

# Working Paper

## A Universal Bifurcation Diagram for Seasonally Perturbed Predator-Prey Models

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## *ABSTRACT*

The bifurcations of a periodically forced predator-prey model (the chemostat model), with a prey feeding on a limiting nutrient, are numerically detected with a continuation technique. Eight bifurcation diagrams are produced (one for each parameter in the model) and shown to be topologically equivalent. These diagrams are also equivalent to those of the most commonly used predator-prey model (the Rosenzweig-McArthur model). Thus, all basic modes of behavior of the two main predator-prey models can be explained by means of a single bifurcation diagram.

# ***A UNIVERSAL BIFURCATION DIAGRAM FOR SEASONALLY PERTURBED PREDATOR-PREY MODELS***

Alessandra Gragnani

## ***1. INTRODUCTION***

During the last ten years, a number of studies have been performed on the interactions between seasons (or, more generally, environmental cycles) and internal biological rhythms of ecosystems. By and large, these studies show that these interactions can have spectacular consequences, such as multiplicity of attractors, catastrophes and deterministic chaos (for a recent review see Hastings et al., 1993). Even the simplest predator-prey model has been considered by many authors (Inoue and Kamifukumoto, 1984; Schaffer, 1988; Toro and Aracil, 1988; Allen, 1989; Gary et al., 1993) who have found, mainly through simulations, that chaos can be obtained by increasing the strength of the seasons. A more systematic and complete analysis of the bifurcations of the periodically forced Rosenzweig-McArthur predator-prey model (Kuznetsov et al., 1992; Rinaldi et al., 1993) has shown that chaos can be obtained in the two classical ways, i.e., through torus destruction and through cascade of period doublings. Strange attractors of the first kind are obtained by introducing a low 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 seasonality, even when the system does not autonomously cycle. This means that chaos can be present in a predator - prey community provided that the exogenous and endogenous sources of periodicities are, as a whole, sufficiently strong. This

conclusion was possible after recognizing that the bifurcations of the model were always the same, no matter which parameter was periodically forced. In other words, there exists a bifurcation diagram which qualitatively applies to all possible seasonality mechanisms.

In this paper, we repeat this systematic analysis for a more complex predator-prey model, namely the chemostat model, in which the prey feeds on a limiting nutrient. Thus, the model is three-dimensional and the extension is not trivial. The bifurcations of such a model have already been found for two cases: (i) periodically varying inflow rate (Pavlou and Kevrekidis, 1992) and (ii) periodically varying nutrient concentration of the inflow (Kot et al., 1992). Here we complete the analysis by periodically perturbing the six other parameters: the efficiency and the two parameters identifying the functional response of both populations. Again, the comparison of the eight bifurcation diagrams shows that they are topologically equivalent. But what is even more interesting, is that they are also equivalent to those of the Rosenzweig-McArthur model. We have therefore found a kind of "universal" bifurcation diagram which can be used to interpret all modes of behavior of the two most commonly used predator-prey models when they are periodically forced in all possible ways.

## ***2. THE PERIODICALLY FORCED CHEMOSTAT***

The chemostat model we consider in this paper is the following:

$$\dot{n} = Dn_i - Dn - a_x \frac{n}{b_n + n} x \quad (1a)$$

$$\dot{x} = -Dx + e_x a_x \frac{n}{b_n + n} x - a_y \frac{x}{b_x + x} y \quad (1b)$$

