborhood of point A_2 is different. Crossing $f^{(1)}$ just above point A_2 from region 5 to region 2 results in the disappearance of a pair of saddle type period two fixed points while the period one fixed point which is stable in region 5 becomes a saddle in region 2. Crossing $f^{(1)}$ just below point A_2 from region 6′ to region 2 results in the disappearance of a pair of period two saddle fixed points while the repelling period one fixed point bifurcates into a saddle.

Tangent bifurcation of period two fixed points[$t^{(2)}$]

The tangent bifurcation curve $t^{(2)}$ has two branches ($t_1^{(2)}$ and $t_2^{(2)}$) originating at point K_2 on the b_0-axis where the limit cycle of the unperturbed system has period 2. Branch $t_1^{(2)}$ terminates at point D_3 which is a codimension two bifurcation point on the flip bifurcation curve $f^{(1)}$. Some details concerning the system behavior near point K_2 can be found in [Guckenheimer & Holmes, 1986] where an example of this bifurcation is considered. On the branch $t_1^{(2)}$ and on the branch $t_2^{(2)}$ close to point K_2 two pairs of period two fixed points appear, namely a pair of stable points and a pair of saddle points.

At point B on curve $t_2^{(2)}$ the Poincaré map has a period two fixed point with two multipliers $\mu_{1,2}^{(2)} = 1$. This is a codimension two bifurcation which has also been studied in [Arnold, 1982]. The Hopf bifurcation curve $h^{(2)}$ originates at this point.

Hopf and flip bifurcations of period two fixed points [$h^{(2)}$ *and* $f^{(2)}$]

The Hopf bifurcation curve $h^{(2)}$ can be constructed by continuation starting from point B and terminating at point C where the multipliers $\mu_{1,2}^{(2)}$ of the second iterate of the Poincaré map are both equal to -1. This is again a codimension two bifurcation point. A curve $f^{(2)}$ corresponding to the flip bifurcation of period two fixed points goes through point C. Of course, fixed points of period four appear when crossing curve $f^{(2)}$.

Cascade of period doublings

The analysis shows that flip bifurcation curves $f^{(4)}$, $f^{(8)}$, ..., exist in the vicinity of curve $f^{(2)}$, and that this cascade of period doublings results in a strange attractor which can be found in some subregion of regions 8 and 9. One of these attractors is shown in Fig.5.

Bifurcations of closed invariant curves

As in the previous case, closed and regular invariant curves bifurcate. For example, in accordance with [Guckenheimer & Holmes, 1986], the stable torus appearing through the Hopf bifurcation on curve $h^{(1)}$ disappears through a homoclinic structure on a bifurcation set resembling a curve connecting point A_2 with a point on curve $t_1^{(2)}$ near the b_0-axis.

5.3. Case $r > r_1$ (see Fig.6)

If $r > r_1$ then the period T_H of the limit cycle appearing through the Hopf bifurcation in the unperturbed system is smaller than 1. In the following we assume that r is fixed at some generic value ($r = 3.3\cdot 2\pi$) and we present bifurcation curves on the (ε,b_0)-plane (Fig.6).

For $r \geq r_1$ the bifurcation curves described in the previous section still remain. Moreover, a triangular region $K_1E_1E_2$ bounded by the bifurcation curve $t^{(1)}$ appears (this region shrinks to a point when r tends to r_1). The curve has two branches ($t_1^{(1)}$ and $t_2^{(1)}$) starting at point K_1 on the b_0-axis at which the unperturbed system has a stable limit cycle of period 1 (note that point K_1 is above point K_2). The first branch $t_1^{(1)}$ terminates at point E_1 and the second one $t_2^{(1)}$ terminates at point E_2. These two points of codimension two correspond to the cusp bifurcation of the period one fixed points. The two cusps are connected by the third branch $t_3^{(1)}$ of $t^{(1)}$. Inside the triangle the Poincaré map has three fixed points of period one: one saddle point and two non-saddle points.

There are two codimension two bifurcation points G_1 and G_2 on $t^{(1)}$ characterized by $\mu_{1,2}^{(1)} = 1$. The Hopf bifurcation curve $h^{(1)}$ starting from point H on the b_0-axis terminates at point G_1 and originates again at point G_2. The stable closed invariant curve appearing on $h^{(1)}$ bifurcates inside the triangle through homoclinic structures.

6. Concluding Remarks

The canonical model used in ecology to describe damped or sustained oscillations of predator-prey communities has been analyzed in this paper under the assumption that one of its parameters is periodically varying in time with period 1 year. This corresponds to deal with a specific seasonality mechanism affecting the dynamics of prey and predator populations. The analysis is much more detailed and complete than in other contributions on the same subject [Inoue & Kamifukumoto, 1984; Toro & Aracil, 1988; Schaffer, 1988; Allen, 1989] where simulation is the only tool of investigation. On the contrary, we have used an interactive package implementing a continuation method which allows one to detect codimension one and two bifurcations as well as to continue bifurcation curves. By means of this method we have shown that the model has stable and unstable periodic solutions of various periods, as well as stable and unstable quasi-periodic solutions and chaotic motions. Two different routes to chaos have been detected: in the case analyzed in Sec. 5.1 the strange attractor (see **Fig.** 3) arises from a torus which first loses smoothness and then is destroyed, while in the case analyzed in Sec. 5.2 the strange attractor (see **Fig.** 5) arises from a cascade of period doublings.

