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Multiple Attractors, Catastrophes and Chaos in Seasonally Perturbed Predator-Prey Communities

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Foreword

This paper presents the analysis of a periodically forced second order nonlinear dynamical system describing predator-prey communities. Six different seasonality mechanisms are identified and compared in terms of bifurcation diagrams. The analysis is carried out by means of an interactive package which detects Hopf, flip and fold bifurcations curves as well as codimension two bifurcation points. The results are in agreement with the general theory of periodically perturbed Hopf bifurcations. This work shows that complex environmental issues can be highlighted by suitably combining basic results of nonlinear system theory and powerful numerical techniques.

Alexander B. Kurzhanski
Chairman
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Abstract

The classical predator-prey model is considered in this paper with reference to the case of periodically varying parameters. Six elementary seasonality mechanisms are identified and analyzed in detail by means of a continuation technique producing complete bifurcation diagrams. The results show that each elementary mechanism can give rise to multiple attractors and that catastrophic transitions can occur when suitable parameters are slightly changed. Moreover, the two classical routes to chaos, namely, torus destruction and cascade of period doublings, are numerically detected. Since in the case of constant parameters the model cannot have multiple attractors, catastrophes, and chaos, the results support the conjecture that seasons can very easily give rise to complex population dynamics.

Acknowledgements

The first author would like to thank C.S. Holling with whom in the Summer of 1985 he had stimulating discussions which have originated this study. Some of the results presented in this paper were actually anticipated by Holling on a purely intuitive basis.

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1 Introduction

The study of ecological systems driven by periodic external forces is of great importance since, with almost no exception, population communities are imbedded in periodically varying environments. Temperature variations strongly influence the reproduction rate of bacteria during the day, moon and tide cycles regulate migration rates of numerous species in aquatic and terrestrial ecosystems, light intensity controls photosynthesis during the seasons, hunting perturb game stocks once a year. It is therefore quite natural to try to identify the functional role that seasons play in the behavior of population communities. In particular, a basic problem is to understand if the magnitude of the seasonal variations is related with the complexity of the system. Indeed, it is known since long ago that nonlinear mechanical and electronic systems described by Duffing and Van der Pol equations have a very simple dynamic behavior in the constant parameter case, but become very complex (multiplicity of attractors, catastrophes, and chaos) when they are periodically perturbed (Guckenheimer and Holmes, 1986). Another important example in a different field is the classical SEIR epidemic model which has a globally stable equilibrium in the constant parameter case and a great number of modes of behavior in the periodically varying case (Schwartz and Smith, 1983; Aron and Schwartz, 1984; Kot *et al.*, 1988; Olsen *et al.*, 1988).

In this paper we prove that the classical predator-prey model, composed by a logistic prey and a Holling's type predator, is also very sensitive to seasonality. In the constant parameter case the model has a supercritical Hopf bifurcation and therefore has only one mode of behavior for each combination of the parameters: a globally stable equilibrium or a globally stable limit cycle. For small magnitudes of the seasonal variations of the parameters the equilibrium is replaced by a periodic solution with the same period of the perturbation (say, period 1), while the limit cycle is, in general, replaced by a quasi-periodic solution (torus). Nevertheless, if the parameter values are such that the period of the limit cycle of the unperturbed system is approximately k times bigger than the period of the forcing function ($k =$ integer), then even a small periodic perturbation of a parameter can give rise to "phase-locking", i.e., to stable period k periodic solutions (called subharmonics). This well-known phenomenon (Guckenheimer and Holmes, 1986) is particularly relevant (and therefore easy to detect numerically) for $k = 2$ and $k = 3$. Period 2 and 3 subharmonics can coexist with the basic period 1 solution as well as with quasi-periodic solutions or with strange attractors obtained through torus destruction. Obviously, the presence of two (or more) attractors, each one having its own basin of attraction, makes the system particularly sensitive to random disturbances. Moreover, some of the bifurcations characterising the system (for example, tangent and flip bifurcations) are such that small variations of a parameter can entail "catastrophic transitions" between different attractors. Finally, for high magnitudes of the seasonal variations the period 2 and 3 subharmonics can very easily undergo a cascade of period doublings ending in a strange attractor. Some of these attractors are quite similar to those discovered by Ueda for the periodically perturbed Duffing equation (Guckenheimer and Holmes, 1986).