$$\dot{y} = -Dy + e_y a_y \frac{x}{b_x + x} y \quad (1c)$$

where  $n$ ,  $x$  and  $y$  are nutrient, prey and predator concentrations;  $D$  is through-flow;  $n_i$  is nutrient concentration of the inflow;  $a_x$  and  $a_y$  are maximum nutrient uptake of prey and maximum prey uptake of predator;  $b_n$  and  $b_x$  are half-saturation constants, and  $e_x$  and  $e_y$  are efficiencies of prey and predator. The model can be used to describe microbial processes such as those going on in a chemostat or in a wastewater treatment plant where the prey, a bacterial population, feeds on a substrate and the predator, a protozoan population, feeds on bacteria. But chemostat experiments in the laboratory can also be carried out with algae (prey) and zooplankton (predator) in order to mimic the interactions going on in a lake or in a marine environment. In other words, model (1) can be considered a minimum model for plankton dynamics in eutrophic water bodies. Finally, in a more abstract sense, eq. (1) represents the dynamics of any predator-prey assembly with the prey feeding on a limiting resource flowing through the environment. The literature on this model and its extensions is quite rich. For recent reviews, the reader can refer to Pavlou and Kevrekidis, 1992, and Kot et al., 1992.

In the constant parameter case, the chemostat can be studied by means of a reduced (second order) model, since all the trajectories approach exponentially (or lie in) a particular plane of the state space  $(n, x, y)$ . In such a case the model has four different modes of behavior:

1. washout of both populations;
2. washout of predator only;
3. steady coexistence of the two populations;
4. cyclic coexistence of the two populations;

The transitions from 1 to 2 and from 2 to 3 are transcritical bifurcations, while the transition from 3 to 4 is a supercritical Hopf bifurcation (Guckenheimer and Holmes, 1983; Afrajmovich et al., 1991). Thus, except for the first mode, which is obviously non interesting and typical of a chemostat with a very high through-flow, the model has the same modes of behavior (and bifurcations) as the well-known Rosenzweig-McArthur model (see Rinaldi et al., 1993). In the following, we will show that this is also true for the case of periodically varying parameters.

Model(1) has eight parameters  $(D, n_i, a_x, a_y, b_n, b_x, e_x, e_y)$ . If the environment is not constant in time, each one of these parameters must vary in order to keep track of the variations of the interactions between environment and populations. In particular, in the case of a periodically varying environment (seasons), any parameter  $p$  can be assumed to vary sinusoidally, i.e.,

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

where  $p_0$  is the average value of  $p$  and  $\varepsilon$  is the strength of the season (notice that  $\varepsilon p_0$  is the magnitude of the perturbation). Obviously,

$$0 \leq \varepsilon \leq 1$$

because  $p$  cannot be negative. Also notice (see (2)) that the period of the season has been normalized to 1.

In real ecosystems there are many independent mechanisms that transform the seasonality of the environment into a periodicity of many, if not all, population parameters. To be consistent, the lag existing between different sinusoids should also be taken into account, as done in Rinaldi and Muratori, 1993. In fact, not all parameters vary in phase: for example, if  $x$  and  $y$  are algae and zooplankton of a lake in a resort area, the efficiency of algae  $e_x$  peaks on the summer equinox when light intensity is at its maximum, while the nutrient

concentration of the inflow  $n_i$  might peak one month later when the touristic activities reach their maximum level. Nevertheless, in order to simplify the analysis, we only deal with "elementary" seasonality mechanisms, namely with phenomena that entail periodic variations of a single parameter in model (1). These mechanisms are the following:

(i) *Inflow variations ( $D$ )*

This is the case analyzed by Pavlou and Kevrekidis, 1992. It simulates, for example, the case of daily variations of the inflow of a waste-water treatment process.

(ii) *Nutrient concentration of the inflow ( $n_i$ )*

This is the case analyzed by Kot et al., 1992. As in the preceding case, it can be simulated in the laboratory with a chemostat in which a bacterial population (the prey) interacts with a protozoan population (the predator).

(iii) *Temperature variations ( $a_x$ )*

If the nutrient uptake of the prey is influenced by temperature (as in plankton communities, see Doveri et al., 1993), the parameter  $a_x$  varies periodically with a period of 1 year.

(iv) *Resting time of predator ( $a_y$ )*

If the resting time of the predator varies seasonally, as in populations characterized by a certain degree of diapause, then  $a_y$  varies periodically (see Rinaldi et al., 1993).