Although the bifurcation diagrams presented in **Figs. 2,4,6,7** are not complete because bifurcations of periodic solutions of period greater than or equal to three as well as homo- and heteroclinic tangencies of the saddle invariant manifolds and bifurcation sets of the closed invariant curves are not presented, the structure of bifurcations of periodic solutions of period one and two is completely understood and proves that forced *ecological* *oscillators* are as reach as the well known mechanic and electronic oscillators.

It is also interesting to notice that our numerical results near the parameter values at which the period of the appearing limit cycle of the unperturbed system is one ore two times the period of the forcing function are in perfect agreement with the local theory of periodically forced Hopf bifurcation. The comparison becomes straightforward if one considers bifurcation curves near the resonance 1:2 in the (r,b_0)-plane for ε = const (see, for example, our **Fig.7** and Fig.25 in [Gambaudo, 1985] and Fig.1 in [Bajaj, 1986]). Nevertheless, the bifurcations far from these resonances (for example, the flip bifurcation of period two fixed points) are not predicted by the local analysis performed in [Gambaudo, 1985; Bajaj, 1986].

The results of our analysis are also very interesting from a biological point of view, because they confirm that seasonality has the power of transforming simple ecosystems into complex ecosystems. In fact, our predator-prey model has always a single attractor in the case of no seasonality, while the perturbed model may have multiple attractors. For example, in region 5 of **Fig. 4** the system has a stable period one solution as well as a stable period two solution. The coexistence of a stable period two solution with a strange attractor is also possible in region 2 of **Fig. 2**.

Moreover, in the unperturbed case the attractor varies smoothly with parameters and catastrophic transitions cannot occur. On the contrary, in the case of sufficiently pronounced seasonality, the system can sharply change its mode of behavior if a strategic parameter is only slightly perturbed. Suppose, for example, that the parameters are such that the system is in region 2" of **Fig.2** and that the mode of behavior is a stable period two limit cycle. Then, if b_0 decreases so that the bifurcation curve $h^{(2)}$ is crossed, the stable period two solution becomes unstable and the system moves toward a completely different attractor which may be even a strange attractor like the one shown in **Fig.3**.

As a last remark we would like to point out that the number of possible asymptotic modes of behavior of the system is not as high as it might appear from a superficial analysis of our figures. Indeed, many of the bifurcation curves shown in **Fig. 2, 4, 6** concern only unstable solutions. Nevertheless, these curves are needed if one likes to fully understand the ultimate structure of the bifurcations of this predator-prey system.

REFERENCES

Allen, J.C. [1989] "Are natural enemy populations chaotic ?", in *Estimation and Analysis of Insect Populations*, eds. McDonald, L., Manly, B., Lockwood, J. & Logan, J., *Lecture Notes in Statistics*, 55 (Springer Verlag, Berlin) pp. 190-205.

Arnold, V.I. [1982] *Geometrical Methods in the Theory of Ordinary Differential Equations* (Springer-Verlag, New-York, Heidelberg, Berlin).

Arnold, V.I., Afraimovich, V.S., Il'yashenko ,Yu. S.& Shil'nikov, L.P. [1986] "Bifurcation theory" in *Dynamical Systems, V*, eds. Anosov, D.V. & Arnold, V.I. (VINITI, Moscow) pp. 5-218 [in Russian].

Aron, J.L. & Schwartz, I.B. [1984] "Seasonality and period-doubling bifurcations in an epidemic model", *J. Theor. Biol.* 110, 665-679.

Bajaj, A.K. [1986] "Resonant parametric perturbations of the Hopf bifurcation". *J. Math. Anal. Appl.* 115, 214-224.

Bardi, M. [1981] "Predator-prey models in periodically fluctuating environments", *J. Math. Biol.* 12, 127-140.

Butler, G.J., Hsu, S.B. & Waltman, P. [1985] "A mathematical model of the chemostat with periodic washout rate", *SIAM J. Appl. Math.* 45, 435-449.

Cheng, K.S. [1981] "Uniqueness of a limit cycle for a predator-prey system", *SIAM J. Math. Anal.* 12, 541-548.

Cushing, J.M. [1977] "Periodic time-dependent predator-prey systems", *SIAM J. Appl. Math.* 32, 82-95.

Cushing, J.M. [1980] "Two species competition in a periodic environment", *J. Math. Biol.* 10, 384-400.

Cushing, J.M. [1982] "Periodic Kolmogorov systems", *SIAM J. Math. Anal.* 13, 811-827.

De Mottoni, P. & Schiaffino, A. [1981] "Competition systems with periodic coefficients: a geometric approach", *J. Math. Biol.* 11, 319-335.

Gambaudo, J.M. [1985] "Perturbation of a Hopf bifurcation by an external time-periodic forcing", *J. Diff. Eqs.* 57, 172-199.

Gilpin, M.E. [1972] "Enriched predator-prey systems: theoretical stability", *Science* 177, 902-904.

Guckenheimer, J. & Holmes, P. [1986] *Nonlinear Oscillations, Dynamical Systems, and Bifurcations of Vector Fields* (Springer-Verlag, New-York, Heidelberg, Berlin, Tokyo).