This is not the first contribution on periodically forced ecosystems. Discrete-time models (maps), in which the unit time step coincides with the period of the forcing function, have been used to show that quasi-periodic and chaotic solutions are possible in population dynamics (see, for example, May, 1974; Kot and Schaffer, 1984; Lauwerier and Metz, 1986). Models of this kind are very 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). More interesting continuous time models with periodically varying parameters have been used to show that seasonality can support coexistence of competing species (Cushing, 1980; De Mottoni and Schiaffino, 1981; Smith, 1981; Butler *et al.*, 1985; Namba, 1986), and that periodic Lotka-Volterra predator-prey systems can have a great variety of periodic solutions (Cushing, 1977; Bardi, 1981; Cushing, 1982). Nevertheless, these studies are somehow incomplete, because they do not touch the problem of deterministic chaos. On the contrary, more recent contributions on second order periodically varying predator-prey systems (Inoue and Kamifukumoto, 1984; Schaffer, 1988; Toro and Aracil, 1988; Allen, 1989; Kuznetzov *et al.*, 1991) deal with such a problem and are much closer, at least in spirit, to the present analysis. Specific comments on these contributions can be found in the following sections. Here it suffices to say that the analysis presented in this paper is much more accurate and complete and allows one to synthetically interpret the results. Some interesting analogies can also be found with a very recent work (Kot *et al.*, 1991) on a third order chemostat model with periodically varying concentration of the inflowing substrate.

Finally, we would like to mention that 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 nonlinear phenomena (Sugihara and May, 1990). 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 (Roberston *et al.*, 1990). A low dimensional strange attractor has been ascertained in the Canadian Lynx population by applying Taken's 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 and Almiral, 1989). But the most convincing and detailed analysis showing evidence of chaos in a periodically perturbed population is, with no doubt, the study on 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. Nevertheless, we would like to stress that the ultimate goal of this paper is only to show that the analysis of the classical predator-prey model supports the conjecture that seasons can generate very complex ecosystems dynamics, comprising catastrophes and chaos. The reinforcement of this conjecture through the analysis of field data and laboratory experiments is certainly a much more ambitious and difficult task.

2 THE MODEL AND THE SIX SEASONALITY MECHANISMS

The model we discuss in this paper is the classical predator-prey model used in the last twenty years to interpret the behavior of many predator-prey communities, namely

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

$$\dot{y} = y[e\frac{ax}{b+x} - d] \tag{2}$$

where the six parameters r, K, a, b, d, e are positive and x and y are the numbers of individuals of prey and predator populations or suitable (but equivalent) measures of their density or biomas. 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 quality and amount of food available to the prey population and can therefore undergo synchronous periodic variations during the year.

The function

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

appearing in Eqs. (1), (2) is the type 2 *functional response* proposed by Holling (Holling, 1965), which is, by far, the most commonly used in these kind of studies. It represents the prey biomass destroyed by each predator in one unit of time and can be justified as follows (for a more detailed interpretation see Metz and 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 (resting time) of the predator occupy a fraction u of its time, we can write

$$\frac{s}{x}q(x) + hq(x) + u = 1$$

from which Eq. (3) follows with

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

Thus, $q(x)$ 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. Finally, 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.

Of course, the parameters must be time-varying if relevant environmental factors periodically fluctuate in time. For simplicity we consider only sinusoidal perturbations so that for any periodic parameter p in Eqs. (1), (2) we write

$$p = p_0(1 + \varepsilon \sin 2\pi t)$$

where p_0 is the average value of p and ε is the "degree" of seasonality (notice that εp_0 is the magnitude of the perturbation). Obviously, $0 \leq \varepsilon \leq 1$ because p cannot be negative: $\varepsilon = 0$ corresponds to absence of seasonality, while $\varepsilon = 1$ means that the maximum value of the parameter is twice its average value.

Real predator-prey communities are characterized by many seasonality mechanisms so that many, if not all, parameters of model (1), (2) vary periodically. Moreover, these periodic variations are often not in phase, because, even when the different seasonality mechanisms have a common physical origin, their influence reaches its maximum at different times. For example, light intensity and water temperature influencing in different ways phytoplankton-zooplankton communities are out of phase of one or two months in relatively large lakes, although they both depend upon the sun cycle. In order to avoid a too heavy analysis, we only deal with "elementary" seasonality mechanisms, namely with phenomena that entail periodic variations of a single parameter in model (1), (2) or periodic but synchronous variations of two parameters. At this aim, we identify six elementary mechanisms denoted by $(i), (ii), \ldots, (vi)$ in the following. The first one entails the synchronous variation of the intrinsic growth rate r and of the carrying capacity K, while all others imply the periodic variation of one parameter.