(v) *Searching time of prey ( $b_n$ ).*

Seasonal variations of the structure of the nutrient and of the environment might entail some differences in the searching time of the prey and, hence, in the half-saturation constant  $b_n$ . (This is possibly the less relevant among the eight elementary mechanisms.)



(vi) *Searching time of predator ( $b_x$ )*

Seasonal variations of the habitat might protect the prey in some specific season, so that  $b_x$  varies. For example, the presence of filamentous blue-green algae in a shallow lake during the summer protects other algae (prey) from zooplankton (predator).

(vii) *Light variations ( $e_x$ )*

If the prey population is also limited by light intensity (as in the case of phytoplankton) the efficiency  $e_x$  can vary during the year, in particular in temperate zone (see Doveri et al., 1993).

(viii) *Quality of the prey ( $e_y$ )*

If the quality of the prey varies during the year (as in phytoplankton communities), the energy available to the predator (zooplankton) varies consistently. Hence, the efficiency  $e_y$  varies periodically.

Of course, the values of the eight parameters depend upon the application (a chemostat, a wastewater treatment plant, a shallow lake, etc.). The interested reader can refer to Kot et al., 1992, for microbial systems, and to Doveri et al., 1993, for shallow lakes. Since, in the present paper, we are not interested in a specific application, the values of the parameters have been fixed in such a way that the bifurcation diagrams discussed in the next section are easily readable. The reference setting is the following

$$\begin{array}{cccc} D=7.56 & n_i=150 & a_x=43.2 & a_y=17.82 \\ b_n=27 & b_x=9 & e_x=0.4 & e_y=0.6 \end{array}$$

For these values of the parameters, model (1) oscillates on a limit cycle with period equal to 1.65. In the following, all these parameters will be perturbed

sinusoidally as in (2), but always one at a time. For example, if the perturbed parameter is  $D$ , eq. (1) will be written with

$$D = D_0(1 + \varepsilon \sin 2\pi t)$$

and bifurcation curves will be computed in the two-dimensional space  $(\varepsilon, D_0)$ , keeping the seven remaining parameters at their reference values. The strength of the season will be varied from 0 to 0.5, while  $D_0$  will be varied around its reference value.

### 3. BIFURCATION ANALYSIS

The analysis of the bifurcations of model (1) with one periodically varying parameter, say  $p(t) = p_0(1 + \varepsilon \sin 2\pi t)$ , and all other parameters at their reference values, has been performed numerically by means of LOCBIF, a package implementing a powerful continuation method. The package produces local bifurcations of cycles of periodically forced dynamical systems (Khibnik et al., 1993) and displays them in two-dimensional spaces. The use of the package is described in detail in Rinaldi et al., 1993 and is therefore not repeated here.

The results of the analysis are shown in Fig. 1, where the diagrams (i), (ii), ..., (viii) refer to the eight cases described in the previous section. In these diagrams each bifurcation curve is identified with a symbol, namely h (for Hopf), t (for tangent) and f (for flip). When curve  $h^{(k)}$  is crossed, an attracting (repelling) cycle of period  $k$  bifurcates into an attracting (repelling) quasi-periodic solution (torus) and a repelling (attracting) cycle of period  $k$ . On curve  $t^{(k)}$  a saddle and a non-saddle cycle of period  $k$  collide and disappear. Finally, when curve  $f^{(k)}$  is crossed, a non-saddle (saddle) cycle of period  $k$  bifurcates into a saddle (non-saddle) cycle of period  $k$  and a non-saddle (saddle) cycle of period

$2k$  (period doubling). In Fig. 1, only the bifurcation curves involving attractors are shown, because this simplifies the biological interpretation of the diagrams. Nevertheless, other bifurcation curves (involving only saddles and repellers) are also present and must actually be computed in order to identify the whole bifurcation structure (see Kuznetsov et al., 1992, for more details). Moreover, the figure does not show bifurcations of periodic solutions with period greater than 2, which, nevertheless, exist and are actually very complex, as shown in great detail by Pavlou and Kevrekidis, 1992, for case (i). The bifurcation curves  $f^{(4)}$  and  $f^{(8)}$  have also been obtained, but they are not shown in the figure 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).