Gutierrez, E. & Almiral, H. [1989] " Temporal properties of some biological systems and their fractal attractors", *Bull. Math. Biol.* 51, 785-800.

Holling, C.S. [1965] "The functional response of predators to prey density and its role in mimicry and population regulation", *Mem. Entomol. Soc. Can.* 45, 5-60.

Inoue, M. & Kamifukumoto, H. [1984] "Scenarios leading to chaos in a forced Lotka-Volterra model", *Progr. Theor. Phys.* 71, 930-937.

Kath, W.L. [1981] "Resonance in periodically perturbed Hopf bifurcation", *Studies in Appl. Math.* 65, 95-112.

Khibnik, A.I. [1990a] "LINLBF: A program for continuation and bifurcation analysis of equilibria up to codimension three", in *Continuation and Bifurcations: Numerical Techniques and Applications*, eds. Roose, D., de Dier, B. & Spence, A. (Kluwer Academic Publishers, Netherlands) pp. 283-296.

Khibnik, A.I. [1990b] "Numerical methods in bifurcation analysis of dynamical systems: parameter continuation approach", in *Mathematics and Modelling*, eds. Zarhin, Yu.G. & Bazykin, A.D. (Center of Biological Research of the USSR Academy of Sciences, Pushchino) pp. 162-197 [in Russian].

Kolmogorov, A.M. [1936] " Sulla teoria di Volterra della lotta per l'esistenza", *Giornale dell'Istituto Italiano degli Attuari* 7, 74-80 [in Italian].

Kot, M. & Schaffer, W.M. [1984] "The effects of seasonality on discrete models of population growth", *Theor. Pop. Biol.* 26, 340-360.

Kot, M., Schaffer, W.M., Truty, G.L., Grasser, D.J. & Olsen, L.F. [1988] "Changing criteria for imposing order", *Ecol. Modelling* 43, 75-110.

Kuznetsov, Yu.A. & Rinaldi, S. [1991] "Numerical analysis of the flip bifurcation of maps", *Appl. Math & Comp.* 43, 231-236.

Lancaster, P. & Tismenetsky, M. [1985] *The Theory of Matrices* (Academic Press, San Diego).

Lauwerier, H.A. & Metz, J.A.J. [1986] "Hopf bifurcation in host-parasitoid models", *IMA J. Math. Appl. Med. & Biol.* 3, 191-210.

May, R.M. [1972] "Limit cycles in predator-prey communities", *Science* 17, 900-902.

May, R.M. [1974] "Biological populations with nonoverlapping generations: stable points, stable cycles, and chaos", *Science* 186, 645-647.

May, R.M. & Seger, J. [1986] "Ideas in ecology", *Am. Sci.* 74, 256-267.

Metz, J.A.J. & van Batenburg, F.H.D. [1985] "Holling's "hungry mantid" model for the invertebrate functional response considered as a Markov process. Part I: the full model and some of its limits", *J. Math. Biol.* 22, 209-238.

Namachchivaya, S. N. & Ariaratnam, S.T. [1987] "Periodically perturbed Hopf bifurcation", *SIAM J. Appl. Math.* 47, 15-39.

Namba, T. [1986] "Bifurcation phenomena appearing in the Lotka -Volterra competition equation: a numerical study", *Math. Biosci.* 81, 191-212.

Olsen, L.F., Truty, G.L. & Schaffer, W.M. [1988] "Oscillations and chaos in epidemics: a nonlinear dynamic study of six childhood diseases in Copenhagen, Denmark", *Theor. Pop. Biol.* 33, 344-370.

Robertson, D.R., Petersen, C.W & Brawn, J.D. [1990] "Lunar reproductive cycles of benthic-broading reef fishes: reflections of larval biology or adult biology ?", *Ecol. Monogr.* 60, 311-329.

Rosenblat, S. & Cohen, D.S. [1981] "Periodically perturbed bifurcation - II. Hopf bifurcation", *Studies in Appl. Math.* 64, 143-175.

Schaffer, W.M. [1984] "Stretching and folding in Lynx fur returns: evidence for a strange attractor in nature ?", *Amer. Nat.* 124, 798-820.

Schaffer, W.M. [1988] "Perceiving order in the chaos of nature", in *Evolution of Life Histories of Mammals*, ed. Boyce, M.S. (Yale University Press, New Haven) pp. 313-350.

Schwartz, I.B & Smith, H.L. [1983] "Infinite subharmonic bifurcation in an SEIR epidemic model", *J. Math. Biol.* 18, 233-253.