(i) Amount of food available to prey (r, K)

The intrinsic growth rate r in (1) is the difference between basic birth and death rates of the prey. Hence r increases with the amount of food available to the prey community, so that, $r = r_0\ (1 + \varepsilon \sin 2\pi t)$. Since, on the contrary, the prey intraspecific competition (r/K) is not influenced by the amount of food available to the prey it follows that $K = K_0\ (1 + \varepsilon \sin 2\pi t)$.

(ii) Prey intraspecific competition (K)

Surplus of prey mortality at high densities due to competition for special niches or to epidemics can be enhanced in some seasons. If this is the case, the carrying capacity varies periodically, i.e., $K = K_0\ (1 + \varepsilon \sin 2\pi t)$.

(iii) Caloric content of the prey (e)

If the caloric content of the prey varies during the year, like in some plant-herbivore communities, the energy available to the predator for reproduction varies consistently. Hence the efficiency varies periodically, i.e., $e = e_0\ (1 + \varepsilon \sin 2\pi t)$.

(iv) Predator exploitation (d)

The periodic presence of a superpredator exploiting the predator community gives rise to periodic variations of the predator death rate, i.e., $d = d_0\ (1 + \varepsilon \sin 2\pi t)$. Phytoplankton-zooplankton communities with first year class fish feeding on zooplankton during the Summer and tree-insect pest systems controlled by migratory insectivores are examples of this class.

(v) Predator and prey mimicry (b)

When the degree of mimicry of the prey (predator) is not constant during the year or when variations of the habitat facilitate the escape or the capture of the prey in some specific season, the parameter identifying the searching time in Eq. (4) varies periodically. This implies (see Eq. (4)) that the half saturation constant varies in the same way, i.e. $b = b_0\ (1 + \varepsilon \sin 2\pi t)$.

(vi) Predator resting time (a)

If the resting time of the predator fluctuates during the year, as in populations characterized by some degree of diapause, the parameter u in (4) varies periodically. Thus the maximum harvest rate of the predator varies in the same manner, i.e., $a = a_0\ (1 + \varepsilon \sin 2\pi t)$.

The only "single parameter" perturbation we have excluded in our analysis is that of the intrinsic growth rate r, because we have not found an interesting biological interpretation for it.

In this respect we must point out that the analysis carried out in (Inoue and Kamifukumoto, 1984; Toro and Aracil, 1988; Allen, 1989) refers exactly to this case. Moreover, the discussion in (Inoue and 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 and Aracil, 1988; Allen, 1989) only the results of a few simulations are shown. On the contrary, the discussion in (Schaffer, 1988) (corresponding to our third elementary mechanism) is more systematic and points out that chaos can be obtained through torus destruction. This is confirmed by our analysis which, nevertheless, shows that the period doubling route to chaos is also present as was already proved for the fifth elementary mechanism in (Kuznetsov *et al.*, 1991) and for a third order chemostat model composed by limiting substrate, heterotrophic prey and holozoic predator in (Kot *et al.*, 1991).

3 THE CONSTANT PARAMETER CASE

In the absence of seasonality ($\varepsilon = 0$), system (1), (2) is an autonomous second order system where all parameters and state variables are nonnegative. The analysis of the local stability of its equilibria (May, 1972) shows that there is a *Hopf* bifurcation at

$$K = b\frac{ea + d}{ea - d} \tag{5}$$

and a *transcritical* bifurcation at

$$K = b\frac{d}{ea - d} \tag{6}$$

The Hopf bifurcation is always supercritical (the computation of its Liapunov number is relatively easy if one considers the orbitally equivalent system obtained by multiplying Eqs. (1), (2) by $(b + x)$) and the asymptotic period of the appearing limit cycle is

$$T_H = 2\pi\left(\frac{K}{rbd}\right)^{1/2} \tag{7}$$

Moreover, the limit cycle does not bifurcate since it is unique (Cheng, 1981; Wrzosek, 1990). Thus the parameter space is partitioned into three regions separated by the manifolds (5) and (6). 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 sufficiently high values of the carrying capacity K, the attractor is a stable limit cycle. For decreasing values of K this cycle shrinks and disappears through a Hopf bifurcation. Then the attractor is a stable equilibrium which is positive for intermediate values of K and trivial (absence of predator population) for low values of K.