It should be noticed that on the vertical axis of each bifurcation diagram there are two points, namely  $H$  and  $T_2$ , which are, respectively, the points of departure of a Hopf bifurcation curve  $h^{(1)}$  and of two branches ( $t_1^{(2)}$  and  $t_2^{(2)}$ ) of a tangent bifurcation curve. These two points can be easily detected by analyzing model (1) with constant parameters ( $\varepsilon = 0$ ). Point  $H$  is the value of the parameter for which steady coexistence (mode 3 of Sect. 2) is substituted by cyclic coexistence (mode 4 of Sect. 2). Therefore, it corresponds to a Hopf bifurcation of model (1) with constant parameters. Point  $T_2$ , on the contrary, is not a bifurcation point: it simply corresponds to the value of the parameter for which the period of the limit cycle of the unperturbed model is equal to 2. Since for the reference setting of the parameters the period of the limit cycle is 1.65, we can conclude that in all eight diagrams the reference value of the perturbed parameter is somewhere between point  $H$  and point  $T_2$ .

#### 4. A UNIVERSAL BIFURCATION DIAGRAM

If the bifurcation diagrams of Fig. 1 are compared, turning the first, third, fifth and sixth upside down, it can be immediately recognized that the eight diagrams are topologically equivalent. This fact is very important: it means that all seasonality mechanisms give rise to the same phenomena. But what is even more surprising is that these diagrams are also topologically equivalent to those of the periodically forced Rosenzweig-McArthur model (compare Fig. 1 with Fig. 2 in Rinaldi et al., 1993). This is a very interesting discovery, because it allows the observation that all complex dynamic phenomena detected in the last decade by studying with different models the influence of seasons on predator-prey communities can be interpreted by means of a unique bifurcation diagram. This "universal" diagram, shown in Fig. 2, is, therefore, the same as that already discussed in Rinaldi et al., 1993. The parameter  $p_0$  of this diagram is directly (in cases (ii), (iv), (vii), (viii)), or inversely (in cases (i), (iii), (v), (vi)) related to the average value of the periodically varying parameter. Reading the diagram is relatively easy if not too technical questions are asked about the codimension-two bifurcation points A, B, C and D (the reader interested in this kind of details should refer to Rinaldi et al., 1993). In the following paragraphs, the main consequences of the diagram are summarized.

On the  $p_0$ -axis there is point H 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  $\varepsilon$  and below point H are period 1 periodic solutions, while for small values of  $\varepsilon$  and above point H are 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.

Point A is a codimension-two bifurcation point, called *strong resonance* 1:2, from which a flip curve  $f^{(1)}$  starts. Along  $f^{(1)}$  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. 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. However, 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. 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. 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. Points C and D are also codimension-two bifurcation points. When curve  $h^{(2)}$  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  $f^{(4)}$ ,  $f^{(8)}$ ... exist in the vicinity of curve  $f^{(2)}$  (the difference between curves  $f^{(2)}$  and  $f^{(4)}$  is intentionally magnified in Fig. 2). 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, through a homoclinic 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 there are strange attractors obtained through torus destruction.

The universal bifurcation diagram proves that seasons can generate rather complex dynamics. First of all, they can support multiple attractors. For example, a stable cycle of period 2 coexists with a stable cycle of period 1 in region 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. Moreover, very small variations of a parameter can entail a radical change of behavior of the system because some of the bifurcations are catastrophic. For example, crossing the flip curve  $f^{(1)}$  from region 3 to region 4 will give rise to a transition from a period 1 cycle to a period 2 cycle (frequency switching). Finally, there are two distinct routes to chaos. The first one (torus destruction) is characterized by low values of  $\varepsilon$  but requires values of  $p_0$  for which the unperturbed system behaves on a limit cycle (in other words a predator-prey system that does not autonomously cycle in a constant environment cannot become chaotic through torus destruction). On the contrary, the second route to chaos (cascade of period doublings) is characterized by higher values of  $\varepsilon$  and can sometimes be present in predator-prey systems which would not cycle in a constant environment. In summary predator-prey communities can be expected to be chaotic when the exogenous and endogenous sources of periodicities are, as a whole, sufficiently strong.