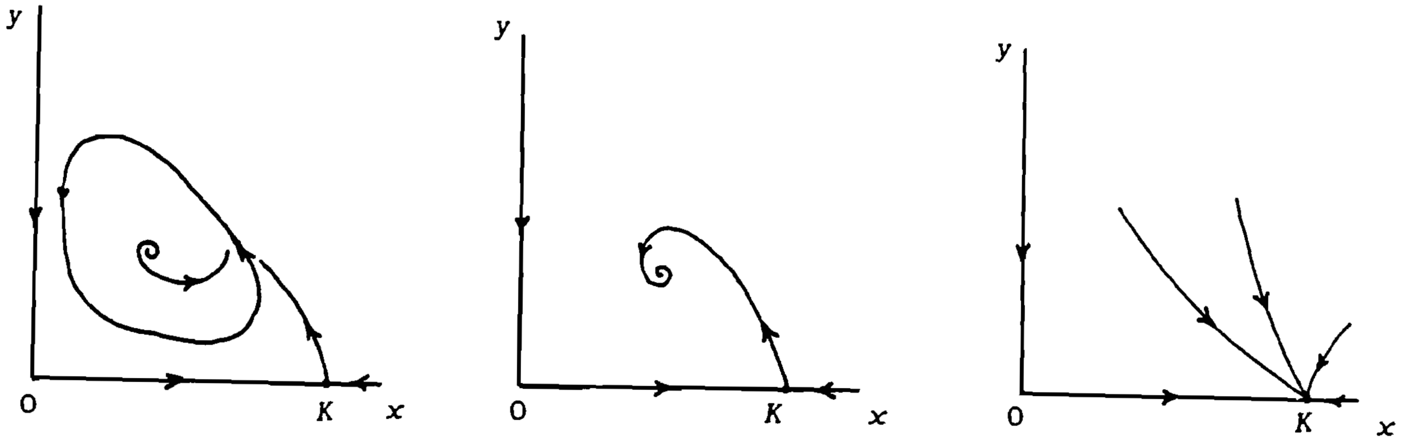
Shimazu, Y., Sugiyama, K., Kojima, T. & Tomida, E. [1972] "Some problems in ecology oriented environmentology", *J. Earth Sci. Nagoya Univ.* 20, 31-89.

Smith, H.L. [1981] "Competitive coexistence in an oscillating chemostat", *SIAM J. Appl. Math.* 40, 498-522.

Toro, M. & Aracil, J. [1988] "Qualitative analysis of system dynamics ecological models", *Syst. Dyn. Review* 4, 56-80.

Verhulst, P.F. [1845] "Recherches mathématique sur la loi d'accroissement de la population", *Mem. Acad. Roy. Belg.* 18, 1-38 [in French].

Wrzosek, D.M. [1990] "Limit cycles in predator-prey models", *Math. Biosci.* 98, 1-12.



(a) (b) (c)

Fig.1. Phase portraits of the constant parameter system (8),(9):

(a): $b_0 < \dfrac{K(ea - d)}{ea + d}$;

(b): $\dfrac{K(ea - d)}{ea + d} < b_0 < \dfrac{K(ea - d)}{d}$;

(c): $b_0 > \dfrac{K(ea - d)}{d}$.