4 METHOD OF INVESTIGATION

For $\varepsilon > 0$ system (1), (2) 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 $(x(0), y(0)) \to (x(1), y(1))$ can be defined (Arnold, 1982; Guckenheimer and Holmes, 1986). Fixed points of the k-th iterate of the map correspond to periodic solutions (cycles) of Eqs. (1), (2) with period k (we will refer to these points as *period k fixed points*). Closed and regular invariant curves of the Poincaré map correspond to quasi-periodic solutions (*invariant tori*), while irregular invariant sets correspond to chaotic solutions (*strange attractors*).

Non-saddle (i.e., attracting or repelling) and saddle cycles of period k of system (1), (2) can bifurcate at some parameter values. We use the following notation for the corresponding 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: $\mu_{1,2}^{(k)} = e^{\pm i\omega}$, $\omega > 0$. When curve $h^{(k)}$ is crossed an attracting (repelling) cycle of period k bifurcates into an attracting (repelling) quasi-periodic solution and a repelling (attracting) cycle of period k.

$t^{(k)}$ – **tangent (fold) bifurcation curve.** For parameter values on this curve the map has a period k fixed point with a multiplier $\mu_1^{(k)} = 1$. When this curve is crossed a saddle and a non-saddle cycle of period k collide and disappear.

$f^{(k)}$ – **flip (period doubling) bifurcation curve.** For parameter values on this curve the map has a period k fixed point with a multiplier $\mu_1^{(k)} = -1$. When this curve is crossed a saddle (non-saddle) cycle of period k bifurcates into a non-saddle (saddle) cycle of period k and a saddle (non-saddle) cycle of period $2k$.

The behavior of the system for parameter values close to these curves are described in (Arnold, 1982; Guckenheimer and Holmes, 1986). It is worthwhile noticing that tangent and flip bifurcations always involve saddle cycles, while Hopf bifurcations are only concerned with attractors and repellors. Moreover, Hopf bifurcations always involve an attractor, while tangent and flip bifurcations sometimes do not. Although all curves $h^{(k)}$, $t^{(k)}$, $f^{(k)}$ are needed if one likes to fully understand the structure of the bifurcations of a dynamical system, only those concerning attractors are useful to classify the asymptotic modes of behavior of the system. In the following, in order to facilitate the biological interpretation of the results, we will not display bifurcation curves which do not refer to attractors. Readers interested in the bifurcation structure of the model can refer to (Kuznetsov *et al.*, 1991), where the bifurcation curves corresponding to our fifth elementary mechanism are fully displayed.

The bifurcation curves presented in the next section have been computed by means of a continuation method interactively supported by the program LOCBIF developed by the third 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 (1), (2). 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

$$\begin{aligned} &R[\det(A-\mu I),\ \det(\mu A - I)] = 0 && \text{(for } \textit{Hopf} \text{ bifurcation)},\\ &\det(A - I) = 0 && \text{(for } \textit{tangent} \text{ bifurcation)},\\ &\det(A + I) = 0 && \text{(for } \textit{flip} \text{ bifurcation)}, \end{aligned}$$

where $R[\cdot,\cdot]$ stands for the *resultant* of two ponlynomials (Lancaster and 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. The program LOCBIF also produces phase portraits of the Poincaré map, continues fixed points in any (x, y, p_1)-space and detects codimension one bifurcations.

5 BIFURCATION CURVES

In this section we present and discuss the bifurcation curves of system (1), (2) for the six elementary seasonality mechanisms identified in Sec. 2. The reference values of the parameters are the following

$$e = K = 1 \quad r = d = 2\pi \quad a = 2.2\pi \quad b = 0.3. \tag{8}$$

For these values, the system oscillates on a limit cycle (K is slightly bigger than $b(ea+d)/(ea-d)$ (see Eq. (5)), and the period of the cycle (evaluated numerically) is $T = 1.85$. Thus, in the parameter space we are not too far from Hopf bifurcations (5) and from $k = 2$ resonances, i.e., values of parameters giving rise to a cycle of period two times bigger than the period of the forcing function. Actually, the reference values of the parameters have been tuned intentionally in this way, because these are the most favourable conditions to point out periodic and quasi-periodic behavior, as well as phase-locking of a periodically forced dynamical system. The reader interested in the analysis of the bifurcations of system (1), (2) in other regions of the parameter space can refer to (Kuznetsov *et al.*, 1991) where the fifth seasonality mechanism is discussed in some more detail.