## ***5. CONCLUDING REMARKS***

The bifurcations of the periodically forced chemostat model already studied by Pavlou and Kevrekidis, 1992, and Kot et al., 1992, have been analyzed in this paper. Eight bifurcation diagrams have been produced (one for each parameter) and recognized to be topologically equivalent. This allows the casting of all modes of behavior of the chemostat in a single frame. Moreover, these

bifurcation diagrams are also topologically equivalent to those of the seasonally perturbed predator-prey model of Rosenzweig-McArthur (see Rinaldi et al., 1993). This means that the two models have the same modes of behavior (except for the extreme case of washout of both populations) not only in the constant case, as has been known for quite a long time, but also in the case of periodically varying parameters. In a sense, this should not be a surprise, in view of the general theory of periodically perturbed Hopf bifurcations (Kath, 1981; Rosenblat and Cohen, 1981; Gambaudo, 1985; Bajaj, 1986; Namachchivaya and Ariaratnam, 1987). Nevertheless, as already pointed out by Kuznetsov et al., 1992, this general theory predicts only some of the bifurcation curves of our universal diagram.

The equivalence of the two models (the chemostat and the Rosenzweig-McArthur model) has been only partially ascertained. In fact only the bifurcations of periodic solutions of period 1 and 2, namely those which are described in our universal diagram, have been compared. Pavlou and Kevrekidis, 1992, have shown, however, that there are many other bifurcations in a chemostat with periodically forced inflow rate (case (i)) and that some of them are definitely very subtle. Of course, it would be interesting to know if also these bifurcations are universal, i.e., if they are present even in cases (ii), ..., (viii) and in the Rosenzweig-Mc Arthur model.