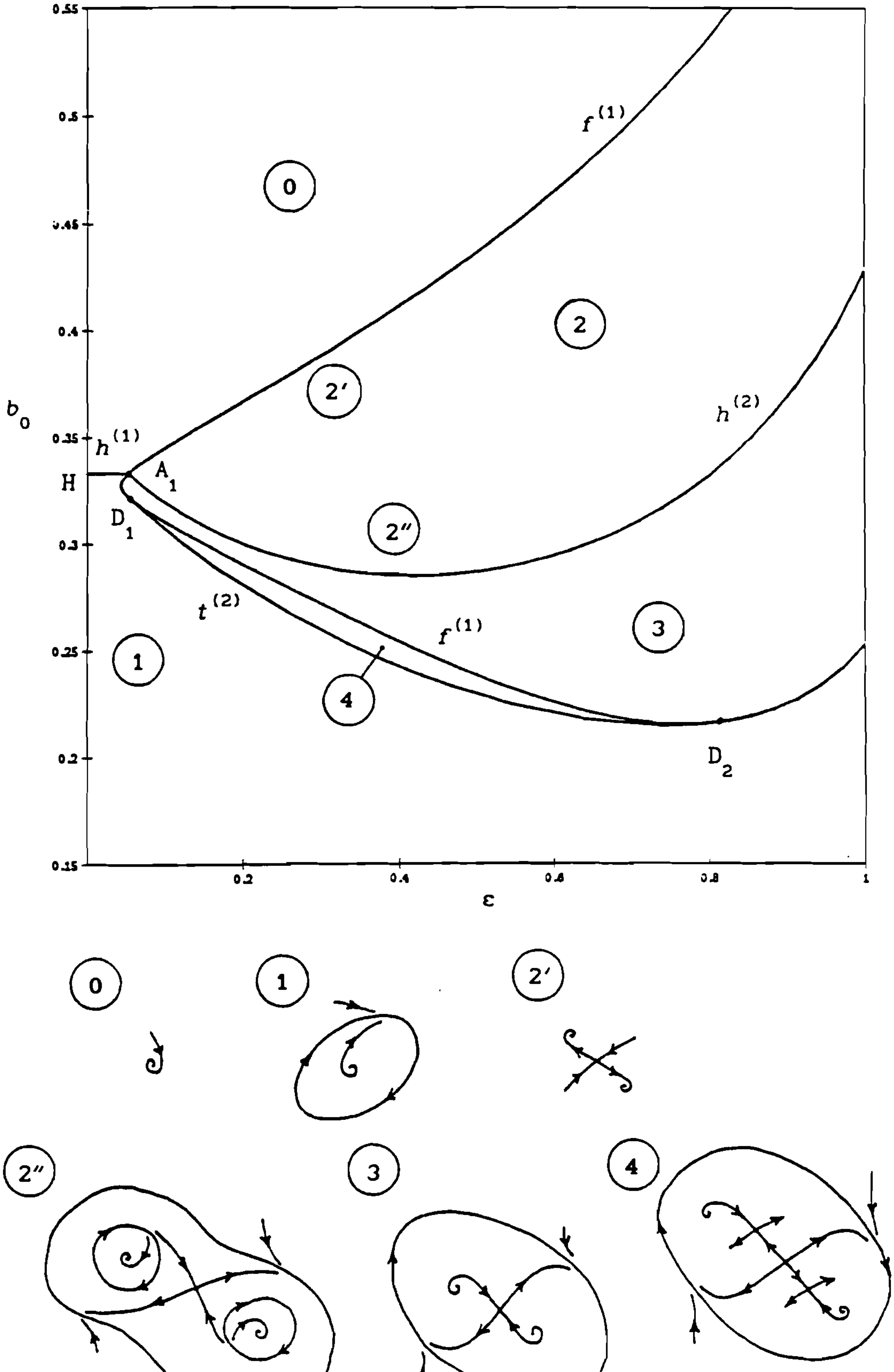


Fig.2. Bifurcation diagram of system (5)-(7) for the case $r < r_2$. The parameter values are $r = 0.73 \cdot 2\pi$, $e = 1$, $a = 2 \cdot 2\pi$, $d = 2\pi$.

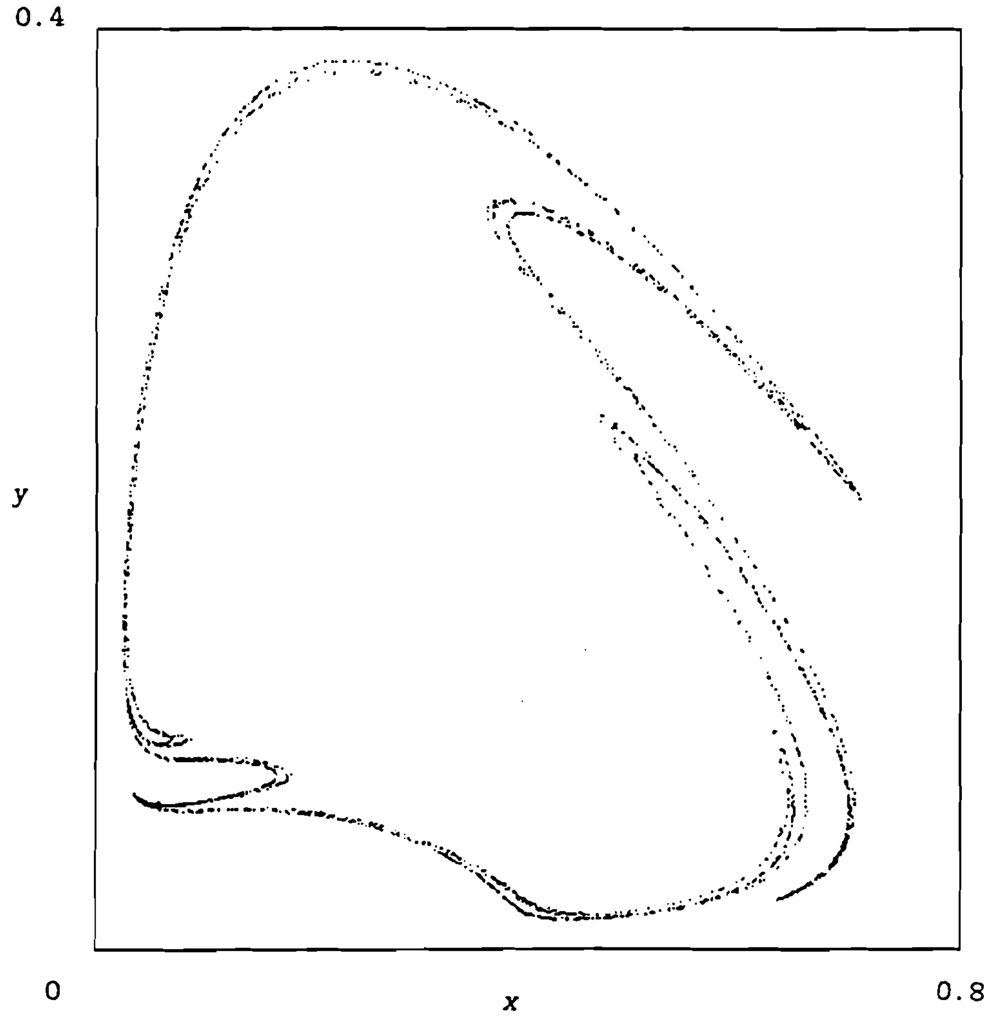


Fig.3. A strange attractor of system (5)-(7) appearing through torus destruction. The parameter values are $r = 0.73\cdot 2\pi$, $b_0 = 0.28$, $e = 1$, $a = 2\cdot 2\pi$, $d = 2\pi$, $\varepsilon = 0.35$.