For each seasonality mechanisms the discussion is carried out with respect to two parameters. The first is the degree of seasonality ε, which varies from 0 to 1, and the second is the average value of the periodically varying parameter, i.e., K_0 (with $r_0 = 2\pi \cdot K_0$) in case (i), K_0 in case (ii), e_0 in case (iii), and so on. All other parameters are kept constant at their reference value (8). The second parameter varies in a range that contains the value for which the unperturbed system has a Hopf bifurcation (easily computable from (5)) and the resonant value for which the period of the limit cycle for $\varepsilon = 0$ is equal to 2.

The six diagrams $(i), (ii), \ldots, (vi)$ of Fig. 2 display the bifurcation curves of system (1), (2) for the corresponding six seasonality mechanisms. Five bifurcation curves are drawn on these diagrams, namely, $h^{(1)}$, $h^{(2)}$, $f^{(1)}$, $f^{(2)}$, and $t^{(2)}$, the last one composed by two branches ($t_1^{(2)}$ and $t_2^{(2)}$). These bifurcation curves are present in all cases, but curve $h^{(2)}$ cannot be seen in cases (i), (ii), (iii), (vi) because of the particular range of the parameters. The curves $f^{(1)}$, $f^{(2)}$ and $t^{(2)}$ are not complete, because the branches not involving attractors have been disregarded. The bifurcation curves $f^{(4)}$ and $f^{(8)}$ have also been obtained but they are not shown in Fig. 2 because they almost coincide with $f^{(2)}$. Nevertheless, they must be kept in mind because they clearly indicate one of the two routes to chaos (i.e., cascade of period doublings).

If we compare the six diagrams 2(i), ..., 2 (vi) we immediately recognize that turning the fourth and fifth upside down we obtain six topologically equivalent diagrams. This fact is very important and clearly indicates that the six seasonality mechanisms give rise to the same phenomena. Let us therefore consider and interpret in detail the qualitative bifurcation diagram of Fig. 3 which is equivalent to those of Fig. 2, but contains, for the sake of clarity, the bifurcation curves $f^{(4)}$ and $h^{(4)}$. The parameter p_0 of this diagram is directly (in cases (i), (ii), (iii), and (vi)) or inversely (in cases (iv) and (v)) related to the average value of the periodically varying parameter. On the p_0-axis there is point H (computable from (5)) corresponding to the Hopf bifurcation of the unperturbed system. Below that point, the attractor of the unperturbed system is an equilibrium, while above it the attractor is a limit cycle. Thus, for small values of ε and below point H we have period 1 periodic solutions, while for small values of ε and above point H we have quasi-periodic solutions. Consistently, a bifurcation curve $h^{(1)}$ rooted at point H separates the two regions. When this curve is crossed from below, the forced stable cycle of period 1 smoothly bifurcates into a stable quasi-periodic solution. While continuing curve $h^{(1)}$

from the left to the right the multipliers $\mu_{1,2}^{(1)} = e^{\pm i\omega}$ of the Poincaré map vary and become equal to -1 when the terminal point A is reached.

Point A is a codimension two bifurcation point, called *strong resonance* 1:2, studied in (Arnold, 1982) by means of the normal form approach. The two coefficients of the normal form are of opposite sign and this suffices to say that only two bifurcation curves, namely, a Hopf $h^{(1)}$ and a flip $f^{(1)}$, are rooted at point A (as already said, the branch of $f^{(1)}$ not involving attractors is not shown in the figure). Curve $f^{(1)}$ can be generated by the continuation technique starting from point A. Along curve $f^{(1)}$ the normal form coefficient (computed as in (Kuznetsov and Rinaldi, 1991)) varies and becomes equal to 0 at point B, which is therefore a codimension two bifurcation point. Thus, curve $f^{(1)}$ is divided into two segments (AB and BE) and the period doubling takes place in opposite directions on these two segments, namely from region 4 on segment AB and from region 1 on segment BE. More precisely, when curve $f^{(1)}$ is crossed from region 1 to region 4 the forced cycle of period 1 loses stability and smoothly bifurcates into a stable period 2 cycle. On the contrary, if $f^{(1)}$ is crossed from region 3 to region 4, the stable cycle of period 1 collides with a saddle cycle of period 2 and becomes a saddle cycle of period 1.