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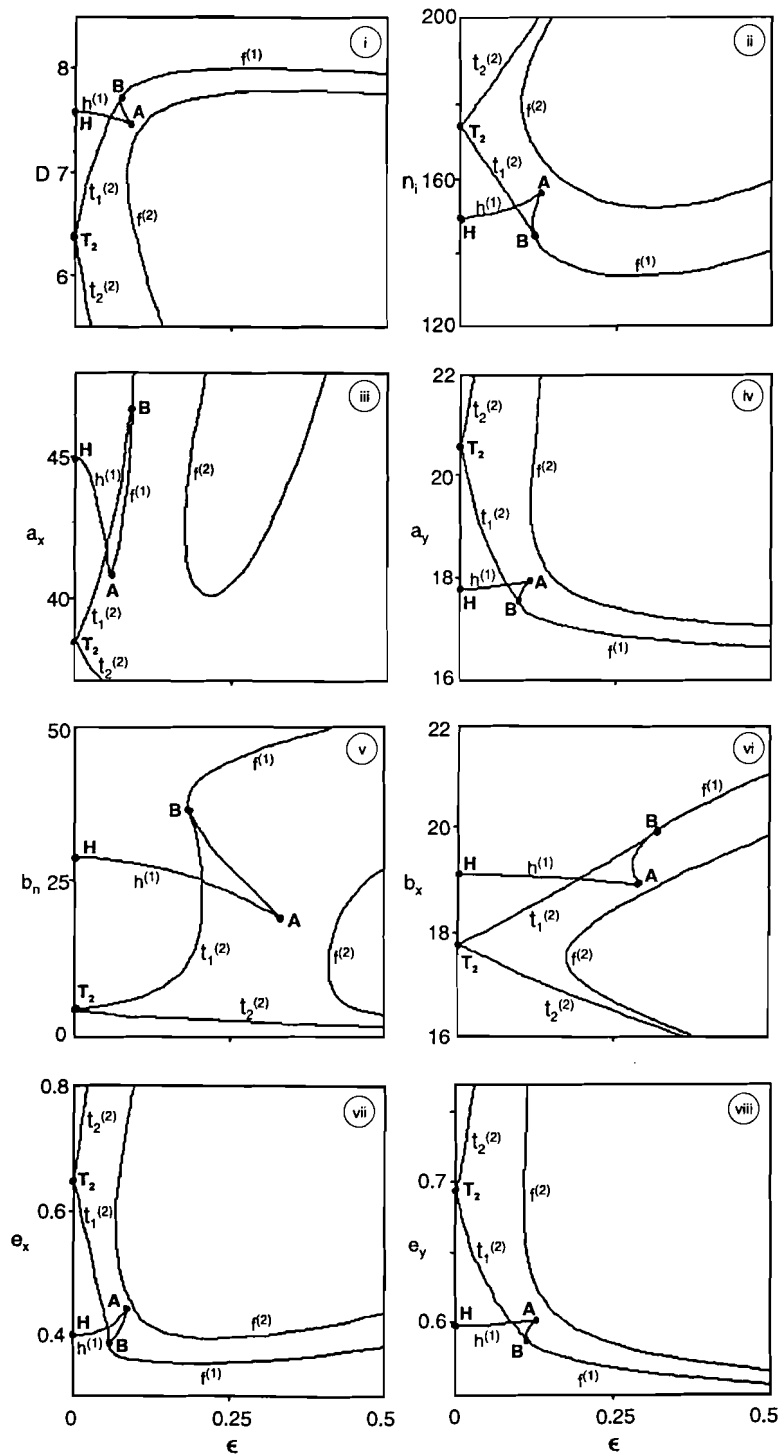


Figure 1 Bifurcation diagrams for model (1), (2). Each case (i),..., (viii) refers to the corresponding seasonality mechanism identified in the text. Curve  $h^{(k)}$ ,  $t^{(2)}$  and  $f^{(k)}$ ,  $k=1, 2$  are Hopf, tangent and flip bifurcation curves respectively. Points A and B are codimension-two bifurcation points. All parameters are fixed at the reference value indicated in the text.

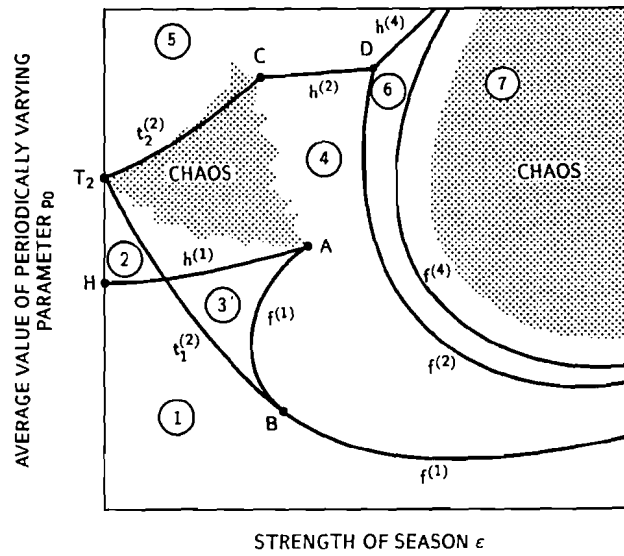


Figure 2 The universal bifurcation diagram. Curves  $h^{(1)}$ ,  $h^{(2)}$ ,  $h^{(4)}$ ,  $f^{(1)}$ ,  $f^{(2)}$ ,  $f^{(4)}$ ,  $t^{(2)}$  are bifurcation curves. Points A, B, C, D are codimension-two bifurcation points.