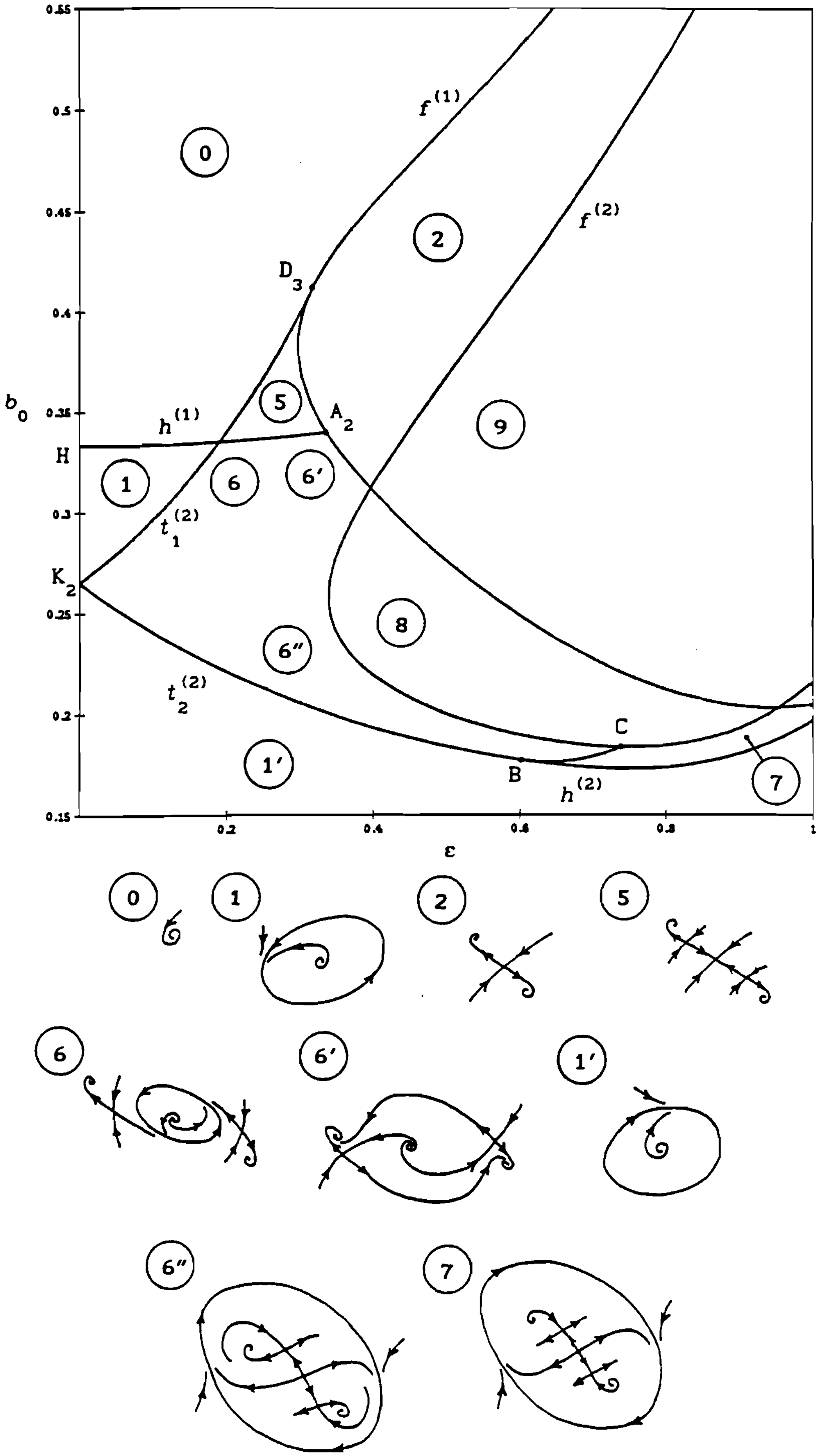


Fig.4. Bifurcation diagram of system (5)-(7) for the case $r_2 < r < r_1$. The parameter values are $r = 2\pi$, $e = 1$, $a = 2\cdot 2\pi$, $d = 2\pi$.