The codimension two bifurcation point B is the terminal point of one of the two branches of a tangent bifurcation curve $t^{(2)}$ (Afrajmovich *et al.*, 1991). The two branches ($t_1^{(2)}$ and $t_2^{(2)}$) originate at point T_2 on the p_0-axis where the limit cycle of the unperturbed system has period 2. Some details concerning the system behavior near point T_2 can be found in (Guckenheimer and Holmes, 1986). When $t_1^{(2)}$ and $t_2^{(2)}$ are crossed from the left, close to point T_2, a stable cycle of period 2 and a saddle cycle of period 2 appear. When branch $t_2^{(2)}$ is continued from point T_2 the first multiplier $\mu_1^{(2)}$ remains equal to 1 while the second $\mu_2^{(2)}$ varies smoothly and becomes equal to 1 at the codimension two bifurcation point C. After this point, the bifurcation curve $t_2^{(2)}$ does not involve attractors and has not been drawn in Fig. 3.

Point C is the root of a Hopf bifurcation curve $h^{(2)}$ ending at point D where the two multipliers are equal to -1 and the two coefficients of the normal form have the same sign. When $h^{(2)}$ is crossed from below, a stable cycle of period 2 bifurcates into an unstable cycle of period 2 and in a stable quasi-periodic solution.

Point D is the root of a bifurcation curve $f^{(2)}$ (and of a bifurcation curve $h^{(4)}$). When curve $f^{(2)}$ is crossed from region 4 to region 6, a stable periodic solution of period 2 smoothly bifurcates into a stable periodic solution of period 4.

Finally, the analysis shows that flip bifurcation curves $f^{(4)}$, $f^{(8)} \ldots$ exist in the vicinity of curve $f^{(2)}$ (the difference between curves $f^{(2)}$ and $f^{(4)}$ is intentionally magnified in Fig. 3). This cascade of period doublings results in strange attractors which can be found in some subregions of region 7.

The quasi-periodic solutions also bifurcate, but their bifurcation sets can not be computed with our continuation technique. Nevertheless, in accordance with (Guckenheimer and Holmes, 1986), we can say that the stable quasi-periodic solution appearing on $h^{(1)}$ disappears through a homoclimic structure on a bifurcation set resembling a curve connecting point A with a point on branch $t_1^{(2)}$ close to point T_2. Thus, in this region we have strange attractors obtained through torus destruction see (Schaffer 1988 and Kuznetsov *et al*, 1991) for some examples.

Finally, we must point out that the same kind of bifurcations exist for cycles of period 3 (as well as for cycles of higher period). Indeed, two branches $t_1^{(3)}$ and $t_2^{(3)}$ of a tangent bifurcation originate at a point on the p_0-axis where the period of the limit cycle of the unperturbed system is equal to 3. When these branches are crossed from the left, a stable cycle of period 3 appears together with a saddle cycle of period 3. Then, the stable cycle undergoes a cascade of period doublings $f^{(3)}$, $f^{(6)}$, ... None of these bifurcation curves is shown in our figures in order to maintain them as readable as possible.

6 MULTIPLE ATTRACTORS, CATASTROPHES AND CHAOS

The qualitative bifurcation diagram of Fig. 3 points out a number of interesting facts which prove that seasonalities can generate rather complex dynamics.

The first and most important fact is the existence of multiple attractors. Indeed, for a constant value of ε and for increasing values of p_0, a stable cycle of period 2 first coexists with a stable cycle of period 1 (in region 3 of Fig. 3), then with a quasi-periodic solution (in region 4, just above curve $h^{(1)}$) and, finally, with a strange attractor obtained through torus destruction (in a subregion of region 4). Coexistence of cycles of period greater than or equal to 3 with quasi-periodic solutions and strange attractors are also possible in the regions delimited by the branches $t_1^{(k)}$ and $t_2^{(k)}$, $k \geq 3$ of tangent bifurcation curves not shown in Fig. 3. Moreover, coexistence of triplets of attractors like, for example, cycles of period 2 and 3 and strange attractors, cannot be excluded although we have not found numerical evidence of it during our computational experiments.

A second relevant fact is that some of the bifurcations shown in Fig. 3 are catastrophic, so that even very small variations of a parameter can sometimes entail a radical change of behavior of the system. Assume, for example, that the system behaves in region 1 of Fig. 3, just below the Hopf bifurcation curve $h^{(1)}$. In this region the system has only one stable mode of behavior, namely a cycle of period 1. If p_0 is kept constant and ε is slowly increased, the stable cycle of period 1 varies smoothly but gradually loses stability when approaching the flip curve $f^{(1)}$.