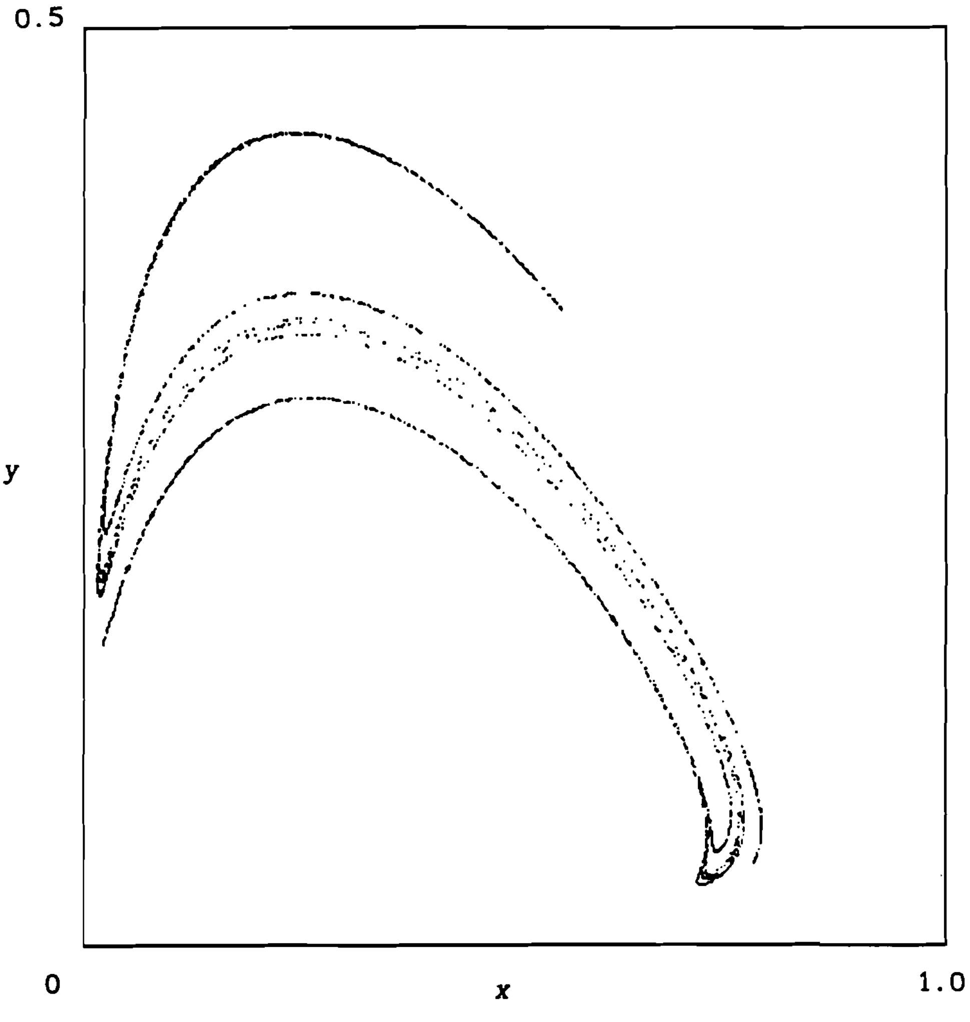


Fig.5. A strange attractor of system (5)-(7) appearing through a cascade of period doublings. The parameter values are $r = 2\pi$, $b_0 = 0.4$, $e = 1$, $a = 2\cdot 2\pi$, $d = 2\pi$, $\varepsilon = 0.7$.