When line AB is crossed the attractor disappears because on that line the stable cycle of period 1 collides with a saddle cycle of period 2 and becomes a saddle cycle of period 1. Therefore, after $f^{(1)}$ has been crossed, the system moves toward another attractor, which, in the present case, is a period 2 cycle. After this catastrophic transition has occured, the system is trapped in the new attractor. Indeed, even if ε is now slowly decreased, so that $f^{(1)}$ is crossed from the right, the stable mode of behavior remains the cycle of period 2. Of course, if ε is further reduced, so that the tangent bifurcation curve $t_1^{(2)}$ is crossed from the right, we will have another catastrophic transition that brings the system back to a period 1 cycle. All this can be summarized by saying that if ε is alternatively increased and decreased so that curves $t_1^{(2)}$ and $f^{(1)}$ are crossed we will have a "hysteresys" involving transitions between cycles of period 1 and 2. Therefore, the catastrophic transitions characterizing the hysteresis involve a sudden variation of the frequency at which the system operates: a rather interesting behavior.

Finally, the third important fact is the existence of deterministic chaos in two different regions of parameter space (see dotted regions of Fig. 3). The first region is characterized by relatively small values of ε and is delimited from below by the bifurcation set on which stable quasi-periodic solutions disappear through homoclimic structures (torus destruction). If p_0 is increased at constant ε starting from a point just above curve $h^{(1)}$ in Fig. 3, a small closed and regular curve on the Poincaré section (stable invariant torus) will first become bigger and bigger and then smoothly lose continuity and degenerate into a fractal set (strange attractor). It is clear from Fig. 3 that these strange attractors can be present only for values of p_0 for which the unperturbed system behaves on a limit cycle. In other words, a predator-prey system which does not autonomously cycle in a constant environment, cannot become chaotic through torus destruction.

The second region of deterministic chaos is characterized by relatively high values of ε and corresponds to the second well-known route to chaos, namely cascade of period doublings $f^{(2)}$, $f^{(4)}$, $f^{(8)}, \ldots$. This region is delimited by a curve $f^{(\infty)}$ where the attractor loses periodicity and becomes chaotic. The curve $f^{(\infty)}$ cannot be found by numerical analysis because it is not possible to distinguish between a periodic cycle with an extremely large period and a genuine chaotic solution. Nevertheless, we can reasonably conjecture that curve $f^{(\infty)}$ is quite close to $f^{(2)}$ because the flip bifurcation curves $f^{(2)}$, $f^{(4)}$, $f^{(8)}, \ldots$ follow, in general, the Feigenbaum accumulation law (Guckenheimer and Holmes, 1986) and all our computations point out that $f^{(4)}$ and $f^{(8)}$ are already almost coinciding with $f^{(2)}$. Fig. 4 shows six chaotic attractors, one for each seasonality mechanism, while Fig. 5 shows the corresponding time series of the y variable (predator) for a time interval equal to 25. All attractors have been obtained with the same degree of seasonality $\varepsilon = 0.7$ and with the other parameters (except the time varying ones) at their reference values (8). The corresponding points are denoted by Q in Fig. 2.

The analysis of Figs. 2, 3 proves that the value of p_0 at which curve $f^{(\infty)}$ is minimum is sometimes lower than the value of p_0 corresponding to point H. This implies that this kind of chaotic behavior can occur even if the corresponding unperturbed system does not autonomously cycle. The attractors (iii), (iv), and (v) of Fig. 4 are three examples. This characteristics allows one to further distinguish between the two types of chaos: the first (torus destruction) does not need high degrees of seasonality but requires a strong endogenous tendency to cycle, while the second (period doubling) requires high degrees of seasonality but can develop also in systems that would not cycle in a constant environment.

7 CONCLUDING REMARKS

The classical predator-prey model has been studied in this paper with reference to the case of periodically varying parameters. Six elementary seasonality mechanisms have been identified and analyzed in detail by means of a continuation technique automatically producing Hopf, tangent and flip bifurcation curves of periodic solutions of any period. The results have been compared and summarized through a general qualitative bifurcation diagram (Fig. 3) which allows one to classify and interpret the main modes of behavior of the model. The general conclusion is that for suitable values of the parameters there are multiple attractors, catastrophes and strange attractors. Since, on the contrary, the unperturbed system has always a unique attractor (an equilibrium or a limit cycle) our analysis proves that seasons can easily give rise to very complex predator-prey dynamics. This fact had already been established (Inoue and Kamifukumoto, 1984; Schaffer, 1988; Toro and Aracil, 1988; Allen, 1989) but not synthetically interpreted in terms of bifurcations, since the analysis was carried out only through simulation.

From a biological point of view the most interesting results are the following. If the degree of seasonality is small, the predator and the prey populations asymptotically vary in a periodic or in a quasi-periodic way. The period of the oscillations coincides with that of the forcing function (normalized to 1) if the system does not autonomously cycle when there are no seasons. On the contrary, if the unperturbed system behaves on a limit cycle, then the introduction of a small degree of seasonality transforms the cyclic behavior into a quasi-periodic one. Moreover, in some subregions of the parameter space, there are also subharmonics, namely periodic solutions of period k times bigger than that of the forcing function ($k =$ integer). In particular, subharmonics of period 2 and 3 are relevant and have indeed been detected numerically in all cases we have analyzed. Thus, multiplicity of attractors, for example, coexistence of periodic solutions of period 2 or 3 and quasi-periodic solutions is possible even at very low degrees of seasonality. This is also true for higher magnitudes of the seasonal variations at which, for example, subharmonics of period 2 can coexist with the basic period 1 solution (region 3 of Fig. 3). Actually, if the degree of seasonality is slowly varied and alternatively increased and decreased, the system can repeatedly undergo catastrophic transitions between periodic solutions of period 1 and 2 (hysteresys with frequency switches). Finally, the two classical routes to chaos, i.e., torus destruction and cascade of period doublings, are present. Strange attractors of the first kind are obtained by introducing a low degree of seasonality in a predator-prey community which, in the absence of seasons, behaves on a limit cycle, while the second type of attractors can be generated, with a higher degree of seasonality, even when the system does not autonomously cycle. This means that chaos can be present in a predator-prey community provided that the exhogeneous and endogeneous sources of periodicities are, as a whole, sufficiently strong.

As far as the method of analysis is concerned, we can summarize our experience by saying that continuation techniques producing bifurcation curves are very effective when they are used in conjunction with "detectors" of codimension two bifurcation points. Indeed, our bifurcation diagrams have been obtained in the following way. We have first generated curve $h^{(1)}$ starting from the Hopf bifurcation of the unperturbed system (point H in Fig. 3) and ending at point A, which is a codimension two bifurcation point. Then, we have produced the flip curve $f^{(1)}$, starting from point A, thus finding a second codimension two bifurcation point, namely point B. From this point we have generated the tangent bifurcation curve $t^{(2)}$ and found the third codimension two point, namely point C. Continuing like so, we have alternatively obtained bifurcation curves ($h^{(2)}$, $f^{(2)}$, $h^{(4)}$, $f^{(4)}$) and codimension two bifurcation points. Finding these codimension two points is therefore necessary for producing in a systematic way all the bifurcation curves. Of course, at each codimension two bifurcation point one must use the normal form approach to find out how many and which bifurcation curves are rooted at that point. For this reason we believe that packages which incorporate "detectors" and "analyzers" of codimension two bifurcation points are very powerful for discussing the qualitative behavior of nonlinear dynamical systems. Moreover, they are the only serious tool for finding bifurcation curves which are not predicted by the available theories. For example, our bifurcation curves $f^{(2)}$ are not predicted by the known theory of periodically forced Hopf bifurcations (Kath, 1981; Rosenblat and Cohen, 1981; Gambaudo, 1985; Bajaj, 1986; Namachchivaya and Ariaratnam, 1987) (the interested reader can find more details on this matter in (Kuznetsov *et al.*, 1991).

Although the analysis presented in this paper is quite detailed, we believe that there are still interesting questions to be answered and meaningful extensions to be performed. For example, it would be of interest to extend the analysis presented in this paper to predator-prey models which have also tangent and homoclinic bifurcations when they are not periodically perturbed. Among these models we have the case of a logistic prey, a Holling's type predator and a constant Holling's type superpredator, i.e. the most rudimentary food chain model (a more complete study of periodically forced food chain systems involving third order models appears to be very difficult because such models can have chaotic behavior even in the case of constant environment (Hogeweg and Hesper, 1978; Scheffer, 1990; Hastings and Powell, 1991). Another interesting extension would be to revisit the analysis of the periodically forced chemostat model carried out in (Kot *et al.,* 1991) with the use of circle maps. In fact, our continuation technique allows one to find codimension two bifurcation points and is therefore more powerful than the circle map technique. Finally, an interesting direction for further research is the investigation of the synergism among independent sources of periodicity. In particular, it would be interesting to know how chaos could be reinforced or damped by suitably "controlling" the phase between different elementary seasonality mechanisms. Information on this matter would be of particular relevance in the field of renewable resources management, where the time and intensity of stocking and harvesting must be well tuned with the natural periodicity mechanisms in order to avoid undesirable modes of behavior.

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