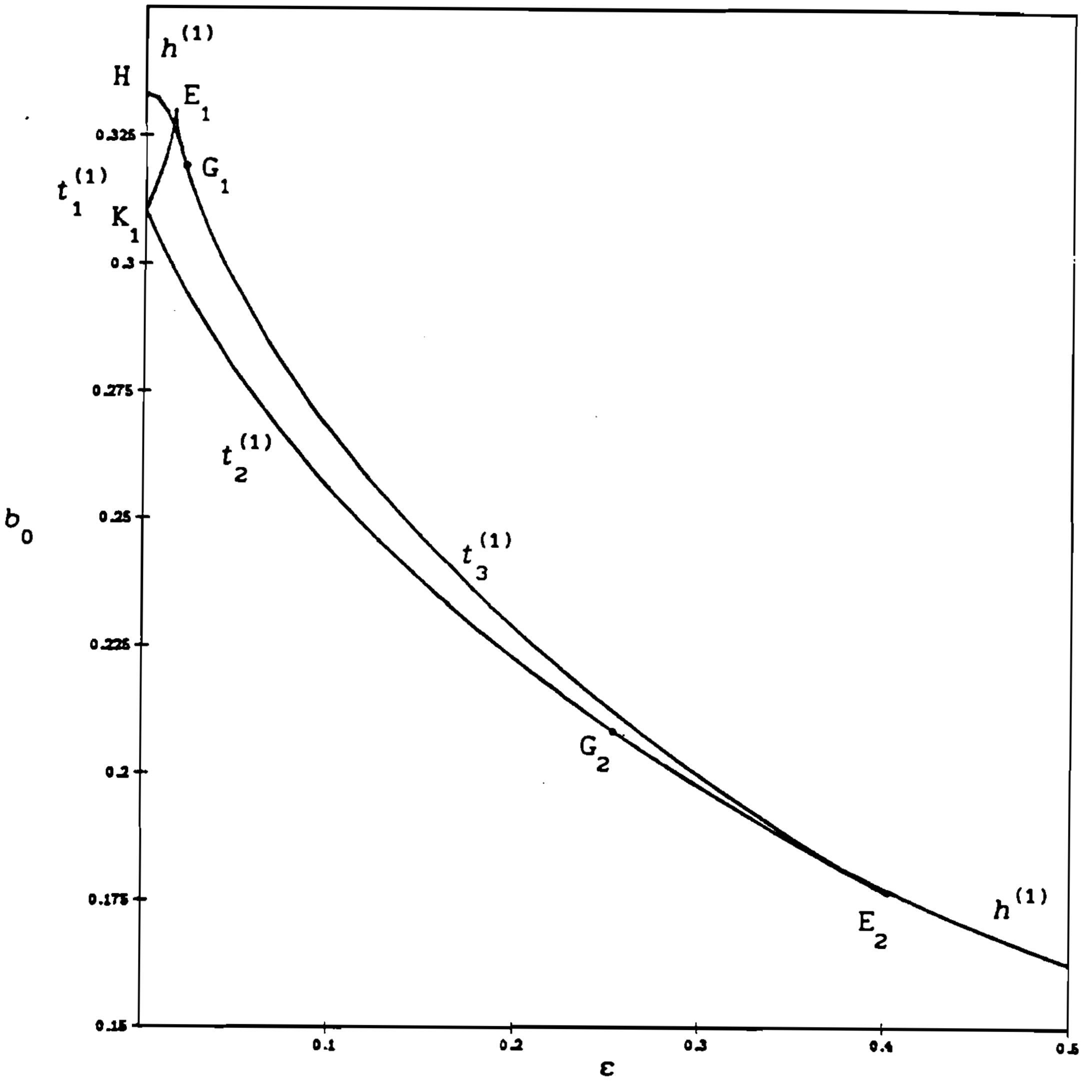


Fig.6. Part of the parametric portrait of system (5)-(7) for the case $r > r_1$ (the rest of the portrait is like in **Fig.4**). The parameter values are $r = 3.3 \cdot 2\pi$, $e = 1$, $a = 2 \cdot 2\pi$, $d = 2\pi$.

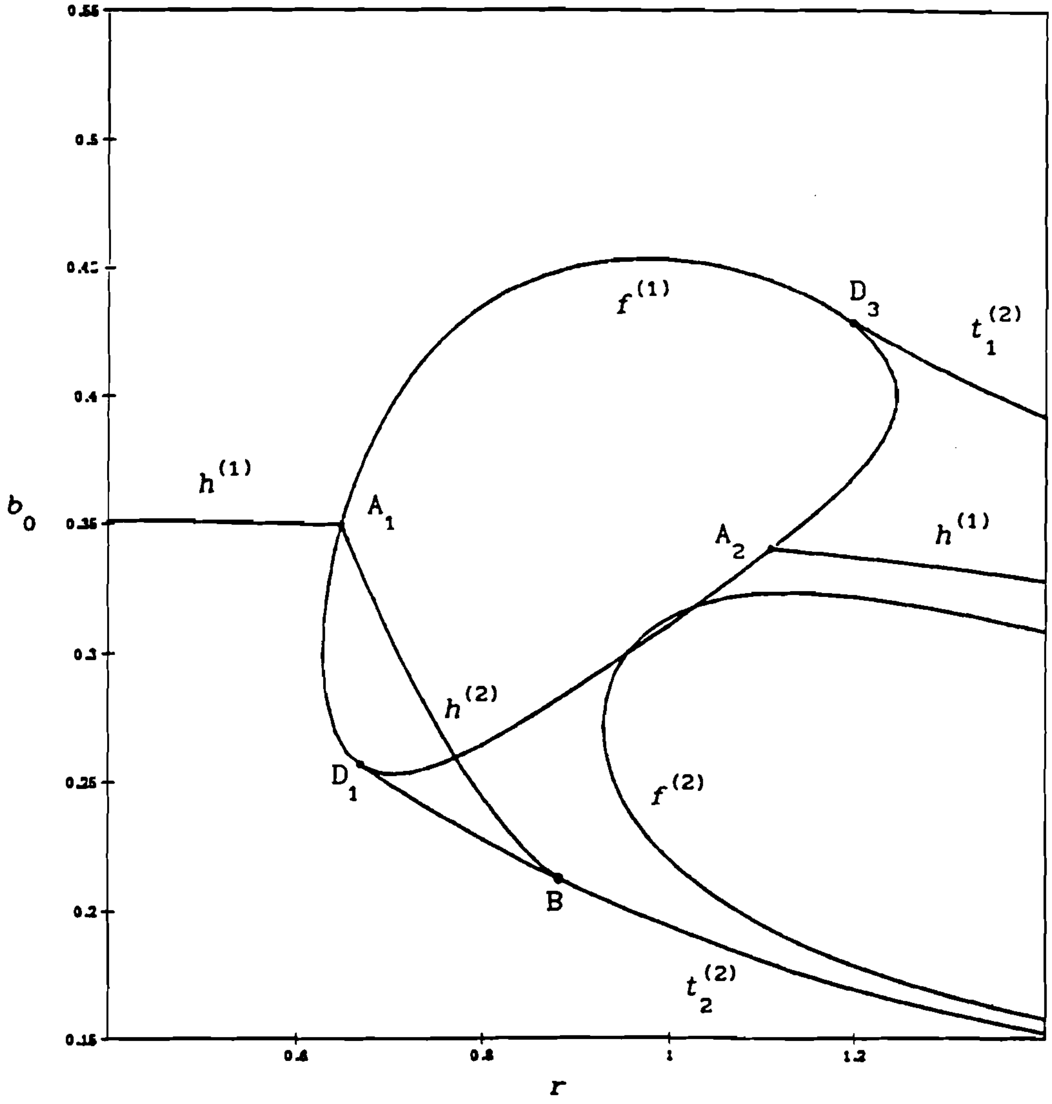


Fig.7. Parametric portrait of system (5)-(7) in the (r,b_0)-plane for ε = 0.4 and e = 1, a = $2\cdot 2\pi$, d = 2π. Note that the flip bifurcation curve $f^{(1)}$ is closed. Labels of points and curves correspond to those in Figs.2, 4.